INTERACTIONS BETWEEN ATLANTIC SPOTTED (*STENELLA FRONTALIS*) AND BOTTLENOSE (*TURSIOPS TRUNCATUS*) DOLPHINS OFF BIMINI, THE BAHAMAS 2003 – 2007

by

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Abstract

Interspecific interactions have been observed in a variety of social animals. Functional explanations include foraging, antipredatory and social advantages. These behaviors are little 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 the *S. frontalis* since 2003. The interactions were documented with underwater video using focal animal sampling. Mating or sexual play are the primary activities observed in nearly 50% of these interactions, with male *T. truncatus* as the initiators. The most likely functional explanation for these interactions is social. The *T. truncatus* males may be failing to gain access to *T. truncatus* females because of immaturity or lack of social status. Alternatively, these interactions may be attempts to diffuse aggressive tensions that might exist between the populations.

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Chapter 1 Interspecific Interactions and Hybridization Among Cetaceans: A Review

Although most animals form groups consisting of only one species, mixed species groups have been observed across mammalian taxa (primates, Hardie and Buchanan-Smith 1997, Mendes-Pontes 1997, McGraw and Bshary 2002, ungulates, Keast 1965, Sinclair 1985, terrestrial carnivores, Kiliaan *et al.* 1991, Minta *et al.* 1992, and pinnipeds, Kerley 1983, Kovacs *et al.* 1997, Lancaster *et al.* 2006). These groups are often referred to as interspecific, polyspecific, heterospecific or mixed species groups (Stensland *et al.* 2003). Mixed species groups are distinguished from aggregations in that they occur irrespective of concentrated resources (Stensland *et al.* 2003). Aggregations of scavengers or sympatric species (domestic or wild) that are not observed in clear groups are therefore excluded from the discussion of mixed species groups.

Cetacean species observed in mixed species groups are summarized in Table 1.1. The functional explanations for these mixed species groups are often unclear (Sheldon *et al.* 1995, Frantzis and Herzing 2002). However, combinations of foraging, antipredatory and/or social functions (e.g. mating) have been suggested (Norris and Dohl 1980, Corkeron 1990, Kenney 1990, Scott and Chivers 1990, Herzing and Johnson 1997, Baraff and Asmutis-Silva 1998, Scott and Cattanach 1998, Stensland *et al.* 1998, Forestell *et al.* 1999, Herzing *et al.* 2003, Kristiansen *et al.* 2007). Mating attempts can be grouped into four categories: 1) mating attempts or courtship behavior with no copulation, 2) copulation with no fertilization, 3) copulation with fertilization, but with reproductively sterile offspring and 4) copulation with fertilization and reproductively viable offspring. When the latter two scenarios involve different species, meaning they are from different and reproductively isolated gene pools, the resulting offspring is considered a hybrid (Bérubé 2002).

Table 1.1: Summary of observed cetacean mixed species groups

Species 1	**Species 2**	**Reference(s)**
Bottlenose dolphins (*Tursiops truncatus)*	Pilot whales (*Globicephala* spp.)	Kenney 1990, Scott and Chivers 1990
	Pantropical spotted dolphins (*Stenella attenuata*)	Scott and Chivers 1990
	Atlantic spotted dolphins (*Stenella* frontalis)	Herzing and Johnson 1997, Herzing *et al.* 2003
	Indo-Pacific humpback dolphins (*Sousa chinensis*)	Corkeron 1990, Stensland *et al.* 1998
	Tucuxi dolphins (*Sotalia guianensis or S. fluviatilis*)	Acevedo-Gutierrez *et al.* 2005, Forestell *et al.* 1999, Kristiansen *et al.* 2007
Spinner dolphins (*Stenella longirostris*)	*S. attenuata*	Norris and Dohl 1980, Scott and Cattanach 1998
Long-finned pilot whales (*Globicephala melas*)	Atlantic white-sided dolphins (*Lagenorhynchus acutus*)	Baraff and Asmutis-Silvia 1998
Risso's dolphins (*Grampus griseus*)	Gray whales (*Eschrichtius robustus*)	Shelden *et al.* 1995
Dall's porpoises (*Phocoenoides dalli*)	Harbor porpoises (*Phocoena phocoena*)	Baird *et al.* 1998, Willis *et al.* 2004
Striped dolphins (*Stenella coeruleoalba*)	Short-beaked common dolphins (*Delphinus delphis*) and *Grampus*	Frantzis & Herzing 2002

Genetically, marine mammals are relatively similar. For example, the mean transition difference in rRNA genes between fin (*Balaenoptera physalus*) and blue whales (*B. musculus*) is 3.8% (Arnason and Gullberg 1993). This is comparable to the 3.4% difference between humans (*Homo sapiens sapiens*) and chimpanzees (*Pan troglodytes, P. paniscus*) (Arnason and Gullberg 1993). Nearly all cetacean species have the same number of chromosomes ($2n = 44$) and this similar genetic background, coupled with a high frequency of sympatric ranges, may favor hybridization (Bérubé 2002).

Numerous hybrid cetaceans have been documented in the literature (Nishiwaki and Tobayama 1982, Spilliaert et al. 1991, Heide-Jørgensen and Reeves 1993, Reyes 1996, Baird et al. 1998, Bérubé and Aguilar 1998, Herzing et al. 2003, Zornetzer and Duffield 2003, Willis et al. 2004), both in the wild and in captive settings. The first review of intergeneric mammalian hybrids included two cetacean crosses, one wild and one captive (Van Gelder 1977). Suspected wild cetacean hybrids are typically observed without prior observations of parental interactions. Classification is, therefore, based on morphology and/or genetics. This review examines known cases of hybridization in cetaceans and examines hypotheses addressing the mechanisms for interspecific interactions, particularly mating. Interspecific mating may occur due to a lack of available conspecific mates. This may be a result of reduced population of one or both species (Spilliaert *et al.* 1991) or inadequate social ranking, strength or health of one or both individuals. Interspecific mating may also be a technique for reducing aggression in sympatric species. This is a well documented practice among bonobos (*Pan paniscus*) (de Waal 1997); the same strategy may be employed in mixed species groups.

Wild Cases

Cetacean remains have provided evidence of potential hybrids, although confirmation of these cases is challenging. The first recorded cetacean specimens to be considered hybrids were three dolphins that stranded at Blacksod Bay, Ireland in 1933 (Fraser 1940). The parents were assumed to be *Tursiops truncatus* and *Grampus griseus*, based primarily on the reduction or complete absence of the rostrum and a reduction in the number of teeth (Fraser 1940). In a more recent case, a skull found after a subsistence hunt in Greenland is believed to belong to a narwhal (*Monodon monoceros*) × beluga (*Delphinapterus leucas*), based again on intermediate skull and dentition characteristics (Heide-Jørgensen and Reeves 1993). In both cases morphological evidence points to multiple hypotheses, including hybridization, unknown species or anomalous known species. None of these hypotheses were sufficiently supported or rejected, however all authors favored the possibility of hybridization, particularly in light of the parental species' overlapping ranges and breeding seasons (Fraser 1940, Heide-Jørgensen and Reeves 1993).

Potential hybrids have also been described based on catches and/or general observations. Reyes (1996) notes an atypical animal captured among dusky dolphins (*Lagenorhynchus obscurus)* off the coast of Peru. The post-mortem condition of the body hindered the notation of distinctions in coloration; however, skull measurements suggest similarities with both *L. obscurus* and common dolphins (*Delphinus spp*.), as well as intermediate characteristics of the two species (e.g., rostrum length/width index, Reyes 1996). As with Fraser (1940) and Heide-Jørgensen and Reeves (1993), no interactions between the two species were observed. Acevedo-Gutierrez *et al.* (2005) and Kristiansen and Forestell (2007), however, describe interactions between *T. truncatus* and *S. fluviatilis* and have photographic documentation of possible hybrids. Acevedo-Guitierrez *et al.* (2005) consider these interactions to be social in nature; however, they offer no conclusions regarding the mechanisms driving such interactions.

Herzing and Johnson (1997) documented the interactions between *S. frontalis* and *T. truncatus* in the Bahamas and Herzing *et al.* (2003) report a potential hybrid calf. Although photographs of the presumed hybrid calf are provided, as with Acevedo-Guitierrez *et al.* (2005), DNA studies would be required to confirm hybridization (Spilliaert *et al.* 1991, Arnason and Gullberg 1993). This is particularly important when the morphological similarities (color, size, etc.) between calves of the two species are great as with *T. truncatus* and *S. frontalis*. *T. truncatus, S. frontalis,* and *S. fluviatilis* are all listed as data deficient with respect to their status, according to the IUCN Red List (IUCN 2007), however the regularity with which these species are observed suggests that populations are stable enough to reject the hypothesis that interactions are occurring due to population stress.

The first genetically confirmed report of a wild cetacean hybrid was a cross between a *B. musculus* and a *B. physalus* (Spilliaert *et al.* 1991). In 1986, a large, pregnant Balaenopterid whale was caught in Iceland (Spilliaert *et al.* 1991). Morphologically, the adult female hybrid, which was estimated to be 6-7 years old and in her second pregnancy, exhibited characteristics (color and size) intermediate between the parental species (*B. musculus* and *B. physalus*) (Spilliaert et al. 1991). Molecular analyses showed that she was a hybrid between a female *B. musculus* and a male *B. physalus*. This was also the first genetically confirmed, *fertile* cetacean hybrid discovered in the wild – the fetus was fathered by a *B. musculus* (Spilliaert et al. 1991). Whaling records indicate the possibility of *B. musculus* × *B. physalus* individuals, based on morphology, as early as 1887 (Bérubé 2002). In this case, the whaler's logbook indicated that the whale was found swimming with a group of three other *B. physalus* (Spilliaert et al. 1991). This suggests that it would have been accepted into the female nursing group. If population declines were the driving force behind the mating, then *B. physalus* should be the fetus' father, as *B. musculus* was the species in decline at the time (Spilliaert et al 1991). However, it is possible that the decline in *B. musculus* resulted in a lack of available mates for a reproductively mature male *B. musculus* which, without geographic and morphological barriers, mated with the hybrid female. Since the actual courting and copulation were not witnessed, the physical state of the fathers, the pregnant female or her calf cannot be assessed, nor can potential aggression levels be ascertained. Therefore, the hypotheses of mating due to a lack of mates because of inadequate social standing or physical condition and mating as an outlet for aggression can neither be supported nor rejected. Since then, additional observations of *B. musculus/B. physalus* groups and hybrids have been documented, indicating that interactions and hybridization between these two species may be relatively frequent (Bérubé and Aguilar 1998).

A more recent, genetically confirmed hybrid is between *Phocoenoides dalli* and *Phocoena phocoena* populations off British Columbia, Canada. Baird *et al.* (1998) and Willis *et al.* (2004) described a hybrid *P. dalli* × *P. phocoena* fetus recovered within a dead *P. dalli* in southern British Columbia in 1994. There have also been multiple observations of presumed hybrids in the waters surrounding Vancouver Island, traveling with and behaving like *P. dalli*, but with atypical pigmentation (Baird *et al.* 1998). Recent genetic analyses have confirmed that these individuals are hybrids (Willis *et al.* 2004). The hybrids were never observed in the company of *P. phocoena*, which might be because the maternal species has always been a *P. dalli*, thus the offspring are reared with the *P. dalli* group. These hybrids are easily distinguished visually from others in the group by their intermediate physical characteristics, in particular their pale gray pigmentation (Willis *et al.* 2004).

Hybridization between these two species is facilitated by their overlapping ranges, although *P. dalli's* range extends into deeper water than *P. phocoena* (Baird *et al.* 1998). Despite the overlap, mixed species groups are rarely observed, accounting for only three out of over 1500 (< 2%) recorded sightings for the two species (Baird *et al.* 1998). This, however, may not be the most representative assessment of their interactions, since the *P. phocoena* avoid boat traffic more than *P. dalli* (Baird *et al.* 1998).

These two species also have overlapping breeding seasons and ranges (Willis *et al.* 2004). Sexual dimorphism differs between the two species; male *P. dalli* are slightly longer than females and female *P. phocoena* are slightly larger overall than males (Reeves *et al.* 2002). Baird *et al.* (1998) suggest that the reverse sexual dimorphism and large testes in *P. phocoena* correspond to male *P. phocoena* being less particular about mate choice and more promiscuous than *P. dalli*. Given this behavioral tendency and the population decline in *P. phocoena* (Baird *et al.* 1998), it is possible that the male *P. phocoena* are seeking out female *P. dalli*, or pursuing matings indiscriminately (Willis *et al.* 2004).

Captive Cases

Although an examination of hybridization in a captive setting has limitations in its application to the behavioral assessment of interspecific interactions between free-ranging animals, it is useful in informing genetic and taxonomic discussions, particularly when the hybrid offspring survive to adulthood and are fertile. The first well documented hybrid birth occurred in 1971 at Oceanic Institute in Oahu, Hawaii (Dohl *et al.* 1974), where a female roughtooth dolphin (*Steno bredanenis*) gave birth to a healthy *Tursiops spp.* × *S. bredanenis* calf. Although molecular data were not collected, the father was one of two male bottlenose dolphins, one a *T. truncatus*, the other a *T. t. gilli*, with which the *S. bredanenis* shared its tank. Staff observed numerous matings between the female *S. bredanenis* and male *T. truncatus*, and, therefore, the *T. truncatus* was assumed to be the father, although this was not confirmed (Dohl *et al.* 1974).

The pregnancy was considered normal and it was immediately apparent that the calf had intermediate characteristics of both parents, although it more closely resembled a *Tursiops* calf (Dohl *et al.* 1974). The head shape and coloration were intermediate. The melon was more sharply defined than seen in *S. bredanenis*, but more sloping than seen in *Tursiops spp*. The coloration included the pale gray “blaze” along the peduncle as seen in *S. bredanenis* and the pale coloring above the eye as seen in *Tursiops spp.* (Dohl *et al.* 1974). At the end of two months, the calf closely resembled a *Tursiops spp.*, but by the end of 18 months, its *S. bredanenis* -like characteristics (lack of melon groove, lengthened rostrum, protruding eyes) had become more prominent. Behavior between the mother and calf was consistent and nurturing and the calf grew at a healthy rate. No rejection of the calf by the mother was observed (Dohl *et al.* 1974).

There have also been cases of hybridization between *T. t. gilli* and false killer whales (*Pseudorca crassidens*) in captivity (Nishiwaki and Tobayama 1982). In 1981, a female hybrid calf was born to a *T. t. gilli* mother at Kamogawa Sea World in Chiba, Japan. It was presumed, and later genetically confirmed, that the paternal animal was a *P. crassidens* that shared the same pool (Nishiwaki and Tobayama 1982). This was not the first case of hybridization at this facility; however, it was the first live birth and there had been multiple observations of mating attempts and copulations between the male *P. crassidens* and female *T. t. gilli*. The calf lived for 277 days. The calf appeared to develop relatively normally, but on day 273 its food consumption decreased and the calf died several days later. The cause of death was determined to be acute pneumonia (Nishiwaki and Tobayama 1982). Analyses of the morphology of the calf and previous hybrid fetuses show four noteworthy characteristics: 1) the beak of the hybrids was shorter than a typical *T. t. gilli.*, 2) the body color was darker than similar stages in *T. t. gilli*, 3) the shape of the pectoral fin was morphologically similar to that of *P. crassidens,* and 4) the dental configuration of hybrids was intermediate between *T. t. gilli* and *P. crassidens* (Nishiwaki and Tobayama 1982).

Between 1992 and 1993, four hybrid calves were born at Sea World California. Each of these calves was born to a different *T. truncatus* female and all were sired by a long-beaked common dolphin (*Delphinus capensis*) male. Of the four, two died within three days, one of which was a first calf for its mother

(Zornetzer and Duffield 2003). It is difficult, if not impossible, to assess whether these calves did not survive because they were hybrids or because survival of captive offspring in general is low (Van Gelder 1977). In 2003, two of the four hybrids were still alive and one of these had given birth to a calf sired by another *T. truncatus* in 2000. This live-born backcross calf died within one day (Zornetzer and Duffield 2003). Body length and tooth counts for the surviving first generation hybrids were intermediate between parental species, but proportions of various body parts varied. The coloration pattern was also intermediate, however, the degree varied between the two hybrids. Both are successfully trained animals and appear behaviorally and socially normal within their captive group (Zornetzer and Duffield 2003).

Because these calves were conceived and born in captivity, under conditions which unnaturally placed the parents together, application to wild populations is limited. However, captive cases do offer insight into the occurrence of interspecific mating in a scenario in which there is a lack of appropriate mates. Nishiwaki and Tobayama (1982) do not explicitly mention whether there were female *P. crassidens* available to the male, but in captive situations, the lack of mate choice is likely the strongest driving force behind interspecific matings.

Morphological analyses of captive-born hybrid dolphins show consistently intermediate characters (Dohl *et al.* 1974, Nishiwaki and Tobayama 1982, Zornetzer and Duffield 2003). However, Zornetzer and Duffield (2003) point out that many smaller dolphins have substantial variation in intraspecific morphology; therefore, the visual detection of hybrids in the wild may be quite difficult. For example, within *Tursiops* alone there is great geographic diversity in morphology. Genetic studies suggest that *T. aduncus* might actually be more closely related to species of *Stenella* and *Delphinus* than to *T. truncatus* (LeDuc *et al.* 1999, Wells and Scott 2002).

Discussion

Even when no offspring are produced, what drives members of different species to mate? First, interspecific matings may occur due to an inaccessibility of conspecific mates. The animals may be driven outside their own species because of declining population (Spilliaert *et al.* 1991). This hypothesis can be extended to both the captive and free-ranging cases. In a captive scenario, the individuals in question have an obvious lack of available mates. Spilliaert *et al.* (1991) suggest and simultaneously discredit this mechanism to explain the *B. physalus* × *B. musculus* hybrid pregnant with a fetus fathered by *B. musculus*, as *B. musculus* whale numbers were in decline. However, this hypothesis should still be considered since either species has the potential to be the mother or father of this hybrid combination (Bérubé and Aguilar 1998) and the lack of available conspecific females may have driven the *B. musculus* to mate with the hybrid, but *B. physalus* associated, female.

Lack of conspecific mates may also occur in stable, wild populations and interspecific mating might, in those cases, serve as an outlet for immature or weaker individuals of one species with respect to social interactions. Individuals who lack access to conspecific mates might seek partners outside their species. This may be the case in *T. truncatus* and *S. frontalis* interactions involving sub-adult male *T. truncatus* (Bimini, The Bahamas, personal observations). More information is needed on the conspecific social ranking of the adult male *T. truncatus* observed mating with *S. frontalis* (Herzing and Johnson 1997, personal observations).

Second, interspecific mating may occur as a mechanism to diffuse interspecies aggression. When two species are sympatric, competition may result in aggression. Sexual behavior could be a mechanism by which these tensions might be released, as seen in *P. paniscus* groups (de Waal 1997). Sexual aggression as a reproductive strategy is well documented in *T. truncatus* (Ostman, 1991). *T. truncatus* are involved in many interspecific mating observations in the wild (Herzing and Johnson 1997, Herzing *et al.* 2003, Acevedo-Gutierrez *et al.* 2005, Kristiansen *et al.* 2007) and their conspecific aggression may extend into interactions with sympatric species.

Hybridization in mammals occurs rarely compared to other animal groups (Bérubé 2002, Willis *et al.* 2004). However, cetaceans may have a greater ability to hybridize than other mammals because of their slow chromosomal evolution and often sympatric distributions (Bérubé 2002, Willis *et al.* 2004). In all of the captive examples discussed above, *T. truncatus* was one parent. Although this is likely a factor of the abundance of *T. truncatus* in captivity, *Tursiops spp.* is also one of the most cosmopolitan genera of small cetaceans in the wild (Zornetzer and Duffield 2003). For this reason, understanding other genera with which *Tursiops* is potentially reproductively compatible should be of interest to behaviorists, geneticists, taxonomists and conservationists alike. Continued genetic research will provide taxonomists with tools previously unavailable for species classification. If hybridization is more common than previously thought, becomes more predominant over time or results in changes in cetacean taxonomy, decisions regarding stock assessments and subsequent management efforts may need to be reconsidered.

Fertilization resulting in reproductively viable offspring might, over time, result in the elimination of reproductive barriers, whether physical or geographic (Bérubé 2002). The long-term potential for a group of such offspring is introgression, whereby the genes of one species are present in individuals that seem, morphologically, to be a different species. This has been documented in coyote (*Canis latrans)* and gray wolf (*C. lupus)* populations in North America (Lehman *et al.* 1991). Marine mammal hybridization does not appear to be at the level of introgression, but it is important to remember how little is known of marine mammal populations and the potential that many hybrids are simply not encountered, overlooked or incorrectly described. Rates of hybridization could also rise with anthropogenic effects on populations or habitats and should be considered.

The importance of both identifying successful hybrids and understanding the mechanisms driving the parental individuals is twofold. First, our current definition of species indicates that individuals of different species, and certainly different genera, are not expected to successfully reproduce with each other (Van Gelder 1977). As illustrated in this review, individuals of different genera have successfully hybridized in nature. This calls into question the classic definition of a species (Van Gelder 1977), or requires that the taxonomic classifications of these animals be reconsidered. Second, if hybridization continues to the point of introgression, particularly among threatened or endangered species, this might affect the conservation efforts of at-risk populations. With these larger issues lingering, it is crucial that observational research of mixed species groups and hybrid cetaceans continue and include genetic elements as practicable.

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Chapter 2 Interactions between Atlantic spotted (*Stenella frontalis*) and bottlenose (*Tursiops truncatus*) dolphins off Bimini, The Bahamas

Introduction

Interspecific interactions, including sexual encounters, occur between a variety of species in both terrestrial and marine habitats (Stensland *et al.* 2003). There are three primary hypotheses to explain these mixed species groups: foraging advantages, predatory avoidance and social advantages, including reproductive advantages (Stensland *et al.* 2003). The primary functions of interspecific interactions in mixed species primate groups are foraging and/or antipredatory (Hardie and Buchanan-Smith 1997, Mendes-Pontes 1997, McGraw and Bshary 2002), antipredatory in ungulates (Sinclair 1985, Keast 1965), foraging in terrestrial carnivores (badgers-coyotes, Kiliaan *et al.* 1991, Minta *et al.* 1992), and possibly social in pinnipeds (Kerley 1983, Kovacs *et al.* 1997, Lancaster *et al.* 2006). Among cetaceans, the functional explanations are less clear (Sheldon *et al.* 1995, Herzing and Johnson 1997, Frantzis and Herzing 2002, Herzing *et al.* 2003). However, combinations of foraging, antipredatory and/or social functions have been suggested (Norris and Dohl 1980, Corkeron 1990, Kenney 1990, Scott and Chivers 1990, Baraff and Asmutis-Silva 1998, Scott and Cattanach 1998, Stensland *et al.* 1998, Acevedo-Gutierrez *et al.* 2005, Kristiansen and Forestell 2007).

There are cases in which mixed genera and higher taxa groups occur, including groups of pantropical spotted dolphins (*Stenella attenuata*) or spinner dolphins (*Stenella longirostris*) that associate with yellowfin tuna (*Thunnus albacares*) to feed on smaller prey in the eastern tropical Pacific Ocean (ETP) (Scott and Cattanach 1998). In this case, Scott and Cattanach (1998) suggest both foraging advantages as well as potential antipredatory advantages. The dolphins may follow the tuna, which regularly drive dolphin prey to the surface or the tuna may follow the dolphins (Scott and Cattanach 1998). However both tuna and dolphins are at risk from shark predation, so their associations may reduce their individual risk via the dilution effect, confusion effect and/or detection effect (Scott and Cattanach 1998).

S. longirostris have also been observed traveling to groups of *S. attenuata* during their daytime rest periods in the ETP (Norris and Dohl 1980). In this case, *S. attentuata* were alert and feeding in the open ocean and it is suspected that they provided refuge for the resting *S. longirostris* (Norris and Dohl 1980). Considering the different foraging strategies of these two Delphinid species and the primary activity of resting by one of the species, the function of these mixed species groups is likely antipredatory on the part of *S. longirostris* (Norris and Dohl 1980, Scott and Cattanach 1998).

Stensland *et al.* (2003) describe interactions between young Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) engaged in sexual behavior with female Indo-Pacific humpback dolphins (*Sousa chinensis*) off the coast of Zanzibar. While it is unknown if these interactions have resulted in hybrid offspring, the young age of the *T. aduncus* involved suggests the practice of adult behaviors and, thus, a social and reproductive function (Stensland *et al.* 2003).

The extent to which interspecific interactions result in hybridization among cetaceans is also poorly understood, but is an increasingly studied phenomenon in sympatric populations (Fraser 1940, Spilliaert *et al.* 1991, Heide-Jørgensen and Reeves 1993, Baird *et al.* 1998, Herzing *et al.* 2003, Willis *et al.* 2004). During a 2003 research effort off the coast of Bimini, The Bahamas, two male common bottlenose dolphins (*T. truncatus*) were observed entering an Atlantic spotted dolphin (*Stenella frontalis*) group with penile erections directed at the *Stenella*. This paper describes the repeated interactions between *Stenella* and *Tursiops* off the coast of Bimini, The Bahamas, from 2003 – 2007. Durations of observations and interactions, environmental conditions, group composition, individual reoccurrence, and behavioral contexts are reported, and potential functional explanations are considered. I hypothesize that social advantages are the most likely explanation for the *Stenella*/*Tursiops* groups documented in this area.

Methods

Study Area

The study was conducted immediately west and north of North Bimini, The Bahamas (Figure 2.1). The main 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 to the east/west from 79° 11' W to 79° 16' W. Although there are scattered ledges and coral heads present, the study area consists primarily of 6-12 m depths with a white sandy sea floor, which occasionally extends over the continental shelf immediately west.

Surveys were conducted aboard a local ecotour vessel (42-foot Stapleton, 38-foot Delta or 42-foot Hatteras) typically during the 4 - 5 hours prior to sunset. A total of 233 boat trips were completed over a 5 year period (Table 2.1). Sightings are defined as time with dolphins in view from the surface or under water. Encounters are defined as underwater observations > 3 min in duration.

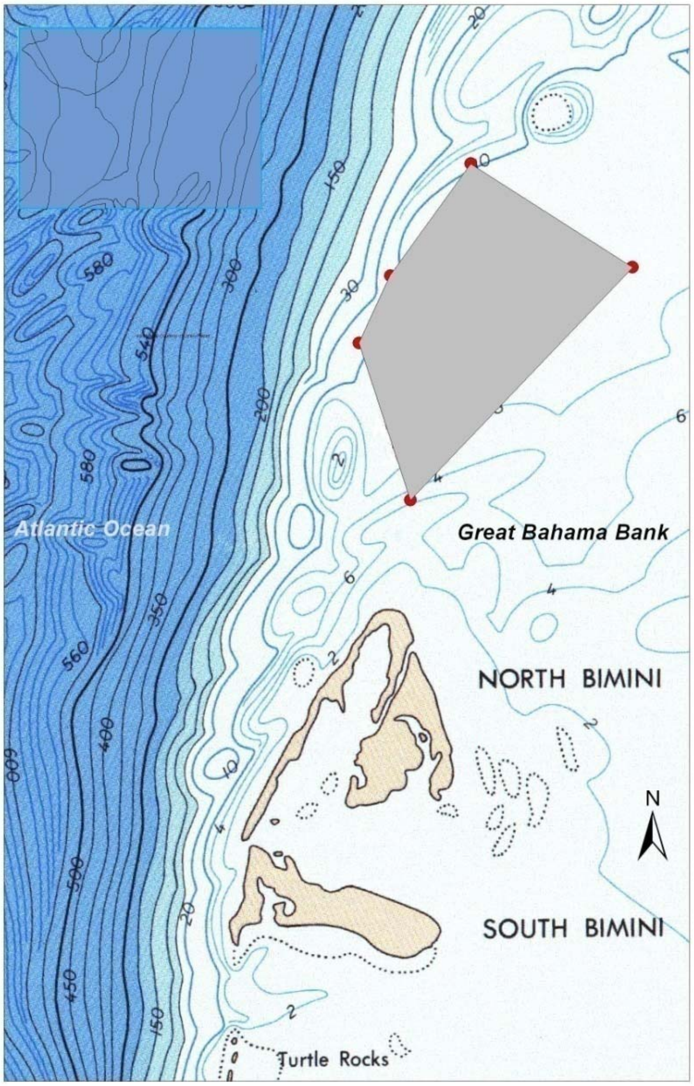

Figure 2.1: Study area along the Great Bahama Bank, north of North Bimini, The Bahamas. The shaded area represents the focus of the study area, however, dolphins that were sighted along the western coastline of Bimini as the boat traveled to the study area were included in the analysis.
Map credit: NOAA.

Table 2.1: Boat trips and effort hours by field season.

Field Period	**Boat Trips Completed**	**Total Effort (Hours)**
June – August 2003	33	139.60
June – September 2004	40	178.22
June – August 2005	44	187.35
May – September 2006	55	233.38
January 2007	4	16.57
May – September 2007	57	240.95
TOTAL	**233**	**996.07**

Study Animals

Stenella have been the focus of longitudinal population and behavioral studies conducted by the Dolphin Communication Project (DCP) around Bimini, The Bahamas, since 2001 (DCP, unpublished data, 2001 – 2007). *Stenella* were classified by age class 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 2.2, Perrin 1969). *Stenella* exhibit subtle sexual dimorphism in size. Adult males can reach 2.26 m in length and 140 kg, while adult females can reach 2.29 m and 130 kg (Reeves *et al.* 2002).

Tursiops are also observed within the study area. Individuals are recognized by the shape of the dorsal fin and any nicks or scars present on the dorsal fin (Wursig and Wursig 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 2.3, 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 in this study, unknown age classification for *Tursiops* indicates an inability to distinguish between sub-adult and adult. Size varies between inshore and offshore populations, but males tend to be larger among all *Tursiops* groups (Reeves *et al.* 2002). Adult males can reach 3.8 m in length and 500 kg and adult females can reach 3.7 m and 260 kg (Reeves *et al.* 2002).

Stenella in this area are in frequent contact with boats and human swimmers, as they are the primary subjects of commercial swim-with-dolphin programs and of DCP's longitudinal research studies. They are considered habituated to humans and boats (e.g., Dudzinski 1998). *Tursiops* appear less tolerant of boats or human swimmers in close proximity than *Stenella*; however, the former were observed throughout the study period.

Table 2.2: Age class designations and descriptions of *Stenella*, after Perrin 1969.

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

Table 2.3: 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 yrs)	Approximately ½ length of adult; no fetal folds, slender
3	Juvenile (4 < 7 yrs)	Approximately 2/3 length and slender
4	Subadult (7 < 10 yrs)	¾ to similar length as adult, but girth < adult
5	Adult (11+ yrs)	Largest girth; female often with calf

Data Collection

Photographic and behavioral data were collected using video cameras encased in underwater housings (Sony digital 8 TRV230 in 2003, 2004 and January 2007, Sony digital 8 TRV510 in 2004, Sony DCR PC105 in 2005 and 2006 and Sony DCR PC101 in 2007). Two underwater housings were used. The digital 8 cameras were housed in a TopDawg (Light in Motion, Monterey, CA) unit without external hydrophones (2003 and January 2007). The digital mini-DV cameras were housed inside a mobile video/acoustic system (Dudzniski *et al.* 1995) with two omni-directional hydrophones (2005-2007; digital 8 camera in 2004). Video data were collected using a focal-animal-follow sampling protocol (Altman 1974, Mann 1999); however, in mixed species encounters with a focal group rather than a focal individual, effort was biased towards *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 was used above water to photograph *Tursiops* dorsal fins for identification 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 identifications from video and still pictures were confirmed by at least two trained DCP researchers.

A handheld Garmin GPS was used to mark the dolphins' location at each sighting. Depth was documented when possible at each dolphin sighting from the onboard depth sounder. Environmental data were also recorded for each dolphin sighting (Table 2.4).

Table 2.4: Environmental variables

Underwater Visibility:	Estimated and grouped in increments of 3m (<3m, 3-9m, 9-12m, 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)

Data Filtering and Analyses

Video segments with clear focal and affiliate animals and positively identifiable species were examined for species confirmation, age class and 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 order of appearance (affiliate1, affiliate2, etc.). Sex was determined by clear observation of genital area or penile erection. Behaviors were classified according to the ethogram defined by Dudzinski (1996, 1998) and are applicable to both species. A subset of behaviors from this ethogram, 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, etc., Appendix A) was used for interspecific interactions. Behaviors were then categorized as sexual, aggressive, affiliative (travel, play and neutral associations, Herzing and Johnson 1997), investigative (head scanning or echolocation clicks) or foraging. Each time the focal animal changed, the behavior of a focal or affiliate animal changed, or a new affiliate animal entered the video frame, a new focal observation was designated.

SPSS v.15 for Windows was used to determine frequencies of behaviors and group composition (species, age class, sex and individuals) of focal groups. Because not all individuals could be positively identified with their catalog identification number, a subset of video data where all individuals were identified was analyzed for the reoccurrence of individuals over time. Results are reported as mean ± 1 standard error unless otherwise stated.

Results

Sighting and encounter summary

From June 2003 – September 2007, a total of 451 sightings of and 262 encounters with *Stenella* and/or *Tursiops* in single or mixed species groups were recorded (Table 2.5). 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 2.2). Mean durations of mixed species sightings and encounters were 27.24 ± 3.53 and 15.35 ± 2.88 min, respectively (Table 2.6). Mean group size of mixed species groups observed from the boat was 12 total animals. Of the 34 mixed species encounters, 15 yielded useable video data segments, totaling 73 min 32 sec ($\bar{x}$ = 5 min 15 sec ± 67.76 sec), 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 3-9 m, cloud cover of 50% and sea state of 2 (wavelets, but no whitecaps).

Table 2.5: Summary of total observations of *Stenella*, *Tursiops* or mixed species groups between 2003-2007

Total sightings	Total encounters	Mixed species sightings	Mixed species encounters	Mixed species encounters with useable video
451	262	40	34	15

Table 2.6: Summary of mean duration, group size and environmental data for mixed species observations (n = 15, except depth, n = 9)

Mean sighting duration	Mean encounter duration	Mean group size	Mean time before sunset	Mean water depth	Mode underwater visibility	Mode cloud cover	Mode sea state
27.24 min	15.35 min	12	98.33 min.	13 m	3-9 m	50%	2

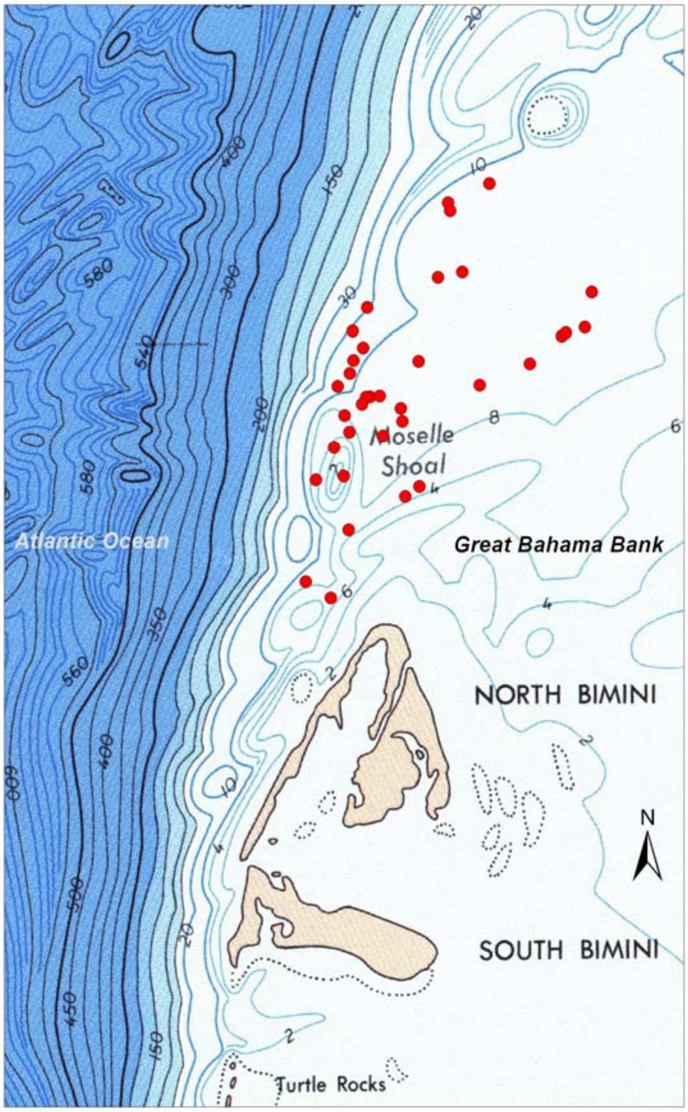

Figure 2.2: Mixed species observations were distributed throughout the study area along the western edge of the Great Bahama Bank. Map credit: NOAA.

Photo-Identification

A total of 89 individual *Stenella* and 24 individual *Tursiops* were identified and cataloged during the 5 year study period. The distribution of these animals across species, age classes and sex is summarized in Table 2.7. The high proportion of unknown sex and age classes among *Tursiops* is a result of identification from above-water dorsal fin photographs, which do not include a view of the genital region. Similarly, above-water photographs do not facilitate positive distinction between sub-adult and adult age classes for *Tursiops* and such individuals were given the age classification of unknown. *Tursiops* identified thus far around Bimini match the description (size, coloration, etc.) for the coastal ecotype (Rossbach and Herzing 1999, Reeves *et al.* 2002 and Parsons *et al.* 2006), although potential offshore *Tursiops* were observed on at least one occasion off Bimini during this study period and once previously by another team of researchers (Herzing *et al.* 2003).

Table 2.7: Breakdown of age class and sex of known individuals among *Stenella* and *Tursiops*

	Stenella	***Tursiops***
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

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 4 per species. The total number of animals in view at one time ranged from 1-5 (Table 2.8). Most commonly, there was 1 *Stenella* (36.6%) and 1 *Tursiops* (58.8%) in any given video frame. These smaller group sizes (versus the average mixed species group size of 12 observed from the boat, Table 2.6) 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 allowed.

Table 2.8: Total number of animals (*Stenella* and/or *Tursiops*) in view (n = 284 focal observations)

Total number of animals	1	2	3	4	5
Percent in view	22.9%	27.8%	19.0%	21.1%	9.2%

The breakdown of focal and affiliate animals by species, age class and sex is summarized in Table 2.9. During mixed species observations, *Tursiops* more commonly (66.2%) represented the focal animal; however, *Stenella* represented the majority of all other positions (affiliate animals 1 – 4; 68.7%, 72.3%, 90.0%, 75.0%, respectively). The predominance of *Tursiops* as focal animals is a byproduct of the bias toward this species in data collection previously described. There were no confirmed *Tursiops* calves or juveniles in any position during mixed species observations and the most commonly observed *Tursiops* were subadults (34.0% of focal *Tursiops*). All age classes of

Stenella were observed at least once during mixed species observations, but were most often juvenile (56.3% of focal *Stenella*). Both males and females of each species were observed at least once; however, when the sex of *Tursiops* was confirmed, it was overwhelmingly male (64.4% of focal *Tursiops*). These trends hold across all positions for both species.

Table 2.9: 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 (n=188)	0%	0%	34.0%	7.4%	58.5%	64.4%	4.8%	30.9%
Focal Sf (n=96)	16.7%	56.3%	5.2%	14.6%	7.3%	7.3%	39.6%	53.1%
Affiliate1 Tt (n=67)	0%	0%	10.4%	0%	89.6%	56.7%	1.5%	41.8%
Affiliate1 Sf (n=147)	25.9%	56.5%	0%	4.8%	12.9%	10.2%	12.2%	77.6%
Affiliate2 Tt (n=39)	0%	0%	2.6%	0%	97.4%	61.5%	0%	38.5%
Affiliate2 Sf (n=102)	33.3%	52.0%	1.0%	3.9%	9.8%	5.9%	10.8%	83.3%
Affiliate3 Tt (n=9)	0%	0%	22.2%	11.1%	66.7%	22.2%	0%	77.8%
Affiliate3 Sf (n=81)	19.8%	58.0%	0%	2.5%	19.8%	1.2%	29.6%	69.1%
Affiliate4 Tt (n=7)	0%	0%	28.6%	0%	71.4%	0%	0%	100%
Affiliate4 Sf (n=21)	9.5%	61.9%	4.8%	0%	23.8%	33.3%	9.5%	57.1%

Known individuals observed in mixed species encounters are summarized in Table 2.10. 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.

Table 2.10: Individual 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	3/4	2
Sf14	Female	2/3	3
Sf17	Male	5	1
Sf36	Female	3/4	1
Sf38	Female	4	1
Sf76	Female	2/3	3
Sf78	Male	3	2
Sf79	Male	3	2
Sf80	Female	3	2
Sf87	Female	2	1

Behaviors

In seven of the 15 video segments, mating or sexual play behaviors occurred at least once. For both focal and affiliate animals, the most common behavior was a slow swim and the most common behavioral category was affiliative (travel, play and neutral associations; Herzing and Johnson 1997). For the focal, affiliate1 and affiliate2 animals, the second and third most common behavior categories were sexual and aggressive, respectively. Investigative behaviors were the fourth most commonly observed behaviors among the focal, affiliate1 and affiliate2 animals and only the focal and affiliate1 animals were ever observed foraging. For affiliate3 animals, aggressive and investigative were the second and third most common behavioral categories. For affiliate4 animals, investigative behaviors were the second most common, with both sexual and aggressive behaviors the third most common.

Discussion

Interactions between *Stenella* and *Tursiops* off Bimini, The Bahamas were observed 40 times during the 5 year study period. During this time, there were 281*Stenella*-only observations and 110 *Tursiops*-only observations indicating that mixed species groups are relatively uncommon. Age class and sex were often unknown for individuals in mixed species groups, however *Tursiops* focal, affiliate1 and affiliate 2 animals were typically sub-adult males and *Stenella* in the same positions were typically juvenile females (Figures 2.3 – 2.8). Focal animals were more often *Tursiops* and all affiliate positions were most often *Stenella* (Figure 2.9). This was expected based on the focal animal sampling bias and the larger *Stenella* numbers in mixed groups. Common behavioral categories among focal and affiliate animals are summarized in Figure 2.10. Removing the overwhelmingly dominant affiliative behaviors, the inverse relationship between sexual and aggressive behaviors among focal and affiliate1-3 animals is more obvious (Figure 2.11). Of the three functional explanations for mixed species groups described by Stensland *et al.* (2003), observations of *Stenella-Tursiops* groups off Bimini might have some anti-predator advantages, but are most likely social/reproductive in nature. The social and reproductive advantages possible through mixed species groupings can be divided into at least three categories, reproduction, aggression diffusion and alloparenting.

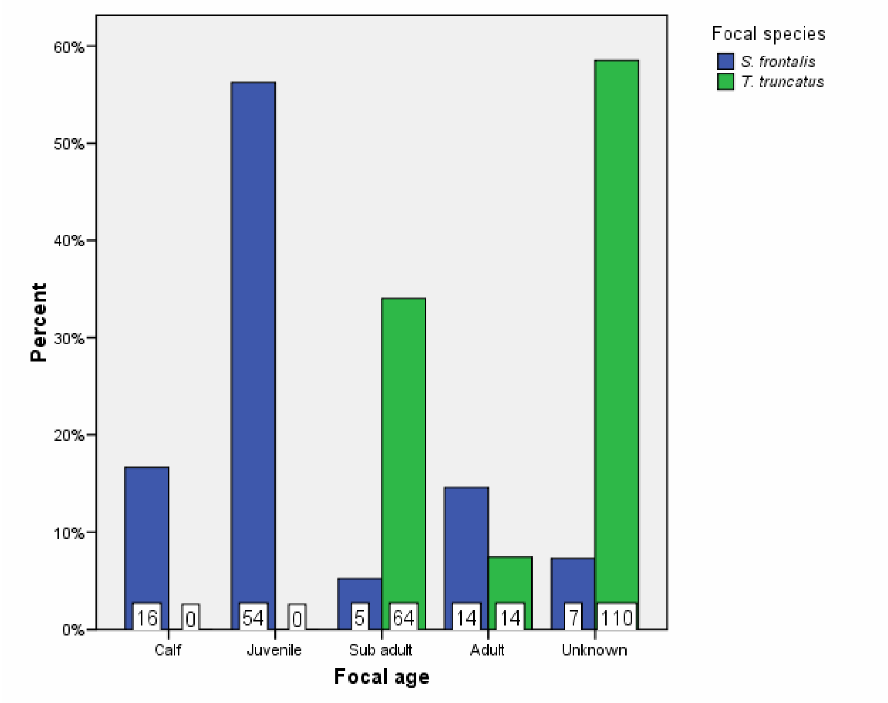

Figure 2.3: Among focal animals, age class was often unknown for *Tursiops;* however, when it was confirmed, the *Tursiops* was most often a sub-adult. *Stenella* was most often a juvenile.

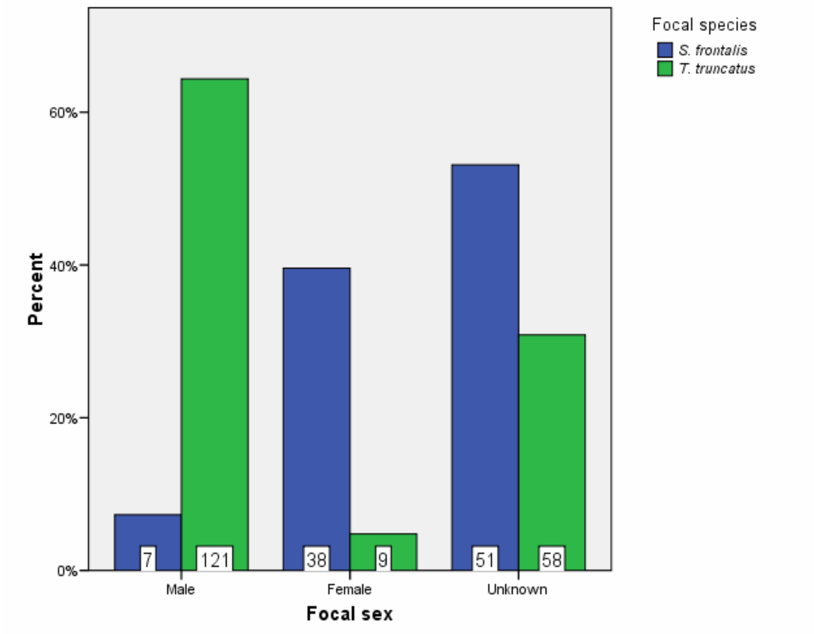

Figure 2.4: Among focal animals, sex was often unknown for both species*;* however, when it was confirmed, the *Tursiops* was most often a male. *Stenella* was most often a female.

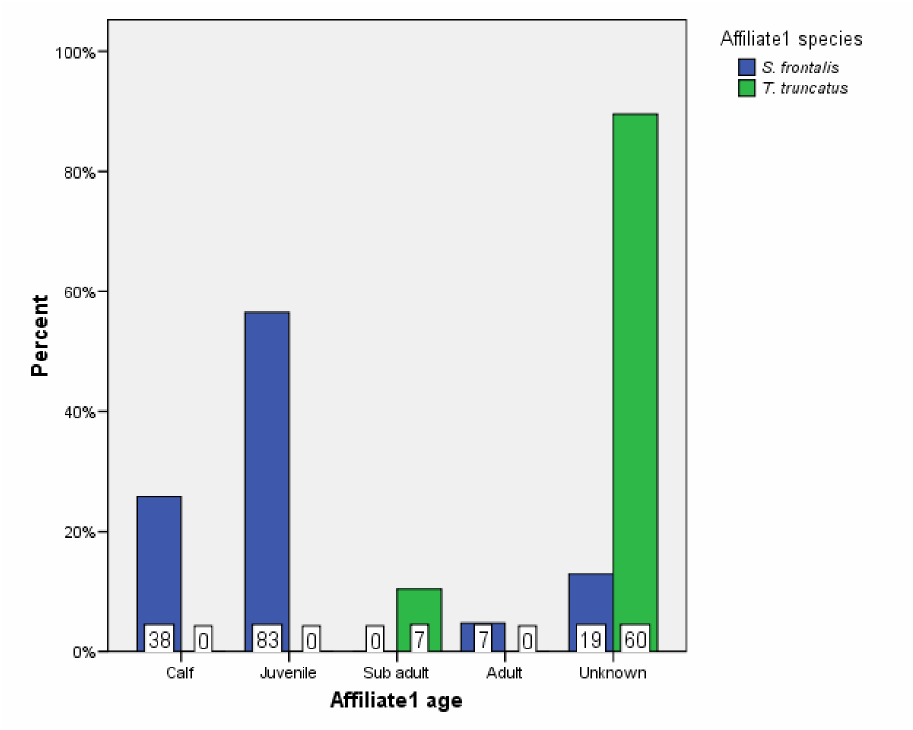

Figure 2.5: Among affiliate1 animals, age class was often unknown for both species; however, when it was confirmed, the *Tursiops* was most often a sub-adult. *Stenella* was most often a juvenile.

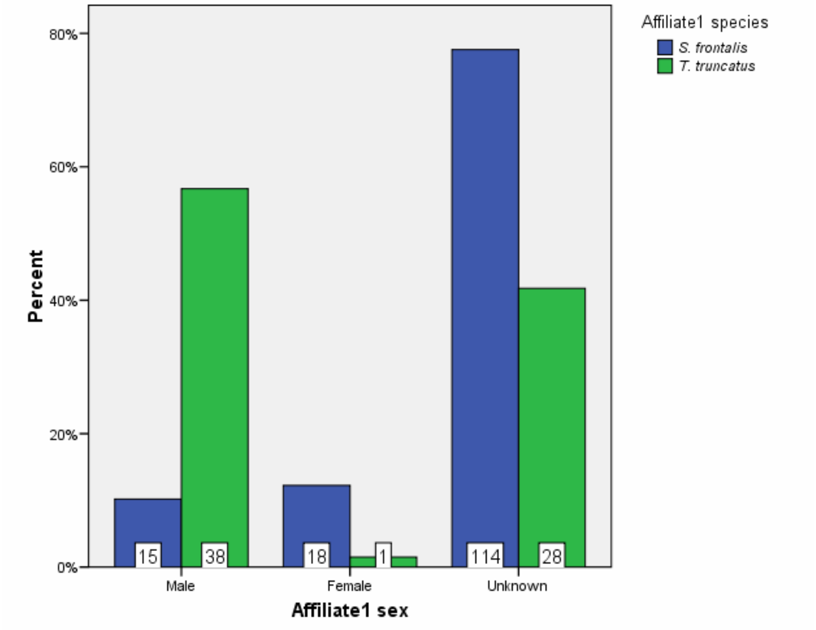

Figure 2.6: Among affiliate1 animals, sex was often unknown for both species; however, when it was confirmed, the *Tursiops* was most often a male. *Stenella* was most often a female.

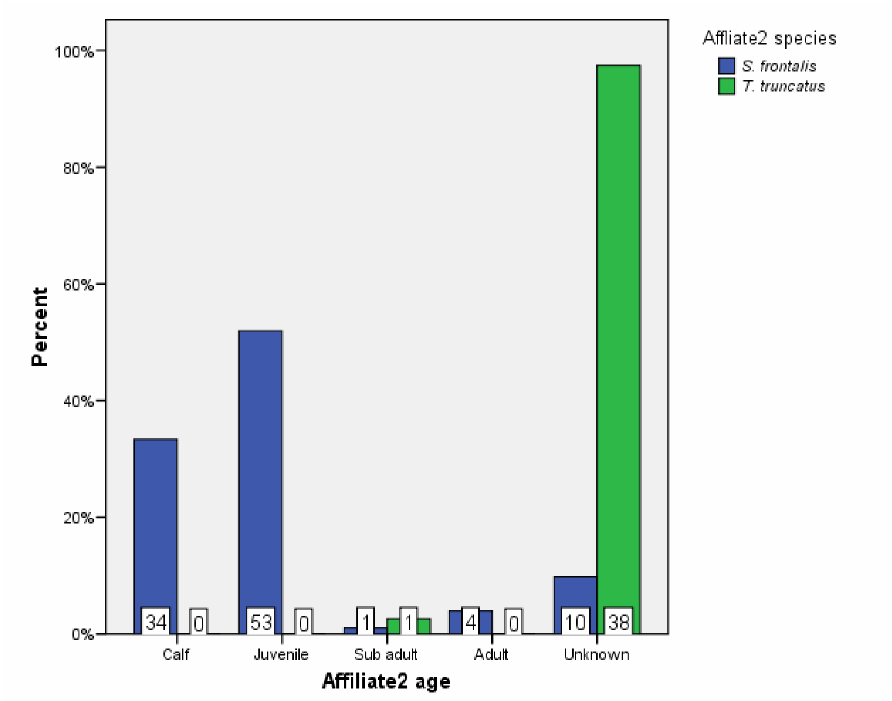

Figure 2.7: Among affiliate2 animals, age class was often unknown for both species. The only confirmed *Tursiops* was a sub-adult. *Stenella* was most often a juvenile.

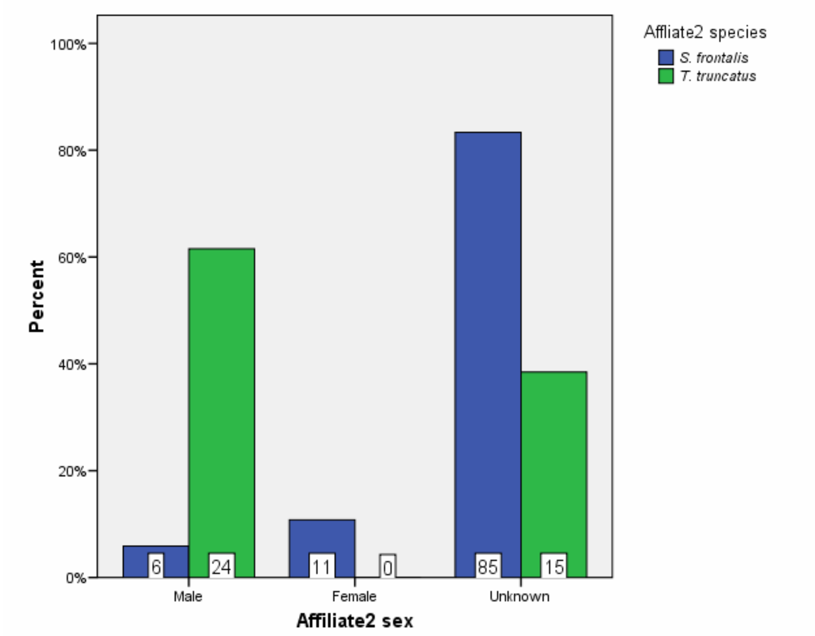

Figure 2.8: Among affiliate2 animals, sex was often unknown for both species; however, within *Tursiops* only males were confirmed. *Stenella* was most often a female.

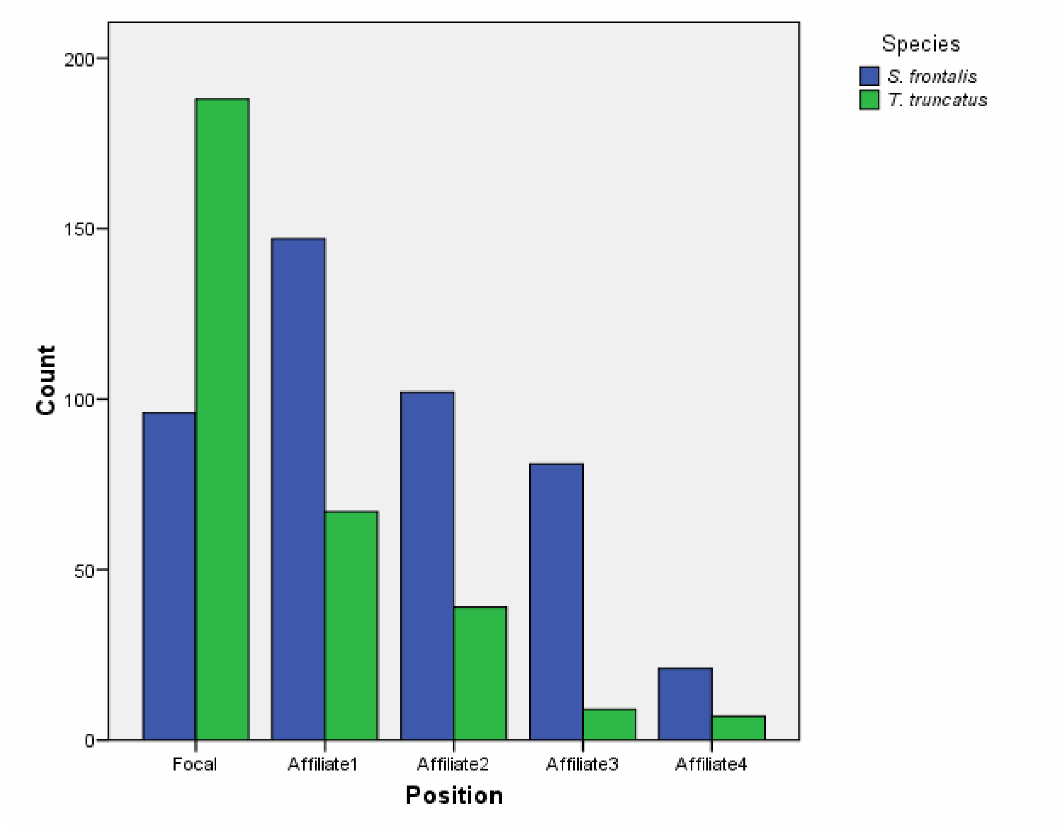

Figure 2.9: Each species was represented in each position during the study. Focal animals were most likely to be *T. truncatus*, however this is an expected byproduct of the sampling bias. As expected with greater numbers of *S. frontalis* in all mixed species groups, each affiliate position was most likely to be *S. frontalis.* Sample sizes as follows: focal n=284, affiliate1 n=213, affiliate2 n=141, affiliate3 n=90, affiliate4 n=28.

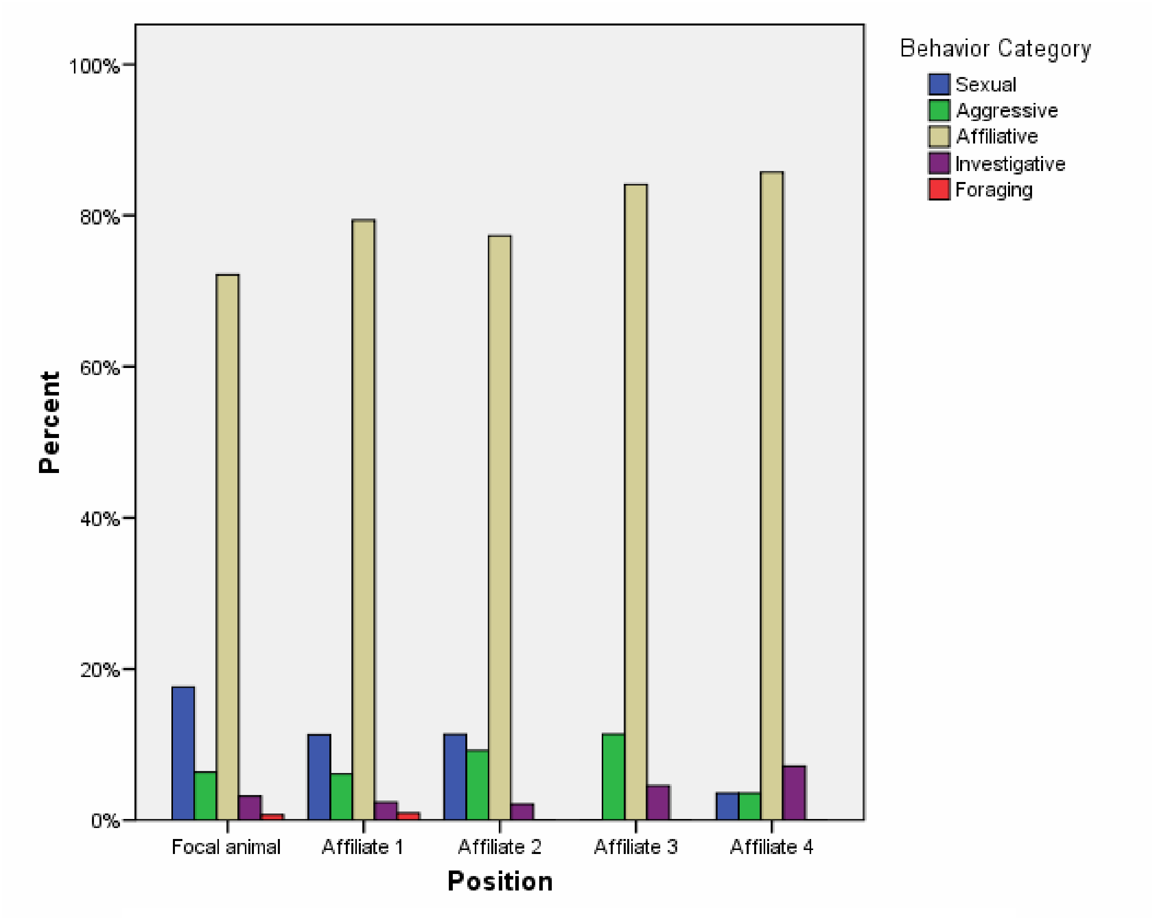

Figure 2.10: The most common behavior category among all positions was affiliative. For focal, affiliate 1 and affiliate 2 animals this was followed by sexual and then aggressive behaviors. Sample sizes as follows: focal n=284, affiliate1 n=213, affiliate2 n=141, affiliate3 n=90, affiliate4 n=28.

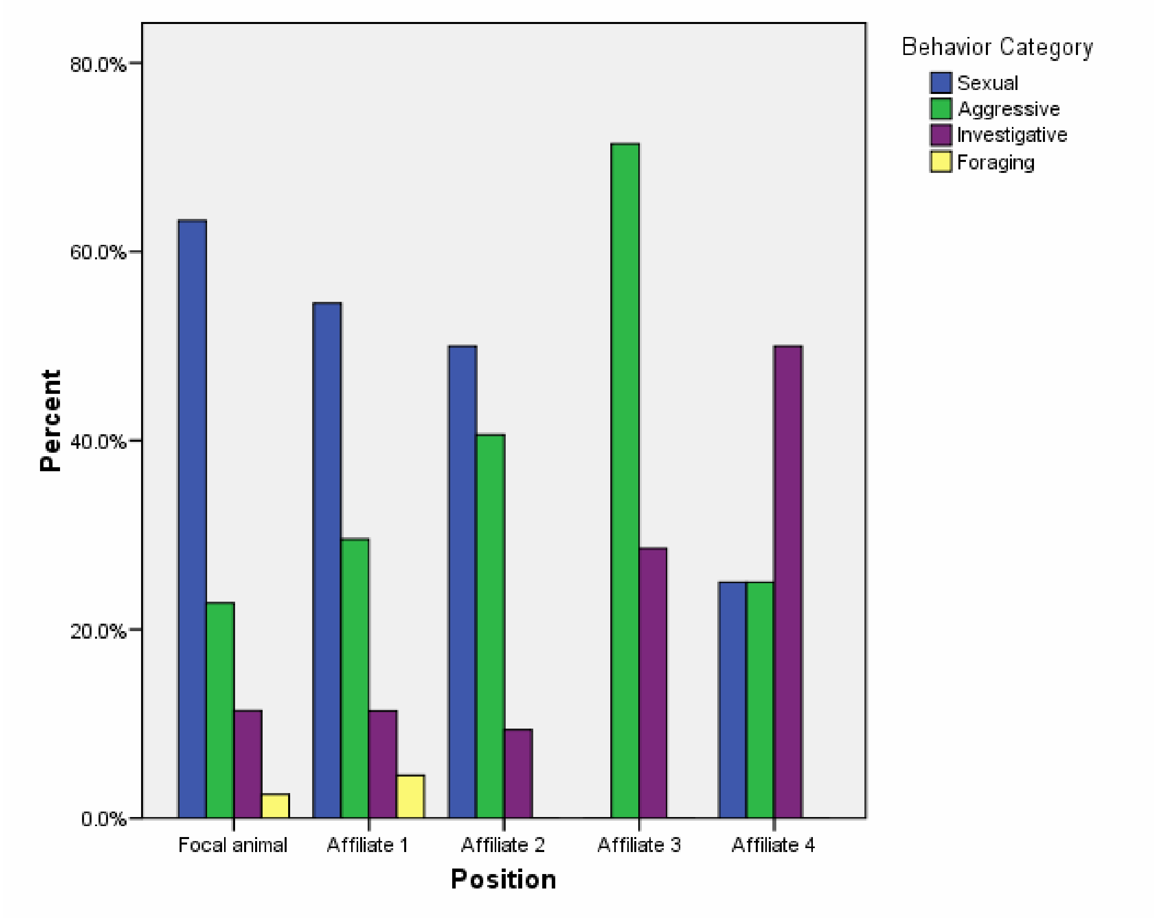

Figure 2.11: Removing affiliative behaviors from consideration, the most common behavior category among focal, affiliate 1 and affiliate 2 animals was sexual. Aggressive behavior among these individuals appears inversely related to sexual behaviors with a peak in aggression among affiliate 3 animals. Sample sizes as follows: focal n=284, affiliate1 n=213, affiliate2 n=141, affiliate3 n=90, affiliate4 n=28.

Nearly 50% of the recorded mixed species interactions during this study included mating or sexual play, suggesting a reproductive function for these encounters. These behaviors were always initiated by sub-adult or unknown (indicating borderline between sub-adult and adult) *Tursiops*. Mating strategies of *Stenella* and *Tursiops* differ among regional conspecific groups and between the two species, but all are polygynandrous (both males and females have multiple partners; Dudzinski 1996, Mesnick and Ralls 2002). Although *Tursiops*-only groups are rarely observed mating in the study area, male *Tursiops* in other areas have been observed creating alliances and multiple males often herd individual females (Connor *et al.* 2000, Connor *et al.* 2001).

Alliance formation has been observed among male *Tursiops* in the Little Bahama Bank (Rogers *et al.* 2004), but not among male *Stenella* in the same area (Dudzinski 1996). The role of alliances is currently unknown for either species in Bimini. Patterson *et al.* (1998) provide evidence for intra- and interspecific infanticide in a *Tursiops* population and suggest this behavior may be a result of limited access to females. No such behavior has been observed in the Bimini population and is not reported in Little Bahama Bank studies. Such variations support the idea that mating strategies differ among *Tursiops* populations globally (Parsons *et al.* 2003) and do not eliminate the possibility that the same is true of *Stenella* populations. Less is known about *Stenella* mating strategies*;* however, observations of *Stenella*-only mating groups in Bimini were generally mixed-gender groups of at least 10 individuals clustered at the surface.

The movement of a *Stenella* mating group was often too swift to allow for underwater observations and mating *Stenella* showed little interest in the boat.

Sexual behaviors in *Stenella-Tursiops* groups more closely resemble *Tursiops*-only groups in that the activity generally progresses toward the sea floor with 1-2 *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 the *Tursiops* allows for their behavior to dominate; however, the ability of *Stenella* to retaliate (Herzing and Johnson 1997, Dudzinski 2007, personal communication) suggests that *Stenella* do not perceive the *Tursiops* advances as threatening. Male *Stenella* were never observed instigating sexual interactions (indicated by erections) with *Tursiops.* However, Herzing *et al.* (2003) reported a single observation off Bimini in which multiple male *Stenella* side-mounted a male *Tursiops*, held it to the sea floor, and forced it into a passive float. Although this shows that male *Stenella* may instigate sexual interactions with *Tursiops,* it was not the typical scenario observed in Bimini during this study. Herzing and Johnson (1997) also reported adult female *Tursiops* soliciting sexual interactions from juvenile male *Stenella*. Given that only one female *Tursiops* was observed in mixed-species groups in the Bimini population, interspecies sexual interactions are likely a *Tursiops* male strategy at this site.

Dolphins, like primates (particularly *Pan paniscus*, de Waal 1997, Hohmann and Fruth 2003), engage in sex with multiple partner combinations, including those incapable of reproduction (e.g., non-ovulating female-male, male-male, female-female, adult-juvenile). The slogan, “Make Love, Not War” has been applied to *P. paniscus* social relationships (de Waal 1997) and may be appropriate for certain Delphinid groups, including those in this study. The fact that *Stenella* in Bimini have not been observed fighting off *Tursiops* may be related to the *Tursiops* size advantage; however, the *Stenella* may also gain from these interactions 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, may 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 suggests that these sexual interactions provide reproductively immature *Tursiops* males, which likely lack the size or social ranking to gain access to mature conspecifics, a sexual outlet outside their own group. *Tursiops* males also typically initiate these encounters.

Direct reproductive benefits in the form of *Tursiops* genes being successfully passed on is the least likely functional explanation for these behaviors, given that sexual interactions between reproductively mature *Tursiops* and *Stenella* were not observed during this study. Even if reproduction was successful, both species would benefit less than when mating with conspecifics. Given the very few recordings of intraspecific mating for either species, mature animals might be least likely to stay within close proximity of humans when actively mating, despite their habituation. It is possible, therefore, that we are not observing interspecific interactions of reproductively mature individuals, if they do occur. However, if the hypothesis that the *Tursiops* joining *Stenella* are those that are being denied conspecific mates is correct, then mature *Tursiops* would not be expected to attempt to mate with *Stenella*. It is also likely that receptive *Stenella* females are monopolized by conspecific males (Herzing and Johnson 1997).

Because *Tursiops* and *Stenella* have overlapping ranges in The Bahamas (Herzing and Johnson 1997, Herzing *et al.* 2003), as well as similar diets and social systems (Herzing *et al.* 2003), it is not surprising that mixed species groups occur. These overlapping ranges, along with the lack of evidence related to cetaceans defending space for exclusive use (Miller 2002), suggest that neither species is specifically territorial. It is possible, however, for conflicts to arise when the two species encounter one another. Interspecific sexual interactions might serve to diffuse tensions when groups of each species mix. The diffusion of aggression through sexual behaviors is common within *P. paniscus* groups (de Waal 1997). *Stenella* and *Tursiops*, like *P. paniscus,* both have complex, fission-fusion social systems (Dudzinski 1996). The similarities between the two groups, both morphologically and socially, allow mixed species groups to occur and allow the interspecific interactions to include sexual behaviors. Perhaps, like bonobos, *Stenella-Tursiops* groups substitute sexual behaviors for rivalries (de Waal 1997) as indicated by the spike in aggression as individuals become further removed from sexual interactions (Figure 2.11).

Alloparental care has been observed in both captive and wild mixed species groups. Bearzi (1996) describes a *Tursiops* calf associated with an adult short-beaked common dolphin (*Delphinus delphis*) while the mother *Tursiops* fed with her conspecific group. 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 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 general, slow swim behaviors.

The behavior of *Stenella* and *Tursiops* in mixed species groups cannot be generalized across regional groups (Little Bahama Bank/White Sand Ridge and Bimini/Great Bahama Bank, for example). Herzing and Johnson (1997) observed short-term, mixed species male alliances in the Little Bahama Bank population in which male *Stenella* joined male *Tursiops* to chase away intruding *Tursiops*. Herzing and Johnson (1997) also reported *Stenella* behavior as generally passive when being pursued sexually by *Tursiops* males, unless the *Stenella* outnumbered the *Tursiops*. In that case, *Stenella* were repeatedly observed driving away the *Tursiops*. Neither interspecific alliances nor *Stenella* driving away *Tursiops* have been observed in the Bimini population.

Throughout the study period, only two mixed species focal groups were observed in close proximity to potential prey. During the first of these sessions, 2 female *Stenella* calves approached two *Tursiops* (unknown sex). The 2 *Tursiops* were actively bottom grubbing (crater-feeding) and showed no sexual, aggressive or investigative behaviors toward the *Stenella*. Rather, the *Stenella* investigated the *Tursiops* by gliding along the bottom next to the *Tursiops* and jawing at and circle chasing the *Tursiops*. There was no feeding on the part of the *Stenella;* therefore, this encounter is not indicative of foraging advantages. The second mixed species observation in close proximity to potential prey was also the deepest observation (27.5 m) during which a single adult *Tursiops* (unknown sex) approached a mixed-age group of *Stenella,* which were investigating a school of jacks (*Carangidae*). No dolphins of either species made any attempt to capture any of the fish, possibly because the jacks were too large. No dolphins of either species exhibited any sexual, aggressive or investigative behaviors toward each other; both species only investigated the fish prior to going out of view. Interspecific foraging behaviors have been observed in the more northern Little Bahama Bank population of *Stenella* (Herzing and Johnson 1997). The lack of observed foraging behaviors in mixed species groups in Bimini may be related to the small sample size of mixed species observations in the Bimini study population relative to the Little Bahama Bank population.

Predatory sharks (e.g., bull (*Carcharhinus leucas*), tiger (*Galeocerdo cuvier*) hammerhead (*Sphyrna mokarran, S. lewini)*) are a source of injury and mortality, as indicated by the presence of scars on *Stenella* and *Tursiops* in the study area (personal observation). *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 and Schilt 1988, Herzing and 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 and Dohl 1980). Rather, the sexual and aggressive behaviors observed in the mixed species groups in this study suggest a reduced level of vigilance. This lack of vigilance may be offset by increased group size, such that mixed groups offer no added protection, but also no added risk, in terms of predator avoidance or detection.

Even with reduced vigilance, both species may benefit from the dilution effect when in larger groups (Norris and Schilt 1988). The dilution effect implies that if a predator comes upon a group of prey, each individual prey is safer because of the ratio of prey to predators (Norris and Schilt 1988). Mixed species groups in the study area, however, have not been observed in greater numbers than those in single species groups. The largest mixed species group was 20 individuals, whereas the largest *Stenella* group observed was 30 individuals and the largest *Tursiops* group observed was also 20 individuals. Therefore, the mixed species group does not offer more protection via the dilution effect than is possible for either single species group. Individual *Tursiops,* however, may gain added protection via the dilution effect when traveling alone or in small groups and joining a larger *Stenella* group. For example, on 18 August 2007, a single *Tursiops* joined a *Stenella* group of at least 21 individuals. There was no visible predator and the *Tursiops* remained with the *Stenella* group only briefly with little interaction.

Orange Cay

An exploratory research trip was conducted from 23-25 July 2007 to Orange Cay, The Bahamas with the primary goal of documenting the *Stenella* in this area. Orange Cay is approximately 60 miles south of Bimini. Preliminary photo-ID work supports the possibility of Orange Cay as home to a third resident *Stenella* population in The Bahamas (in addition to Little Bahama Bank/White Sand Ridge and Bimini/Great Bahama Bank populations). This research trip also included an observation of a *Stenella/Tursiops* group. This single observation, however, did not fit the typical mixed species observations off Bimini. Here, a group of at least 10 *Tursiops* (mixed ages and sex) was encountered at 13:13 in less than 10 m of water. While observing this group underwater, four *Stenella* (sub-adult and adult) entered the area. In Bimini, nearly all mixed species observations have involved *Tursiops* joining *Stenella* groups and interacting primarily with younger *Stenella.* The sub-adult *Stenella* approached the *Tursiops* and both species proceeded to swim slowly between the bottom and the surface with occasional interruptions for interspecific rubbing and circle swims. *Tursiops* raked *Stenella* with their teeth and displayed erections. At one point, three male *Tursiops* (between sub-adult and adult) attempted intromission with a single sub-adult *Stenella*, while swimming away from the rest of the group. At no point were aggressive behaviors (jaw claps, loud vocalizations, flaring pectoral fins) observed. Further population and behavioral studies are needed in this area in order to provide a thorough comparison to observations of the Bimini and other dolphin populations.

Conclusions

The waters off Bimini are home to a resident population of *Stenella* who have regular interactions with *Tursiops*. With many of these interactions including sexual behaviors, it is valuable to monitor the population for potential hybrids. *Tursiops* have successfully reproduced with other odontocete species in captivity (Dohl *et al.* 1974, Nishiwaki and Tobayama 1982, Zornetzer and Duffield 2003) and possibly in the wild (e.g., Fraser 1940, Herzing *et al.* 2003, Acevedo-Gutierrez *et al.* 2005, Kristiansen and Forestell 2007) and the potential for hybridization with *Stenella* cannot be ruled out. All mixed species observations during this study included immature *Tursiops*; however, this age classification is based solely on external morphology, so the state of reproductive maturity cannot be confirmed. Although these interactions are relatively infrequent, they do occur with some consistency over time and between populations, therefore continued observations of these dolphin groups are required to determine whether interspecific interactions represent a significant exchange between species. It would also be interesting to note if any of the immature *Tursiops* individuals continue their sexual pursuit of *Stenella* once they are reproductively active and socially mature.

Genetic studies would be useful to confirm suspected 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 2003, personal communication) and in the Bimini *Stenella* populations (Herzing *et al.* 2003). *Tursiops* in other areas of The Bahamas and the southern Caribbean have been observed with atypical ventral spotting (Dudzinski, 2003, 2006 personal communication). The Bimini *Stenella* population is estimated at between 125 – 145 individuals and the *Tursiops* population is unknown. If the two Delphinid species around Bimini successfully hybridize, the potential impact on their separate populations, including introgression of mtDNA (Lehman *et al.* 1991), should be monitored. 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).

Examinations of intra- and interspecific communication during mixed species encounters would also be valuable. Continuing to compare the nature of these behaviors between different *Stenella* and *Tursiops* populations in the Bahamas and elsewhere will enhance the discussion of behavioral variations between different populations of the same species, particularly in the context of potential cultural transmission of behavior in species with complex social structures. The definition of culture, as well as the methods (experimental or field-based) to test for its presence, are far from agreed upon (Rendell and Whitehead 2001); however *Tursiops* males should be observed in order to determine if there is cultural transmission of these behavioral strategies within or between overlapping generations and populations. Comparative studies of *Tursiops* within the Bahamas (e.g. Little Bahama Bank, Bimini and Orange Cay) could provide insight into potential exchanges between *Tursiops* groups, given that regional *Tursiops* groups may not be absolutely discrete (Shane *et al.* 1986). There does not appear to be mixing between the Little Bahama Bank and Bimini *Stenella* populations (Herzing 2007, personal communication), so transmission of information between *Stenella* groups in the region is unlikely unless the two populations are mixing at the most southern and northern (respectively) bounds of their ranges.

Finally, 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 in Bimini and the Little Bahama Bank, serve as baseline information with which to inform the scientific, governmental and public communities.

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Appendix A

Subset of the catalog of surface and underwater behaviors created for *Stenella* by Dudzinski (1996). Applicable to both *Stenella* and *Tursiops* during this study.

CODE	**Behavior**	**CODE**	**Behavior**
ERE	Erection	HDO	Head down
EOR	Erection w. direction	DEP	Depart
INT	Intromission	OSD	Turn body on side
GOS	Goose	BUP	Belly up
GPS	Group on one sex	GAB	Glide along bottom
HRD	Herding	SUS	Suspended vertical swim
MNT	Mounting	RSM	Move horizontally
FTG	Fluke to genital	SYB	Synch breathe
JCP	Jaw Clap	MLL	Milling
ATK	Chase & bite	LOB	Lying on bottom
BTE	Bite or rake	APP	Approach
CCH	Circle chase	HSC	Head scanning
PDD	Pushing down	BTG	Bottom grubbing
NDG	Nudging	P6	Calf under adult
FLW	Follow	BTB	Belly to belly
SSW	Slow swim	RUB	Rubbing
CSW	Cruising swim	PET	Petting w. pec fin
FSW	Fast swim	CNT	Contact
UTS	Swim to surface	BBT	Bubble trail
STB	Swim to bottom	BBS	Bubble stream
HUP	Head up		