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NOTE

Marine Mammal Science

Food sharing in rough-toothed dolphins off southwestern Mexico

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Food sharing can be defined as a resource owner allowing a conspecific to consume part of a food item originally acquired by this owner, although the latter could defend this resource (Hadjichrysanthou & Broom, 2012; Stevens & Gilby, 2004). This behavior has been widely documented in a range of species, including insects (Boggs, 1995) and birds (Elgar, 1986; Heinrich, 1988), but has been more frequently documented in mammals, including the common vampire bat (*Desmodus rotundus*; Carter & Wilkinson, 2013) and primates (De Waal, 1989; Goodall, 1986; Ruiz-Miranda et al., 1999).

Documentation of food sharing has been rare in cetaceans as this behavior (and feeding in general) can be inconspicuous to boat-based observers. Most reports are anecdotes from both captive and wild delphinids (Connor & Norris, 1982; Johnson, 1982), including in killer whales (*Orcinus orca*; Hoelzel, 1991; Wright et al., 2016), false killer whales (*Pseudorca crassidens*; Baird et al., 2008; Connor & Norris, 1982), Guiana dolphins (*Sotalia guianensis*; Spinelli, de Jesus, & do Nascimento, 2008), and common bottlenose dolphins (*Tursiops truncatus*; Fedorowicz, Beard, & Connor, 2003). Food sharing is certainly underreported, and its occurrence is probably underestimated. However, reporting prey sharing is relevant for determining how ecological factors (e.g., food availability) might affect its occurrence (Wright et al., 2016), and to understanding the degree to which it shapes odontocete societies (Ford & Ellis, 2014).

Rough-toothed dolphins (*Steno bredanensis*) are oceanic and often island-associated delphinids distributed globally in tropical and warm temperate waters where they feed on a variety of large and high trophic level prey, primarily teleosts (see Jefferson, 2017; Kiszka, Baird, & Braulik, 2019 for reviews). This species displays long-lasting associations with conspecifics, indicating that rough-toothed dolphins may have more stable grouping patterns than other small delphinids (Baird et al., 2008; Kuczaj & Yeater, 2007).

Despite numerous reports of prey handling and cooperative feeding in rough-toothed dolphins (Addink & Smeek, 2001; Götz, Verfuß, & Schnitzler, 2006; Ortega-Ortiz et al., 2014; Pitman & Stinchcomb, 2002), to the best of our knowledge there are only two reported cases of food sharing in this species (Brower & Curtsinger, 1979) and

one report of possible food sharing (Lodi & Hetzel, 1999). In the first case, in a group of 10 dolphins swimming slowly and close together, one dolphin deemed the "keeper" carried a large (~9 kg) mahi-mahi (*Coryphaena hippurus*) crosswise in its mouth and shifting the fish to the corner of its mouth to "chew" it (likely ripping off a piece of flesh; Brower & Curtsinger, 1979). The keeper dolphin handling the fish repeatedly dropped it, appearing to pass to two other dolphins, who repeatedly picked up the fish, "chewed" it once and released it to another dolphin. The group eventually dived out-of-sight still carrying the remainder of the fish. In the second case, 6 days later, the divers observed from the boat a group of rough-toothed dolphins with one dolphin carrying a mahi-mahi. Once underwater, they witnessed similar behavior to the first case: a single dolphin holding the fish within a slow-moving group. The keeper individual consumed several pieces of the fish, "chewing" by undulating its body from its flukes to its head. It repeatedly released the fish and allowed group members to carry the entire fish and tear pieces of flesh off the fish. The dolphins continued these behaviors until they dived out of sight still holding a small portion of the fish. It is unknown if these two groups were composed of the same dolphins. Lodi and Hetzel (1999) documented a case of possible food sharing involving two dolphins within a group of 12 dolphins sighted feeding in Ilha Grande Bay, Brazil (Lodi & Hetzel, 1999). Within the group, an adult dolphin and a calf held a cutlass fish (*Trichiurus lepturus*) in their mouths and repeatedly alternated who would hold the fish, one dolphin releasing it at the surface of the water and the other picking it up. The fish was released alive and captured by the researchers.

Here, we report two cases of food sharing in rough-toothed dolphins off the southwestern Pacific coast of Mexico. We observed one case of food sharing between five dolphins from a small boat and a second case between two adult rough-toothed dolphins directly observed with a UAV (unmanned aerial vehicle, hereafter drone). We describe these observations in detail.

We sighted rough-toothed dolphins during boat-based cetacean surveys conducted as part of the long-term monitoring efforts of Whales of Guerrero (https://www.whalesinmexico.com/science/research-projects/), a community-based research organization based in Barra de Potosí that studies marine mammals in the state of Guerrero (e.g., Ramos et al., 2018b; International Whaling Commission, 2018). From January to April each year from 2014 to 2020, we surveyed the Bay of Potosí and along the adjacent coastline within 5 km of shore from small boats (7.5 m long) with outboard engines (60–85 HP). The region is dominated by sandy bottoms and waters with a depth range of 2–80 m. We attempted to photograph both sides of each dolphin's dorsal fin for individual identification using a Canon EOS 80D digital SLR camera equipped with a telephoto lens (100–400 mm) or a Nikon D7000 digital SLR camera with a telephoto lens (55–300 m). Data on survey effort, sighting location, and *ab libitum* notes on animal behavior were recorded manually. We identified the water depth range (in meters) at sighting locations using the Navionics Boating application on an iPhone 8 (Apple Inc.).

In one sighting, we launched a small drone (DJI Mavic Pro 2) equipped with a high-resolution camera (3,700 × 2,900 dpi) and piloted the drone to altitudes of 20–30 m to track dolphin movements and conduct a drone-based focal group follow to record their behavior. The video was transmitted live to an iPhone 8 (Apple Inc.) and monitored via the DJI GO application to remotely pilot the drone and to maintain sight of the group in the field-of-view (FOV) of the camera. We flew the drone continuously while matching their swimming speed in a fixed orientation relative to the centroid of the group, and approximately 5 m to one side of the group. The aerial video recording continued until all dolphins were lost from sight.

We reviewed aerial videos in QuickTime Player 10 (Apple Inc.) to isolate footage of dolphins and to identify behaviors involved in food sharing. To determine if the behaviors we observed constituted food sharing and which dolphins participated in the behavior, we undertook individual focal follows (Altmann, 1974) of all dolphins using BORIS behavioral observation software (Friard & Gamba, 2016). To construct detailed activity budgets of dolphin activity, we coded dolphin behavior according to the following behavior states; *directional swimming*: continuous swimming movement in one direction; *feeding*: tearing pieces off the fish for consumption with head jerk, shaking of the body, and opening and closing movements of the mouth during consumption; *fish handling*: handles prey item, including holding the fish in its mouth, picking the fish up, and dropping the fish; and *sociosexual*: social and sexual behaviors, including direct approaches, close contact, genital touches, pectoral and fin rubbing, and possible intromission.

To identify individual dolphins, we compared images of the dorsal fin of each dolphin to the reference images of known individuals in the *Whales of Guerrero* photo-identification catalog through matching of scarring on their dorsal fins (Würsig & Jefferson, 1990). We identified dolphins in aerial video by matching the unique pigmentation patches on the bodies of each dolphin from video stills to archived boat-based images of their bodies in the regional catalog for the species.

From 2014 to 2020, we sighted rough-toothed dolphins 158 times. Dolphins were detected feeding in 43 sightings (27.2% of total) where dolphins engaged in a variety of feeding behaviors, including swimming in circles around prey fish, short dives, tail slaps, fast darting with repeated leaps during fish chases, and carrying of prey fish at the surface in their mouths. In two of these sightings, we observed evidence of multiple dolphins in the same group handling and passing the same prey item back and forth.

In the first sighting at 11:56 a.m. on February 19, 2016, we encountered a group of at least eight dolphins feeding 4.4 km east of the coast and northeast of the Isla Ixtapa at a depth range of 36–43 m (Figure 1). As many as five dolphins repeatedly passed an unidentified species of jack (*Caranx* spp.) back and forth, likely Pacific crevalle jack (*Caranx caninus*). The dolphins tore pieces of flesh off the fish and dropped the fish in place and another dolphin would pick it up and perform a similar behavior. These behaviors continued for 15 min until the dolphins were lost from sight.

In the second sighting at 10:38 a.m. on January 15, 2020, we encountered a group of four adult rough-toothed dolphins traveling and feeding 1.5 km east of Playa Tortuga at a depth range of 34–40 m (Figure 1). At 1056, we hand-launched the small drone to document dolphin behavior. We reviewed a total of 7.9 min of continuous aerial video observations of four adult rough-toothed dolphins (Figure 2a–f; Supplementary Video S1). The four dolphins were photo-identified as known individuals in the Whales of Guerrero catalog: Pickles (RTD163), Blue (RTD165), Fuji (RTD171), and Moby (RTD174).

Figure 3 is a detailed plot of the activity budget of each of the four dolphins sighted on January 15, 2020. Moby and Fuji were visible in the FOV of the drone's camera for the entire observation. Pickles went out-of-sight for 4.5 s and Blue went out-of-sight for 78.5 s (Figure 3). In the following section, we provide a descriptive summary of the event:

FIGURE 1 Map of the two sightings of rough-toothed dolphins observed food sharing off the southwestern Pacific coast of Guerrero, Mexico on February 19, 2016 and January 15, 2020. The inset map on the right depicts: the location of the beginning and ending of the drone-based group follow on January 15, 2020; the takeoff location of the DJI Mavic Pro 2; the GPS track of the drone flown over the group; and the section of the track where food sharing was observed.

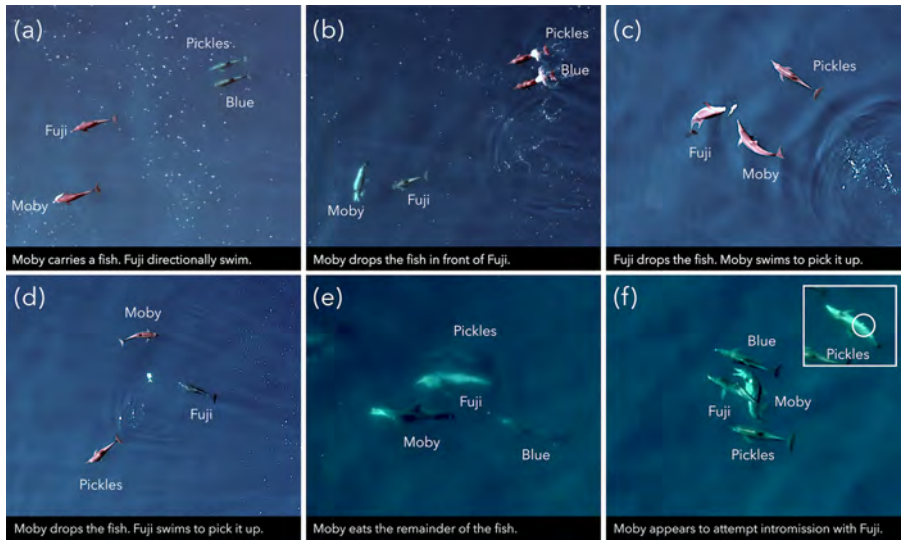

FIGURE 2 Images of rough-toothed dolphins and different behaviors they exhibited during aerial video observations gathered on January 15, 2020 with a DJI Mavic Pro 2 off the Pacific coast of Guerrero, Mexico. (a) Moby carried the prey fish at the beginning of the observation and Fuji, Blue, and Pickles directionally swam nearby. (b) Moby then fed, dropped the fish and Fuji picked it up and fed. (c) Both feeding dolphins repeatedly grabbed the prey fish, jerked their heads to tear a piece of flesh off, and ate the piece while opening and closing its mouth. (d) Moby and Fuji passed the fish back and forth between them again. Blue and Pickles did not engage in feeding or food sharing behaviors. (e) Moby consumed the remainder of the fish. (f) Pickles and Moby engaged in sociosexual behaviors with Fuji. The smaller inset image shows Pickle's extruded penis.

00:18–01:07: All four dolphins were first observed swimming at the surface. Moby carried the body of a large fish (0.7–1.0 m long) crosswise in its mouth and directionally swam <1 m to the left of Fuji. Pickles and Blue directionally swam <1 m apart, 7 m behind them (Figure 2a).

01:08–02:45: Moby began feeding on the fish, jerking its head several times to rip pieces of flesh off it and opening and closing its mouth while eating (Figure 2b). Immediately before releasing the fish, Moby turned on its right side, changed its swim direction, and turned its body more than 90° to meet the approaching Fuji (Figure 2b). As they swam past each other in a perpendicular orientation, Fuji picked up the fish in its mouth, jerked its head and turned its body more than 90° while swimming on its right side, ripping a piece of flesh off the fish and releasing the fish near Pickles and Blue as they swam past.

Fuji picked up the fish again and repeated the same sequence of feeding behaviors. Fuji dropped the fish as Moby approached the fish ventrum-up and grabbed it (Figure 2c). Moby accelerated and dropped the fish near Pickles as it swam past it perpendicularly. Pickles did not pick up the fish and Fuji grabbed the fish again. Moby and Fuji repeated the sequence of feeding behaviors on two more occasions, and both dolphins repeatedly dropped the fish in front of Pickles and Blue, both of whom did not pick it up and continued to swim directionally (Figure 2d).

03:00–07:27: Pickles reentered the FOV and approached and engaged in sociosexual behavior with Fuji, swimming up underneath Fuji and turning on its right side while aligning its genital region with Fuji while appearing to attempt intromission. Pickles opened and closed its mouth repeatedly while maintaining its position with Fuji (Figure 2f). Both dolphins slowed their swim speed for 3 s before Pickles separated with its penis partially extruded (Figure 2f). Pickles repeated this approach four times. Moby handled and fed on the fish during this period.

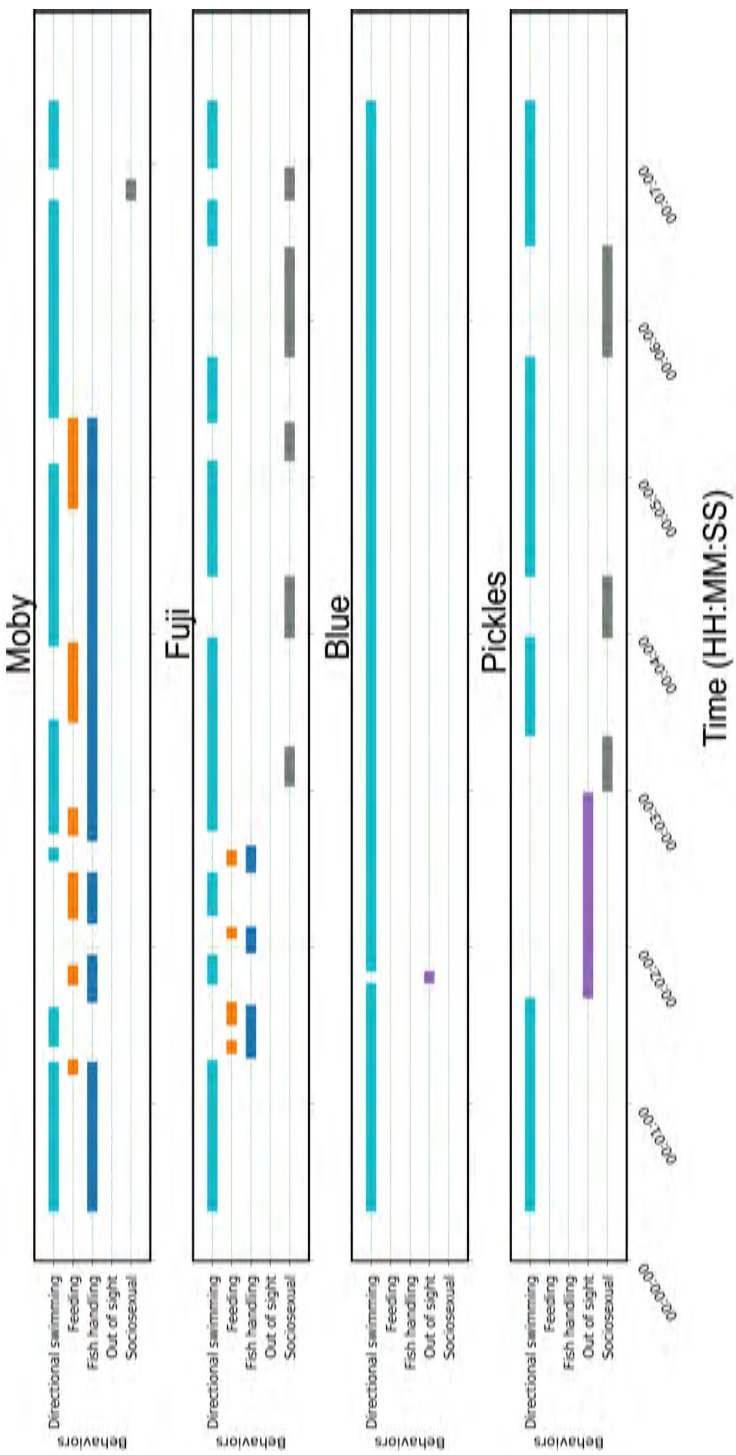

FIGURE 3 Plots of the behavioral activity of four rough-toothed dolphins in aerial video observations gathered with a small drone off the Pacific coast of Guerrero, Mexico on January 15, 2020. Graphic produced in BORIS behavioral analysis software (Friard & Gamba, 2016).

Fuji accelerated and approached Moby and turned on its side, but the fish was not exchanged. Moby fed on the fish and consumed the remainder of the body (Figure 2e). Moby then approached and engaged in sociosexual behaviors with Fuji, including extruding its penis, swimming up underneath Fuji ventrum-to-ventrum, and appeared to engage in a sexual interaction (Figure 2f).

07:28: All four dolphins dived and went out-of-sight.

Behavioral analysis revealed that only Moby and Fuji were involved in handling, feeding on, and exchanging the fish. Moby handled the fish for a total of 256.4 s (91.1% of total handling time; mean handling time = 64.1 s; $n = 4$) and fed on the fish for 106.0 s. Fuji handled the fish for 25.0 s (8.9% of total handling time; mean handling time = 13.5 s; $n = 3$) and fed on the fish for 23.8 s. Moby and Fuji passed the fish between them six times in 4.3 min. Moby continued to carry the fish for another 2.6 min following the final exchange before consuming the remainder of the fish (Figure 3). Prior to exchanging the fish, Moby and Fuji repeatedly fed on the prey fish by jerking their heads to rip pieces off. Pickles and Blue swam within 5 m of Moby and Fuji throughout the food sharing and interacted with them but did not feed or handle the prey. Given the headless state of the fish at the beginning of dolphin detection from the drone, this behavior may have preceded our observation for a longer period of time. Fuji was the only dolphin observed engaging in sociosexual behavior with multiple dolphins (Moby and Pickles).

The "2020" group swam in close proximity throughout the observation and visual inspection of the GPS track of the drone indicated all four dolphins maintained the same swim direction throughout the aerial follow, traveling nearly parallel to the coastline at a compass direction of 145°–160° (Figure 1).

The fish exchanged and eaten by Moby and Fuji in this observation of food sharing was most likely Pacific crevalle jack according to its physical characteristics as viewed in the high-resolution drone imagery including the "V" shape and yellow color of the caudal fin (Figure 2c).

Our observations provide additional evidence that rough-toothed dolphins engage in food sharing. Pitman and Stinchcomb (2002) hypothesized rough-toothed dolphins could specialize in large pelagic prey, particularly mahi-mahi, and suggested that coordinated foraging and food sharing could indicate high levels of cooperation, enabling them to capture large fast-moving prey. Rough-toothed dolphins may have evolved cooperative hunting tactics to optimize hunting efficiency in capturing large prey similar to killer whales (Hoelzel, 1991; Pitman & Durban, 2012). Our observations and previous reports of rough-toothed dolphin foraging also indicate these dolphins regularly target smaller prey fish and cooperatively hunt to herd fish schools and to feed on numerous fish at the same time for individual consumption (Addink & Smeek, 2001; Ortega-Ortiz et al., 2014). Thus, food sharing in this species may have evolved as a tactic to improve food intake when targeting large and unpredictable prey, and as a means to reinforce social relationships between individuals.

Similar to previous accounts food sharing in rough-toothed dolphins, feeding dolphins in our observations swam in close proximity while feeding and exchanged the prey item by repeatedly releasing the fish and allowing another dolphin to pick it up (Brower & Curtsinger, 1979; Lodi & Hetzel, 1999). The two feeding dolphins in the second sighting used swimming and body movements, and biting behaviors (i.e., jerking their heads and turning rapidly as they released the fish) to facilitate tearing pieces of flesh from the fish, similar to descriptions of rough-toothed dolphin prey exchanges during food sharing (Brower & Curtsinger, 1979; Lodi & Hetzel, 1999). This feeding behavior may be an important component of food sharing, allowing each dolphin to feed while facilitating the ultimate consumption of the remainder of the fish's body.

The occurrence of this rarely observed behavior in rough-toothed dolphins provides insights into their social lives and should stimulate additional research on understanding the frequency of food sharing in this species. For example, we observed dolphins engage in a variety of sociosexual behaviors during feeding and food sharing, and it is unclear how sexual behavior may be related to feeding behavior in this species. Our findings illustrate the power of small aerial drones to track and document the fine-scale behavior of dolphins (Orbach et al., 2020; Ramos et al., 2018a; Weir et al., 2018). Similar to other marine mammals (e.g., Hartman, van der Harst, & Vilela, 2020; Landeo-Yauri et al., 2020), individual rough-toothed dolphins can be identified by their scarring and skin pigmentation patterns. Future studies should focus on understanding the long-term social structure of this

species (stability of associations), in particular as it relates to cooperative foraging (e.g., prey sharing and group hunting).

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AUTHOR CONTRIBUTIONS

Eric Angel Ramos: Conceptualization; data curation; formal analysis; investigation; methodology; resources; validation; visualization; writing-original draft; writing-review and editing. **Jeremy Kiszka:** Conceptualization; formal analysis; investigation; methodology; writing-original draft; writing-review and editing. **Victoria Pouey-Santalou:** Data curation; formal analysis; investigation; methodology; validation; writing-original draft; writing-review and editing. **Raúl Ramírez Barragán:** Data curation; formal analysis; methodology; resources; validation; writing-review and editing. **Andrea García Chávez:** Data curation; formal analysis; investigation; methodology; resources; validation; writing-review and editing. **Katherina Audley:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; writing-original draft; writing-review and editing.

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SUPPORTING INFORMATION

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