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Octopuses punch fishes during collaborative interspecific hunting events

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Cooperation is ubiquitous in nature, and occurs at all levels of biological complexity, providing immediate direct benefits and/or future indirect benefits to participating partners (Lehmann and Keller 2006, Bshary and Bergmüller 2008). In interspecific interactions, the lack of relatedness between individuals ensures that the underlying dynamics and potential feedback mechanisms can be interpreted in terms of direct, personal benefits. Moreover, in multispecific collaborative hunting groups, ecology and game theory are implicitly linked, as the life history and evolved hunting strategy of each species often leads to specialized roles within a group (asymmetric conditions), which facilities coordination (Bshary et al. 2006, Bshary and Bergmüller 2008). For instance, collaborative hunting between moray eels and groupers provides one of the most elaborate examples on how different species with complementary hunting techniques (groupers hunt in the water column and eels enter rock crevices) can join forces and increase their predation success (Bshary et al. 2006, Vail et al. 2013, 2014). Involving active recruitment and referential gestures, the nature of this relationship is mutually beneficial (byproduct mutualism); that is, both can increase their hunting success rate from the presence of the other species, which likely played an important role in the emergence of complex interactions between groupers and eels.

Concurrently, groupers and various other species of coral reef fishes are also known to form hunting associations with octopuses (Fig. 1), often involving numerous partners from several species at the same time (Diamant and Shpigel 1985, Forsythe and Hanlon 1997, Bayley and Rose 2020). These events can last over 1 h, with octopuses pursuing prey within rock and coral crevices (identically to the moray eel), while other fishes search the seafloor around a larger perimeter (bottom feeders, e.g. yellow-saddle goatfish *Parupeneus cyclostomus*) and others guard the water column (semibenthic predators, e.g. smooth cornetfish *Fistularia commersonii*; Video S1). Although the octopus plays a central role, some of its followers are opportunistic predators that join the group, and do not actively seek prey (e.g. tailspot squirrelfish *Sargocentron caudimaculatum*). With these species, interspecific interactions may be commensalistic or even parasitic (Diamant and Shpigel 1985). However, octopuses also follow fish partners for more prey opportunities, namely, groupers, which use referential gestures to signal prey locations to octopus in the same way as

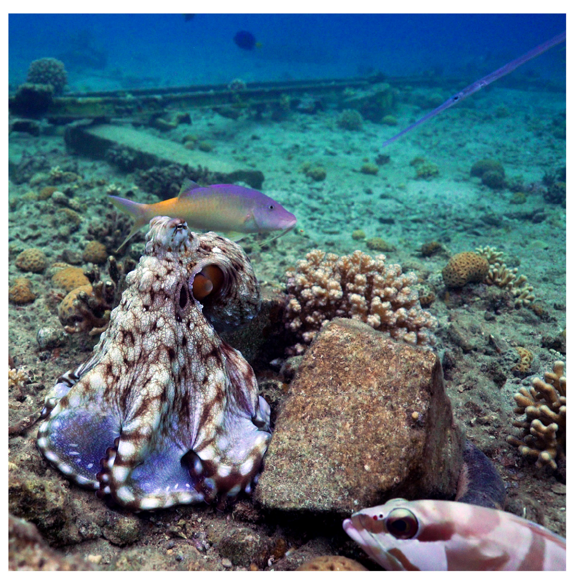

FIG. 1. Example of a multispecific hunting group composed by a day octopus *Octopus cyanea*, a yellow-saddle goatfish *Parupeneus cyclostomus*, a smooth cornetfish *Fistularia commersonii*, and a blacktip grouper *Epinephelus fasciatus* (Video S1).

they do to moray eels (Vail et al. 2013), and goatfishes, which also scour the sea bottom and crevices (Video S2; see also Bayley and Rose 2020). These observations suggest that with certain species of fish partners, interspecific interactions can be mutualistically beneficial (Bshary and Bergmüller 2008). As a result, in heterogeneous multispecific groups, conflicts between partners can arise over the level of investment or the distribution of payoffs (Lang and Farine 2017). Thus, in this complex social network of interactions, partner control mechanisms might emerge in order to prevent exploitation and ensure collaboration (Raihani et al. 2012).

Here we report a series of events, dating between 1 October 2018 and 1 November 2018 (29.5577° N, 34.9519° E, Eilat, Israel), and 10 May 2019 and 10 July 2019 (26.2032° N, 34.2165° E, El Quseir, Egypt), where different *Octopus cyanea* individuals engage in active displacement of partner fish during collaborative hunting. To this end, the octopus performs a swift, explosive motion with one arm directed at a specific fish partner, which we refer to as punching (Fig. 2). We recorded punches (n = 8 events; see Video S2) targeting different fish species: tailspot squirrelfish (*S. caudimaculatum*, Event 1), blacktip (*Epinephelus fasciatus*, Events 2 and 3) and lyretail (*Variola louti*, Event 4) groupers, yellow-saddle (*P. cyclostomus*, Events 5 and 6) and Red Sea goatfishes (*Parupeneus forsskali*, Event 7), and halfspotted hind (*Cephalopholis hemistiktos*, Event 8). These multiple observations involving different octopuses in different locations suggest that punching serves a concrete purpose in interspecific interactions. From an ecological perspective, actively punching a fish partner entails a small energetic cost for the actor (i.e., octopus), and simultaneously imposes a cost on the targeted fish partner. From the fish's standpoint, this cost can take several forms, such as subtraction of an immediate opportunity to catch prey (e.g. Events 3 and 8), relocation to a more external or less advantageous location in the group (e.g. Event 5), or even permanent eviction (e.g. Event 1). Thus, from the octopus's perspective, punching serves as a partner control mechanism, the nature of which is dependent on the ecological context of the interaction, and on how the octopus benefits from inflicting costs on fish partners (Clutton-Brock and Parker 1995, Bshary and Bergmüller 2008).

In cases where continuous interactions over time and collaboration are not evident—*S. caudimaculatum* has an opportunistic hunting strategy and is not reported to be commonly included in these interspecific hunting groups (Diamant and Shpigel 1985)—simple competition for similar food resources can explain the punching behavior (Event 1; Raihani et al. 2012). In situations

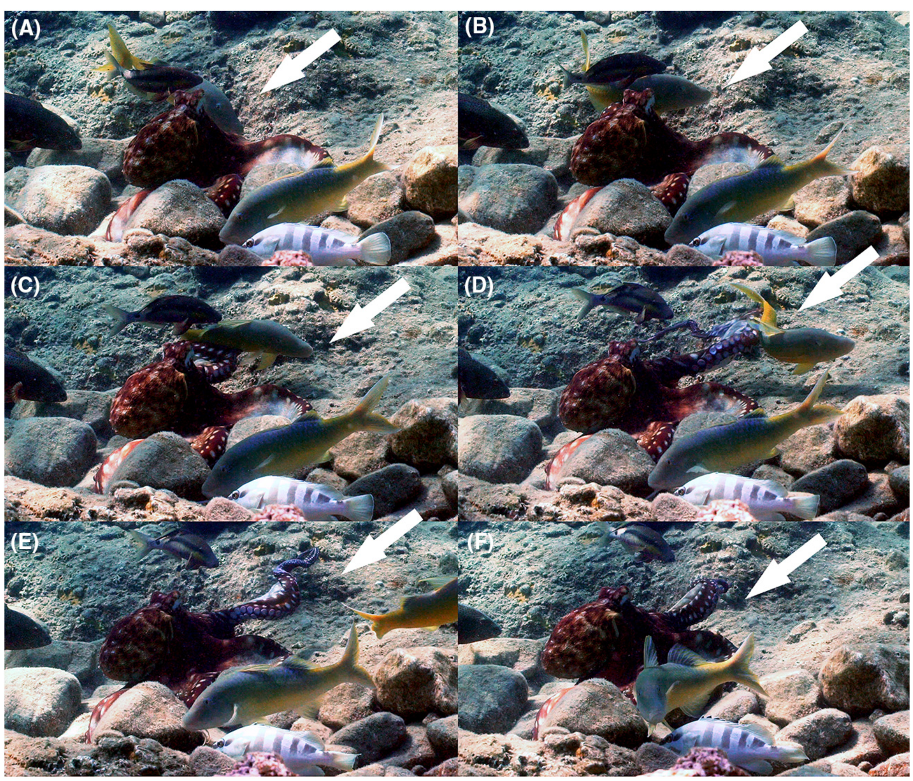

Fig. 2. Image sequence depicting the behavioral action of *Octopus cyanea* punching (white arrows) a yellow-saddle goatfish (*Parupeneus cyclostomus*) partner during interspecific multicollaborative hunting (see Video S3).

where collaboration does exist, and the octopus punches a specific partner to gain direct access to prey (performing a web-over immediately after punching, e.g. towards *E. fasciatus* or *C. hemistiktos* in Events 3 and 8, respectively), immediate benefits are yielded from that aggressive action. That is to say, in this scenario the octopus performs a self-serving behavior (displacing a fish to access prey), which despite a small energetic cost produces immediate benefits. This action simultaneously imposes a cost to the partner (subtraction of prey opportunity) and can promote cooperation in future interactions. This mechanism is a form of direct negative pseudo-reciprocity, that is, sanctions (Raihani et al. 2012). Thus, when the octopus punches and obtains immediate benefits from that action, the underlying mechanisms and ecological role are relatively simple and direct.

However, other events show that punching is not always followed by an attempt to retrieve prey (e.g. Events 5 and 6), indicating it also occurs in the absence of immediate benefits. In a collaborative context, such as with the yellow-saddle goatfish *P. cyclostomus* (Bayley and Rose 2020; Video S2) or with certain species of groupers (Vail et al. 2013), other mechanisms might explain punching. In these cases, two different scenarios are possible according to game theory. In the first one, benefits are disregarded entirely by the octopus, and punching could be a case of spite (no emotional connotation), used to impose a cost on the fish regardless of self-cost, for example, after defection (stealing prey) by a usually collaborative partner (Clutton-Brock and Parker 1995). In the other theoretical scenario, punching may be a form of aggression with delayed benefits (i.e., direct negative reciprocity or punishment), where the octopus pays a small cost to impose a heavier one on the misbehaving partner, in an effort to promote collaborative behavior in the following interactions (Clutton-Brock and Parker 1995). In other words, punching might impose an immediate cost to both partners, but because hunting groups promote additional subsequent interactions, such negative feedback can yield an overall higher benefit for players in the long run (Raihani et al. 2012). Documented cases of consistent change in partner behavior after negative feedback are rare in nonhuman species (Raihani et al. 2012), making its potential use by octopuses during collaborative hunting worthy of further investigation. However, in order to disentangle between the numerous mechanisms that may underlie punching behavior, careful studies of previous and subsequent interactions between the octopus and the targeted fish, within the changing dynamics of the group, are warranted.

Comparatively to the paired structure of the grouper–moray eel system (Bshary et al. 2006), the existence of direct negative feedback mechanisms when one octopus and multiple fish partners hunt together indicates that additional rules shape these ecological relationships. Thus, the multilayered network of interactions suggests that the underpinnings of these interspecific groups, are more complex than what both pairwise collaborative associations or group nuclear-follower ecological models describe (Diamant and Shpigel 1985, Vail et al. 2013). Detailed quantitative analyses of these multispecific hunting events can explore several other important ecological questions, such as the potential existence of privileged relationships between octopuses and specific fish partners (e.g. are some species or individuals more punched than others?), and how individual dynamics are modulated by the network of social interactions (e.g. do fishes also provide feedback to each other?).

Further work on this severely understudied system can shed light on costs, benefits, and control mechanisms in underlying game structures (Bshary and Bergmüller 2008, Raihani et al. 2012), unexplored cognitive processes (Vail et al. 2013, 2014), particularly for an otherwise-solitary marine invertebrate (Schnell and Clayton 2019), as well as the ecological role and conditions promoting the emergence of multispecific cooperation (Lehmann and Keller 2006, Lang and Farine 2017).

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