ANIMAL BEHAVIOUR, 2005, **69**, 899–909
doi:10.1016/j.anbehav.2004.04.024

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Surviving at sea: ecological and behavioural predictors of calf mortality in Indian Ocean bottlenose dolphins, *Tursiops* sp.

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*(Received 5 June 2003; initial acceptance 27 August 2003;
final acceptance 29 April 2004; published online 8 February 2005; MS. number: A9628R)*

We examined the behavioural ecology of mothers and calves during the first year of life to identify variables predicting calf mortality among bottlenose dolphins. Specifically, we investigated whether the primary cause of calf mortality was poor calf condition or shark predation. Seventy-five per cent of calves that died ($N = 12$) showed visible signs of poor health compared with 4.7% of the survivors ($N = 21$). Calves that spent more time swimming in infant position (in contact under the mother) in the first year of life were more likely to die by 3 years of age than calves that spent less time swimming in infant position. No other behavioural or ecological measures tested were associated with calf mortality. We suggest that the mother and/or calf may compensate for poor calf health by increasing the time spent in contact with the mother. In contrast, frequent mother–calf separation and high rates of calf socializing and foraging are proposed to be indicators of vigour. Although most of our results do not support the predation hypothesis, mothers altered one behaviour in relation to predation risk. Mothers rested less in deep water during the warm months, where and when predation risk was high, than during the cool months, when predation risk was low, suggesting that predation risk influenced maternal vigilance. However, calf mortality was not higher in warm months than in cool months. Our results suggest that poor calf condition, not predation, is the primary cause of calf mortality.

Infancy is the most vulnerable period in a mammal's life, and bottlenose dolphins are no exception. In Shark Bay, Australia, 44% of calves die before weaning (Mann et al. 2000). By identifying the sources of calf mortality, we may better understand the selective pressures that have shaped delphinid ecology, social structure and life-history characteristics, including the extensive 3–6 year period of dependence on maternal care (Mann et al. 2000). Two potential sources of mortality for young cetaceans are predation by sharks and infant body condition.

Maternal care and the social, demographic and ecological factors that influence such care play critical roles in determining offspring survivorship (e.g. savannah baboons, *Papio cynocephalus*: Altmann 1980; vervet monkeys, *Cercopithecus aethiops*: Hauser & Fairbanks 1988; Fairbanks & McGuire 1995; bighorn sheep, *Ovis canadensis*: Festa-Bianchert & Jorgenson 1998; roe deer, *Capreolus capreolus*: Andersen et al. 2000; cheetah, *Acinonyx jubatus*: Laurenson 1995). For example, maternal experience and social rank affect patterns of maternal care and offspring survivorship in a number of mammals (red deer, *Cervus elaphus*: Clutton-Brock et al. 1982; Wass et al. 2003; primates: Nicolson 1987; Pryce 1993, 1996; Silk 1993; rabbits, *Oryctolagus cuniculus*: von Holst et al. 2002). Numerous studies also demonstrate relationships between measures of maternal condition, maternal care and offspring survival (e.g. cheetah: Laurenson 1995; fur seals, *Arctocephalus tropicalis*: Georges & Guinet 2000; spotted hyaenas, *Crocuta crocuta*: Hofer & East 1993; bighorn sheep: Festa-Bianchert & Jorgenson 1998; vervet monkeys: Hauser & Fairbanks 1988; Lee et al. 1991).

Although increased maternal care may result in higher survivorship, such care may be influenced by infant characteristics, particularly behaviours that reliably indicate offspring condition (Godfray 1995; Agrawal et al. 2001). Few studies have examined how patterns of offspring behaviour might affect or reflect chances of offspring survival (Wilson et al. 1994; Wilson 1998), although Hauser (1993) found that maternal care by female vervet monkeys is influenced by their infants' cry rate, and that lack of maternal responsiveness combined with high cry rate predicts infant mortality.

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0003–3472/04/$30.00/0

The behaviour of offspring may be particularly important in precocial mammals such as dolphins, where calves venture hundreds of metres away from their mothers throughout the prolonged period of dependence on maternal care (Smolker et al. 1993; Mann et al. 2000). Here we observed behaviours of mothers and calves during the first year of calf life, and examined whether they predicted survival of calves to the end of their third year. We also examined whether any of several ecological variables predicted calf survival to 3 years of age. Two-thirds of dependent calf deaths occur during the first year of life, and nursing calves often die before 3 years of age (Mann et al. 2000). Therefore, we presented relevant behavioural and ecological data from the first year of calf life, but used survival to 3 years of age as our dependent variable. We tested two hypotheses: the 'predation hypothesis' suggests that predation by sharks is the primary cause of calf mortality, and the 'condition hypothesis' suggests that dolphin calves die primarily because they are in poor physical condition. The latter hypothesis is intrinsically linked to maternal condition and care, since these factors are likely to play a large role in determining calf condition. If the predation hypothesis is correct, calf mortality should correlate with variables associated with predation risk. If the condition hypothesis is correct, factors relating to calf condition should correlate with calf mortality. Here we examined these predictions in Shark Bay dolphins.

Tiger shark (*Galeocerdo cuvier*) density in Shark Bay is high in warm months (September–May, with mean temperatures $\geq 22^{\circ}$C) and very low in cool months (June–August, $\leq 19^{\circ}$C; Heithaus & Dill 2002). Other sharks, mostly *Carcharhinus* sp. are commonly sighted during the warm months, but this has not been quantified. Although large sharks probably pose the greatest threat to calves, calves and adults also bear small shark scars. In our longitudinal study, the semicircular scars characteristic of shark attacks range from an estimated 5 to over 50 cm. Heithaus (2001) found that 74.2% of dolphins (noncalves) in Shark Bay bear shark bite scars. One-third of nursing calves bear shark bite scars as well (Mann & Barnett 1999). Bites from small carcharhinid sharks occurred on 6.2% of juvenile and adult dolphins (Heithaus 2001). Small bites leave less visible scars and are more likely to go undetected. Alternatively, large bites may kill the animal and never be observed. The impact of different shark species and their habitat use on dolphins is not yet well understood.

During shark season we expected calves to die at a higher rate than when sharks were absent. Since dolphin breeding is seasonal, peaking in October–December (Mann et al. 2000) and younger calves are more likely to die than older calves, we expected warm season deaths to be more common than cool season deaths even if predation rates were generally low. Furthermore, if predation is a primary cause of calf death, we expected calf mortality to correlate positively with time separated from the mother when shark density was high. Finally, specific habitats (shallow versus deep water) may seasonally vary in predation risk. Mothers and/or calves might be expected to alter their behaviour (e.g. rest less) when predation risk is high because of season or habitat.

The calf condition hypothesis proposes that the physical state (size, health) of the calf is the most important factor influencing calf mortality. Without capturing dolphins, calf condition cannot be measured directly, but it can be visually assessed based on calf size and skin condition. If the calf condition hypothesis is correct, high rates of calf foraging, socializing and separation from the mother (which are indicators of calf competence) should be associated with lower calf mortality. Calves that separate from their mothers to forage may be particularly robust, or they may be supplementing their diet with sufficient amounts of solid food to enhance survival. Calf condition is related to maternal condition, which in turn is influenced by food availability (e.g. Lee et al. 1991). The physical conditions of both mother and calf are likely to influence patterns of maternal care including contact and nursing access. If the calf condition hypothesis is correct, there should be no seasonal bias in mortality, since the food supply available to Shark Bay dolphins does not vary seasonally (Heithaus & Dill 2002). Our study documented dolphin activity budgets and identified factors contributing to calf mortality. We present our two hypotheses with numbered predictions in Table 1 for clarity.

METHODS

Field Site

Shark Bay is located at 25°47′S, 113°43′E in Western Australia. A long-term study of the Shark Bay dolphins was established in 1984 off a fishing camp (now resort) called Monkey Mia (Connor & Smolker 1985). Shark Bay bottlenose dolphins have haplotypes common to *Tursiops truncatus* and *T. aduncus*, leaving their taxonomic status uncertain (M. Krützen & W. Sherwin, unpublished data). The main study area extended 250 km^2 off the east side of the Peron Peninsula and included over 600 animals. Most of the dolphins were well habituated to small boats (4–5 m), allowing us to follow individuals for many hours (Smolker et al. 1993; Mann & Smuts 1998). The habitat consisted mostly of embayment plains (5–13 m in depth) and shallow seagrass beds (0.5–4 m) bisected by deeper channels (7–12 m).

Subjects

During 1988–1999, we conducted focal follows on mother–calf pairs from calf birth to weaning or calf death. Thirty-three calves (16 males, 14 females, three of unknown sex) and 23 mothers were observed for 3–23 h during 147 follows in the first year of life (4–12 months). The total amount of observation time was 412.5 h. Newborns (0–3 months) do not forage, rarely socialize, and separate infrequently from their mothers (Mann & Smuts 1999), so our sample included only calves older than 4 months. Our sample was subject to slight pseudoreplication (Machlis et al. 1985) because seven females were observed with more than one calf. However, the bias was minimal because only three of those females had more than one calf that survived to age 3 years.