



Nurturant behavior toward dead conspecifics in free-ranging mammals: new records for odontocetes and a general review

MELISSA A. L. REGGENTE,* FILIPE ALVES, CÁTIA NICOLAU, LUÍS FREITAS, DANIELE CAGNAZZI, ROBIN W. BAIRD, AND PAOLO GALLI

Department of Biology, University of Milano-Bicocca, piazza della Scienza 3, 20126 Milano, Italy (MALR, PG)

MaRHE Centre (Marine Research and High Education Centre), Magoodhoo Island, Faafu Atoll, Republic of Maldives (MALR, PG)

Madeira Whale Museum, 9200-031 Caniçal, Madeira, Portugal (FA, CN, LF)

CIIMAR-Madeira, Interdisciplinary Centre of Marine and Environmental Research of Madeira, Edifício Madeira Tecnopolo, 9020-105 Funchal, Portugal (FA)

Marine Ecology Research Center, School of Environment, Science and Engineering, Southern Cross University, Lismore, New South Wales 2480, Australia (DC)

Cascadia Research Collective, 218 ½ W. 4th Avenue, Olympia, WA 98506, USA (RWB)

* Correspondent: m.reggente@campus.unimib.it, mel.regg@hotmail.it

Nurturant behavior toward dead conspecifics has been documented in several free-ranging marine and terrestrial mammals but still remains undocumented and poorly understood for most species. This study describes observations of adults carrying dead calves and juveniles in 7 odontocetes (toothed cetaceans) species and discusses the subject in mammals in general. Observations are based on 14 events from 3 oceans and constitute the 1st records for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), spinner dolphins (*Stenella longirostris*), killer whales (*Orcinus orca*), Australian humpback dolphins (*Sousa sahulensis*), and sperm whales (*Physeter macrocephalus*), as well as presenting additional records for Risso's dolphins (*Grampus griseus*) and short-finned pilot whales (*Globicephala macrorhynchus*). Information on how the adults supported and carried the dead conspecifics, on the gender of both adults and dead young, and on the age class of the dead young, is presented. Moreover, a comparison with terrestrial mammals, including a compilation of published literature, and a discussion on possible hypotheses to explain this particular type of behavior are given. The present study helps to corroborate that adults mourning their dead young is a common and globally widespread behavior in long-lived and highly sociable/cohesive species of mammals.

Key words: Delphinidae, mammalian, mourning, perinatal mortality, Physeteridae, supportive behavior

The term “epimeletic behavior” was used by Scott (1958) to indicate behavior which involves the giving of care or attention to another individual. Caldwell and Caldwell (1966) later differentiated it in nurturant behavior if toward young and in succorant behavior if toward individuals in distress. Such behaviors have been described in a wide range of marine and terrestrial mammalian taxonomic groups, including sea otters (e.g., Kenyon 1969), manatees (e.g., Hartman 1979), seals (e.g., Rosenfeld 1983), and cetaceans (see Fertl and Schiro 1994; Alves et al. 2015), as well as elephants (e.g., Douglas-Hamilton et al. 2006), giraffes (e.g., Muller 2010), and non-human primates (e.g., Fashing et al. 2011). Yet, information on nurturant behavior still remains undocumented for most

of species, especially for cetaceans and when directed toward dead conspecifics.

The most common target (age) group of nurturant behavior toward dead conspecifics is newborns (e.g., Ritter 2007; Sugiyama et al. 2009), which may be due to the higher mortality rate in newborns than in older calves and juveniles (Caughley 1966; Whitehead and Mann 2000). Dead newborns may include animals in advanced state of decay (Rosenfeld 1983), or even mummified (Fashing et al. 2011), and typically involves the carrying of the carcasses by adults of the group (Park et al. 2013). However, this type of behavioral response toward dead young is still poorly understood.

This study uses observational data from anecdotal events of adults supporting and carrying dead conspecifics in the wild, to

describe such types of behavioral responses for the first time in 5 odontocetes (toothed cetaceans) species and to add information in another 2 odontocetes. In the “Discussion,” the subject is extended to terrestrial mammals in order to provide a broader overview, and a compilation based on published literature is also included. Finally, possible hypotheses to explain this particular type of behavior are also presented.

MATERIALS AND METHODS

Data from 14 observational events of adults displaying nurturant behavior toward dead calves and juveniles were collected from 7 species in 7 geographic regions covering 3 oceans: 1 of Risso’s dolphin (*Grampus griseus*) in the Indian Ocean (Maldives), 1 of Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and 1 of spinner dolphin (*Stenella longirostris*) in the Red Sea (Egypt), 6 of short-finned pilot whale (*Globicephala macrorhynchus*) in 3 areas of the North Atlantic Ocean (Madeira, Azores, and Canary Islands), 1 of sperm whale (*Physeter macrocephalus*) in the Azores, 1 of killer whale (*Orcinus orca*) in the North Pacific Ocean (Washington, United States), and 3 of Australian humpback dolphin (*Sousa sahulensis*) in the South Pacific (Queensland, Australia). These correspond to records #1–14 (see “Results”). Such data were collected opportunistically from 8 different sources, which implied using unstandardized methodological protocols. Nevertheless, photographs and/or videos, which were available from all events except 1 (record #12), were used to confirm species and extract/corroborate biological and behavioral information, in addition to postmortem exams, when available. Biological information included the gender of both adults and dead young, and the age class of the dead young (according to definitions in [Supporting Information S1](#)). Behavioral information included the adults’ response in supporting and carrying the dead conspecifics.

The information compiled for all mammals, which was used for the general review on nurturant behavior toward dead conspecifics in free-ranging mammals (see “Discussion”), was based on peer-reviewed literature. The compiled list of studies presented as [Supporting Information](#) includes other type of scientific literature in order to allow a broader coverage and a larger comprehensive review. The present study focused on nurturant behavior (i.e., attention given to offspring/young), and in particular to dead conspecifics, and not to epimeletic behavior in general. Moreover, the study covered only information from free-ranging animals, given it was considered that captivity may artificially influence animals behavior. Finally, observations on animals from whaling were not considered.

RESULTS

Record #1: Risso’s dolphin, Indian Ocean (Maldives).—On July 2012, in South Maldivian waters, a tourist operator observed an adult Risso’s dolphin interacting with a dead calf (A. Gherli, White Wave Maldives, pers. comm.). Apart from the cruise boat, at least a fishing boat and a small yacht were also present in the vicinity. The adult was filmed for 2 min

while swimming with the dead animal upon its back (held by its dorsal fin). The adult was seen moving away and coming back to the carcass, swimming in circles under the carcass, touching the carcass with several parts of its body (rostrum, and pectoral and dorsal fin), and remaining in vertical position (with the head down) near the dead calf. Then, the adult pushed the carcass away from the boats, and the observers did not attempt to follow them. From the video, the dead animal was identified as a Risso’s dolphin calf based on its size and lack of rostrum. The body showed signs of decay with about 90% of the skin missing. No other information, such as presence of marks or wounds potentially related to cause of death, were visible in the video.

Record #2: Indo-Pacific bottlenose dolphin, Red Sea (Egypt).—On 17 December 2012, near the coast of Hurghada, an adult Indo-Pacific bottlenose dolphin was observed swimming and pushing a smaller dead dolphin in an advanced status of decay (M. Fumagalli, University of Otago, New Zealand; A. Cesario, The University of Hong Kong; and M. Costa, St Andrews University, United Kingdom, pers. comm.). Observations were made from a small zodiac, and no other animals were in the vicinities. The video shows the adult pushing and touching the carcass repeatedly. Then, the biologists decided to fix a rope around the fluke and dragged the carcass to the shore, where it was buried. While the carcass was being dragged, the video shows the adult following, swimming around, and touching the carcass until it reached very shallow waters. The adult was observed remaining in the area and swimming in shallow waters long after the removal of the carcass. Two days later, a biologist from the Hurghada Environmental Protection and Conservation Association (HEPCA) recovered the buried carcass and confirmed that the dolphin was a juvenile.

Record #3: spinner dolphin, Red Sea (Egypt).—On 1 September 2011, a tourist boat arrived in the protected area of Samadai reef where spinner dolphins usually rest during daylight hours. The crew immediately spotted a group of spinner dolphins swimming calmly and bobbing around a floating object in the southern lagoon of the reef. The dive guide approached the animals with a small zodiac and noticed an adult dolphin pushing a small dead dolphin. The adult was observed pushing the carcass toward the zodiac. The carcass was lifted into the zodiac and the group of dolphins’ reaction was to circle the boat twice, with 1 individual jumping once, and then leaving the lagoon. The carcass was transported to land for members of the Egyptian Environmental Affairs Agency (EEAA) perform a necropsy before the carcass was buried. The exam showed that the dolphin was a newborn female spinner dolphin with 98 cm (total) length, and that the rostrum was broken.

Records #4–7: short-finned pilot whale, North Atlantic Ocean (Madeira).—In the south/south-east of Madeira Island, 4 different sightings, occurring in 3 different years (2 and 16 September 2007, 3 July 2009, and 11 September 2011; records #4–7, respectively), were recorded by the Madeira Whale Museum research team. The sightings lasted about 20 min each. The adults carrying dead calves were, in all cases, surrounded by other whales, with groups ranging from 8 to 30 individuals.

However, for the whole period of the observations, only 1 adult individual remained constantly in contact with the decomposed calf, using the mouth to hold it by the peduncle and fluke, while the other individuals (both adults and juveniles) swam slowly around the pair. In records #4–6, the whales were observed swimming slowly and cohesively, while in record #7, the whales were first seen swimming in different directions and then gathering around the adult and dead calf. In records #4 and #6, at least 1 member of the group was observed spy-hopping. All carcasses were classified as newborns, based on their small size and pale skin coloration (see [Supporting Information S1](#)). The carcasses presented different states of decomposition, ranging from light (with color pattern still visible) to moderate-advanced (when the skin was missing from about 90% of the body).

Record #8: short-finned pilot whale, North Atlantic Ocean (Azores).—On 25 August 2003, a group of short-finned pilot whales with a dead calf was encountered in the channel between Pico and São Jorge Islands (M. Silva and S. Magalhães, Center of the Institute of Marine Research (IMAR) & Department of Oceanography and Fisheries, University of the Azores, pers. comm.). Only the research boat was present in the area during the observation. The observation lasted 109 min and involved a single adult short-finned pilot whale interacting with a dead calf while 10 other individuals were swimming around, divided into 2 subgroups. The 1st subgroup was composed of 2 subadults and 1 calf, and the 2nd by 2 adults, 2 subadults, and 1 calf. The adult and the carcass were recorded to be closer to the 2nd subgroup. The adult carried the carcass with its mouth or pushing it with the melon. The members of the 2nd subgroup kept very close to the pair during period of observation. The carcass was in an advanced state of decay with no skin.

Record #9: short-finned pilot whale, North Atlantic Ocean (Canary Islands).—On 2 August 2013, a dispersed group of approximately 15–20 pilot whales was observed off La Gomera Island in calm sea conditions (F. Ritter, M.E.E.R. e.V. Bundesallee, Berlin, pers. comm.). The observation lasted 5 min. When the boat approached the group at a distance of about 100 m, a whale carrying either a dead pilot whale calf or a smaller dolphin was spotted. The dead animal showed signs of decomposition, and due to the body size, it was considered to be a juvenile.

Record #10: sperm whale, North Atlantic Ocean (Azores).—On September 1997, during a whale-watching trip (R. Seitre and S. Viallelle, Espaço Talassa team, Azores, pers. comm.), a group of approximately 10 sperm whales was seen south of Pico Island. Only 1 boat was present and 2 photographers dropped in the water far in front of the group. An adult female sperm whale (based on the body size) was swimming in front of the group with a dead calf in her mouth. While the photographers were around the boat, some sperm whales, including the female and the dead calf, passed under the boat, and the other whales were observed to gather in small groups. Approximately 6 h later, the female was sighted again, but alone with the carcass.

Record #11: killer whale, North Pacific Ocean (Washington).—On 10 September 2010, during a study on Southern Resident killer whales in Haro Strait off of San Juan

Island, Washington, a 24-year-old female (known as L72) accompanied by L105, her 6-year-old son (her only known offspring), was noticed with a dead neonate in her mouth. Individual identities and age/sex were confirmed by comparison of photos to a long-term photo-identification catalogue. The neonate was neutrally buoyant, indicating it had not been dead for long. No information was available to assess whether it was stillborn or born alive. Based on estimated size, it was likely full term and was identified as a female based on photos of the genital area. The umbilicus was still attached and visible as were obvious fetal folds, and L72's genital area and teats were also distended, indicating she had given birth to the calf. L72 was at least 1 km away from the rest of the killer whales that were spread out and foraging. L105 was nearby the entire time but was not seen to interact with the neonate. L72 was observed carrying the calf on her rostrum, but every few surfacings had to double back and retrieve it. When she was seen by whale watching boats the next day, the neonate was not seen. In subsequent encounters with L72 (within a week), the behavior appeared normal. She was observed in her typical social group and foraging normally.

Records #12–14: Australian humpback dolphin, Queensland (Australia).—Nurturant behaviors displayed by Australian humpback dolphins were recorded on 3 different occasions (22 September 2006, 16 September 2010, and 6 July 2014; records #12–14, respectively) in the inshore waters of the southern Great Barrier Reef Marine Park and World Heritage Area. In record #12, 2 individuals, an adult and a juvenile humpback dolphin, were observed near a floating dead calf. The observation lasted for 20 min, until weather conditions deteriorated. The adult was identified from photo-identification data as being a female (individual #132) and she was assumed to be the mother of the calf as no other adult dolphin was present in the area. The adult was seen circling around the carcass, and occasionally trying to push it forward with her melon. The carcass was estimated to be several days old. In record #13, a carcass of a humpback dolphin calf was observed floating in the Fitzroy River. An adult (individual #181), identified as the mother by both photo-identification and genetic data, was observed circling around the carcass. The mother always remained within 1 body length from the carcass and tried repeatedly to move it with her melon. For the entire observation (32 min), a group of other 6 dolphins, 4 adults and 2 juveniles, remained within 100 m of the pair. The same adult female humpback dolphin was observed with a live calf 8 days before this sighting. One side of the carcass' body was sunburnt and the tongue was distended; due to the cold weather conditions, it was likely that the juvenile died at least the day before. The carcass was not recovered but samples were taken from both the adult and the carcass for genetic analyses. In record #14, a group composed of 1 juvenile and 3 adult humpback dolphins was spotted near Yeppoon in Keppel Bay. One of the adults (individual #224) was seen carrying a dead calf and briefly attempting to hold the calf at the surface with the melon and rostrum on 3 occasions. After 13 min, the adult abandoned the carcass. The carcass

was identified as newborn, probably a stillborn, based on its body size and color.

DISCUSSION

This study adds 5 species to the list of mammals displaying intraspecific nurturant behavior toward dead calves, either by supporting or carrying the young at the surface. These are Indo-Pacific bottlenose dolphins, spinner dolphins, sperm whales, killer whales, and Australian humpback dolphins. It also adds information on this type of behavior for Risso's dolphins and short-finned pilot whales, where documented events of such cases in the literature are scarce (Palacios and Day 1995; Norris and Prescott 1961; see Supporting Information S2). Furthermore, the 14 events described in the present study occurred over a wide geographic range, having been recorded in the North and South Pacific, in several regions of the North Atlantic, and in the Indian Ocean, including the Red Sea. This supports that nurturant behavior toward dead young is commonly displayed in cetaceans and that it occurs worldwide. This is corroborated by the fact that such behavior has been described in other species as well, including common bottlenose dolphins (*Tursiops truncatus*), belugas (*Delphinapterus leucas*), Franciscana (*Pontoporia blainvillei*), and humpback whales (*Megaptera novaeangliae*), and in a diversity of habitats including oceanic waters, bays, rivers, and inlets (Caldwell and Caldwell 1966; Smith and Sleno 1986; Cockcroft and Sauer 1990; Cremer et al. 2006).

The compilation of studies describing intraspecific nurturant behavior toward dead cetaceans in the wild (see Supporting Information S2) evidences that all reports on odontocetes. Possible explanations are that baleen whales: 1) exist in much lower numbers (species and abundance) than odontocetes (that includes delphinids) worldwide, 2) inhabit more offshore/oceanic waters during their migratory courses when compared with odontocetes that can more easily be observed in coastal areas, 3) have more difficulties in carrying carcasses for longer periods due to the absence of teeth, and 4) exhibit less chances of alloparental care (due to generally living in small groups). Nevertheless, the behavioral patterns were observed to be similar in both taxonomic groups (Krushinskaya 1986). All reports found of baleen whales displaying nurturant behavior toward dead were related with whaling episodes (Caldwell and Caldwell 1966), which were not considered in this study (as well as in Supporting Information S2).

Nurturant behavior toward dead young, which may include individuals in a wide range of decay (see Supporting Information S2), has been also described in other marine mammals, as well as in terrestrial relatives (see Supporting Information S3). It has been reported in sea otters, manatees, and seals (Kenyon 1969; Hartman 1979; Rosenfeld 1983), as well as in elephants, giraffes, chimpanzees, and lemurs (Nakamichi et al. 1996; Payne 2003; Biro et al. 2010; Bercovitch 2013). This suggests that such behavior is common and widespread in many mammalian species and occurs globally.

In this study, different behaviors were observed on how the cetacean adults support and carry the dead young. These

include using the dorsal fin, the melon, or the rostrum (by typically holding the carcass's fins or peduncle with the mouth). Other behaviors displayed by the adults include stationing near the floating carcass, circling the carcass, and in 1 case (in the Risso's dolphin, record #1), the adult was observed in vertical position (with the head down) near the carcass. The latter behavior, together with circling and touching the carcass, constitutes new information for that species. As well, holding the carcass's fluke also constitutes new information for short-finned pilot whales. Nevertheless, the behavioral responses described here are generally in agreement with other studies (e.g., Caldwell and Caldwell 1966; Connor and Norris 1982; Fertl and Schiro 1994; Alves et al. 2015). Different behaviors in cetaceans have been described in the literature, such as sexual activity, but only when toward dead adults (Dudzinski et al. 2003; Park et al. 2013), or in interspecific interactions (Parsons 1998). In terrestrial mammals, the mother's range of interaction with dead offspring is also wide, from staying nearby the carcass to carrying it. For example, giraffes (*Giraffa camelopardalis rothschildii* and *G. c. thornicrofti*) were reported to sniff, nuzzle, and inspect a carcass (Muller 2010; Bercovitch 2013). African elephants (*Loxodonta africana*) are known to stay in an evident state of distress near a dead or dying calf (Douglas-Hamilton et al. 2006). Common chimpanzees (*Pan troglodytes*) have been observed carrying (usually between neck and shoulder) and grooming a dead infant (Biro et al. 2010), and gelada monkeys (*Theropithecus gelada*) carrying (usually in the mouth) a dead infant for so long that the bodies mummified (Fashing et al. 2011). Ring-tailed lemurs (*Lemur catta*) have been described moving back and forth between a dead infant and their troop (Nakamichi et al. 1996). Dingos (*Canis dingo*) have been observed carrying a dead pup along the litter and sleeping area (Appleby et al. 2013), and wolves (*C. lupus*) have been seen burying a dead pup (Boyd et al. 1993).

The age class of the dead young (see Supporting Information S1) was determined in all 14 records in the present study. These include 8 newborns, 3 calves, and 3 juveniles (see Supporting Information S4). In the case of the common chimpanzee, the age of the dead young may range up to 2.6 years old (Biro et al. 2010), and in the common squirrel monkey (*Saimiri sciureus*) and Japanese macaque (*Macaca fuscata*), the older the dead infant is, the shorter period of time it will be carried (Kaplan 1973; Sugiyama et al. 2009).

In the present study, the gender was confirmed in only 3 of the adults and 2 of the dead young, and all were females. These adults correspond to the killer whale (from record #11) and the Australian humpback dolphins (from records #12 and #13), while the dead young correspond to the spinner dolphin (from record #3) and the killer whale (from record #11). Although it could be expected for the adults involved with the dead young to be their mothers, as presumed in several records in this study, such parental bond was only confirmed in records #11 and #13 (see "Results"). This agrees with most of the described cases in the literature when the sex of both the adult and the dead young were known, in both marine (e.g., Lodi 1992; Ritter 2007) and terrestrial mammals in which motherhood is easier to assess

(e.g., Sugiyama et al. 2009; Bercovitch 2013). Nevertheless, in future events of similar nature, researchers should be aware that the adult involved with the dead young can be a male, as shown by a short-finned pilot whale (Herrero and Martín 2010), a common chimpanzee (Kooriyama 2009), and in macachi (Merz 1978; Taylor et al. 1978).

In this study, 3 pairs of adults and their dead conspecifics were observed with no other animals in the vicinity. In the remaining records, the other individuals of the group did not interact with the carcass but were observed swimming cohesively and slowly around the pair, with the exception of the short-finned pilot whales from record #7 and the killer whales (record #11). In the former case, the whales gathered around the pair in a protective behavior (which constitutes new information for the species), and in the latter, the older brother of the dead calf was seen near the mother/infant pair. The presence of multiple individuals from the same group around a dead young, as observed in this study, has been also described in other studies with cetaceans (e.g., Cockcroft and Sauer 1990; Ritter 2007). And in terrestrial mammals, this behavioral pattern is also commonly reported, with the mother and dead infant being rarely left alone, as observed, for example, in African elephants and common chimpanzees (Biro et al. 2010; King 2013). Generally, in primates, the attention toward dead infants is not restricted to the infants' mothers given that juvenile females and even females from other groups have been observed carrying them (Anderson 2011). In some cases, as for macachi and baboon species, males of the group were observed defending the mother/infant pair (Merz 1978; Mori et al. 1997).

What are the possible explanations for such nurturant behavior toward dead young? Dolphins, and generally all odontocetes, as well as other marine and terrestrial mammal species documented displaying such behavior (Supporting Information S3), are gregarious animals (Whitehead and Mann 2000). Many of these species are known to rely on cooperation and social bonds, which often includes allomothering (Bates et al. 2008). In some mammal species, as of dolphins and nonhuman primates, the calves were in care of adults that were not the parents (Mann and Smuts 1998), which could include adoption (Riedman 1982; Anderson 2011). From that perspective, epimeletic behaviors between members of the same group may be very useful for the survival of relatives (Smith 1964; Kuczaj et al. 2015) and can have a positive evolutionary adaptive consequence (Cockcroft and Sauer 1990).

While it is not mutually exclusive, Smith and Sleno (1986) and Kilborn (1994) proposed that such behaviors may be a result from the incapacity of the mother to accept the death of an offspring. It is known that females are considered to be the caretakers of young, while males seem to have a minor role in such activity (Brodie 1969; Fertl and Schiro 1994). The long period of infant dependency in cetaceans appears to correspond to an intense learning period for the calf (Brodie 1969). And this period of infant dependency can be prolonged, depending on the species, up to 6 or 8 years (Mann et al. 2000). The "normal" nurturant behavior of dolphin mothers toward their calves is clearly evident during lactation (Cockcroft and Ross 1990). This is supported by observations of mothers and other

adults of a group trying to rescue calves from nets or other dangers (Pilleri 1984). In nonhuman primates, it is suggested that it could be a way of showing a "mourning attitude" to subadult females from the group (Warren and Williamson 2004) or simply due to hormonal causes (Biro et al. 2010).

Another theory, which was proposed to explain a belugas similar behavior but toward a variety of objects (e.g., a caribou skeleton), suggests this behavior could be a form of play rather than a nurturant one (Smith and Sleno 1986; Shane 1994). This may be supported by juvenile common chimpanzees that showed play-oriented behavior toward dead infants (Kooriyama 2009; Biro et al. 2010). Furthermore, cetaceans have been also reported to display interspecific epimeletic behavior, similar to those toward dead conspecifics (Norris and Prescott 1961). That included mainly other cetacean species, but in some cases also different taxonomic groups such as sea otters, turtles, or sharks (Caldwell and Caldwell 1966; Herzen and dos Santos 1992; Fertl and Schiro 1994; Fertl and Fulling 2007). While the intraspecific epimeletic behavior could be explained by kin selection, even for other mammalian species, the interspecific one is more difficult to interpret, and may be a form of object-oriented play, as reported for Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) playing with a neonate harbor porpoise (*Phocoena phocoena*—Baird 1998). In the cases we report, such an explanation seems unlikely, given that the individuals expressing such behavior were adults and the behavior was directed toward young conspecifics, many of which were the likely the offspring of the adults involved. As noted by King (2013), nurturant behavior toward dead young in long-lived and highly sociable mammalian species likely represents the individuals mourning their dead conspecifics, reflecting the strong social bonds in group-living species where cooperation in acquiring food and raising offspring is critical for survival.

ACKNOWLEDGMENTS

Special thanks to the following persons that helped collecting and/or provided images/data/information to the present study: A. Gherli (on record #1); A. Cesario, M. Costa, and M. Fumagalli (on record #2); the rangers from the Egyptian Environmental Affairs Agency in Marsa Alam (on record #3); A. Dinis, C. Ribeiro, R. Ferreira, and C. Silva (on records #4–7); M. Silva and S. Magalhães (on record #8); F. Ritter (on record #9); R. Seitre and S. Viallelle (on record #10); and C. K. Emmons (on record #11). F. Alves was partially supported by the Oceanic Observatory of Madeira (M1420-01-0145-FEDER-000001-OOM) and by ARDITI - Madeira's Regional Agency for the Development of Research, Technology and Innovation (Madeira 14-20-FSE). Special thanks to an anonymous reviewer for valuable suggestions and contributions for the literature review, which was a precious help.

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online

(jmmamm.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Definition of age classes used in this study.

Supporting Information S2.—List of studies describing intra-specific nurturant behavior toward dead in free-ranging cetaceans, including general information.

Supporting Information S3.—List of species displaying epimeletic behavior toward dead offspring in mammalians, except cetaceans (that are covered in [Supporting Information S2](#)).

Supporting Information S4.—Data reports for each of the 14 records described in this study.

LITERATURE CITED

- ALVES, F., C. NICOLAU, A. DINIS, C. RIBEIRO, AND L. FREITAS. 2015. Supportive behavior of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) toward dead neonates, with data on perinatal mortality. *Acta Ethologica* 18:301–304.
- ANDERSON, J. R. 2011. A primatological perspective on death. *American Journal of Primatology* 73:410–414.
- APPLEBY, R., B. SMITH, AND D. JONES. 2013. Observations of a free-ranging adult female dingo (*Canis dingo*) and littermates' responses to the death of a pup. *Behavioural Processes* 96:42–46.
- BAIRD, R. W. 1998. An interaction between Pacific white-sided dolphins and a neonatal harbor porpoise. *Mammalia* 62:129–134.
- BATES, L. A., ET AL. 2008. Do elephants show empathy? *Journal of Consciousness Studies* 15:204–225.
- BERCOVITCH, F. B. 2013. Giraffe cow reaction to the death of her newborn calf. *African Journal of Ecology* 51:376–379.
- BIRO, D., T. HUMLE, K. KOOPS, C. SOUSA, M. HAYASHI, AND T. MATSUZAWA. 2010. Chimpanzee mothers at Bossou, Guinea carry the mummified remains of their dead infants. *Current Biology* 20:R351–R352.
- BOYD, D. K., D. H. PLETSCHER, AND W. G. BREWSTER. 1993. Evidence of wolves, *Canis lupus*, burying dead wolf pups. *Canadian Field-Naturalist* 107:230–231.
- BRODIE, P. F. 1969. Duration of lactation in Cetacea: an indicator of required learning? *American Midland Naturalist* 82:312–314.
- CALDWELL, M. C., AND D. K. CALDWELL. 1966. Epimeletic (care-giving) behavior in Cetacea. Pp. 755–789 in *Whales, porpoises and dolphins* (K. S. Norris, ed.). University of California Press, Berkeley.
- CAUGHLEY, G. 1966. Mortality patterns in mammals. *Ecology* 47:906–918.
- COCKCROFT, V. G., AND G. J. B. ROSS. 1990. Observations on the early development of a captive bottlenose dolphin calf. Pp. 461–478 in *The bottlenose dolphin* (S. Leatherwood and R. R. Reeves, eds.). Academic Press, New York.
- COCKCROFT, V. G., AND W. SAUER. 1990. Observed and inferred epimeletic (nurturant) behavior in bottlenose dolphin. *Aquatic Mammals* 16:31–32.
- CONNOR, R. C., AND K. S. NORRIS. 1982. Are dolphins reciprocal altruists? *American Naturalist* 119:358–374.
- CREMER, M. J., F. A. S. HARDT, AND A. J. T. JÚNIOR. 2006. Evidence of epimeletic behavior involving a *Pontoporia blainvillei* calf (Cetacea, Pontoporiidae). *Biotemas* 19:83–86.
- DOUGLAS-HAMILTON, I., S. BHALLA, G. WITTEMYER, AND F. VOLLRATH. 2006. Behavioural reactions of elephants towards a dying and deceased matriarch. *Applied Animal Behaviour Science* 100:87–102.
- DUDZINSKI, K. M., M. SAKAI, K. MASAKI, K. KOGI, T. HISHII, AND M. KURIMOTO. 2003. Behavioral observations of adult and sub-adult dolphins towards two dead bottlenose dolphins (one female and one male). *Aquatic Mammals* 29:108–116.
- FASHING, P. J., ET AL. 2011. Death among geladas (*Theropithecus gelada*): a broader perspective on mummified infants and primate thanatology. *American Journal of Primatology* 73:405–409.
- FERTL, D., AND G. L. FULLING. 2007. Interactions between marine mammals and turtles. *Marine Turtle Newsletter* 115:4–8.
- FERTL, D., AND A. SCHIRO. 1994. Carrying of dead calves by free-ranging Texas bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals* 20:53–56.
- HARTMAN, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. Special Publication No. 5. The American Society of Mammalogists. Pittsburgh, Pennsylvania.
- HERRERO, R., AND V. MARTÍN. 2010. Amazing pilot whale footage. <http://zendesk.wetpixel.com/articles/amazing-pilot-whale-footage-by-rafa-herrero>. Accessed 16 January 2015.
- HERZEN, S., AND M. E. DOS SANTOS. 1992. Three encounters with wild bottlenose dolphins (*Tursiops truncatus*) carrying dead calves. *Aquatic Mammals* 18:49–55.
- KAPLAN, J. 1973. Responses of mother squirrel monkeys to dead infants. *Primates* 14:89–91.
- KENYON, K. W. 1969. Sea otter in eastern Pacific Ocean. *North American Fauna* 68:1–352.
- KILBORN, S. S. 1994. Object carrying in a captive beluga whale (*Delphinapterus leucas*) as a possible surrogate behavior. *Marine Mammal Science* 10:496–501.
- KING, B. 2013. When animals mourn. *Scientific American* 309:62–67.
- KOORIYAMA, T. 2009. The death of a newborn chimpanzee at Mahale: reactions of its mother and other individuals to the body. *Pan African News* 16:19–21.
- KRUSHINSKAYA, N. L. 1986. The behaviour of cetaceans. *Invest Cetacea* 19:115–273.
- KUCZAJ, S. A., II, E. E. FRICK, B. L. JONES, J. S. E. LEA, D. BEECHAM, AND F. SCHNÖLLER. 2015. Underwater observations of dolphin reactions to a distressed conspecific. *Learning & Behavior* 43:289–300.
- LODI, L. 1992. Epimeletic behavior of free-ranging rough-toothed dolphin, *Steno bredanensis* from Brazil. *Marine Mammal Science* 8:284–287.
- MANN, J., R. C. CONNOR, L. M. BARRE, AND M. R. HEITHAUS. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology* 11:210–219.
- MANN, J., AND B. B. SMUTS. 1998. Natal attraction: allomaternal care and mother–infant separations in wild bottlenose dolphins. *Animal Behaviour* 55:1097–1113.
- MERZ, E. 1978. Male-male interactions with dead infants in *Macaca sylvanus*. *Primates* 19:749–754.
- MORI, A., T. IWAMOTO, AND A. BEKELE. 1997. A case of infanticide in a recently found gelada population in Arsi, Ethiopia. *Primates* 38:79–88.
- MULLER, Z. 2010. The curious incident of the giraffe in the night time. *Giraffa* 4:20–23.

- NAKAMICHI, M., N. KOYAMA, AND A. JOLLY. 1996. Maternal responses to dead and dying infants in wild troops of ring-tailed lemurs at the Berenty Reserve, Madagascar. *International Journal of Primatology* 17:505–523.
- NORRIS, K. S., AND J. H. PRESCOTT. 1961. Observations of Pacific cetaceans of California and Mexican waters. University of California Publications in Zoology 63:291–402.
- PALACIOS, D. M., AND D. DAY. 1995. A Risso's dolphin (*Grampus griseus*) carrying a dead calf. *Marine Mammal Science* 11:593–594.
- PARK, K. J., H. SOHN, Y. R. AN, D. Y. MOON, S. G. CHOI, AND D. H. AN. 2013. An unusual case of care-giving behavior in wild long-beaked common dolphins (*Delphinus capensis*) in the East Sea. *Marine Mammal Science* 29:508–514.
- PARSONS, E. C. M. 1998. The behaviour of Hong Kong's resident cetaceans: the Indo-Pacific hump-backed dolphin and the finless porpoise. *Aquatic Mammals* 24:91–110.
- PAYNE, K. 2003. Sources of social complexity in the three elephant species. Pp. 57–85 in *Animal social complexity: intelligence, culture, and individualized societies* (F. B. M. de Waal and P. L. Tyack, eds.). Harvard University Press, Cambridge, Massachusetts.
- PILLERI, G. 1984. Epimeletic behaviour in Cetacea: intelligent or instinctive? *Investigations on Cetacea* 16:30–48.
- RIEDMAN, M. L. 1982. The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology* 57:405–435.
- RITTER, F. 2007. Behavioral response of rough-toothed dolphin to a dead newborn calf. *Marine Mammal Science* 23:429–433.
- ROSENFELD, M. 1983. Two female northwest Atlantic harbor seals (*P. vitulina concolor*) carry dead pups with them for over two weeks - some unusual behavior in the field and its implication for a further understanding of maternal investment. Abstract, pp. 87, in the 5th Biennial Conference on Biology of Marine Mammals, 27 November–1 December, Boston, Massachusetts.
- SCOTT, J. P. 1958. *Animal behavior*. University of Chicago Press, Chicago, Illinois.
- SHANE, S. H. 1994. Pilot whales carrying dead sea lions. *Mammalia* 58:494–498.
- SMITH, J. M. 1964. Group selection and kin selection. *Nature* 201:1145–1147.
- SMITH, T. G., AND G. A. SLENO. 1986. Do white whales, *Delphinapterus leucas*, carry surrogates in response to early loss of their young? *Canadian Journal of Zoology* 64:1581–1582.
- SUGIYAMA, Y., H. KURITA, T. MATSUI, S. KIMOTO, AND T. SHIMOMURA. 2009. Carrying of dead infants by Japanese macaque (*Macaca fuscata*) mothers. *Anthropological Science* 117:113–119.
- TAYLOR, H., J. TEAS, T. RICHIE, C. SOUTHWICK, AND R. SHRESTHA. 1978. Social interactions between adult male and infant rhesus monkeys in Nepal. *Primates* 19:343–351.
- WARREN, Y., AND E. A. WILLIAMSON. 2004. Transport of dead infant mountain gorillas by mothers and unrelated females. *Zoo Biology* 23:375–378.
- WHITEHEAD, H., AND J. MANN. 2000. Female reproductive strategies of cetaceans: life histories and care. Pp. 219–246 in *Cetacean societies: field studies of dolphins and whales* (J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead, eds.). University of Chicago Press, Chicago, Illinois.

Submitted 30 March 2015. Accepted 2 May 2016.

Associate Editor was Jeanette A. Thomas.