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Survival of Bottlenose Dolphin (*Tursiops sp.*) Calves at a Wild Dolphin Provisioning Program, Tangalooma, Australia

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ABSTRACT Mortality of calves born to provisioned mothers is identified in the literature as an issue of concern in dolphin provisioning programs. Wild dolphin provisioning at Tangalooma, Moreton Island, Australia has been occurring since 1992. Each evening, up to eight dolphins are provided with fish in a regulated provisioning program. In this paper, calf survival at the Tangalooma provisioning program is reported and contrasted with that from wild populations and from a similar provisioning program at Monkey Mia, Western Australia. At Tangalooma, the calf survival rate is 100%, including both orphaned and first-born calves, both of which are expected to have relatively low survival rates. Possible explanations for the high calf survival rate are explored. These include site attributes such as isolated location and high water quality, aspects of foraging ecology likely to benefit calves of provisioned mothers, and the management regime used in the provisioning program (e.g., duration and timing of provisioning; quality of provisioned fish).

Keywords: bottlenose dolphin, calf survival, Moreton Bay, provisioning, Tangalooma



Historically, cetaceans have been regarded as unique among wild animals because of their sociable behavior toward humans (Frohoff and Packard 1995), although recent studies indicate that

avoidance behaviors may also occur in relation to swim-with-dolphin programs (Constantine 2001) and increased "ecotourism" boat traffic (e.g., Lusseau 2003, 2004), particularly where boats approach groups including calves (Santos et al. 2006). Many associations between free-ranging

Address for correspondence: Dr David Neil, School of Geography, Planning and Architecture, The University of Queensland, Brisbane 4072, Australia. E-mail: d.neil@uq.edu.au dolphins and humans have developed when both are attracted to locations where mutual reinforcement of social behavior occurs (Lockyer 1990). Examples of such mutual reinforcement, where the dolphin receives food, include cooperative fishing (Neil 2002), by-catch utilization (Orams 1995), and hand feeding (provisioning) (Conner and Smolker 1985). Many swim-with-dolphin programs do not provide such reinforcement, which may result in increased avoidance behaviors by the dolphins associated with increased long-term exposure to humans (Constantine 2001).

In Moreton Bay, Queensland, Australia, inshore bottlenose dolphins (*Tursiops sp.*) have a long history of interacting with humans (e.g., see Corkeron, Bryden and Hedstrom 1990; Orams 1995; Neil 2002). In 1992, Tangalooma Resort on Moreton Island (Figure 1) established a wild dolphin provisioning program on the beach adjacent to the resort, the details of which are documented elsewhere (e.g., Green and Corkeron 1991; Orams 1994, 1995, 1996; Neil and Brieze 1998). Planning for management of the program at Tangalooma was carried out with the benefit of information from similar programs elsewhere, and was intended to minimize possible adverse effects on the dolphins (Neil and Brieze 1998). Familial relationships of the dolphins provisioned at Tangalooma are provided in Figure 2. The group consists predominantly of two matrilines, one mother (Bess) and her two male calves, and one mother (Beauty) and her two female calves that in turn have given birth to two calves and one calf, respectively. The provisioned group currently includes six adults (4 male and 2 female), two sub-adults (1 male and 1 unknown), and two calves born in August and September, 2004 (sex unknown). Thus, in 2007, eight adult and sub-adult bottlenose dolphins regularly attended the nightly provisioning sessions, accompanied by two non-provisioned calves.

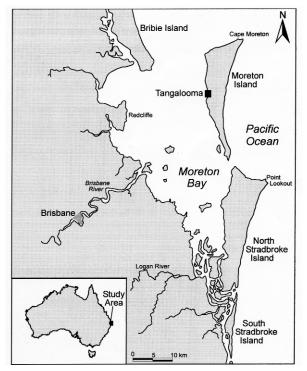
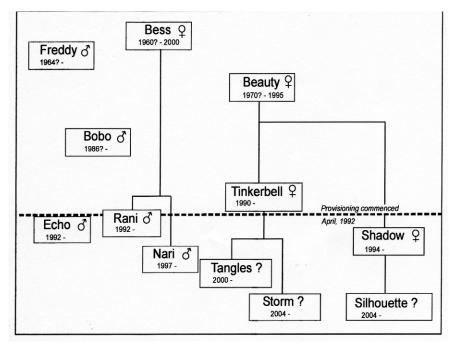
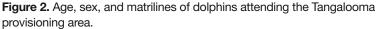


Figure 1. Location of Tangalooma in Moreton Bay, Australia.





This paper presents a brief overview of issues relating to wild dolphin provisioning programs. Mortality of calves born to provisioned mothers is identified as an issue of concern in these programs. The life history of each of the calves associated with the Tangalooma provisioning program, the overall calf survival rate for the program, and possible explanations for the observed calf survival rates are discussed.

Issues with the Provisioning of Wild Dolphins

Provisioning of wild animals may lead to aggression toward humans, associated with decreased wariness and awareness that humans may be associated with food sources. Examples include various primate species (Wrangham 1974; Brennan, Else and Altmann 1985; Goodall 1986; Fa 1992), bears (Albert and Bover 1991), cassowaries (Casuarius casuarius; Kofron 1999) and dolphins (Lockyer 1990, Orams, Hill and Baglioni 1996). Provisioned dolphins may become aggressive to the point of being dangerous to humans engaging in feeding, by biting and/or physically pushing against humans for food (Wilson 1994; Orams, Hill and Baglioni 1996). Under provocation, dolphin aggression has resulted in serious injury or death of humans (Santos 1997). There are also reports of humans having adverse effects on dolphin welfare by causing changes to natural behavioral patterns and significant increases in infant mortality and behavioral changes (NMFS 1994; Wilson 1994; Frohoff and Packard 1995; Orams 1996; Mann and Smuts 1999; Mann et al. 2000). The US National Marine Fisheries Service (NMFS 1994) reported that wild dolphin-feeding charter boat operations caused significant habituation to hand feeding, resulting in increased dependency and modified foraging strategies, as well as changes in social behavior within each group. It was concluded that disturbing such natural behaviors would likely disadvantage the dolphins, making them less able to search for food on their own.

In Shark Bay, Western Australia, a high mortality rate of bottlenose dolphin (*Tursiops sp.*) calves was associated with tourist feeding of lactating mothers (Mann et al. 2000). The hand fed mothers were found to neglect their calves, resulting in malnourishment and death by disease and shark attack (Wilson 1994). Subsequently, feeding regulations were changed in order to minimize the impacts on the dolphins. At Tin Can Bay, on the east Australian coast, Indo-Pacific humpback dolphins have been provisioned since the early 1970s. Inappropriate behaviors reported from this site include provisioning of fish of unknown quality and quantity, children riding a dolphin by holding onto the dorsal fin, and an adult trying, unsuccessfully, to climb onto the back of a dolphin (Garbett and Garbett 1997). These examples demonstrate the potential for adverse impacts on dolphins as a result of inappropriate behavior by human participants.

Bottlenose Dolphin Calf Survival

Studies on the population ecology of wild bottlenose dolphin populations have demonstrated that large odontocetes have extremely low adult mortality but substantial infant mortality, believed to be largely caused by predation (Jefferson, Stacey and Baird 1991). An important determinant of female reproductive success may be the ability to protect infants from harm (Conner et al. 1998). Hersh, Odell and Asper (1990) reported an annual mortality rate (1976– 1983) of 9.2% for bottlenose dolphins in the Indian/Banana River system, Florida, with females tending to live longer than males. Similarly, Stolen and Barlow (2003) reported an annual mortality rate of 9.8% for bottlenose dolphins in the Indian River Lagoon for the period 1978–1997. Bottlenose dolphins are long-lived, reach reproductive maturity late in life, and have a great deal of parental investment in offspring (Mann et al. 2000). Protection of calves from predators is a function of the close physical association between mothers and calves, sometimes lasting for 3 to 6 years from birth (Navarro 1990). Lactating females have also been known to exhibit punitive behavior toward calves that stray too far or for too long, further demonstrating the parental care involved in protecting infants from predators (Chirighin 1987).

By contrast with the 9.8% annual mortality rate of the Indian River Lagoon bottlenose dolphin population, the modeled calf mortality in the first year of life is 16.4% per annum (Stolen and Barlow 2003). Reported wild bottlenose dolphin calf mortality rates in the first year of life are 33% (Shark Bay, 1985–1993; Richards 1993, cited in Wilson 1994), 29% (Shark Bay, 1988–1998; Mann et al. 2000) and 19% (Sarasota Bay, Florida; Wells and Scott 1990). Similarly, Herzing (1997) reported first-year calf mortality of 24% for *Stenella frontalis* in the Bahamas. Bottlenose dolphin mortality in the period to weaning (3 years) is reported as 46% (Sarasota Bay; Wells and Scott 1990) and 44% (Shark Bay; Mann et al. 2000). Thus, although mortality rates vary in space and time and there are uncertainties in many of the calf mortality rate estimates, in the order of 20 to 30% of calves are likely to die in their first year, and almost half will die in their first three years (i.e., before they are weaned). For first-born calves (i.e., of primiparous females) mortality rates may be much higher. In Sarasota Bay, calves born to first-time mothers have a mortality rate of 86% compared to approximately 18% for experienced females (Weiss 1998).

A case study which provides a useful benchmark for the outcomes of provisioning at Tangalooma is the long-running provisioning program at Monkey Mia, Shark Bay, Western Australia, where bottlenose dolphins have been provisioned since 1964. A formally structured and government-sanctioned dolphin provisioning program commenced at Monkey Mia in 1986 when Parks and Wildlife service rangers were stationed in the area, and an interpretive centre built (Orams 1994). Since that time the program has been subject to much public and scientific scrutiny, as it was reported that, even with a cautious feeding regime, the calves born into this program (post 1986) had a mortality rate of more than 80% (Wilson 1994). Richards (1993) investigated calf survival in Shark Bay for the period 1985–1993 and reported a dramatically reduced survival rate for offspring of provisioned females compared with offspring of non-provisioned females. The cumulative survivorship of infant bottlenose dolphins before 2 years of age remained significantly lower for the calves born of provisioned mothers (Figure 3). The most significant difference was in survival of infants in the first year of life: 36% for provisioned compared with 67% for non-provisioned mothers (Wilson 1994).

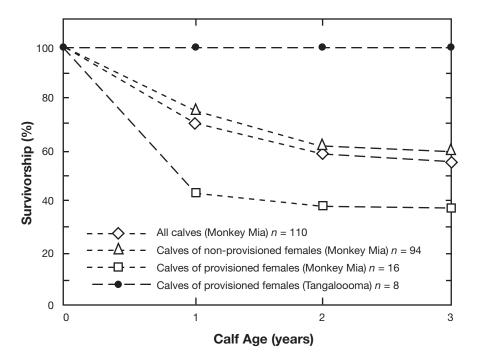


Figure 3. Calf survivorship from birth to age 3 years at Monkey Mia and Tangalooma (modified from Mann et al. 2000).

Wilson (1994) considered it most unlikely that the very high infant mortality rates of calves born to the provisioned females could be attributed entirely to natural causes, and suggested that one or several of the following may cause mortality to calves of provisioned mothers at Monkey Mia:

- prolonged exposure to polluted near shore waters;
- exposure to human pathogens;
- provisioning may distract mothers and offspring from attending to potential threats, especially shark attack;
- provisioned dolphins may accept poor quality fish items from boats;
- provisions supplied during feeds may be nutritionally inappropriate;
- the provisioned females sampled may have included a disproportionate number of individuals that are at the beginning or the end of their reproductive career, thus affecting the survival of their offspring.

Wilson (1994) suggested that although a biased sample of females in the study was a possibility, it was not considered to be a likely explanation of the low infant survivorship of provisioned mothers at Monkey Mia.

Observation of infant mortality in provisioned dolphins, and contrasting it with infant mortality in non-provisioned dolphins, is one of the most non-invasive methods of monitoring the impacts provisioning may have on wild dolphin health. This is particularly the case given the importance of calf survival to a species of naturally low fecundity.

Calf Survival at the Tangalooma Provisioning Program

Calves provisioned at Tangalooma include two born to mothers who were subsequently provisioned, five born to mothers who were provisioned at the time of the birth (one of which was subsequently orphaned), and one apparently orphaned. The life history of each of these calves of all provisioned mothers for the 15-year history of the program is outlined in chronological order below.

Tinkerbell

At the time hand feeding commenced (April, 1992), Beauty (Figure 2) was accompanied by a female calf (Tinkerbell) estimated to be one and a half years old (Orams 1995). Beauty's attendance rate at the daily provisioning sessions during Tinkerbell's 3rd year was 70% (Figure 4; insufficient data from Tinkerbell's 1st and 2nd years). Tinkerbell began to accept hand-fed fish in October 1992. She continues to participate in the provisioning program and has given birth to two calves (in 2000 and 2004).

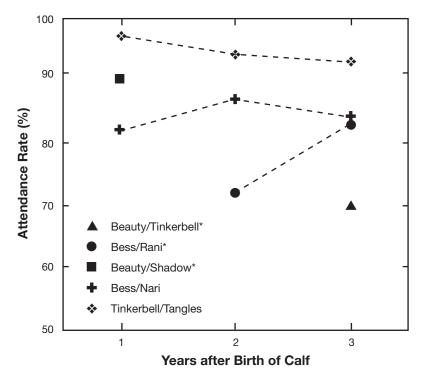


Figure 4. Attendance rate (% of nights present) of mothers at the provisioning area in the three years following calf birth. * Tinkerbell and Rani born before program commenced; Beauty died when Shadow was aged 14 months.

Rani

When Bess (Figure 2) first attended provisioning sessions, she was accompanied by a male calf (Rani) estimated to be approximately 6 months old at the time (Orams 1995). Bess' attendance rate at the daily provisioning sessions during Rani's 2nd and 3rd years was 77% (Figure 4; insufficient data from Rani's 1st year). Rani began to accept hand-fed fish in January 1993, and continues to participate in the provisioning program.

Echo

Echo was first observed adjacent to the provisioning area on the July 15, 1993. His age was estimated at 8–10 months. Echo was not accompanied by an adult dolphin, then or subsequently, and therefore was assumed to have been orphaned. Echo, who was in poor physical condition, immediately began to accept fish from the provisioning program (Orams 1996). Echo is a regular participant in the provisioning program.

Shadow

On October 14, 1994, Beauty gave birth to another female calf, Shadow. Beauty last attended the provisioning program at Tangalooma on December 23, 1995 and is assumed deceased. Shadow, then 14 months old and still a dependent calf, visited the provisioning program alone on December 26, 1995 and was then included in the program to enhance her probability of survival. Beauty's attendance rate at the daily provisioning sessions during Shadow's first year was 89% (Figure 4). Shadow continues to participate in the provisioning program and, in September 2004, gave birth to her first calf.

Nari

Nari, a male, was born to Bess on January 29, 1997. Bess last attended the provisioning program on February 22, 2000 and is presumed deceased. Bess' attendance rate at the daily provisioning sessions during Nari's first three years was 84% (Figure 4). Nari accepted hand-fed fish for the first time on February 27, 1999. He has been a consistent participant in the provisioning program since that time.

Tangles

Tangles (sex unknown at the time of writing) was born to Tinkerbell on September 20, 2000. Tinkerbell's attendance rate at the daily provisioning sessions for the 3 years following Tangles' birth was 95% (Figure 4). Tangles began accepting provisioned fish at two years of age, and has since been a regular participant in the provisioning program.

Storm

On August 27, 2004 Tinkerbell gave birth to her second calf, Storm (male). During Storm's first year of life, Tinkerbell's attendance rate was 87%.

Silhouette

Silhouette (sex unknown) was born to Shadow on September 7, 2004 and during Silhouette's first year of life Shadow attended 89% of provisioning sessions. Provisioning of Storm and Silhouette commenced when they reached two years of age.

The survival rate of the eight dolphin calves, born to females provisioned in the program at Tangalooma, is 100%. No mortality has occurred despite that two of the calves were orphaned (Echo and Shadow) and two were first-born calves (Tangles and Silhouette), both factors expected to yield high mortality rates. Furthermore, as indicated in Figure 4, attendance rates of the provisioned mothers were consistently high (> 80% for mothers of calves born in the last ten years [attendance rates were generally lower in the early years of the program]). These data clearly indicate that all of the mothers are consistent participants in the program and not occasional visitors. This outcome represents a marked contrast with mortality rates observed elsewhere (see above).

Perhaps the most comprehensive data set is that of Mann et al. (2000) from Monkey Mia. Western Australia. Calf mortality in the first 3 years of life at Monkey Mia was 44% (n = 110). For calves born to non-provisioned dolphins the mortality rate was 40% (n = 94), and for those born to provisioned dolphins the mortality rate was 60% (n = 16). By contrast, calf survival at Tangalooma is 100% (n = 8) (Figure 3). Furthermore, there has been no mortality of weaned juveniles at Tangalooma. By contrast, Mann et al. (2000) report that five (11%) of 46 juveniles at Monkey Mia disappeared one year or more after weaning and are presumed dead. Although there are no mortality data for calves born to non-provisioned dolphins in Moreton Bay, and thus no control population, we assume that non-provisioned calf mortality rates in this area would be similar to those reported from other locations, that is, in the order of 20 to 30% of calves are likely to die in their first year, and almost half will die in their first three years. This is likely to be a conservative assumption given the high incidence of shark wounds observed on bottlenose dolphins in Moreton Bay (Corkeron et al. 1987). Furthermore, the estimates of calf mortality from wild populations are likely to be minimum estimates because newborn calves may die before being observed by researchers. This is not the case at Tangalooma, where dolphins are observed on a daily basis and an impending birth is recognized.

It is acknowledged that the sample size at Tangalooma (8 calves) is small relative to that for the provisioned population at Monkey Mia (16 calves; Mann et al. 2000), and is too small to allow statistical analysis. However, we believe that the 100% survival rate for the calves at Tangalooma is of sufficient significance to warrant reporting. This is particularly the case as, given the present age/reproductive status of the female dolphins at Tangalooma, it will be several years before any additional first-year calf survival can be reported and, at historical rates of reproduction, about 28 years until the Monkey Mia sample size of 16 is attained. There has been no calf mortality associated with the Tangalooma provisioning program over the fifteen years it has been operating.

Although high calf mortality rates are often cited as a consequence of dolphin provisioning (e.g., Wilson 1994; Orams 2002), the observations from Tangalooma indicate that this is not necessarily the case. This finding is consistent with the observation of Mann and Kemps (2003) that, subsequent to changes in provisioning practices at Monkey Mia in 1995, all calves born to provisioned dolphins had survived to weaning. Furthermore, it seems likely that the provision of fish to the orphaned dolphins Echo and Shadow may have contributed to their survival.

Possible Explanations for High Calf Survival Rates

Although under some circumstances it is possible to attribute a specific cause of death to a particular calf, the reciprocal position is clearly not possible, that is, it is not possible to attribute a specific cause to the long-term survival of a particular calf. Thus, although we cannot provide specific explanations for the 100% calf survival at Tangalooma, some factors which may have contributed to this outcome are suggested. These relate to aspects of the location and characteristics of the provisioning area at Tangalooma, to dolphin foraging ecology and to the provisioning management regime.

Location and Characteristics of the Provisioning Area

Tangalooma is located on an island in eastern Moreton Bay. The island's population is small (several hundred) with access only by boat, limiting the potential for unregulated human-dolphin

interactions. Similarly, small boat access from urban centers on the mainland is restricted by often hazardous sea conditions, limiting the potential for interactions between dolphins and boat operators. The Tangalooma Resort is located on the leasehold site of the former Tangalooma whaling station. This lease gives tenure to low tide level, thus giving provisioning program managers jurisdiction over the beach, a key aspect of effective management of the program. Furthermore, a condition of the permit under which the provisioning is conducted gives the resort jurisdiction over the sub-tidal dolphin provisioning area and immediate surrounds (Hassard, personal communication).

The northeast part of Moreton Bay, where the provisioning area is located, has the best tidal flushing, the best water quality, and is the most remote from sources of pollution of any area within the Bay (Milford and Church 1977; Wallace and Moss 1979; Moss, Connell and Bycroft 1992; Patterson and Witt 1992; Islam et al. 1995), with water quality similar to oceanic conditions. Thus, the risk of pollution-related morbidity or mortality is low at this site compared with other areas of the Bay (Neil and Brieze 1998), particularly given the limited time dolphins spend in the provisioning area. A regime of weekly water quality monitoring is maintained at the provisioning area.

Foraging Ecology

Mann and Sargeant (2003) suggest that, on average, female dolphins spend in the order of 20 to 40% of their time foraging, and separations of calves from mothers occur primarily while the mother is foraging (Mann and Smuts 1998). As dolphin mothers are unable to cache or carry offspring, accelerated chases during foraging result in repeated separations of mothers and calves, increasing the risk of predation (Connor et al. 2000). Acquisition of 10 to 30% of their daily food intake from provisioning in less than 5% of the day may proportionately reduce foraging-related mother–calf separations for the dolphins provisioned at Tangalooma, thus reducing predation risk. Furthermore, this component of dietary intake is acquired in shallow water, where predation risks are reported to be lower because mothers and calves who spend more time in very shallow water may be able to detect and avoid sharks more readily than in deeper water (Mann et al. 2000).

There is a significant nursing cost in feeding a calf (Mann et al. 2000), with associated increases in food intake by up to 50% in captive bottlenose dolphins (Cheal and Gales 1991), as well as the energetic cost of chasing, shepherding and defending a calf. Provisioned mothers are able to increase their food intake during nursing by the simple expedient of increasing their attendance rates at the provisioning sessions. Similarly, dolphin food intake varies seasonally, commonly increasing during cooler months (e.g., Shane 1990, wild dolphins; Cheal and Gales 1992, captive dolphins), perhaps as a basis for producing and maintaining an adequate blubber layer (Shane 1990). Provisioned mothers have the opportunity to increase provisioning attendance rates to respond to the combined nutritional requirements of cool temperatures and lactation. These foraging ecology factors associated with provisioning have the potential to enhance the health of both calves and mothers (by facilitating increased food intake by mothers when needed), and to reduce predation risk (by reducing foraging-related mother–calf separations).

Management Regime: Provisioning Duration and Feeding Times

Provisioning is limited to one session daily of approximately one hour duration. Thus, dolphins with a 100% attendance rate spend less than 5% of their time in the provisioning area. Provisioning occurs shortly after sunset, which minimizes opportunities for interaction with vessels and other beach users in the vicinity, and is also consistent with widely reported late afternoon–evening peaks in bottlenose dolphin foraging (e.g., Saayman, Tayler and Bower 1973; Shane,

Wells and Wursig 1986; Shane 1990). The floodlights are extinguished at the completion of provisioning and all of the dolphins leave within about 3 minutes.

Management Regime: Pathogen Induced Disease and Feeder Management

In order to reduce any risk of pathogen transfer from humans to dolphins (Wilson 1994), staff and feeders are required to wash hands and forearms in a Milton® anti-bacterial solution prior to fish handling. This solution is commonly used to provide hygienic protection for baby bottles and to disinfect drinking water, making it a suitable mild and non-toxic anti-bacterial solution to use for the provisioning program. Further to this, no feeder or staff member is permitted to touch or swim with the dolphins at any time, further reducing the risk of human pathogen transfer to the dolphins and minimizing the risk of injury to human feeders. Appropriate behavior of feeders is controlled by conducting a pre-provisioning briefing, explaining appropriate and inappropriate behaviors, and by maintaining a feeder: staff ratio generally of 2:1 and not exceeding 3:1. Provisioning is conducted on a rotational basis, with staff and feeders moving into the water to feed the dolphins (c. 30 s duration) and then leaving the water (for c. 30 s duration) before the next group moves into the water to feed. Thus, close proximity of humans to the dolphins occurs only for brief and intermittent periods and, similarly, separation of calves from their mothers and from the other dolphins also occurs only for brief and intermittent periods. Signs at the provisioning area beach advise that no boating, swimming, or fishing is permitted in the buoyed-off provisioning area at any time, a prohibition enforced by staff.

Management Regime: Fish Quality

Nutritional quality of the fish provided at the Monkey Mia feeding program may have been inadequate or inappropriate and contributed to malnutrition and subsequent high mortality of calves there (Wilson 1994). There is little information available on fish species selection by dolphins under differing conditions and locations, or on the relative nutritional values of the fish species eaten (Wilson 1994). Tangalooma's provisioning program attempted to overcome this by trialing several species including Squid (*Loligo spp.*), Squire (*Chrysophrys auratus*), Grinner (*Saurida undosquamis*), Flounder (*Pseudorhombus spp.*), Whiting (*Sillago spp.*), Silver Biddies (*Gerres subfasciatus*) and Mullet (*Mugil spp.*). Silver Biddies proved to be the most popular choice of the dolphins (Orams 1995). They are locally caught, frozen within four hours of netting and stored in freezers for no more than one month.

Several of the possible explanations for 100% calf survival at Tangalooma provided above may also apply at Monkey Mia, particularly those factors associated with feeding ecology. It seems likely that provisioning may either increase or decrease calf survival relative to mortality rates in non-provisioned populations. Which outcome occurs is likely to be determined by the characteristics of the site (e.g., location, isolation, water quality, potential for management controls) and the management regime itself (control of timing and duration of provisioning, control of contact between humans and dolphins, control of the quality of food). The combination of site and management characteristics at Tangalooma appear to have resulted in calf survival rates greater than in non-provisioned populations, while those at Monkey Mia have had the opposite effect. We reiterate that Mann and Kemps (2003) reported that no calf mortality had occurred at Monkey Mia after the management regime was altered in 1995.

Conclusion

Wild dolphin provisioning for the benefit of human enjoyment and education has been shown to have significant effects on dolphin behavior and survival. The death of a large proportion

of dolphin calves at Monkey Mia in the 1980s and early 1990s, far in excess of natural mortality rates, is evidence of this. However, no calf mortality has occurred at Tangalooma in 15 years of the provisioning program's operation, despite the presence of first-born and orphaned calves, both of which are factors likely to increase calf mortality rates. This outcome is probably related to three main factors. First, the high water quality and limited public access inherent in the physical setting of the provisioning area assists in minimizing adverse impacts on the dolphins. Second, provisioned food may play a role in both reducing foraging-related mother–calf separations and allowing nursing mothers to increase their food intake by increasing their attendance rate. Third, the management regime of fixed feeding times of short duration, no physical contact with humans, and control of the quantity and quality of fish provided limits the risks associated with dependency, malnutrition, predation, pathogens, and pollution (Neil and Brieze 1998). Although provisioning at Tangalooma has been undertaken for the past 15 years with no calf mortality, continued monitoring and assessment of the program is essential.

The results from Tangalooma indicate that dolphin provisioning does not inevitably lead to high calf mortality. However, there are numerous factors which are likely to contribute to this outcome at this particular site. The 100% calf survival rate at Tangalooma, possibly due largely to the site-specific attributes of Tangalooma and the management regime implemented there, is not an argument for the development of dolphin provisioning programs at other locations, because of the other well-documented risks inherent in the provisioning of wild animals.

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References

- Albert, D. M. and Boyer, R. T. 1991. Factors related to grizzly bear-human interactions in Denali National Park. *Wildlife Society Bulletin* 19: 339–349.
- Brennan, E. J., Else, J. G. and Altmann, J. 1985. Ecology and behaviour of a pest primate: Vervett monkeys (*Cercopithecus aethiops*) in a tourist lodge habitat. *African Journal of Ecology* 23: 35–44.
- Cheal, A. J. and Gales, N. J. 1991. Body mass and food intake in captive, breeding bottlenose dolphins, *Tursiops truncatus*. <u>Zoo Biology 10: 451–456.</u>
- Cheal, A. J. and Gales, N. J. 1992. Growth, sexual maturity and food intake of Australian Indian Ocean bottlenose dolphins, *Tursiops truncatus*, in captivity. *Australian Journal of Zoology* 40: 215–223.
- Chirighin, L. 1987. Mother–calf spatial relationships and calf development in the captive bottlenose dolphin (*Tursiops truncatus*). Aquatic Mammals 13: 5–15.
- Conner, R. C., Mann, J., Tyack, P. L. and Whitehead, H. 1998. Social evolution in toothed whales. <u>Trends in</u> <u>Ecology and Evolution 13: 228–232.</u>
- Conner, R. C. and Smolker, R. A. 1985. Habituated dolphins (*Tursiops sp.*) in Western Australia. <u>Journal of</u> <u>Mammalogy 66: 398–400.</u>
- Conner, R. C., Wells, R. S., Mann, J. and Read, A. J. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. In *Cetacean Societies: Field Studies of Dolphins and Whales*, 91–126, ed. J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead. Chicago: University of Chicago Press.
- Constantine, R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science* 17: 689–702.
- Corkeron, P. J., Bryden, M. M. and Hedstrom, K. E. 1990. Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. In *The Bottlenose Dolphin*, 329–336, ed. S. Leatherwood and R. R. Reeves. San Diego: Academic Press.
- Corkeron, P. J., Morris, R. J., Bryden, M. M. and Hedstrom, K. E. 1987. Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. *Aquatic Mammals* 13: 111–114.
- Fa, J. E. 1992. Visitor-directed aggression among the Gibraltar macaques. Zoo Biology 11: 43-52.

Frohoff, T. G. and Packard, J. M. 1995. Human interactions with free-ranging and captive bottlenose dolphins. Anthrozoös 8: 44–53.

Garbett, D. and Garbett, P. 1997. An update on interaction between humans and dolphins *Sousa chinensis* at Tin Can Bay, Queensland. Brisbane: Australian Whale Conservation Society.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behaviour. Cambridge: Harvard University Press.

Green, A. and Corkeron, P. J. 1991. An attempt to establish a feeding station for bottlenose dolphins (*Tursiops truncatus*) on Moreton Island, Queensland, Australia. *Aguatic Mammals* 17: 125–129.

Hersh, S. L., Odell, D. K. and Asper, E. A. 1990. Bottlenose dolphin mortality patterns in the Indian/Banana River system of Florida. In *The Bottlenose Dolphin*, 155–164, ed. S. Leatherwood and R. R. Reeves. San Diego: Academic Press.

Herzing, D. L. 1997. The life history of free-ranging Atlantic spotted dolphins (Stenella frontalis): age classes, color phases and female reproduction. <u>Marine Mammal Science 13: 576–595.</u>

Islam, M. A., Neil, D. T., Bell, P. R., Ahmad, W. and Gabric, A. 1995. Water quality parameter mapping in a shallow coastal water area, Moreton Bay, Brisbane, Australia, through the integration of remote sensing and geographic information systems. In *The Marine Environment Conference—Program and Abstracts*, 89, ed. D. T. Neil, N. J. Hall and I. R. Tibbitts. Brisbane: The University of Queensland.

Jefferson, T. A., Stacey, P. J. and Baird, R. W. 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. *Mammal Reviews* 21: 151–180.

Kofron, C. P. 1999. Attacks to humans and domestic animals by the southern cassowary (*Casuarius casuarius johnsonii*) in Queensland, Australia. *Journal of Zoology* (London) 249: 375–381.

Lockyer, C. 1990. Review of incidents involving wild, sociable dolphins, worldwide. In *The Bottlenose Dolphin*, 337–353, ed. S. Leatherwood and R. R. Reeves. San Diego: Academic Press.

Lusseau, D. 2003. Male and female bottlenose dolphins (*Tursiops spp.*) have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology Progress Series* 257: 267–274.

Lusseau, D. 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioural information. *Ecology and Society* 9: Art. No. 2. www.ecologyandsociety.org/vol9/iss1/art2 Accessed November 2007.

Mann, J., Connor, R. C., Barre, L. M. and Heithaus, M. R. 2000. Female reproductive success in bottlenose dolphins (*Tursiops sp.*): life history, habitat, provisioning, and group-size effects. <u>Behavioral Ecology 11: 210–219.</u>

Mann, J. and Kemps, C. 2003. The effects of provisioning on maternal care in wild bottlenose dolphins, Shark Bay, Australia. In *Marine Mammals: Fisheries, Tourism and Management Issues*, 304–317, ed. N. Gales, M. Hindell and R. Kirkwood. Collingwood: CSIRO Publishing.

Mann, J. and Sargeant, B. 2003. Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops sp.*). In *The Biology of Traditions: Models and Evidence*, 236–266, ed. D. M. Fragaszy and S. Perry. New York: Cambridge University Press.

Mann, J. and Smuts, B. 1998. Natal attraction: allomaternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour* 55: 1097–1113.

Mann, J. and Smuts, B. 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops sp.*). *Behaviour* 136: 529–566.

Milford, S. N. and Church, J. A. 1977. Simplified circulation and mixing models of Moreton Bay. *Australian Journal of Marine and Freshwater Research* 28: 23–34.

Moss, A., Connell, D. and Bycroft, B. 1992. Water quality in Moreton Bay. In *Moreton Bay in the Balance*, 103– 114, ed. O. N. Crimp. Brisbane: Australian Littoral Society and Australian Marine Science Consortium.

National Marine Fisheries Service (NMFS). 1994. Report to Congress on results of feeding wild dolphins: 1989– 1994. National Marine Fisheries Service, Office of Protected Resources, Silver Springs: Maryland.

Navarro, T. 1990. Behavioural traits of a female dolphin (*Tursiops truncatus*) with her calf. <u>Aquatic Mammals 16:</u> <u>65–69.</u>

Neil, D. T. 2002. Cooperative fishing interactions between Aboriginal Australians and dolphins in eastern Australia. Anthrozoös 15: 3–18.

Neil, D. T. and Brieze, I. 1998. Wild dolphin provisioning at Tangalooma, Moreton Island: An evaluation. In Moreton Bay and Catchment, 239–252, ed. I. R. Tibbetts, N. J. Hall and W. D. Dennison. Brisbane: School of Marine Science, The University of Queensland.

Orams, M. B. 1994. Tourism and marine wildlife: The wild dolphins of Tangalooma, Australia: A case report. *Anthrozoös* 11: 195–201.

- Orams, M. B. 1995. Development and management of a feeding program for wild bottlenose dolphins at Tangalooma, Australia. <u>Aquatic Mammals 21: 137–147.</u>
- Orams, M. B. 1996. Managing interaction between wild dolphins and tourists at a Dolphin Feeding Program, Tangalooma, Australia. Ph.D. Thesis, The University of Queensland, Australia.
- Orams, M. B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. <u>Tourism</u> <u>Management 23: 281–293.</u>
- Orams, M. B., Hill, G. J. E. and Baglioni, Jr., A. J. 1996. "Pushy" behavior in a wild dolphin feeding program at Tangalooma, *Australia. Marine Mammal Science* 12: 107–117.
- Patterson, D. and Witt, C. 1992. Hydraulic processes in Moreton Bay. In *Moreton Bay in the Balance*, 25–39, ed. O. N. Crimp. Brisbane: Australian Littoral Society and Australian Marine Science Consortium.
- Richards, A. F. 1993. Reproductive parameters of bottlenose dolphins in Shark Bay, Western Australia. Paper presented at the Tenth Biennial Conference on the Biology of Marine Mammals, Galveston, Texas, USA, November 11–15, 1993.
- Saayman, G. S., Tayler, C. K. and Bower, D. 1973. Diurnal activity cycles in captive free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus Ehrenburg*). <u>Behaviour 44: 212–233</u>.
- Santos, M. C. D. 1997. Lone sociable bottlenose dolphin in Brazil: Human fatality and Management. <u>Marine</u> <u>Mammal Science 13</u>: 355–356.
- Santos, E., Pansard, K. C., Yamamoto, M. E. and Chellappa, S. 2006. Behavior of estuarine dolphin, Sotalia guianensis (Van Beneden) (Cetacea, Delphinidae) in the presence of tourist boats in Pipa Beach, Rio Grande do Norte, Brazil. Revista Brasileira de Zoologia 23: 661–666.
- Shane, S. H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In *The Bottlenose Dolphin*, 245–265, ed. S. Leatherwood and R. R. Reeves. San Diego: Academic Press.
- Shane, S. H., Wells, R. S. and Wursig, B. 1986. The ecology, behavior and social organization of the bottlenose dolphin—a review. *Marine Mammal Science* 2: 34–63.
- Stolen, M. K. and Barlow, J. 2003. A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon System, Florida, USA. *Marine Mammal Science* 19: 630–649.
- Wallace, H. D. and Moss, A. J. 1979. Some aspects of water quality in Northern Moreton Bay. In Northern Moreton Bay Symposium, 33–46, ed. A. Bailey and N. C. Stevens. Brisbane: Royal Society of Queensland.
- Weiss, C. 1998. Differential calf survival of bottlenose dolphins. Sarasota Dolphin Research Program. December, 1998: 7–8. http://www.mote.org/~rwells/1998news/news.phtml Accessed September 14, 2004.
- Wells, R. S. and Scott, M. D. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Reports of the International Whaling Commission*, Special issue 12: 407–415.
- Wilson, B. 1994. Review of dolphin management at Monkey Mia. Perth: Department of Conservation and Land Management.
- Wrangham, R. W. 1974. Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behaviour* 22: 83–93.