# Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects

**Janet Mann,**[a] **Richard C. Connor,**[b] **Lynne M. Barre,**[a] **and Michael R. Heithaus**[c]
[a]Departments of Biology and Psychology, Georgetown University, Washington DC 20057, USA, [b]Department of Biology, UMASS-Dartmouth, Dartmouth, MA 02747, USA, and [c]Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

This study examines factors influencing female reproductive success in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Australia. Eighty-three females and their 142 calves were surveyed between 1988 and 1998 (3457 surveys); 42 calves were also observed during focal follows for 1330 h. Calf mortality is 44% by age 3 ($n = 110$). Reproduction is moderately seasonal (September–January), peaking from October to December. Calf loss between August and December is followed by rapid conception (1–2 months), whereas conception is delayed (2–9 months) if calf loss occurs between January and July. Weaning ages ranged from 2.7 to 8.0 years, but 66.7% (42 calves) were weaned by their fourth birthday. Females tended to wean mid-pregnancy. Accordingly, median interbirth interval was 4.1 years. Female reproductive success was classified as 0, 1, 2, or 3 according to the number of calves who survived to age 3 over a 10-year period ($n = 38$ females with complete histories). We examined whether factors affecting predation or food availability, water depth, and group size, were related to female reproductive success. Group size was unrelated to water depth or female reproductive success, but reproductive success was predicted by water depth ($p < .002$). Shallow water may allow mothers and calves to detect and avoid predatory sharks. Alternatively, or additionally, prey density may be higher in shallow water compared to deep water. *Key words:* birth, bottlenose dolphins, female reproductive success, interbirth interval, lactation, mortality, sociality, *Tursiops,* water depth, weaning. *[Behav Ecol 11:210–219 (2000)]*

Long-term studies of bottlenose dolphins (*Tursiops* sp.) at several sites (Sarasota, Florida: Wells et al., 1987; Moray Firth, Scotland: Wilson et al., 1997; Shark Bay, Australia: Connor et al., 1992b) have revealed complex societies for these long-lived, large-brained mammals. Dolphins are also characterized by extensive maternal investment (Mann and Smuts, 1998; Oftedal, 1997). Yet factors affecting variation in female reproductive success remain virtually unexplored. The current study examined how factors such as calf mortality, weaning, interbirth intervals, breeding season, provisioning, group size, and habitat influence female reproductive success.

Everywhere they have been studied, dolphins live in a fission-fusion society where individuals join and leave groups on a fluid basis, with associations lasting minutes to years (e.g., Smolker et al., 1992; Wells et al., 1987). Grouping patterns within this flexible system likely reflect sex-specific reproductive strategies. In Shark Bay, males form two levels of alliances in which they herd and compete for females (Connor et al., 1992a,b, 1999). Associations within male alliances are strong and stable over time. Females may be highly social or solitary, associating with related and unrelated females (Shark Bay: this paper; Smolker et al., 1992; Sarasota: Duffield and Wells, 1991). Whereas male reproductive strategies clearly focus on gaining and maintaining access to cycling females, female reproductive strategies are likely to center on calf protection (from predators and/or conspecifics) and access to food. Thus, female reproductive success is expected to correlate with social and ecological factors such as group size and water depth. Grouping is expected to afford protection against sharks. Visibility and distribution of prey and predatory sharks may correlate with water depth.

Other social factors that may influence female reproductive success in dolphins include mate choice and protection from conspecifics. Females appear to opportunistically form coalitions against males, but how females exercise mate choice has not been systematically explored (Connor et al., 1992a, 1996). Polyestrus cycling and spontaneous ovulation (Kirby and Ridgway, 1984; Schroeder, 1990) in dolphins may allow females greater choice in mating partners or reduce paternity certainty and thus protect their offspring from infanticide (Connor et al., 1996). Indeed, calves who died from dolphin-inflicted injuries have washed ashore in the Moray Firth and Virginia, USA, although the relationships between the victims and perpetrators remain unknown (Patterson et al., 1998; Dunn et al., 1999). Infanticide has not been documented in Shark Bay, but the unpopulated coastline and high shark density make carcass recovery unlikely (also see Connor et al., 1996).

Female reproductive success is also influenced by breeding season and other demographic and reproductive parameters. After a 12-month gestation, females typically give birth in the spring or summer (Connor et al., 1996; Kasuya et al., 1997; Urian et al., 1996; Wells et al., 1987). Studies of dolphins in captivity report an 18-month lactation period (Cockcroft and Ross, 1990; Tavolga, 1966), although field studies report approximately twice that duration (Mann and Smuts, 1998; Wells et al., 1987). Females typically begin reproduction between 7 and 12 years of age (Kasuya et al., 1997; Schroeder, 1990; Wells et al., 1987). Maximum life span for Shark Bay females is not known, but Sarasota females may live to their early 50s

(Hohn et al., 1989; Wells and Scott, 1999). This study investigated factors affecting female reproduction.

## Birth seasonality

We reexamined birth seasonality with a larger sample size than published previously (Connor et al., 1996) and also investigated the relation between temperature and birth peaks. Studies at other sites found that these peaks coincided (Urian et al., 1996; Wells et al., 1987), possibly due to homeothermic or ecological factors. Studies of the relationship between season and predator and prey density and distribution are currently underway in Shark Bay.

Seasonal breeding is likely to be primarily in the female's reproductive interests because she bears the costs of lactation, calf care, and protection. Calves may be most vulnerable to predation or harassment soon after birth (Mann and Smuts, 1998), although the precise cause of calf death is rarely known. Females should favor larger group sizes when they have young calves (0–3 months), compared to when they have older calves, but whether group size protects primarily against predation and/or conspecifics cannot currently be tested.

With a narrow breeding season or loss of calf late in the season, females would be forced to delay conception until the next breeding season if their calf died. With a longer breeding season or loss of calf early in the season, females may resume cycling quickly after calf death.

Male reproductive strategies, specifically their ability to monopolize females, will also be influenced by the degree of seasonal breeding. Infanticide is unlikely to be a successful strategy unless males have an opportunity to monopolize the mother of the deceased infant at the time of her subsequent conception. We examined seasonal variation in the time lag between infant death and the female's subsequent pregnancy to determine whether there is a seasonal "window of opportunity" for male infanticide to be an adaptive strategy. Alternatively, if neonatal death is high from other causes (e.g., disease, predation), males may peacefully associate with new mothers to increase the chances of monopolizing her should the calf die. Interactions among newborns, mothers, and adult males are rarely observed (Mann and Smuts, 1998, 1999) but are needed to distinguish between these hypotheses.

## Calf mortality

Age-specific patterns of calf mortality from birth to age 3 (close to minimum weaning age) were examined. Sixteen of 110 calves in our study were born to 5 females provisioned with dead fish on a daily basis. We compared mortality for calves born to provisioned and nonprovisioned females. Field studies of several mammals suggest artificial provisioning typically increases female reproductive rate (e.g., vervets, *Cercopithecus aethiop*: Lee et al., 1986; baboons, *Papio cynocephalus*: Altmann and Muruthi, 1988).

## Weaning and interbirth intervals

The variation in weaning age and its relation to interbirth intervals with surviving calves was examined. We examined the timing of weaning in relation to female reproductive status. Females might wean before the next pregnancy, allowing them to regain body condition. Alternatively, females might wean during the pregnancy and, if fetal loss occurs, continue nursing their dependent calf for another year (potentially explaining some of the variation in age of weaning).

## Age at first birth and female reproductive success

We compared age at first birth, survivorship of first-born calves, and female reproductive success over a 10-year interval. Water depth and group size factors were examined in relation to female reproductive success. Some habitats may offer better food or safety from predators, and associates may offer protection from predators or conspecifics, although potentially enhance feeding competition. The association between group size and habitat is also explored to determine if solitary and social females use different habitat types.

## METHODS

### Field site

Shark Bay is located 25°47′S, 113°43′E in Western Australia. After an initial visit in 1982, a long-term study of the Shark Bay dolphins was established in 1984 off of a fishing camp called Monkey Mia. The study area currently extends 300 km² off the east side of the Peron Peninsula and includes more than 600 animals. Most dolphins are well habituated to small boats (4–5 m), allowing us to follow individuals for many hours (Mann and Smuts, 1998; Smolker et al., 1993). The habitat consists mostly of embayment plains (5–13 m) and shallow seagrass beds (0.5–4 m) bisected by deeper channels (6–10 m).

Since the 1960s, several dolphins have visited the camp to accept fish handouts from fishers and tourists (Connor and Smolker, 1985). The number of provisioned dolphins has varied over the past 30 years, as has the amount of fish fed to them, both daily and seasonally. Currently, three adult females and their offspring visit Monkey Mia on a daily basis. The feedings are controlled by rangers, who allow only the adult females to be fed up to 2 kg per day.

### Subjects

The complete sample includes 83 females and their 142 calves. Sexes were determined primarily by sighting of the genital area, reliable presence of a dependent calf, and in three cases via genetic sampling (Krützen M, unpublished data). Sample sizes vary by analysis according to the quality of the data (i.e., whether exact birthdates, weaning dates, sex, and survivorship were known). For example, if a mother and newborn calf were sighted together one year, but neither mother nor calf were sighted for several years, and the calf was not sighted again, we could not determine calf survivorship, but can use the case for birth seasonality. Calves' dorsal fins are less distinctive than their mothers', making it difficult to keep track of juveniles. Similarly, exact birth month or year was not known for all calves due to gaps between sightings. However, such calves might still survive to weaning, and documentation of association pre- and postweaning is still possible.

### Surveys

Most of the data come from 3457 surveys of females and calves during 77 months of fieldwork between 1988 and 1998. Additional sighting, demographic, and behavioral information was added from 1330 hours of focal follows on 42 calves who were also surveyed, field notes from researchers, rangers at the Monkey Mia Dolphin Information Centre, and a tour operator who photographed new calves when researchers were not in the field. Twenty of the focal calves were observed to weaning, and in 17 of those cases, either mother or calf was observed postweaning. Each of the 83

females was sighted during surveys on average 69 times (SD = 84, median = 46).

Surveys were conducted regularly by all researchers in Shark Bay. When a dolphin was sighted, we recorded identity of animals in the group using a 10-m chain rule (Smolker et al., 1992). Nongroup members were also indicated. For association and group size analyses, all animals within the 10-m chain during the first 5 min of the survey were considered, regardless of their activities. Dorsal fins were photographed for all animals not readily identifiable and later matched to a catalogue photo. Location (GPS or compass bearings), water depth, temperature, and activities were systematically recorded. If mother and calf were observed swimming in infant position (calf swims under the mother, lightly touching her abdomen), a reliable indicator of continued dependency and nursing (Mann and Smuts, 1998), this was noted.

Each time a calf was sighted for the first time, the observer recorded estimated size and age, fetal lines, swimming style (chin-up and cork-up surfacings, consistent echelon swimming; Mann and Smuts, 1999), spatial relationship with the mother, and other details to determine age. Detailed observations of newborn calves indicate that fetal lines typically disappear by 3 months of age, and swimming style changes rapidly during the first month of life (Mann and Smuts, 1999).

## Birthdates and birth seasonality

Birthdates were estimated based on last sighting of mother before calf birth and first sighting of mother with calf. If year of birth could not be determined, the calf was not included in age-specific mortality and weaning analysis. All known births that could be estimated within 3 months were used for birth season data. This included 47 mothers and 74 calves, with accurate birth estimates to within 1 month ($N = 50$), 2 months ($N = 16$), and 3 months ($N = 8$).

## Temperature

We collected data on surface water temperature during 2582 surveys. These were averaged by month. No temperature readings were collected during February.

## Calf mortality

If mothers were sighted repeatedly without their calf when the calf was <3 years of age, we presumed that the calf died. Although a few calves were weaned as early as 2.7 years, the two cases of calf disappearance between ages 2 and 3 involved calves who should have been observed often and who had distinctive fins. In cases where we could not be certain if the calf was weaned or died, we excluded these cases from the analysis. Deaths were classified by calf age: <12 months, 12–23 months, and 24–35 months. Calves that survived to 3 years of age were considered survivors, even if they were not yet weaned. Of 110 calves used in the survivorship analysis, 16 were born to 5 provisioned females, and 94 were born to 58 nonprovisioned females. To compare provisioned and nonprovisioned groups, we used survival analysis (Kaplan-Meier method), which is most suitable for small data sets with precisely measured event times. The Wilcoxon chi-square statistic was calculated by taking the weighted sum of the deviations of observed numbers of mortality events from expected numbers of events and squaring them for either group.

## Weaning

Weaning age was estimated by taking a midpoint between two time points. The time points were based on two major behavior changes: (1) last sighting of infant in infant position and cessation of infant position swimming with the mother and (2) marked change in mother–calf association from always/consistently sighted together to always/consistently apart. Calves do not swim in infant position once the next sibling is born. All calves who markedly reduced association with their mothers had ceased swimming in infant position. However, one calf born to a provisioned female continued to associate at high levels with her mother but had ceased swimming in infant position. Detailed focal observational data were collected on 20 calves until weaning, including this mother–calf pair, allowing us to be certain of the weaning date. All nursing occurs from infant position, and once calves cease infant position swimming, they never resume (Mann and Smuts, 1998). That is, in 1330 focal h and 3457 surveys of calves and females, weaning was clearly demarcated by the absence of infant position swimming and a significant drop in mother–calf association. Nursing is virtually never observed during surveys but is often seen during focal follows. Nursing (beak to mammary slit) was observed during the last 6 weeks of infant position swimming for three of four focal mother–calf pairs observed in detail throughout the weaning process. The fourth pair was observed from greater distances (because we used a larger vessel), thus making it unlikely we could detect nursing.

For 42 calves, we had accurate weaning ages (known birth and weaning month) based on survey and follow data. Coefficients of association (COA) between mother and calf were calculated using the halfweight method (Cairns and Schwager, 1987) for preweaning and for up to 2 years postweaning. COA between individual a and b = $2Nab/Na + Nb$, in which $Nab$ is the number of times a and b were in the same group, and $Na$ and $Nb$ are the total number of group sightings for a and b. We multiply this formula by 100 to yield a number between 0 and 100, where 0 = a and b are never sighted together, to 100 = a and b are always sighted together. For some calves, we did not have accurate birth years, but with accurate weaning month, we could calculate COA pre- and postweaning ($N = 45$ calves for COA analysis).

## Interbirth intervals

Years between birth of a surviving calf and another birth were used to determine interbirth intervals (IBI). We used two methods. In the first method, we restricted our sample to 33 cases where the female was sighted often annually, reducing the likelihood that we missed a birth. Of these, only three had a gap large enough between weaning of the first calf and the birth of the second calf that a pregnancy and loss could have occurred. The 30 cases with no gap were most accurate. In two cases the IBI was estimated within 2 years. We added half a case to both possible IBI years. The first method would bias against long IBIs. For the second method, we included all 44 cases with a surviving calf and a known subsequent birth, regardless of the gap between weaning of the first calf and birth of the next. In 14 of these cases, the interval could have been shorter if mothers lost unsighted calves <1 year of age.

## Reproductive success

Female reproductive success (RS) was defined as the number of offspring surviving to age 3 within a 10-year period. Reproductive success was classified as 0, 1, 2, or 3, reflecting the number of calves each female had that survived to age 3. Females ($N = 38$) and "probable" females ($N = 2$) were included in the analysis if (1) they were adult size at the onset of the 10-year period, (2) known to be at least age 12 (known

**Table 1**

**Reproductive success (RS), water depth (m), and group size for 38 females over a 10-year period**

| ID | RS | Depth (m) Median | Mean | SD | No. of depth surveys | Group size Median | Mean | SD | No. of of group surveys |
|----|----|--------|------|----|--------|--------|------|----|--------|
| ol | 0 | 3.0 | 4.0 | 2.9 | 10 | 3 | 3.1 | 2.1 | 12 |
| tw | 0 | 4.9 | 5.2 | 2.4 | 59 | 8 | 7.8 | 3.9 | 87 |
| hh | 0 | 5.2 | 4.8 | 2.3 | 29 | 7 | 7.4 | 3.6 | 58 |
| sc | 0 | 5.8 | 5.7 | 2.2 | 38 | 7.5 | 7.5 | 4.0 | 47 |
| pd | 0 | 6.1 | 6.0 | 1.9 | 56 | 3 | 4.9 | 4.5 | 61 |
| ft | 0 | 6.1 | 5.9 | 1.7 | 134 | 7 | 7.0 | 3.8 | 177 |
| fe | 0 | 6.4 | 7.3 | 1.5 | 17 | 4 | 3.7 | 2.4 | 19 |
| tt | 0 | 7.0 | 7.4 | 1.9 | 13 | 7 | 7.1 | 4.1 | 21 |
| mu | 0 | 7.6 | 7.8 | 1.9 | 52 | 5 | 5.6 | 5.2 | 72 |
| ta | 0 | 8.5 | 8.3 | 1.7 | 27 | 4 | 4.4 | 3.2 | 47 |
| sr | 1 | 4.0 | 4.0 | 1.9 | 149 | 5 | 5.4 | 3.8 | 200 |
| cr | 1 | 4.3 | 4.4 | 1.1 | 83 | 4 | 4.0 | 2.6 | 107 |
| pu | 1 | 4.3 | 4.6 | 1.6 | 212 | 5 | 5.7 | 3.8 | 268 |
| ho | 1 | 4.6 | 4.9 | 1.6 | 102 | 3 | 4.5 | 3.6 | 125 |
| wa | 1 | 5.8 | 8.0 | 2.7 | 15 | 4.3 | 4.4 | 3.2 | 21 |
| tr | 1 | 6.7 | 6.5 | 1.9 | 21 | 7 | 7.4 | 3.6 | 25 |
| to | 1 | 6.7 | 6.7 | 1.8 | 59 | 4 | 5.1 | 3.9 | 68 |
| ya | 1 | 6.7 | 6.4 | 1.5 | 96 | 2 | 3.8 | 4.2 | 128 |
| ha | 1 | 7.3 | 6.8 | 1.9 | 42 | 2 | 3.6 | 3.7 | 59 |
| ps | 1 | 7.3 | 7.4 | 1.9 | 101 | 5 | 5.9 | 4.0 | 129 |
| ja | 1 | 7.6 | 7.8 | 2.3 | 38 | 4 | 5.7 | 5.0 | 42 |
| wy | 1 | 8.4 | 8.6 | 2.3 | 31 | 5.5 | 6.1 | 3.3 | 46 |
| ni | 1 | 8.5 | 8.0 | 3.1 | 16 | 3.8 | 5.0 | 4.1 | 24 |
| go | 1 | 8.5 | 9.4 | 2.4 | 44 | 5 | 6.9 | 4.7 | 66 |
| ty | 1 | 8.7 | 8.8 | 2.4 | 37 | 6 | 6.9 | 3.8 | 52 |
| nc | 2 | 4.3 | 4.5 | 1.7 | 158 | 5 | 5.9 | 4.3 | 205 |
| jf | 2 | 4.3 | 4.3 | 1.6 | 234 | 4 | 5.2 | 4.2 | 312 |
| by | 2 | 5.2 | 5.0 | 1.9 | 38 | 2 | 3.2 | 3.3 | 46 |
| sq | 2 | 5.9 | 6.0 | 2.0 | 199 | 6 | 6.7 | 3.8 | 266 |
| uh | 2 | 6.4 | 6.1 | 2.2 | 131 | 8 | 7.9 | 4.5 | 161 |
| bl | 2 | 7.0 | 7.2 | 1.7 | 68 | 4 | 6.0 | 5.5 | 88 |
| mi | 2 | 7.3 | 8.3 | 3.1 | 108 | 5 | 6.1 | 5.0 | 156 |
| al | 2 | 7.9 | 7.8 | 2.1 | 51 | 6.5 | 7.2 | 5.2 | 79 |
| sa | 2 | 8.1 | 8.1 | 1.4 | 22 | 4 | 4.8 | 3.2 | 39 |
| de | 2 | 9.0 | 9.7 | 3.1 | 56 | 5 | 6.2 | 4.3 | 82 |
| zg | 3 | 4.9 | 5.4 | 2.4 | 45 | 8 | 8.1 | 4.5 | 55 |
| np | 3 | 7.0 | 6.8 | 2.4 | 27 | 6 | 6.7 | 4.0 | 51 |
| ee | 3 | 8.8 | 9.5 | 2.3 | 54 | 7.5 | 7.2 | 4.5 | 67 |

Water depth significantly predicted female reproductive success (weighted least squares linear regression, $\hat{y} = 1.6231 - 0.0112(\times \text{ depth}) - 0.0055(\times \text{ group size}) + 0.0006 \times (\times \text{ depth} \times \text{ group size})$; $t = -3.19$, df = 1, $p < .002$).

for provisioned females and estimated for moderate to heavily speckled females; Smolker et al., 1992), and (3) we had a consistent sighting history without gaps large enough such that a surviving calf might escape our notice. Probable females are those who consistently associate with other females and associate with males only when apparently being herded by them. We did not include probable females in analysis of group size and water depth in relation to female reproductive success. We included only those cases where the death or survival to age 3 of all calves was known. Censored calves (born after 1995, $N = 7$) were excluded because they were not old enough to be weaned. (Censored cases refer to those where the end point, such as survival, death, or weaning, has not yet been determined.) A depth sounder was not used on one boat from 1996 to 1998 because of acoustic recordings. Thus, the sample sizes for depth were smaller than for group size (Table 1).

Because error variance should decrease with an increase in the number of surveys per female, weighted least squares regression was applied. This means that cases (females) with large weight (more surveys) have small variance and were more important in the regression analysis (WLS, weighted least squares linear regression; Hocking, 1996). For the 38 females, an average of 101 surveys per female were collected (SD = 86, median = 72).

## RESULTS

### Birth seasonality

Figure 1 shows the seasonal pattern of births in relation to temperature. October–December were clearly the peak birth months (accounting for 73% of all births), just preceding peak temperatures, but the breeding season broadly extended from September to January (90% of births), with approximately seven out-of-season births February–August.

The interval between the death of a calf and the next conception was calculated using only deaths and pregnancies known within 3 months ($N = 17$ calf deaths followed by a pregnancy within 1 year). A midpoint was used for ranges of deaths and/or conceptions known within 2–3 months. No midpoints were used for 10 of 17 estimates because they were
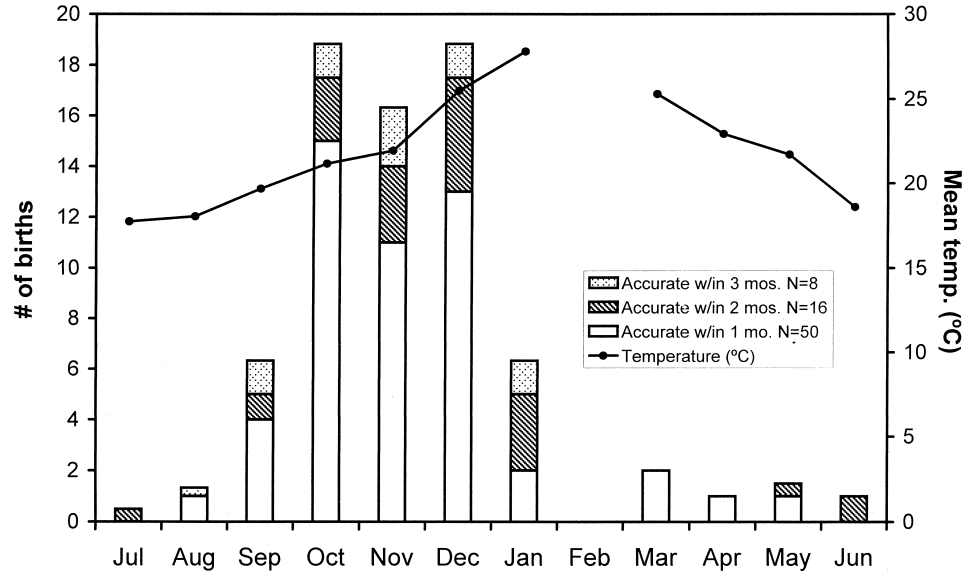
**Figure 1**
Number of births and average temperature by month (SD ranges for temperature = 0.9–1.6). If a birth could not be assigned to one month, it was divided equally among the possible birth months ($N = 74$ calves, 47 mothers).

accurate within 1 month. Month of conception was considered to be 12 months before calf birth; we assumed no births were premature. All mothers conceived within 1–2 months (mean = 1.2 months, SD = 0.4) following loss of calf July–December, but conceived 2–9 months following calf loss in January–June (mean = 5.3, SD = 2.3; Figure 2). Thus, females were still more likely to conceive within season following calf loss (76.5%) than not (binomial test, $p < .02$). The three 2-month intervals that occurred out of season were in late summer, January–March. These were responsible for half the out-of-season births in Figure 1 where the previous calf's status was known. Length of interval to next conception was inversely correlated with month of year (beginning with January, the last month of breeding season) that previous calf died (Spearman $r = -.531$, $p < .05$; Figure 2). Out-of season births were not significantly more likely to be preceded by calf death than within-season births ($\chi^2 = 2.59$, $p = .11$, df = 1, $N = 44$). The sample for out-of-season births is too small to determine if those calves were less likely to survive to age 3 than calves born in season.
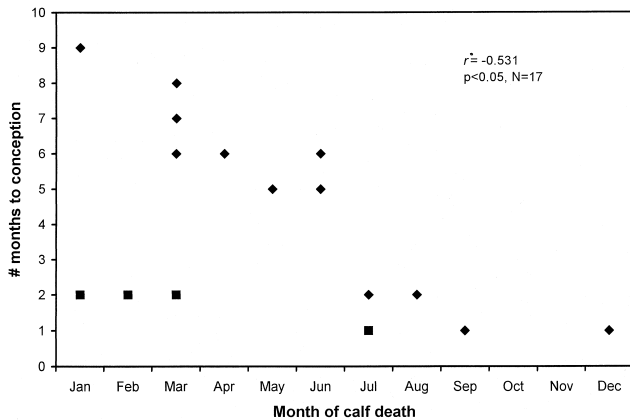


**Figure 2**
Length of interval between calf loss and next conception. The length of interval inversely correlates with month of year (beginning with January, the last month of the breeding season). Conception following loss of calf was delayed long enough to ensure within-season birth. That is, regardless of when a female lost her calf, she was more likely to have the subsequent birth within season than not ($N = 17$, binomial test, $p < .02$).

We hypothesized that females would resume cycling faster after losing a small calf (early in lactation) compared to an older calf. A small newborn calf (<3 month) is likely to be less costly to the mother's fat reserves compared to a larger calf. Loss of a newborn (<3 months, $N = 5$) always resulted in pregnancy within the year, but in one-third of the losses of older calves (3–18 months, $N = 23$), females did not become pregnant within the year ($\chi^2 = 2.44$, $p = .12$, df = 1). The small newborn sample suggested a trend.

**Age at first birth**

To examine age at first birth, only females sighted >10 times annually were included so births were unlikely to be missed. Four females gave birth to their first calf at age 12, one had her first at age 14, and another at age 15. However, seven females between ages 12 and 15 have not given birth, although some of these may have lost calves before being sighted. Two of nine first-born calves documented in our population survived to age 3, one is currently age 2, and the other less than 1 year (three mothers were of unknown age but were judged as subadult in the late 1980s or early 1990s). The sample size of first-born calves is too small to determine whether survivorship is significantly lower than for later-born calves.

**Calf mortality**

Survival analysis (Kaplan-Meier method) of calf mortality from birth to age 3 revealed high first-year mortality at 29% (Figure 3), with mortality rates declining in the second (18%) and third (3%) years. Forty-four percent of 110 calves died by age 3.

A comparison of calves born to provisioned and nonprovisioned females revealed a significant difference in first-year mortality and overall (Wilcoxon $\chi^2 = 4.86$, $p = .027$). First-year mortality was 56% for calves born to provisioned females compared to 24% for calves born to nonprovisioned females. By age 3, 62% of calves born to provisioned and 40% of calves born to nonprovisioned females died. Mortality rates for calves born to provisioned and nonprovisioned females did not differ significantly for the second or third year.

**Weaning and COA**

Weaning ages are shown in Figure 4. The majority of calves (66.7%) were weaned before their fourth birthday ($N = 42$
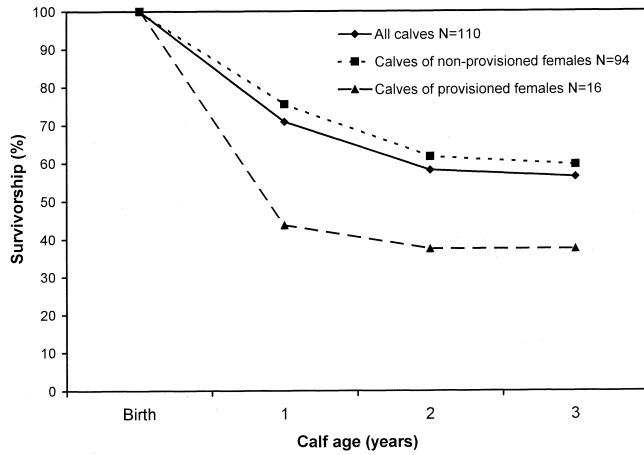
**Figure 3**
Calf survivorship from birth to age 3. Survival analysis (Kaplan-Meier method) revealed significant differences in calf mortality when provisioned and nonprovisioned females were compared (Wilcoxon $\chi^2 = 4.86$, $p = .027$). Although 83.3% of calves were weaned after their third birthday (see Figure 4), we know of no deaths for nursing calves older than 3 years. Mortality rates for weaned juveniles are not known.
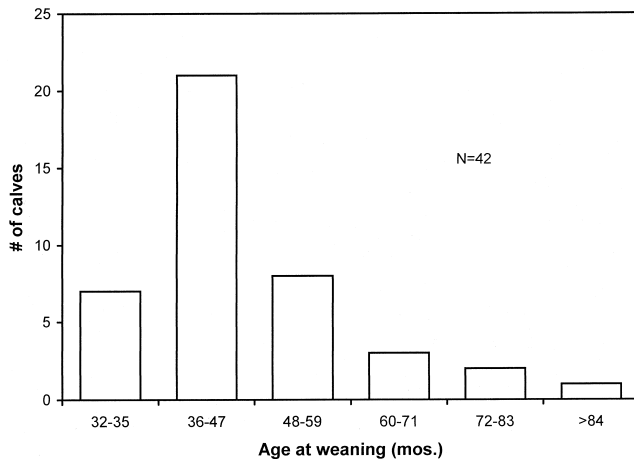


**Figure 5**
Interbirth intervals when first calf survived to weaning ($N = 33$) and mother gave birth within 1–2 years (no gap). If she gave birth >1 year after weaning for first calf, then she could have lost a fetus in the interim (possible gap, shaded bar). Average interbirth interval was 4.55 (SD = 1.00, median = 4.07).

calves). Three calves were weaned in their sixth year, two calves in their seventh year, and one in her ninth year.

The COA of all calves preweaning averaged 94.0 (SD = 6.5, median = 96.0, range = 77.4–100) and averaged 25.3 postweaning (SD = 24.2, median = 20.2, range = 0–82.5). The only calf with a postweaning COA within the range of preweaned calves was the daughter of a provisioned female.

For seven calves, we knew the precise weaning age (within 1 month) and gestational status of the mother at time of weaning. Gestational status of the mother was determined by the birth of the next calf. Five calves were weaned during month 5, one during month 6, and one during the month 10 of the mother's next pregnancy.

**Interbirth intervals**

As expected from weaning data, IBIs for surviving calves were between 3.0 and 6.2 years ($N = 33$ intervals). Four-year inter-

vals were most typical (47% of intervals; mean = 4.55 ± 1.00, median = 4.07; Figure 5). If we include all intervals after a surviving calf, irrespective of whether we may have missed a birth in between, then the mean IBI is 4.71 ± 1.38 years (median = 4.06, range = 3.0–9.9, $N = 44$ intervals). Only two IBIs were >7 years.

**Female reproductive success**

Figure 6 shows the variation in female RS based on the number of surviving calves over a 10-year period. Thirty percent of the females had no surviving calves, 37.5% had one surviving calf, 25% had two surviving calves, and 7.5% had three. We know the lifetime RS of one provisioned female, who died at approximately age 35 based on tooth-layer analysis (Hohn AA, personal communication) and who left two daughters who survived to reproduction. Based on the density and distribution of her ventral speckles (see Smolker et al., 1992), she was one of the oldest dolphins in the study area. Few females have comparable speckle density. However, her death was caused by a ray spine, not old age. If females typically have



**Figure 4**
Weaning ages for 42 calves are shown; 16.7% were weaned at age 2 (32–35 months), 50% at age 3, 19% at age 4, 7.1% at age 5, 4.8% at age 6, and 2.4% at age 8.
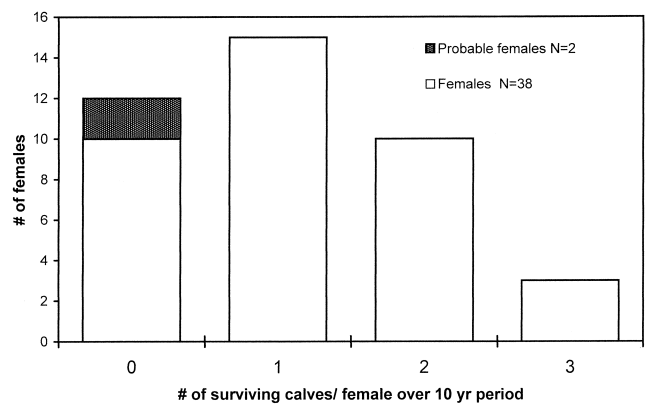


**Figure 6**
Variation in female reproductive success based on number of surviving calves per female over a 10-year period. Thirty percent of the females had no surviving calves, 37.5% had one surviving calf, 25% had two surviving calves, and 7.5% had three ($N = 40$).

**Table 2**

**Comparison of median group sizes for surviving calves from birth to 24 months**

| | Calf age (months) | | | |
|---|---|---|---|---|
| | 0–3 | 4–6 | 0–6 | 7–24 |
| No. of calves | 9 | 9 | 22 | 22 |
| No. of surveys | 50 | 28 | 122 | 224 |
| Group size (mean ± SD) | 6.3 ± 3.6 | 4.5 ± 4.0 | 5.4 ± 2.5 | 5.5 ± 4.5 |
| Group size (median) | 5.0 | 3.0 | 4.0 | 4.1 |

Nine calves surveyed in the newborn period (0–3 months) were in significantly larger groups compared to when they were 4–6 months of age (Wilcoxon matched-pairs, signed-ranks test, t = 2, $p$ < .006). Median group size did not significantly change between 0–6 and 7–24 months.

a 20-year reproductive period (early teens to early 30s), then maximum lifetime RS is likely to be five to six calves; but if female reproductive life span approaches that of larger *Tursiops* in other populations, this estimate may be too conservative.

To examine if group size and water depth are predictors for female RS, we used the WLS linear regression, including an interaction term for group size and water depth. Water depth alone predicted female RS ($y_{RS}$ = 1.6231 − 0.0112 − 0.0055 + 0.0006; $t$ = −3.19, df = 1, $p$ < .002; Table 1). Group size did not interact with or relate to water depth. Mean group size for females was 5.9 (SD = 4.2, median = 4.2, range = 1–40). Some females were fairly solitary, with median group sizes of two (typically mother and offspring), while others were quite sociable, with median group sizes of eight. Depth averaged 6.3 m (SD = 2.5, median = 6.0, range = 0.7–14.5 m). The WLS regression model indicated that for each 3.5 m increase in depth, female RS declined by 1/10 of one calf.

The number of surveys per female was significantly correlated with the mean (Pearson $r$ = −.46, $p$ < .01) and median (Pearson $r$ = −.43, $p$ < .01) water depth. That is, shallow-water females were sighted more often than deep-water females. However, the provisioned females, who were surveyed often, account for this difference. If the five provisioned females are removed, this relationship is no longer significant ($r$ = −.24, −.29, respectively). Mean and median group size did not significantly correlate with number of surveys (Pearson $r$ = .10 and .04, respectively).

As the mortality data indicate, first-year calves were more vulnerable than older calves. Thus, we examined group size in relation to calf age. Because female sociability varies, we included only surviving calves who were surveyed in all relevant age classes so that the change within each calf could be determined. Group size did not differ when we compared group size for calves 0–6 months with calves 7–24 months (22 calves, 346 surveys; Table 2), but during the newborn period (0–3 months), calves were in significantly larger groups than when aged 4–6 months (Wilcoxon matched-pairs, signed-ranks test, $t$ = 2, $p$ < .006, N = 9 calves, 78 surveys; Table 2).

**DISCUSSION**

Birth seasons appear to be more pronounced in Shark Bay and Sarasota, Florida (Wells et al., 1987), than other in *Tursiops* field sites (see Kasuya et al., 1997; Urian et al., 1996), although different sampling methods (live animal sightings versus newborn strandings and fetal lengths) may account for these differences. Females may give birth seasonally because warm water is thermally efficient for small calves or for moth-

ers. Food availability may fluctuate sufficiently to favor seasonal births, allowing females to maximize intake when nutritional stress is likely to be greatest, at mid-lactation (Oftedal, 1997). The availability of weaning foods for calves is unlikely to favor seasonal births because calf foraging is so variable, beginning years before weaning. Predator densities may also influence birth seasonality.

The birth season and mortality data suggest that females resume cycling rapidly if the timing of calf loss allows them to give birth within season the following year. Calf age and seasonal factors are likely to influence vulnerability to predation or infanticide. Newborn calves are probably most vulnerable, and this is when mothers stayed in the largest groups compared to other age classes. Most calf growth occurs in the first year (Read et al., 1993). Captive female *Tursiops truncatus* increase food intake by 50% during mid-lactation, suggesting a significant nursing cost (Cheal and Gales, 1992). Once the mother has invested her fat reserves in nursing an older calf (>3 months), she may be unlikely to cycle rapidly following calf loss.

If male dolphins are infanticidal, we predict that females with young calves would avoid less familiar males more often during this period of risk (August to December), relative to periods of lower risk (January to July). Because females mate promiscuously and associate with multiple males during the months before conception, paternity confusion might be sufficient to minimize any infanticide risk (Connor et al., 1996). Because adult males rarely associate with mothers of new calves (Mann and Smuts, 1998), it is difficult to determine whether such associations are affiliative or not. More extensive observations of cycling females and mothers with new calves may help resolve some of these issues. At this point we can only suggest that male mating opportunities following calf loss appear to be limited by season and calf age.

First-year calf mortality (24%) for nonprovisioned females is similar to rates reported for *Tursiops truncatus* at Sarasota, Florida (19%; Wells et al., 1987) and for *Stenella frontalis* in the Bahamas (24%; Herzing, 1997). We likely underestimated mortality for young calves, given that some calves probably died before being sighted. Although infancy, and the first year in particular, is the period of greatest mortality risk, juveniles also disappear. Of 46 juveniles, all were repeatedly sighted in the study area after weaning, but five disappeared 1 year or more after weaning and are presumed dead.

Mortality data on calves born to provisioned and nonprovisioned females was first provided to the Australian Department of Conservation and Land Management (CALM) in 1994 (Wilson, 1994). Monkey Mia has been the longest operating site permitting the provisioning of wild dolphins. In response to the mortality figures provided in 1994, feeding procedures were changed to reduce the amount provisioned

and to encourage the dolphins to spend more time away from the provisioning area. Since the changes were implemented in 1995, no calf deaths have occurred, and three calves have been successfully weaned. Although this analysis included those surviving calves and the mortality differences remain significant, we are cautiously optimistic that the policy changes are working and reducing calf mortality.

Possible causes of the higher mortality may be or may have been: (1) disease resulting from human contact or septic pollution (EPA, 1989); (2) change in mother–calf contact, behavior, or associations (see Mann and Smuts, 1999); (3) change in diet or predator or prey concentrations near shore; and (4) sampling biases (infrequent sightings of nonprovisioned females would increase likelihood of missing a calf that died soon after birth). Although the first-year mortality rate for calves born to nonprovisioned females is likely to be higher than what we report, it is unlikely to be as twice as high, comparable to the rate for calves born to provisioned females. Photographs of new calves from a year-round daily tour operator since 1993 have allowed us to monitor more births and deaths regardless of season or weather.

Preweaning association coefficients are not 100 (as reported in Smolker et al., 1992) because mother and calves separate for brief periods, particularly during foraging (Mann and Smuts, 1998; Smolker et al., 1993). In this study, we included all sightings; Smolker and colleagues (1992) excluded sightings where foraging was the predominant activity. Thus our preweaning coefficients ranged between 77 and 100.

The weaning ages reported here are similar to those for *Tursiops* in Florida (Wells et al., 1987). Although association patterns can be used to estimate weaning age, infant position is a more reliable indicator. Opportunistic observations indicate that calves nurse, at least occasionally, for the entire period of infant position swimming, typically 3–6 years and occasionally up to 8 years. Age-specific changes in milk composition and/or intake from birth to weaning are unknown. Even if nursing rate could be determined, this is poorly correlated with milk intake in mammals (Cameron, 1998). Similar to spotted dolphins (*Stenella frontalis*; Herzing, 1997), females continue nursing their offspring nearly halfway through the next pregnancy (based on infant position, observations of nursing attempts, and subsequent birth of sibling). This strategy may assure a viable pregnancy before weaning the previous calf. Simultaneously lactating and pregnant females are reported in other *Tursiops* populations (Kasuya et al., 1997). Minimum IBIs are shorter than those we had previously reported (Connor et al., 1996), but still longer than the 2-year minimum reported in Sarasota (Wells et al., 1987).

The ages at first birth in Shark Bay (12–15) are within the ranges reported for other *Tursiops,* although several births to 6- to 7-year-old females occurred in Sarasota, Florida (Wells et al., 1987). In captivity, female *Tursiops* typically begin reproduction at 7–10 years, but may begin cycling between 5 and 7 years (Schroeder, 1990). Age at first birth may be later in Shark Bay than in Sarasota because of differences in body size. Adult Shark Bay females, at 2 m length, are roughly the same size of Sarasota 2- to 3-year-olds (Read et al., 1993). A calf born to a 6- to 7-year-old Shark Bay female may be too small and vulnerable to predators, and the female may not be large enough or fat enough to nurse a growing calf.

The variation in female RS has implications for attractivity. We would expect males to compete vigorously for females with a history of calf-rearing success, especially given that such females are likely to cycle only for a few months every 3–4 years. Genetic studies underway may indicate that some male coalitions are more likely to father offspring of successful females compared to less successful females.

Group size was not related to female RS. However, group sizes were largest when calves were most vulnerable, in the first 3 months of life. Group size alone may not offer significant advantages against predators or conspecifics, except during this initial period. Because cooperative hunting has not been observed in Shark Bay, group size would not contribute directly to foraging success, although detection of prey or accessibility to optimal habitats may be enhanced by group size. For example, there could be subtle forms of female cooperation in defending home ranges and excluding other females. Although degree of sociality does not appear to influence RS, our measures of sociality may be too crude to detect important behavioral and ecological factors. In a fission-fusion society, the context-dependent timing of associations is likely to be critical.

Similarly social and solitary strategies may represent trade-offs. For example, gregarious females and calves may suffer competitive costs that are outweighed by social benefits such as reduced male harassment, ectoparasite removal through reciprocal petting and rubbing, or development of strong bonds (e.g., potentially important for male calves in the development of alliances), or improved access to habitats of high prey density. Alternatively, social and foraging costs may be offset by reduced predation rates. Two of the three most solitary females in our sample specialize in sponge foraging and spend most of their time hunting with "sponge tools" (Smolker et al., 1997), suggesting that this foraging technique favors a solitary lifestyle. Detailed comparisons of foraging behavior in social and solitary females may reveal such trade-offs.

We found that water depth significantly predicted female RS. Norris and Dohl (1980) first suggested that many cetaceans move into shallow water to give birth and rear calves because shallow water affords protection against predation. Our data are consistent with this hypothesis. We found this effect even though, by most cetacean standards, our entire study area is shallow. Mothers and calves who spend more time in very shallow water may be able to detect and avoid sharks readily compared to those in deeper water. One-third of the calves in the focal study bore shark bite scars, and several calves were killed by sharks (Mann and Barnett, 1999). Prey availability may also be greater in shallow water compared to deep water habitats, affording females better diets (Heithaus MR, unpublished data). Current studies of predator and prey distributions in Shark Bay habitats may provide insights into the causes of this pattern.

Despite the differential mortality, we included provisioned females in the analysis of female RS. All provisioned females spend most of their time in shallow water. If we excluded provisioned females from the analysis, the relationship between water depth and female RS would be greater. Although shallow water may contribute to female RS, the nature of that contribution is unknown.

Our definition of female RS was limited to number of calves surviving to age 3 over a 10-year period. Both calf mortality and weaning age contribute to female RS. Approximately one-third of calves are weaned at later ages; thus late-weaning mothers would have lower RS by our measure but potentially raise calves more likely to reproduce in adulthood.

Bottlenose dolphin females invest heavily in their calves. Few terrestrial mammals except great apes (e.g., chimpanzees, *Pan troglodytes*; Goodall, 1986) and elephants (*Loxodonta africana*; Lee and Moss, 1986) exhibit such prolonged nursing and maternal investment; no terrestrial mammals reliably show such ranges in weaning age. Within the Shark Bay population, female dolphins appear to vary widely in habitat use, sociability, and life-history strategy. Continued study of Shark Bay dolphins will help explain the relevance of such flexibility to female reproductive success.

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