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Infanticide attacks and associated epimeletic behaviour in free-ranging common bottlenose dolphins (*Tursiops truncatus*)

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Infanticide is considered a conspicuous expression of sexual conflict amongst mammals, including bottlenose dolphins. Although reported previously in this species, confirmed cases of infanticide and associated epimeletic behaviour are very rare and their socio-behavioural context remains poorly understood. Here, we provide evidence of epimeletic and infanticide behaviours in free-ranging bottlenose dolphins in Galicia, NW Spain. After describing the observed events, we include a complete description of the post-mortem examinations (where the carcasses were recovered) in order to confirm the cause of death. With evidences of blunt trauma in two of the presented cases, we confirm that the calves were intentionally killed by adult individuals. The aggressive interaction between adult individuals and the neonates together with the observed ante-mortem injuries bore a strong resemblance to the behaviours and traumatic injuries described in other cases of violent dolphin interactions in other parts of the world. The circumstances under which these infanticides occurred at our site fit the conditions proposed under the sexual selection hypothesis. The difficulties for researchers to observe this type of behaviour in the field and to find carcasses in good enough condition to determine the cause of death, emphasizes the importance of this type of study.

Keywords: infanticide, epimeletic behaviour, bottlenose dolphin, socioecology, traumatic injuries, care giving

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INTRODUCTION

The primary reasons for group formation in mammals are suggested to be environmental variables such as protection and prey resources (Alexander, 1974). Female grouping patterns tend to be more directly related to these parameters, while male social strategies are more related to mate access (Trivers, 1972; Connor *et al.*, 2000).

Infanticide by males, or the killing of dependent offspring by males, is considered one of the most conspicuous expressions of sexual conflict between males and females in mammalian societies (Hrdy, 1979; Palombit, 2015). It is regularly observed in primates, equids, rodents, carnivores and cetaceans (van Schaik, 2000). These are species in which lactation is longer than gestation and females experience lactational amenorrhea, so postpartum mating does not occur (van Schaik, 2000). Males, therefore, benefit from killing a female's offspring if they are not the sire, if they can mate with the female when she returns to oestrous, and if they have a chance of siring her next offspring (i.e. the sexual selection hypothesis; Hrdy, 1979). This would suggest, therefore, that adult males who have not invested time and energy toward rearing the offspring may carry out infanticide and gain the chance to mate with the newly receptive female whose infant has been killed.

Bottlenose dolphins have relatively long inter-birth periods during which time young are dependent on the mother (Mann & Smuts, 1998). If a female loses her offspring prematurely, she soon becomes sexually receptive, reducing time between births (Hrdy, 1979). The first description of infanticide by common bottlenose dolphins (*Tursiops truncatus*, Montagu 1821), and by any cetacean species, was done by Patterson *et al.* (1998) from post-mortem examinations of stranded specimens in the Moray Firth (Scotland). Direct observations of this behaviour at sea are rare, which makes it difficult to understand the context or the cause of such infanticide. To date, only three cases of observed or suspected infanticide have been witnessed in long-term studies of common bottlenose dolphins. The most detailed and compelling description of calf-directed aggression by males in the field was recorded by Robinson (2014) during a long-term study on *T. truncatus* at Moray Firth, in Scotland, where several adult males directed an attack towards an adult female and her male infant; after intense fighting, the infant was severely injured. Two other additional cases of suspected infanticide attacks have also been reported for *T. truncatus* by Kaplan *et al.* (2009) off the coast of Florida and Perrtree *et al.* (2016) in Georgia (USA). All these observations were considered an attempt of infanticide based on the nature of the attacks; nonetheless the calf did not die suddenly after the attacks. In all these cases the causes of the death of the calves were not supported

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by post-mortem examinations because it was not possible to recover the carcasses.

Although reported previously in this species, cases of infanticide and associated epimeletic behaviour are very rare and their socio-behavioural context remains poorly understood (Reggente *et al.*, 2016). Epimeletic behaviour, care or attention giving, can be associated with an infanticide episode. This assistance is generally conducted by a healthy adult dolphin (presumably the mother) swimming with a dead or incapacitated calf, helping it to stay floating at the surface, or maintaining it away from an apparent source of danger (Cockcroft & Sauer, 1990; Connor & Smolker, 1990; Harzen & dos Santos, 1992; Fertl & Schiro, 1994; Félix, 1994; Ritter, 2007; Moura *et al.*, 2009).This type of behaviour may be considered generally adaptive for the survival of possibly genetically related individuals within specific groups (Cockcroft & Sauer, 1990), particularly for dolphins that appear to be dependent on group structure for survival (Norris & Dhol, 1980).

Here, we provide evidence of infanticide and associated epimeletic behaviours in free-ranging bottlenose dolphins along the NW coast of Spain. After describing the observed events, we include a complete description of the post-mortem examinations (where the carcasses were recovered) in order to confirm the cause of the death. Furthermore, we discuss the potential factors that may help explain the observed behaviours and the implications for understanding dolphin socioecology.

MATERIALS AND METHODS

Data for this study were collected as part of a longitudinal study of common bottlenose dolphins inhabiting the Galician coast, Spain (Figure 1). Galicia is a region situated in the north-west of the Iberian Peninsula with 1195 km of coastline, where there are a series of ancient drowned tectonic valleys that were taken over by the sea (also referred to as 'rías') (Evans & Prego, 2003).

Systematic recording of stranded cetaceans along the Galician shoreline commenced in 1990 with the establishment of the NGO Coordinadora para o Estudio dos Mamiferos Mariños (CEMMA), a group which records strandings, conducts boat and land-based surveys, carries out necropsies and provides samples for biological studies (López, 2003; Santos *et al.*, 2007; Pierce *et al.*, 2010; Fernández *et al.*, 2011; Louis *et al.*, 2014). Since 2014, as a result of the cooperation between the CEMMA and the Bottlenose Dolphin Research Institute (BDRI), regular year-round boat surveys were conducted as part of a multi-year mark–recapture study along Galician waters, improving the photo-identification work carried out by the CEMMA (Fernández *et al.*, 1996; Vázquez *et al.*, 2006; López *et al.*, 2011). Individuals were identified by photo-identification based on the distinctive characteristics of their dorsal fins and surrounding area as unique natural markers (Würsig & Jefferson, 1990). Sex was determined primarily by observations and photographs of the genital region. Digital photographs and videos were taken using DSLR cameras equipped with telephoto zoom lenses.

This study reports three cases, provided by the Galician Marine Mammal Stranding Network (coordinated by the CEMMA), of free-ranging bottlenose dolphin reactions to dead calves and the results of the necropsy examinations. The described field observations are presented chronologically, as

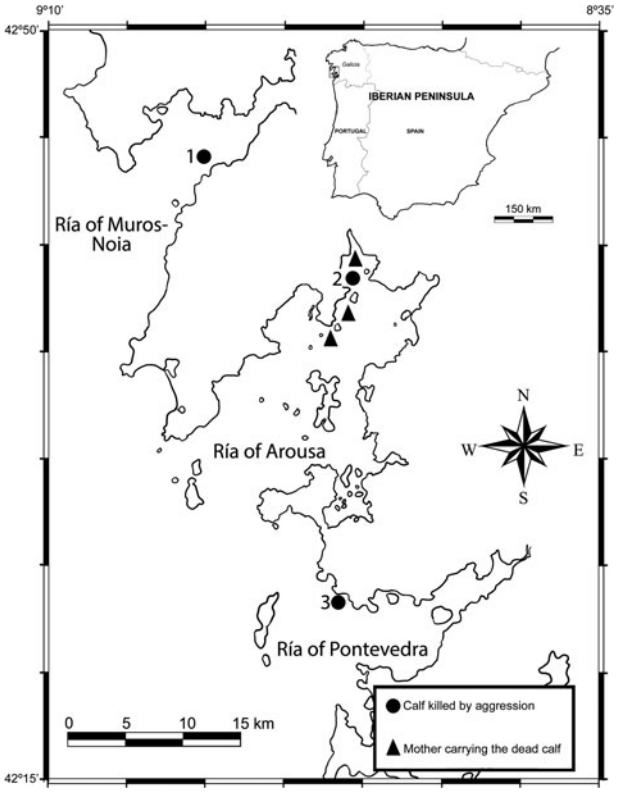

Fig. 1. Geographic locations of the three reported cases of calf-directed aggression carried out by adult common bottlenose dolphins (represented by circles) and cases of observed epimeletic behaviour (one reported and two anecdotal cases represented by triangles), in Galicia (NW Spain).

observed, filmed and photographed from two motor vessels (cases 1 and 3) and the BDRI research vessel (case 2). Onboard the BDRI research vessel, six observers monitored the bottlenose dolphins, either with the naked eye or with binoculars, in order to collect behavioural data and to record changes in group composition. During these observations, continuous data (Altmann, 1974) were collected on the behaviour and occurrence of affiliative and agonistic interactions between the participants, including the identities of actors and recipients and the time of onset and termination for each bout.

In two of the three observed cases (cases 2 and 3), the carcass of the calf was recovered immediately after the field observations, and necropsied within 24 h according to a standard protocol defined by the European Cetacean Society (Kuiken, 1996). Photographs of the necropsy were taken. Dead calves were measured, weighed, sexed and classified following Smithsonian Condition Codes (Geraci & Lounsbury, 2005). The carcasses received a complete standard necropsy with systematic examination of all organ systems. Necropsies were attended by experienced personnel of the CEMMA.

RESULTS

– Case 1. Ría of Muros, 14 July 2014.

Field observations

Opportunistic observers in a motor boat reported to the CEMMA the observation of one group of bottlenose dolphins

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in the Ría of Muros (42°44.29′N 009°00.22′W; UTM 29T, *x* 499,700, *y* 4,731,740, Figure 1). The observation supported by photographs began at 17:00 h UTC and lasted around 30 min.

At 17:00 h a group of bottlenose dolphins were seen moving hurriedly close to the shore. An adult bottlenose dolphin accompanied by a neonate in echelon position (Figure 2A) were observed, together with at least six other bottlenose dolphin adults circling around. For the next 20 min, the adults were seen harassing the adult-neonate pair in an apparently coordinated manner, with some perpetrators sandwiching the pair while others rammed and separated the neonate from the accompanying adult (presumably the mother) and occasionally tossed the neonate out of the water (Figure 2B). Subsequently, surface activity increased with tail slaps, after which an adult resurfaced with the calf lying motionless on its head. During the next minutes it was possible to observe the accompanying adult (presumably the mother) lifting the corpse above the surface.

The adult individuals present in the observed group were not identified from previous encounters by the authors. Opportunistic observers confirmed the death of the neonate by the observation of the body floating motionless at the surface of the water. Unfortunately, it was not possible to retrieve the body of the dead calf but the cause of death was likely to be related to the aggressive interactions.

– Case 2. Ría de Arousa, 11 September 2016.

Field observations

At 11:30 UTC on 11 September 2016, the Galician stranding network was notified of a dead newborn bottlenose dolphin floating in the Bay of Rianxo at 42°36.98′N 008°49.91′W (UTM 29T, *x* 520,300, *y* 4,694,349), 9.4 m depth, and ∼0.4 nautical miles from the coast (Figure 1). Upon the arrival of the BDRI's research vessel at 13:00 h, local fishermen related having observed other bottlenose dolphins swimming around the carcass. According to the local fishermen, the dolphins were continuously pushing the carcass away from their boat and towards the surface with their rostrum and other parts of their bodies.

The behavioural activities of the group of dolphins were monitored continuously from the arrival of the researchers, between 13:09 and 15:25 h (UTC). The research vessel remained in the same position (at a distance of around 100 m from the dolphins) to minimize the effect of the observers' presence on the dolphins' behaviour. The following events are presented chronologically, as observed, filmed and photographed from the research vessel.

13:09 UTC – A group of bottlenose dolphins was observed swimming between mussel rafts in close formation at ∼400 m from the shore in the inner part of the Ría of Arousa. The presence of a dead newborn was confirmed together with two adult bottlenose dolphins swimming around the carcass. Both adults were identified by direct observation of their dorsal fins (one male known as ID#A9 and one female known as ID#C7). The female (ID#C7) was keeping the dead calf afloat, while the male (ID#A9) circled around them in an anticlockwise direction.

13:20 UTC – All at once, the two adult individuals became notably more active. Suddenly the large adult male dolphin (ID#A9) rapidly emerged pushing the body of the newborn calf underwater.

13:26 UTC – The male (ID#A9) began circling energetically with continuous tail stock dives with abrupt changes in direction. The mother then positioned herself between the calf and male (ID#A9) as he circled around them.

13:28 UTC – The mother held the dead calf on her rostrum while swimming (Figure 3A). A second male dolphin (ID#C9) was spotted swimming 80 m away from the other individuals.

13:40 UTC – The male (ID#A9) launched itself directly into the mother-calf pair, driving his body between the two animals and forcing them apart. Thereafter, the same male breached and charged towards the body of the infant, holding the calf beneath the water from above.

13:46 UTC – The male aggressor (ID#A9) rammed the calf with his peduncle with enough impact that the carcass was tossed into the air 2–3 m high and flipped on its side.

13:51 UTC – The mother was observed doing sequences of regular dives followed by tail stock dives as she circled around the male (ID#A9) and the dead newborn (Figure 3B).

14:03 UTC – Followed by the male (ID#A9), the mother (ID#C7) surfaced with her dead calf lying across her back. Afterwards, the mother (ID#C7) lifted the corpse above the surface during several seconds (Figure 3C).

14:09 UTC – The female (ID#C7) was seen repeatedly trying to come in between the body of the calf and the adult male (ID#A9).

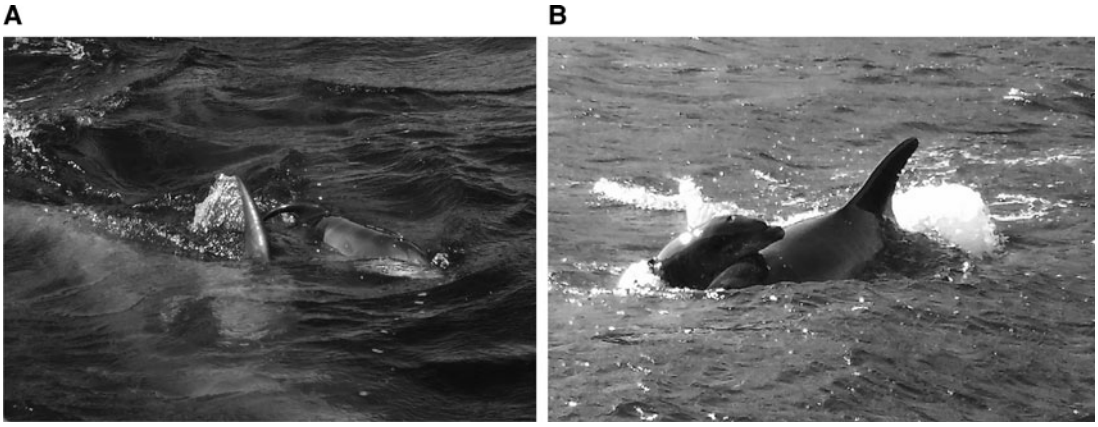

Fig. 2. Photographs authenticating the attempted infanticide of the newborn bottlenose dolphin calf observed on 14 July 2014 in the Ría of Muros (NW Spain). (A) Image of an adult bottlenose dolphin accompanied by a neonate in echelon position. The foetal folds and furled dorsal fin are still evident. (B) Image of the calf being abducted by one adult that rises partially out of the water and slaps the neonate with its front upper body and rostrum. Photographs: Miguel Prado.

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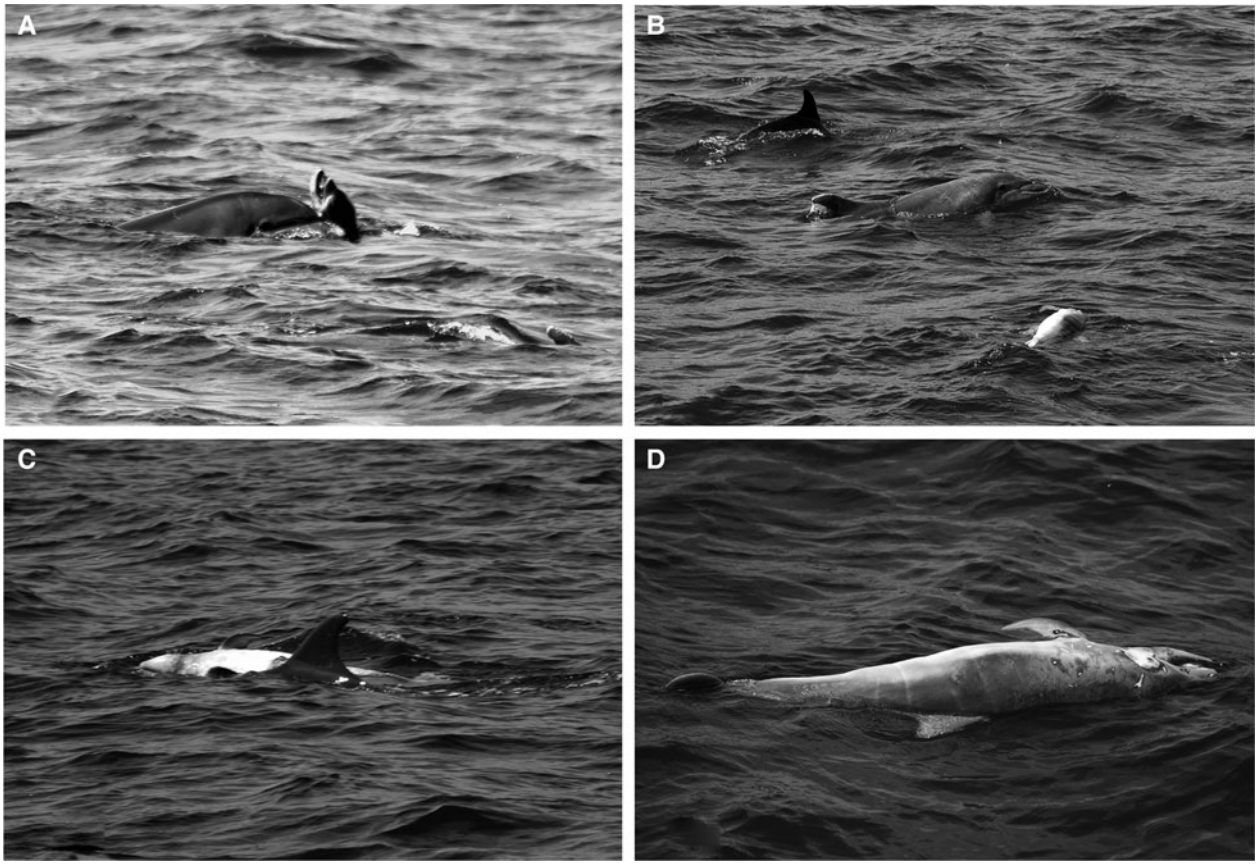

Fig. 3. Photographs of the epimeletic and infanticide behaviour observed in the Ría of Arousa (NW Spain) on 11 September 2016. (A) The female carried the carcass on its rostrum and repeatedly blocked the male (ID#A9) from reaching the dead neonate. (B) The mother doing sequences of regular dives followed by tail stock dives as she circled around the male (ID#A9) and the newborn. The foetal folds are still evident. (C) The mother (ID#C7) surfaced with her calf lying motionless across her back; she lifted the corpse above the surface. (D) The carcass of the calf before its recovery hours after the first sighting of the group.

14:19 UTC – The male (ID#A9) continued his aggressions, charging towards the calf hard from one side, and with such velocity that the newborn was launched clear out of the water.

14:21 UTC – The female carried the carcass on its rostrum and repeatedly blocked the male (ID#A9) from reaching the dead neonate.

14:28 UTC – The dead calf was pushed away from the immediate area by the male aggressor (ID#A9). Then, the mother, after a sequence of tail stock dives, got closer to the carcass and the adult (ID#A9) that was pushing it. During these social bouts, both adult dolphins exhibited rapid movements including sudden changes in direction and compact circling behaviour with repeated tail stock dives.

14:40 UTC – Over the course of several minutes the female's response, with rapid movements and tail stock dives, became gradually less vigorous. The female always remained close to the body of the calf, but was never seen in physical contact with the male aggressor (ID#A9).

14:49 UTC – After a tail stock dive and subsequent long dive period, the female – male (ID#A9) pair was observed heading south-west leaving the carcass of the newborn calf 200 m away. This pair of dolphins was swimming on a consistent course, spaced within a few body lengths of each other, and with rhythmic surfacings followed by shallow dives.

14:56 UTC – The second male dolphin appeared thereafter (known as ID#C9) and started to regroup around the female dolphin. At this point the male (ID#A9) was observed swimming on a consistent course (south) with regular dives and short ventilations.

15:02 UTC – The male (ID#A9) stayed 100 m away from the other two individuals (ID#C7 and ID#C9) swimming slowly (less than ~1 knot), with shallow dives and floating. This dolphin did not engage in any other activities during this apparently resting behaviour.

15:10 UTC – The second male (ID#C9) and the female (ID#C7) were seen exhibiting long dives and changes in direction with repeated tail stock and flukes up dives. The carcass of the calf was adrift by the swell 600 m away from the position of the adult dolphins.

15:25 UTC – All three dolphins (ID#A9, ID#C7 and ID#C9) were observed swimming on a consistent course (south), spaced within a few body lengths of each other and with synchrony ventilations followed by shallow dives. The carcass of the calf was adrift by the swell 900 m away from the position of the adult dolphins.

15:30 UTM – The research vessel moved towards the position of the dead calf to recover the carcass (Figure 3D).

All three adult individuals present during the encounter (ID#C7, ID#C9 and ID#A9) were well-known due to a long-term study of the *T. truncatus* population in this location by the authors, including data on the sex, reproductive history and associations of the animals reported since 2014. The known female detailed in the present report (ID#C7) was seen eight times in the area since first recorded by the

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authors in May 2014. Between May and September 2014 the female was observed four times in company of a 2–3-year-old calf, so we can assume that she was not a first-time mother. Mother–newborn pair was sighted for the first time during the reported encounter on 11 September 2016. The two adult males detailed in the present report (ID#A9 and ID#C9), were re-sighted 14 times and 7 times in the study area, respectively. Both the female (ID#C7) and the male (ID#C9) were seen three times together since 2014. The adult male (ID#A9) was never seen previously with the female (ID#C7).

During the period of most likely conception of the infant (between August and October 2015) a total of 58 encounters with bottlenose dolphins were done in the Ría of Arousa (N = 27 days at sea). While the female (ID#C7) was not seen during any of these encounters, both males were observed in the area during this period (ID#A9 was seen on 5 different days and ID#C9 was seen on 2 different days). Following the reported field observations on 22 September 2016 and during photo-identification surveys in the Ría of Arousa, the female (ID#C7) and the male (ID#C9)) were seen swimming in association as part of a group of bottlenose dolphins in which the male (ID#A9) was not present. This male (ID#A9) was sighted in two different groups of dolphins (23 September and 27 October) where the second male (ID#C9) and the female (ID#C7) were not present.

Summary of necropsy data

The bottlenose dolphin neonate was a male weighing 32 kg and measuring 150.5 cm from the tip of the rostrum to the tail notch. From its length, evident foetal folds, marginal papillae, rostral hairs, un-erupted teeth, and furled flukes and dorsal fin, it was estimated to be within its first days of life and therefore would still be dependent (Mead & Potter, 1990). The animal was assessed to be in good body condition, and the preservation of the carcass was determined to be between codes 2 and 3 (Geraci & Lounsbury, 2005).

The regularly spaced, parallel lacerations observed on the skin of this neonate were characteristic of rake marks produced when an adult bottlenose dolphin slides its teeth across a cutaneous surface. These lesions, mainly involving the epidermis, were organized in parallel groups of 2–4 regularly spaced lacerations on both sides of the thorax with inter-tooth distances between 11 and 13 mm.

The individual exhibited multiple, internal, ante-mortem injuries including bruising around the head and thorax, rib fractures with associated haemorrhage, large bruise on its lower jaw (Figure 4A), atlanto-occipital dislocation (Figure 4B), and the thoracic vertebrae (T-6) fractured and luxated with a concomitant severed spinal cord (Figure 4B). Rib fractures occurred only on the left side of the thorax in a linear pattern involving 1st and 2nd adjacent ribs in correspondence with the position of the scapula. Other findings included occipital haematoma, abdominal haemorrhage, liver lacerations and contusions and multiple soft tissue contusions. Soft tissue contusions and bruises were bilateral, separate and discrete.

Gross necropsy findings indicated severe blunt-force trauma was the cause of death which is consistent with the aggressive behaviours seen during our field observation. The pattern of bilateral, multiple fractures and discrete soft tissue injuries, suggests repeated trauma and trauma inflicted from multiple directions.

– Case 3. Ría de Pontevedra, 12 September 2016.

Field observations

On 12 September 2016, in Raxó, Poio (42°24.07′N 008°45.20′W; UTM 29T, *x* 520,300, *y* 4,694,349), local fishermen observed a dead bottlenose dolphin calf. Moments before the carcass was recovered, people related having observed other bottlenose dolphins swimming in the vicinity and around the carcass. When one of the observers was confident that the calf was dead, the body was recovered for further examination of the carcass in the laboratory. When they carried the body to the shore the other dolphins went very close to the coastline and became notably more active with continuous tail stock dives and full leaps with abrupt changes in direction. It was not possible to identify the adult individuals present during the encounter.

Summary of necropsy data

The bottlenose dolphin neonate was a female weighing 28 kg and measuring 128 cm from the tip of the rostrum to the tail notch. The animal was assessed to be in moderate decomposition, and the preservation of the carcass was determined to be

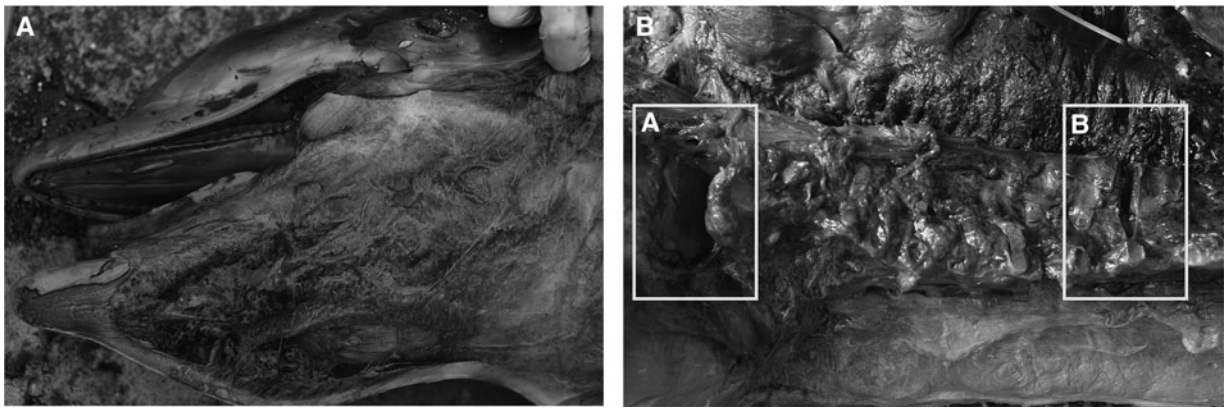

Fig. 4. Post-mortem photographs of the wounds inflicted on the neonate male common bottlenose dolphin recovered in Ría of Arousa (NW Spain) where the cause of death was diagnosed to be blunt-force trauma. (A) Large bruise on the neonate calf's lower jaw. (B) Atlanto-occipital dislocation (box A), and the thoracic vertebrae (T-6) fractured and luxated with a concomitant severed spinal cord (box B).

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code 3 (Geraci & Lounsbury, 2005). The calf had external evidence of injury with a large wound across the lower jaw region (Figure 5A). From its length, evident foetal folds, un-erupted teeth, and furled flukes and dorsal fin, it was estimated to be within its first days of life and therefore would still be dependent (Mead & Potter, 1990).

The skull presented several fractures and the lower jaw and inner ears were absent. Multiple superficial cutaneous lacerations were present on the left flank, belly and flukes of the animal (Figure 5B). These lesions (rake marks), mainly involving the epidermis, were organized in parallel groups of 3–8 regularly spaced lacerations with inter-tooth distances between 12 and 13 mm.

The individual exhibited multiple, internal, ante-mortem injuries including bruising around the head and thorax, disarticulated ribs on both sides of the thorax in a linear pattern involving adjacent ribs, large bruise around the thoracic vertebrae (T-5) fractured and luxated. Other findings included multiple soft tissue contusions and bruises bilateral, separate and discrete. Gross necropsy findings indicated severe blunt-force trauma was the cause of death.

DISCUSSION

Because observing and interpreting social interactions among wild dolphins is difficult, it is likely that the best opportunity for recognizing epimeletic and infanticide behaviours lies in documenting field observations and, whenever is possible, the associated post-mortem findings.

Here we provide for the first time evidence for infanticide and associated epimeletic behaviour along the NW coast of Spain. Epimeletic behaviour in bottlenose dolphins has been recognized for some time (Caldwell & Caldwell, 1966), however this type of behaviour is rarely observed in the field during sightings or strandings research (Reggente *et al.*, 2016). While there are previous accounts of epimeletic behaviour in bottlenose dolphins in relation to the death of a calf (e.g. Cockcroft & Sauer, 1990; Connor & Smolker, 1990; Harzen & dos Santos, 1992; Fertl & Schiro, 1994), these studies did not confirm the causes of the death of the neonate.

In two cases presented in this study (cases 2 and 3), the reports involved calves that were dead when the observations were made and in both cases the cause of the death was confirmed by further post-mortem examinations. In both cases, we conclude that purposeful violent dolphin interaction was the cause of the death of the bottlenose dolphin neonates. With evidence of blunt trauma in both of these cases, the hypothesis that emerged from field observations during the first case (that the calf was intentionally killed by adult individuals) is supported.

The aggressive interaction that we observed between adult bottlenose dolphins and the neonate during the first and second cases bears a strong resemblance to the behaviours seen in the intra- and inter-specific interactions in other parts of the world (Ross & Wilson, 1996; Cotter *et al.*, 2012; Robinson, 2014; Perrtree *et al.*, 2016). Moreover, in the last two cases, the traumatic lesions observed in addition to the rake marks on the body of the calves were consistent with lesions reported by Ross & Wilson (1996), Jepson & Baker (1998), Dunn *et al.* (2002), Barnett *et al.* (2009), Cotter *et al.* (2012)

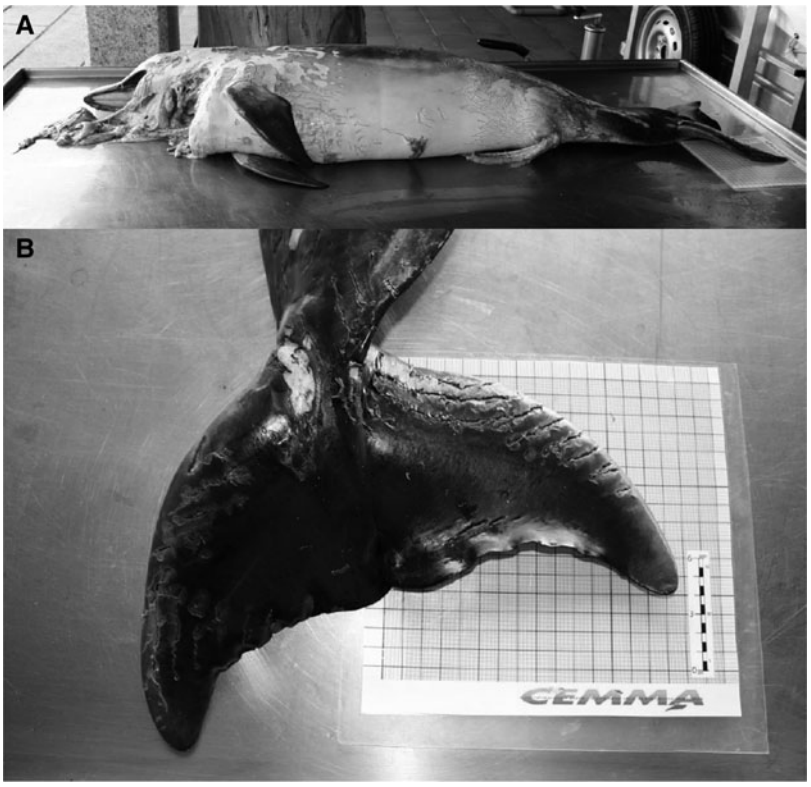

Fig. 5. Post-mortem photographs of the wounds inflicted on the neonate female common bottlenose dolphin recovered in Ría of Pontevedra (NW Spain) where the cause of death was diagnosed to be blunt-force trauma. (A) Body of the calf with an external evidence of injury with a large wound across the lower jaw region. (B) Numerous rake marks are present on the fluke region (grid 1 × 1 cm).

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and Robinson (2014), in attacked bottlenose dolphin calves and harbour porpoises (*Phocoena phocoena*, Linnaeus 1758).

These observations provide a new and plausible explanation for earlier reports of interspecific interactions in Galician waters, NW Spain. A comparison of the post-mortem findings in the observed cases with traumatic injuries described in one stranded harbour porpoise (López & Rodríguez, 1995) and one striped dolphin (*Stenella coeruleoalba*, Meyen 1833) (Alonso *et al.*, 2000) in Galicia, revealed remarkable similarities. Therefore, the cases presented here provide the evidence that attacks of adult bottlenose dolphins may also lead to the stranding and death of other small cetaceans in Galician waters (NW Spain).

The regularly spaced, parallel lacerations observed on the skin of the neonates were characteristic of rake marks produced when an adult bottlenose dolphin slides its teeth across a cutaneous surface with intertooth distances between 10.97 and 12.32 mm (Ross & Wilson, 1996). The presence of these marks on the body of the examined neonates can be related with purposeful violent dolphin interaction and/or the epimeletic behaviour of the mother. The presence of rake marks as a result of the epimeletic behaviour of the mother is supported by: (i) neonate carcasses had tooth marks on the thorax and (ii) during field observations the mother had tried to keep the body of the neonate afloat with her rostrum. Di Beneditto *et al.* (2001) attributed conspecific tooth marks on the body of *Pontoporia blainvillei* (Gervais & d'Orbigny 1844) specimens accidentally caught on the northern Rio de Janeiro coast to rescue attempts by one or more members of the group. In addition, the calves or young dolphins that have been the subject of care-giving behaviour have exhibited fresh parallel scratches on their bodies from the adults' teeth (Félix, 1994; Cremer *et al.*, 2006; Moura *et al.*, 2009). The damage to the head of case 3 (mandible detached) might be related to the moderate degree of autolysis and water pressure, as the dead calf was carried by the mother/group, rather than being a 'wound' inflicted pre-mortem. Two more anecdotal observations of adult bottlenose dolphins insistently trying to keep the body of a neonate carcass afloat were also reported to the CEMMA in Galician waters.

In the Galician population, infanticidal events may be orchestrated by one male (as the aggressive attacks seen in case 2) or by several cooperating individuals at once (as seen in case 1). Nonetheless, all reported events essentially involve the same prolonged chasing, compact circling behaviour, repeated ramming, tossing out of the water, and pushing the body of the targeted neonates. Robinson (2014) and Perrtree *et al.* (2016) reported similar coercive strategies associated with infanticide behaviours used by common bottlenose dolphins towards newborn calves in Moray Firth (Scotland) and in Georgia (USA) respectively. The circumstances under which infanticide occurred at our site fit the conditions proposed under the sexual selection hypothesis (e.g. Hrdy, 1979). First, the observed newborns were still nursing and potentially vulnerable to infanticide by males (Mann & Smuts, 1998). Moreover, during the two month period following the second case, one of the males involved in the aggression was observed in close association with the mother, reinforcing the hypothesis that an infanticidal male may gain the chance to mate with the newly receptive female whose infant has been killed (Hrdy, 1979).

This study adds new information on infanticide and associate epimeletic behaviour for *T. truncatus*. Documented events of such cases are scarce and their socio-behavioural context remains poorly understood (Reggente *et al.*, 2016). The difficulties for researchers to observe this type of behaviour in the field and to find carcasses in good enough condition to determine the cause of death, emphasizes the importance of this type of study.

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REFERENCES

Alexander R.D. (1974) The evolution of social behaviour. *Annual Review of Ecology and Systematics* 5, 325–383.

Alonso J.M., López A., González A.F. and Santos M.B. (2000) Evidence of violent interactions between bottlenose dolphin (*Tursiops truncatus*) and other cetacean species in NW Spain. In Evans P.G.H., Pitt-Aiken R. and Rogan E. (eds) *Proceedings of the 14th Annual Conference of the European Cetacean Society, Cork, Ireland, 2–5 April 2000. Cork: European Cetacean Society*, pp. 105–106.

Altmann J. (1974) Observational study of behavior: sampling methods. *Behaviour* 49, 227–267.

Barnett J., Davison N., Deaville R., Monies R., Loveridge J., Tregenza N. and Jepson P.D. (2009) Post mortem evidence of interactions of bottlenose dolphin (*Tursiops truncatus*) with other dolphin species in south-west England. *Veterinary Record* 165, 441–444.

Caldwell M. C. and Caldwell D.K. (1966) Epimeletic (care-giving) behavior in Cetacea. In Norris K.S. (ed.) *Whales, dolphins and porpoises*. Berkeley, CA: University of California Press, pp. 755–789.

Cockcroft V.G. and Sauer W. (1990) Observed and inferred epimeletic (nurturant) behaviour in bottlenose dolphins. *Aquatic Mammals* 16, 31–32.

https://doi.org/10.1017/S0025315417001266 Published online by Cambridge University Press

Connor R.C. and Smolker R.A. (1990) Qualitative description of a rare behavioural event: a bottlenose dolphin's behavior toward her deceased offspring. In Leatherwood S. and Reeves R.R. (eds) *The bottlenose dolphin*. San Diego, CA: Academic Press, pp. 355–360.

Connor R.C., Wells R.S., Mann J. and Read A.J. (2000) The bottlenose dolphin: social relationships in a fission–fusion society. In Mann J., Connor R.C., Tyack P.L. and Whitehead H. (eds) *Cetacean societies*. Chicago, IL: University of Chicago Press, pp. 91–126.

Cotter M.P., Maldini D. and Jefferson T.A. (2012) 'Porpicide' in California: killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science* 28, E1–E15.

Cremer M.J., Hardt F.A.S. and Junior A.J.T. (2006) Evidence of epimeletic behavior involving a *Pontoporia blainvillei* calf (Cetacea, Pontoporidae). *Biotemas* 19, 83–86.

Di Beneditto A.P.M., Ramos R.M.A. and Lima N.R.W. (2001) Sightings of *Pontoporia blainvillei* (Gervais & ÓOrbigny, 1844) and *Sotalia fluviatilis* (Gervais, 1853) (Cetacea) in South-eastern Brazil. *Brazilian Archives of Biology and Technology* 44, 291–296.

Dunn D.G., Barco S.G., Pabst D.A. and McLellan W. A. (2002) Evidence for infanticide in bottlenose dolphins of the western north Atlantic. *Journal of Wildlife Diseases* 38, 505–510.

Evans G. and Prego R. (2003) Rias, estuaries and incised valleys: is a ria an estuary? *Marine Geology* 196, 171–175.

Félix F. (1994) A case of epimeletic behaviour in a wild bottlenose dolphin *Tursiops truncatus* in the Gulf of Guayaquil, Ecuador. *Investigations on Cetacea* 25, 224–234.

Fernández A., Torrado F., Pérez R., Garci M. and Rodríguez A. (1996) The bottlenose dolphin *Tursiops truncatus* along the Galician coast, with special reference to the Ria de Vigo herd. In Evans P.G.H., Vella A. and Stockin K. (eds) *Proceedings of the tenth annual Conference of the European Cetacean Society, Lisbon, Portugal, 11–13 March 1996. Lisbon: : European Cetacean Society*, pp. 213–216.

Fernández R., Santos M.B., Pierce G.J., Llavona A., López A., Silva M., Ferreira M., Carrillo M., Cermeño P., Lens S. and Piertney S. (2011) Fine-scale genetic structure of bottlenose dolphins, *Tursiops truncatus*, in Atlantic coastal waters of the Iberian Peninsula. *Hydrobiologia* 670, 111–125.

Fertl D. and Schiro A. (1994) Carrying of dead calves by free-ranging Texas bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals* 20, 53–56.

Geraci J.R. and Lounsbury V.J. (2005) *Marine mammals ashore: a field guide for strandings*. Baltimore, MD: National Aquarium.

Harzen S. and dos Santos M.E. (1992) Three encounters with wild bottlenose dolphins (*Tursiops truncatus*) carrying dead calves. *Aquatic Mammals* 18, 49–55.

Hrdy S.B. (1979) Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology* 1, 13–40.

Jepson P.D. and Baker J.R. (1998) Bottlenose dolphins (*Tursiops truncatus*) as a possible cause of acute traumatic injuries in porpoises (*Phocoena phocoena*). *Veterinary Record* 143, 614–615.

Kaplan J.D., Lentell B.J. and Lange W. (2009) Possible evidence for infanticide among bottlenose dolphins (*Tursiops truncatus*) off St. Augustine, Florida. *Marine Mammal Science* 25, 970–975.

Kuiken T. (1996) Review of the criteria for the diagnosis of by-catch in cetaceans. In Kuiken T. (ed.) *Diagnosis of by-catch in Cetaceans. Proceedings of the Second ECS Workshop on Cetacean Pathology, newsletter 26 (Special Issue)*. Saskatoon, SK: European Cetacean Society, pp. 38–43.

López A. (2003) Estatus dos pequenos cetáceos da plataforma de Galicia. PhD thesis. Universidade de Santiago de Compostela, Santiago de Compostela, Spain. 337 pp.

López A., Covelo P., Vázquez J.A., Martínez J.A., Caldas M., Lago R., Llavona A. and Alonso J.M. (2011) Bases para a conservación e xestión das especies de cetáceos ameazadas nas augas Atlánticas e Cantábricas. *Eubalaena* 12, 30–33.

López A. and Rodríguez A. (1995) Agresión de arroás (*Tursiops truncatus*) a toniña (*Phocoena phocoena*). *Eubalaena* 6, 23–27.

Louis M., Viricel A., Lucas T., Peltier H., Alfonsi A., Berrow S., Brownlow A., Covelo P., Dabin W., Deaville R., de Stephanis R., Gally F., Gauffier P., Penrose R., Silva M., Guinet C. and Simon-Bohuet B. (2014) Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. *Molecular Ecology* 23, 857–874.

Mann J. and Smuts B.B. (1998) Natal attraction: allomaternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour* 55, 1097–1113.

Mead J.G. and Potter C.W. (1990) Natural history of bottlenose dolphins along the central Atlantic coast of the United States. In Leatherwood S. and Reeves R.R. (eds) *The bottlenose dolphin*. New York, NY: Academic Press, pp. 165–195.

Moura J. F., Rodrigues E. S. and Siciliano S. (2009) Epimeletic behavior in rough-toothed dolphins (*Steno bredanensis*) on the east coast of Rio de Janeiro State, Brazil. *Marine Biodiversity Records* 2, e12.

Norris K.S. and Dhol T.P. (1980) The structure and function of cetacean schools. In Herman L.M. (ed.) *Cetacean behavior: mechanisms and processes*. New York, NY: Wiley, pp. 211–261.

Palombit R.A. (2015) Infanticide as sexual conflict: coevolution of male strategies and female counterstrategies. *Cold Spring Harbor Perspectives in Biology* 7, a017640.

Patterson I.A.P., Reid R.J., Wilson B., Grellier K., Ross H.M. and Thompson P.M. (1998) Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbor porpoises? *Proceedings of the Royal Society: Biological Sciences* 265, 1167–1170.

Perrtree R.M., Sayigh L.S., Williford A., Bocconcelli A., Curran M.C. and Cox T.M. (2016) First observed wild birth and acoustic record of a possible infanticide attempt on a common bottlenose dolphin (*Tursiops truncatus*). *Marine Mammal Science* 32, 376–385.

Pierce G.J., Caldas M., Cedeira J., Santos M.B., Llavona A., Covelo P., Martinez G., Torres J., Sacau M. and López A. (2010) Trends in cetacean sightings along the Galician coast, north-west Spain, 2003–2007, and inferences about cetacean habitat preferences. *Journal of the Marine Biological Association of the United Kingdom* 90, 1547–1560.

Reggente M.A., Alves F., Nicolau C., Freitas L., Cagnazzi D., Baird R.W. and Galli P. (2016) Nurturant behavior toward dead conspecifics in free-ranging mammals: new records for odontocetes and a general review. *Journal of Mammalogy* 97, 1428–1434.

Ritter F. (2007) Behavioral responses of rough-toothed-dolphins to a dead newborn calf. *Marine Mammal Science* 23, 429–433.

Robinson K.P. (2014) Agonistic intraspecific behavior in free-ranging bottlenose dolphins: calf-directed aggression and infanticidal tendencies by adult males. *Marine Mammal Science* 30, 381–388.

Ross H.M. and Wilson B. (1996) Violent interactions between bottlenose dolphins and harbor porpoises. *Proceedings of The Royal Society of London B* 263, 283–286.

Santos M.B., Fernández R., López A., Martínez J.A. and Pierce G.J. (2007) Variability in the diet of bottlenose dolphin, *Tursiops truncatus*, in Galician waters, northwest Spain, 1990–2005. *Journal of the Marine Biological Association of the United Kingdom* 87, 231–241.

Trivers R. (1972) Parental investment and sexual selection. In Campbell B. (ed.) *Sexual selection and the descent of man*. Chicago, IL: Aldine Publishing Co, pp. 136–179.

van Schaik C.P. (2000) Vulnerability to infanticide by males: patterns among mammals. In van Schaik C.P. and Janson C.H. (eds) *Infanticide by males and its implications*. Cambridge: Cambridge University Press, pp. 61–71.

Vázquez J.A., Caldas M., Guzmán I., López A., Olondo M., Lago R. and Covelo P. (2006) Evidences of bottlenose dolphins movements in the Cantabrian sea. In Kuklik I. (ed.) *Proceedings of the 20th Annual Conference of the European Cetacean Society, Gdynia, Poland, 2–7 April 2006*. Gydinia: European Cetacean Society, p. 215.

and

Würsig B. and Jefferson R.A. (1990) Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission Special Issue* 12, 43–52.

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