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White-Beaked Dolphins (*Lagenorhynchus albirostris*) Cooperating with Humans and Showing Altruism Toward Harbor Porpoises (*Phocoena phocoena*)

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Abstract

In an odontocete rehabilitation center in the Netherlands, repeated observations were made over several days of interspecific cooperative behavior initiated by three white-beaked dolphins (*Lagenorhynchus albirostris*)—that is, mutually beneficial cooperation with humans and altruism toward three harbor porpoises (*Phocoena phocoena*). In the first observation (mutually beneficial cooperation), a white-beaked dolphin cooperated on her own initiative with humans to herd a harbor porpoise toward a veterinary treatment/feeding area in the pool. In the second observation (altruism), two recently recovered white-beaked dolphins assisted newly arrived harbor porpoises with swimming. These first recorded examples of interspecific mutually beneficial cooperation and altruism initiated by white-beaked dolphins will help to elucidate the motivation behind such behavior and the potential fitness benefits resulting from it.

Key Words: across species, altruism, behavior, cooperation, inter species, odontocete, social interactions

Introduction

In evolutionary biology, *cooperation* can be broadly defined as any behavior by an individual (the actor) that either fully or partially functions to increase the fitness of the actor's social partner(s)—the recipient(s). If this results in direct fitness benefits for both actor and recipient, cooperation is said to be mutually beneficial. However, if the recipient's fitness is increased at the cost of the fitness of the actor, regardless of the actor's underlying motivation, the cooperative behavior is referred to as *altruism* (Gardner et al., 2016).

Mutually beneficial cooperation and altruism are widespread in animals and have been described in, for instance, insects (e.g., Ratnieks & Wenseleers, 2007; Tang et al., 2014), fish (e.g., Dugatkin & Mesterton-Gibbons, 1996; Bshary, 2002), birds (e.g., Olendorf et al., 2004; Beecher et al., 2010), bats (e.g., DeNault & McFarlane, 1995; Carter & Wilkinson, 2013), primates (e.g., Seyfarth & Cheney, 1984; Kappeler & Van Schaik, 2006), and cetaceans (e.g., Benoit-Bird & Au, 2009; Pitman et al., 2017).

In contrast to mutually beneficial cooperation, which has direct fitness benefits for all parties, altruistic behavior is difficult to reconcile with natural selection. Various mechanisms have been proposed to explain the evolution and persistence of altruism, the most common being kin selection and reciprocity (Hamilton, 1963; Trivers, 1971; Rothstein & Pierotti, 1988; Brinkers & Den Dulk, 1999). Non-reciprocal altruism toward unrelated individuals is rare and poorly understood. Besides in humans, in which it is thought to arise from empathy, such altruism has only been described in the large-brained taxa of great apes, elephants, and cetaceans (see De Waal, 2008). Studying cooperative behavior in taxa that are distantly related to humans and have evolved under very different selective pressures (e.g., cetaceans) may help us understand the evolution of intentionally altruistic altruism (i.e., an animal consciously helping another animal; De Waal, 2008) and its climax in humans.

Cetaceans, especially dolphins, are known for their cooperative behavior toward both conspecifics and members of other species. Examples are cooperative prey herding (e.g., Simões-Lopes et al., 1998; Benoit-Bird & Au, 2009), the formation of mixed-species groups as an anti-predator and/or foraging advantage strategy (e.g., Quérouil et al., 2008; Kiszka et al., 2011), play (e.g., Deakos et al., 2010), and epimeletic, or caregiving, behavior. Epimeletic behavior includes assisting sick or injured individuals by keeping them afloat, "standing by" individuals in distress (see Caldwell & Caldwell, 1966; Connor & Norris, 1982; Bearzi & Reggente, 2018), and maternal behavior, which includes nursing (Mann, 2018) and swimming in echelon position (a form of aquatic "infant carrying"; Noren, 2008). Maternal behavior is sometimes directed toward a calf other than the mother's own (e.g., Simard & Gowans, 2004). Some of these costly cooperative behaviors cannot easily be explained by kin selection or reciprocity, especially when they occur interspecifically. The addition of records of such behaviors to the existing literature is required to increase our understanding of cooperation in cetaceans.

Temporary captivity provides a unique opportunity to study behavior in wild cetaceans. In 1991, the Dolfinarium Harderwijk in the Netherlands opened a rehabilitation and research center for stranded odontocetes. Since that time, five stranded white-beaked dolphins (*Lagenorhynchus albirostris*) and over 50 stranded harbor porpoises (*Phocoena phocoena*) have been brought to the center, ~50% of which have been deemed healthy enough to be released in the North Sea. While caring for the rehabilitating dolphins and porpoises, staff kept meticulous records of husbandry techniques and behavioral observations of the animals. We describe two such observations, each lasting several days. The first suggests mutually beneficial cooperation (hereafter "cooperation") between a white-beaked dolphin and humans, and the second demonstrates altruism of white-beaked dolphins toward harbor porpoises. To our knowledge, these are the first recorded observations of interspecific cooperative behavior initiated by white-beaked dolphins.

Observation 1: Cooperation—a White-Beaked Dolphin Cooperates with Humans to Herd a Harbor Porpoise

On 15 November 1993, an adult male harbor porpoise (Pp031; Table 1) stranded on the coast of the Dutch island of Terschelling. He was transported to the rehabilitation center and placed in a pool with a juvenile female white-beaked dolphin (Lal009; Table 1) that had stranded on the same day on the Dutch island of Texel. Both animals were emaciated but were able to swim independently. They both swam in clockwise circles but did not dive or breathe simultaneously.

The dolphin started to eat fish (with medication) from the hands of the staff soon after arrival, but the porpoise did not, and, therefore, he required tube feeding. To tube-feed and medicate the porpoise, two people in waders holding a net fence panel herded him to a veterinary treatment/feeding area at a specific location at the side of the pool (Figure 1a; Kastelein et al., 1997). The herding process took time, but once the porpoise was confined to a small area (2 to 3 m^2), he floated calmly, as is typical for captive harbor porpoises (Kastelein et al., 1997). One of the herders then entered the treatment/feeding area and held the porpoise at the water surface. A person on the edge of the pool then tube-fed the porpoise (providing fish porridge, oral medication, and vitamins) and administered antibiotics via injection.

After 2 days of this procedure (approximately six times per day), the white-beaked dolphin started to cooperate with the human staff by herding the porpoise toward the treatment/feeding area as soon as the herders and the net fence entered the pool on the opposite side to the treatment/feeding

Table 1. Details of the six animals involved in the two observations. Harbor porpoises (*Phocoena phocoena*) are indicated by Pp in their identification code (ID) and white-beaked dolphins (*Lagenorhynchus albirostris*) by Lal. M = male; F = female. Observation 1 = Cooperation; Observation 2 = Altruism. Age = estimated age on arrival at the rehabilitation center, Mass = body mass, Length = total body length, and NL = the Netherlands.

ID code	Sex	Observation	Stranding date	Location	Age	Mass (kg)	Length (cm)	Release date
Pp031	M	1	15 Nov. 1993	Terschelling, NL	> 10 y	37.0	134	17 June 1994
Lal009	F	1	15 Nov. 1993	Texel, NL	17 mo	110.0	201	15 April 1994
Lal010	F	2	17 March 1994	Westenschouwen, NL	9 mo	56.2	170	16 Aug. 1994
Lal011	F	2	17 March 1994*	Calais, France	9 mo	54.1	171	16 Aug. 1994
Pp035	M	2	24 March 1994	Callantsoog, NL	9 mo	26.2	113	17 June 1994
Pp036	M	2	24 March 1994	Terschelling, NL	9 mo	23.2	111	21 Oct. 1997

*All animals arrived at the rehabilitation center on the day they stranded, except for dolphin Lal011, who stranded in France and arrived within 5 days of stranding.

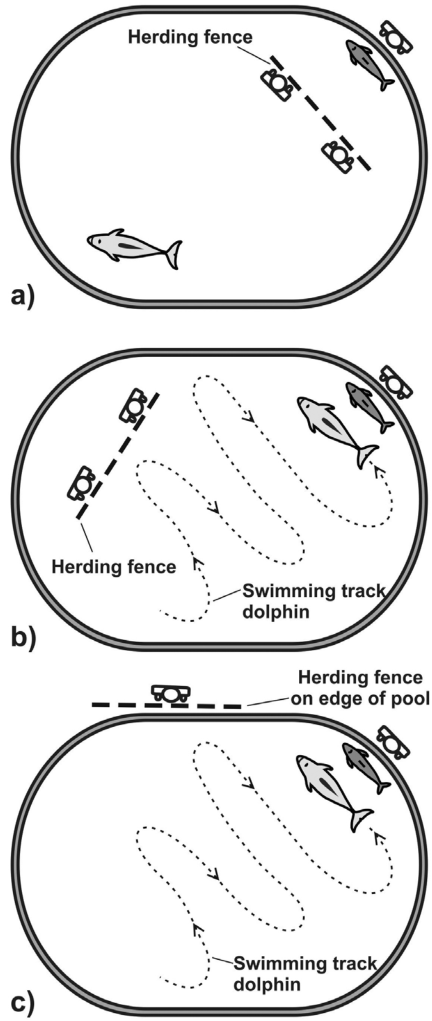

Figure 1. Observations of mutually beneficial cooperation between a white-beaked dolphin and humans. The panels (a–c) provide a schematic top view of the three phases of the observed cooperative interactions: (a) a harbor porpoise (*Phocoena phocoena*; dark gray) being slowly herded by two people holding a net fence panel toward a veterinary treatment/feeding area at the side of the pool; the white-beaked dolphin (*Lagenorhynchus albirostris*; pale gray) did not participate during this phase, which lasted around 2 days; (b) once the fence panel and the people are in the water (stationary), the white-beaked dolphin slowly herds the porpoise to the treatment/feeding area; this phase continued for around 4 days; and (c) upon seeing the fence panel and one person on the edge of the pool, the white-beaked dolphin herds the porpoise slowly toward the treatment/feeding area. This phase continued for around 10 days. Dimensions of the concrete oval pool were 8.6 × 6.3 m, 1.2 m deep. The water level was kept constant, with an average water temperature of 19.5°C and an average salinity of 2.2% NaCl.

area. Before the staff arrived, the dolphin swam clockwise circles ~90% of the time; this behavior stopped as soon as the herders entered the pool. When herded by the dolphin, the porpoise slowly swam toward the treatment/feeding area where he floated calmly (Figure 1b). No fish or secondary reward was given to the dolphin.

Four days after the white-beaked dolphin started to cooperate with the staff, she began to herd the harbor porpoise calmly toward the treatment/feeding location when she saw only one person with the fence panel on the edge of the pool waiting to put the panel into the water behind the porpoise if needed. From this point on, there was no need for the staff to enter the water. This not only reduced the number of people involved in the veterinary treatment/feeding procedure from three to two, but it also saved time and effort, and reduced stress for the animals (Figure 1c). The white-beaked dolphin continued to cooperate with staff by herding the harbor porpoise until the porpoise was able to eat voluntarily, and treatment was no longer needed after approximately 10 days. After the porpoise recovered, the dolphin and porpoise frequently engaged in physical contact (side to side and chest to chest) for almost 4 months. Once they were deemed healthy enough, the white-beaked dolphin and harbor porpoise were released into the North Sea on 15 April and 17 June 1994, respectively.

Observation 2: Altruism—White-Beaked Dolphins Assist Swimming Harbor Porpoises

In March 1994, two juvenile female white-beaked dolphins arrived at the rehabilitation center within 5 days of each other. Both had stranded on 17 March—the first (Lal010) on the Dutch coast of Westenschouwen and the second (Lal011) on the coast of Calais, France (Table 1). On arrival, both animals had similar body mass and length (Table 1). Both were emaciated and suffered from bacterial infections. They also appeared to have pain in their tail stocks (i.e., the tail stocks were hard, stiff, and trembling), which had probably been caused by overheating and intense and/or prolonged tail-slapping on land while beached. As they were unable to eat or swim voluntarily, the dolphins were tube-fed and put in swimming support hammocks (Lal010 for 6 days and Lal011 for 2 days; Figure 2a; Kastelein et al., 1995). They were also treated with antibiotics. During this period, they were taken out of the hammocks several times per day for 15 to 60 min to assess their ability to swim independently. Once the animals had recovered sufficiently to be able to swim and eat thawed fish voluntarily, they swam clockwise

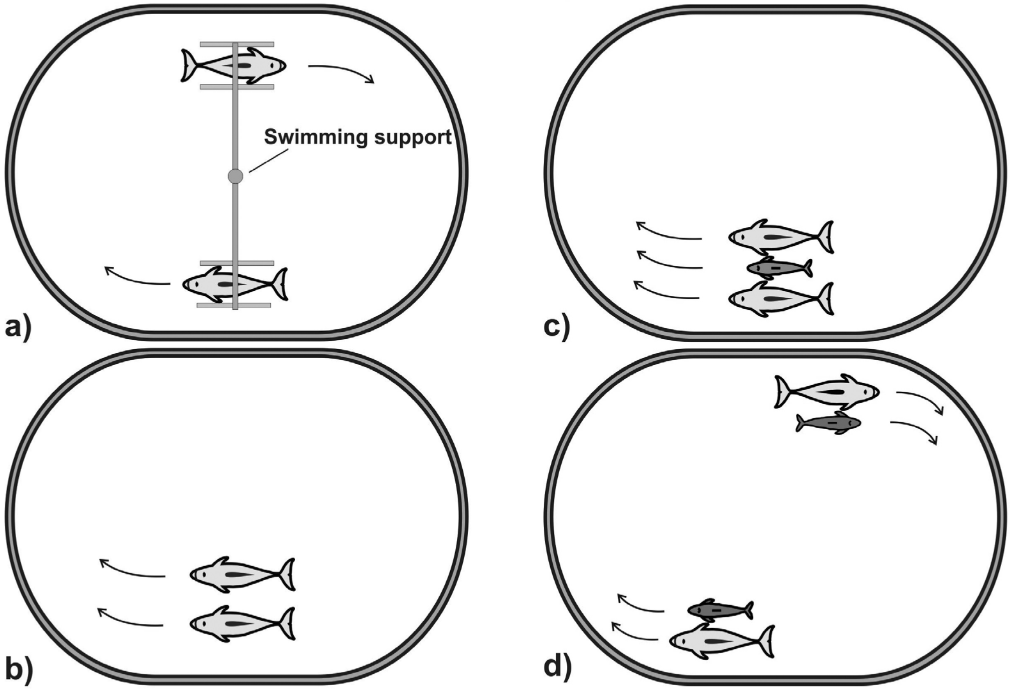

Figure 2. Observations of altruism by white-beaked dolphins (pale gray) toward harbor porpoises (dark gray). Panel (a) shows the two newly arrived dolphins in the swimming support hammocks, while panels (b-d) provide a schematic top view of the phases of the observed altruistic interactions: (b) the two white-beaked dolphins swimming side by side and breathing simultaneously; (c) the two dolphins flanking a newly arrived harbor porpoise, all three animals diving and breathing simultaneously; and (d) each white-beaked dolphin swimming parallel to a harbor porpoise, with each pair diving and breathing simultaneously. Dimensions of the concrete oval pool were 8.6 × 6.3 m, 1.2 m deep. The water level was kept constant, with an average water temperature of 19.5°C and an average salinity of 2.2% NaCl.

circles in the pool and breathed simultaneously (Figure 2b). At that time, they were still emaciated but were not receiving any medication.

On 24 March, a juvenile male harbor porpoise (Pp035; Table 1) stranded on the Dutch coast near Callantsoog and was sent to the rehabilitation center. As no other pools were available, the sick and emaciated porpoise was put in the same pool as the two white-beaked dolphins. The porpoise was able to swim independently. Within 1 h, the two dolphins both flanked the porpoise on either side, and all three odontocetes started to dive and breathe simultaneously, continuing almost all day (Figure 2c).

Later that day, another juvenile male harbor porpoise (Pp036; Table 1) stranded on the Dutch island of Terschelling. He was transported to the rehabilitation center and was added to the pool with the white-beaked dolphins and the harbor porpoise (Pp035). Like Pp035, Pp036 was sick and emaciated but able to swim independently. After he was placed in the pool, each white-beaked dolphin swam to the left of one of the porpoises, thereby shielding it from the pool wall. Then, each pair started to dive and breathe simultaneously while swimming in a clockwise direction (Figure 2d). This situation continued for several days until the porpoises recovered. All four animals were eventually deemed sufficiently healthy to be released into the North Sea. The white-beaked dolphins were released together on 16 August 1994; Pp035 was released on 17 June 1994, and Pp036 was released on 21 October 1997.

Discussion

All three white-beaked dolphins we observed were female. Adult white-beaked dolphins are 240 to 310 cm long (Reeves et al., 1998), so, based on their body length, the stranded individuals were deemed to be juveniles (Table 1). The two harbor porpoises that received altruistic behavior were also juveniles (Table 1), as adult males reach about 145 cm (Bjørge & Tolley, 2018). Due to the significant interspecific size differences, all three harbor porpoises may have appeared similar to newborn calves to the dolphins, as white-beaked dolphins are about 120 cm long at birth (Reeves et al., 1998). Common bottlenose dolphins (*Tursiops truncatus*) are also believed to have "mistaken" harbor porpoises for infants of their own species but through violent attacks with the presumed intention of infanticide, or while practicing skills for infanticide, rather than in epimeletic behavior (Patterson et al., 1998; Cotter et al., 2011). Sexual maturity in female white-beaked dolphins is reached at a mean length of 240 cm (Galatius et al., 2012), so it is highly unlikely that any of the three dolphins had given birth to a calf before stranding. The two species produce different acoustic signals: white-beaked dolphins use whistles for social communication and clicks for echolocation (Rasmussen & Miller, 2002), while harbor porpoises produce high-frequency clicks for both communication and echolocation (Hansen et al., 2008). These sounds were produced by the animals in the rehabilitation center, as the pulse repetition rate could be heard by staff, and should have reduced the likelihood of the dolphins mistaking the porpoises for calves. Nevertheless, the dolphins may have felt an instinctive need to take care of the porpoises with which they shared their pool.

In the case of Observation 1, the white-beaked dolphin was neither trained to herd the harbor porpoise to the treatment/feeding area nor given food or other rewards for this behavior. This contrasts with, for instance, wild bottlenose dolphins cooperating with artisanal fisheries in Laguna, Brazil, where dolphins share the catch after herding fish toward fishermen waiting with nets (Simões-Lopes et al., 1998, 2016). However, by herding the porpoise herself, the dolphin reduced, and later eliminated, the need for people and the net fence to be present in the water, increasing her own swimming area and decreasing disturbances within it (i.e., reducing stress). Therefore, her behavior was interpreted as mutually beneficial cooperation with humans, but it could also be interpreted as altruistic toward the porpoise. Being herded non-aggressively by a fellow odontocete that was larger than itself, as its mother was when it was young, may have reduced stress in the porpoise, though this particular porpoise was probably fully grown and > 10 y old (Table 1). From her own experience, the dolphin may have associated any activity near the side of the pool with food, whether or not she was aware of what happened to the porpoise while he was at the treatment/feeding area. Therefore, she may have intended to help the porpoise feed by guiding him toward the food, though the dolphin had not been fed in the same area as the porpoise.

Observation 2 was interpreted as altruistic, epimeletic behavior of the white-beaked dolphins toward the harbor porpoises, which may have been mistaken for calves. Flanking the porpoises not only protected them from hurting themselves on the unfamiliar concrete wall of the pool, but it is also likely to have aided them in swimming by hydrodynamic facilitation, as observed in dolphin mother–calf pairs (Mann & Smuts, 1999; Weihs, 2004; Fellner et al., 2006). This echelon position, where a calf swims very close and parallel to its mother's mid-lateral flank, is a type of maternal care that improves the calf's swimming performance at the cost of its mother's (Noren, 2008; Noren et al., 2008). Both intra- and interspecific allomaternal behavior (i.e., maternal behavior toward a calf by a female other than its mother) have been reported in bottlenose dolphins (*Tursiops* spp.; e.g., Mann & Smuts, 1998; Sakai et al., 2016; Carzon et al., 2019), and Simard & Gowans (2004) described allomaternal behavior in Atlantic white-sided dolphins (*Lagenorhynchus acutus*), a species closely related to white-beaked dolphins. However, the function of such behavior and its costs and benefits for the calves, mothers, and allomothers involved are still poorly understood. One possibility is the Learning to Parent hypothesis in which both calf and allomother (an inexperienced female) may benefit from their association (Mann & Smuts, 1998). In the study by Mann & Smuts (1998), however, the allomothering females and calves were of the same species; and although they were subadults, the allomothering females were significantly older than the female dolphins involved in the present observations.

The synchronous swimming and breathing may have served a different, cooperative, purpose, benefiting all parties. Behavioral synchrony in dolphins has been linked to communication, social bonding, defense against predators, and reduction of stress and social tension (Hastie et al., 2003; Connor & Mann, 2006; Connor et al., 2006; Perelberg & Schuster, 2008). As the two white-beaked dolphins were the same sex and similar in age, their synchronous swimming before the arrival of the porpoises probably had a social function (Perelberg & Schuster, 2008) and may have provided them with reassurance in their captive environment. However, it is unclear whether synchronicity among the dolphin–porpoise pairs provided any benefit to the dolphins other than possible (additional) reassurance. If they were seeking a social benefit, the two dolphins could have swum together, as they did before arrival of the porpoises. Therefore, the most likely explanation for the white-beaked dolphins' behavior remains altruism directed at the harbor porpoises, perhaps due to mistaking them for white-beaked dolphin calves (although dolphin and porpoise communication signals are considerably different, as mentioned earlier). In the wild and in captivity, harbor porpoises usually do not swim in synchrony, except as mother–calf pairs (Kastelein & Staal, 1997).

The two observations described herein add to the limited list of examples of cooperative behavior in cetaceans, in which white-beaked dolphins are underrepresented. To our knowledge, these observations are the first recorded examples of mutually beneficial cooperation and interspecific altruism initiated by white-beaked dolphins. Observations such as these may aid in understanding the proximate and ultimate explanations of cooperative behavior in cetaceans—the motivation behind the behavior and the potential fitness benefits resulting from it, respectively.

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