

Short Note

Interspecific Interactions Between Cetacean Species in Algoa Bay, South Africa

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When individuals of different species meet in a non-predatory context, a trade-off is made between the costs (i.e., competition for food) and benefits (i.e., reduced predation risk, energetic benefits, and benefits of alloparental behaviour) of group formation (Gygax, 2002). In general, nonpredatory interspecific interactions (hereafter referred to as interspecific interactions) are classified as either positive or negative for either party involved (i.e., mutualism and competition, respectively) or at least for one of the interacting species (i.e., commensalism and parasitism, respectively) (Krebs, 1985).

Positive interactions often result in the formation of mixed-species groups, providing either social and foraging advantages or protection from predators for at least one of the species involved (Norris & Dohl, 1980; Stensland et al., 2003; Bearzi, 2006). Competition is often the result of an overlap in preferred resources and/or habitat between two or more species. When competitors meet, a trade-off is made between the costs of fighting (i.e., time, energy, injury, or mortality) and the costs of tolerance or avoidance (i.e., loss of resources or habitat) (Tanner & Adler, 2009). High costs of competition can lead to tolerance, resulting in the coexistence of two competing species (Tannerfeldt et al., 2002; Tanner & Adler, 2009), or, alternatively, the inferior species could choose to avoid its competitor.

Reports on interspecific interactions among cetacean species are numerous (e.g., Jefferson et al., 1991; Herzing & Johnson, 1997; Migura & Meadows, 2002; Kiszka, 2007; Mellilo et al., 2009; Cotter et al., 2012; Smultea et al., 2014). We know little, however, on interactions involving the Indian Ocean humpback dolphin (*Sousa plumbea*, formerly *Sousa chinensis*) (Saayman & Tayler, 1979; Karczmarski et al., 1997) or on interactions between suborders (Jefferson et al., 1991; Shelden

et al., 1995; Ciano & Jørgensen, 2000; Wedekin et al., 2004b; Rossi-Santos et al., 2009). In addition, the actual frequency of occurrence as well as functional explanations of interspecific interactions among cetaceans are currently unclear (Shelden et al., 1995; Herzing & Johnson, 1997; Frantzis & Herzing, 2002; Herzing et al., 2003). It is, thus, important to report on these interactions to facilitate our understanding of their significance as well as their effect on animal behaviour and ecology (Fertl & Fulling, 2007). Herein, we report on a series of observations of interspecific interactions among cetaceans in Algoa Bay, South Africa, and discuss their potential functions.

Interspecific interactions were observed during both land- and boat-based surveys conducted between May 2010–2011 and June 2008–2011, respectively. Land-based surveys were carried out daily from four vantage points along a 10-km stretch of coastline in the westernmost part of Algoa Bay (Figure 1). Boat-based strip-transect surveys were conducted approximately four times a month and focused on the coastal area of the bay, with three main tracks carried out monthly (Figure 1). No surveys were conducted if there were Beaufort Sea States above 3, poor visibility, a swell exceeding 2 m, or on rainy days. For more detailed information on the study area and survey methodologies, see Koper et al. (2016) and Melly (2011), respectively.

We classified the interspecific interactions observed as either an association (i.e., two species in such close proximity that they can be regarded as members of the same group) or an avoidance (i.e., abrupt and immediate departure by one species away from the other species usually followed by the disappearance of one of the interacting groups in response to the action of the other) (Stensland et al., 2003; Parra, 2005). The term *group* refers to

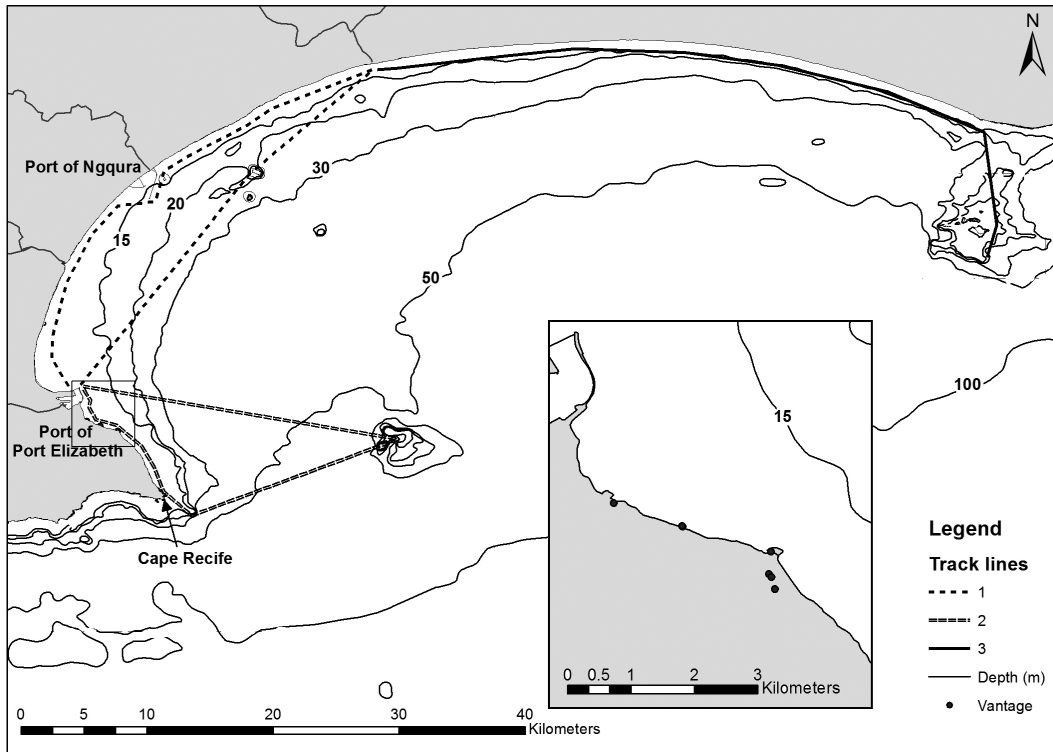


Figure 1. Study areas for land-based (insert) and boat-based (i.e., track lines 1, 2, and 3) surveys carried out in Algoa Bay, South Africa, during which interspecific interactions between cetacean species were observed

any aggregation of individuals engaged in similar activities as well as solitary individuals. Dominant behaviours of Odontocetes followed the definitions provided by Karczmarski et al. (1997, 2000), Karczmarski & Cockcroft (1999), and Constantine et al. (2004). Dominant behaviours of Mysticetes followed the definitions provided by Cummings (1985) and Best (2007).

The search effort reached for land- and boat-based observations was 512 h and 5,000 km, respectively, resulting in 722 sightings of cetaceans combined. We classified 14 of the 722 sightings as interspecific associations. Six of these (42.86%) included Indian Ocean humpback and Indo-Pacific bottlenose (*Tursiops aduncus*) dolphins (Events 1 to 6), four instances (28.57%) included long-beaked common (*Delphinus capensis*) and bottlenose dolphins (Events 7 to 10), three instances (21.43%) included humpback whales (*Megaptera novaeangliae*) and bottlenose dolphins (Events 11 to 13), and one instance (7.14%) included southern right whales (*Eubalaena australis*) and humpback dolphins (Event 14) (Table 1).

All Odontocete-Odontocete associations included the bottlenose dolphin, which was always,

with one exception, the most abundant species in the sighting. Events 1, 7, and 8 included potential hybrids as the bottlenose dolphin observed in Event 1 appeared to have a small hump similar to the appearance of a humpback dolphin, while both common dolphins observed in Events 7 and 8 had, in addition to a saddle marking, colour patterns closely resembling the colour pattern of bottlenose dolphins. The majority (i.e., 90%) of Odontocete-Odontocete associations comprised a small group of humpback or common dolphins in association with bottlenose dolphins in the absence of any evident interspecific tactile or nontactile interactions. Humpback dolphins were primarily observed on the outskirts of bottlenose dolphin groups, while common dolphins were always found in a well-mixed association (i.e., in the middle of a bottlenose dolphin group). The predominant behaviour of these associations was primarily travelling (66.67%), although foraging (22.22%) and socialising (11.11%) were also observed.

Three Mysticete-Odontocete associations were comprised of humpback whales and bottlenose dolphins (Events 11 to 13; Table 1). Event 11 included a humpback whale mother-calf pair and

Table 1. Interspecific associations including Indian Ocean humpback dolphins (*Sousa plumbea*), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), long-beaked common dolphins (*Delphinus capensis*), humpback whales (*Megaptera novaeangliae*), and southern right whales (*Eubalaena australis*) observed during land- and boat-based observations between 2008 and 2011 in Algoa Bay, South Africa

Event	Species 1	Species 2	Group sizes Sp. 1 : Sp. 2	Behaviour Sp. 1: Sp. 2
1	Humpback dolphin	Bottlenose dolphin	4 : 1	Foraging : Foraging
2	Humpback dolphin	Bottlenose dolphin	3 : 80	Milling : Socialising
3	Humpback dolphin	Bottlenose dolphin	2 : 80	Foraging : Foraging
4	Humpback dolphin	Bottlenose dolphin	2 : 180	Travelling : Travelling
5	Humpback dolphin	Bottlenose dolphin	2 : 7	Travelling : Travelling
6	Humpback dolphin	Bottlenose dolphin	2 : 50	Travelling : Travelling
7	Common dolphin	Bottlenose dolphin	1 : 50	Travelling : Travelling
8	Common dolphin	Bottlenose dolphin	1 : 40	Foraging : Foraging
9	Common dolphin	Bottlenose dolphin	2 : 200	Travelling : Travelling
10	Common dolphin	Bottlenose dolphin	1:12	Travelling : Travelling
11	Humpback whale	Bottlenose dolphin	2 : 12	Travelling/Breaching : Travelling
12	Humpback whale	Bottlenose dolphin	2 : 15	Breaching : Foraging
13	Humpback whale	Bottlenose dolphin	1 : 100	Travelling/Twirling : Travelling
14	Southern right whale	Humpback dolphin	2 : 2	Travelling : Travelling

12 bottlenose dolphins (10 adults and two calves) travelling in association. Both the humpback whale mother and calf displayed breaching and side fluking behaviour. Event 12 consisted of a humpback whale mother-calf pair surrounded by 15 foraging bottlenose dolphins and a large amount of foraging Cape gannets (*Morus capensis*). Again, the humpback whale calf displayed breaching behaviour. Event 13 consisted of a juvenile humpback whale continuously rolling around its axis, swimming belly up, with pectoral fin slapping, while travelling in association with a large group (100 individuals) of bottlenose dolphins. Again, a group of foraging Cape gannets surrounded the group. The fourth Mysticete-Odontocete association consisted of a southern right whale mother-calf pair and two adult humpback dolphins travelling in association (Event 14).

Of the 722 sightings recorded during the two surveys, we classified 14 as interspecific avoidance interactions (Events 15 to 28; Table 2). All of these events consisted of the avoidance of bottlenose dolphins by humpback dolphins. During all avoidance interactions, bottlenose dolphins were the most abundant species. Humpback dolphins either changed their direction of travel (21.43%), changed their behaviour to move away from the group of bottlenose dolphins (21.43%), increased their dive duration and disappeared (21.43%), split

up (14.29%), increased their dive duration until the bottlenose dolphins had passed (7.14%), increased their dive duration and temporarily changed direction of travel until the bottlenose dolphins had passed (7.14%), or increased their dive duration and temporarily changed their behaviour until the bottlenose dolphins had passed (7.14%).

The primary behaviour of travelling observed for Odontocete-Odontocete associations suggests two likely functional explanations: (1) protection from predators and/or (2) energetic benefits. The main predators of dolphin species in South Africa are sharks, evident from individuals bearing scars in KwaZulu-Natal (Cockcroft, 1991), Plettenberg Bay (Saayman & Tayler, 1979), and Gansbaai (Weisel et al., 2010). The presence of at least five predatory shark species in Algoa Bay (Compagno et al., 1989; Ebert, 1991; Smale, 1991; Dicken, 2011; Dicken & Booth, 2012) could drive smaller groups of humpback and common dolphins to join larger groups of bottlenose dolphins to decrease the risk of a shark attack. Smaller groups of humpback and common dolphins may also join larger groups of bottlenose dolphins to conserve energy as previously indicated by studies on fish schools (Weihs, 1973; Herskin & Steffensen, 1998; Hemelrijk et al., 2015).

Although no tactile or nontactile interactions were observed, social or foraging advantages

Table 2. Interspecific avoidance interactions including Indian Ocean humpback dolphins and Indo-Pacific bottlenose dolphins observed during land-based observations between May 2010 and May 2011 in Algoa Bay, South Africa

Event	Species 1	Species 2	Group size Sp. 1 : Sp. 2	Start behaviour Sp. 1 : Sp. 2	Avoiding species	Reaction
15	Humpback dolphin	Bottlenose dolphin	--	Travelling : Travelling	1	Change in direction
16	Humpback dolphin	Bottlenose dolphin	--	Travelling : Travelling	1	Change in direction
17	Humpback dolphin	Bottlenose dolphin	5 : 50	Travelling : Travelling	1	Change in direction
18	Humpback dolphin	Bottlenose dolphin	1 : 150	Resting : Travelling	1	Change in behaviour
19	Humpback dolphin	Bottlenose dolphin	3 : 50	Foraging : Travelling	1	Change in behaviour
20	Humpback dolphin	Bottlenose dolphin	7 : 45	Milling : Travelling	1	Change in behaviour
21	Humpback dolphin	Bottlenose dolphin	3 : 8	Travelling : Travelling	1	Change in dive duration; disappeared out of sight
22	Humpback dolphin	Bottlenose dolphin	1 : 50	Travelling : Travelling	1	Change in dive duration; disappeared out of sight
23	Humpback dolphin	Bottlenose dolphin	7 : 80	Milling : Travelling	1	Change in dive duration; disappeared out of sight
24	Humpback dolphin	Bottlenose dolphin	1 : 4	Travelling : Travelling	1	Change in dive duration
25	Humpback dolphin	Bottlenose dolphin	2 : 5	Travelling : Travelling	1	Change in dive duration, direction
26	Humpback dolphin	Bottlenose dolphin	?	Travelling : Travelling	1	Change in dive duration, behaviour
27	Humpback dolphin	Bottlenose dolphin	4 : 14	Travelling : Travelling	1	Group split
28	Humpback dolphin	Bottlenose dolphin	6 : 50	Travelling : Travelling	1	Group split

should not be excluded (Paulos et al., 2010). The observation of potential hybrids could indicate the occurrence of interspecific mating (Fraser, 1940; Reyes, 1996; Yazdi, 2002; Herzing et al., 2003; Silva et al., 2005; Amaral et al., 2014; Hodgins et al., 2014), whereas various nontactile interactions (e.g., eye contact or body postures) may have taken place beneath the surface (Pryor, 1990). Additionally, humpback dolphins may receive foraging advantages from associating with bottlenose dolphins with whom they show some dietary overlap (Ross, 1984; Cockcroft & Ross, 1990; Barros, 1991; Barros et al., 2004). A recent study by Koper et al. (2016) suggested that the humpback dolphins in Algoa Bay might suffer from a decline in prey abundance. The observation of humpback dolphins swimming on the outskirts of, rather than integrated in, a group of bottlenose dolphins, therefore, possibly indicates that humpback dolphins associate to obtain information on the location of food resources when there is a decrease in food abundance (Norconk, 1990) to increase their food detection success (Stensland et al., 2003). This hypothesis is unlikely for the

associations between common and bottlenose dolphins as the dietary overlap between these two species is less pronounced (Cockcroft & Ross, 1990; Best, 2007).

Three Mysticete-Odontocete associations were comprised of humpback whales and bottlenose dolphins, with the humpback whales displaying agonistic defence movements (i.e., breaching, pectoral fin slapping, and rolling around axis) during the interactions (Baker & Herman, 1984; Ford & Reeves, 2008; Cartwright & Sullivan, 2009). Bottlenose dolphins could be attracted by the fauna associated with the presence of humpback whales, including potential prey, such as the whalesucker (*Remora australis*) and shark-sucker (*Echeneis naucrates*), on the body of the humpback whales (Wedekin et al., 2004b; Rossi-Santos et al., 2009). Hence, the bottlenose dolphins observed might have been feeding on prey attached to as well as around the humpback whales. Rapid movements related to foraging around vulnerable mother-calf pairs or juveniles might scare or agitate the whales, with consequent behavioural responses related to fear or agitation

and defence (Shelden et al., 1995). Alternatively, the bottlenose dolphins may have associated with humpback whales to experience a reduced energy expenditure, riding the waves created by the movement of the whales (i.e., bowriding) (Weihs, 1973; Wedekin et al., 2004b). The latter seems a likely functional explanation for the observed association between a southern right whale mother-calf pair and two humpback dolphins as neither species appeared disturbed, and their movements seemed finely attuned.

In addition to associations, we observed an equal amount of avoidance interactions during which humpback dolphins avoided bottlenose dolphins. Avoidance is a sign of interference competition, which means that the presence of a dominant competitor can reduce a species willingness to utilise an area (Tannerfeldt et al., 2002). Consequently, the inferior species could become excluded to breed or feed in an area (Tannerfeldt et al., 2002). A change in prey abundance for humpback dolphins in Algoa Bay, as mentioned above, could have caused an increase in dietary overlap with the bottlenose dolphins and, thus, an increase in competition for food with consequent interference competition (Corkeron, 1990). Alternatively, avoidance behaviour could be the result of previous aggressive or harassing encounters (Wobber, 1975; Kutsukake & Clutton-Brock, 2008). Bottlenose dolphins are known for their aggressive and harassing behaviour towards conspecifics (Connor et al., 1996, 1999; Parsons et al., 2003; Scott et al., 2005) as well as allospesifics (Saayman & Tayler, 1979; Ross & Wilson, 1996; Herzog & Johnson, 1997; Patterson et al., 1998; Wedekin et al., 2004a; Flores & Fontoura, 2006; Cotter et al., 2012). Although no aggressive encounters between humpback and bottlenose dolphins were observed, previous encounters could have taught humpback dolphins to avoid bottlenose dolphins to prevent high costs as a result of conflicts (Bolles, 1970).

Our data highlight the complexity of Odontocete-Odontocete interactions with multiple functional explanations for associations such as protection from predators, provisioning of energetic benefits, social advantages, or foraging advantages. However, the existence of these benefits might be determined by the species' group sizes as well as the behaviour displayed at the time of encounter as suggested by the observations of humpback dolphin avoidance of, as well as amicable associations with, bottlenose dolphins. Mysticete-Odontocete associations primarily seem to benefit the Odontocete species by either providing foraging or energetic advantages.

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