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SHORT COMMUNICATION

INTRASPECIFIC AGGRESSION TOWARDS COMMON BOTTLENOSE DOLPHIN CALVES, NORTHERN GULF OF MEXICO

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INTRODUCTION

Infanticide has been widely documented throughout the animal kingdom, and is generally viewed as an evolved, or adaptive behavior for the aggressor (Hrdy 1979). In his review of mammalian infanticide, Ebensperger (1998) identified 91 terrestrial mammals observed to purposely kill young conspecifics. Hypotheses for the occurrence of infanticide include: 1) cannibalism (predation), 2) elimination of potential competition (resource competition), 3) increased sexual access for males (sexual selection), 4) elimination of defective, ill-timed, or unrelated young (adoption-avoidance), and 5) non-adaptive, pathological infanticide (social pathology) that does not provide a clear survival advantage (Hrdy 1979, Ebensperger 1998). Marine mammal infanticide observed among pinniped species and polar bears (Ursus maritimus) appears to be driven by nutritional and sexual-access rewards derived from the consumption or elimination of the infant (Taylor et al. 1985, Campagna et al. 1988). Infanticide motivated by increased sexual access to females with calves, or the elimination of potential genetic competition has also been proposed for delphinids. Examples include killer whales (Orcinus orca, Towers et al. 2018), Indo-Pacific humpback dolphins (Sousa chinensis, Zheng et al. 2016), Guiana dolphins (Sotalia guianensis, Nery and Simao 2009), and bottlenose dolphins (Tursiops spp., Dunn et al. 2002, Scott et al. 2005, Kaplan et al. 2009, Robinson 2014, Perrtree et al. 2016). However, reports of dolphin aggression towards calves are infrequent, and accounts of confirmed infanticide are rarer still. To increase our understanding of the socio-behavioral context of these aggressive interactions, Dunn et al. (2002) recommend reporting such observations. Here, we describe an incident of conspecific aggression towards a calf in a small group of common bottlenose dolphins (Tursiops truncatus) in Sabine Lake on the Texas-Louisiana border, and relate some details of 36 other reports of bottlenose dolphin calf-directed aggression observed in the northern Gulf of Mexico (GOM).

MATERIALS AND METHODS

During August 2016 and February/June 2017, photographic identification (photo-ID) surveys (Würsig and Würsig 1977) were conducted in Sabine Lake (~240 km², mean depth 2 m, USEPA 1999) on the Texas-Louisiana border in the northwestern GOM. Surveys were conducted to examine common bottlenose dolphin spatio-temporal distribution patterns and estimate abundance for the Sabine Lake bottlenose dolphin stock (Hayes et al. 2019). Survey methods were consistent with Melancon et al. (2011) and results are reviewed in detail in Ronje et al. (2020). We documented dolphins, with few exceptions, in the Sabine Pass Channel, adjacent coastal waters, and the extreme southern end of Sabine Lake. The individual dorsal fin photographs collected were included in a FinBase catalog (Adams et al. 2006) that houses photo-ID data for estuarine and coastal waters used by multiple purported estuarine bottlenose dolphin stocks in the northwestern GOM (NorTex catalog, Ronje et al. 2020).

During the Sabine Lake surveys, we observed one case of apparent intraspecific aggression toward a bottlenose dolphin calf that resembled the accounts of attempted infanticide noted by other researchers. Given that observations of attempted infanticide are rare, we describe in detail the aggressive interaction observed during our photo-ID survey. To understand the frequency and broader context of these types of observations, we reviewed the literature and surveyed other bottlenose dolphin researchers focused on northern GOM waters. We contacted 10 non-profit, academic, state, or federal agencies with bottlenose dolphin research programs representing photo-ID studies from all northern GOM states (Texas, Louisiana, Mississippi, Alabama, Florida) including 18 bay, sound, and estuarine stock areas for bottlenose dolphins as defined by the National Marine Fisheries Service (Hayes et al. 2019). Where applicable, we asked the respondents to query the sighting notes in their databases (e.g., using keywords) for possible calf-directed aggression events and we synthesized behavioral descriptions relative to observations during our surveys.

RESULTS AND **D**ISCUSSION

During a bottlenose dolphin survey on 24 June 2017 we encountered a dolphin group traveling upstream in the Sabine Pass Channel (29.7009'N, -93.8442'W) against an ebbing tide. Environmental conditions during this sighting were water depth 5.1 m, water temperature 29.3°C, salinity 9.5, and Beaufort sea state 2. Photo-ID analysis revealed 10 unique dorsal fins in the sighting, belonging to 9 adults and one calf. Group cohesiveness (the estimated greatest distance between individuals) was < 10 m except for one adult/ calf pair that consistently maintained proximity to each other (< 1 m distance). The calf was a young-of-the-year estimated at about 1/3 the length of the adult (presumed mother; hereafter referred to as the "mother"). The calf presented neonatal skin folds and surfaced synchronously in the echelon position (beside and slightly behind an adult; Fellner et al. 2013) to the mother. We documented the initial behavioral state of the group as "slow travel" towards Sabine Lake. Immediately after the group encounter began, we observed a single dolphin partially breaching the surface of the water with a kingfish (Menticirrhus spp.) in its mouth. This dolphin repeatedly cleared the surface of the water, released the fish into the air (or "tossed" it), retrieved it, and resumed swimming with the fish in its mouth. We observed this pattern 5 times in the first 11 minutes of the sighting when our attention was then diverted to a different behavioral interaction between an adult-sized dolphin and the mother/calf pair.

During the next behavior sequence, the adult-sized dolphin (hereafter referred to as the "aggressor") swam between and separated the calf from its mother, rammed the calf with its rostrum, and dove on top of the calf in an apparent attempt to submerge it (Figures 1A–C). The aggressor then forcefully pushed the calf up out of the water, resulting in the calf being "tossed" in the air (Figure 2), and then rammed the calf when it fell back to the surface of the water. The mother maintained proximity (about ≤ 3 m) to the calf and moved between the calf and the aggressor during the attack. We could not completely describe the mother's behavior in these interactions because she was often out of view underwater. The observed calf-directed aggression lasted < 1 min, and during that short span of time photographs indicated the calf was alternately submerged and tossed from the water at least 6 times before the attack subsided. Immediately post--attack, the calf resumed the echelon position alongside the mother, but exhibited noticeably shorter inter-breath intervals and a pronounced lack of coordinated swimming (e.g., side-to-side rocking that was not observed prior to the attack). The mother/calf pair continued to swim in the same direction as the rest of the group, but appeared to slow their pace

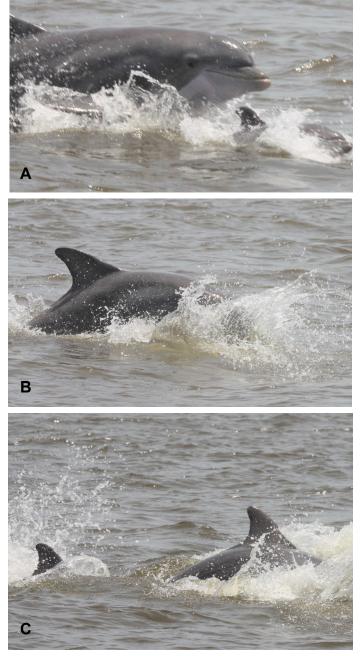


FIGURE 1. Example sequence of events as the aggressor dolphin attempts to ram and submerge the calf. A. Aggressor dolphin arches out of the water towards the calf. B. Aggressor dolphin begins dive while possibly ramming or attempting to submerge calf. C. Presumed mother of the calf being attacked is on the left, while the aggressor dolphin continues its attack.

relative to their pre—attack swimming speed, allowing some distance (≥ 100 m) between them and the original group that continued to swim upstream in the Sabine Pass Channel. We continued to monitor the mother/calf pair at about 25 m distance before ending the sighting with a total encounter time of 23 min. For the remainder of the sighting, the mother/calf pair did not close the distance to the original group and the calf continued frequent respirations. The aggressor changed swim direction after the attack subsided and did



FIGURE 2. Common bottlenose dolphin calf tossed clear of the water's surface by an aggressor dolphin.

not appear in subsequent photographs of the group, but it is not clear if it left the group entirely or remained undetected. With the exception of the mother/calf pair and one other dolphin, each individual in the group was previously photographed in summer 2016/2017. We previously encountered 4 individuals, including the fish—tossing dolphin and the aggressor, in Sabine Lake during February 2017.

The aggressor dolphin was photo-identified during 3 encounters in 2017, but its fin was marginally distinct relative to other adult dolphins in the associated catalog. Dolphins tend to accumulate unique notches on the trailing edge of their dorsal fin with age, and the few trailing edge notches on the aggressor may indicate the animal was not advanced in years (Pleslić et al. 2018), but its relative size (estimated > 250 cm) suggests an adult age class (Read et al. 1993). While the sex of the aggressor was not determined during surveys, subadult or adult males have been identified as the aggressor in 84% of intraspecific aggressive interactions among delphinids (Scott et al. 2005), suggesting a high likelihood that the aggressor was male. The sexual selection hypothesis predicts that killing the offspring of a competitor reduces the reproductive success of that competitor, and increases the aggressor's opportunity to breed, thereby conferring a reproductive advantage to the aggressor (Hrdy 1979). Female cetaceans with nursing calves are not reproductively available, but they may return to estrus relatively quickly (within 1-2 weeks) if a calf is lost (Connor et al. 1996), thus providing males with an additional reproductive option. The intraspecific calf-directed aggression described here, and the apparent effort of the mother to intervene in the attack on her calf, are similar to field reports of other attacks on dolphin calves (Kaplan et al. 2009, Robinson 2014). Perrtree et al. (2016) distinguished their observed bottlenose dolphin calf-directed aggression as unique due to "submergence behavior" that differed from the calf tossing described in other reports. Our observations involved both forced calf submergence and ejections from the water, similar to Kaplan et al. (2009), indicating these actions may be more common behavioral sequences than previously thought. We conducted only one additional survey in Sabine Lake after this event and did not observe the mother/calf pair again. Although the calf initially survived the attack described here, the long—term survival status of the calf is unknown, and it is possible the calf later succumbed to internal injuries incurred during the attack. Aggression toward a dolphin calf has reportedly resulted in death as much as 7 months after the event due to severe spinal deformity (Robinson 2014).

The co-occurrence of fish tossing and calf-directed aggression by 2 members of a focal group has not been previously reported. The fish-tossing dolphin flanked the mother/calf pair before the attack and continued to swim with fish in-mouth (fish oriented perpendicular to its rostrum) and toss the fish while the aggressor was attacking the calf. Finally, the fish-tossing dolphin flanked the mother/calf pair shortly after the attack (opposite the calf) and continued the fish carrying/tossing after the mother/calf pair fell behind the group, never having appeared to tear the fish apart or make other obvious efforts to ingest the fish. Fish tossing is a common behavior by bottlenose dolphins and is likely a food processing tactic used to disable or "tenderize" fish prior to swallowing (Bloom 1991, Kuczaj and Yeater 2007, Miller et al. 2010, Kumar et al. 2012), but has also been hypothesized as a "play" behavior (Shane 1977). Because no other dolphins in the group appeared to be foraging (e.g., travel was consistent and without localized dives or quick changes in direction indicative of chasing fish), it seems feasible that the fish observed in this study served as the "object" in object-oriented play.

Review of the literature and data from 10 researchers representing 8 organizations in the northern GOM resulted in additional evidence of calf-directed aggression. We found 2 references describing similar aggressive behavior towards bottlenose dolphin calves in the northern GOM. Shane (1987) observed bottlenose dolphins "rough housing" on 5 occasions during photo-ID surveys in Sanibel Island, FL, describing "rough housing" as "vigorously tumbling with and tossing small or newborn calves," and indicated the adult bottlenose dolphins used their rostrums and flukes to toss the calves into the air. Shane (1987) also observed similar behavior in captive bottlenose dolphins and in freeranging bottlenose dolphins in Texas waters. Contrary to our observation, the calves subjected to the rough treatment did not appear to try and escape in either context (Shane 1987, 1988).

Four organizations contributed 32 records collected during small–boat fieldwork and 2 records collected during stranding recovery that potentially demonstrate calf–directed aggression (Table 1). These reports (and percentage of total records queried) were from Galveston Bay, TX (0.5%, n = 1,005, pers. comm. K. Fazioli, Galveston Bay Dolphin Research Program, Galveston, TX), Barataria Bay, LA (0.1%, n = 2,635, pers. comm. T. Speakman, National Marine Mammal Foundation, Charleston, SC), Perdido Bay, AL (1.3%, n = 75, pers. comm. T. Bouveroux, Dauphin Island Sea Lab, Dauphin Island, AL), and Sarasota Bay, FL (0.1%, n = 24,165, pers. comm. J. Allen, Chicago Zoological Society's Sarasota Dolphin Research Program, Sarasota, FL). We also obtained necropsy and histopathology reports from the Alabama Marine Mammal Stranding Network (ALMMSN) that included 2 cases of trauma (5.7% of total calves and perinates having gross necropsies and histology and 1 calf, 133 cm and 1 perinate, 112.5 cm, pers. comm. M. Russell, Dauphin Island Sea Lab, Dauphin Island, AL) in young bottlenose dolphins. These data were consistent with confirmed or suspected infanticide descriptions of trauma (Patterson et al. 1998, Dunn et al. 2002). The NorTex catalog included 3 additional sightings where possible calf-directed aggression was observed, including 2 observations off the Louisiana coast near the Sabine Pass Channel, and one in Galveston Bay, TX for a percentage of total sightings queried = 0.61% (n = 494).

Reports from the Chicago Zoological Society's Sarasota Dolphin Research Program (SDRP) further indicate certain individuals may exhibit a possible pattern of aggressive behavior. The SDRP identified 15 individual bottlenose dolphins out of 24 observations of aggressive interactions as aggressors, and 33% of those individuals were involved in 46% of the sightings. All aggressors in the SDRP records were identified as male except for 2, and both females (ID# F277, \sim 5 – 6 years of age and HWK3, ~7 years of age) were observed harassing calves alongside males. Notably, HWK3 was observed "chasing calves of Tampa (Bay) transients" alongside F173, a male identified as an aggressor or present during observed calf-directed aggression in three separate incidents (italics added for clarity). Individual F173 was also carrying a fish in-mouth, like the individual we observed in Sabine Lake, shortly before "chasing" a "porpoising" (fast-traveling) mom/ calf pair across the bay. This individual was accompanied by another male (F238) in what was described as "coordinated and synchronous" behavior. Additionally, SDRP reports included aggressive attacks on a calf (ID# 1254) observed on 2 different occasions (4 Nov 2015 and 20 May 2016) with the same male present (ID # BRD3). Of the male bottlenose dolphins specifically identified as aggressors in the SDRP database, the ages ranged from 11 – 26 years (age estimated from observed year of birth) and the mean (± SD) age was 16.7 (± 4.3) years.

Inconsistent protocols and terminology for documenting opportunistic behavioral observations in the field limit estimating the prevalence of bottlenose dolphin infanticide from the results of this data query. Agonistic behavioral interactions, often rapid and short—lived, are obfuscated by splashing or are underwater, and the focal individuals and interactions may be difficult to visually track and photograph. Such opportunistic observations are often ancillary to the primary research goals of some population studies (e.g., photo—ID mark—recapture for abundance estimation), thus research teams may not be in a position to conduct focal—follows and collect detailed behavioral observations in the field for prolonged periods. Describing and attempting

Agency	Study area	Date range	Total records queried	Calf-directed aggression observations (% of total)	Query keywords
Dauphin Island Sea Lab	Perdido Bay AL	2010 - 2020	75	1 (1.3%)	N/A
Alabama Marine Mammal Stranding Network	Mobile Bay AL	2010 - 2020	35	2 (5.7%)	N/A
National Marine Mammal Foundation	Barataria Bay LA	2010 - 2020	2,635	2 (0.1%)	neonate, calf, aggression, infanticide
National Marine Fisheries Service/ Texas Marine Mammal Stranding					
Network	North Texas Coast	2014 - 2020	494	3 (0.6%)	aggress*, toss*, infanticide, calf, neonate, social
Galveston Bay Dolphin Research Program	Galveston Bay TX	2013 - 2020	1,005	5 (0.5%)	aggress*, toss*, bash*, yoy, calf
Chicago Zoological Society's Sarasota Dolphin Research Program	Sarasota Bay FL	1989 - 2020	24,165	24 (0.1%)	agg*, chas*, cal*, chas*, yoy, hurt*, kill*, beat*, heav*, social, bite, push, shove, agon*, throw, kick, charge, back-ender*

to define aggressive interactions may be hindered by a low vantage point from a small research vessel with relatively poor maneuverability. One published account of possible attempted infanticide in a bottlenose dolphin group was aided by use of an aerial blimp that captured video footage (Kaplan et al. 2009). In recent years, unmanned aerial vehicle (UAV) technology has become a highly effective tool for observing and analyzing behavior in cetaceans (Torres et al. 2018), including the mating behavior and mother/calf interactions of small delphinids (Weir et al. 2018, Orbach et al. 2020). The interactions in Sabine Lake reported here were brief ($\leq 1 \text{ min}$); however, it is possible the proximity of the research boat to the sighting influenced the behavior of the dolphins and the interactions were prematurely truncated. The presumed attempted infanticide reported by Kaplan et al. (2009) lasted for 51 minutes, and the use of UAVs to record high quality video without unduly influencing the behavior of the dolphins may be an additional tool to consider improving opportunistic boat-based observations of rarely reported behavior. If water clarity and field conditions are suitable, researchers might consider the routine use of UAVs to record such behavioral interactions when encountered.

During our review of survey results, it was difficult to maintain our definition of "calf–directed aggression" as strictly related to attempted infanticide, as some reports used "aggression" in a socio–sexual context or to describe other aggressive interactions. While some reports we reviewed explicitly stated, "attempted infanticide" or described adult males attempting to separate mother/calf pairs with the presumed intention of harassing the calf, it is not possible to assign motive to the observed behaviors. The word "toss" or "tossing" was used to describe behavior consistent with presumed attempted infanticide, but numerous instances of the words "aggressive", "harass," "chase," or "push," were possibly indicative of, but not necessarily descriptors of, attempted infanticide, leaving a wide margin of interpretation for the observed behavior in these reports. The diverse keywords used by researchers to query their databases in our survey indicate the variety of terms that may be used to record aggressive interactions (Table 1). Consistent terminology to describe behavior would have been helpful to classifying perceived aggressive behavior as potentially attempted infanticide, or some other interaction interpreted as aggressive. It would also be useful to develop an ethogram with objective terminology to catalog behaviors observed during encounters to enable comparison among studies. Despite the variable behavioral descriptions for aggressive interactions among the reports we reviewed, this information can be used to guide and promote future research in calf-directed aggression behavior. We encourage standardization of behavioral observation recording methods, and targeted research to quantify social behavior in bottlenose dolphins not only in the northern GOM but also throughout their range.

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