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Forum

Novel social behaviors in a threatened apex marine predator, the oceanic whitetip shark *Carcharhinus longimanus*

The cryptic life history and ecology of top predators

The timing, drivers and mechanics of animal mating systems have long been among the most perplexing and mysterious aspects of organismal biology. Today, these concepts are of critical importance for the conservation of species in the face of mounting biodiversity loss. Top predators such as African wild dogs (*Lycaon pictus*), killer whales (*Orcinus orca*), and grizzly bears (*Ursus arctos*) play critical roles in shaping ecosystem structure and function, yet exhibit high extinction risk (ESTES et al. 2011). Thus, understanding the biology and behaviors of top predators is central to ecology as well as for predicting how they will be impacted by aspects of global change. Studies of this kind are especially relevant in the case of large sharks, whose populations are becoming increasingly threatened on a global scale (FERRETTI et al. 2010; GALLAGHER et al. 2012). However, elucidating the most fundamental aspects of large predatory shark life history and behavior is extremely challenging as these rare and elusive animals frequently dive to depths inaccessible by most humans, migrate thousands of kilometers across oceans and cannot be maintained in captivity (HAMMERSCHLAG et al. 2011). Here we present an ethological case study that may have provided clues into the cryptic life history of a highly mobile top marine predator. We hope this case study underscores the utility of in-situ observations and provides a forum for stimulating discussion on how to best combine methodological approaches in future work targeting highly threatened, yet difficult to observe and study marine species.

Case study of an open-ocean predatory fish

The oceanic whitetip shark (*Carcharhinus longimanus*) is a solitary, large open-ocean apex predatory shark found in subtropical waters around the globe, whose populations are highly threatened due to overfishing (BONFIL et al. 2008). In the Northwest Atlantic Ocean, they are classified as 'Critically Endangered' by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. One of the few known dense aggregation sites for this species appears around Cat Island, Bahamas, each year from April to early June. This aggregation supports a few shark diving ecotourism operations where bait is offered to bring them in close proximity to dive tourists (GALLAGHER & HAMMERSCHLAG 2011). Sexually mature

females dominate the aggregation, with the occasional males transiently appearing throughout the season (Howey-Jordan et al. 2013). Here we present and describe novel social behaviors for this species that were obtained on a week-long expedition to the Bahamian aggregation site. We hypothesize that these social behaviors may be related to either reproduction or competition, and compare our findings to those seen in other species of predatory sharks. We also describe the ecological and conservation implications of these behaviors on apex predators.

This study was conducted off the southern point of Cat Island, the Bahamas (~ 24.30°N, 75.40°W), about 3 km offshore on a shallow reef which quickly drops off into a deep oceanic trench. Observations ran from 22 to 25 April 2013, from approximately 11:00–19:00 each day. Shark abundance ranged from 8 to 15 unique individuals per day, all of which were adult females (Fig. 1a). On 25 April at around 11:00, the first male shark of the expedition appeared, and was recorded exhibiting high-speed, erratic and aggressive swimming behavior towards both the divers and nearby females (Fig. 1b). At 12:00, we recorded a group of three female sharks joining together in an evenly-spaced straight-line formation, spaced approximately 0.5 m apart (Fig. 2a). Although size was not estimated, the largest female was positioned in the center of the line. The group remained together for 8.5 min before breaking up. This behavior was observed an additional 4 times that day until dusk. Our observations were corroborated by anecdotal evidence from a local dive operator who reported that these behaviors are common during the 2-month aggregation season (Fig. 2b).

Drivers of behaviors

Congregations of otherwise solitary marine predators may drive intraspecific interactions such as sociality and mating that are otherwise less common due to their wide-ranging nature (e.g., Fallows et al. 2013). We hypothesize that the unique social behaviors we observed exhibited by female oceanic whitetip sharks are driven by (a) courtship and/or (b) competition. Although our observations were only conducted over a week, the types of behaviors we documented are difficult to identify and record given the cryptic nature of pelagic sharks and the limited tools available to detect such behaviors in marine systems.

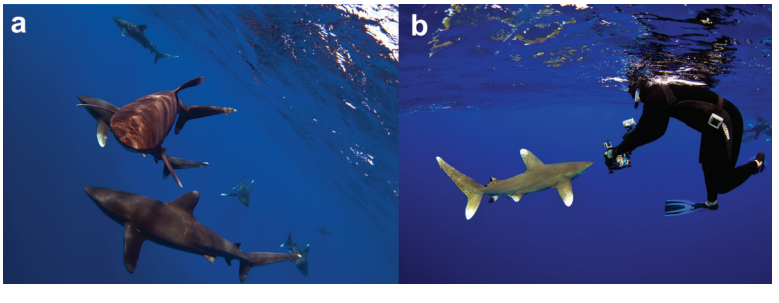

Fig. 1. — Wild behaviors of the oceanic whitetip shark: (a) the most common formation of free-ranging oceanic whitetip sharks at the aggregation, defined by randomized, non-linear clusters (photo: Austin Gallagher), and (b) the first male of the expedition (note the smaller size than females) exhibiting aggressive posture and charging the author (photo: Christine Shepard).

Fig. 2. — Nose-to-tail following behavior in free-ranging oceanic whitetip female sharks at a distance of (a) ~ 150 m away from the photographer on the April 2013 expedition (photo: Austin Gallagher), and (b) in close proximity to divers during a 2012 expedition (photo: Deb Canabal).

The type of nose-to-tail 'follow' swimming patterns we observed (Fig. 2) have been proposed to be linked to mating in basking sharks (*Cetorhinus maximus*, SIMS et al. 2000) and white sharks (*Carcharodon carcharias,* MARTIN 2003), with most displays occurring with the arrival of a newcomer to the group (MARTIN 2003). The social formation of female oceanic whitetip sharks we observed may function to signal courtship while also defending females from harassment by sexually-charged males. Furthermore, this signal may support the theory of olfaction-mediated pair formation in which male sharks follow females in straight-line formation to discriminate between ovulated and nonovulated individuals (JOHNSON & NELSON 1978), as seen in goldfish (PARTRIDGE et al. 1976). KLIMLEY & NELSON (1981) observed schooling behavior in the scalloped hammerhead shark (*Sphyrna lewini*) where the largest females were typically located centrally in non-linear formations and proposed that it was a form of sexual selection, allowing males to identify the fittest females in a group to mate. Mating scars are infrequently observed on resident female oceanic whitetip sharks at the site (authors' direct observation; E. BROOKS pers. comm.). Our ethograms were also documented in the absence of males. Whether males trigger these behaviors is unknown; males may be present but out of the view of divers, or the behaviors may preempt male arrival. If mating is indeed occurring, recently copulated females would benefit by retreating to depths to recover from mating-induced trauma in cooler, oxygen-rich temperatures, or they may leave the area altogether to avoid further harassment.

Alternatively, these behaviors could be a type of agonistic signaling among individuals resulting from heightened intraspecific competition for the bait being offered by divers. In such a case, individuals may be 'sizing each other up,' to determine dominance or willingness to fight, as has been suggested in white sharks (MARTIN 2007; SPERONE et al. 2010). This could also be a form of predatory mimicry, as proposed by MYRBERG (1991). We also cannot rule out that the behaviors observed were due to human presence in the water and the use of chum to attract sharks near the boat.

While we cannot determine the specific driver of the behaviors observed, the fact that they are social and occurring when otherwise solitary species convene over small spatiotemporal scales suggests that they may be related to an otherwise cryptic phenomenon of their life history. Conducting ethological research on pelagic sharks is extremely difficult, and we propose that future work on relatively rare pelagic species could benefit from combining natural in-situ observations and quantitative analysis of behavior with recent technological advances in shark tracking (e.g. HAMMERSCHLAG et al. 2011) to better understand their life history and conservation needs.

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