



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

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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.

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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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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  $\geq 22^\circ\text{C}$ ) and very low in cool months (June–August,  $\leq 19^\circ\text{C}$ ; 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  $25^\circ 47'\text{S}$ ,  $113^\circ 43'\text{E}$  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<sup>2</sup> 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.

**Table 1.** Hypotheses and predictions

<p><b>Shark predation hypothesis</b></p> <p>Prediction 1. Close proximity and contact with the mother decreases mortality risk.</p> <p>1A. Increased contact with the mother (infant position) decreases mortality risk.</p> <p>1B. Increased separation time (&gt; 10 m) from the mother increases mortality risk.</p> <p>Prediction 2. Calves are more likely to disappear when sharks are prevalent (warm months) than when sharks are uncommon (cool months).</p> <p>Prediction 3. Prevalence of sharks by season affects calf behaviour.</p> <p>3A. Calves spend more time in contact with their mothers during warm than cool months.</p> <p>3B. Calves separate from their mothers less often during warm than cool months.</p> <p>3C. Calves rest less during warm than cool months.</p> <p>Prediction 4. Prevalence of sharks by season affects maternal behaviour.</p> <p>4A. Mothers (and calves) are in larger groups during warm than cool months.</p> <p>4B. Mothers rest less often during warm than cool months.</p> <p>Prediction 5. If there are habitat differences in shark density, then calves that spend more time in habitats with more sharks will have higher mortality risk than those that spend time in habitats with fewer sharks.</p> <p>Prediction 6. High-risk (shark) habitats affect calf behaviour by season.</p> <p>6A. Calves rest less in high-risk habitats during warm months than cool months.</p> <p>6B. Calves spend more time in contact with their mothers in high-risk habitats during warm months than cool months.</p> <p>6C. Calves spend less time separated from their mothers in high-risk habitats during warm months than cool months.</p> <p>Prediction 7. High-risk (shark) habitats affect maternal behaviour by season.</p> <p>7A. Mothers (and calves) spend less time in high-risk habitats during warm months than cool months.</p> <p>7B. Mothers rest less in high-risk habitats during warm than cool months.</p> <p>7C. Mothers (and calves) spend more time in large groups in high-risk habitats during warm than cool months.</p> <p><b>Calf condition hypothesis</b></p> <p>Prediction 1. Calf activity relates to calf mortality.</p> <p>1A. Contact patterns with the mother positively relate to mortality.</p> <p>1B. Social activity is negatively related to mortality risk; calves in good condition socialize more than calves in poor condition.</p> <p>1C. Foraging is negatively related to mortality risk; calves in good condition forage more than calves in poor condition.</p> <p>1D. Time separated from the mother relates to decreased mortality risk (calves in good condition separate from their mothers more than calves in poor condition).</p> <p>Prediction 2. Calves in poor condition are more likely to disappear than calves in good condition.</p>
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## Analyses of Behaviour, Group Size and Water Depth

Maternal and calf activities are defined in Table 2. Infant position (swimming in contact under the mother) affords protection and nursing access to the calf. All nursing takes place from infant position. Infant position was almost always initiated by the calf, but could be terminated by either mother or calf. In thousands of infant position bouts that have been observed over the last 14 years, a mother was seen to initiate infant position only once. Time spent in infant position was recorded continuously (onset and offset determined by subsurface observation or first surfacing of calf in or out of infant position). Separations were also recorded continuously based on the first observation of the calf farther than 10 m from the mother, to the first observation of the calf less than 10 m from the mother. Calves initiate and terminate over 90% of all separations (J. M., unpublished data). Separation time and time in infant position, although mutually exclusive, are not necessarily negatively correlated since the calf can remain close to the mother (< 10 m) for extended periods, without assuming infant position. Infant position, resting, travelling, socializing and foraging were scored as mutually exclusive behaviours that were observed continuously but were recorded by either point sampling (1-min intervals), predominant activity sampling (2.5- or 5-min intervals, Mann 1999) or continuous sampling. Infants could be

**Table 2.** Ethogram

Activity	Definition
Infant position	Calf swims under the mother, in intermittent contact, with the calf's head touching the mother's abdomen. Indicated for calf only.
Social	Rubbing, petting (flipper or flukes actively moving on a body part of another), chasing, mounting, poking, contact swimming (excluding infant position), and other forms of active contact.
Forage	Characterized by fast swims, rapid direction changes, bottom-grubbing, fish catches and fish fleeing.
Rest	Slow (< 3 km/h) nondirectional movement, frequent hanging at the surface.
Travel	Steady, moderate or fast (> 3 km/h) directional movement. Speeds were often tracked by boat speed.
Separation	Mother and calf surface > 10 m apart. Onset and offset of each separation recorded. Predominant maternal and calf activity and maximum distance during the separation was also recorded. Separations are not mutually exclusive from any other activities except infant position.

resting or travelling while in the infant position if the mother was resting or travelling, but in these cases, calf behaviour was scored as infant position. If mother and calf separated, we typically remained with the calf but assessed maternal activity at 1- or 5- min intervals when possible. If no predominant activity could be recorded, or if the observer was uncertain which activity occupied more than 50% of the interval, then both were scored and each weighted by a half for analysis. The most common difficulty arose between forage and travel, because dolphins often travel short distances between foraging sites and it is difficult to identify the moment they stop foraging and begin travelling. Group size was determined by scan sampling at 1- or 5-min intervals, where any animal within 10 m of another in the group was considered to be part of the group. Water depth data were collected at 5-min intervals using a depth sounder. The deepest water sampled was 12.5 m. We divided the water column into three depth classes: less than 4 m (shallow), 4–7 m (moderate), and greater than or equal to 7 m (deep).

### Calf Survivorship

Survivorship analysis involved classifying 33 calves according to whether or not they died before the minimum weaning age of 3 years. To examine seasonal patterns of calf mortality, we used the larger long-term database from survey records (see Mann et al. 2000 for survey methods and age-specific mortality for calves). This included 56 calves that died or disappeared in the first 3 years of life. Seasonal timing of death was certain for 26 of these calves.

### Shark Sightings

Over an 11-year period we recorded the size (visually estimated) and species (if identifiable) of every shark sighted. Sharks over 1 m long were classified as 'large', and those less than 1 m were classified as 'small'. Shark sightings occurred during routine surveys of the dolphin population, searches for dolphins, and during focal follows. To examine predation risk for calves, we analysed the distribution of shark sightings according to water depth. For this comparison, we determined the proportion of time we spent in shallow, moderate and deep water (935 h, 11 220 depth readings). Then, water depth, shark size and species (if identifiable) were recorded for each shark sighting. In 79 shark sightings, depth readings were not taken because of either equipment failure or interference by sonar equipment with acoustic recordings. If sharks were evenly distributed by water depth, then the percentage of sharks sighted should be proportional to the time we spent at that depth. However, because sharks are more easily sighted in shallow than deep water, a disproportionate number of sightings in shallow water might merely reflect observation bias.

### Calf and Maternal Condition

Poor condition is obvious by a sunken flank, 'neck', or area around the blowhole, or by skin condition (e.g.

ectoparasite load) and was noted for nine focal calves. Two had extensive skin conditions and seven were thin. The remaining 24 calves were considered to be in good condition. For all 23 mothers in years in which they had calves, poor body condition was noted in only three cases (two had skin conditions and one was emaciated). In all three cases, mothers subsequently lost their calves that year. Otherwise, maternal condition was not noted, and was assumed to be good.

### Data Analyses

We used parametric and nonparametric tests depending on sample size and distribution. Ontogenetic differences in calf behaviour were assessed with a Kruskal–Wallis ANOVA. Sex differences in calf activity budgets were evaluated with a Mann–Whitney *U* test. A Wilcoxon matched-pairs signed-rank test was used to compare maternal and calf behaviour when together (<10 m) and separated (>10 m). A chi-square test was used to test prediction 2 of the calf condition hypothesis, that body condition is associated with mortality, and Mann–Whitney *U* tests were used to test prediction 1A. Binomial tests were used to determine whether sharks were sighted more frequently at depths or during a particular season than would be expected from our field effort. Logistic regression analysis (SAS v.8) was used to examine how maternal behaviour, calf behaviour, group size and water depth (continuous independent variables) predicted calf mortality (binary dependent variable). The logistic regression tested our predation predictions 1 and 5, and calf condition prediction 1. We used dummy variables (averages) in up to six cases where water depth or relevant behavioural variables were not available. Pearson correlations were used to elucidate relationships between behavioural and ecological variables. Wilcoxon matched-pairs signed-ranks tests were used to evaluate seasonal variation in activity, testing predation hypothesis predictions 3 and 4. Because we found seasonal and depth differences in shark distribution, we examined variation in maternal and calf behaviour by season and depth using ANCOVA, comparing calves that were observed during warm and cool seasons within the same year. We used two ANCOVAs to evaluate the percentage of time a mother and calf rested as dependent variables. These ANCOVAs were used to test predictions 6 and 7 of the predation hypothesis. The full model of both ANCOVAs included focal calf, season, day of observation and depth as independent class variables, and percentage of time in a group of more than four, as well as percentage of time the mother and calf were separated, as covariates. For both models, interactions between class variables were removed (hierarchically) if they did not significantly contribute ( $P > 0.2$ ; Hendrix et al. 1982). To account for variation in minutes observed per day (30–530), we weighted each day by the number of minute point samples taken that day ( $N = 138$  days), treating each calf as independent. We calculated variance between depths using an autoregression model, and analysed the other variances (within focal between seasons and within focal within seasons between days).



assuming compound symmetry, which requires that the variances and covariances of the different repeated measures are homogeneous.

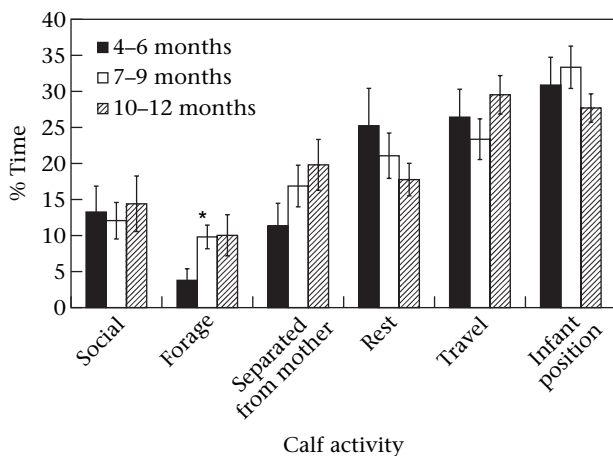
## RESULTS

### Ontogenetic Changes in Calf Behaviour

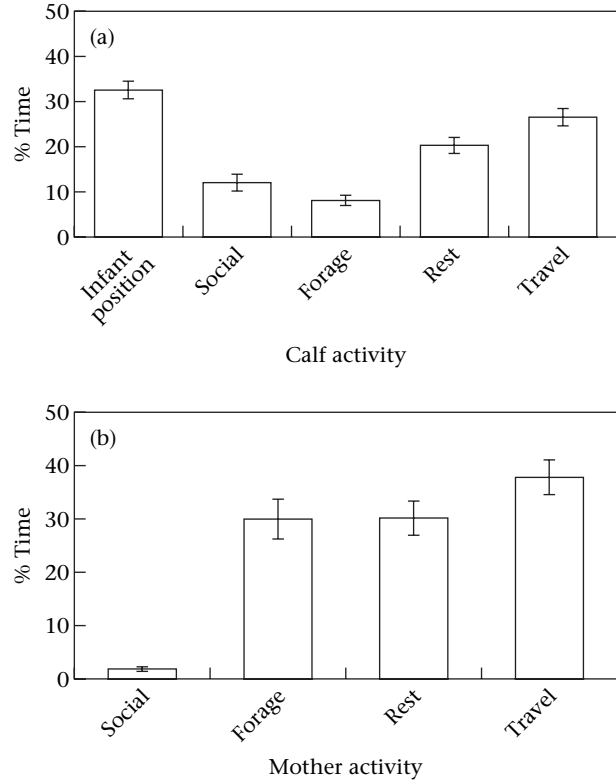
We first examined developmental changes in behaviour for 32 calves in three age classes: 4–6, 7–9, and 10–12 months (Fig. 1). One calf was excluded because of insufficient behavioural data in one age class. Calf foraging time (Kruskal–Wallis ANOVA:  $H_2 = 6.40$ ,  $P = 0.04$ ) increased during the first year, but there were no other significant developmental changes (socializing:  $H_2 = 0.27$ ,  $P = 0.88$ ; resting:  $H_2 = -1.15$ ,  $P = 0.56$ ; travelling:  $H_2 = 2.40$ ,  $P = 0.30$ ; time separated from the mother:  $H_2 = 3.13$ ,  $P = 0.21$ ). Of particular importance to this study, infant position did not significantly increase or decrease in the first year across those three age periods (Kruskal–Wallis ANOVA:  $H_2 = 1.34$ ,  $P = 0.51$ ). There was some pseudoreplication because 12 calves were counted in two age categories. For subsequent analyses, all calves over 4 months but less than 1 year of age were treated equally, but results including time foraging might have been influenced by the ages of the calves used in those analyses (Fig. 1).

### Maternal and Calf Activity Budgets

The most common activity for calves in the first year was infant position swimming with the mother. Foraging occupied the smallest proportion of their activity budget (Fig. 2a). One calf was not observed foraging at all (range 0–31.6%). There were no significant sex differences in calf behaviour during the first year (Mann–Whitney  $U$  tests: infant position:  $U = 79.0$ ,  $N_1 = 16$ ,  $N_2 = 13$ ,  $P = 0.29$ ; socialize:  $U = 93.5$ ,  $P = 0.65$ ; forage:  $U = 93.0$ ,  $P = 0.65$ ; travel:  $U = 73.0$ ,  $P = 0.18$ ; rest:  $U = 63.0$ ,  $P = 0.08$ ; separation:  $U = 69.0$ ,  $P = 0.13$ ; average group size:  $U = 80.0$ ,



**Figure 1.** Calf behavioural development during the first year of life (mean  $\pm$  SE percentage of time spent in each behavioural activity) at three age periods (4–6, 7–9 and 10–12 months of calf age).  $N = 43$  for all behavioural activities except separation time, where  $N = 44$ .



**Figure 2.** (a) Activity budgets averaged for 33 calves aged 4–12 months, showing means with standard error bars. (b) Activity budgets averaged for 23 mothers with dependent calves (4–12 months of age), showing means with standard error bars.

$P = 0.31$ ). Mothers spent much of their time travelling, resting and foraging (Fig. 2b) and little time socializing. Seventy-five per cent of the mothers spent less than 2% of their time in social activities (range 0–13.0%). All mothers foraged, although the proportion of time varied considerably, from 2.1 to 76.8%.

### Separations and Group Size

Calves spent an average  $\pm$  SD of  $16.0 \pm 10.6\%$  (range 1.8–43.6%) of their time farther than 10 m from their mothers. Separations occurred an average  $\pm$  SD of  $2.1 \pm 1.0$  times per hour (range 0.6–4.7 times/h). During each separation, the predominant activity ( $\geq 50\%$  of separation) of calf and/or mother was scored. Calf activities during separations varied; travel occurred less often during separations than did other behaviours (Table 3). Mothers predominantly foraged during separations. Resting occupied roughly 22% (median) of separations. For 15.6% of mother–calf separations, the mother was too far away to assess her activity. Because foraging animals are more difficult to keep track of, it is likely that maternal foraging was underrepresented in this sample.

Mothers were significantly more likely to forage during separations than when they were together with their calves (Wilcoxon matched-pairs signed-ranks test:  $Z = 4.84$ ,  $N = 31$ ,  $P < 0.0005$ ). Mothers were also less likely to socialize ( $Z = -3.94$ ,  $N = 27$ ,  $P < 0.0005$ ) and travel

**Table 3.** Descriptive statistics of calf and maternal behaviour during separations

Activity during separations	$\bar{X} \pm SD$	Median	Range
<b>Calf</b>			
Forage	26.58 ± 21.90	23.64	0–100
Social	26.47 ± 22.08	26.85	0–93.75
Travel	16.83 ± 17.04	12.28	0–83.33
Rest	27.66 ± 26.16	22.60	0–100
<b>Maternal</b>			
Forage	47.02 ± 29.66	44.88	0–100
Social	0.26 ± 0.87	0	0–3.45
Travel	8.96 ± 11.95	3.65	0–44.44
Rest	28.09 ± 25.57	21.53	0–100

( $Z = -4.86$ ,  $N = 31$ ,  $P < 0.0005$ ) during separations. Calf proximity did not affect time mothers spent resting ( $Z = -1.44$ ,  $N = 32$ ,  $P = 0.15$ ). Calves significantly increased foraging ( $Z = 4.53$ ,  $N = 31$ ,  $P < 0.0005$ ) and social activities ( $Z = 4.53$ ,  $N = 31$ ,  $P < 0.0005$ ) during separations and, like their mothers, were less likely to travel during separations ( $Z = -3.24$ ,  $N = 32$ ,  $P = 0.001$ ). Separation from the mother did not affect the time calves spent resting ( $Z = -1.23$ ,  $N = 32$ ,  $P = 0.22$ ). Sample sizes varied because not all mothers and calves engaged in all behaviours.

### Shark Distribution, Water Depth and Seasonal Factors

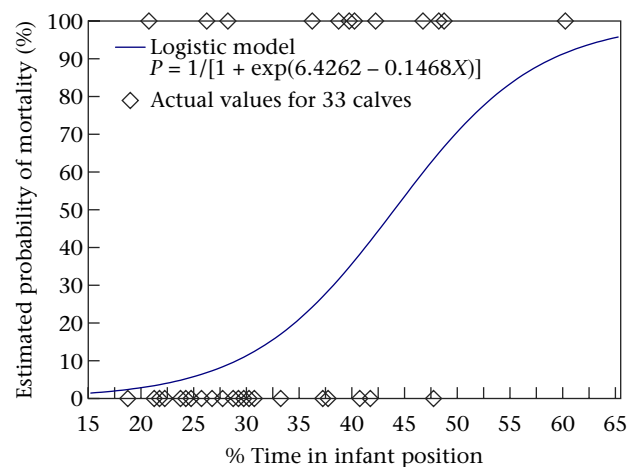
Almost all (99.3%) of 290 shark sightings occurred during warm months (September–May), although only 50.6% of our time on the water occurred in these months. Disproportionately more sharks were sighted during warm months than expected, given our field effort (binomial test:  $P < 0.0001$ ). Most of the sharks sighted were small (89.9%) and *Carcharhinus* species, but large hammerheads (*Sphyrna* spp.) and tiger sharks, *Galeocerdo cuvier*, were also sighted. Many of the shark species in Shark Bay have not been identified.

We spent 37.5% of our time in deep, 38.0% in moderate, and 24.5% in shallow water. Significantly more sharks were sighted in deep water (81.5%) and significantly fewer in both moderate (6.2%) and shallow water (12.3%) depths than expected (all tests were binomial tests: all  $P < 0.0001$ ,  $N = 211$  sharks). When separated by size, this pattern held for small sharks (<1 m; binomial tests: all  $P < 0.001$ ,  $N = 172$ ), but not for large sharks (>1 m; binomial tests: all  $P > 0.05$ ,  $N = 19$ ). In 22 cases, shark size was not noted. We sighted significantly more small sharks in deep water than expected (85.5%), and significantly fewer small sharks in moderate and in shallow water (4.1% and 10.5%, respectively). Of 19 large sharks, 42.1% were sighted in deep, 21.1% in moderate, and 36.0% in shallow water. Because only 19 large sharks were sighted (including seven tiger sharks), we only had 5, 41 and 24% power to detect a significant difference in deep, moderate and shallow water, respectively. Therefore, we could not accept or reject the null hypothesis that large sharks are distributed evenly across all depths.

### Behavioural, Physical and Ecological Predictors of Calf Mortality

Seven predictors of calf mortality were selected for logistic regression analysis: time spent in infant position, infant socializing, infant foraging, mother–calf separation, maternal foraging, median group size and water depth. For all variables except group size and depth, we used the proportion of time engaged in that activity. For water depth, we chose the proportion of time spent in deep ( $\geq 7$  m) water. We ran the regression for survival to age 3 years. Only one variable predicted calf mortality: time spent in infant position. Calves that spent more time in infant position were more likely to die before their third birthday than calves that spent less time in infant position (Fig. 3). The logistic model accurately predicted 78.8% of the cases correctly (odds ratio = 1.14, Wald  $\chi^2_1 = 6.69$ ,  $P < 0.01$ ).

Although only infant position predicted calf mortality, the relationship between infant position and other variables may help to explain why this was the case. A Pearson correlation matrix of the seven variables appears in Table 4. These data should be interpreted with caution since time spent in infant position was defined as mutually exclusive from all other infant behaviours, with the exception of time spent in deep water. Time in infant position also positively correlated with time spent in deep water (Pearson correlation:  $r = 0.482$ ,  $N = 28$ ,  $P = 0.009$ ). Similarly, the time a calf spent separated from the mother negatively correlated with time spent in deep water ( $r_p = -0.436$ ,  $N = 28$ ,  $P = 0.02$ ). Group size correlated with infant socializing (Pearson correlation:  $r = 0.402$ ,  $N = 32$ ,  $P = 0.023$ ), as might be expected, but did not relate significantly to any other variables. Maternal foraging did not significantly correlate with any behavioural or ecological variable we measured. Although separations and infant position were significantly correlated with calf socializing and foraging, calf socializing and foraging were



**Figure 3.** Results of the logistic regression analysis of the percentage of time spent in infant position in relation to calf mortality before 3 years of age. Twenty-one infants survived to age 3 years and 12 infants died.

**Table 4.** Pearson correlation matrix of social, behavioural and ecological variables considered in relation to calf mortality

	Infant position	Calf social	Calf forage	Separation	Deep water	Group median	Mother forage
Infant position	—						
Calf social		—					
<i>r</i>	<b>-0.424</b>						
<i>P</i>	<b>0.015</b>						
<i>N</i>	<b>32</b>						
Calf forage			—				
<i>r</i>	-0.306	-0.076					
<i>P</i>	0.088	0.679					
<i>N</i>	32	32					
Separation				—			
<i>r</i>	<b>-0.411</b>	<b>0.402</b>	<b>0.526</b>				
<i>P</i>	<b>0.017</b>	<b>0.022</b>	<b>0.002</b>				
<i>N</i>	<b>33</b>	<b>32</b>	<b>32</b>				
Deep water					—		
<i>r</i>	<b>0.482</b>	-0.183	-0.238	<b>-0.436</b>			
<i>P</i>	<b>0.009</b>	0.360	0.232	<b>0.020</b>			
<i>N</i>	<b>28</b>	27	27	<b>28</b>			
Group median						—	
<i>r</i>	-0.158	<b>0.402</b>	-0.048	-0.080	0.032		
<i>P</i>	0.381	<b>0.023</b>	0.792	0.656	0.872		
<i>N</i>	33	<b>32</b>	32	33	28		
Mother forage							—
<i>r</i>	0.037	-0.079	0.201	0.269	-0.025	-0.089	
<i>P</i>	0.840	0.667	0.270	0.137	0.902	0.627	
<i>N</i>	32	32	32	32	27	32	

Significant ( $P < 0.05$ ) relationships are in bold.

not significantly related to each other (Pearson correlation:  $r = -0.076$ ,  $N = 32$ ,  $P = 0.70$ ).

### Behavioural Changes by Season and Water Depth

We divided the focal follows for each calf into those occurring during the warm spring–autumn (September–May) and cool winter (June–August). To control for developmental changes and variation between mother–calf pairs, we chose 14 calves that were observed from either warm (September–May) to cool (June–August) months ( $N = 6$ ) or cool to warm months ( $N = 8$ ) within the first year. We contrasted the change from warm to cool months, regardless of which came first. Using a Wilcoxon matched-pairs signed-ranks test, we examined whether infant behaviours (time spent in infant position, socializing, foraging, separation time) and median group size or water depth use changed with season. By season, calves did not significantly change their time in infant position ( $T = 31.0$ ,  $N = 13$ ,  $P = 0.31$ ), socializing ( $T = 44.0$ ,  $N = 13$ ,  $P = 0.92$ ), foraging ( $T = 45.0$ ,  $N = 13$ ,  $P = 0.97$ ), or separated from their mothers ( $T = 30.0$ ,  $N = 14$ ,  $P = 0.16$ ). Calves did not significantly change their movements in shallow water by season ( $T = 35.0$ ,  $N = 14$ ,  $P = 0.75$ ), but they did tend to spend less time in moderate depth in warm months ( $T = 25.0$ ,  $N = 14$ ,  $P = 0.08$ ) and more time in deep water ( $T = 6.0$ ,  $N = 14$ ,  $P = 0.05$ ); median group size tended to be larger in the cool months than in warm months ( $T = 5.5$ ,  $N = 14$ ,  $P = 0.08$ ).

The next set of analyses, using an ANCOVA model, focused on behavioural changes by season and water depth. We used data from 68 focal follows ( $\bar{X} \pm \text{SD} = 180 \pm 14$  min/day, range 30–530) of 14 calves ( $\bar{X} \pm \text{SD} = 4.8 \pm 0.55$  days/calf, range 2–8). We determined that both sets of residuals for both the calf resting ANCOVA ( $W = 0.99$ ,  $N = 138$ ) and the mother resting ANCOVA ( $W = 0.94$ ,  $N = 138$ ) were approximately normally distributed, and the variances appeared to be homogeneous for both ANCOVAs by evaluation using the Schwarz's Bayesian criterion. Mothers spent more time resting in deep water than in shallow water during cool months ( $\bar{X} \pm \text{SD}$ : deep:  $47 \pm 7.4\%$ ; shallow:  $17 \pm 5.6\%$ ; ANCOVA:  $t_{63} = 3.64$ ,  $P = 0.0006$ ), but not warm months (deep:  $30 \pm 5.5\%$ ; shallow:  $23 \pm 5.8\%$ ; ANCOVA:  $t_{63} = 0.94$ ,  $P = 0.353$ ). There was no significant interaction between season and depth in the time calves spent resting ( $P = 1.0$ ). Calves did not significantly alter the percentage of their time resting in the warm ( $\bar{X} \pm \text{SD} = 43 \pm 4.3\%$ ) versus the cool ( $39 \pm 4.7\%$ ) season regardless of depth (ANCOVA:  $t_{12} = -0.66$ ,  $P = 0.52$ ); but calves rested more in deep water ( $49 \pm 5.1\%$ ) than in shallow water ( $31 \pm 4.7\%$ ) during both seasons ( $t_{63} = 3.31$ ,  $P < 0.002$ ). Neither group size nor time spent separated significantly interacted with season and depth to affect either the mother's or the calf's time resting (mother resting: group size by season by depth interaction:  $P = 0.81$ ; time separated by season by depth interaction:  $P = 0.65$ ; calf resting: group size by season by depth interaction:  $P = 0.24$ ; time separated by season by depth interaction:  $P = 0.38$ ).

## Calf Mortality

Death date for 26 of 56 calves could be narrowed down to either September to May or June to August. If calf death was equally likely to occur all year round, then 75% would occur in September–May and 25% in June–August. In fact, 23.08% (6 of 26) calves disappeared in the cool months (June–August), when predation pressure is quite low (binomial test:  $N = 26$ ,  $P = 0.5$ ). Calves that died by age 3 years had poor body condition relative to that of survivors (Fisher's exact test:  $\chi^2_1 = 14.74$ ,  $N = 33$ ,  $P < 0.001$ ). Seventy-five per cent of calves that died (8 of 12) showed visible signs of poor health compared with 4.7% of the survivors (1 of 21).

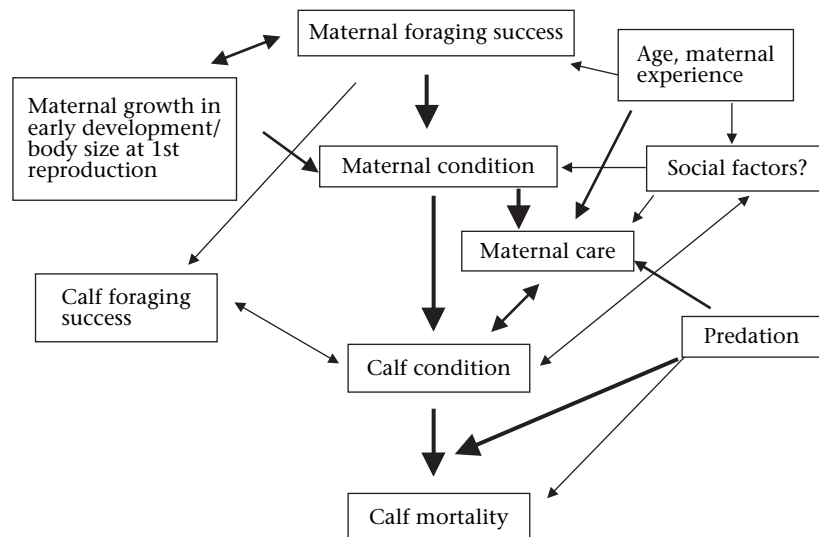
## DISCUSSION

We sought to answer two major questions. First, what behavioural, social and ecological factors predict calf mortality? Second, are these findings consistent with the calf condition or the predation hypothesis? We suggest that calf condition is likely to be the primary cause of calf mortality, but predation risk, although apparently secondary, influences maternal behaviour. Our results supported only part of prediction 7 (7B) and contradicted prediction 1 of the predation hypothesis. Group sizes were larger during cool than warm months, in contradiction to prediction 4A of the predation hypothesis. None of the remaining 13 predictions for the predation hypothesis were supported. For the calf condition hypothesis, all five of the predictions were largely supported. Most calves that died showed signs of poor condition prior to their disappearance, and these calves also may have been more vulnerable to predation. Although only one behaviour,

time spent in infant position, was directly related to calf mortality, we suggest that infant position may be an indirect measure of calf condition. Other factors probably contribute to infant position patterns and some calves in poor condition may have escaped detection. The calf's condition is likely to be a product of maternal condition and experience. Maternal condition may be linked to a number of factors (e.g. age, experience and early growth patterns), but foraging success is likely to be the key contributor. Figure 4 shows a model of how behavioural, physiological, developmental and ecological factors are expected to shape calf mortality risk. We discuss this model below in relation to two categories of results: behavioural ecology of calves and their mothers, and predation risk.

## Behavioural Ecology of Calves and Their Mothers

Our results on calf mortality and calf behaviour appear somewhat counterintuitive. How could calves that spent more time in contact with their mothers be less likely to survive than other calves? We suggest that calves compensate for poor condition by seeking additional care. Whether calves are successful in receiving more milk or better protection with this strategy is not known. Vigorous or healthy calves, which socialized, foraged and separated more than their less vigorous counterparts, may have further enhanced their condition by supplemental feeding and reducing the costs of maternal care. For example, calves that separated more often may not only have fed themselves, but also enhanced foraging opportunities for the mother by allowing her to hunt alone.



**Figure 4.** A schematic representing a possible network of factors leading to calf mortality in bottlenose dolphin (in boxes), the direction of their effects (arrowheads), and the strength of their relationships (indicated by the width of the line). Shallow water habitats (possibly indicating higher maternal foraging success) have been correlated with increased reproductive success in bottlenose dolphins (Mann et al. 2000). In the present study, we examined the relationship between calf condition, predation and calf mortality. Further insights into the causes of calf mortality will be derived from a better understanding of how variations in maternal foraging behaviour, habitat use and development relate to maternal and calf condition.



Calf behaviour did not vary seasonally, and thus calf behaviour did not appear to vary with predation risk. Calves tended to rest more in deep than in shallow water during both seasons, perhaps because calves often move slowly at the surface while their mothers make deep foraging dives. This behaviour fits our definition of 'resting', although the calves are probably not inattentive since they appear to be tracking their mothers from the surface. Water depth significantly correlated with the time spent in infant position, as expected if calves were being more cautious because of predation risk, their condition, or both. However, calves separated from their mothers equally during warm and cool months. Furthermore, calves tended to spend more time in larger groups during cool than warm months, precisely opposite that expected if either group size offered protection from predation or if predation exerted a significant pressure on dolphin calf behaviour.

In general, our data suggest that mothers were tolerant of calves maintaining contact through infant position, and that by doing so, they may have been compensating for poor calf condition. If habitat quality varies by water depth, then mothers in deeper water may use compensatory strategies by being more tolerant of calf bids for contact. Other compensatory mechanisms, such as late weaning, may also be important. In other mammals, mothers sometimes increase care under poor conditions when sources of infant mortality are dependent on care (e.g. mountain baboons, *Papio cynocephalus ursinus*: Lycett et al. 1998). In red deer (Clutton-Brock et al. 1982) and primates (reviewed in Lee 1999), mothers in good condition have offspring in good condition, and therefore may reduce maternal care.

Mothers were more likely to forage during separations than when close to their calves. Unlike their calves, mothers socialized little, and when they did so, the calf was typically their partner, potentially explaining why mothers were less likely to be separated from their calves during social activities. Group size, which is largely controlled by the mother, did not predict calf mortality. This was consistent with our earlier findings that group size does not predict female reproductive success (Mann et al. 2000).

The time mothers spent foraging was not correlated with calf behaviour, group size, water depth use, or calf mortality. Time spent foraging is likely to be only weakly correlated with food intake, and may be inversely related. Foraging success is likely to be a key factor in determining maternal condition but is difficult to assess because catches of small prey are more likely to be missed than catches of large prey, which are often brought to the surface and take time to process (heads and pieces of large fish are routinely broken off before swallowing). Furthermore, prey catches in shallow water are easier to observe than prey catches in deep water. Although we cannot measure foraging success directly, foraging success, rather than time spent foraging, is likely to contribute to the female's growth during development, maternal condition, and calf growth prenatally and during lactation. In addition, successful foraging may indirectly foster calf condition because efficient foragers may be able to direct more effort towards maternal care than those that are less

efficient. Figure 4 models the predicted direction and strength of these interactions.

### Predation Risk

Our data suggest that predation risk was a secondary, not primary, cause of calf mortality. First, calves were equally likely to disappear during shark (warm) and nonshark (cool) seasons. Second, most calves already had signs of poor condition prior to their disappearance. Third, mothers and calves were not avoiding large or small sharks. Heithaus & Dill (2002) found that large tiger sharks occur in shallow water (<4 m) about 35% of the time, significantly more than expected, given that only 17% of the habitats they surveyed (a subset of our study area) were shallow. We found that small sharks were disproportionately found in deeper water. Mothers and calves did not move out of shallow water in the warm months, only from moderate to deep. If tiger sharks are disproportionately found more in shallow water than deep water during warm months, then mothers and calves were not avoiding them. However, sharks may still have influenced maternal behaviour. Mothers were less likely to rest in deep water during the warm months than during the cool months, suggesting that they were more vigilant in habitats with higher overall shark density. Similarly, female elk (*Cervus elaphus*) in habitats with predators (wolves) and higher calf mortality spend more time vigilant and less time foraging than those in predator-free environments (Wolff & Van Horn 2003).

Reactions to sharks by dolphins vary and seem to depend on the size of the shark, the size and composition of the dolphin group, and when the shark is detected. A number of shark-dolphin encounters have been observed with calves present. Females and calves have been observed speeding away from large sharks (e.g. Connor & Heithaus 1996), as well as attacking and mobbing large tiger sharks (Mann & Barnett 1999; J.M., personal observation). In the only case where a lethal shark attack was observed, the calf was emaciated, alone (~70 m from her mother), and in water of moderate depth. Several females sped to the scene and fought the shark after the attack began, and the mother subsequently chased the shark from her deceased calf after the other dolphins had left (Mann & Barnett 1999). Although dolphins are clearly concerned about the presence of sharks and alter some aspects of their behaviour accordingly, dolphins, with their superior manoeuvrability, are adept at defence or avoiding lethal attacks if the shark is detected early enough. It is possible that shark attacks could cause changes in calf condition, but none of the calves in poor condition in the current study had recently been attacked by sharks.

In Shark Bay, fish density is higher in shallow than deep water (Heithaus & Dill 2002). Thus, mothers and calves that live in shallow water habitats may be in better condition than those living in deeper water. This is consistent with our previous findings (Mann et al. 2000) that water depth predicts long-term (10-year) female reproductive success, with shallow-water mothers having higher success than deep-water mothers. Reproductive

success combines mortality with weaning age, not just calf mortality per se. This may be why water depth alone does not predict calf mortality, but does predict female reproductive success. Maternal body condition (see Fig. 4), particularly limited access to resources, may be the most critical factor explaining female reproductive success. We suggest that patterns of maternal care, development and behaviour in Shark Bay bottlenose dolphins are similar to life histories for other large-brained mammals with delayed maturation, in that energetic constraints, rather than predation pressure, are the primary factors affecting female calving success.

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