



Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises?

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Most harbour porpoises found dead on the north-east coast of Scotland show signs of attack by sympatric bottlenose dolphins, but the reason(s) for these violent interactions remain(s) unclear. Post-mortem examinations of stranded bottlenose dolphins indicate that five out of eight young calves from this same area were also killed by bottlenose dolphins. These data, together with direct observations of an aggressive interaction between an adult bottlenose dolphin and a dead bottlenose dolphin calf, provide strong evidence for infanticide in this population. The similarity in the size range of harbour porpoises and dolphin calves that showed signs of attack by bottlenose dolphins suggests that previously reported interspecific interactions could be related to this infanticidal behaviour. These findings appear to provide the first evidence of infanticide in cetaceans (whales, dolphins and porpoises). We suggest that infanticide must be considered as a factor shaping sociality in this and other species of cetaceans, and may have serious consequences for the viability of small populations.

Keywords: aggression; bottlenose dolphin; Cetacea; conservation biology; infanticide; social structure

1. INTRODUCTION

Over 60% of harbour porpoises (*Phocoena phocoena*) found dead on the north-east coast of Scotland show signs of attack by sympatric bottlenose dolphins (*Tursiops truncatus*) (Ross & Wilson 1996). The occurrence of these violent attacks has been confirmed by direct observations, but the reason(s) for the interactions remain(s) unclear (Ross & Wilson 1996). Post-mortem evidence in other areas of the UK where the two species coexist (P. Jepson and J. Baker, personal communication) now suggests that the attacks are not simply due to the aberrant behaviour of one or two individuals off north-east Scotland, but are more widespread. Possible explanations for this behaviour have included competition for prey, feeding interference, play or practise fighting, and sexual frustration (Ross & Wilson 1996). However, current constraints on the study of diet and behaviour in these two species have prevented systematic tests of these hypotheses.

Here we provide evidence for infanticide in the Moray Firth population of bottlenose dolphins. We suggest that these findings provide a new and plausible explanation for earlier reports of interspecific interactions. Importantly, this is also the first record of infanticide among cetaceans. We suggest that infanticide may therefore be an important factor shaping the social structure of bottlenose dolphins and perhaps other cetacean species, and could also have

serious consequences for the viability of small populations of such species.

2. STUDY AREA AND METHODS

The study was carried out in the Moray Firth and adjacent coasts of north-east Scotland. This area forms the core range of the North Sea's only resident population of bottlenose dolphins, which is estimated to number approximately 129 (95% CL=110–174) individuals (Wilson *et al.* 1997, 1998). Harbour porpoises are also present in the Moray Firth throughout the year. Their abundance within this area is not known, but their distribution is widespread, and an estimated 341 366 (95% CL=260 000–449 000) harbour porpoises occur throughout the North Sea and adjacent waters (Hammond *et al.* 1995).

Since 1992, post-mortem examinations have been conducted on cetaceans found dead on these coasts using standard protocols outlined in Kuiken & Garcia Hartmann (1991). Between January 1990 and September 1997, standardized twice-monthly boat surveys were also carried out in the inner Moray Firth to record the distribution and behaviour of individually recognizable bottlenose dolphins (for details, see Wilson *et al.* (1997)). The presence and behaviour of other cetaceans were also noted during boat surveys.

3. RESULTS

Between 1992 and 1996, 90 out of 142 harbour porpoises (63.4%) found stranded within the Moray Firth exhibited multiple skeletal injuries and/or damage

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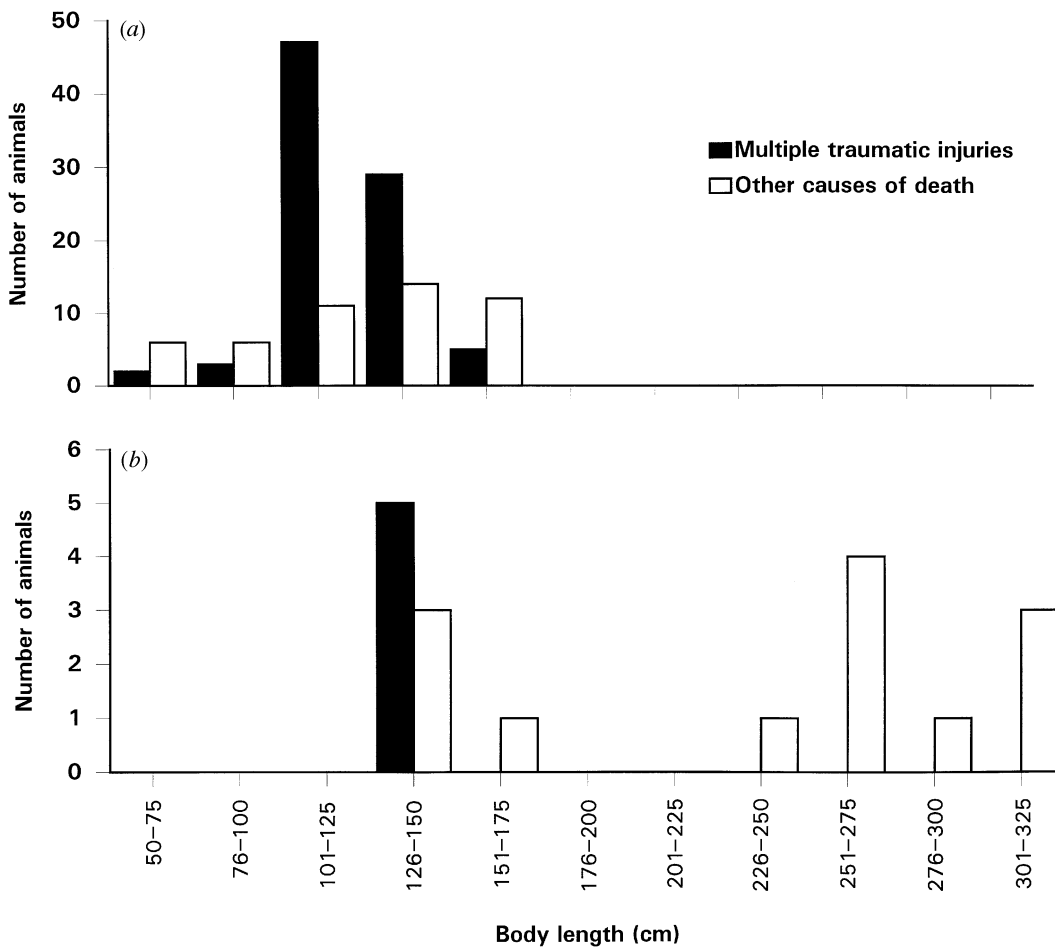


Figure 1. Frequency distribution of the body sizes of (a) harbour porpoises and (b) bottlenose dolphins found stranded in the Moray Firth between 1992 and 1997. Data are shown separately for those individuals possessing multiple traumatic injuries indicative of attack by bottlenose dolphins (filled bars), and those individuals that had died from other causes (open bars).

to internal organs. These injuries were consistent with attack by bottlenose dolphins, as described for a sample of 105 porpoises examined between 1991 and 1993 (Ross & Wilson 1996). The total body length of the porpoises showing signs of attack by bottlenose dolphins ranged from 0.74 to 1.66 m, but 84% were in the 1.0–1.5 m size range (figure 1a).

During the same period, 18 bottlenose dolphins were found stranded within the study area. Five individuals (three females, two males) exhibited multiple, internal, ante-mortem injuries including bruising around the head and thorax, multiple rib fractures with associated haemorrhage and bruising, ruptured lungs resulting from penetration by fractured ribs, and, in two cases, spinal dislocation. In each case the skin bore fresh parallel tooth marks but in no cases were parts of the dolphin eaten. All of the dolphins with these multiple traumatic injuries were less than 1.5 m in length. From their lengths, they were estimated to be within their first year of life (Mead & Potter 1990) and therefore would still be dependent upon their mothers (Wells *et al.* 1983; Connor *et al.* 1996). In contrast, a wide size range of both male and female dolphins had died from other causes (figure 1b).

Violent interactions between bottlenose dolphins and harbour porpoises were observed on two boat surveys, and two other observations were recorded by members of

the public (Ross & Wilson 1996). In addition, one of us (B.W.) observed an aggressive interaction involving two adult bottlenose dolphins and a dead bottlenose dolphin calf during a survey on 2 September 1994. All three dolphins were observed for 53 min in the inner Moray Firth, and the two adults were recognized from photo-identification studies; ID22 was of unknown sex, and ID192 was assumed to be a female through earlier associations with a previous calf (which was born in 1990 and last seen in 1992). ID22 repeatedly jumped and lunged at the surface and was seen gripping the calf in its jaws, pushing it around underwater, and butting it clear of the surface with its head. ID192 always remained close to or over the calf, but was never seen in physical contact with either the calf or ID22. The calf appeared to be freshly dead, but on each occasion that it was released by ID22 it sank, and could not therefore be retrieved for post-mortem examination.

4. DISCUSSION

The injuries on the young bottlenose dolphins (a combination of extensive ante-mortem damage and parallel tooth scarring) were the same as those previously reported in harbour porpoises that had been attacked by bottlenose dolphins (Ross & Wilson 1996). These findings

indicate that these calves were killed by conspecifics, while their small size (figure 1b) provides strong evidence for infanticide. Field observations of the violent interaction between an adult bottlenose dolphin and a dead calf further support this suggestion, although we were unable to confirm that this interaction, or the resulting injuries, had been responsible for the calf's death. Similarities in the size range of conspecifics and harbour porpoises killed by bottlenose dolphins (figure 1) further suggest that reported interspecific interactions (Ross & Wilson 1996) could be related to infanticidal behaviour. The violent nature of ID22's behaviour made the alternative interpretation of epimelitic behaviour seem unlikely. The aggressive interaction that we observed between this adult bottlenose dolphin and calf also bore a strong resemblance to the behaviours seen in the interspecific interactions (Ross & Wilson 1996). Violent attacks on porpoises could be a form of object-orientated play, as proposed for an interaction between two Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and a neonatal harbour porpoise (Baird 1998). Such play could serve to develop or practise those skills used in infanticidal attacks. Alternatively, as seen in other marine mammals, attacks may result from re-directed aggression or sexual frustration, where access to females or other resources is limited (Higgins & Tedman 1990; Rose *et al.* 1991; Le Boeuf & Campagna 1994). Discriminating between these hypotheses now depends upon better information on the age and sex of the dolphins initiating both the inter- and intraspecific attacks, but collection of such data is severely constrained by the animals' extensive geographical range and the low frequency of attacks.

Although infanticide inflicted by both males and females is widely reported from other mammals (Hrdy 1979; Wolff 1997), this seems to be the first evidence that this behaviour occurs in cetaceans. As well as providing a new explanation for observed interspecific interactions, these findings highlight how infanticide could influence cetacean social structure and behaviour. Mating strategies in male bottlenose dolphins include both alliance formation to herd females and individuals roving between female groups (Wells *et al.* 1983; Connor & Richards 1992). Female bottlenose dolphins typically calve only every 2–4 years, but they become attractive to males within a few days of losing a calf (Connor *et al.* 1996). In certain situations, male-inflicted infanticide may therefore increase individual reproductive fitness, as reported in other mammals (Hrdy 1979; Breden & Hausfater 1990; Pusey & Packer 1994). Alternatively, infanticide may be inflicted by females when resources are limited (Wolff 1997).

The importance of infanticide in shaping social behaviour has been widely recognized within other mammalian groups (Wolff 1997), but studies of cetaceans have generally overlooked this possibility and focused on the potential role of predation and food distribution. Connor *et al.* (1996), on the other hand, speculated that the high frequency of observed matings in bottlenose dolphins could be a female strategy that reduced the risk of infanticide. However, they found no direct or indirect evidence of such behaviour during their field studies in Western Australia. Our findings support their speculation, and suggest that infanticide must be considered as a factor shaping sociality in this and other cetacean species.

Violent sexual behaviour is common intraspecifically in other marine mammals and, in extreme cases such as the endangered Hawaiian monk seal, can influence demography (Gilmartin & Eberhardt 1995). Interspecific attacks on harbour porpoises have generally been considered to be of little conservation importance because North Sea bottlenose dolphins are known to be relatively rare and localized in comparison to harbour porpoises (Hammond *et al.* 1995). However, the population of bottlenose dolphins in the Moray Firth is estimated to consist of only 129 individuals, and appears to produce only six or seven calves per annum (Wilson *et al.* 1998). Stochastic variations in population sex ratio (Gilmartin & Eberhardt 1995), or disruption of social bonds owing to human activities, could increase the potential impact of infanticidal behaviour on population viability (Swenson *et al.* 1997). Furthermore, no dead calves were recovered in the period following our observation of the interaction between the adult bottlenose dolphins and the dead calf. Infanticide may therefore be more common than the number of reported strandings suggest, and could have important consequences for the conservation of this and other small populations of cetaceans.

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