Rare Mixed-Species Associations Between Sperm Whales and Risso's and Northern Right Whale Dolphins Off the Southern California Bight: Kleptoparasitism and Social Parasitism?

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Source: Northwestern Naturalist, 95(1):43-49. 2014.
Published By: Society for Northwestern Vertebrate Biology
DOI: http://dx.doi.org/10.1898/NWN13-11.1
URL: http://www.bioone.org/doi/full/10.1898/NWN13-11.1

NORTHWESTERN NATURALIST 95:43–49 SPRING 2014

RARE MIXED-SPECIES ASSOCIATIONS BETWEEN SPERM WHALES AND RISSO'S AND NORTHERN RIGHT WHALE DOLPHINS OFF THE SOUTHERN CALIFORNIA BIGHT: KLEPTOPARASITISM AND SOCIAL PARASITISM?

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Key words: aerial survey, *Grampus griseus*, kleptoparasitism, *Lissodelphis borealis*, mixed-species association, Northern Right Whale Dolphin, social parasitism, *Physeter macrocephalus*, Risso's Dolphin, southern California, Southern California Bight, Sperm Whale

Inter-specific behavioral interactions between large whales and small odontocetes are rarely described and little understood. Reasons for such associations have been proposed but are difficult to substantiate empirically given the challenges inherent with studying deep- and long-diving cetaceans at sea. Proposed reasons include some of those described for schooling fish, birds, ungulates, and primates, such as reduced predation through the dilution or predator startle effect, competition for resources, aggression, kleptoparasitism, social parasitism, and play and sociality (Norris and Prescott 1961; Fritz and De Garine-Wichatitsky 1996; Weller and others 1996; Clua and Grosvalet 2001; Cameron and Du Toit 2005; Cords and Würsig 2014). Herein, we describe the first published social interactions of Sperm Whales (*Physeter macrocephalus*), Risso's Dolphins (*Grampus griseus*), and Northern Right Whale Dolphins (*Lissodelphis borealis*) as photo- and video-documented off southern California in spring 2011.

We hypothesize based on our observations and other studies that this association stemmed from a combination of kleptoparasitism and social parasitism. Kleptoparasitism is described as acquiring food captured or harvested by another individual or the transfer (stealing) of food already procured from one individual to another (Brockmann and Barnard 1979; Brown and others 2004). It has been suggested for a few interspecific observations among odontocetes involving aggression and pieces of squid/flesh in nearby waters; for example, False Killer Whale (*Pseurdorca crassidens*) and Short-finned Pilot Whale (*Globicephala macrorhynchus*) harassment of Sperm Whales (Palacios and Mate 1996; Weller and others 1996). Social parasitism is defined as an association of 2 or more species where at least 1 species is believed to benefit from another species' food-finding abilities, and has been suggested as an odontocete foraging

practice among Bottlenose Dolphins (*Tursiops truncatus*), California Sea Lions (*Zalophus californianus*), common dolphins (*Dephinus* spp.), and Pantropical Spotted Dolphins (*Stenella attenuata)* (Norris and Dohl 1980; Shane 1994; Clua and Grosvalet 2001; Bearzi 2006; Cords and Würsig 2014).

The 3 odontocete species discussed herein belong to stocks inhabiting the eastern North Pacific south to southern California (Jefferson and others 2008; Carretta and others 2012). Sperm Whales occupy primarily offshore deep waters (over 1000-m depth) off Washington, Oregon, and California (Barlow and others 2010; Carretta and others 2012), while Risso's Dolphins and Northern Right Whale Dolphins are closely tied to continental shelf and slope waters (Leatherwood and Walker 1979; Dohl and others 1980, 1983; Carretta and others 2012). Sperm Whales can dive over 2000-m deep for well over an hour, but typically forage at depths near 400 m (Watkins and others 1985, 1993; Amano and Yoshioka 2003; Jefferson and others 2008), though little is known about how they capture their preferred squid prey (Watwood and others 2006). Similarly, Risso's Dolphins and Northern Right Whale Dolphins are believed to feed primarily on mesopelagic squid associated with the deep scattering layer that ranges from approximately 0–100 m depth at night to 300–400 m during the day (Würtz and others 1992; Jefferson and others 1994; Clarke 1996; Fiedler and other 1998; Shoham-Frider and others 2002; Jefferson and others 2008). Notably, these 2 species are known to dive to considerably shallower depths (in excess of 200 m) (Jefferson and others 1994; Bearzi and others 2010) than Sperm Whales. The association of these 3 species is considered unusual and has not been previously published, nor has the observed apparent aggressive harassment of the Sperm Whales by the Risso's Dolphins as described below.

Inter-species Interaction

On 14 May 2011, during a line-transect aerial survey focused on marine mammals in the Southern California Bight (SCB) off southern California, a rare interaction was recorded between a group of Sperm Whales (16 adults and 4 calves), 11 Risso's Dolphins, and 50 Northern Right Whale Dolphins approximately 44 km west of San Diego, California (Fig. 1). No mature Sperm Whale males were observed (they are typically one-third larger than mature females [Rice 1989]). The group was circled for 67 min (10:36–11:43 PDT) by a small, Partenavia P68-C aircraft flying at an altitude of 290–445 m and radial distance of 500–1000 m, which was outside of the hearing distance range of the animals for an overflying aircraft (see Urick 1972 and Richardson and others 1995). The sighting was documented using high-definition (HD) photographs and video, as well as systematic behavioral protocol and notes on a notebook computer using real-time Mysticetus observational software and mapping (described in Smultea and Bacon 2012).

FIGURE 1. Sperm Whales mixed with Northern Right Whale Dolphins (white arrow) and Risso's Dolphins (red arrow). Note the tight flank-to-flank parallel staggered line-abreast group formation by the Sperm Whales early in this encounter. Also note the much smaller body size (up to 3 m long) of the black Northern Right Whale Dolphins relative to the larger grayish Risso's Dolphins (approximately 3.5 m long) and the approximately 13-m-long non-calf Sperm Whales. The Sperm Whales are heading to the left. Photo by David Steckler taken under NMFS permit #14451 on 14 May 2011.

The Sperm Whales traveled slowly east and over the edge of a steep (37° slope) underwater ridge where water depth was 425–1150 m. All but one of the adult Sperm Whales undertook 2 long dives lasting approximately 20 min each; the calves surfaced earlier accompanied by 1 adult whale while the dolphins remained at the surface. During this encounter, Risso's Dolphins often swam in-between the Sperm Whales, and the Northern Right Whale Dolphins generally remained with or near the Risso's Dolphins but on the periphery of the Sperm Whale group. On 7 occasions, a Risso's Dolphin was seen rapidly

FIGURE 2. Sperm Whale with a calf at its rear right flank as a Risso's Dolphin approaches from the front. Note the Sperm Whale's open white lower jaw (whitish color through water). Photo by David Steckler taken under NMFS permit #14451 on 14 May 2011.

approaching (and once in contact with) an adult Sperm Whale, then quickly retreating; on 4 of these 7 occasions, the adult Sperm Whale was seen (and photographed or video recorded) opening its mouth exposing its white lower jaw coloration (Fig. 2). The Sperm Whales initially closed ranks by decreasing inter-individual spacing while the calves moved toward the middle of the group. The whales later appeared to spread out with calves seen on the periphery of the Sperm Whale group while the Risso's Dolphins and Northern Right Whale Dolphins were interspersed with the Sperm Whales. Details of what we consider the most interesting aspects of the behavior and interactions of the Sperm Whales and dolphins are described in Table 1.

A Case for Kleptoparasitism

A number of characteristics support our hypothesis that this interspecific encounter involved kleptoparasitism. In this case, we think that the Risso's Dolphins instigated aggression to induce regurgitation and potential consumption of Sperm Whale prey remains based on the following: (1) Risso's Dolphins behaved aggressively only toward adult Sperm Whales that had recently dove; (2) the Sperm Whales behaved defensively; (3) similarly sized squid-eating odontocetes have behaved aggressively toward Sperm Whales, resulting, in some cases, in pieces of squid flesh floating nearby; and (4) all species involved consume squid.

We interpreted Risso's Dolphin behavior as aggressive when they swam among, rapidly and directly toward (charged), bumped into, and breached near the heads of (only) adult Sperm Whales (which we recorded 12 times), followed by fast retreats (Table 1). We termed this behavior ''playing chicken''. Such behavior was not directed toward the 4 adult-calf whale pairs or the single adult that remained at the surface while the other whales dove. Long Sperm Whale dives typically involve foraging (Whitehead 2009), presumably on squid. Thus, Risso's Dolphins would be expected to preferentially harass non-calf whales that most recently dove and fed, we assume, on squid and are likely to have prey in their stomachs (as opposed to young whales nursing on milk). The single adult that remained at the surface between group dives we presume had fed less recently.

We interpreted Sperm Whale behavior as defensive based on several events indicative of avoidance. First, the Sperm Whales decreased their inter-individual spacing, apparently herding calves toward the middle of the group (Table 1). Adults typically protect calves from predators, including whalers, by tightly surrounding the calves, often with the adults' wide tails facing outside the group as a means of defense to hit potential predators (for example, Weller and others 1996; Smultea and others 2008). Second, when the Risso's Dolphins charged their heads, the Sperm Whales opened their mouths, dropped their lower jaws, and exposed their white gums and teeth (note that Sperm Whales have teeth only on their lower jaw) while making forceful blows-exhalations (Fig. 2). The latter Sperm Whale behavior has been noted in response to perceived threats, including whaling vessels, Pilot and False Killer Whales (Palacios and Mate 1996; Weller and others 1996), and aircraft flying directly overhead (Smultea and others 2008). Sperm Whales clapped their jaws together in response to being aggressively surrounded by Short-finned Pilot Whales in the Gulf of Mexico (Weller and others 1996). Thus, jaw displays by Sperm Whales may be a counter-aggressive behavior.

Risso's Dolphins have reportedly behaved aggressively toward other cetacean species, including Short-finned Pilot Whales (Shane 1995; Baird 2008). False Killer Whales have also been reported attacking Sperm Whales (Palacios and Mate 1996). A similar interaction as the one

TABLE 1. Chronological description of some of the events observed during an encounter with Sperm Whales, Risso's Dolphins (Risso's), and Northern Right Whale Dolphins (NRWD) off of the coast of southern California.

Time	Behavior event
10:36	20 Sperm Whales (4 calves) sighted in staggered line-abreast formation with 11 Risso's and 50 NRWD, 44 km west of San Diego
10:40	Sperm Whales move closer together (nearest neighbor distance changes from 1–10 to ¼ -3 body length [BL] minimum and maximum), group formation changes to huddled clump as Risso's approach
10:43	Risso's swim among Sperm Whales, 1 Risso's bumps mouth of Sperm Whale then retreats rapidly
10:44	One Risso's breaches directly in front of, charges, then quickly retreats from Sperm Whale. NRWD swim just in front of Sperm Whale group
10:45	Sperm Whales move closer together (less than ½ BL apart) in flank-to-flank echelon formation with calves in center of group, slow travel/rest at surface, some touching each other
10:50	A NRWD crosses and mills directly in front of calves. No observed response by adult Sperm Whales
10:51	Three Risso's move between main Sperm Whale group and 4 outlying whales, Risso's widely dispersed from each other (up to 10 BL apart). One Risso's swims perpendicularly in front of Sperm Whale heads, then all Sperm Whales on left side of group fluke-up dive
10:52	Single Risso's swims rapidly toward Sperm Whale head then quickly retreats. NRWD in front of Sperm Whale group
10:54	Only 1 Sperm Whale at surface, logging; all others dove. NRWD and Risso's interspersed with each other, slow travel, not interacting with Sperm Whale
11:02–04	A 2nd Sperm Whale surfaces. Risso's and NRWD milling/interspersed. Single Risso's rapidly approaches Sperm Whale who defecates and turns sharply toward Risso's
11:05–07	On 4 occasions, single Risso's swims rapidly toward Sperm Whale head, Sperm Whale opens mouth (lower white jaw visible) and Risso's quickly retreats
11:08	Sperm Whale that had been charged dives, leaving only a single adult Sperm Whale at surface. Risso's and NRWD interspersed/logging at surface ~250 m away–no interaction with remaining Sperm Whale
11:12	Mother-calf Sperm Whale surfaces. NRWD and Risso's still milling/logging ~250 m away
11:17	No more Sperm Whales visible at surface. NRWD and Risso's travel slowly
11:21	Mother-calf Sperm Whale surfaces
11:26	Three adult Sperm Whales surface in fan formation, Risso's surround them and 1 Risso's swims rapidly toward Sperm Whale head then retreats
11:30	Risso's interspersed with Sperm Whales. Nine Sperm Whales now at surface including 3 calves. One Risso's repeatedly approaches Sperm Whale calf, adult Sperm Whales move closer to calf
11:37	17 Sperm Whales at surface. One calf separate from adults. Risso's swim in-between Sperm Whales but are not rapidly approaching them in short bursts like before. One Risso's passes perpendicularly close and in front of 7+ Sperm Whales
11:41	All Sperm Whales dive and no longer in view

we report between Risso's Dolphins and Sperm Whales was observed near the Azores in the North Atlantic Ocean. During this interaction, 10 Risso's Dolphins swam around a group of 4 resting Sperm Whales, made repeated close approaches, performed active surface behavior (such as breaching), and actively dove in close proximity to the Sperm Whales. During this interaction, the Sperm Whales moved closer together (0–1 body lengths) and performed several short dives.

While Sperm Whales opening their mouths in response to a charging Risso's Dolphin may have been a threat display, we believe that this behavior may have also involved regurgitation of recently captured and ingested food remains. According to Weller and others (1996), squid remains were found floating in the water after Sperm Whales lowered their jaws when charged by Pilot Whales. These Pilot Whales may have induced the Sperm Whales to regurgitate their squid prey so that they could prey upon the remains (Weller and others 1996). Certainly, all 3 species are known to forage on squid and thus presumably compete for food. It may also be that deeper-diving adult Sperm Whales can prey upon larger squid than the dolphins. Thus, kleptoparasitism may be an opportunistic alternative foraging strategy that may occur on those apparently relatively rare occasions when these species encounter one another.

A Case for Social Parasitism

That the Northern Right Whale Dolphins generally remained on the periphery of the Sperm Whales and were not overtly aggressive towards them suggests that their association was inspired by social parasitism. They closely followed the Risso's Dolphins, and we assume

that they were apparently attentive to their interactions with the Sperm Whales. Thus, we conjecture that the Northern Right Whale Dolphins were anticipating the regurgitation of squid remains by the Sperm Whales as induced by the actions of the Risso's Dolphins. We have video-documented Northern Right Whale Dolphins closely following foraging Risso's Dolphins on several other occasions in the Southern California Bight (Smultea and others 2011a, 2011b; Smultea and Bacon 2012). It is possible that the smaller Northern Right Whale Dolphins associate with the larger Risso's Dolphins to locate prey, to prey on scattered remains of Risso's Dolphin prey, or for defense from predators such as sharks and Killer Whales (*Orcinus orca*). The reason(s) for this interspecific association have not been empirically established due to the small number of observations. However, squid comprise a large portion of the diets of all of these species (for example, see Jefferson and others 2008) and this is likely an influencing factor.

Conclusion

As far as we are aware, we report the 1st documented head-on charges by Risso's Dolphins to a larger cetacean species, resulting in Sperm Whales opening their mouths and dropping their lower jaws. Although we were unable to determine if there were pieces of food in the water based on examination of photographs and video, given our high altitude of approximately 360 m, we speculate that the apparent harassment of Sperm Whales by Pilot Whales and Risso's Dolphins may cause Sperm Whales to regurgitate their food, allowing the aggressors to eat the regurgitated food. Regurgitation of stomach contents by Sperm Whales when disturbed has been reported by Caldwell and others (1966) and Whitehead and others (1990). This feeding technique is commonly displayed by some birds, including jaegers (*Stercorarius* spp.) and Roseate Terns (*Sterna dougallii*) (Brockmann and Barnard 1979; Brown and others 2004; Shealer and others 2005). Squid tentacles could also remain externally attached to Sperm Whales, or pieces of squid may remain in their mouths when they surface, and these are the parts of the prey that are released at the surface or when the whales open their mouths, allowing other species to take advantage of this food source.

We postulate that the harassment of the Sperm Whales by Risso's Dolphins that we observed represents kleptoparasitism, and that the Northern Right Whale Dolphin association with the Risso's Dolphins represents social parasitism. Alternatively, they may simply have been foraging for pieces of prey remains brought to the surface by the Sperm Whales. Such kleptoparasitism and social parasitism are considered a viable foraging strategy among many animal species (Höner and others 2002; Cords and Würsig 2014), and may be either a primary or opportunistic-alternative foraging strategy. In our observed case, given the extreme rarity of such reported observations and particularly this interspecific mix of 3 species, we propose that both strategies are opportunistic. However, the social parasitism hypothesis remains to be further investigated, given that we have commonly observed Northern Right Whale Dolphins closely following foraging Risso's Dolphins off the coast of southern California. In these cases, the Northern Right Whale Dolphins remain at the surface while a Risso's Dolphin dives abruptly and steeply, presumably chasing prey, after which the Northern Right Whale Dolphins closely follow the resurfacing Risso's Dolphin. Social parasitism has been commonly documented among terrestrial animals (for example, Sumner and others 2004; Dietemann and others 2006), but is inherently difficult to document among at-sea odontocetes that spend the majority of their lives below the ocean surface.

Acknowledgments.—We are grateful to Navy personnel, C Johnson (NAVFAC Southwest), S Hanser, and R Uyeyama (NAVFAC Pacific) for their support, coordination, and facilitation in implementing these marine mammal and sea turtle aerial monitoring surveys. Thanks to field personnel during this survey: V James, M MacKay, M Moore, and D Steckler. Special thanks to our excellent and safe Aspen pilots: B Hansen and A Blasingame, and Aspen's manager, R Throckmorton. Research was conducted under National Marine Fisheries Service Scientific Permit No. 14451. Funding for this study was provided by the US Navy, Pacific Fleet, through Smultea Environmental Sciences (SES) and HDR|EOC. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the US Navy.

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