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MARINE MAMMAL SCIENCE, **(*) : ***_*** (***) 2016)
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DOI: 10.1111/mms.12346

Spatial variation in shark-inflicted injuries to Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of the southwestern Indian Ocean

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Predation risk can be critical in shaping the behavior and population dynamics of prey taxa (*e.g.*, Lima and Dill 1990) that, in turn, may have cascading consequences for communities (Heithaus *et al.* 2008). Although often considered top predators, many populations of small delphinids are at risk from predators. Killer whales (*Orcinus orca*) are a threat primarily in temperate waters, while risk from large sharks dominates in tropical ecosystems (see Heithaus 2001*a*, Weller 2009 for reviews). Although often overlooked, these predators may influence small cetacean (Delphinidae and Phocoenidae) behavior—including daily movements (*e.g.*, spinner dolphins *Stenella longirostris*, Norris and Dohl 1980), group size (Gygax 2002), and habitat use at multiple spatial scales (Heithaus and Dill 2006, Srinivasan *et al.* 2010)—as well as body condition (MacLeod *et al.* 2007).

Of key importance to identifying areas where predation risk might be important in shaping behaviors and population dynamics is understanding spatial and temporal variation in predation risk. For most populations of small cetaceans such as delphinids, however, there is no information on the relative risk of predation they face. Because predation events are uncommon enough to preclude direct estimates of mortality risk, evidence of unsuccessful predation attempts (*e.g.*, scars and injuries) have been used to gain insights into predation risk to many taxa, including dolphins (*e.g.*, Corkeron *et al.* 1987, Heithaus 2001*b*). The use of scars, however, has many

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limitations because the probability of an individual surviving an attack to display a wound will vary with numerous factors including the relative size of predator and prey, relative prey escape ability and predator efficiency, as well as wound healing rates (see Heithaus 2001a for discussion). Still, in the absence of other data, the proportion of individuals with predator-inflicted injuries provides an important first step in elucidating predator-prey interactions.

Here, we estimated the proportion of individual Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) bearing injuries inflicted by sharks at four locations in the southwestern Indian Ocean (southern Kenya, Réunion, Mauritius, and Mayotte; Fig. 1) during photo-identification surveys (see Kiszka *et al.* 2012, Webster *et al.* 2014 for details). In Kenya, the sampling focused on the Kisite-Mpunguti Marine Protected Area ($4^{\circ}04'S$, $39^{\circ}02'E$) and adjacent waters (~ 200 km²), and was conducted from January 2006 to December 2009. Photo-identification surveys were conducted every month (except from January to June 2008 due to national political conflicts). This area mostly covers shallow waters (0–15 m), including coral reefs, where Indo-Pacific bottlenose dolphins are common (Pérez-Jorge *et al.* 2015). Mayotte ($12^{\circ}50'S$, $45^{\circ}10'E$) is located in the northeastern Mozambique Channel and is part of the Comoros archipelago (Fig. 1). The island is almost entirely surrounded by a 197 km barrier reef, forming the largest coral lagoon in the Indian Ocean and averages 20 m in depth (1,500 km²). Adjacent to the northern part of the lagoon, there is a submerged reef bank (*Iris*) that is about 215 km². Indo-Pacific bottlenose dolphins occur

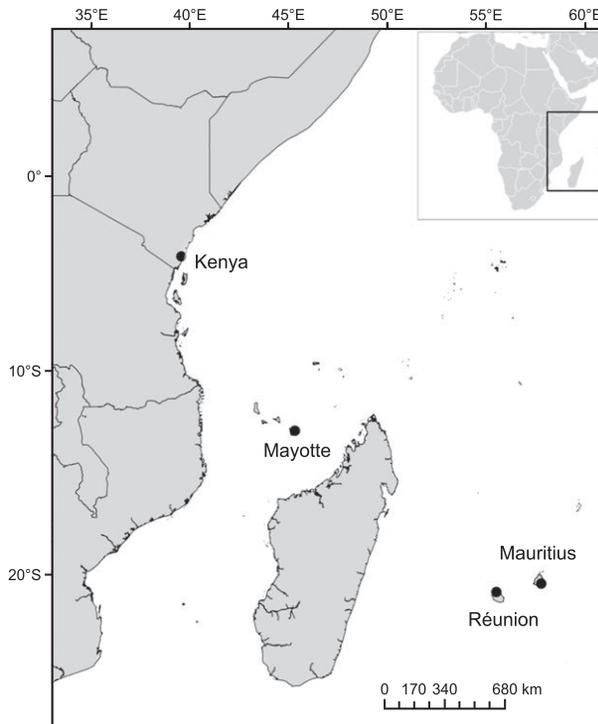


Figure 1. Location of study sites in the southwestern Indian Ocean.

both in the lagoon and the *Iris* bank and were sampled from July 2004 to April 2009 (Kiszka *et al.* 2012). In La Réunion, photo-identification data were collected from January 2005 to December 2012 in the coastal waters of the west coast of the island, over an area of about 1,000 km². The island shelf is very narrow (200 m depth contour lies, on average, *ca.* 3 km from the coast) and Indo-Pacific bottlenose dolphins occur in waters <80 m depth (Dulau-Drouot *et al.* 2008). Off Mauritius (20°17'S, 57°33'E), the study area encompassed ~30 km of coastline along the southwest coast, including sandy bays and fringing reefs where Indo-Pacific bottlenose dolphins are commonly encountered (Webster *et al.* 2014). Sampling in the study area was conducted from April 2008 to June 2010. For Mayotte, Réunion, and Mauritius, photo-identification surveys were conducted year round throughout the range of studied locations.

Injuries to dolphins were assessed from photographs taken during standard photo-identification surveys. We only included individuals in analyses if they were identified based on photo-identification. Therefore, a single individual could not be counted more than once. We considered an injury to be shark-inflicted if it was crescent shaped and/or contained deep and widely spaced tooth impressions that could only have been caused by a shark (Fig. 2). For all individuals included in the sample from all locations, photographs of each individual were available for the dorsal surface and upper flanks of the dolphin from the head to the peduncle on both sides. Therefore, the majority of shark bites on the upper body surfaces likely were recorded. Because previous studies of bottlenose dolphins (*Tursiops cf. aduncus*; Heithaus 2001b) and Atlantic spotted dolphins (*Stenella frontalis*; Melillo-Sweeting *et al.* 2014) suggest



Figure 2. Representative photographs of shark-inflicted injuries on Indo-Pacific bottlenose dolphins (*T. aduncus*) from Réunion. Photo credit: Globice Réunion.

that injuries are less likely to occur ventrally, it is unlikely that spatial patterns in injury rates were largely affected by this bias. Calculated injury proportions, however, should be considered to be minimum estimates because of the incomplete coverage of dolphins' bodies and the likelihood that old injuries that had healed well were missed (*e.g.*, Heithaus 2001*b*).

Two experienced observers (MRH and JJK) independently assessed the species potentially responsible for a particular bite based on characteristic tooth impressions of upper and lower jaws. Most bites were scored as "unknown" and a species was only considered a likely attacker when both observers' assessments matched.

We observed a total of 27 individuals with shark-inflicted injuries across 345 individually identifiable dolphins based on photo-identification data (Fig. 2). Of these 27 injuries, five were fresh and the rest had healed. Based on photographs, it was impossible to determine the species responsible for inflicting injuries in most cases. Tiger sharks (*Galeocerdo cuvier*) were identified as the likely attacker for three injuries, bull sharks (*Carcharhinus leucas*) for two, and unknown species of requiem sharks (*Carcharhinus* spp.) for two others. Based on the estimated size of injuries on two individuals attacked by tiger sharks, the attacking sharks were likely up to 400 cm in total length. There was significant spatial variation in the probability of an identified individual having a shark-inflicted injury (Fig. 3; logistic regression, $df = 3$, $\chi^2 = 33.9$, $P < 0.001$). The probability of encountering a known individual with a shark-inflicted injury was highest off the west coast of Réunion (20 of 101 identified individuals) and lowest off southern Kenya (1 of 138 individuals) and Mayotte (2 of 71 individuals). The probability of a dolphin having a shark-inflicted injury was intermediate off southwest Mauritius (4 of 35 individuals).

The proportions of individual bottlenose dolphins with shark-inflicted injuries off southern Kenya and Mayotte are similar to those (<5%) reported for shallow coastal and inshore waters of Florida Bay, U.S.A., offshore of Aruba in the Caribbean, and the Adriatic Sea (Table 1). In contrast, shark-inflicted injury rates on *T. aduncus* off western Réunion were similar to *Tursiops* sp. (10%–19%) and Indian Ocean

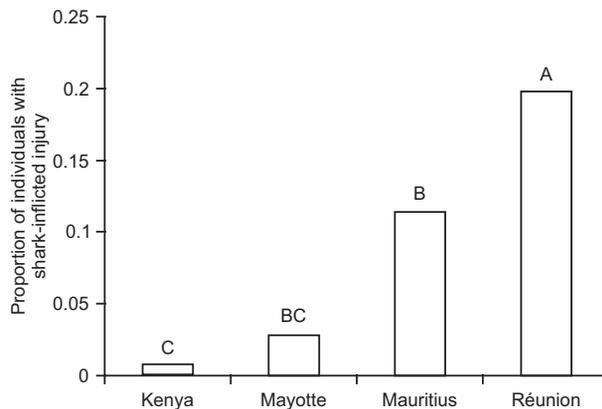


Figure 3. Spatial variation in the probability of dolphins having a shark-inflicted injury. Values are the proportion of individuals where shark bites were observed in photographs of the dorsal surfaces and upper flanks. Bars with the same letter are not significantly different based on *post hoc* Tukey's tests.

Table 1. Reported proportions of shark-inflicted injuries on coastal dolphin populations worldwide.

Location	Species	Proportion ^a	Reference
Atlantic Ocean			
Sarasota, Florida	<i>Tursiops truncatus</i>	31%	Heithaus 2001b
Florida Bay	<i>Tursiops truncatus</i>	1%–5%	Sarabia 2012
Aruba	<i>Tursiops truncatus</i>	1.3%	Luksenberg 2014
Aruba	<i>Stenella frontalis</i>	0.6%	Luksenberg 2014
Bimini, Bahamas	<i>Stenella frontalis</i>	15%–31%	Melillo-Sweeting <i>et al.</i> 2014
Adriatic Sea	<i>Tursiops truncatus</i>	0%	Bearzi <i>et al.</i> 1997
Pacific Ocean			
Moreton Bay, Australia	<i>Tursiops aduncus</i>	36.6%	Corkeron <i>et al.</i> 1987
Indian Ocean			
Shark Bay, Australia	<i>Tursiops cf. aduncus</i>	74.2%	Heithaus 2001b
Réunion	<i>Tursiops aduncus</i>	19.8%	This study
Kenya	<i>Tursiops aduncus</i>	0.7%	This study
Mayotte	<i>Tursiops aduncus</i>	2.8%	This study
Mauritius	<i>Tursiops aduncus</i>	11.4%	This study
Durban, South Africa	<i>Tursiops aduncus</i>	10%–19%	Cockcroft <i>et al.</i> 1989
Durban, South Africa	<i>Sousa plumbea</i>	28%	Cockcroft 1991

^aProportion injured: low estimates where ranges are provided represent definitive shark-inflicted injuries while high estimates represent the inclusion of injuries possibly caused by sharks.

humpback dolphins (*Sousa plumbea*; 28%) from South Africa and Atlantic spotted dolphins of Bimini, Bahamas (15%–30%). *T. aduncus* off western Réunion were less likely to have scars than *T. aduncus* of Moreton Bay, Australia (37%) and much less likely to have scars than *T. cf. aduncus* of Shark Bay, Australia (74%).

Off South Africa, Cockcroft *et al.* (1989) were able to measure both shark-inflicted injury rates and the presence of dolphin remains in the stomachs of sharks. They estimated that *ca.* 2% of the dolphin population is killed by sharks each year. If comparable or greater shark-inflicted mortality rates, relative to scarring rates, are present in the locations we sampled in the southwest Indian Ocean, sharks may be an important source of mortality for dolphins off western Réunion and southwest Mauritius but direct predation by sharks may be less important in the particular areas where sampling occurred in southern Kenya and Mayotte. Further long-term studies of dolphin and shark populations in these locations may provide important insights into the relationship between scarring rates and predation risk as well as the role of shark predation in shaping coastal dolphin habitat use patterns and population dynamics. Because dolphins are upper trophic level predators and have the potential to structure ecosystems through inducing risk effects in prey and consuming a large biomass of prey (Bowen 1997, Heithaus *et al.* 2008) studies of shark-dolphin interactions will provide insights into the dynamics of marine ecosystems where they are sympatric.

ACKNOWLEDGMENTS

We thank the numerous colleagues and volunteers who helped collect data in the field across the southwest Indian Ocean. In Mayotte, data were collected during a joined program of

the University of La Rochelle, the Office National de la Chasse et de la Faune Sauvage and the Collectivité Départementale de Mayotte, and dolphin surveys funded by the later institutions, as well as the Ministère de l'Énergie, de l'Écologie, du Développement Durable et de la Mer (MEEDDM). In Kenya, we would also like to thank the authorities and elders of Mkwiro and Shimoni and their communities at large for their hospitality and their support from 2006 to 2015. Permission to work in the Kisite-Mpunguti Marine Protected Area was provided by Kenya Wildlife Service (KWS). We are grateful for all the support from KWS staff. Funding in Mauritius was provided to the Mauritius Marine Conservation Society by TOTAL Foundation, the United Nations Development Programme – Global Environment Facility. Research permits were provided by Albion Fisheries Research Centre, Ministry of Fisheries, Republic of Mauritius (F7532/27/2/2) with ethics approval from Murdoch University, Western Australia (W2249/09). This is contribution 796 of the Southeast Environmental Research Center and #9 of the Marine Education and Research Center in the Institute of Water and the Environment at Florida International University.

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Received: 23 November 2015

Accepted: 11 June 2016