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Agonistic intraspecific behavior in free-ranging bottlenose dolphins: Calf-directed aggression and infanticidal tendencies by adult males

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Common bottlenose dolphins (*Tursiops truncatus*) are well-known for their overtly aggressive behavior (Herzing *et al*. 2003, Blomqvist and Amundin 2004, Coscarella and Crespo 2009). Indirect indicators include the prevalence of tooth rake marks on individuals, which have been used to document relative rates of intraspecific antagonism by age, sex, reproductive status and season in these odontocetes (*e.g.*, McCann 1974, Scott *et al.* 2005). The contexts and causes of intraspecific aggression vary widely, with agonistic interactions arising from social, affiliative behaviors, copulation, coercion, or even as a result of anthropogenic factors (Herzing 1996; Connor *et al*. 2000*a*, 2001). When observed directly, these may include head-to-head posturing, acoustic threats, and even physical violence (*e.g.*, body slamming, tail hitting, charging, jawing, and biting) (Herzing 1996, Connor *et al*. 2000*b*, Blomqvist and Amundin 2004). Indeed, in one case scenario reported by Parsons *et al*. (2003), a solo adult male was actually rendered unconscious by two smaller bottlenose rivals (constituting a well-known male alliance) during repeated, violent exchanges.

Perhaps the most striking example of targeted intraspecific aggression in these delphinids, however, is the practice of infanticide, as revealed from postmortem examinations of stranded calves (Patterson *et al*. 1998, Dunn *et al*. 2002) and from several anecdotal observations at sea (*e.g.*, Wilson,[2] Dunn *et al*. 2002, Eisfeld 2003). The most detailed and compelling account in the field was recorded by Kaplan *et al*. (2009) off the coast of Florida from an aerial blimp, and describes a prolonged, 51 min attack on a newborn calf by several adult males that was thought to result in the death of the infant (although this was never actually confirmed). However, direct observations of

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[2]Personal observation by Ben Wilson, University of Aberdeen Lighthouse Field Station, School of Biological Sciences, George Street, Cromarty, Ross-shire IV11 8YJ, Scotland, 2 September 1994 (in Patterson *et al.* 1998).

this behavior at sea are rare, which makes it difficult to understand the context or cause of such elevated, potentially lethal, intraspecific aggression/infanticide.

The following report, recorded on 14 September 2009 in the outer Moray Firth in northeast Scotland (57°41 N, 2°40 W), describes elevated aggression towards a newborn bottlenose calf by an identified adult male, which was interpreted as attempted infanticide. The individuals involved in this encounter were well-known further to a 12 yr study of the *Tursiops* population in this location by the author, including data on the sex reproductive history, and associations of the animals reported. The following events are presented chronologically, as observed and photographed from a 5.4 m rigid-hulled inflatable boat (see Robinson *et al.* 2007 for survey methodology):

1242—A large, mixed-sex group of 42 dolphins were recorded travelling in a tight-knit "line formation" (after Bel'kovich 1991) approximately 40 m from the shore.

1244—Several subgroups pulled away from the core group, leaving behind a central band of mothers with young calves in tow, which were tracked moving westwards close inshore. Lots of logging and rolling were observed as the group milled at the surface between long, slow dives.

1247—All at once, the group became notably more active. The animals began circling energetically and were then observed surface rushing (charging through the water's surface at speed), with abrupt changes in direction. Suddenly a large adult male dolphin rapidly emerged in the center of the group clutching a newborn calf in its jaws.

1248—A high speed chase ensued as the young calf was butted, rammed and head-spun away from the maternal group by the identified male (ID#021, Fig. 1A), a mature male resighted 68 times since first recorded by the author in July 1997. The calf received multiple strikes to the head, flanks, abdomen, and tail stock, as it was driven into deeper waters by the male.

1250—Accompanied by several female affiliates, the identified mother (ID#387), a young female sighted 32 times since her birth in 2001, gave chase, and managed to catch up with her calf. She then swam in echelon with the calf (Noren *et al.* 2008), positioning herself between the calf and male ID#021 as he circled around them. The male then launched himself directly into the mother-calf pair, driving his body between the two animals and forcing them apart (Fig. 1B). Thereafter, the male aggressor leapt upon the calf, holding it beneath the water from above.

1251—Flanked by a known female associate, the mother moved in again, surfacing with her calf lying motionless across her back (Fig. 1C), which she held up above the waterline for at least 20 s to recover.

1252—The calf was observed swimming, though somewhat awkwardly, by its mother's side once again. However, ID#021 continued his assault, this time striking the calf hard from below, and with such velocity that the infant was launched clear out of the water (Fig. 1D). He then seized the calf in his jaws and tossed it into the air a second time, but at this point several other large males converged on the scene and encircled ID#021 obstructively.

1253—Further dolphins appeared thereafter as many of the original animals started to regroup around the mother and calf and aggressive male. Lots of circling was observed and, amongst the commotion, the calf was escorted away from the immediate area by its mother.

1300—The mother-calf pair were subsequently relocated heading west, close inshore, within a mixed-sex group of 26 animals including six other females with calves.

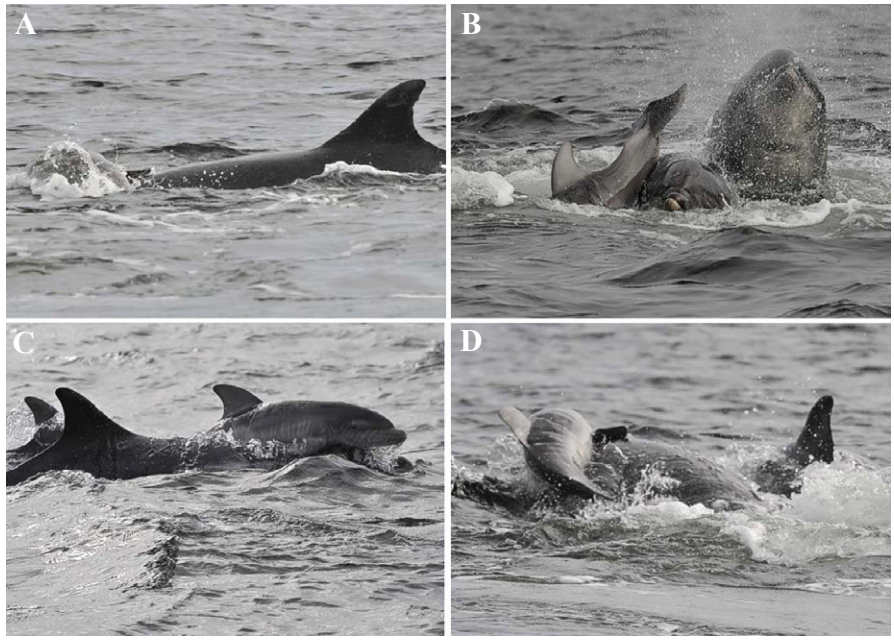

Figure 1. Photographs authenticating the attempted infanticide of the newborn bottlenose calf observed on 14 September 2009. (A) Image of the calf being abducted by the identified adult male (ID#021). (B) Female ID#387 (right) and her calf (far left) being driven apart by the male aggressor (ID#021) (center). (C) Flanked by a known affiliate, female ID#387 raises her calf to the surface following its attempted asphyxiation by the large male. (D) Male ID#021 strikes the calf hard from below, projecting the infant clear out of the water.

1318—Male ID#021 was eventually located heading east and offshore within a smaller, residual subgroup.

Initial concerns as to whether the calf had survived its ordeal or not were put to rest the following day when the mother and infant were encountered together at sea by the author. However, when identified off the coast of Aberdeen approximately seven months later, the recaptured calf had developed a prominent deformity "affecting its ability to swim in a normal, coordinated manner" (Fig. 2).[3] The calf consequently live-stranded and died at the Bridge of Don, Aberdeen, just one month later, and a necropsy was carried out on the deceased animal by the Scottish Agricultural College that revealed an acute scoliosis with observed kyphosis in body posture (Fig. 3). According to the veterinary report, this gross deformity was concluded to be long-standing—based on remodeling and realignment of the lateral spinal processes to accommodate the axial musculature as the calf developed—and was therefore either manifest at birth or acquired from trauma as a neonate (Brownlow[4]). Since the condition could not be distinguished in photographs taken during the attack, however, it

[3]Personal communication from Caroline Weir, Ketos Ecology, 4 Compton Road, West Charleton, Kingsbridge, Devon, U.K., 12 April 2010.

[4]Unpublished necropsy report by Andrew Brownlow, Wildlife Unit, SAC Consulting: Veterinary Services, Drummondhill, Stratherrick Road, Inverness IV2 4JZ, Scotland, June 2010.

Figure 2. Female ID#387 and calf photo-identified on 10 April 2010 approximately six months after the attack. Note the acute scoliosis developed by the calf (pictured here left of its mother) (photo credit Caroline Weir, Ketos Ecology).

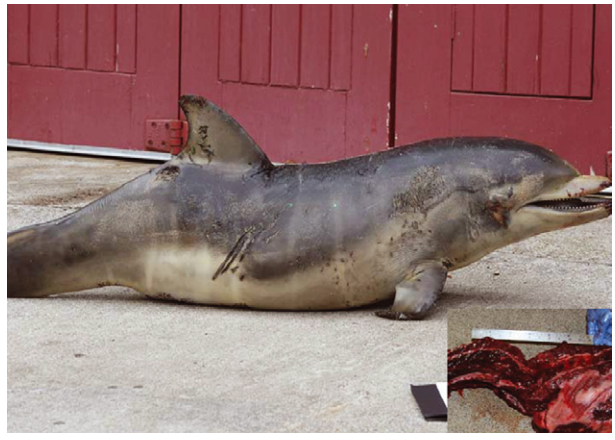

Figure 3. The deceased calf after its recovery from the Bridge of Don in Aberdeen on 11 May 2010. Inset: shows the pronounced S-shaped deformation of the spine, which is now housed at the National Museums Scotland in Edinburgh (photo credits Barbara Cheney, University of Aberdeen Lighthouse Field Station).

is likely to have occurred as a direct result of the events reported here. Indeed, the high incidence of scoliotic calves in the Moray Firth bottlenose population reported by Haskins and Robinson (2007) could thus be attributed, in part at least, to the trauma-inducing capabilities of infanticidal males within this population, in addition to the list of other possible causes (*e.g.*, Cowell *et al*. 1972, Giddens *et al*. 1984, Wilson *et al*. 1997).

By nature of their small size and dependency, newborn dolphins are evidently most at risk from infanticidal males (Patterson *et al*. 1998, Kaplan *et al*. 2009, Nery and Simão 2009). However, first-time mothers might further be targeted in view of their lack of parental experience. At just 8 yr of age, the known female detailed in the present report was a first-time mother and the calf was just several days old (the last sighting of female ID#387 was made just four days earlier and there was no calf present at this time). The sex of the calf was also incidentally male (Brownlow[4]), although there is no evidence to suggest that infant males might be preferentially targeted over females by infanticidal adult males. Besides, the driving factor behind this behavior seems to be the elimination of rival offspring to increase reproductive success, rather than the removal of future male competitors (Dunn *et al*. 2002). However, newborn bottlenose calves may possess a remarkable ability to survive such brutal interactions, even in the face of resulting gross structural deformation (present report, Watson *et al.* 2004).

As with other species practicing this behavior (*e.g*., Breden and Hausfater 1990, Pusey and Packer 1994, Derocher and Wiig 1999, Soltis *et al.* 2000, Wilkinson and Childerhouse 2000), such a strategy requires a flexible reproductive physiology allowing conception by the female soon after losing an infant. According to Mann *et al*. (2000), bottlenose females may become pregnant within two months following the loss of a newborn, but conception is considerably longer (up to a year or more) upon losing an older calf, presumably due to the considerable investment by the female in lactation and the resulting loss of condition. This would suggest, therefore, that adult males would only benefit from infanticide by targeting very young calves (of females that they had not previously mated with) and having access to the mother when she resumed cycling within a month or so afterwards.

Thus, while infanticide may be a realistic strategy for these delphinids, particularly when the ratio of available females to males is unevenly skewed or if the population is close to carrying capacity (*e.g.*, van Schaik *et al*. 2004, Henzi *et al*. 2010), there are a number of qualifying conditions which need to be met. Resumption of cycling by the female is clearly paramount if the male has any chance of fathering the next offspring in the weeks thereafter (Mann *et al*. 2000). In addition, the animals involved must not have previously mated or be familiar to one another (Henzi *et al*. 2010). In the present case example, male ID#021 and female ID#387 were not known associates (KPR, unpublished data) and they were only seen together on one occasion thereafter, two weeks after the documented attack. However, since the attempted infanticide was not successful and the calf survived, perhaps male ID#021 had no immediate interest in guarding this female from other male conspecifics in this particular case.

As in other social mammal groups also practicing this behavior (*e.g.*, Hrdy 1979), the close relatives of targeted calves would be expected to resist against potential attackers. In this respect, a large majority of infanticidal attacks may in fact be thwarted by the defensive efforts of the mother, her female affiliates and even her male consorts, as observed in the event described herein. The counter-strategies employed by females in defense of their young have been well-reviewed by Agrell *et al*. (1998) and may include approaches such as faking estrus, promiscuity or polygamous behavior, actively defending offspring, avoiding unfamiliar males, and/or associating with other conspecifics for protection. All of these factors, accompanied by the present evidence that attacks may transpire in just a matter of minutes, might certainly explain the lack of *in situ* observations of this behavior in the field to date.

In the Moray Firth population, infanticidal events may be orchestrated by single males (as seen in the present report and by Wilson[2]) or by several cooperating males at once (*e.g.*, Eisfeld 2003). Nonetheless, all events essentially involve the same prolonged chasing, repeated ramming, tossing out of the water, and attempted asphyxiation of targeted newborns. Nery and Simão (2009) reported similar coercive strategies used by marine tucuxi (*Sotalia guianensis*) towards an early newborn calf. Moreover, the mechanisms used by other delphinids in predatory and nonpredatory interspecific events alike (*e.g.*, killer whale, *Orcinus orca*, attacks on baleen whales as described by Ford *et al*. 2005 and Barrett-Lennard *et al*. 2011, and lethal attacks on harbor porpoises, *Phocoena phocoena*, by bottlenose dolphins, *e.g.,* Ross and Wilson 1996, Cotter *et al*. 2012) are clearly comparable, in both method and execution, to the event described herein.

The present paper contributes a valuable, first-hand account of infanticidal behavior in free-ranging bottlenose dolphins, adding further to our understanding of the mechanisms and conditions that may elicit such responses in these highly-social, aquatic mammals.

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