



## Perspective

# Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins



Vivienne Foroughirad<sup>a</sup>, Janet Mann<sup>a,b,\*</sup>

<sup>a</sup> Georgetown University, Department of Biology, 3700 O St. NW, Washington, DC 20057, USA

<sup>b</sup> Georgetown University, Department of Psychology, 3700 O St. NW, Washington, DC 20057, USA

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## ABSTRACT

To promote close encounters with wildlife, humans sometimes provision wild animals with food. However such practices can be harmful, and the impacts of human provisioning on wild animals can be difficult to determine, especially indirect effects such as those on the offspring of provisioned animals. In Shark Bay, Australia, a small subset of the resident population of bottlenose dolphins is regularly provisioned with fish handouts under the supervision of the West Australian Department of Environment and Conservation (DEC). Previous studies have shown that calves born to provisioned females experienced reduced care and higher mortality relative to calves of non-provisioned mothers. These results led to changes in the management practices in 1994, which we assessed the efficacy of by comparing (1) calf mortality before and after the intervention and (2) behavior of provisioned with non-provisioned dolphins in the population. Although calves born to provisioned females exhibited higher survivorship (86.7%) than before the intervention (23.1%,  $\chi^2 = 9.05$ ,  $df = 1$ ,  $p = 0.003$ ,  $N = 28$ ), group differences in maternal and calf activity budgets were still observed over the course of calf development. Provisioned mothers provided less care to their calves and their calves appeared to compensate by foraging more and separating more from their mothers compared to their non-provisioned counterparts ( $N = 114$  calves). Our study shows that careful regulation and reduced wildlife provisioning can increase calf survivorship, but behavioral development continues to be affected.

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Abbreviations: DEC, West Australian Department of Environment and Conservation; BACI, Before-After-Control-Impact.

\* Corresponding author at: Georgetown University, Department of Biology, 3700 O St. NW, Washington, DC 20057, USA. Tel.: +1 202 687 1307; fax: +1 202 687 5662.

E-mail address: [mannj2@georgetown.edu](mailto:mannj2@georgetown.edu) (J. Mann).

## 1. Introduction

Wildlife conservation efforts often have a complex dynamic with ecotourism ventures. Ecotourism can offer vital economic support for wildlife protection and promote public awareness, but can also degrade wildlife and their habitat (Krüger, 2005), especially as tourism increases (Duffus and Dearden, 1990). Though their motives differ, conservationists and tour operators often share the objective of maintaining ecosystem health. Tourism contributes to economic stability, particularly for those in developing countries or in poor communities (Andam et al., 2010; Ferraro et al., 2011). Habituation to humans also facilitates close monitoring of animals for basic research (Asquith, 1989; Connor and Smolker, 1985) and health assessment (e.g., Robbins et al., 2011).

Though cetacean tourism is often cited as an ecologically preferred and economically viable alternative to more consumptive practices such as whaling (Cisneros-Montemayor et al., 2010), its growth has prompted an emerging body of research on potentially negative impacts (Constantine et al., 2004; Stamation et al., 2010; Visser et al., 2011). Cetacean tourism is especially popular in Australia, involving over 1.6 million whale-watchers that support a 172 million dollar industry and hundreds of jobs each year (O'Connor et al., 2009). In addition, Australia permits feeding of wild dolphins at four locations, Tin Can Bay, Tangalooma, Bunbury, and Monkey Mia (Orams, 1995; Samuels et al., 2000), although unregulated feeding occurs at these and several additional sites (Finn et al., 2008; Garbett and Garbett, 1997). Western Australia prohibited feeding of wild marine mammals in 1998 under the Wildlife Conservation Notice, but the bottlenose dolphin provisioning program based at Monkey Mia in Shark Bay was grandfathered in since it is the oldest provisioning site in Australia.

Shark Bay provides an ideal dolphin population for examining the costs and benefits of tourism, particularly wildlife provisioning, because (1) basic research preceded the growth in tourism; and (2) anthropogenic impacts are relatively small. While Shark Bay as a whole is a relatively low-recreation area, two boats currently operate wildlife viewing tours in the eastern gulf, with one specifically licensed for dolphin-watching operations in a zoned area near shore. In addition, only a very small subset (<0.002%) of the resident population of about 3000 dolphins participates in the daily provisioning program managed by the West Australian Department of Environment and Conservation (DEC), enabling comparisons between provisioned and non-provisioned dolphins. Approximately 100,000 people visit Monkey Mia annually, supporting a multi-million dollar industry and an estimated 20–42% of the local Shark Bay economy (Stoeckl et al., 2005). The reliability of observing provisioned dolphins and their proximity to shore facilitates research efforts as well (Connor and Smolker, 1985; Mann and Kemps, 2003), and both provisioned and non-provisioned dolphins have been intensively studied since 1984. Although dolphins have large home ranges, longitudinal study of individuals is feasible because both sexes remain in their natal areas for life (Tsai and Mann, 2013). The long-term study of individually known dolphins over periods with different management protocols and between provisioned and non-provisioned groups allows us to apply the powerful 'BACI' (Before-After-Control-Impact) design (Underwood, 1991).

Although wildlife feeding is popular with tourists, provisioned animals experience altered behavior patterns and population dynamics (Laroche et al., 2007; Unwin and Smith, 2010; Villanueva et al., 2012), physiological costs (Semeniuk et al., 2009), and increased intra- and inter-specific aggression (Hodgson et al., 2004; Orams et al., 1996; Smith et al., 2008). Previous studies in Shark Bay have shown that dolphin calves born to provisioned females received less care and had higher mortality rates than calves of

non-provisioned females (Mann et al., 2000; Mann and Kemps, 2003). In response to research, DEC implemented specific protocols designed to reduce time that females spent at the provisioning site with the hope that this would lessen calf mortality (Mann and Kemps, 2003). The current study examines the effectiveness of this intervention.

For long-lived, socially-complex species such as bottlenose dolphins, evaluating the long-term impacts of tourism and provisioning can be complicated by many issues (Bejder et al., 2006; Samuels and Bejder, 2003). First, species with slow life histories may not show significant demographic changes for many years, making survival or reproductive rates alone an impractical metric. Second, baseline data or control data from comparable populations are rarely available. Third, short-term effects are difficult to interpret and often affect long-term changes non-linearly (Higham et al., 2008). Fourth, social transmission of behaviors can influence animals that are not directly exposed to tourism (Donaldson et al., 2012). Finally, the long-term social bonds and fission–fusion nature of bottlenose dolphin societies, where groups change frequently in size and composition (Connor et al., 2000), makes it challenging to detect key changes in social dynamics.

Shark Bay dolphin calves nurse for an average of 4 years and occasionally as late as age 8 (Mann et al., 2000). Altered maternal activity budgets and care are likely to affect calf experience and skill development, and because dolphins are not in stable groups, weaned juveniles face a range of social and ecological challenges on their own (Stanton and Mann, 2012). Although several studies have examined the impacts of human provisioning on wildlife, behavioral development has received little attention, perhaps because immature animals, such as the dependent offspring of provisioned animals, are affected only indirectly. Using the BACI design we investigated whether (1) management changes resulted in increased calf survival and, (2) maternal and calf behavior and development in the provisioned group differs from mother–calf pairs that had no involvement in the program.

## 2. Methods

### 2.1. Study site

Monkey Mia, located in Shark Bay, Western Australia (26°S, 114°E), was historically a small seasonal fishing camp that became a resort in 1991 and has served as a field base for dolphin researchers since 1984. Shark Bay contains a population of about 3000 resident bottlenose dolphins (Preen et al., 1997), with about 600 dolphins residing within our 250 km<sup>2</sup> study site. Research on demography, genetics, life history, and behavior of the resident population has been ongoing since 1984, with information on approximately 1500 individuals collected.

Since the 1960s, several dolphins have received fish handouts from humans at Monkey Mia (Connor and Smolker, 1985). The feeds were originally unregulated; fishermen often fed baitfish or some of their catch to dolphins, and tourists could purchase buckets of fish to feed to the dolphins ad libitum while standing in knee-deep water. In 1989, DEC began regulating feeds, limiting them to members of three well-known matrilineal groups. Unregulated shore- and boat-based feeding were discouraged and park rangers selected individual tourists to feed each dolphin up to 60 kg of fish per month, or more if the female had recently calved (up to 120 kg of fish per month, although this total amount was rarely fed). In response to elevated calf mortality (Mann et al., 2000), protocols were revised in late 1994 to further limit each dolphin to 2 kg of fish per day, rather than averaged over the month, with feeds occurring for a maximum of three times and only between the

hours of 7:30 and 13:00. Although only one calf had been regularly fed in the early 1990s, juvenile and adult males were also fed prior to 1994. Only non-calf female members of the three matrilineal groups were subsequently fed to maintain vertical transmission of female foraging traditions (Mann and Sargeant, 2003; Mann et al., 2008) and reduce dolphin aggression (Scott et al., 2005). Fish quality control and handling procedures were strictly controlled, and any physical contact or unsupervised feeding of the dolphins was prohibited. Each feeding session is now preceded by an educational talk on the biology and history of the Shark Bay dolphins given by a DEC park ranger, and field scientists present research seminars to the public each week.

## 2.2. Data collection

Dolphin activity budgets were calculated from 2181 h of mother-calf focal follows (Altmann, 1974; Mann, 1999) conducted from 1988 to 2011. Both non-provisioned adult females ( $N = 53$ ) and their offspring ( $N = 82$ ; 1614 h) and provisioned adult females ( $N = 7$ ) and their offspring ( $N = 22$ ; 567 h) were observed from small boats (<5.7 m) for 1–9 h per follow away from the provisioning area. Each mother-calf pair was observed for a minimum of 2 h in total, but usually for much longer ( $\bar{x} \pm sd = 20.98 \pm 19.04$  h). Boat-based follows are referred to as “offshore follows.” These were used for comparisons between provisioned and non-provisioned mother-calf pairs. “Calves” were defined as dependent, nursing offspring and females first calve at approximately age 12 (Mann et al., 2000).

Focal observations (30 min each) of provisioned mothers and their calves were also conducted from shore during provisioning sessions (380 h;  $N = 19$  calves and 7 adult females; Fig. 1). These are referred to as “onshore follows” because the observers were limited to shore-based observations of the provisioning area and are used for comparisons to offshore follows of provisioned mothers and their calves. During provisioning sessions, mothers and calves typically visit a 90 m stretch of beach that border an “interaction area” extending about 45 m offshore. No swimming or boating activity is allowed in this area and calves typically remain within the deeper part of that area while their mothers wait closer to shore for fish handouts. Tourists are allowed to stand about knee deep in the water but are currently not allowed to approach or

touch dolphins, although dolphins occasionally touch them. After about 30 min, tourists are asked to step out of the water as the buckets of fish arrive. Adult females are fed simultaneously several meters apart, each with their own bucket and attendant. Rangers select individual tourists to come into the water and hand-feed one fish to a dolphin, with up to four fish per feed per dolphin based on total weight. All fish are caught locally, frozen and defrosted in fresh water. Almost without exception, mothers and calves leave the interaction area immediately after the feeding session. Since 1991, DEC rangers have recorded the total amount of time that each individual spends in the provisioning area (interaction area) daily from 7:30 to 16:00.

## 2.3. Analyses

Activities for adults were collapsed into the categories resting, foraging, socializing, travelling, and “other”. Calf activity also included “infant position”, defined as when the calf swam underneath the mother, with the head lightly touching the mother’s abdomen. The time a mother permits her calf to maintain infant position is a proxy for maternal care because this position provides protection, contact, and nursing access (for detailed definitions of behavior categories see Mann and Smuts, 1999). All activity budgets were sampled with point sampling (during onshore and offshore follows) and infant position was recorded continuously. Group composition was recorded as scan samples during offshore follows, using a 10-m chain rule where any individual within 10 m of another group member is considered part of the group. We extracted mother–infant separation time from group composition data, defining separation as not being in the same group.

Mann–Whitney  $U$  tests were used for between group (provisioned vs. non-provisioned mothers) comparisons and calf activity budgets were compared using student  $t$ -tests or Welch’s  $t$ -test where appropriate. Calf behavior during provisioning sessions was compared to their behavior offshore using Wilcoxon Matched Pairs Signed-Ranks tests.

After comparing overall calf activity budgets, we examined developmental patterns of foraging, infant position, and maternal separations, since the relative amount of time devoted to these activities varies over the course of the long infancy period and may contribute directly to a calf’s probability of survival.



**Fig. 1.** A typical feeding session. Volunteers, supervised by rangers, hold buckets of fish in shallow water and tourists are individually selected from the crowd to take a fish and place it in the water in front of the dolphin. Photo credit: Brittany Baschuk.

Observations were binned according to calf age (in months), and only calves that were observed for at least 2 h per month were included. For all datasets, each calf was observed for about 5 h per month and during five separate months. Foraging and infant position datasets included 1870 h on 74 calves (59 non-provisioned, 15 provisioned). Separation data included 2351 h of observations on 114 calves (91 non-provisioned, 23 provisioned). Calves ranged in age from less than one week to 70 months. One calf was observed while still nursing at 97 months but that data point was excluded from our sample as an outlier.

We compared provisioned and non-provisioned animals using generalized linear mixed models. The response variable was the proportion of observations in each state (foraging, infant position, maternal separation). By definition, infant position cannot co-occur with maternal separation or calf foraging. The fixed effects of interest were age (in months), maternal provisioning status, and their interaction. We also included sex, maternal age at birth, and calf weaning age as fixed effects in our models to help explain some of the variance. Since calf foraging and infant position combined could cumulatively represent calf nutritional intake, we also included the number of infant position observations in our model of foraging, and vice versa. Infant position data appeared to vary quadratically with age, so a second degree polynomial was included for the age term. Calf identity was included as a random factor. Models were compared using AIC criteria and the best models that included our interactions of interest are presented. All models were run with a binomial distribution using the logit link function in the package 'lme4' in R version 2.12.1 (Bates et al., 2011).

The average duration of visits to the provisioned area by the provisioned females and the survival of their calves to age 3 (minimum weaning age) pre- and post the 1994 management changes were compared using Welch's *t* test and Chi-square tests respectively. Calves under one year of age when the management changes were implemented were considered in the post-intervention group. Because very few calves born to provisioned females survived between 1988 and 1994, we could not compare activity budgets of mothers and calves between time periods. Alpha values below 0.05 were deemed significant and all values under 0.20 are reported. Means and standard deviations are presented unless otherwise indicated.

### 3. Results

#### 3.1. Management changes

From 1991 to 1994, provisioned adult females spent an average of  $146.7 \pm 46.6$  min per day in the provisioning area. From 1995–2010, that time was reduced by over an hour to only  $78.5 \pm 32.2$  min per day (Welch's,  $t = 2.82$ ,  $df = 6.7$ ,  $p = 0.027$ ; Fig. 2). Survival of calves born to provisioned females improved substantially ( $\chi^2 = 9.05$ ,  $df = 1$ ,  $p = 0.003$ ,  $N = 28$ ) from 23.1% for calves born before the management changes to 86.7% for calves born after. The survival rate for calves born to non-provisioned females over the same time period was 62.2% ( $N = 288$ ), not significantly different from calves born to provisioned mothers at present ( $\chi^2 = 2.71$ ,  $df = 1$ ,  $p = 0.100$ ).

#### 3.2. Maternal behavior

Provisioned adult females did not significantly differ from non-provisioned adult females in terms of resting, socializing, travelling, or overall foraging behaviors (Table 1). However our measure of maternal care, infant position, was different between groups with calves born to provisioned mothers spending less time in

infant position ( $33.14 \pm 8.66\%$ ) than calves of non-provisioned mothers ( $39.01 \pm 14.4\%$ ;  $t = 2.42$ ,  $df = 53$ ,  $p = 0.020$ ). During provisioning sessions (onshore follows), calves spent even less time in infant position, averaging only  $15.02 \pm 5.06\%$  of their time in infant position compared to  $33.14 \pm 8.66\%$  during offshore follows ( $w = -188$ ,  $z = -3.77$ ,  $p < 0.001$ ).

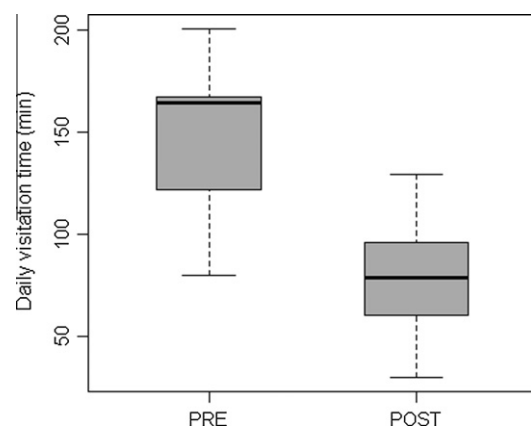
#### 3.3. Calf behavior

Activity budgets of calves in the provisioned and non-provisioned groups differed (Table 1). Calves born to provisioned mothers spent less time resting (Welch's,  $t = 2.42$ ,  $df = 52.83$ ,  $p = 0.023$ ) and more time foraging (Welch's,  $t = 2.42$ ,  $df = 52.83$ ,  $p = 0.020$ ) than calves with non-provisioned mothers. They also spent about  $22.37 \pm 15.78\%$  of their time separated from their mothers (not in the same group as defined by a 10 m chain rule), whereas non-provisioned mother-calf pairs only spent  $15.36 \pm 15.30\%$  of their time separated ( $t = -1.95$ ,  $df = 112$ ,  $p = 0.054$ ). In addition, calves born to provisioned mothers spent, on average, 15% less time travelling ( $z = -3.33$ ,  $p < 0.001$ ) and about 17% more time resting ( $z = 3.25$ ,  $p = 0.001$ ) during the provisioning sessions than when away from the provisioning beach. Calves also tended to socialize more during the provisioning sessions than during offshore follows ( $z = 1.92$ ,  $p = 0.0549$ ).

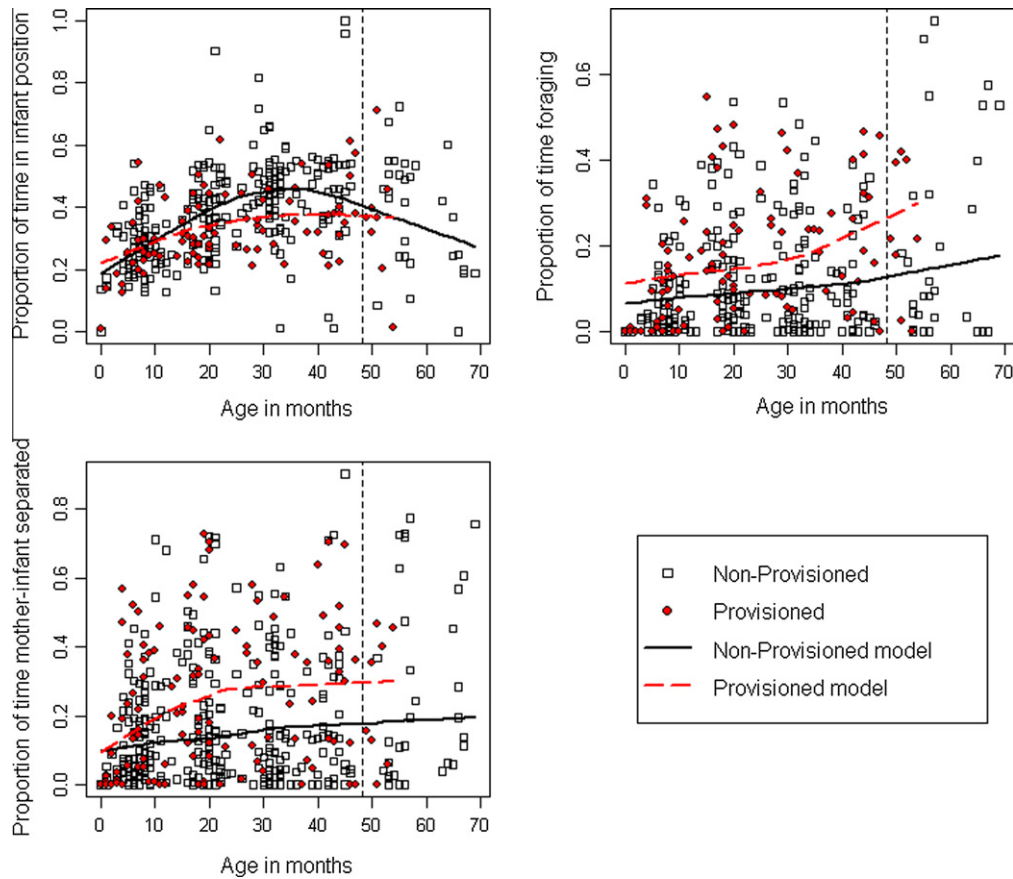
#### 3.4. Calf development

Our final model for foraging development included the terms for age, maternal provisioning status, their interaction, and the number of observations in infant position (Table 2). All terms were significant except for the interaction between age and maternal provisioning status at  $p = 0.073$ . Infants increased the relative amount of time spent foraging as they aged, and maternal provisioning also had a positive effect on the proportion of time spent foraging, though this effect lessened with age (Fig. 3). Time in infant position was inversely related to time spent foraging.

The final infant position model included the terms for age, age<sup>2</sup>, maternal provisioning status, weaning age, and the interactions of the age and provisioning terms. Age contributed a positive linear effect in our model until time in infant position reached a peak at about 28 months and then leveled off and finally decreased toward weaning age (Fig. 3). Maternal provisioning status tended to have a negative effect ( $p = 0.099$ ) on the time spent in infant



**Fig. 2.** Boxplot of average daily visitation time for provisioned adult females pre- ( $N = 5$ ) and post- ( $N = 6$ ) the 1994 management, i.e., when the amount of fish fed and the duration of provisioning sessions were reduced. Thick lines represent the median, the shaded boxes represent the 25–75th percentiles, and the whiskers represent the remaining data range.



**Fig. 3.** Proportion of time spent in each activity across development. Provisioned animals are shown in red and non-provisioned in black. Lines represent our model's predicted values for each group with a smoothing function applied. The vertical dotted line represents the mean weaning age ( $48.24 \pm 14.29$  months) for animals in our sample. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**  
Mother and calf activity budgets (% time  $\pm$  SD). Statistically significant results appear in bold.

|        |                 | Forage   | Rest  | Travel  | Social           | Infant position                                |
|--------|-----------------|--|---|---|------------------|--|
| Mother | Provisioned     | 27.16 $\pm$ 6.05                               | 31.12 $\pm$ 8.34                                | 38.78 $\pm$ 8.18                              | 1.74 $\pm$ 0.68  | N/A  |
|        | Non-provisioned | 31.51 $\pm$ 21.32                              | 33.55 $\pm$ 16.65                               | 33.02 $\pm$ 12.68                             | 1.85 $\pm$ 2.27  | N/A  |
| Calf   | Provisioned     | <b>16.30 <math>\pm</math> 9.08<sup>a</sup></b> | <b>18.47 <math>\pm</math> 7.51<sup>a</sup></b>  | <b>23.47 <math>\pm</math> 8.81</b>            | 8.05 $\pm$ 6.35  | <b>33.14 <math>\pm</math> 8.66<sup>a</sup></b> |
|        | Non-provisioned | <b>10.94 <math>\pm</math> 9.69</b>             | <b>23.30 <math>\pm</math> 11.41</b>             | 19.41 $\pm$ 7.87                              | 6.82 $\pm$ 8.07  | <b>39.01 <math>\pm</math> 14.40</b>            |
|        | Onshore         | 22.96 $\pm$ 12.61                              | <b>35.73 <math>\pm</math> 14.88<sup>b</sup></b> | <b>8.93 <math>\pm</math> 7.92<sup>b</sup></b> | 13.17 $\pm$ 6.12 | <b>15.02 <math>\pm</math> 5.06<sup>b</sup></b> |

<sup>a</sup> Significant differences between provisioned and non-provisioned groups.

<sup>b</sup> Significant differences between calves of provisioned animals observed offshore and during the provisioning sessions.

position. Weaning age had a slightly positive effect, with calves weaned later spending more time in infant position over the course of development. Maternal provisioning interacted significantly with age, so that while provisioned calves had similar or higher rates of infant position compared to non-provisioned calves in their first year, their relative rates dropped for later years. While the oldest provisioned calf that we had data for was 54 months old and the oldest non-provisioned was 69 months old, weaning ages did not differ between groups (Welch's,  $t = 1.88$ ,  $df = 56.0$ ,  $p = 0.070$ ).

The best separation model included only the terms for age, maternal provisioning status, and their interaction. Separation rates were similarly low for very young animals in both groups, and increased significantly with age. Calves in the provisioned group spent more time separated from their mothers, and this difference increased with age (Fig. 3).

#### 4. Discussions

The marked increase in calf survival rates among offspring with provisioned mothers demonstrates that the changes in feeding protocols were successful. After 1994 when provisioning periods were shortened and feeding was reduced, provisioned dolphins spent more time away from shore where mothers engaged in relatively normal activities. We attribute the increase in calf survival primarily to this shift. Since feeds no longer occurred after 13:00, dolphins spent less time near the beach where calves had minimal nursing access. Offshore, calves had more opportunities to socialize with non-provisioned animals, hunt, and learn skills from their mothers and others (Mann et al., 2007; Sargeant and Mann, 2009). Eliminating the feeding of calves and juveniles also reduced dependency on fish handouts, even if those individuals were later introduced to the provisioning program as adults.

**Table 2**Parameter estimates from the models for time spent foraging, in infant position, and maternal separation. Age is age in months and *prov* is maternal provisioning status.

|                 | Parameter               | Estimate | St Error | z-Value | p-Value  |
|-----------------|-------------------------|----------|----------|---------|----------|
| Forage          | (Intercept)             | -2.89371 | 0.16558  | -17.476 | <0.00001 |
|                 | Age                     | 0.02308  | 0.00088  | 26.136  | <0.00001 |
|                 | Prov                    | 0.99729  | 0.35816  | 2.784   | 0.00536  |
|                 | Infant position         | -0.00263 | 0.00014  | 19.200  | <0.00001 |
|                 | Age * Prov              | -0.00266 | 0.00148  | -1.794  | 0.07280  |
| Infant Position | (Intercept)             | -0.86617 | 0.23400  | -3.70   | 0.00021  |
|                 | Age                     | 4.51082  | 0.17952  | 25.13   | <0.00001 |
|                 | Age <sup>2</sup>        | -5.62875 | 0.17746  | -31.72  | <0.00001 |
|                 | Prov                    | -0.26187 | 0.15880  | -1.65   | 0.09912  |
|                 | Weaning age             | 0.00866  | 0.00453  | 1.91    | 0.05577  |
|                 | Age * Prov              | -3.94068 | 0.38823  | -10.15  | <0.00001 |
|                 | Age <sup>2</sup> * Prov | 0.70555  | 0.43826  | 1.61    | 0.10743  |
| Separation      | (Intercept)             | -2.48119 | 0.15103  | -16.428 | <0.00001 |
|                 | Age                     | 0.01081  | 0.00069  | 15.618  | <0.00001 |
|                 | Prov                    | 0.50891  | 0.33192  | 1.533   | 0.12500  |
|                 | Age * Prov              | 0.00832  | 0.00123  | 6.733   | <0.00001 |

However, despite the increase in calf survival, the offspring of provisioned dolphins differed behaviorally from offspring of non-provisioned females. While there were not enough surviving calves to test for behavioral differences pre- and post-1994, behavioral differences were still evident in the provisioned population with calves continuing to receive less maternal care, separate from their mothers more often, and forage more than other calves. Near shore and the provisioning area, the increase in time devoted to socializing, though not significantly different, was probably a result of the relatively high density of animals in the provisioning area compared with offshore. Although the calves spent relatively little time with their mothers during the sessions, they could still socialize with each other or with other dolphins that occasionally entered the area. Likewise the decrease in travelling and increase in resting near shore compared to offshore were likely an artifact of the small size of the provisioning area; given that calves spent about 79 min per day in the provisioning area, rest near shore would not compensate for lack of rest offshore compared with the non-provisioned group. Calves born to provisioned mothers foraged more than non-provisioned, possibly as a way to compensate for (1) lower milk intake; (2) increased energy expenditure during daily travels to and from the provisioning area; or (3) inefficient foraging due to lack of experience (including maternal and non-maternal foraging behavior). We suggest that increased calf foraging mitigates the impact of reduced maternal care. While social time was not different, resting was lower among calves born to provisioned females compared to non-provisioned. Since small environmental changes can have significant impacts on the amount of “enforced-rest” an organism needs, such events could cause these low-resting individuals to experience activity budget conflicts (Korstjens et al., 2010). We were surprised to find that calves born to provisioned females rested less often given that their home ranges are smaller than the non-provisioned group (Patterson, 2012). Reduced rest is probably exacerbated by less time in infant position, which can also allow calves to rest if the mother is resting. Additionally, calves with provisioned mothers did not spend more time travelling than their non-provisioned counterparts (consistent with the home range pattern), suggesting that increased energy expenditure is unlikely to explain the difference in foraging between groups.

While the impacts of provisioning are apparent, it is unclear whether the effects are due to the current provisioning program, or are residual effects from the way the program was previously managed. Dolphins born under the new protocols can still learn harmful behaviors, such as begging for fish and following boats, from older generations that grew up under less stringent management

(Donaldson et al., 2012). The calves of the provisioned animals are especially at risk because of the strong vertical transmission of foraging techniques from mother to offspring (Sargeant and Mann, 2009). Notably, five offspring born to provisioned females after 1994 survived infancy, but did not survive the juvenile period. This might be related to insufficient social and hunting experience pre-weaning, especially since four of these offspring were born to one female who consistently spent more time in the provisioning area than the other females and often begged from boats offshore, both before and after 1994. To date, none of her offspring have survived beyond their 8th year and all were noticeably small in size. The fifth juvenile that disappeared was thought to have died from wounds inflicted by a tiger shark attack. Other studies have shown that the juvenile period is especially vulnerable to anthropogenic stressors (Müllner et al., 2004). Comparisons with findings from other studies are difficult because few are based on individually specific data and activity budgets vary widely among species and between populations in different environments. Similarly, Shark Bay dolphins are known for their diverse foraging tactics and habitat heterogeneity (Sargeant et al., 2007), which could further complicate comparisons. There is a dearth of information regarding how such behavioral effects translate into fitness costs, though data from the continuation of this study and other long-term projects should help elucidate these relationships.

Despite high survival rates, parent-offspring interactions and activity budgets were markedly affected by participation in a provisioning program. While initial results on dolphin calf mortality in a licensed provisioning program have been described elsewhere (Neil and Holmes, 2008), this is to our knowledge the first study that has been able to: (1) implement a BACI design; (2) examine the effects of wildlife provisioning across early development; and, (3) identify the impacts of provisioning by comparing provisioned dolphins with a well-studied non-provisioned group. Although other provisioning programs sometimes keep detailed records on individual dolphin visitation, they know little about their behavior away from the tourist site and have few records on behavior and survivorship of the non-provisioned population. It is arguable that a limited and carefully monitored provisioning program can allow humans to have close wildlife encounters with few deleterious impacts. However such programs are justifiable only when relevant data on impacts are available.

## 5. Conclusions

The dolphins of Monkey Mia are an excellent example of the positive effects of managerial responses to sustained research efforts

on a population in conflict with ecotourism. Faced with unusually high levels of calf mortality among provisioned females when compared to the rest of the population, the management at Monkey Mia took action to limit the impacts of the provisioning program. The Department of Environment and Conservation reduced the amount of time that tourists were allowed to spend at the provisioning beach, the amount of food that could be fed, and the time period that fish could be distributed. These changes succeeded in reducing the amount of time that the dolphins spent in the provisioning area, which corresponded to an increase in calf survival. Our study highlights the importance of the infancy period as a susceptible point in development with regard to wildlife provisioning. We therefore recommend that the ontogeny of a species' behavioral repertoire be incorporated to the extent possible when evaluating anthropogenic impacts.

While some successes are evident, the long-term fitness outcomes of calves born to provisioned females are not yet known and may be affected by their altered behavioral development. Further research, particularly on habitat use, social bonds, foraging development, survival, and reproduction is needed to ensure that a responsible balance between dolphin welfare and human interests is achieved.

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