

eScholarship

International Journal of Comparative Psychology

Title

Behavioural responses of Irrawaddy dolphins (*Orcaella brevirostris*) to a dead conspecific

Permalink

<https://escholarship.org/uc/item/68h1b3rs>

Journal

International Journal of Comparative Psychology, 34(0)

ISSN

0889-3675

Authors

Jones, Amy L

Tubbs, Sarah E

Croxford, Eve M

Publication Date

2021-07-27

DOI

10.46867/ijcp.2021.34.00.04

Copyright Information

Copyright 2021 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed



Behavioral Responses of Irrawaddy Dolphins (*Orcaella brevirostris*) to a Dead Conspecific

Amy L. Jones¹, Sarah E. Tubbs¹, and Eve M. Croxford²

¹*Marine Conservation Cambodia*

²*University of Sheffield, United Kingdom*

Cetacean behavior has long attracted scientific attention as humans endeavor to discover what makes these mammals so emotive and engaging. To date, much of this research has focussed on abundant and widely distributed cetacean species such as bottlenose dolphins (*Tursiops truncatus*) and humpback whales (*Megaptera novaeangliae*). As an endangered and often evasive species, research regarding Irrawaddy dolphin (*Orcaella brevirostris*) behavior is limited. This study uses data collected by The Cambodian Marine Mammal Conservation Project, to investigate the behavioral responses of Irrawaddy dolphins towards a dead conspecific. During a routine boat survey of Cambodia's Kep Archipelago, the carcass of an adult female Irrawaddy dolphin was recovered and attached to the stern of the research vessel and promptly towed to the research island for further examination. During this survey, there was a four-fold increase in the number of Irrawaddy dolphin groups observed compared to the seasonal average (post-monsoon), in addition to an atypically positive response towards the research vessel and an atypical increase in the number of behavioral events observed. These behavioral variations were believed to be in response to the towed dead conspecific. The authors propose future dedicated research to assess the complexity of wild Irrawaddy dolphin behavior, cognition, and awareness to robustly exemplify the species' apparent sentience and intelligence.

Keywords: atypical behavior, behavioral responses, cetacean, comparative thanatology, curiosity, dead conspecific, Irrawaddy dolphin, *Orcaella brevirostris*

As higher-order thinking mammals with large brains, it is widely accepted that cetaceans are intelligent beings capable of complex cognition and social bonding (Connor, 2007; Herman, 2006; Marino et al., 2007; Whitehead & Rendell, 2015; Wursig, 2009). Behavioral observations allow preliminary insight into the complex inter and intraspecific interactions of cetaceans. These observations underpin our understanding of cetacean society, culture, and cognition (Whitehead & Rendell, 2015).

Behavioral responses of delphinids towards living conspecifics has been well-documented worldwide (Mann et al., 2000; Perrin, 2009; Pryor & Norris, 1991; Schusterman et al., 1986; Shane et al., 1986). While the behavioral responses of delphinids towards dead and dying conspecifics have only been documented in 10 of the 42 delphinid species: Atlantic spotted dolphins (*Stenella frontalis*; Alves et al., 2015), Australian humpback dolphins (*Sousa sahulensis*; Reggente et al., 2016), bottlenose dolphins (*Tursiops truncatus*; Diaz Lopez, 2020), Indo-pacific bottlenose dolphins (*Tursiops aduncus*; Reggente et al., 2016), Indo-pacific humpback dolphins (*Sousa chinensis*; Bearzi et al., 2018), killer whales (*Orca orcinus*; Reggente et al., 2016), long-beaked common dolphins (*Delphinus capensis*; Park et al., 2013), Risso's dolphins (*Grampus griseus*; Reggente et al., 2016), short-finned pilot whales (*Globicephala macrohynchus*; Reggente et al., 2016), and spinner dolphins (*Stenella longirostris*; Reggente et al., 2016); and yet, these behavioral responses are still poorly understood (Reggente et al., 2016). Previously, behavioral responses towards dead conspecifics have been attributed to epimeletic behavior (Alves et al., 2015; Caldwell & Caldwell, 1966; Cockcroft & Sauer, 1990; Connor & Smolker, 1990; Fertl & Schiro, 1994; Harzen & Santos, 1992; Kilborn, 1994; Lodi, 1992; Santos et al., 2000; Smith & Sleno, 1986), grief (Bearzi et al., 2018), mate-guarding (Dudzinski et al., 2003), infanticide (Dunn et al., 2002; Diaz Lopez et al., 2018; Patterson et al., 1998; Towers et al., 2018), empathy (Frohoff, 2011; Kuczaj et al., 2001; Nakahara et al., 2016; Perez-Manrique & Gomila, 2018; Reggente et al., 2016), inclusive fitness (Bearzi et al., 2017), and personality (Diaz Lopez, 2020; Kuczaj et al., 2012).

The Irrawaddy dolphin (*Orcaella brevirostris*) is a marine and freshwater dwelling species, classified as “Endangered” by the IUCN (Minton et al., 2017), with a discontinuous and fragmented distribution across the Indo-Pacific region (Perrin et al., 1995; Stacey & Arnold, 1999). Irrawaddy dolphins face threats from habitat loss and degradation, bycatch, pollution, and live capture for aquaria (Dolar et al., 2002; Food and Agriculture Organization of the United Nations, 1978; Jaaman et al., 2009; Kannan et al., 2005; Minton et al., 2017; Perrin et al., 2005; Peter, Ngeian, et al., 2016; Peter, Poh, et al., 2016; Reeves et al., 2003; Smith et al., 2008; Smith et al., 2004; Smith & Jefferson, 2002). At present, literature on Irrawaddy dolphin behavior is sparse and focuses on habitat use (de la Paz et al., 2020; Ponnampalam et al., 2013; Kuit et al., 2019; Stacey & Hvenegaard, 2002; Sutaria et al., 2019; Tubbs et al., 2020), dolphin-vessel interactions (D’Lima et al., 2014; Hashim & Jaaman, 2011 Mahmud et al., 2018), interspecific delphinid interactions (Kummaruzzan & Jaaman 2013; Jaaman, 2010), foraging and mating behaviors (Ponnampalam et al., 2013; Stacey & Hvenegaard, 2002), and acoustic behavior (Bahl et al., 2006; Hoffman et al., 2017; Inoue et al., 2007; Sugimatsu et al., 2013; Tubbs & Keen, 2019). Literature regarding Irrawaddy dolphin behavioral responses towards dead and dying conspecifics is non-existent.

Cambodia’s Kep Archipelago is home to a population of Irrawaddy dolphins (Tubbs et al., 2019, Tubbs et al., 2020) threatened by illegal, unregulated and unreported (IUU) fishing activities, specifically bottom trawling and electric trawling (Beasley & Davidson, 2007; Bohm, 2019; Hines et al., 2020; Tubbs et al., 2019). The region is recognised as a Marine Fisheries Management Area (MFMA) and an Important Marine Mammal Area (IMMA; MMPATF, 2019). In 2017, Marine Conservation Cambodia established The Cambodian Marine Mammal Conservation Project (CMMCP), subsequently Kep’s Irrawaddy dolphins have become the subject of increased research focus over recent years (Tubbs et al., 2019; Tubbs et al., 2020).

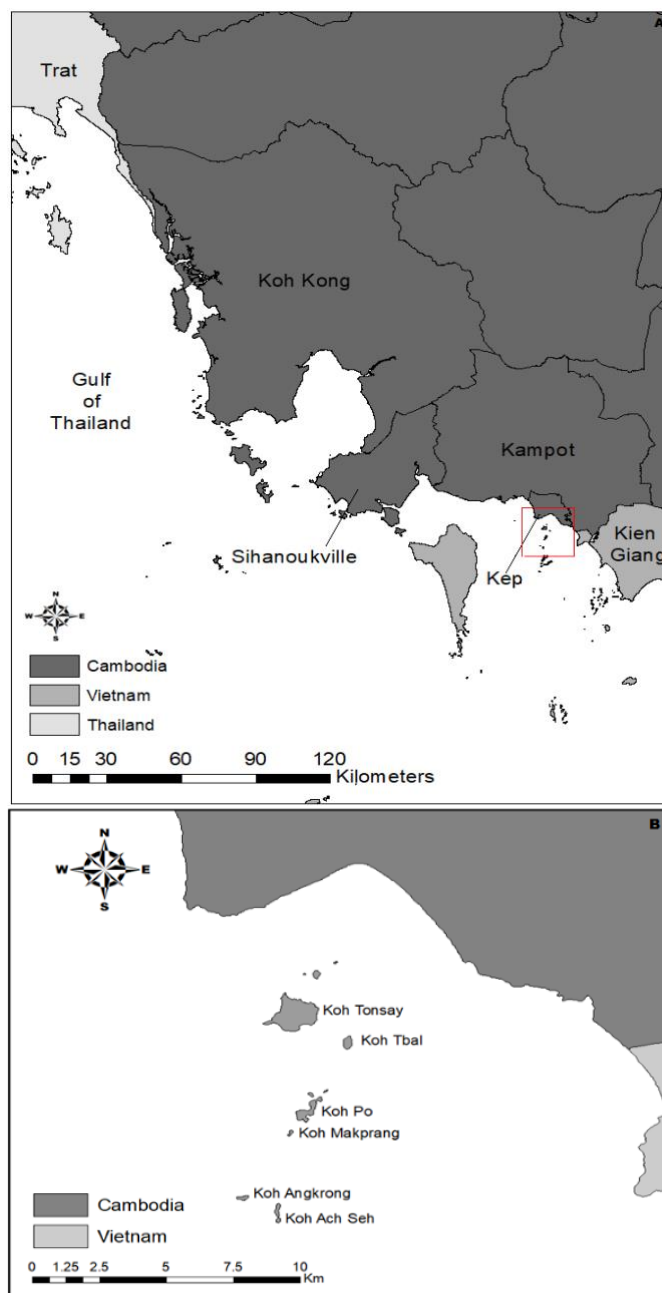
During a routine boat-based survey conducted by CMMCP on November 7, 2019, the carcass of an Irrawaddy dolphin was discovered and promptly towed to land to conduct a necropsy and collect tissue samples. The current study investigated the responses of Irrawaddy dolphin focal groups to the carcass by comparing survey sightings data (number of dolphin groups, directional response to the research vessel, and number of behavioral events) from the towed survey to the seasonal average (post-monsoon season 2017 and 2018). Regarding published literature, this is the first report of towing an Irrawaddy dolphin through an identified hotspot. Prior to this event, CMMCP had never towed a dead Irrawaddy dolphin and thus never monitored conspecific responses to such an event. The findings aim to formally record and acknowledge the unusual behavior displayed by these dolphins in response to the dead conspecific and aim to stimulate further research into the behavioral repertoire and responses of wild Irrawaddy dolphins.

Method

The Kep Archipelago consists of 13 islands situated in the coastal waters of Kep Province, Cambodia (Figure 1). The waters of the archipelago are shallow (2-12 m) and support seagrass, mangrove, and coral reef habitats, as well as commercial fish and crustacean species. Irrawaddy dolphins are the only cetacean observed in the region (Tubbs et al., 2019).

Figure 1

Maps of the East Gulf of Thailand and the Kep Archipelago



Note. A: The east coast of the Gulf of Thailand, displaying the Cambodian and Vietnamese coastal provinces (map from Tubbs and Keen, 2019). B: The islands of the Kep Archipelago, Kep Province (map from Tubbs, 2018).

CMMCP conduct weekly cetacean boat-based surveys in the Kep Archipelago. Surveys follow a triangular route onboard a converted Seine net vessel with a 200HP in-board engine. The research vessel travels at an average speed of 4 knots with a minimum observation team of five. Three observers scan the sea surface with Bushnell 8×42 binoculars, while two rest to avoid fatigue effects. Upon a cetacean sighting, a group number is assigned, and time is recorded. If a group, defined as a collection of individuals with coordinated behavior over several minutes (Connor et al., 1998), is not sighted for 20 minutes or longer after the original sighting, they are recorded as a separate group. Five-minute-interval sampling is used to record group size, behavioral state (Table 1), behavioral events (Table 1), distance and reaction to research vessel (Table 2), vessel type and quantity within 400 m of the dolphins, and the angle of the dolphins from north. The research vessel tracklines and cetacean groups are recorded using Garmin 64s GPS device.

Table 1

Ethogram Defining Dolphin Behavioral States and Behavioral Events

Behavioral State	Operational Definition
Surface-Feeding (SU-FE)	Individuals show active, rapid directional changes just under the surface.
Diving (DV)	Individuals disappear from the surface for between 30 s and several minutes. Individuals resurface within 100 m from where they submerged.
Travel-Diving (TR-DV)	Individuals disappear from the surface for between 30 s and several minutes. Individuals reappear more than 100 m from where they submerged, making directional progression with their location.
Travelling (TR)	Individuals show directional travel at a constant speed, with diving interval of 3-5 s.
Travel-Fast (TR-F)	Individuals swim rapidly at the surface of the water, rarely submerging.
Socialising (SOC)	Individuals show various interactive behaviors with body contact.
Resting (RE)	Individuals are drifting at the surface, submerging, and reappearing in the same location.
Milling (MI)	Individuals are facing different directions and often change direction. The group shows no net movement. Dive intervals are variable but short.
Behavioral Event	Operational Definition
Breaching (BR)	Individual leaps partly out of the water and lets their body slap the surface of the water upon re-entry.
Tail Slap (TS)	Individual slaps their fluke on the surface of the water.
Fluke Up (FU)	Individual raises only their tail fluke above the surface of the water, followed by controlled re-entry.
Spy Hopping (SH)	Individual raises only their head above the surface of the water.
Full Leap (FL)	Individual leaps out of the water, their body clears the surface of the water.
Belly Up (BU)	Individual turns ventral side up displaying their belly.

Note. Adapted from Lusseau (2003, 2006), Parra (2006), Bas et al. (2015) and Tubbs et al. (2020).

Table 2*Definitions of Positive (POS), Neutral (NEU) and Negative (NEG) Directional Responses of Dolphin Groups Towards a Vessel*

Reaction to Vessel	Operational Definition
Positive (POS)	The group shows directional travel towards the vessel, or individuals interact with the vessel
Neutral (NEU)	The group shows no change in directional response, or behavior, as a result of the vessel.
Negative (NEG)	The group shows directional travel away from the vessel, or a change in behavior, as a result of the vessel.

The number of dolphin groups, reactions of groups to the research vessel, and number and type of behavioral events observed on November 7, 2019, were compared with the seasonal average from 2017 and 2018 (post-monsoon season; Tsujimoto et al., 2018; Tubbs et al., 2020) to analyze how these observations differ from the seasonal norm and to highlight the atypical nature of the observations. No statistical analysis was conducted due to the serendipitous circumstances and limited comparable dataset. The seasonal average (post-monsoon season; PoM-season) was calculated as the mean number from every observation made throughout the season during 2017 and 2018. This composed of 59 observations, 20 separate Irrawaddy dolphin groups, which displayed six of the eight behavioral states (diving, travelling, travel-diving, surface-feeding, socialising, and resting; Table 1) and two of the six behavioral events (fluke up and spy hopping; Table 1). Tubbs et al. (2020) found no significant relationship between the behavioral states and events displayed by Irrawaddy dolphins in Kep during PoM-season. Photographs were taken using a Canon Rebel T6i Digital SLR camera and EF 75-300 mm f/4-5.6 III lens, although the dolphins observed on November 7, 2019, were not identifiable due to the lack of high-quality photographs taken during the survey.

The research vessel trackline and dolphin sighting locations were uploaded to Esri® *ArcGIS*TM as point data and converted into line data. Arrow heads were added to dolphin and boat tracklines to show the direction of travel. Only a single line of datum was recorded for Group 3, preventing the construction of a trackline. RStudio (Version 1.2.5042) was used to analyse and plot the relative frequency of dolphin groups and the directional response of dolphins to the research vessel. Relative frequency of groups (Figure 4) was plotted using the *gridExtra* (2.3; R Core Team, 2019) and *lattice* (0.20-41; Sarkar, 2008) R packages. *GGPlot2* (3.3.0; Wickham, 2016) and *dplyr* (0.8.5; Wickham *et al.*, 2021) packages were used to create Figure 5. The number and types of behavioral events (Figure 6) were analyzed and plotted using Microsoft Excel (Version 2101).

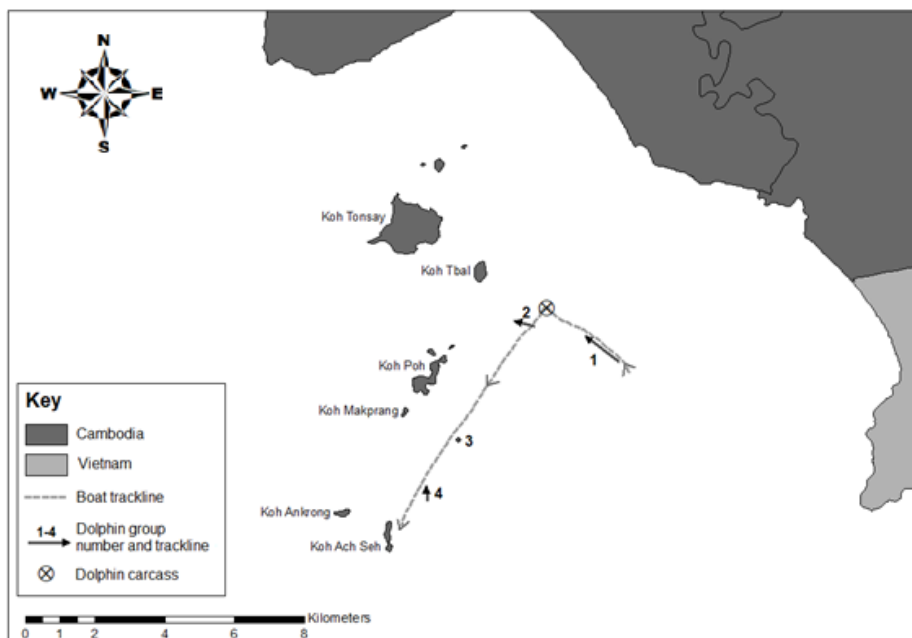
Results

The following observations were made on November 7, 2019, during a routine CMMCP boat-based survey of the Kep Archipelago:

7:13 a.m.: A group of three Irrawaddy dolphins, labelled Group 1, was sighted for two 5-min intervals east of Koh Poh with a positive reaction to the research vessel (Figure 2). This group was travelling in a northwest direction, towards the location where the carcass would be found.

Figure 2

Route of Research Vessel and Observed Dolphin Groups



Note. The route and direction of travel of the research vessel, from when the first dolphin group was sighted, including location of the dolphin carcass recovery, and the locations and directions of travel of the four dolphin groups encountered.

7:35 a.m.: The carcass of an adult female Irrawaddy dolphin was sighted south-west of Koh Tbal (Figures 1 and 2) and attached to the stern of the research vessel via a 5-m length rope (Figure 3). The survey route was altered in a southerly direction through the central archipelago back to Koh Ach Seh to promptly tow the carcass to shore for sample collection and burial (Figure 2). A speed of 4 knots was maintained while towing the carcass.

Figure 3

Towed Irrawaddy Dolphin Carcass



Note. The carcass of an adult female Irrawaddy dolphin was found in the Kep Archipelago and attached to the stern of the research vessel via a 5-m rope. The carcass was promptly towed to the research island, Koh Ach Seh, for post-mortem examination and burial.

7:49 a.m.: During the tow, four Irrawaddy dolphins, labelled Group 2, were sighted diving for two 5-min intervals with one fluke-up event per interval. Group 2 maintained the closest proximity (approximately 300 m) of the four groups to the research vessel and the attached carcass. This group travelled in a northwest direction as the research vessel approached, displaying a neutral response towards the research vessel in the first interval, followed by a positive response in the second interval (Figure 2).

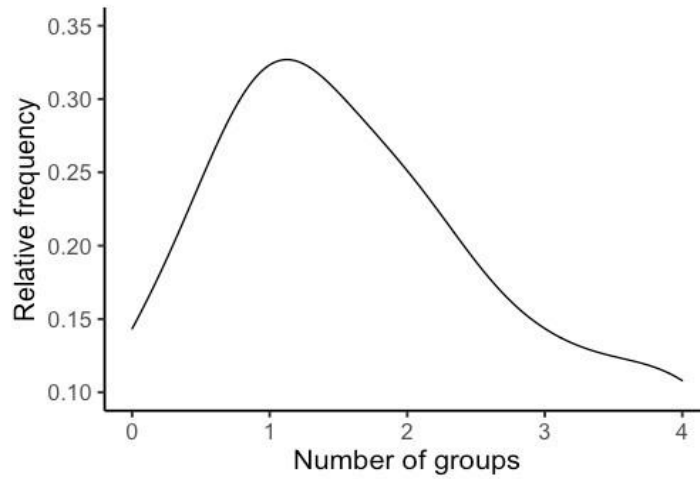
8:25 a.m.: Six Irrawaddy dolphins, labelled Group 3, were observed diving for one 5-min interval with a positive response towards the research vessel (Figure 2). Group 3 approached the research vessel from a southerly direction at a distance of approximately 300 m (Figure 2).

8:37 a.m.: Five individuals, labelled Group 4, were sighted travelling north for two 5-min intervals, with a positive reaction to the research vessel at a distance of approximately 550 m (Figure 2). Group 4 displayed two tail slaps in the first interval and two breaches in the second interval.

Results showed a four-fold increase in the number of groups sighted on November 7 (four groups; approximately 0.1 relative frequency) when compared to the seasonal average (one group; approximately 0.3 relative frequency; Figure 4). An atypically positive response towards the research vessel with the attached carcass was also observed (83% positive), when compared to the seasonal average (0% positive; Figure 5). A discrepancy was also found when comparing the events from the towing survey to the seasonal average (Figure 6). Breaching (BR) showed the most prominent deviation from the average with a 14-fold increase in breaching events, followed by tail slapping (TS; 13-fold increase) and fluke up (FU; 0.5-fold increase). Conversely, spy-hopping (SH) and belly-up (BU) events had previously been observed during the PoM-season but were not witnessed during this towing survey. No full leaps (FL) were observed during the towing survey or any previous survey during the PoM-season (Figure 6).

Figure 4

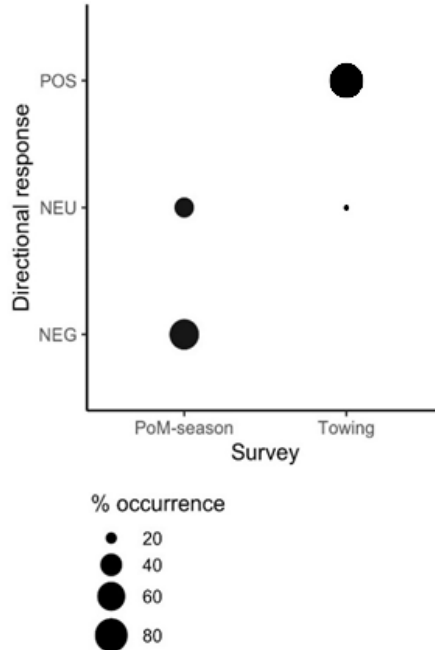
Relative Frequency of Group Number



Note. The relative frequency of the number of groups observed during post-monsoon season (October to November). Post-monsoon season data from 2017 and 2018 was accessed from the CMMCP database. Relative frequency of 1 = 100% likelihood of sighting during a single survey effort.

Figure 5

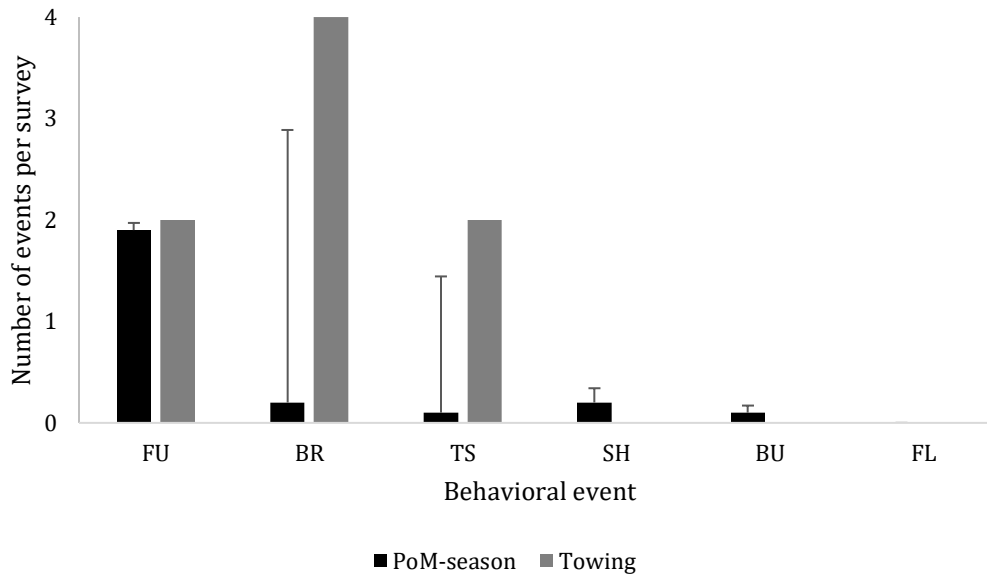
Comparison of POS (Positive Response), NEG (Negative Response) and NEU (Neutral Response) Responses of Irrawaddy Dolphin Groups to the Research Vessel



Note. Comparisons were made between previous CMMCP post-monsoon season surveys (2017 and 2018) and the towing of the dead conspecific on November 7, 2019.

Figure 6

Number and Types of Behavioral Events Observed



Note. Number of behavioral events (FU, Fluke Up; BR, Breaching; TS, Tail Slap; SH, Spy Hopping; BU, Belly Up; FL, Full Leap) displayed during the towing survey (dark grey) compared to the average number of events observed during post-monsoon season (PoM-season) surveys in 2017 and 2018 (black). Error bars display the standard deviation of the seasonal average.

The dorsal fin of the deceased female was compared with CMMCP’s photo-identification catalogue, revealing that the individual was known to the research team and had first been identified using dorsal fin mark-recapture photo identification in December 2018. CMMCP’s catalogue consists only of Irrawaddy dolphins sighted within the Kep Archipelago. Fin analysis of the observed groups was inconclusive due to the limited photo-ID data and lack of high-quality photos collected during this specific towing survey. However, the stranded individual was known to associate with four other identified individuals (adults) within the archipelago. The basic necropsy conducted could not determine cause of death due to carcass decomposition.

Discussion

During a CMMCP boat-based survey around the Kep Archipelago on November 7, 2019, a dolphin carcass was discovered and promptly towed to Koh Ach Seh, where a basic necropsy and burial were conducted. En route from the carcass recovery site to Koh Ach Seh, four separate Irrawaddy dolphin groups were sighted. The behavioral and directional responses of these four groups to the towed carcass were investigated. Comparing this towing survey with previous post-monsoon season data found an atypical increase in: the number of dolphin groups observed (Figure 4), positive reactions towards the research vessel (Figure 5), and the type and quantity of behavioral events (Figure 6). It is hypothesized that these observed behavioral differences were a result of increased awareness in response to the dead conspecific.

The difference in the number of groups observed could be explained by the alternative route that was taken on November 7. The route was altered to promptly tow the carcass back to Koh Ach Seh for examination and to reduce further decomposition of the carcass. The research vessel travelled south via the eastern side of the central islands compared to the typical survey route which travels south on the western side of the central islands (typical survey route $n = 49$). Tubbs et al. (2020) reported that the highest Irrawaddy dolphin density was west of the central islands in PoM-season, whereas observations from November 7 found highest density to the east of the central islands, supporting the hypothesis that the towed carcass attracted conspecifics.

Vessel traffic may also have contributed to the increased number of dolphin groups observed. During the PoM-season, an average of five boats were observed within 400 m of the dolphin groups, whereas during this towing survey, an average of one boat was sighted within 400 m of the dolphin groups. Research on other cetacean species has found that vessels within 400 m of the dolphin groups are believed to have a significant impact on dolphin behavior and directional movement (Aguilar de Soto et al., 2006; Dans et al., 2008; Baş et al., 2015; Baş et al., 2017). As an evasive and often boat-shy species (Jaaman, 2010; Jaaman et al., 2009; Mahmud et al., 2018), the heavier seasonal average vessel traffic may have deterred dolphin groups from the area or elicited more evasive behaviors such as diving and travel-diving, reducing the likelihood of a sighting. Therefore, the five-fold decrease in vessel traffic observed during the towing survey is likely to have positively affected dolphin presence, behavior, and directional travel and may also have increased their awareness of both the research vessel and the attached carcass. Vessel type remained consistent across both the PoM-season average and the towing survey with the presence of only the research vessel and small fishing boats (defined as vessels less than ≤ 5 m in length, with an outboard engine).

The atypically high number of groups observed and their positive directional response towards the vessel could be a result of curiosity, non-instrumental or otherwise (Kidd & Hayden, 2015; Shani et al., 2011). During this study, 83% of the directional responses towards the research vessel were positive, with the remaining 17% neutral. This was the first record of a positive directional response towards the research vessel during this season. Previous PoM-season data found 0% positive, 34% neutral, and 66% negative (Figure 6). This uncharacteristically positive response towards the vessel may have been a result of the attached carcass and curiosity.

Curiosity, as a result of a bold or novelty-seeking personality, has been shown to have evolutionary benefits for delphinids, as it allows for improved future actions and survival chances (Diaz Lopez, 2020; Kuczaj et al., 2012). Diaz Lopez's (2020) exploration of bold and shy personalities is consistent with that of Kuczaj et al.'s (2012) Five Factor Model of dolphin personality. These models suggest that the cumulative personalities of Groups 1, 3, and 4 may have been more curious and extroverted when approaching the research vessel, whereas Group 2 was more shy, cautious, and hesitant. This evasive response towards vessels has been previously documented in Kep's Irrawaddy dolphins during socializing and travelling behaviors (Tubbs & Croxford, 2019). Similar evasive behavior has also been documented in other populations of Irrawaddy dolphins in areas of high vessel density and traffic (Hashim & Jaaman, 2011; Mahmud et al., 2018). The research vessel used to tow the carcass could have deterred cautious personalities from the immediate vicinity, as the immediate risks associated with vessel proximity (disorientation, vessel strike, bycatch) outweighed the benefits of non-instrumental curiosity.

Non-instrumental curiosity, such as wider area exploration, appears to have no immediate fitness benefit to the informed recipient. However, the information gathered could contribute towards behavioral plasticity in a fluctuating environment (Whitehead, 2010; Whitehead et al., 2004; Wong & Candolin, 2015), such as the IUU-threatened Kep Archipelago. Behavioral plasticity has been observed in Indo-Pacific humpback dolphins, where dolphins follow low-speed fishing vessels to forage but avoid high-speed, non-fishing vessels, due to increased acoustic disturbance and associated disorientation and noise fatigue (Ng & Leung, 2003; Dey et al., 2019). Irrawaddy dolphins in the Kep Archipelago face similar anthropogenic

pressures. In Kep, non-instrumental curiosity of groups and individuals can lead to increased knowledge acquisition and consequent behavioral plasticity. This search for non-instrumental information suggests that Irrawaddy dolphins could be capable of foresight and higher-level cognition as they seek out “knowledge for knowledge’s sake” (Shani et al., 2011). However, further in-depth research would be required to confirm these findings.

Analyses found an atypical increase in the occurrence of breaching (14-fold increase) and tail slapping (13-fold increase) events and a reduction in the prevalence of spy hopping and belly-up events performed by the dolphin groups (Figure 6). This shift in the types and quantity of events observed may have been functional and emotional responses to the dead conspecific. Tail slapping (also known as fluke slapping, tail whips and lobtailing) have been observed in bottlenose dolphins interacting with a dead conspecific (Dudzinski et al., 2003). Tail slaps are accepted examples of aggression (Dudzinski, 1998; Ostman, 1991; Shane et al., 1986; Slooten, 1994). Although tail slapping may simply be a form of non-vocal communication (Connor et al., 2000), it may also indicate emotion, motivation, and intent (Ponnampalam et al., 2013; Slooten, 1994). No such conclusions have been formally drawn from the events of Irrawaddy dolphins, although the behavioral events observed here may have been emotional displays yet to be translated (e.g., tail-slapping to display distress).

Dorsal fin photo identification of the towed individual revealed that the adult female was resident to the Kep Archipelago and was known to associate with four other adult Irrawaddy dolphins within the archipelago. Photo analysis of the dolphin groups sighted during the towing survey was inconclusive due to the lack of high-quality photos captured during this event. However, the unusual behaviors displayed by the groups could be due to recognition and social alliances. These factors may have caused the groups to atypically approach the research vessel with the attached carcass (83% positive responses) and to display an atypical increase in behavioral events, for communicative purposes or otherwise, as has been witnessed in other delphinid species responding to dead conspecifics (Dudzinski et al., 2003).

Previous comparative thanatology research has largely focused on bottlenose dolphins (Bearzi et al., 2018; Dudzinski et al., 2003; Harzen & Santos, 1992), due to their extensive coastal distribution and relatively large population size (Wells et al., 2019). In bottlenose dolphins, atypical behaviors and positive directional responses to dead conspecifics have been attributed to epimeletic behavior (Bearzi et al., 2018; Harzen & Santos, 1992), grief (Bearzi et al., 2018), herding, and mate-guarding (Dudzinski et al., 2003). Such conclusions cannot be drawn from the present observations due to the lack of understanding of the social networks and alliances of these dolphins. The groups also lacked physical contact and maintained proximity with the dead conspecific discounting epimeletic behavior and mating guarding.

It is plausible that the interpretations of the observed behaviors have been subject to anthropomorphism, the ascription of human characteristics to nonhuman beings or events (Guthrie, 1997). However, an unwillingness to draw parallels between the behaviors and motivations of intellectually and socially similar mammals such as humans and dolphins may be more hindering than helpful in attempting to uncover the unknowns of animal behavior (Safina, 2015).

Conclusion

By comparing the data collected during the towing survey to the post-monsoon season average, this study found a four-fold increase in the number of groups observed, an atypically positive response towards the research vessel (83% compared to 0%), and an atypical increase in the number of behavioral events observed (14-fold increase in breaching events, 13-fold increase in tail slapping events). These behavioral variations were attributed to the towing of the dead dolphin, attracting conspecifics to the vicinity. However, due to the anomalous circumstances and limited comparable dataset, no statistical methods were used to test for the significance of these results.

This study suggests that the dolphins were aware of and curious about the dead conspecific. However, there are many unknowns in the field of comparative psychology and thanatology, and the full extent of cetaceans' intellectual and emotional spectrum is yet to be comprehended and translated by scientists. This example of experiential knowledge, combined with awareness and understanding, forms the basis of subjective perception and sentience, demonstrating that Irrawaddy dolphins are complex thinking mammals. This case study and its findings therefore aim to stimulate further research into Irrawaddy dolphin behavior, cognition, and awareness, with a view to ensuring the essential protection of this intelligent, endangered species.

Acknowledgments

Many thanks to Marine Conservation Cambodia, International Conservation Fund of Canada, Heinrich Boll Foundation, The Rufford Foundation, Foundation Ensemble and Idea Wild for funding this research. To the Cambodian Fisheries Administration, notably Mr. Vibol Ouk, Mr. Phay Somany and Mr. Chheng Touch, for their continued support and collaboration. To Dr. Gill Notman, Miss. Lucy Coals and Mr. Paul Ferber for manuscript improvements. To the volunteers at Marine Conservation Cambodia for assisting with data collection.

References

- Aguilar de Soto, N., Johnson, M., Madsen, P. T., Tyack, P. L., Bocconcelli, A., & Borsani, J. F. (2006). Does intense ship noise disrupt foraging in deep-diving Cuvier's beaked whales (*Ziphius cavirostris*). *Marine Mammal Science*, 22(3), 690–699. <https://doi.org/10.1111/j.1748-7692.2006.00044.x>
- Alves, F., Nicolau, C., Dinis, A., Ribeiro, C., & Freitas, L. (2015). Supportive behaviour of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) toward dead neonates, with data on perinatal mortality. *Acta Ethologica*, 18(3), 301–304. <https://doi.org/10.1007/s10211-014-0210-8>
- Bahl, R., Ura, T., Sugimatsu, H., Ioune, T., Kojima, J., Akamatsu, T., Takahashi, H., Behera, S. K., Pattnaik, A. K., Kham, M., & Kar, S. K. (2006). Acoustic survey of Irrawaddy dolphin populations in Chilika Lagoon: First test of a compact high-resolution device. *OCEANS*, 1–6. <https://doi.org/10.1109/OCEANSAP.2006.4393872>
- Bas, A. A., Ozturk, A. A., & Ozturk, B. (2015). Selection of critical habitats for bottlenose dolphins (*Tursiops truncatus*) based on behavioral data, in relation to marine traffic in the Istanbul Strait, Turkey. *Marine Mammal Science*, 31(3), 979–997. <https://doi.org/10.1111/mms.12202>
- Bas, A. A., Christiansen, F., Ozturk, A. A., Osturk, B., & McIntosh, C. (2017). The effects of marine traffic on the behaviour of Black sea harbour porpoises (*Phocoena phocoena relicta*) within the Istanbul Strait, Turkey. *PLoS One*, 12(8), e0183597. <https://doi.org/10.1371/journal.pone.0172970>
- Bearzi, G., Eddy, L., Piwetz, S., Reggente, M. A. L., & Cozzi, B. (2017). Cetacean behavior toward the dead and dying. In J. Vonk & T. K. Shackelford (Eds.), *Encyclopaedia of Animal Cognition and Behaviour* (pp. 1–8). Springer International. https://doi.org/10.1007/978-3-319-47829-6_2023-1
- Bearzi, G., Kerem, D., Furey, N. B., Pitman, R. L., Rendell, L., & Reeves, R. R. (2018). Whale and dolphin behavioural responses to dead conspecifics. *Zoology*, 2010, 1–42. <https://doi.org/10.1016/j.zool.2018.05.003>
- Beasley, I., & Davidson, P. (2007). Conservation status of marine mammals in Cambodian waters, including seven new cetacean records of occurrence. *Aquatic Mammals*, 33(3), 368–379. <https://doi.org/10.1578/AM.33.3.2007.368>
- Bohm, A. B. (2019). Marine harvesting networks in Cambodia: Technical report on transnational fishing activities. *Technical Report*. Marine Conservation Cambodia. <https://www.marineconservationcambodia.org/academicinternships/reports-and-documents>
- Caldwell, M. C., & Caldwell, D. K. (1966). Epimeletic (care-giving) behavior in *Cetacea*. In K. S Norris (Ed.), *Whales, porpoises and dolphins* (pp. 755–789). University of California Press. <https://doi.org/10.1525/9780520321373-041>
- Cockcroft, V. G., & Sauer, W. (1990). Observed and inferred epimeletic (nurturant) behaviour in bottlenose dolphins. *Aquatic Mammals*, 16(1), 31–32.

- Connor, R. C. (2007). Dolphin social intelligence: Complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), 587–602. <https://doi.org/10.1098/rstb.2006.1997>
- Connor, R. C., & Smolker, R. A. (1990). Quantitative description of a rare behavioral event: A bottlenose dolphin's behavior toward her deceased offspring. In S. Leatherwood & R. R. Reeves (Eds.), *The Bottlenose Dolphins* (pp. 355–360). Academic Press. <https://doi.org/10.1016/B978-0-12-440280-5.50023-8>
- Connor, R. C., Mann, J., Tyack, P. L., & Whitehead, H. (1998). Social evolution in toothed whales. *Trends in Ecology and Evolution*, 13(6), 228–232. [https://doi.org/10.1016/S0169-5347\(98\)01326-3](https://doi.org/10.1016/S0169-5347(98)01326-3)
- Connor, R. C., Heithaus, M., Berggren, P., & Miksis, J. (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>
- Dans, S. L., Crespo, E. A., Pedraza, S. N., Degradi, M., & Garaffo, G. V. (2008). Dusky dolphin and tourist interaction: Effect on diurnal feeding behavior. *Marine Ecology Progress Series*, 369, 287–296. <https://doi.org/10.3354/meps07629>
- de la Paz, M. E., Palomar-Abesamis, N., Sabater, E., Seneron, J. A., & Dolar, M. L. (2020). Habitat use and site fidelity of Irrawaddy dolphins (*Orcaella brevirostris*) in the coastal waters of Bago-Pulupandan, Negro Occidental, Philippines. *The Raffles Bulletin of Zoology*, 68, 562–573. <http://doi.org/10.26107/RBZ-2020-0072>
- Dey, M., Krishnaswamy, J., Morisaka, T., & Kelker, N. (2019). Interacting effects of vessel noise and shallow river depth elevate metabolic stress in Ganges river dolphins. *Nature*, 9, 15426. <https://doi.org/10.1038/s41598-019-51664-1>
- Diaz Lopez, B. (2020). When personality matters: Personality and social structure in wild bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour*, 163, 73–84. <https://doi.org/10.1016/j.anbehav.2020.03.001>
- Diaz Lopez, B., Lopez, A., Methion, S., & Covelo, P. (2018). Infanticide attacks and associated epimeletic behaviour in free-ranging common bottlenose dolphins (*Tursiops truncatus*). *Marine Mammals*, 98(5), 1159–1167. <https://doi.org/10.1017/S0025315417001266>
- D’Lima, C., Everingham, Y., Diedrich, A., Mustika, P. L., Hamann, M. & Marsh, H. (2018). Using multiple indicators to evaluate the sustainability of dolphin-based wildlife tourism in rural India. *Journal of Sustainable Tourism*, 26(10), 1687–1707. <https://doi.org/10.1080/09669582.2018.1503671>
- Dolar, M. L. L., Perrin, W. F., Gaudio, J. P., Yaptinchay, A. A. S. P., & Tan, J. M. L. (2002). Preliminary report on a small estuarine population of Irrawaddy dolphins *Orcaella brevirostris* in the Philippines. *The Raffles Bulletin of Zoology*, 10, 155–160. <https://lknhm.nus.edu.sg/wp-content/uploads/sites/10/2020/12/s10rbz0155-160.pdf>
- Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals*, 24(3), 129–142.
- Dudzinski, K. M., Sakai, M., Kogi, K., Hishii, T., & Kurimoto, M. (2003). Behavioural observations of bottlenose dolphins towards two dead conspecifics. *Aquatic Mammals*, 29(1), 108–116.
- Dunn, D. G., Barco, S. G., Pabst, D. A., & McLellan, W. A. (2002). Evidence for infanticide in bottlenose dolphins of the western north Atlantic. *Journal of Wildlife Diseases*, 38(3), 505–510. <https://doi.org/10.7589/0090-3558-38.3.505>
- Fertl, D., & Schiro, A. (1994). Carrying of dead calves by free-ranging Texas bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammal*, 20(1), 53–56.
- Food and Agriculture Organization of the United Nations. (1978). Small cetaceans: Live-capture fisheries. *Mammals in the Sea: Report*. www.fao.org
- Frohoff, T. (2011). Lessons from dolphins. In P. Brakes & M. P. Simmonds (Eds.), *Whales and dolphins: Cognition, conservation and human perceptions* (pp.136–145). Earthscan. <https://doi.org/10.1111/mms.12019>
- Guthrie, S. E. (1997). Anthropomorphism: A definition and a theory. In R. W. Mitchell, N. S. Thompson, & H. L. Miles (Eds.), *Anthropomorphism, Anecdotes, and Animals* (pp. 50–58). State University of New York Press. <https://doi.org/10.1086/420189>
- Harzen, S., & Santos, M. E. (1992). Three encounters with wild bottlenose dolphins (*Tursiops truncatus*) carrying dead calves. *Aquatic Mammals*, 18(2), 49–55.
- Hashim, N. A. N., & Jaaman, S. A. (2011). Boat effects on the behaviour of Indo-Pacific humpback (*Sousa chinensis*) and Irrawaddy dolphins (*Orcaella brevirostris*) in Cowie Bay, Sabah, Malaysia. *Sains Malaysiana*, 40(12), 1383–1392. http://www.ukm.edu.my/jsm/pdf_files/SM-PDF-40-12-2011/08%20Nur%20Azeyanti.pdf
- Herman, L. M. (2006). Intelligence and rational behaviour in the bottlenosed dolphin. In S. Hurley & M. Nudds (Eds.), *Rational Animals?* (pp. 439–467). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780198528272.001.0001>

- Hines, E., Ponnampalam, L., Junchompoo, C., Peter, C., Vu, L., Huynh, T., Caillat, M., Johnson, A., Minton, G., Lewison, R., & Verutes, G. (2020). Getting to the bottom of bycatch: A GIS-based toolbox to assess the risk of marine mammal bycatch. *Endangered Species Research*, 42, 37–57. <https://doi.org/10.3354/esr01037>
- Hoffman, J. M., Ponnampalam, L. S., Arauji-Wang, C., Kuit, S. H., Hung, S. K., & Wang, J. Y. (2017). Description of whistles of Irrawaddy dolphins (*Orcaella brevirostris*) from the waters of Matang, Peninsular Malaysia. *Bioacoustics*, 26(1), 15–24. <https://doi.org/10.1080/09524622.2016.1169558>
- Inoue, T., Ura, T., Sugimatsu, H., Sakamaki, T., Kojima, J., Bahl, R., Panda, S., Kham, M., Behera, S. K., Takahashi, H., Kar, S., & Kar, C. (2007). Long duration real-time observation of Irrawaddy dolphins in Chilika lagoon. *OCEANS*, 2007, 1–7. <https://doi.org/10.1109/OCEANS.2007.4449268>
- Jaaman, S. A., Lah-Anyi, Y. A., & Pierce, G. J. (2009). The magnitude and sustainability of marine mammal by-catch in fisheries in East Malaysia. *Journal of the Marine Biological Association of the United Kingdom*, 89(5), 907–920. <https://doi.org/10.1017/S002531540800249X>
- Jaaman, S. A. (2010). *Marine mammal in East Malaysia: Distribution and interactions with fisheries*. VDM Verlag Dr.Muller Akiengesellschaft & Co: Saarbrucken. <https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.430421>
- Kannan, K., Ramu, K., Kajiwara, N., Sinha, R. K., & Tanabe, S. (2005). Organochlorine pesticides, polychlorinated biphenyls, and polybrominated diphenyl ethers in Irrawaddy dolphins from India. *Archives of Environmental Contamination and Toxicology*, 49, 415–420. <https://doi.org/10.1007/s00244-005-7078-6>
- Kidd, C., & Hayden, B. Y. (2015). The psychology and neuroscience of curiosity. *Neuron*, 88(3), 449–460. <https://doi.org/10.1016/j.neuron.2015.09.010>
- Kilborn, S. S. (1994). Object carrying in a captive beluga whale (*Delphinapterus leucas*) a possible surrogate behavior. *Marine Mammal Science*, 10(4), 496–501. <https://doi.org/10.1111/j.1748-7692.1994.tb00510.x>
- Kuczaj, S., Tranel, K., Trone, M., & Hill, H. (2001). Are animals capable of deception or empathy? Implications for animal consciousness and animal welfare. *Animal Welfare*, 10, 161–173.
- Kuczaj, S. A., Highfill, L., & Byerly, H. (2012). The importance of considering context in the assessment of personality characteristics: Evidence from ratings of dolphin personality. *International Journal of Comparative Psychology*, 25(4), 309–329. <https://doi.org/10.46867/ijcp.2012.25.04.01>
- Kuit, S. H., Ponnampalam, L. S., Ng, J. E., Chong, V. C., Then, A. Y. (2019). Distribution and habitat characteristics of three sympatric cetacean species in the coastal waters of Matang, Perak, Peninsular Malaysia. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(10), 1681–1696. <https://doi.org/10.1002/aqc.3121>
- Kummaruzzan, A. S., & Jaaman, S. A. (2013). Interactions between Indo-Pacific humpback and Irrawaddy dolphins in Cowie Bay, Sabah, Malaysia. *Malayan Nature Journal*, 64(4), 185–191.
- Lodi, L. (1992). Epimeletic behavior of free-ranging rough-toothed dolphins, *Steno bredanensis*, from Brazil. *Marine Mammal Science*, 8(3), 284–287. <https://doi.org/10.1111/j.1748-7692.1992.tb00410.x>
- Lusseau, D. (2003) Effects of boat tours on the behaviour of bottlenose dolphins: using Markov chains to model anthropogenic impacts. *Conservation Biology*. 17(6), 1785–1793. <https://doi.org/10.1111/j.1523-1739.2003.00054.x>
- Lusseau, D. (2006). Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins (*Tursiops sp.*) in Doubtful Sound, New Zealand. *Behavioural Processes*, 73(3), 257–265. <https://doi.org/10.1016/j.beproc.2006.06.006>
- Mahmud, A. I., Jaaman, S. A., Muda, A. M., Muhamad, H. M., Zhang, X., & Scapini, F. (2018). Factors influencing the behaviour of Irrawaddy dolphins *Orcaella brevirostris* (Owen in Gray, 1866) in Brunei Bay, Malaysia. *Journal of Ethology*, 36, 169–180. <https://doi.org/10.1007/s10164-018-0549-9>
- Mann, J., Connor, R. C., Tyack, P. L., & Whitehead, H. (2000). *Cetacean societies: Field studies of dolphins and whales*. The University of Chicago Press. <https://doi.org/10.1023/A:1017339526569>
- Marino, L., Connor, R. C., Fordyce, R. E., Herman, L. M., Hof, P. R., Lefebvre, L., Lusseau, D., McCowan, B., Nimchinsky, E. A., Pack, A. A., Rendell, L., Reidenberg, J. S., Reiss, D., Uhen, M. D., Gucht, E. V., & Whitehead, H. (2007). Cetaceans have complex brains for complex cognition. *PLoS Biology*, 5(5), e139. <https://doi.org/10.1371/journal.pbio.0050139>
- Minton, G., Smith, B. D., Braulik, G. T., Krebs, D., Sutaria, D., & Reeves, R. (2017). *Orcaella brevirostris*. The IUCN Red List of Endangered Species. <http://www.iucnredlist.org/details/15419/0>
- MMPATF (Marine Mammal Protected Area Task Force) (2019) IMMA e-Atlas – Marine Mammal Protected Area Task Force. <http://www.marinemammalhabitat.org/imma-eatlas>
- Nakahara, F., Komaba, M., Sato, R., Ikeda, H., Komaba, K., & Kawakbo, A. (2016) Spontaneous prosocial choice by captive bottlenose dolphin, *Tursiops truncatus*. *Behavioural Processes*, 135, 8–11. <https://doi.org/10.1016/j.beproc.2016.11.009>

- Ng, S. L., & Leung, S. (2003). Behavioral response of Indo-Pacific humpback dolphin (*Sousa chinensis*) to vessel traffic. *Marine Environment Research*, 56(5), 555–567. [https://doi.org/10.1016/S0141-1136\(03\)00041-2](https://doi.org/10.1016/S0141-1136(03)00041-2)
- Ostman, J. (1991). Changes in aggressive and sexual behavior between two male bottlenose dolphins (*Tursiops truncatus*) in a captive colony. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 305–317). University of California Press.
- Parra, G. J. (2006). Resource partitioning in sympatric delphinids: Space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins. *Journal of Animal Ecology*, 75(4), 862–874. <https://doi.org/10.1111/j.1365-2656.2006.01104.x>
- Park, K. J., Sohn, H., An, Y. R., Moon, D. Y., Choi, S. G., & An, D. H. (2013). An unusual case of care-giving behavior in wild long-beaked common dolphins (*Delphinus capensis*) in the East Sea. *Marine Mammal Science*, 29(4), 508–514. <https://doi.org/10.1111/mms.12012>
- Patterson, I. A. P., Reid, R. J., Wilson, B., Grellier, K., Ross, H. M., & Thompson, P. M. (1998). Evidence for infanticide in bottlenose dolphins: An explanation for violent interactions with harbour porpoises. *Proceedings of the Royal Society London*, 265, 1167–1170. <https://doi.org/10.1098/rspb.1998.0414>
- Perez-Manrique, A., & Gomila, A. (2018). The comparative study of empathy: Sympathetic concern and empathic perspective-taking in non-human animals. *Biological Reviews*, 93(1), 248–269. <https://doi.org/10.1111/brv.12342>
- Perrin, W. F., Armstrong W. A., Baker, A. N., Barlow, J., Benson, S. R., Collet, A. S., Cotton, J. M., Everhart, D. M., Mellon, R. M., Miller, S. K., Philbrick, V., Quan, J. L., & Rodriguez, H. R. L. (1995). An anomalously pigmented form of the short-beaked common dolphin (*Delphinus delphis*) from the Southwestern Pacific, Eastern Pacific, and Eastern Atlantic. *Marine Mammal Science*, 11(2), 241–247. <https://doi.org/10.1111/j.1748-7692.1995.tb00522.x>
- Perrin, W., Reeves, R., Dolar, M., Jefferson, T., Marsh, H., Wang, J., & Estacion, J. (2005). Report of the second workshop on the biology and conservation of small cetaceans and dugongs of South East Asia'. *CMS Technical Series Publication No. 9. UNEP/CMS Secretaria. Bonn, Germany.* <http://www.vliz.be/imisdocs/publications/ocrd/120086.pdf>
- Perrin, W. F. (2009). Common dolphins: *Delphinus delphis* and *D. capensis*. In W. F. Perrin, B. Wursig, & J. G. M. Thewissen (Eds.), *Encyclopaedia of Marine Mammals* (pp. 255–259). Elsevier. <https://doi.org/10.1016/B978-373553-9.00063-8>
- Peter, C., Poh, A. N. Z., Ngeian, J., Tuen, A. A., & Minton, G. (2016). Identifying habitat characteristics and critical areas for Irrawaddy dolphin, *Orcaella brevirostris*: Implications for conservation. In I. Dasi & A. A. Tuen (Eds.), *Naturalists, explorers and field scientists in South-East Asia and Australasia: Topics in Biodiversity and Conservation 15*. Springer. https://doi.org/10.1007/978-3-319-26161-4_15
- Peter, C., Ngeian, J., Minton, G., Zulkifli Poh, A., Grinang, J., & Tuen, A. (2016). *Artisanal fisheries and cetaceans in Kuching Bay, Sarawak, East Malaysia: Threats and potential mitigation* (SC/66b/SM09). Report presented at Scientific Committee of the International Whaling Commission.
- Ponnampalam, L. S., Hines, E. M., Monanunsap, S., Ilangakoon, A. D., Junchompoo, C., Adulyanukosol, K., & Morse, L. (2013). Behavioural observations of coastal Irrawaddy dolphins (*Orcaella brevirostris*) in Trat Province, eastern Gulf of Thailand. *Aquatic Mammals*, 39(4), 401–408. <https://doi.org/10.1578/AM.39.4.2013.401>
- Pryor, K., & Norris, K. S. (1991). *Dolphin societies: Discoveries and puzzles*. University of California Press.
- R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria. <https://www.R-project.org>
- Reeves, R. R., Smith, B. D., Crespo, E. A., & Notobartolo di Sciara, G. (2003). Dolphins, whales and porpoises: 2002–2010. Conservation Action Plan for the World's Cetaceans. *IUCN/SSC Cetacean Specialist Group IUCN*. Cambridge, UK. http://cpps.dyndns.info/cpps-docs-web/planaccion/docs2011/oct/turismo_biodiv/Doc.7.Dolphins_whales_porpoises.pdf
- Reggente, M. A. L., Alves, F., Nicolau, C., Freitas, L., Cagnazzi, D., Baird, R. W., & Galli, P. (2016). Nurturant behavior toward dead conspecifics in free-ranging mammals: New records for odontocetes and a general review. *Journal of Mammalogy*, 97(5), 1428–1434. <https://doi.org/10.1093/jmammal/gyw089>
- Safina, C. (2015). *Beyond words: What animals think and feel*. Macmillan Publishers.
- Santos, M. C., Rosso, S., Siciliano, S., Zerbini, A.N., Zampirolli, E., Vicente, A., & Alvarenga, F. (2000). Behavioral observations of the marine tucuxi dolphin (*Sotalia fluviatilis*) in Sao Paulo estuarine waters, Southeastern Brazil. *Aquatic Mammals*, 26(3), 260–267.
- Sarkar, D. (2008). *Lattice: Multivariate data visualization with R*. Springer. <https://www.r-project.org>
- Schusterman, R. J., Thomas, J. A., & Wood, F. G. (1986). *Dolphin cognition and behavior: A comparative approach*. Psychology Press. <https://doi.org/10.4324/9780203767689>

- Shane, S. H., Wells, R. S., & Wursig, B. (1986). Ecology, behavior and social organisation of the bottlenose dolphin: A review. *Marine Mammal Science*, 2(1), 34–63. <https://doi.org/10.1111/j.1748-7692.1986.tb00026.x>
- Shani, Y., Capicka, M. C., & Shashar, N. (2011). Keeping up with the Joneses: Dolphins' search knowledge for knowledge's sake. *Journal of Economic Psychology*, 32(3), 418–424. <https://doi.org/10.1016/j.joep.2011.02.014>
- Slooten, E. (1994). Behavior of Hector's dolphin: Classifying behavior by sequence analysis. *Journal of Mammalogy*, 75(4), 956–964. <https://doi.org/10.2307/1382477>
- Smith, B. D., & Jefferson, T. A. (2002). Status and conservation of facultative freshwater cetaceans in Asia. *The Raffles Bulletin of Zoology*, 10, 173–187.
- Smith, B. D., Ahmed, B., Mowgli, R. M., & Strindberg, S. (2008). Species occurrence and distribution ecology of nearshore cetaceans in the Bay of Bengal, Bangladesh, with abundance estimates for Irrawaddy dolphins *Orcaella brevirostris* and finless porpoise *Neophocaena phocaenoides*. *Journal of Cetacean Research and Management*, 10(1), 45–58.
- Smith, B. D., Beasley, I., Buccat, M., Calderon, V., Evina, R., Lemmuel De Valle, J., Cadigal, A., Tura, E., & Visitacion, Z. (2004). Status, ecology and conservation of Irrawaddy dolphins (*Orcaella brevirostris*) in Malampaya Sound, Palawan, Philippines. *Journal of Cetacean Research and Management*, 6(1), 41–52.
- Smith, T. G., & Sleno, G. A. (1986). Do white whales, *Delphinapterus leucas*, carry surrogates in response to early loss of their young. *Canadian Journal of Zoology*, 64(7), 1581–1582. <https://doi.org/10.1139/z86-237>
- Stacey, P. J., & Arnold, P. W. (1999). *Orcaella brevirostris*. *Mammalian Species*, 616, 1-8. <https://doi.org/10.2307/3504387>
- Stacey, P. J., & Hvenegaard, G. T. (2002). Habitat use and behaviour of Irrawaddy dolphins (*Orcaella brevirostris*) in the Mekong river of Laos. *Aquatic Mammals*, 28(1), 1-13. <https://doi.org/10.7939/r3-ppqm-er09>
- Sugimatsu, H., Kojima, J., Ura, T., Bahl, R., Behera, S., Pattnaik, A., Tomuro, S., & Krebs, D. (2013). Long-term in-situ monitoring of the Irrawaddy dolphin (*Orcaella brevirostris*) in Borneo. *Proceedings of SYMPOL-2013*, 147–153. <https://doi.org/10.1109/SYMPOL.2013.6701925>
- Sutaria, D., Kalkar, N., Araujo-Wang, C., & Santos, M. (2019). Cetacean sociality in rivers, lagoons, and estuaries. In B. Wursig (Ed.). *Ethology and behavioral ecology of odontocetes. Ethology and behavioral ecology of marine mammals*. Springer. https://doi.org/10.1007/978-3-030-16663-2_19
- Towers, J. R., Halle, M. J., Symonds, H. K., Sutton, G. J., Morton, A. B., Spong, P., Borrowman, J. P., & Ford, J. K. B. (2018). Infanticide in a mammal-eating killer whale population. *Nature*, 8, 4366. <https://doi.org/10.1038/s41598-018-22714-x>
- Tsujimoto, K., Ohta, T., Aida, K., Tamakawa, K., & Im, M. S. (2018). Diurnal pattern of rainfall in Cambodia: Its regional characteristics and local circulation. *Progress in Earth and Planetary Science*, 5(39), 2–18. <https://doi.org/10.1186/s40645-018-0192-7>
- Tubbs, S. (2018). *The Cambodian Marine Mammal Conservation Project*. Technical report for the Cambodia Ministry of Agriculture, Forestry and Fisheries. <https://doi.org/10.13140/RG.2.2.17556.76162>
- Tubbs, S., & Croxford, E. (2019). *The Cambodian Marine Mammal Conservation Project: Annual Report*. Technical report for the Cambodia Ministry of Agriculture, Forestry and Fisheries.
- Tubbs, S. E., & Keen, E. (2019). Passive acoustic monitoring shows diurnal patterns for Irrawaddy dolphins in Kep, Cambodia. Poster Presentation. 45th World Marine Mammal Conference, Barcelona.
- Tubbs, S. E., Bağ, A. A., Cote, G., Jones, A. L., & Notman, G. M. (2019). Sighting and stranding reports of Irrawaddy dolphins (*Orcaella brevirostris*) and Dugongs (*Dugon dugon*) in Kep and Kampot, Cambodia. *Aquatic Mammals*, 45(5), 563–568. <https://doi.org/10.1578/AM.45.5.2019.563>
- Tubbs, S. E., Keen, E., Jones, A. L., & Thap, R. (2020). On the distribution, behaviour and seasonal variation of Irrawaddy dolphins (*Orcaella brevirostris*) in the Kep Archipelago, Cambodia. *The Raffles Bulletin of Zoology*, 68, 37–149. <https://doi.org/10.26107/RBZ-2020-0015>
- Wells, R. S., Natoli, A., & Braulik, G. (2019). *Tursiops truncatus*. The IUCN Red List of Threatened Species. <https://www.iucnredlist.org/es/species/22563/156932432>
- Whitehead, H. (2010). Conserving and managing animals that learn socially and share cultures. *Learning and Behavior*, 38(3), 329–336. <https://doi.org/10.3758/LB.38.3.329>
- Whitehead, H., & Rendell, L. (2015). *The cultural lives of whales and dolphins*. University of Chicago Press.
- Whitehead, H., Rendell, L., Osbourne, R. W., & Wursif, B. (2004). Culture and conservation of non-humans with reference to whales and dolphins: Review and new directions. *Biological Conservation*, 120(3), 427–437. <https://doi.org/10.1016/j.biocon.2004.03.017>
- Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag: New York. <https://www.r-project.org>

- Wickham, H., Francois, R., Henry, L., & Muller, K. (2021). *dplyr: A Grammar of Data Manipulation*. Springer-Verlag: New York. <https://www.r-project.org>
- Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioural Ecology*, 26(3), 665–673. <https://doi.org/10.1093/beheco/aru183>
- Wursig, B. (2009). Intelligence and Cognition. In W. F. Perrin, B. Wursig, & J. G. M. Thewissen (Eds.), *Encyclopaedia of Marine Mammals* (pp. 616–623). Elsevier. <https://doi.org/10.1016/B978-0-12-373553-9.X0001-6>

Financial conflict of interest: No stated conflicts.

Conflict of interest: No stated conflicts.

Submitted: August 17th, 2020

Resubmitted: May 14st, 2021

Accepted: May 28th, 2021