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Risky business? A note on repeated live strandings of common bottlenose dolphins (*Tursiops truncatus*) while foraging in a shallow water environment

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Animals face dangerous situations on a daily basis. Risk assessment underlies all behavioral decisions from predator avoidance or prey capture, to mating strategies or territory defense (Stankowich & Blumstein, 2005). Optimal Foraging Theory (OFT) provides the theoretical framework within which the relative trade-off between the risks and benefits while foraging is commonly assessed (Emlen, 1966; MacArthur & Pianka, 1966; Werner & Hall, 1974). Predation is the most common form of risk considered within OFT, and it can play a significant role in shaping the behavior, habitat use, and survival of both predator and prey (Heithaus & Dill, 2002; Mukherjee & Heithaus, 2013). Predation is an inherently risky foraging strategy and predators themselves take risks while foraging. This trade-off between risk taking and reward in predators is relatively under studied (Berger-Tal, Mukherjee, Kotler, & Brown, 2009; Dietl, 2003; Embar, Raveh, Burns, & Kotler, 2014).

Predation-related injuries to top predators mainly arise from two sources: those sustained during interactions with prey and those sustained due to habitat features (Embar et al., 2014). Predators usually need to be in good physical condition to achieve the necessary levels of energy and maneuverability to capture prey (Berger-Tal et al., 2009; Brown & Kotler, 2004; Combes, Crall, & Mukherjee, 2010). Injuries sustained during predator-prey interactions can reduce the predators' ability to forage and can be fatal. Broken bones, dislocated joints, eye injuries, and broken teeth are common injuries associated with hunting in raptors and carnivores (Brown & Kotler, 2004; Werner & Hall, 1974). Among cetaceans, examples are rare, but fatal stingray injuries have been recorded in both common bottlenose

dolphins (*Tursiops truncatus*) and killer whales (*Orcinus orca*) (Duignan, Hunter, Visser, Jones, & Nutman, 2000; McLellan, Thayer, & Pabst, 1996; Walsh et al., 1988).

There is less known about habitat related risk to predators. Red foxes (*Vulpes vulpes*) exploit low-risk prey patches more intensively than areas with a high risk of injury (Berger-Tal et al., 2009). Similarly, barn owls (*Tyto alba*) and long-eared owls (*Asio otus*), which are susceptible to ocular injuries (Holt & Layne, 2008), manage risk by avoiding foraging in high injury risk areas such as thick forests (Embar et al., 2014). For cetaceans, foraging at the limits of their dive capabilities can be dangerous. Moore and Early (2004) found that some adult sperm whales (*Physeter macrocephalus*) suffered from osteonecrosis from nitrogen loading (i.e., “decompression sickness”), from continued deep dives throughout their lives. Conversely, killer whales have been known to unintentionally strand during foraging bouts in extremely shallow waters (Condy, Van Aarde, & Bester, 1978; Visser & Fertl, 2000) and Cook Inlet beluga whales (*Delphinapterus leucas*) have been reported to strand in shallow tidal lagoons when foraging or fleeing killer whales (Vos & Shelden, 2005). A “strand feeding” foraging strategy, in which animals move themselves far enough out of water that they are no longer floating but resting on land, has been described for several delphinid species (e.g., common bottlenose dolphins, Hoese, 1971; killer whales, Lopez & Lopez, 1985; Indian Ocean humpback dolphins (*Sousa plumbea*), Peddemors & Thompson, 1994; Indo-Pacific bottlenose dolphins (*T. aduncus*), Sargeant, Mann, Berggren & Krützen, 2005; Australian humpback dolphins (*S. sahulensis*), Whiting, 2011); however, to our knowledge, no fatalities have been documented from individuals employing this strategy.

Here we describe several live stranding events that are thought to be related to foraging in a shallow water environment by common bottlenose dolphins inhabiting Namibian waters. The total population consists of fewer than 100 individuals that occur exclusively in very shallow waters (all encounters in <30 m depth) within a narrow strip of coastline stretching approximately 200 km north and 400 km south of Walvis Bay (Elwen, Leeney, & Gridley, 2019). The dolphins are regularly seen in a very shallow lagoon environment, where 59% of their observed behaviors were linked to foraging or possible foraging (Namibian Dolphin Project [NDP], unpublished data) and they can become stranded unintentionally on a receding tide. We discuss the significance of these stranding events for such a small, coastal population. We report on resightings of stranded individuals, by comparing photographic records from strandings data to those taken during shore and vessel-based photo-identification (photo-ID) surveys. In addition, we examined the role of human intervention in strandings events and provide information that is relevant to the broader development of optimal foraging theory.

The NDP has collected photo-ID, acoustic recordings, behavioral observations and stranding information for cetaceans in Walvis Bay, Namibia (22°55'S 14°28'E), since 2008. The NDP currently coordinates the Namibian cetacean strandings network and records. Walvis Bay is a square-shaped bay roughly 10 × 10 km with a maximum depth of approximately 30 m across the mouth (Figure 1). At the southern end of Walvis Bay “First Lagoon” covers approximately 9 km² (Figure 1). First Lagoon (hereafter referred to as “the lagoon”) is very shallow and characterized by extensive mudflats between deeper channels (Figure 2), but the maximum depth does not exceed 4 m. The mean tidal range in Walvis Bay is 1.42 m, with a maximum of 1.97 m (South African Navy, 2007). As the tide recedes, the combination of wide mud flats and channels means large areas of ground can be rapidly exposed, creating a high stranding risk for dolphins (Figure 2). Shore-based observations on the western side of the lagoon are difficult due to lack of road access. However, there is good accessibility to the shore on the northern and eastern banks where a large volume of people, including wildlife-oriented tours, pass throughout the day. Therefore, dolphins stranded in this area are highly likely to be reported. Walvis Bay is at the approximate center of the dolphin's known range and is the only embayment of significant size therein. Bottlenose dolphins are encountered year-round within the bay with approximately half the population resident year-round and the other half seen predominantly during winter months (Elwen et al., 2019).

Vessel based photo-ID surveys were conducted around Walvis Bay and further northwards, however, motor vessels are not permitted inside the lagoon as it is a designated Ramsar site, meaning it is a wetland of international importance to a number of both resident and migratory bird species (Ramsar Convention on Wetlands, 2018), therefore any photo-ID within the lagoon was undertaken from shore. Photo-ID survey effort varied over time but

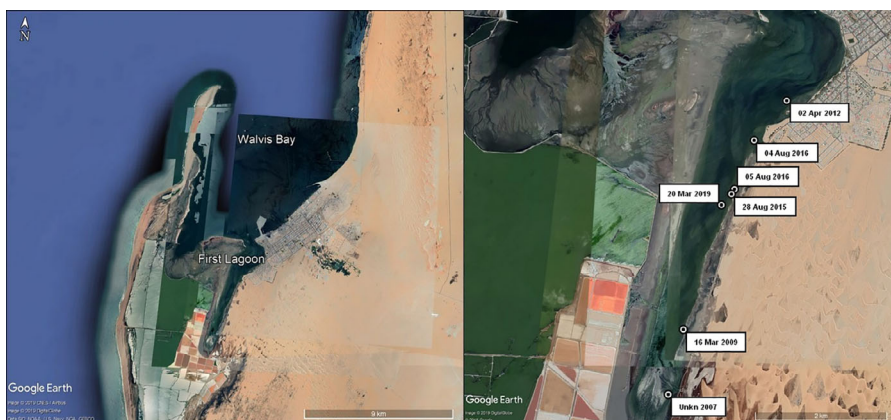


FIGURE 1 Map of Walvis Bay, Namibia, on the left and a closer view of First Lagoon on the right. The known locations of seven strandings are highlighted. All other strandings did not have accurate location data provided.



FIGURE 2 A bottlenose dolphin foraging in First Lagoon. Note the presence of deeper channels where the dolphin is swimming within a few meters of very shallow areas where the great white pelican (*Pelecanus onocrotalus*) is standing; exposed mudflats can be seen in the background but are underwater at higher tides (photo credit: A. Jylhä-Vuorio, NDP).

followed standard protocols (Elwen et al., 2019) where all animals within an encountered group were targeted for high resolution fin images. From 2008 to 2012, boat surveys were conducted in two seasons (February–March and June–August), with between 30 and 70 surveys conducted annually (see Elwen et al., 2019 for details). Fewer surveys were conducted in 2013 ($n = 12$) and 2014 ($n = 9$). In 2015 ($n = 57$) and 2016 ($n = 67$), regular (weekly) surveys were conducted year-round as part of a program monitoring potential impacts of harbor construction in addition to the main winter field season.

Strandings data were collected ad hoc via the Walvis Bay Strandings Network (an informal network of public volunteers who report strandings to the NDP and collect data when needed). Dedicated monthly strandings surveys of the eastern and southern lagoon area and the coastline north of Walvis Bay were conducted throughout 2015 and 2016. We also included five stranding records that were obtained from articles in a local newspaper (The Namib Times) during a review of news archives for marine stories (Shaanika, 2018).

Dedicated behavioral observations of bottlenose dolphins in the lagoon were collected by shore-based observers between 2015 and 2018, as part of a broader project investigating dolphin lagoon-use based on sampling methods described in Heiler, Elwen, Kriesell, and Gridley (2016) and adjusted for land based observations. Data on the surface behavior of dolphins within the lagoon were collected every 3 min during encounters, whereby the predominant group behavior (>50% of individuals) was assigned to a predetermined set of behavioral states. Behavioral states were classified as surface feeding, resting, socializing, traveling, and milling (Heiler et al., 2016).

Since 1991, there have been 13 recorded live bottlenose dolphin stranding events in the lagoon, comprising 56 individuals (25 identified individuals and 31 not identified) (Table 1). All recorded strandings occurred at the south-eastern side of the lagoon (Figure 1), of which eight were attended to by members of the Walvis Bay Strandings Network and five were reported from newspaper articles. No live strandings have been recorded outside the lagoon, but 10 strandings of dead bottlenose dolphins have been confirmed within the wider Walvis Bay area over the study period, including one within the lagoon. Human intervention occurred in 10 live stranding events of 47 dolphins, in which the dolphins were refloated (three by the NDP, three by the Walvis Bay Strandings Network without NDP members and four by members of the public). Three individuals died while stranded: an adult who stranded alone in 1991, an adult who stranded with two others in 2007 and a calf that stranded with 18 others on 16 March 2009. A single individual (ID#: T-012) which stranded and was refloated on 17 March 2009 (Table 1), had stranded the previous day and was thought to be the mother of the deceased calf. The two documented strandings

TABLE 1 Live strandings of bottlenose dolphins in First Lagoon, including information on the date of the stranding, the source of the report, the number of individuals stranded, refloated, deceased and identified, also including number of individuals resighted >5 months, >1 year, and >5 years after refloating. Some reports lacked accurate date information, so the closest known date was used. “Unkn” indicates where individuals were not identified during the stranding, therefore we cannot say whether they were subsequently seen or not. The individuals that stranded on 4 and 5 August 2016 refloated themselves without human intervention and no photographs for identification were taken. “WBSN” indicates where strandings were attended by the Walvis Bay Strandings Network without a member of the NDP.

Date	Source	No. of dolphins	Refloated by humans	Deceased	Photo identified	Resighted >5 months	Resighted >1 year	Resighted >5 years
Jan 1991	Newspaper	1	0	1	0	NA	NA	NA
7 Nov 1995	Newspaper	8	8	0	0	Unkn	Unkn	Unkn
1996	Newspaper	4	4	0	1	1	1	1
9 Mar 2001	Newspaper	1	1	0	0	Unkn	Unkn	Unkn
2002	Newspaper	2	2	0	0	Unkn	Unkn	Unkn
2007	WBSN	3	2	1	0	Unkn	Unkn	Unkn
16 Mar 2009	NDP	19	18	1	17	17	16	12
17 Mar 2009	WBSN	1	1	0	1	1	1	1
2 Apr 2012	WBSN	2	2	0	1	1	1	1
28 Aug 2015	NDP	7	7	0	5	5	5	NA
4 Aug 2016	NDP	3	0	0	0	Unkn	Unkn	NA
5 Aug 2016	NDP	3	0	0	0	Unkn	Unkn	NA
20 Mar 2019	NDP	2	2	0	2	NA	NA	NA

(six individuals) in 2016 did not require human intervention (Table 1), as in both instances the animals refloated themselves when water levels increased on the incoming tide. As some strandings were reported from newspaper articles and some were not attended by members of the NDP (Table 1), there were instances where no photo-ID of the individuals, morphometric measurements, or sex information was available.

Of 27 photographically identified individuals which were refloated, one juvenile, T-017c, which stranded in 2010 was subsequently photographed 6 months later during a dedicated research survey by the NDP but has not been identified since. Excluding the most recent stranding on 20 March 2019, 96% (24/25) of identified refloated dolphins were photographed more than 12 months after being refloated. One adult female, T-017, the mother of the juvenile T-017c, stranded dead approximately 50 km north of Walvis Bay 16 months after being refloated in 2009, but the carcass was partially decomposed when attended, and a cause of death was not determined.

Considering animals that stranded prior to September 2012, 74% (14/19) have been photographed more than five years after stranding (Table 1). On 4 December 2018, the individual (T-015) that stranded on an unknown date in 1996 was photographed alive. Assuming the latest date possible in 1996 (31 December), this indicates that T-015 has survived at least 8,009 days after refloatation. Further, T-015 subsequently restranded twice, once as part of the large mass stranding on 16 March 2009 and once with one other individual on 2 April 2012. On 6 July 2010, T-015 was seen with a large calf. An estimate of body size from the photographs suggests that the calf was more than six months old. Given an estimated gestation period of 376 days for *T. truncatus* (O'Brien & Robeck, 2012), it is likely that T-015 was pregnant when she stranded in 2009. Since 2009, T-015 has given birth to two additional calves, the most recent in 2017. On 30 September 2017, six of the other individuals that stranded on 16 March 2009 were photographed alive, indicating they have been alive for at least 3,121 days after refloating. One individual (T-070) that stranded on 16 March 2009 subsequently restranded in 2015. Three other previously stranded individuals (T-021, T-045 and T-046) were all seen with new calves in 2017. T-070 has been identified as a female from a ventral photograph but has never been observed with a calf, despite being initially identified as a young adult in 2008.

Bottlenose dolphins (*Tursiops* spp.) are widespread throughout temperate and tropical regions (Reynolds, 2000). The diversity in habitat, prey type, and prey accessibility, together with their ability to socially learn (Kopps, Krützen, Allen, Bacher, & Sherwin, 2014; Mann et al., 2008; Sargeant et al., 2005), has resulted in considerable variation in foraging behavior between and within populations worldwide (e.g., Gazda, 2016; Mann & Sargeant, 2003; Sargeant et al., 2005; Torres & Read, 2009; Wursig, 1986). Bottlenose dolphins in Walvis Bay, Namibia forage in a shallow water lagoon which appears to be a risky strategy. Using the largest population estimate from Elwen et al. (2019) ($n = 82$ in 2008) and focusing only on records after the inception of the Namibian Dolphin Project in 2008, we conservatively estimate that 25% of the population has stranded in the lagoon at some point, but the true number may be considerably higher as 31 animals were unidentified, and a large portion of the western side of the lagoon area was not surveyed due to accessibility. However, historical records indicate that this population has used the lagoon for many decades at least, and that this is not a novel foraging behavior with a steep learning curve, but rather well-established behavior. Bottlenose dolphins have been known to use this lagoon for at least 100 years as they were historically hunted "in waist deep water" by the indigenous people of the area using hand harpoons (Budack, 1977).

Dietary information for the Namibian bottlenose dolphin population is sparse, but stomach content analysis of a limited number of specimens has shown that southern mullet (*Liza richardsonii*) are an important prey species (Sekiguchi, Klages, & Best, 1992) and the dolphins are regularly seen chasing these in the lagoon. Mullet are present in large numbers within the lagoon, notably in the very shallow waters around the edges, and this food source is one of the likely driving forces behind the dolphins' use of the lagoon. Feeding (where actual chases are witnessed) accounted for 27% of behaviors observed within the lagoon and was the second most frequently observed behavior after milling (32%), which can include both searching for prey and subsurface foraging where no chases are seen. In the most recent live stranding (20 March 2019), two individuals (T-2015_018 and T-2015_026) were reported stranded while two further individuals (T-006c and T-015 cc) were observed foraging in the lagoon channels just meters away. The same four individuals have regularly been seen foraging in the lagoon. Between 2013 and 2019, there were 83 dolphin encounters in the lagoon and at least one of the four individuals were seen on 70% of these,

and all four were observed together on 14% of them. The day after the two individuals were successfully refloated, all four were once again seen foraging together in the lagoon (NDP, unpublished data). However, the dolphins have also been observed to feed in many other areas of the bay (Heiler et al., 2016), where water is substantially deeper and there is little apparent risk of stranding. Further, there are very few records of the occurrence of any natural predators in these deeper areas, such as killer whales (Elwen & Leeney, 2011) or large sharks (NDP, unpublished data), making them relatively risk free. However, the bathymetry of the lagoon, with a combination of shallow water and deeper channels may act to concentrate fish making them easier to catch (Silber & Fertl, 1995) increasing foraging success. Stranding to catch fish when there are other foraging sites available suggests that the benefits of foraging in the lagoon are high enough to offset the risk involved (Gilby & Wrangham, 2007; Nonacs & Dill, 1990; Stephens, 1981).

Over recent years, additional foraging pressures outside the lagoon may have arisen from a growing Cape fur seal (*Arctocephalus pusillus*) colony at the northwest edge of the bay. The Namibian population is relatively large and regarded as stable in numbers; however, there has been a significant northerly shift in the distribution of the population with several new colonies established, including Walvis Bay (Kirkman et al., 2012) and the colony has grown from ~1,700 pups in 2006 to >12,000 in 2011 and has increased at roughly 12% per annum (see Elwen, Meintjies, & Roux, 2012). The extent of dietary overlap between bottlenose dolphins and Cape fur seals has not been studied within Walvis Bay, but both are generalist predators and so there is likely to be some degree of similarity in prey species. Therefore, the presence of tens of thousands of seals likely feeding at the same trophic level within the bay may have increased food competition between seals and dolphins (Das, Lepoint, Leroy, & Bouquegneau, 2003) over recent years. Seals are rarely seen foraging in the lagoon, so competition for food resources may be much lower there, making the lagoon a more appealing foraging area for the dolphin population. In addition to foraging opportunities, the lagoon may act as a refuge for the dolphins from a large boat-based tourism industry of over 25 boats, which interact daily with the animals throughout the rest of the bay (Leeney, 2014). Marine tourism has been shown to alter bottlenose dolphin behavior (e.g., Bejder et al., 2006; Janik & Thompson, 1996; Nowacek, Wells, & Solow, 2001) and therefore the dolphins may also use the lagoon in Walvis Bay to avoid interactions with the vessels. In addition to potential competition and tourism pressures, the lagoon is a shrinking habitat as it constantly experiences sedimentation at the southern end due to windblown sand from the surrounding dunes (Robertson, Jarvis, Mendelsohn, & Swart, 2012) and from human developments, notably expansion of the harbor to the north and commercial saltworks processing pans to the west of the lagoon. These construction projects have altered the flow of water (P. Botha, personal communication, 22 December 2017) which has the potential to increase sedimentation within the lagoon and restrict access during low tide to historic fishing areas and potentially cause a greater stranding risk. Thus, as sedimentation potentially increases the risk of stranding within the lagoon, the area's value as a refuge from tour boats, and foraging competition, may be simultaneously increasing, potentially leading to an increase in stranding rate.

But is the shallow water foraging strategy as risky as we perceive? In two stranding events in 2016, dolphins refloated themselves on an incoming tide without any human intervention. In one of these events, NDP members noted that the three individuals appeared relatively calm when initially observed from the shore and only showed signs of distress when they were approached to be further assessed. The nature of the environment in Walvis Bay may help reduce two potential causes of death that occur in live strandings: drowning and hyperthermia (Gales, Woods, & Vogelnest, 2008; Herráez et al., 2013). The risk of drowning is higher if animals strand in surf zone environments, where they can be rolled or knocked over easily (Gales et al., 2008). In calm waters, such as the Walvis Bay lagoon, stranded animals may remain upright or be able to maneuver to an upright position, thereby reducing the risk of drowning. The ability of delphinids to orient themselves correctly as the tide comes in is unknown, but given the physical flexibility shown by strand feeding specialists elsewhere (e.g., Hoese, 1971; Lopez & Lopez, 1985), it is likely that animals can do this if healthy. Secondly, the climatic conditions in Walvis Bay may reduce the chances of hyperthermic stress as mornings are typified by sea mist or thick low clouds and afternoons are characterized by strong cool winds resulting in air temperature around 12°C–17°C (Robertson et al., 2012). There are currently no individuals known from Walvis Bay that have scars symptomatic with suffering from sunburn. Sunburn has been

shown to occur in stranded bottlenose dolphins elsewhere (Bossley & Woolfall, 2008; K. Nicholson, personal communication, 17 January 2018), therefore, the environmental conditions in Walvis Bay may enhance the survival rates of stranded animals further by offering protection from the sun. However, even in cool-air environments, such as Walvis Bay, the threat of hyperthermia is always increased with prolonged time out of water (Perrin, Würsig, & Thewissen, 2009). Where it did occur, human intervention assisted the animals to stay upright, stay cool, reunite calves and mothers, reduce the time spent stranded and in orienting the animals correctly when they did start to swim freely, which presumably all increased the chances of survival. In addition, the risk from other sources of danger, such as attack from kelp gulls (*Larus dominicanus*) (Gallagher, Staaterman, & Dreyer, 2015), and intervention by untrained members of the public, was reduced.

Norman et al. (2015) suggested that the live-stranding of beluga whales in the Cook Inlet had negative impacts on their subsequent fitness, and the same might be assumed for bottlenose dolphins. However, the low number of mortalities, long post stranding survival and subsequent reproduction of several of the animals demonstrated in this study, suggests that there are few, if any, long-term, negative impacts on the overall fitness of refloated individuals in the Walvis Bay population. Human intervention likely benefitted the refloated bottlenose dolphins, however, without information on the survivorship of the individuals that refloated themselves, or of animals which have never stranded, it is difficult to assess how necessary it really was. For stranded animals, Wells, Fauquier, Gulland, Townsend, and DiGiovanni (2013) used survival beyond six weeks as an indicator of a successful refloating. Photographic mark-recapture demonstrated that 93% (25/27) of identified individuals refloated in the Namibian strandings surpassed this success metric and 12 individuals surpassed the longest recorded duration (1,490 days) reported by Wells et al. (2013). There are several unpublished accounts of dolphins that were refloated elsewhere and have survived for many years. For example, a bottlenose dolphin which stranded in the Sado Estuary, Portugal, on 7 April 1990, lived until 24 August 2015 (5,984 days) (I. Carvalho, personal communication, 12 September 2017). In the Shannon Estuary, Ireland, a pregnant female bottlenose dolphin was refloated in 2012 (O'Brien et al., 2014) and since then she, and her calf, have regularly been photographed (J. O'Brien, personal communication, 4 September 2017). Multiple and repeat strandings, as well as extensive sunburn of stranded bottlenose dolphins have been reported in Mandurah, Australia. One male live stranded on 1 October 1990 and again on 10 January 2018 (9,963 days) (K. Nicholson, personal communication, 17 January 2018), making him the longest recorded successful refloating of a bottlenose dolphin to the best of our knowledge; however, no formal published description is available. The records from Namibia are the most comprehensive to date involving many individuals from multiple strandings.

The available records do not allow for an assessment of a change in stranding rate or frequency in the Walvis Bay population. However, Walvis Bay provides a potentially useful model for investigating the application of risk assessment in top predators. Detailed data of lagoon usage by the dolphins, prey availability, and changes in the lagoon with sedimentation, will allow for the level of risk to be assessed within a more formal framework. Information on the dietary overlap of the dolphins, seals and other top predators in the area would help identify any natural pressures present. This would in turn help identify if anthropogenic pressures are affecting the dolphins and allow for better and more informed stranding response in the future.

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