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Heterospecific foraging associations between reef-associated sharks: first evidence of kleptoparasitism in sharks

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Social foraging allows groups of predators to search for, pursue, and capture prey with greater efficiency than using solitary hunting. It can vary in complexity and take many forms ranging from cooperative hunting to social information sharing and local enhancement (Lang and Farine 2017). Theoretical and empirical studies support the advantages of group foraging, although there will be trade-offs between benefits, such as increased prey detection or capture success, and costs such as increased competition amongst group members (Gil et al. 2017). Although social foraging is traditionally assumed to occur between conspecifics, recent studies have highlighted the advantages of foraging with heterospecifics including access to prey unavailable to one species alone (Gil et al. 2017). Several heterospecific

associations have been documented among marine predators, including between grouper or lionfish and moray eels (Bshary et al. 2006, Naumann and Wild 2013), and trevally and stingrays (Kiszka et al. 2015). These foraging associations are generally classified as nuclear–follower associations in which one species represents the nuclear species initiating the foraging, with the follower species feeding on parts of or whole prey not consumed by the nuclear associate (Sazima et al. 2006). However, to our knowledge, such heterospecific social associations have never been documented among shark species.

Between June 2014 and July 2018, we observed nighttime predation in the southern pass of Fakarava Atoll, French Polynesia (16°31.137' S; 145°27.660' W). This narrow channel connecting the lagoon and the ocean is home to ~900 reef sharks including gray reef *Carcharhinus amblyrhynchos*, whitetip reef *Triaenodon obesus*, silvertip *Carcharhinus albimarginatus*, and blacktip reef sharks *Carcharhinus melanopterus* (Mourier et al. 2016). The channel is characterized by a locally inverted biomass pyramid in which subsidies in the form of repeated fish spawning aggregations support a population of up to 700 gray reef sharks (Mourier et al. 2016). Throughout these expeditions, we conducted daily dive surveys resulting in a total of ~3,000 h of underwater observations combined across several divers. During the day, opportunistic foraging attempts were rarely observed, as most reef sharks are resting in the current of the channel (Mourier et al. *unpublished data*). Some dives were dedicated to night observations of natural predations, which revealed that gray reef sharks used the channel to feed on a large variety of fish prey every night between dusk and midnight.

During these nighttime observations, we recorded 406 foraging attempts (whether successful or not) by gray reef sharks on fish of which 31 (7.6%) occurred in association with whitetip reef sharks that often initiated the foraging attempt. Whitetip reef sharks have a greater ability than gray reef sharks to find and extract hidden prey from the reef, likely because of whitetip reef sharks' smaller size, slimmer morphology, flexibility, and ability to buccally pump, enabling them to get deeper into holes and crevices. Whitetip reef sharks foraging for prey in crevices attract gray reef sharks that chase disturbed fishes that leave the protection of the reef. Although there might be some effects from using lights during our dives, the same predatory strategies were observed during nighttime dives without artificial lights during our dives, for example, during a full moon which provides sufficient environmental light to observe sharks, during which at least 10 predations (attempted or successful) were observed each dive. In addition, a comparison of the nocturnal activity of sharks tagged with accelerometers during our expedition vs. a month after we left did

not reveal any significant difference in activity (Appendix S1; Fig. S1).

During these heterospecific social predation events (31 events), we observed five possible outcomes (Figs. 1 and 2a; Video S1): (1) the prey escapes unharmed (29% of observations, $n = 9$); (2) the whitetip reef shark successfully captures the prey and the gray reef sharks get nothing (13%, $n = 4$); (3) prey is disturbed by a whitetip reef shark but caught and consumed by gray reef sharks (36%, $n = 11$, kleptoparasitism); (4) the whitetip reef shark disturbs another fish it did not target which is consumed by a gray reef shark (6%, $n = 2$, commensalism); and (5) both species compete for and each partially consumes the same individual prey item (16%, $n = 5$, kleptoparasitism or mutualism depending on whether the gray reef shark steals part of the whitetip reef sharks' prey or helps the whitetip reef shark catch prey, which would have otherwise escaped or too large for its jaws).

Associations between members of different species can vary in their duration and frequency, and are thought to form because of the benefits provided to individual members of one or both associating species. Our observations revealed a previously unknown benefit of these hunting associations for gray reef sharks. By associating with whitetip reef sharks, gray reef sharks can predate on fish hidden in the crevices of the reef, which would typically not be accessible to them (Fig. 2b). Indeed, the proportion of predated hidden prey increased from 17.9% ($n = 47/263$; 95% confidence interval (CI): 13.6–22.9) when gray reef sharks hunted alone to 82.7% ($n = 24/29$; 95% CI: 64.0–92.9) when hunting in association with whitetip reef sharks (melded binomial test for difference: $P < 0.001$). Overall predation success of gray reef sharks increased from 41.8% ($n = 110/263$; 95% CI: 35.9–47.9) to 65.5% ($n = 19/29$;

95% CI: 46.5–81.6) through the presence of whitetip reef sharks (melded binomial test: $P < 0.05$; Fig. 2c) which demonstrates that this association is beneficial for gray reef sharks.

This opportunistic relationship reveals a new facet of shark hunting strategies. It suggests a type of predation particularly beneficial to the gray reef shark that exploits the assets of another species, and which appears to increase its predatory success rate. Although in most cases this association is neutral for the whitetip reef sharks (64%), gray reef sharks can steal the prey from its nuclear associate, shifting the relationship from mutualism to kleptoparasitism. By conducting both intra- and interspecific hunting associations, gray reef sharks get access to a larger number of prey as the proximity to whitetip reef sharks gives them access to prey they would not typically hunt. This foraging strategy is likely efficient, involving simple collective rules that may provide a rapid benefit to gray reef sharks (Steinegger et al. 2018).

These two predatory species share the same ecosystem in most coral reefs of the Indo-Pacific and exploit the same prey communities (Speed et al. 2012, Frisch et al. 2016). Although gray reef sharks outnumber whitetip reef sharks in Fakarava and in most reefs (Robbins et al. 2006, Mourier et al. 2016), it is not surprising that they take advantage of their presence as they compete for the same resources. The benefits of this association appear to be generally one-way: only rarely do whitetip reef sharks potentially benefit from foraging with gray reef sharks. These interactions contribute to the diversity of trophic interactions in coral reef ecosystems. Future research should investigate the role of species occupying central positions in social networks influencing the structure and dynamics of marine communities as has

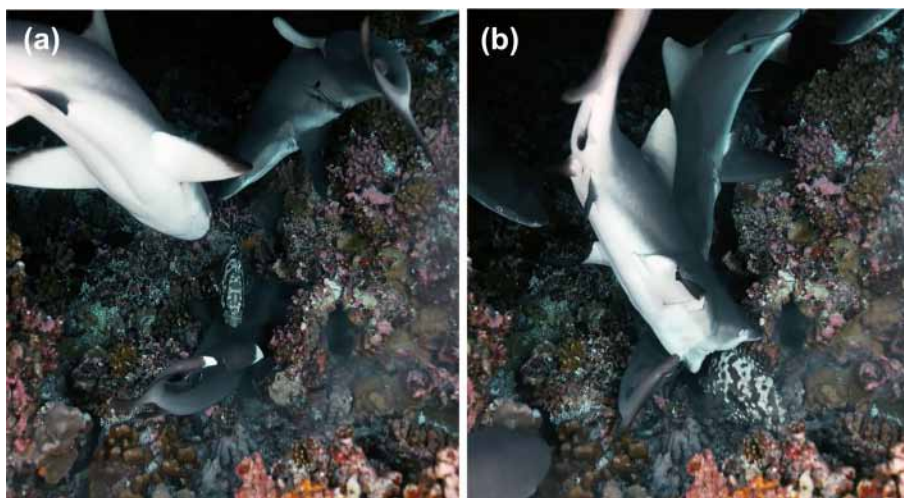


FIG. 1. A whitetip reef shark forages within the crevices of corals and brings out a camouflage grouper (a), which is caught by a gray reef shark that was within proximity of the whitetip reef shark (b).

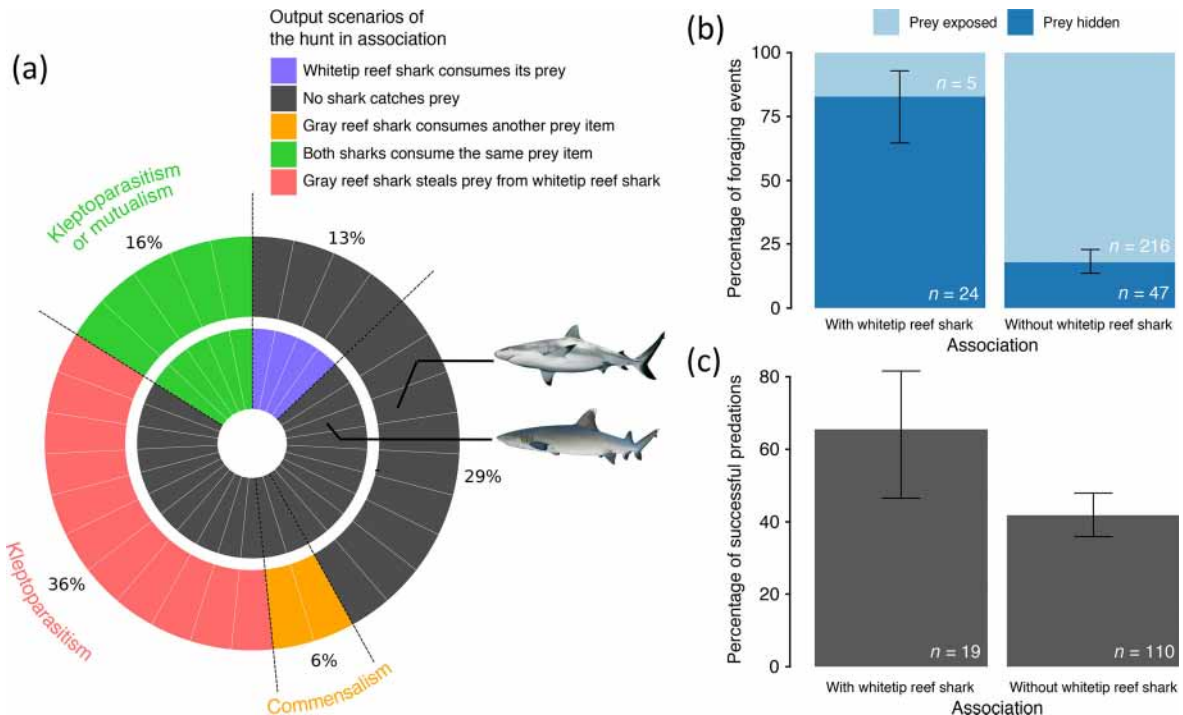


FIG. 2. The outcome of the observed hunting associations. (a) The five outcomes resulting from the associative hunt ($n = 31$). The inner circle represents the result of the foraging association for the whitetip reef shark, and the outer circle is the result for the gray reef shark for the same associative events. (b) This heterospecific foraging association provides gray reef sharks with increased access to concealed prey and (c) increases predation success of gray reef sharks. Error bars represent 95% confidence intervals calculated from exact binomial tests.

been shown in terrestrial environments (Meise et al. 2020). The potential importance of kleptoparasitism between marine predators should also be investigated to determine if payoffs/benefits change relative to other foraging strategies as seen amongst terrestrial predators (Flower et al. 2012).

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