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Rare antagonistic interaction between short-finned pilot whales (*Globicephala macrorhynchus*) and fasting humpback whales *(Megaptera novaeangliae)* off Western Puerto Rico

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Documentation of the occurrence of interspecific interactions and associations (mixed-species associations) (temporary associations of two or more taxa; see Stensland *et al.*, 2003) in large delphinids (Shane, 1995*b*; Bearzi, 2005; Smultea *et al.*, 2014; Bacon *et al.*, 2017), such as pilot whales (*Globicephala macrorhynchus*) (Kraus and Gihr, 1971; Weller *et al.*, 1996; Migura and Meadows, 2002), is uncommon. Pilot whales have been observed with other cetaceans, including large whales and dolphins (Reilly and Shane, 1986; Baraff and Asmutis-Silvia, 1998; Roden and Mullin, 2000). Associations between humpback whales (*Megaptera novaeangliae*) and other marine mammals have also been reported (Brownell, 1964; Glockner-Ferrari and Ferrari, 1985; Ciano and Jørgensen, 2000; Steiger *et al.*, 2008; Deakos *et al.*, 2010; Smultea and Bacon, 2012). The reason for mixed-species associations is unknown, but likely includes coincidence (*e.g.* concurrent feeding opportunities) (Clua and Grosvalet, 2001; Bearzi, 2005; Vaughn *et al.*, 2007), play (*e.g.* observed in groups with whales and dolphins) (Shane *et al.*, 1986; Deakos *et al.*, 2010; Würsig, 2018*a, b*), predation (*e.g.* killer whale predation) (Jefferson *et al.*, 1991; Weller *et al.*, 1996; Weller, 2018), and harassment (*e.g.* aggressive behavior of one species towards another that elicits a response indicative of agitation, annoyance, or distress including - but not limited to - a change in direction, chuffing or percussive activity) (Shane, 1995*a*, *b*; Palacios and Mate, 1996; Herzing *et al.*, 2003; Pereira, 2008; Smultea *et al.*, 2014; MacKay, 2015). Antagonistic behaviors (aggressive; an individual who is hostile to another individual) have been observed by pilot whales towards other cetacean species (Norris and Prescott, 1961; Kraus and Gihr, 1971; Overholtz and Waring, 1991; Shane 1995*a*, *b*; Weller *et al.*, 1996; Baraff and Asmutis-Silvia, 1998; Pereira, 2008) leading to speculation that the motive for the aggressive behavior is kleptoparasitism for obtaining a low energy meal (Palacios and Mate, 1996; Smultea *et al.*, 2014). Kleptoparasitism is the occurrence when food is stolen from one individual that was procured by another individual (Brockmann and Barnard, 1979; Smultea *et al.*, 2014). Pilot whales and humpback whales have been known to associate with other cetacean species throughout their range, although there is only a single documented humpback whale/pilot whale mixed-species association occurring off the feeding grounds in Norway (Ciano and Jørgensen, 2000). Humpback whales foraging in higher latitudes have the potential to regurgitate a free meal for pilot whales, similar to the response of stress including pilot whale harassment, of other large whales (Palacios and Mate, 1996; Weller *et al.*, 1996; Cords and Würsig, 2014; Smultea *et al.*, 2014). Humpback whales fasting on their winter habitats are not a source for kleptoparisitism.

Short-finned pilot whales have a global tropical and sub-tropical distribution (Jefferson *et al.*, 2015). Groups throughout the Western North Atlantic are observed between North Carolina southwards throughout the Lesser Antilles, and the Gulf of Mexico (Leatherwood *et al.*, 1976; Mignucci-Giannoni, 1998; Olson, 2018) including a wide distribution throughout the Caribbean (van Bree, 1975; Watkins and Moore, 1982; Mattila and Clapham, 1989; Swartz and Burks, 2000; Mannocci *et al.*, 2013). They commonly occur offshore in tight social units and are typically found in groups of 15 to several hundred adults (Jefferson *et al.*, 2015). Short-finned pilot whales are known to frequently occupy deep waters, such as those found at the edges of the continental shelf and

submarine canyons, but have been sighted in a wide range of water depths (Roden and Mullin, 2000).

Previously thought to visit only during the summer months in the West Indies (Caldwell and Erdman, 1963; Erdman, 1970; Mignucci-Giannoni, 1998; Roden and Mullin, 2000), pilot whales have been observed throughout the winter months, indicating resident populations (Taruski and Winn, 1976). Aggregations appear to be uncommon nearshore along the islands of the Caribbean (Taruski and Winn, 1976; Roden and Mullin, 2000); however, there are more recent sightings of pilot whales near the shelf edge during the winter and spring (January through April) (Swartz *et al.*, 2003; MacKay, 2015; Rodriguez-Ferrer *et al.*, 2018).

Humpback whales are known to migrate away from their feeding grounds in high latitudes of the North Atlantic (Clapham and Mayo, 1987; Mattila *et al.*, 1989; Kennedy and Clapham, 2018), to the low latitude, low productivity breeding grounds during winter months (Balcomb and Nichols, 1982; Whitehead and Moore, 1982; Goodwin, 1987; Mattila *et al.*, 1989, 1994; Betancourt *et al.*, 2012). Humpback whales are largely solitary although occasionally exhibit behaviors where individuals cooperate with one another in social groups, coordinated feeding, breeding groups, and mother-calf-escort groups. In the Caribbean, they typically occur in relatively shallow waters near islands, over seamounts and offshore banks (Balcomb and Nichols, 1982; MacKay *et al.*, 2016). Despite rare sightings of foraging behaviors (Gendron and Urbán R., 1993) during a considerable amount of research over decades, there is scholarly agreement that they fast while on their breeding and calving grounds (Slijper, 1962; Norris, 1967; Brodie, 1975; Lockyer, 1981; Baraff *et al.*, 1991).

Here, we describe the first antagonistic interactions reported between North Atlantic humpback whales and short-finned pilot whales, which were observed in Mona Passage, off Western Puerto Rico. These observations raise questions of kleptoparisitism as a motive for pilot whale harassment towards wintering humpback whales.

Vessel-based surveys were conducted in Mona Passage during six consecutive winter seasons from 2011-2016. During 2013–2015, pilot whales were observed on five occasions (Table 1). Two of the five sightings were mixed-species associations with humpback whales (Figure 1). In 2013 and 2014, short-finned pilot whales approached a group of North Atlantic humpback whales in a manner that elicited behaviors indicative of agitation and/or distress, including trumpeting, chuffing, and tail slapping. Three humpback whales and nine short-finned pilot whales were observed together in close proximity (less than one body length of the closest humpback whale) off the northwest coast of Puerto Rico on 21 March 2013. A second mixed-species association with three humpback whales and five short-finned pilot whales occurred on 12 February 2014 in a similarly apparent antagonistic interaction between the two species as the one observed encounter in 2013 (Figure 1). In both events, the groups were detected by the blows of the humpback whales from a distance of several kilometers. The survey vessel approached the group to collect data and observed humpback whales blowing, trumpeting, chuffing, and thrashing on and immediately below the surface. The high energetic behaviors of the individuals led the survey team to expect a humpback whale breeding group; however, the smaller blows of the short-finned pilot whales (followed by observations of dorsal fins and rostrum) in the white waters of the thrashing group clarified the observations as mixed-species associations. The smaller blows were visually identified quickly as belonging to short-finned pilot whales in close proximity (less than one humpback whale body length) to the humpback whales. It was not possible to determine if there was direct physical contact between the pilot whale and humpback individuals due to the white water generated from the reaction of the humpback whales and the subsurface behaviors occurring in the group; however, it was clear that the pilot whales movement directly beside the humpback whales were eliciting energetic and vocal responses. The humpback whales dove below the surface leaving the pilot whales remaining at the surface. Several minutes after the humpback whales dove, individual pilot whales turned suddenly, and simultaneously faced a single direction. The humpback whale group resurfaced in the direction indicated by the pilot whales' behavior. The short-finned pilot whales traveled at high speed towards the humpback whales on the surface (sometimes moving in the direction of the humpback whales just prior to surfacing). The following cycle was repeated: pilot whale antagonistic behaviors were observed during four-five min of surface interaction, humpback whales dove below the surface for two-three min, humpback whales resurfaced at a

Table 1. Short-finned pilot whale (*Globicephala macrorhyncus*) sightings and locations in Mona Passage, off Western Puerto Rico.

Date and Time	Group Size	Location	Mixed-Species Group	Species Mixed With
21 Mar 2013 09:27	9	Aquadilla	Yes	Humpback Whale
8 Apr 2013 09:26	6	Aquadilla	No	-
12 Feb 2014 09:49	8	Aquadilla	Yes	Humpback Whale
28 Jan 2015 10:10	16	Aquadilla	No	-
28 Jan 2015 10:38	24	Aquadilla	No	-

Figure 1. One of the mixed-species associations between humpback whales (*Megaptera novaeangliae*) and pilot whales (*Globicephala macrorhynchus*) observed in Mona Passage, off Puerto Rico. The larger animals in the photos are humpback whales. The dorsal fins in the foreground and between the humpback whales are the short-finned pilot whales confirmed by photographic images during this encounter. Photograph taken 21 March 2013 by M. MacKay under DNER permit 2013-EPE-01 and NMFS permit 15682.

distance, and pilot whales moved towards the location where humpback whales resurfaced. The humpback whales finally left the area with the short-finned pilot whales traveling at high speed in the same direction in apparent pursuit. A total of 22 min of antagonistic interaction was observed in 2013 and 48 min of similar interaction in 2014, between the time observations initiated and the humpback whales left the area traveling rapidly.

Speculation exists that pilot whales may harass other cetaceans causing them to regurgitate a recent meal (kleptoparasitism) reducing energy expenditure required while foraging (Palacios and Mate, 1996; Weller *et al.*, 1996; Cords and Würsig, 2014; Smultea *et al.*, 2014; Bacon *et al.*, 2017). Humpback whales are fasting while on the breeding grounds (Chittleborough, 1958; Cartwright *et al.*, 2012; MacKay, 2015) and pilot whales do not typically consume the same prey species humpback whales consume, making a free meal unlikely. The clues provided by these specific cases of antagonistic behaviors by short-finned pilot whales towards fasting humpback whales call into question the hypothesis that pilot whales are gaining any meal via stress-induced regurgitation, and suggest another motive is more plausible for the pilot whales' behavior. Pilot whales harass other cetaceans in what appears to be "fun" (*i.e.* play) (Norris and Prescott, 1961; Shane 1995*a*, *b*; Ciano and Jørgensen, 2000; Pereira, 2008) although in a mixed-species association the playful behavior by one species may be harassment for the other. Würsig (2000) refers to the interaction between dusky dolphins (*Lagenorhynchus obscurus*) and kelp gulls (*Larus dominicanus*) as "playful behavior". In this account, the dusky dolphins appeared to enjoy pulling gulls underwater and releasing them; however, the gulls were clearly not entertained during these encounters. This example is similar to the interaction between the humpback whales and pilot whales in both groups observed during our research when the pilot whales appeared to be entertained at the expense of harassing the humpback whales. Play is often a form of training for young animals (Bekoff, 1997; MacKay, 2015) and we cannot eliminate the possibility that there is another benefit to harassing the humpback whales which was not readily apparent. Antagonizing fasting humpback whales raises the possibility that pilot whales find eliciting a high energy response is simply entertaining. Because these events are either incredibly rare, underreported, or both, discerning

Figure 2. A humpback whale (*Megaptera novaeangliae*) diving in response to pilot whale (*Globicephala macrorhynchus*) (smaller animal in the foreground) harassment observed by the research team during a mixed-species association in Mona Passage, off Puerto Rico on 21 March 2013. Photograph by M. Morel under Departamento de Recursos Naturales de Puerto Rico (DNER) permit 2013-EPE-01 and NMFS permit 15682.

if these were futile attempts at kleptoparasitism, fun via antagonistic behaviors, social harassment (Herzing and Brunnick, 1997; Stensland *et al.*, 2003; Cords and Würsig, 2014), or something else, remains unknown.

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