Received: 10 February 2021 | Accepted: 6 June 2021
DOI: 10.1111/mms.12854

NOTE

Marine Mammal Science

Lords of the Rings: Mud ring feeding by bottlenose dolphins in a Caribbean estuary revealed from sea, air, and space

Eric A. Ramos[1,2] | Leomir Santoya[3] | Joel Verde[3] | Zoe Walker[4] | Nataly Castelblanco-Martínez[2,5,6] | Jeremy J. Kiszka[7] | Guillaume Rieucau[8]

[1]Department of Psychology, The Graduate Center, City University of New York, New York, New York

[2]Fundación Internacional para la Naturaleza y la Sustentabilidad, Chetumal, Quintana Roo, Mexico

[3]Sarteneja Alliance for Conservation and Development, Sarteneja Village, Corozal, Belize

[4]Wildtracks, Sarteneja Village, Corozal, Belize

[5]Consejo Nacional de Ciencia y Tecnología, Mexico City, Mexico

[6]Departamento de Ciencias e Ingeniería, Universidad de Quintana Roo, Chetumal, Quintana Roo, Mexico

[7]Institute of Environment, Department of Biological Sciences, Florida International University, North Miami, Florida

[8]Louisiana Universities Marine Consortium, Chauvin, Louisiana

Correspondence
Eric Angel Ramos, The Graduate Center, City University of New York, 365 Fifth Avenue, New York, NY 10016.
Email: eric.angel.ramos@gmail.com

Bottlenose dolphins (*Tursiops* spp.) display a remarkably diverse array of individual and cooperative foraging tactics across their global distribution that typically reflect local adaptations to habitat conditions and prey types (Finn et al., 2009; Mann & Sargeant, 2003; Torres & Read, 2009). Specialized foraging methods documented to date include strand feeding (Hoese, 1971; Sargeant et al., 2005), kerplunking (Connor et al., 2000; Nowacek, 2002), cooperative foraging with fishermen (Pryor & Lindbergh, 1990), driver-barrier feeding (Gazda et al., 2005), foraging in or around trawl nets (Kovacs & Cox, 2014), and using tools, particularly sponges (Krützen et al., 2014; Smolker et al., 1997) and shells (Allen et al., 2011; Wild et al., 2020).

Mud ring feeding is a tactic used by common bottlenose dolphins (*T. truncatus*) inhabiting the interior of Florida Bay (Engleby & Powell, 2019; Torres & Read, 2009). This tactic involves a single "ring-maker" dolphin (typically in a group) that swims rapidly in a circle near the seafloor along shallow inner-basin mud banks. Strong fluke kicks against the muddy substrate create a large circular mud plume or mud ring barrier used to encircle a fish school, commonly mullet (*Mugil* spp.). Once the prey are encircled, individual dolphins wait with open mouths and lunge to catch airborne fish as they attempt to flee at the water's surface (Engleby & Powell, 2019; Torres & Read, 2009). In the lower Florida Keys, bottlenose dolphins display mud plume feeding behavior where they individually create a semi-circular-shaped mud plume over seagrass beds and lunge into the plumes to capture prey (Lewis & Schroeder, 2003).

Novel remote-sensing techniques such as small unmanned aerial vehicles (UAVs or, commonly, drones) and the analysis of very high-resolution (VHR) satellite imagery (<1 m spatial resolution), have become increasingly affordable and accessible to further document the ecology and behavior of marine mammals (Cubaynes et al., 2018; McMahon et al., 2014). Small UAVs provide unique insights into marine mammal behavior by improving the ability to observe epipelagic animals underwater (Landeo-Yauri et al., 2020; Ramos et al., 2018a; Torres et al., 2018), and in particular, document foraging behaviors that are challenging to detect for boat-based observers (Ramos et al., 2020b; Torres et al., 2020). Similarly, VHR imagery has proven an effective and noninvasive method for detecting and counting marine mammals (Cubaynes et al., 2018; Guirado et al., 2019; Höschle et al., 2021). The power of large data sets of publicly accessible remote-sensing imagery coupled with automated processing techniques were shown to improve the detection of the carcasses of mass stranded whales in a remote and difficult to access region (Fretwell et al., 2019).

Here, we document the occurrence of mud ring feeding in coastal bottlenose dolphins in Chetumal-Corozal Bay in Mexico and Belize using a combination of remote sensing, boat-based, and aerial methods. The distinct circular mud ring trails (observed using VHR satellite imagery) and dolphin behaviors (observed from a small boat, planes, and small UAVs) in Chetumal-Corozal Bay are similar to those reported in Florida Bay (Engleby & Powell, 2019; Torres & Read, 2009) and we hypothesize that similarities between these shallow bay habitats drive dolphins to develop convergent foraging behaviors.

Field data on dolphin foraging were collected opportunistically from 2012 to 2019 during year-round monitoring of Chetumal-Corozal Bay in northern Belize by Wildtracks and the Sarteneja Alliance for Conservation and Development (SACD). Chetumal-Corozal Bay is a large estuarine system in the Western Caribbean Sea located on the southern coastline of the Yucatán Peninsula in northern Belize and the southeastern Mexican state of Quintana Roo (Figure 1). The brackish and marine bay covers an area of 2,560 km^2, comprised of extensive mangrove wetlands, creeks, and lagoons with sparse seagrass beds, and a predominantly sandy/rocky and muddy/silty substrate (Castelblanco-Martínez et al., 2013). Water depths are primarily <6 m in the north and <2 m near the coast (Carrillo, 2009; Castelblanco-Martínez et al., 2013).

Coastal bottlenose dolphins are the only dolphin species known to occur in Chetumal-Corozal Bay and throughout the diverse habitats along the coast of Belize, including its bays, rivers, lagoons, around mangrove cayes, and in offshore atolls (Ramos et al., 2016; Castelblanco-Martínez et al., 2021). The use of mud ring feeding by bottlenose dolphins was confirmed through direct observations of dolphin foraging activity or inferred through the detection of circular mud ring trails (i.e., circular seabed scars left as the byproduct of ring-making) in the substrate in aerial and VHR satellite imagery.

Bottlenose dolphins were opportunistically sighted from small boats (7–12 m) in Chetumal-Corozal Bay during ongoing, year-round boat-based monitoring of the Corozal Bay Wildlife Sanctuary in Belize conducted by SACD several times a month since 2012. Boat-based photographs of dolphins were collected with a Canon 60D digital SLR camera equipped with a 100–300 mm telephoto lens to identify individual dolphins. The dorsal fin of one identified dolphin was matched to photos from an existing catalog in the region (Ramos et al., 2018b, 2020a).

Aerial observations of dolphin foraging were acquired opportunistically during two manned aerial surveys flown on multiple days within a single week from February to March each year from 2011 to 2015. The 13 m single engine Cessna 206 flew a line-transect to cover the bay between altitudes of 80 m and 120 m. Experienced spotters searched for marine megafauna; logged information on sighting locations and the number of animals detected according to a standard protocol (Morales-Vela et al., 2000); and took photos of animals when possible with digital SLR cameras equipped with telephoto lenses, to confirm species identity; count the number of animals, and document behaviors.

Furthermore, dolphin behavior was filmed in one mud ring feeding event with a UAV (DJI Phantom 4 Professional quadcopter). The UAV was hand-launched from the boat and flown between altitudes of 25–35 m above the dolphins. The aircraft was equipped with a gimbal-mounted camera that filmed high definition (3,860 $\times$ 2,870 dpi) video footage and streamed a live-feed to an iPad (Apple Inc.) mounted on the remote control. Aerial videos were reviewed in QuickTime Player 10.7 (Apple Inc.) to identify mud rings and determine dolphin behavior.

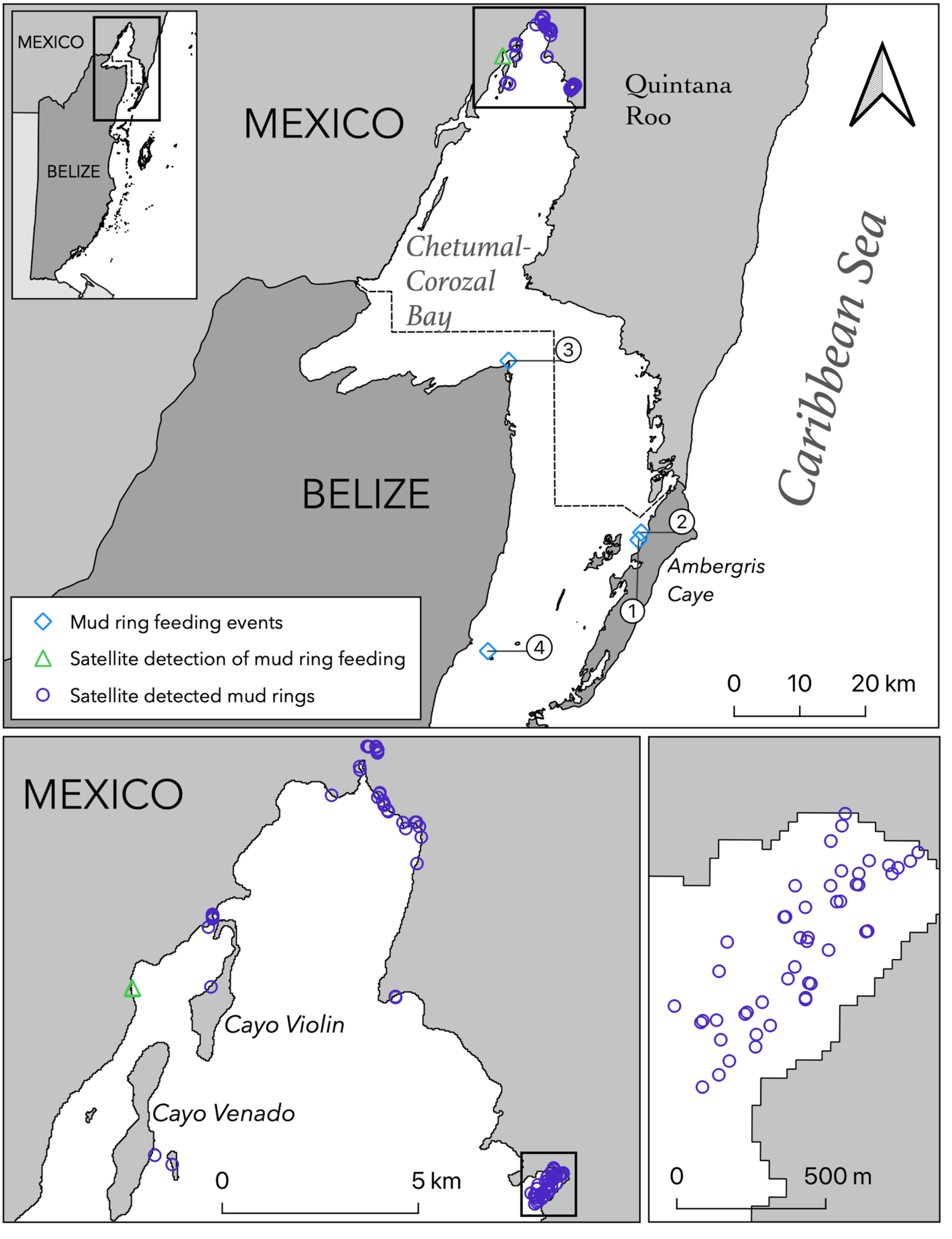

FIGURE 1 Map of Chetumal-Corozal Bay depicting the location of dolphin mud ring feeding events and mud ring trails. Mud ring feeding behavior was observed during aerial surveys, boat trips, and the flight of a small UAV. Mud ring trails ($n = 94$) and a single instance of two dolphins mud ring feeding were detected near the northwest coast of the bay in very high-resolution (VHR) satellite imagery using Google Earth. The four mud ring feeding events we documented in Belize (detailed in Table 1) are numbered by event in the top map.

TABLE 1 Details on four mud ring feeding events of bottlenose dolphins documented from 2012 to 2019 during aerial and boat-based surveys in the Belize side of Chetumal-Corozal Bay. Mud ring feeding was directly observed in three events and its occurrence was inferred from the presence of multiple mud ring trails in the seabed in imagery captured during an aerial survey. UNK = Unknown.

Event no.	Date	Time	Platform	No. dolphins present	No. dolphins foraging	No. mud ring trails
1	January 31, 2012	1000–1030	Plane	6	2	UNK
2	February 6, 2014	1000–1030	Plane	UNK	UNK	6
3	July 30, 2018	0800	Boat	20–25	UNK	UNK
4	January 19, 2019	1143	UAV	6	2	11

Publicly accessible satellite imagery was obtained and analyzed in Google Earth Pro to determine if mud ring trails and mud ring feeding behavior could be visually detected in VHR imagery of Chetumal-Corozal Bay. To identify mud ring trails and direct observations of dolphin mud ring feeding, we searched an area of 470 km^2 of satellite imagery covering Chetumal-Corozal Bay (including its interior and coastlines in Mexico and Belize) (Figure 1). To confirm that these behaviors were similar to those reported in Florida, we searched an area of 1.7 km^2 in Florida Bay, where previous reports have identified regular mud ring feeding (Engleby & Powell, 2019; Torres & Read, 2009). The Historical Imagery feature enabled review of high-resolution satellite imagery of the study area from 2006 to 2019 with minimal cloud cover and where the seabed in the bay was clearly visible. All imagery with poor resolution and excessive cloud cover was excluded from our analysis. The mosaic of satellite images in Google Earth originated from cloudless WorldView-2 satellite imagery (Maxar Technologies) including panchromatic (0.3 m spatial resolution) black and white imagery and RGB multispectral imagery (1.24 m spatial resolution).

Information on water depth and habitat type were acquired from previous studies in Chetumal-Corozal Bay (Castelblanco-Martínez, 2010; Hernández-Arana & Ameneyro-Angeles, 2011) and Florida Bay (Prager & Halley, 1997). Existing spatial data in Florida were overlaid with all detections in QGIS 3.10 to identify the bottom type at each trail. Structural characteristics of the mud ring trails were obtained by measuring the diameter of each mud ring trail by using the measurement tool in Google Earth Pro to draw a straight line between two points on opposing sides of the circular trail. The same tool was used to measure the distance of each trail to the shore by drawing a straight line between the edge of the trail closest to the shore and its nearest point on the shoreline in Chetumal-Corozal Bay. The distance of trails to mudbanks in Florida Bay was determined with the distance to hub (points) vector analysis in QGIS 3.10.

Between 2012 and 2019, mud ring feeding behavior was detected in two of 58 dolphin sightings from a small plane and two of 22 boat-based sightings within Chetumal-Corozal Bay (Table 1). Mud ring feeding behaviors were directly observed in three of these sightings, and their occurrence was inferred from the detection of multiple circular mud ring trails in the seabed in aerial imagery (Figures 2 and 3). In one boat-based sighting, a large group of dolphins was sighted foraging and creating large circular mud plumes. In the second boat-based sighting, detailed aerial observations of dolphin mud ring feeding were gathered with a small UAV (Figure 2).

In the single drone observation of mud ring feeding, an adult female (identified in 2017) and her calf were found feeding near mud ring trails (Figure 2a; see Video S1). The adult female then swam quickly and kicked her flukes against the substrate to create a mud ring (Figure 2b–d). Once the plume was nearly circular (Figure 2c), both dolphins repeatedly displayed fast swimming, pinwheels, and underwater tail slaps within the expanding sediment plume (Figure 2d). After 83 s, the dolphins exited the plume and continued to feed nearby.

Visual searches for mud ring trails in VHR satellite imagery resulted in detections of 94 trails on March 10, 2010 (Figure 1). Mud ring trails were concentrated in a 75 km^2 area of the northern side of the bay in water depths <1 m. Mud ring trails were typically found clustered together (Figure 3b, c). Most trails (53.5%) were concentrated in a sheltered delta in the northeast section of the bay in depths <1 m (Figure 1). Most of the remaining trails were found in

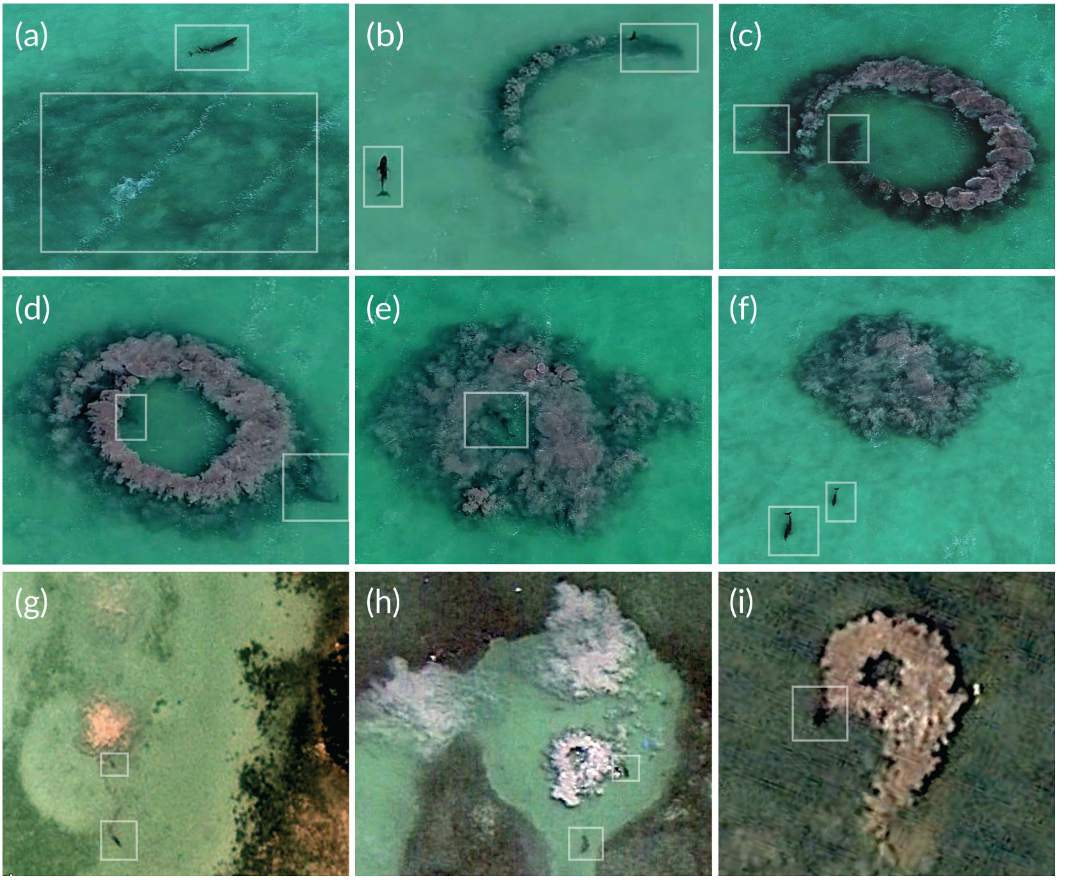

FIGURE 2 Evidence of bottlenose dolphin mud ring feeding from aerial observations with a small UAV and detections in VHR satellite imagery. The white rectangle in (a) marks the location of a mud ring trail and the dolphin nearby. In (b-i), the white rectangles mark the location of a dolphin. (a) Bottlenose dolphin mother-calf pair sighted foraging near recently made mud ring trails on 19 January 2019 (see Video S1). (b) The adult female swam in a circular pattern while hitting her flukes against the muddy substrate to create a mud ring. The calf remained outside of the plume. (c) Once the circular mud ring was complete the calf swam into the plume. (d) Both dolphins were swimming rapidly and exhibiting pinwheels and underwater tail slaps in pursuit of prey within the plume. (e) The plume expanded slowly until (f) the two dolphins emerged and began foraging in another area. (g) Two dolphins exiting a large mud plume similar to (f) in the northwest of Chetumal-Corozal Bay in VHR satellite imagery. (h & i) Bottlenose dolphins engaged in mud ring feeding near large mud plumes in Florida Bay, Florida detected in VHR satellite imagery. Image source for g–i: Google Earth, WorldView-2 satellite imagery (Maxar Technologies/ DigitalGlobe).

mangrove channels in the northern tip of the lagoon and in the northwest along the coast and shores of small cays (Figure 3b, c). In imagery from the same day, one dolphin mud ring feeding event and associated circular mud plumes were detected near the northwest coast of the bay. Two bottlenose dolphins were visible in satellite imagery exiting a recently created plume (Figure 2g). The dolphin pair were similar in appearance to the mother-calf pair previously observed mud ring feeding (Figure 2f) and swimming near similarly sized, circular plumes of sediment.

Three instances of mud ring feeding were detected in VHR satellite imagery of Florida Bay, one in imagery from March 7, 2013 (Figure 2h) and two from February 13, 2017 (Figure 2i). A total of 1,817 mud ring trails were detected in an area of ~1 km^2 in Florida Bay.

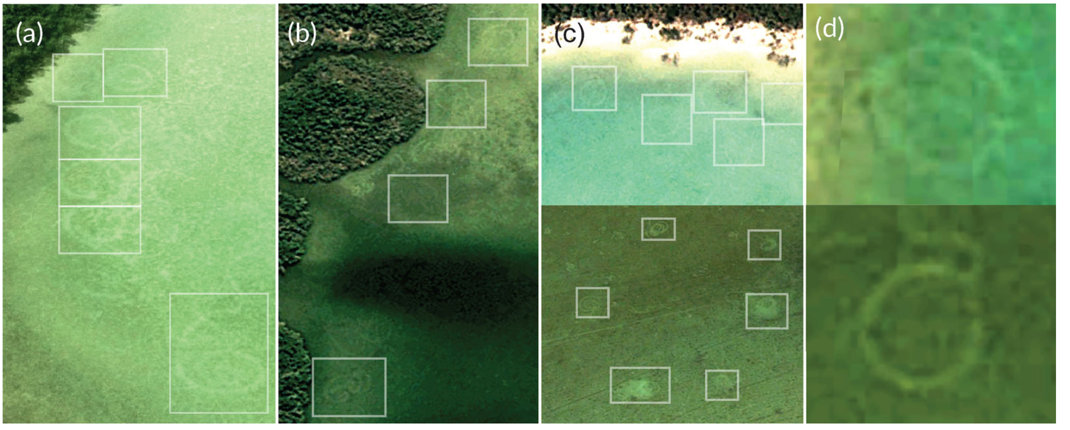

FIGURE 3 Mud ring trails in the substrate captured during aerial surveys and in searches of VHR satellite imagery of Chetumal-Corozal Bay. (a) Mud ring trails near mangrove shores photographed from a small plane in Belize. (b) Satellite detected mud ring trails in a sheltered mangrove channel in the northern tip of the bay. (c) Trails were typically found nearshore in clusters. (d) Individual mud ring trails were shaped circular or spiral and lighter in color than the surrounding substrate. Image source for b–d: Google Earth, WorldView-2 satellite imagery (Maxar Technologies/DigitalGlobe).

In Chetumal-Corozal Bay, all trails and mud ring feeding were located in muddy bottom habitats consisting of sparse algae and silt. Most trails in Florida Bay were detected in muddy substrates (50%) and seagrass beds (48.3%). The water depth at locations of all trails in Chetumal-Corozal and Florida Bays was <1 m.

The diameter of mud ring trails in Chetumal-Corozal Bay was similar (range = 4.6–14.7 m; $M = 9.7$ m; $SD = 2.2$; $n = 85$) to a random sample of trails in Florida Bay (range = 3.4–14.1 m; $M = 8.0$ m; $SD = 1.9$; $n = 100$). Mud ring trails were detected close to shore in Chetumal-Corozal Bay ($M = 106.6$ m; $SD = 97.0$; $n = 85$) and near the edges of mudbanks found within Florida Bay ($M = 221.5$ m; $SD = 286.9$; $n = 1,817$).

In this study, we report the use of mud ring feeding behaviors by coastal bottlenose dolphins in Chetumal-Corozal Bay. To our knowledge, this is the first time that satellite images have been used to document the foraging behavior of small cetaceans. In Chetumal-Corozal Bay, dolphins were directly observed mud ring feeding in small groups. Images of circular mud trails were confirmed to be the remnants of ring-making activity during Event #4 (Figure 2a) and were useful indicators of recent dolphin foraging sites that enabled us to validate the occurrence of this behavior in VHR imagery of the study site.

The mud ring feeding behavior documented in Chetumal-Corozal Bay was remarkably similar to that documented in Florida Bay (Engleby & Powell, 2019; Torres & Read, 2009), occurring nearshore in very shallow waters (<1 m) dominated by mud, sand, and silt substrates (see Video S1). We are confident that these rings have not been caused by other organisms or by boats due to their unique circular characteristics and observed associations with dolphin foraging in both regions. In Florida Bay, boat propeller scars are linear and can be easily discriminated from dolphin mud rings, particularly from the air but also from the surface. Additionally, boats do not have access to these shallow areas in Florida bay and this is not a fishing technique that is known or used in either bay. Trails were circular- or spiral-shaped in both regions, of similar sizes, and generally found in clusters. The detection of dolphin groups engaged in mud ring feeding in Chetumal-Corozal Bay suggests these dolphins may forage cooperatively, as previously reported in Florida Bay (Torres & Read, 2009). However, our observations were limited, and more data are needed to assess the importance of mud ring feeding relative to other foraging tactics in Chetumal-Corozal Bay.

Unlike mud ring feeding reported in Florida Bay where mud ring creation is tightly associated with the capture of schools of mullet, fish were not observed leaping at the end of ring creation and there was no apparent in-air pursuit of fish in our three sightings of this behavior. Repeated foraging behaviors observed by the mother-calf dolphin pair in Chetumal-Corozal prior to ring creation, immediately following the completion of the circular plume, and afterwards in the expanding sediment plume suggest that dolphins use the mud ring's sediment plume either as a means of prey disorientation or as a concentration zone to facilitate prey capture. Similar to mud plume feeding in the Florida Keys (Lewis & Schroeder, 2003), the plumes likely create a temporary visual and physical barrier capable of confusing and disorienting prey and possibly impeding collective antipredator responses (Abrahams & Kattenfeld, 1997). The behaviors we report were more similar to previously reported mud ring feeding behaviors (Engleby & Powell, 2019; Torres & Read, 2009) than to mud plume feeding (Lewis & Schroeder, 2003) due to the creation of a distinct circular ring-shaped mud plume. These observations, however, were of short duration and our sample size was too limited to draw robust conclusions about the regional similarities and differences in mud ring feeding or mud plume feeding between the bays.

Mud ring feeding dolphins in Florida Bay exclusively target species of mullet, such as white mullet (*Mugil curema*; Engleby & Powell, 2019; Torres & Read, 2009). The prey species hunted by bottlenose dolphins during mud ring feeding in Chetumal-Corozal Bay are as yet unknown and dolphin diets or regional prey preferences are yet to be investigated.

As all mud ring trails and the two dolphins mud ring feeding in Chetumal-Corozal Bay were detected in VHR satellite imagery on a single day in 2010 in an area of over 75 km^2, it was not possible to determine when these trails were created. The protected waters of the bay allow seabed disturbances to remain detectable for long periods of time, thus, we could not confirm if these trails were the result of multiple groups of dolphins foraging in different locations at the same time, or one dolphin group foraging over multiple days. Nevertheless, evidence of mud ring feeding detected suggests similarities between these behaviors in Florida and Chetumal-Corozal Bays. Satellite detections in both locations revealed instances of dolphins distinguishable against the sandy bottom as they swam near circular and spiral mud plumes. These findings suggest that VHR imagery may be of use in studies of small marine mammals in coastal habitats, as has already been demonstrated with large whales (Guirado et al., 2019).

Our study supports the idea that habitat characteristics, and/or prey types and their behavior, play a pivotal role in shaping the foraging tactics used by coastal dolphins. We have documented behavioral convergence between two geographically separate locations that share habitat characteristics, leading dolphins to develop similar strategies for prey capture. Future research should investigate the relative contributions of environmental conditions and social transmission, and their possible interplay, on convergent foraging behaviors in geographically distanced dolphin populations.

ACKNOWLEDGMENTS

We owe thanks to the GEF Small Grants Programme for funding the UAV and to all the funders supporting SACD's ongoing area management. Thanks to LightHawk for operating aerial surveys for manatees in Chetumal-Corozal Bay, Belize as part of their partnership with Wildtracks. Special thanks to SACD Park Rangers: Ruby Arrivillaga, Reynel Blanco, Roni Martinez, and Mayeli Guifarro for their help during boat-based monitoring. Thank you to Noemi Ramos for inspiring us to do this study. Thanks to the many colleagues for their valuable input on earlier versions of this manuscript. All field data analyzed in this study were gathered following all local guidelines and regulations. Data collection was permitted by the Belize Forest Department for marine mammal-related monitoring and research. This is contribution #295 from the Coastlines and Oceans Division in the Institute of Environment at Florida International University.

AUTHOR CONTRIBUTIONS

Eric Ramos: Conceptualization; data curation; formal analysis; investigation; resources; writing - original draft; writing-review & editing. **Leomir Santoya:** Conceptualization; data curation; formal analysis; methodology; resources; writing - original draft; writing-review & editing. **Joel Verde:** Conceptualization; data curation; methodology; resources; writing - original draft; writing-review & editing. **Zoe Walker:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; writing - original draft; writing-review & editing. **Nataly Castelblanco-Martínez:** Conceptualization; data curation; formal analysis; methodology; resources; writing - original draft; writing-review & editing. **Jeremy Kiszka:** Methodology; supervision; writing - original draft; writing-review & editing. **Guillaume Rieucau:** Methodology; supervision; writing - original draft; writing-review & editing.

ORCID

Eric A. Ramos https://orcid.org/0000-0003-4803-3170

Nataly Castelblanco-Martínez https://orcid.org/0000-0003-3229-8406

Jeremy J. Kiszka https://orcid.org/0000-0003-1095-8979

Guillaume Rieucau https://orcid.org/0000-0002-8968-4992

REFERENCES

Abrahams, M. V., & Kattenfeld, M. G. (1997). The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology*, *40*, 169–174. https://doi.org/10.1007/s002650050330

Allen, S. J., Bejder, L., & Krützen, M. (2011). Why do Indo-Pacific bottlenose dolphins (*Tursiops* sp.) carry conch shells (*Turbinella* sp.) in Shark Bay, Western Australia? *Marine Mammal Science*, *27*(2), 449–454. https://doi.org/10.1111/j.1748-7692.2010.00409.x

Carrillo, L., Palacios-Hernández, E., Ramírez, A. M., Morales-Vela, B. (2009). Características hidrometeorológicas y batimétricas [Hydrometeorological and bathymetric characteristics]. In J. Espinoza-Ávalos, G. A. Islebe, & H. A. Hernández-Arana (Eds.), *El sistema ecológico de la bahía de Chetumal/Corozal: costa occidental de mar Caribe* [The ecological system of Chetumal/Corozal Bay: western coast of the Caribbean Sea] (pp. 12–20). El Colegio de la Frontera Sur, Chetumal, Quintana Roo, Mexico. Available at: https://www.academia.edu/10094845/El_sistema_Ecol%C3%B3gico_de_la_Bah%C3%ADa_de_Chetumal_Corozal_Costa_Occidental_del_Mar_Caribe

Castelblanco-Martínez, D. N. (2010). *Ecología, comportamiento y uso de hábitat de manatíes en la Bahía de Chetumal* [Manatee ecology, behavior and habitat use in Chetumal Bay] [Doctoral dissertation]. El Colegio de la Frontera Sur, Chetumal, Quintana Roo, Mexico. http://bibliotecasibe.ecosur.mx/sibe/book/000050024

Castelblanco-Martínez, D. N., Padilla-Saldívar, J., Hernández-Arana, H. A., Slone, D. H., Reid, J. P., & Morales-Vela, B. (2013). Movement patterns of Antillean manatees in Chetumal Bay (Mexico) and coastal Belize: A challenge for regional conservation. *Marine Mammal Science*, *29*(2), E166–E182. https://doi.org/10.1111/j.1748-7692.2012.00602.x

Castelblanco-Martínez, D. N., Ramos, E. A., Kiszka, J. J., Blanco-Parra, M. P., Padilla-Saldívar, J. A., García, J., & Niño-Torres, C. A. (2021). Spatial patterns of shark-inflicted injuries on coastal bottlenose dolphins in the Mesoamerican Reef System. *Studies on Neotropical Fauna and Environment*, 1–7. https://doi.org/10.1080/01650521.2021.1877391

Connor, R. C., Heithaus, M. R., Berggren, P., & Miksis, J. L. (2000). "Kerplunking": Surface fluke-splashes during shallow-water bottom foraging by bottlenose dolphins. *Marine Mammal Science*, *16*(3), 646–653. https://doi.org/10.1111/j.1748-7692.2000.tb00959.x

Cubaynes, H. C., Fretwell, P. T., Bamford, C., Gerrish, L., & Jackson, J. A. (2018). Whales from space: Four mysticete species described using new VHR satellite imagery. *Marine Mammal Science*, *35*(2), 466–491. https://doi.org/10.1111/mms.12544

Engleby, L. K., & Powell, J. R. (2019). Detailed observations and mechanisms of mud ring feeding by common bottlenose dolphins (*Tursiops truncatus truncatus*) in Florida Bay, Florida, U.S.A. *Marine Mammal Science*, *35*(3), 1162–1172. https://doi.org/10.1111/mms.12583

Finn, J., Tregenza, T., & Norman, M. (2009). Preparing the perfect cuttlefish meal: complex prey handling by dolphins. *PLoS ONE*, *4*(1), e4217. https://doi.org/10.1371/journal.pone.0004217

Fretwell, P. T., Jackson, J. A., Ulloa Encina, M. J., Häussermann, V., Perez Alvarez, M. J., Olavarría, C., & Gutstein, C. S. (2019). Using remote sensing to detect whale strandings in remote areas: The case of sei whales mass mortality in Chilean Patagonia. *PLoS ONE*, *14*(10), e0222498. https://doi.org/10.1371/journal.pone.0222498

Gazda, S. K., Connor, R. C., Edgar, R. K., & Cox, F. (2005). A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1559), 135–140. https://doi.org/10.1098/rspb.2004.2937

Guirado, E., Tabik, S., Rivas, M. L., Alcaraz-Segura, D., & Herrera, F., 2019. Whale counting in satellite and aerial images with deep learning. *Scientific Reports*, *9*(1), 1–12. https://www.nature.com/articles/s41598-019-50795-9

Hernández-Arana, H. A., & Ameneyro-Angeles, B. (2011). Benthic biodiversity changes due to the opening of an artificial channel in a tropical coastal lagoon (Mexican Caribbean). *Journal of the Marine Biological Association of the United Kingdom*, *91* (5), 969–978. https://doi.org/10.1017/S0025315410002043

Hoese, H. D. (1971). Dolphin feeding out of water in a salt marsh. *Journal of Mammalogy*, *52*(1), 222–223. https://doi.org/10.2307/1378455

Höschle, C., Cubaynes, H.C., Clarke, P.J., Humphries, G., & Borowicz, A. (2021). The potential of satellite imagery for surveying whales. *Sensors*, *21*(3), 963. https://doi.org/10.3390/s21030963

Kovacs, C., & Cox, T. (2014). Quantification of interactions between common bottlenose dolphins (*Tursiops truncatus*) and a commercial shrimp trawler near Savannah, Georgia. *Aquatic Mammals*, *40*(1), 81–94. https://doi.org/10.1578/AM.40.1.2014.81

Krützen, M., Kreicker, S., MacLeod, C. D., Learmonth, J., Kopps, A. M., Walsham, P., & Allen, S. J. (2014). Cultural transmission of tool use by Indo-Pacific bottlenose dolphins (*Tursiops* sp.) provides access to a novel foraging niche. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1784), 20140374. https://doi.org/10.1098/rspb.2014.0374

Landeo-Yauri, S. S., Ramos, E. A., Castelblanco-Martínez, D. N., Niño-Torres, C. A., & Searle, L. (2020). Using small drones to photo-identify Antillean manatees: a novel method for monitoring an endangered marine mammal in the Caribbean Sea. *Endangered Species Research*, *41*, 79–90. https://doi.org/10.3354/esr01007

Lewis, J. S., & Schroeder, W. W. (2003). Mud plume feeding, a unique foraging behavior of the bottlenose dolphin in the Florida Keys. *Gulf of Mexico Science*, *21*(1), 9. https://doi.org/10.18785/goms.2101.09

Mann, J., & Sargeant, B. (2003). Like mother, like calf: the ontogeny of foraging traditions in wild Indian ocean bottlenose dolphins (*Tursiops* sp.). In D. M. Fragaszy & S. Perry (Eds.), *The biology of traditions: Models and evidence* (pp. 237–266). Cambridge University Press.

McMahon, C. R., Howe, H., Van Den Hoff, J., Alderman, R., Brolsma, H., & Hindell, M. A. (2014). Satellites, the all-seeing eyes in the sky: counting elephant seals from space. *PLoS ONE*, *9*(3), e92613. https://doi.org/10.1371/journal.pone.0092613

Morales-Vela, B., Olivera-Gómez, D., Reynolds, J. E., III, & Rathbun, G. B. (2000). Distribution and habitat use by manatees (*Trichechus manatus manatus*) in Belize and Chetumal Bay, Mexico. *Biological Conservation*, *95*(1), 67–75. https://doi.org/10.1016/S0006-3207(00)00009-4

Nowacek, D. (2002). Sequential foraging behaviour of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, FL. *Behaviour*, *139*(9), 1125–1145. https://www.jstor.org/stable/4535977

Prager, E. J., & Halley, R. B. (1997). *Florida Bay bottom types*. (Open-File Report 97-526). U. S. Geological Survey Publication. https://doi.org/10.3133/ofr97526

Pryor, K., & Lindbergh, J. (1990). A dolphin-human fishing cooperative in Brazil. *Marine Mammal Science*, *6*(1), 77–82. https://doi.org/10.1111/j.1748-7692.1990.tb00228.x

Ramos, E. A., Castelblanco-Martínez, D. N., Collom K. A, Barragán-Barrera, D. C., Garcés-Cuartas, N., Prezas-Hernández, B., Anderson, D., Jeffords, A., Niño-Torres, C. A., Carey, B., & Carey, T. (2020a). Where the wild things are: A dedicated vessel-based expedition for marine mammals in the offshore of Belize. *Cashiers de Biologie Marine*, *61*, 447–457. https://doi.org/10.21411/CBM.A.58164306

Ramos, E. A., Castelblanco-Martínez, D. N., Garcia, J., Rojas Arias, J., Foley, J. R., Audley, K., Waerebeek, K. V., & Van Bressem, M. F. (2018b). Lobomycosis-like disease in common bottlenose dolphins *Tursiops truncatus* from Belize and Mexico: bridging the gap between the Americas. *Diseases of Aquatic Organisms*, *128*(1), 1–12. https://doi.org/10.3354/dao03206

Ramos, E. A., Castelblanco-Martínez, D. N., Niño-Torres, C. A., Jenko, K., Gomez, N. A. (2016). A review of the aquatic mammals of Belize. *Aquatic Mammals*, *42*(4), 476–493. https://doi.org/10.1578/AM.42.4.2016.476

Ramos, E. A., Kiszka, J. J., Pouey-Santalou, V., & Audley, K. (2020b). Food sharing in rough-toothed dolphins off the southwestern Pacific coast of Mexico. *Marine Mammal Science*, *37*(1), 352–360. https://doi.org/10.1111/mms.12727

Ramos, E. A., Maloney, B., Magnasco, M. O., & Reiss, D. (2018a). Bottlenose dolphins and antillean manatees respond to small multi-rotor unmanned aerial systems. *Frontiers in Marine Science*, *5*, 316. https://doi.org/10.3389/fmars.2018.00316

Sargeant, B. L., Mann, J., Berggren, P., & Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology*, *83*(11), 1400–1410. https://doi.org/10.1139/z05-136

Smolker, R., Richards, A., Connor, R., Mann, J., & Berggren, P. (1997). Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.): A foraging specialization involving tool use? *Ethology*, *103*(6), 454–465. https://doi.org/10.1111/j.1439-0310.1997.tb00160.x

Torres, L. G., & Read, A. J. (2009). Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. *Marine Mammal Science*, *25*(4), 797–815. https://doi.org/10.1111/j.1748-7692.2009.00297.x

Torres, L. G., Barlow, D. R., Chandler, T. E., & Burnett, J. D. (2020). Insight into the kinematics of blue whale surface foraging through drone observations and prey data. *PeerJ*, *8*, e8906. https://doi.org/10.7717/peerj.8906

Torres, L. G., Nieukirk, S. L., Lemos, L., & Chandler, T. E. (2018). Drone up! Quantifying whale behavior from a new perspective improves observational capacity. *Frontiers in Marine Science*, *5*, 319. https://doi.org/10.3389/fmars.2018.00319

Wild, S., Hoppitt, W. J., Allen, S. J., & Krützen, M. (2020). Integrating genetic, environmental, and social networks to reveal transmission pathways of a dolphin foraging innovation. *Current Biology*, *30*(15), 3024–3030. https://doi.org/10.1016/j.cub.2020.05.069

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Ramos, E. A., Santoya, L., Verde, J., Walker, Z., Castelblanco-Martínez, N., Kiszka, J. J., & Rieucau, G. (2021). Lords of the Rings: Mud ring feeding by bottlenose dolphins in a Caribbean estuary revealed from sea, air, and space. *Marine Mammal Science*, 1–10. https://doi.org/10.1111/mms.12854