BEHAVIORAL DEVELOPMENT IN WILD BOTTLENOSE DOLPHIN NEWBORNS (TURSIOPS SP.)

by

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Summary

Newborn characteristics, patterns of motoric and social behavioural development, and mother-infant relationships in free-ranging and semi-provisioned bottlenose dolphins (*Tursiops* sp.) are examined. Nine newborns were observed for 189 hours over the first 10 weeks of life. Newborn infants breathe more often than their mothers, and synchronize their breathing and swimming with her soon after birth, but show a gradual decline in synchrony as they age. Virtually all patterns of infant behaviour, mother-infant proximity, and spatial relationships with the mother changed as a function of infant age. Maternal activity, however, does not change over time, except that mothers decrease their role in maintaining proximity to their infants from the first month to the second month of infant life. Infants spend less time

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close to their mothers, less time echelon swimming (close, alongside the mother), and more time infant-position swimming (in contact under the mother) as they age. Infants spend more time traveling and socializing independently over time. They also separate from their mothers more often and for longer periods of time. Infants do not forage during the newborn period, but are observed 'practice foraging' by the end of the first month. Rubbing, petting, chasing, and displaying with other animals (including the mother) were common forms of socializing. Infants frequently initiate rubbing with their mothers, with particular focus on her head region. Infants typically associate with young females, adult females and other infants, but not with adult or subadult males. Developmental shifts and overall patterns are discussed in the context of the bottlenose dolphin's fission-fusion social organization and ecology. The effects of provisioning on dolphin behaviour are addressed.

Introduction

Since 1988, we have conducted longitudinal observations of wild bottlenose dolphin (*Tursiops* sp.) mothers and infants in Shark Bay, Western Australia. This paper describes behavioural development in nine newborn infants (first 10 weeks). Using quantitative data derived from focal samples, we examined early physical characteristics and motor development (diving, respiration, and mother-infant respiratory synchrony), developmental changes in spatial relations and mother-infant proximity, and maternal and infant activity budgets, including how mothers and infants coordinate their behaviour.

Some important physical and behavioural characteristics of newborn dolphins have been described in detail for captive animals (McBride & Hebb, 1948; McBride & Kritzler, 1951; Essapian, 1953; Tavolga & Essapian, 1957; Amundin, 1986; Chirighin, 1987; Eastcott & Dickinson, 1987; Reiss, 1988; Cockcroft & Ross, 1990; Peddemors, 1990; Reid *et al*., 1995). This study, however, provides the first quantitative account of early development and behaviour in the wild. Analyses of newborn development within a natural context is important for this species because of their exceptionally complex social structure and unusual combination of ecological and life-history traits.

Bottlenose dolphins form temporary parties whose size and composition changes almost continuously as individuals join and leave in a fluid manner (Wells *et al*., 1987; Smolker *et al*., 1992). Nevertheless, some highly stable patterns of association exist, not only between mothers and infants, but also among female kin (Wells *et al*., 1987), adult females (Wells *et al*., 1987; Smolker *et al*., 1992), and particularly among adult males, who form stable

alliances engaged in reproductive competition against other male alliances (Connor *et al*., 1992a, b). These data, along with evidence of elaborate communication (Richards *et al*., 1984; Tyack, 1986; Janik & Slater, 1997), suggest a social system comparable in complexity to that of great apes, the only other mammalian group in which relative brain size is as large as it is in some delphinids, including *Tursiops* (Connor *et al*., 1992b; Smolker *et al*., 1992; Marino, 1998). Furthermore, like great apes, bottlenose dolphins have very 'slow' life histories characterized by late age of sexual maturity, long interbirth intervals, and long maximum lifespans (Goodall, 1986; Smuts *et al*., 1987; Wells *et al*., 1987; Mann *et al*., in press). In contrast, the dolphin infant's precocious locomotion, post-partum following response, and possible period of maternal imprinting (Mann & Smuts, 1998) closely resemble the follower strategy characteristic of many ungulates (Ralls *et al*., 1987). Finally, delphinid foraging ecology may be compared to that of a terrestrial carnivore, in which mothers must accelerate rapidly to chase prey, but unlike many carnivores, dolphins do not cache their offspring.

Given this particular combination of social structure, life history, and ecology, we would expect selection to favor developmental patterns that enable the newborn to negotiate some tasks rapidly (such as maintaining proximity to the mother), while other skills (such as those associated with foraging and the development of social bonds) may develop much more slowly. Because adult and immature life history variables are closely related (Charnov, 1991), a better understanding of newborn development, combined with data on behavioural development over the entire period of immaturity, should help to clarify the selective pressures that favored delayed maturation, large brains, and complex cognitive abilities in delphinids.

Methods

Study site and population

Our study site incorporates a 130 km^2 area east of the Peron Peninsula that bisects Shark Bay (25°47′S, 113°43′E), Western Australia. After a preliminary visit in 1982 (Connor & Smolker, 1985), a longitudinal field site was established in 1984. By 1998, well over 600 dolphins were identified, and roughly 100 animals are sighted routinely. Sex is determined by views of the genital area or the presence of a dependent calf (adult females). Bottlenose dolphin births peak in the spring and summer (Wells *et al*., 1987; Connor *et al*., 1996). Both captive and wild *Tursiops* infants have high rates of infant mortality, especially during the first few weeks of life (Sweeney, 1977; Cornell *et al*., 1987; Wells *et al*., 1987; Hersh *et al*., 1990; Small & Demaster, 1995).

TABLE 1. *Summary of focal observations*

Infant	Mother	Sex	Ages observed (Wks)	Minutes of observation (PA)	Minutes of observation (non-PA)
Rab[*]	Nic	M	1-8	2054	1110
Nov[*]	Hol	F	1-10	1206	1968
Pep	Puc	M	1-6	1499	0
Hbt	Hol	F	3-8	80	0
Nak	Nic	M	2-8	90	0
Pic	Puc	F	1-10	1142	0
Shd	Sur	M	1-8	571	0
Oys[t]	Alg	M	⩽2-⩽5	0	450
Mou[t]	Min	F	1-8	0	1190
Total				6642	4718

[*] Infant observed both in the provisioning area (PA) and away from the PA (non-PA).
[t] Infant observed away from provisioning area only.
For the provisioned females, date of birth was known within two days. For the two non-provisioned females, Mou's exact date of birth was known but Oys's birthdate was estimated within a two-week range based on the last time his mother was observed pregnant and the first time she was observed with the infant. We could therefore classify Oys's early observations as occurring during the first month of life. Since later observations could have fallen at the end of the first month or the early part of the second month of life, we classified them as occurring during the second month so as to provide conservative estimates of age effects (comparing month 1 to month 2). Fifty-seven percent of observations occurred during the month one. Nov and Pic were observed for 10 hrs during weeks 9 and 10, leaving 179 hrs of observation for the first 8 weeks. Total hours of observation = 189.3 (11,360 minutes), 78.6 hrs away from the provisioning area and 110.7 hrs in the provisioning area.

Since the early 1960s, at least 11 bottlenose dolphins have accepted fish from people, and since the late 1970s, these animals have accepted stroking and 'seagrass games' from tourists standing in knee-deep water at Monkey Mia, a fishing camp on the peninsula. Provisioning is controlled by rangers, who monitor the quality and quantity of fish fed. Females of at least two matrilines are fed up to 2 kg fish per day during 2-3 feedings, most of which occur in the morning. Dolphins occasionally receive hand-outs from fishers, although this practice is strongly discouraged. Several mother-newborn infant pairs that visited the provisioning area (PA) served as subjects in this study (see *Focal observations* below).

This study incorporates 4 field seasons from 1990-1994 totaling 11 months and 189 hrs of focal observations on 9 infants born to 6 mothers (Table 1; of the 9 calves in this study, only 4 survived past their first year. Those four survived to weaning at ages 3-6). Three of the four provisioned adult females that regularly visit the provisioning area (Nic, Hol, Puc) were observed with two newborn infants; the fourth regular visitor (Sur) was observed with one infant. The newborn infants of two non-provisioned females were also included in this study. All mothers in this study were multiparous, with known previous offspring, except for one (Sur), who gave birth to her first offspring (Shd) during the latter part of study. Only two

infants were observed at nine and ten weeks of age (for 10 focal hours), so these data were excluded from most of the analyses (See Table 1).

Focal observations: provisioning area (PA)

For the mother-infant study as a whole, most observations were collected during focal observations away from the provisioning area, obtained by following individuals in small boats (4-5 m dinghies equipped with 6-15 hp motors) for up to 10 hours at a time (Smolker *et al.*, 1993; Mann & Smuts, 1998). However, more than half of the data presented in this paper were collected on the provisioned females and their newborns when they were in or near the provisioning area (Table 1; Fig. 1). These data, termed "PA" focal observations, are included in this study because reliable data on newborns require accurate estimates of birthdates, which were easily obtained for provisioned mothers compared to non-provisioned mothers, who were seen less often. Daily observations of provisioned mothers and their infants allowed us to record neonatal behavioural and physical development in almost as much detail as one can in captivity.

PA observations typically started soon after mother and calf came into the provisioning area (Fig. 1). Observations, conducted from the jetty, were never started during feeds or right after feeds because the dolphins typically left the provisioning area immediately following feeds. Focal samples typically lasted one-half hour, although some were shorter if the dolphins left the provisioning area. A combination of point sampling, event and continuous
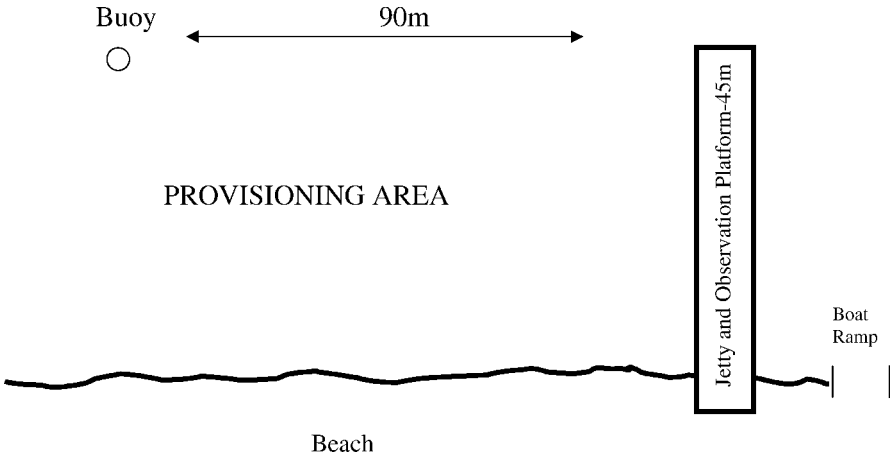

Fig. 1. The provisioning area (not to scale) at Monkey Mia, Shark Bay. Tourists typically stand at the edge of the 90 m beach between the jetty and buoy marker. The jetty height (1-3 m above sea level depending on tides) allows observers to view dolphins within a 200 m radius of the beach. Occasional boat-begging by the provisioned dolphins occurs at the ramp east of the jetty.

TABLE 2. *Ethogram*

Behavior	Definition
Rest	Slow travel, < 2 mph, frequent floating at surface, frequent direction changes.
Travel	Straight movement, > 2 mph (not scored near PA except when arriving or leaving the PA).
Infant position swimming	Infant swims under mother, melon or head lightly touches mother's abdomen. Upon surfacing to breathe, the infant breaks infant position only for a couple of seconds, then angles back under the mother. Infant position swimming can be determined by the infant's surfacing position slightly behind and ≤ 0.5 m from the mother.
Echelon swimming	Also referred to as contact swimming when the calf is close ≤ 30 cm alongside them other — roughly parallel, touching the mother's flank above midline.
Forage	Rapid surfacing, frequent direction changes, fast swims, fish chases, observations of fish catches.
Snack forage	Foraging characterized by belly-up swimming near water surface. Prey are typically trapped at surface.
Beg/people interaction	Dolphin's head < 2 m from and oriented towards boat, or person is within 2 m of dolphin in PA. People interaction also included touching.
Social	Physical contact with conspecifics, including petting, rubbing, mounting, chases, genital inspections, gooses, pokes, play, bonding, displays.
Petting	Type of 'grooming' where one dolphin moves his/her pectoral fin or flukes on body of another.
Rubbing	Gentle body-to-body contact where one individual rubs a body part on another conspecific.
Genital inspections	Rostrum near genital area of conspecific and makes light or no contact to genital area.
Goose	Rostrum makes hard contact with genital area of conspecific.
Poke	Rostrum makes contact with body part (not genital area) of conspecific.
Displays	Surface displays that involve slapping a body part (belly, face, jaw, pectoral fin, dorsal side) on the water surface; also spy hops (bring head vertically out of water, perpendicular to water surface).
Play	Involves chasing, displays, occasionally carrying objects such as seagrass.
Aggressive behavior	Hits with tail, flukes, pectoral fins, head; head jerks (sharp lateral movement of head), open jaw.
Nursing	Rostrum in contact with mammary slit for > 2 s.
Approach	Animal swims within 2 m radius of another.

TABLE 2. *(Continued)*

Behavior	Definition
Leave	Animal departs from 2 m radius of another.
Breath	Determined by seeing the blowhole open at surface, the resulting water spray, or hearing the breath.
Surfacing bout	Breath series in-between dives.
Peduncle dive	Dolphin at surface arches tail-stock before descent, but tail flukes do not break surface.
Tail-out dive	Dolphin at surface arches tail-stock before descent and tail flukes clear water surface.

sampling was used to record maternal and infant activity, the distance between mother and infant, and approaches and leaves within the pair (Table 2). All animals in the vicinity (< 200 m radius from the PA beach) were scored as present and potential associates of the infant during each sample. However, nearest neighbors of the infant were scored at each point sample only if they were within 10 m. For two infants (Nak, Hbt), behaviour and distance from the mother were coded from videotape; their approach/leave data were not included in the analysis due to small sample sizes. For one infant, (Pep), observations were scheduled for 15 minute intervals and certain types of data were not collected (infant and maternal activity and associates in provisioning area).

For two infants (Nov, Rab), we periodically (1-2 times per week) counted exact breath rates of mother and infant for 10 minute periods in order to determine whether infants breathed more often than their mothers.

Focal observations: non-provisioning area (non-PA)

Focal samples of infants away from the provisioning area began as soon as the mother/infant pair was located and lasted for as long as we were able to stay with them or until they returned to the provisioning beach (average follow was 3 hrs). Typical dolphin-boat distance ranged from 2-20 m in 5.7 ± 1.2 m water. Visibility into the water from the boat typically varied between 2-8 m. For behavior definitions, see Table 2.

Four types of observational methods were used (Altmann, 1974). We employed *continuous sampling* (all observed occurrences of a behaviour are recorded and duration and/or frequencies are maintained in the sampling record) to record the durations of surfacing bouts, floating at the surface, and snack foraging, the proportion of time that infants spent in the 'infant' or 'echelon' positions, synchronous breaths/surfacings, and those types of social interactions that generally lasted for at least several seconds occurred at the surface, such that we could reliably detect each occurrence (*e.g.* displays, rubbing, petting). We conducted *instantaneous samples* (at five-minute intervals) of party direction, party composition, distance between mother and infant, identities of nearest neighbors, depth of water, speed (when tracking), and miles traveled.

Predominant activity sampling (PAS, activity must occur for a minimum of 50% of a predefined interval to be considered a predominant activity) was used to record predominant direction, predominant speed (six classifications), and maternal and infant activity. This convention of interval sampling has demonstrated validity (Tyler, 1979; Mann, 1999).

Finally, we used *ad libitum sampling* to record behaviours, such as nursing, that typically have very short durations, such that they can only be observed opportunistically. *Ad libitum* data provided descriptive information outside of focal samples. The rangers also provided us with details about events in the provisioning area that we considered *ad libitum*. Where appropriate, *ad libitum* data are indicated. For some rare behaviors, we describe their first occurrences, but do not present rates or durations.

Party composition was defined using a 10 meter chain rule where for any animal who surfaces within 10 meters of any other animal within the party is considered a party member.

Analyses

To determine the effects of provisioning, we used permutation tests to compare PA and non-PA group size, association, maternal and infant behaviour, and spatial relationships. We combine non-PA observations of provisioned and non-provisioned mothers and their offspring, and contrast them to PA observations (see Table 3).

Age comparisons involved two types of analysis. First, to look at rapid changes in early development, we compared the first week of life to weeks 2-8; for convenience, we refer to this comparison as 'week one *vs* later.' Second, to look at broader changes, the first month (wks 1-4) was compared to the second month of life (wks 5-8); we refer to this comparison as 'month one vs two'. Behaviour durations, frequencies and point samples were collapsed across weeks and converted to rates or proportions. Non-parametric tests were used and all probabilities were two-tailed. Means ± standard deviations are presented for descriptive purposes. For both age comparisons, we increased the sample size by combining non-PA and PA data (for Rab and Nov, who were observed both in and away from the provisioning area, we included only their non-PA data). Three infants were excluded from the weekly comparisons (Hbt and Nak were not observed during week one and Oys was eliminated due to uncertainty about the exact date of birth). Because the sample sizes vary for different analyses, we include a summary table of significant findings with associated sample sizes (see Table 5).

The Hinde Index (Hinde & Atkinson, 1970) was used to calculate who was responsible for maintaining proximity within each mother-infant dyad. The Hinde Index (HI) is determined by the proportion of approaches (A) and leaves (L) that are initiated by the mother (M) and infant (i) (HI = [Am/Am + Ai] − [Lm/Lm + Li].) The index ranges from − 1.0 when the infant is totally responsible for maintaining proximity, to + 1.0, when the mother is totally responsible for maintaining proximity. An index close to 0 would indicate equal responsibility. Approach/Leave data were collected continuously at the provisioning area for 5 infants, but were collected *ad libitum* away from the provisioning area (within focal samples). Only one non-provisioned infant (Mou) had enough non-PA approach/leave data (> 20 approaches and leaves) to include in the analysis.

Results

Description of physical characteristics

At birth, Shark Bay *Tursiops* have 5-7 distinctive fetal folds and white (non-pigmented) lines, called fetal lines, at each crease. Fetal folds, or lumpiness,

are pronounced during the first week after birth, but may not be detectable during the second week (Hbt, Nak, Rab). However, fetal lines, resulting from the folds, remain for many weeks. Their visibility can depend on lighting conditions, individual differences, and, perhaps, the health of the animal. For one infant, fetal lines remained visible through week 6, for another, through week 7, and for a third, through week 10. One small, emaciated infant who was eventually killed by a shark had very faint fetal lines visible until her death at 110 days of age (Mann & Barnett, 1999). In summary, fetal lines are clearly visible in month one, sometimes visible in month two, and barely or not visible in month three.

Newborn coloration varies. Some infants are born a very light grey, whereas others are nearly black in appearance. The underside tends to be white or slightly pink. The pink coloration typically disappears within a few months. Teeth erupt by the 10th or 11th week (Nak, Hbt), but may be present earlier. Rostral whiskers were visible for 3-4 days post-partum on two infants, but not thereafter.

Mother-infant behaviour in provisioning area

All of the provisioned mothers visited the PA within two days after giving birth. During their first two days in the PA, mothers swam rapidly in deeper water with the newborn, avoiding the line of people standing close to shore. The rangers kept tourists from touching the mother and calf or from venturing any deeper than approximately 2 ft of water. During feedings in the first few days after birth, rangers waded into deeper water and often tossed the fish to the mother rather than feeding by hand. Mothers with newborns were offered more than their 2 kg per day quota (up to 4 kg per day), but as of 1994, the practice of feeding extra to new mothers ceased. By the third day, mothers came closer to tourists and would take fish by hand while the newborn swam in circles a meter or two away. As soon as the feed was over, mothers and their calves left the PA (*ad libitum* notes).

Mothers typically kept themselves between the line of tourists and their newborns, sometimes rushing between them if the infant wandered too close. They appeared to be herding or steering their infants away from the beach and tourists. For example, on the first day that Nic brought Rab into the beach area, she herded him away from the people 6 times per hour. Mothers were not always effective, however. Several newborns (Rab, Nov, Pic, Pep,

Shd) temporarily beached themselves during the first few days of life, but were quickly moved back into the water by the rangers. One mother, (Puc) knocked a tourist down in an effort to herd her calf (Pic) away from the beach (*ad libitum* notes).

Newborns were never observed interacting directly with people, but their mothers occasionally did. During the first week, mothers rarely interacted with people outside of feedings, but during subsequent weeks, they occasionally did so (Wilcoxon matched pairs signed ranks: wk one *vs* later, $p < 0.07$). Some of their interactions were aggressive and involved hitting (with tails, flipper, or jaw) or threatening (head jerked at) people attempting to touch them. For example, the most aggressive mother engaged in at least 23 aggressive interactions in the PA over the course of two months (0.7 times per hour). Nine (39%) of those were clearly directed at humans. For all provisioned females pooled, the rate of aggressive behaviour was 0.26 times per hour (compared to 0.01 times per hr non-PA). When in the PA, mothers spent the greatest proportion of their time within 2 m of people ($49.9 \pm 24.6\%$; Table 3). Direct touching, feeding or interacting with humans occurred for a much smaller proportion of the time ($0.2 \pm 0.36\%$).

During the first week of infant life, provisioned mothers continued to chase and beg from incoming boats as their newborns followed. By the second week, the calves typically rested or floated a few meters away from the beach while their mothers stayed close to the people or begged from incoming boats. Mothers no longer herded their infants away from boats or people. The newborns now kept their distance (*ad libitum* notes).

The effects of provisioning on mother-infant behaviour and associations

Maternal behaviour at the provisioning area differed from that away from it in several respects (Table 3). Away from the PA, under natural conditions, mothers foraged and socialized more often than in the PA (permutation tests $p = 0.03$). In the PA, mothers spent roughly 50% of their time attending to people or boats at close range (< 2 m). Even away from the PA, provisioned mothers occasionally begged from boats, but we never observed non-provisioned mothers approaching boats. Travel data could not be compared because traveling mothers rapidly left the provisioning area.

For infants, the clearest behavioural differences between the PA and non-PA involved echelon swimming. Echelon swimming was common away

TABLE 3. *Differences in association and behaviour in non-provisioning and provisioning areas*

	Non-PA (N = 4)		PA (N = 7)		
	Mean	SD	Mean	SD	*p* =
Maternal behaviour					
Rest	48.52	7.78	46.78	23.76	0.45
Travel	19.17	7.95	n/a	n/a	–
Socialize	2.46	2.13	0.26	0.48	**0.03**
Forage	27.46	12.57	3.10	4.05	**0.03**
People/boats	2.39	3.58	49.87	24.59	**0.03**
Infant behaviour					
Rest	20.70	7.99	49.92	5.48	0.73
Travel	8.26	5.20	n/a	n/a	–
Socialize	7.95	4.19	15.32	20.90	0.77
Forage	0	0	0	0	–
People/boats	0	0	0	0	–
Echelon swim	52.10	17.50	27.42	18.72	**0.03**
Infant position swim	11.00	5.62	6.91	4.61	0.20
Mother-infant proximity					
< 2 m	88.73	8.33	78.51	11.70	**0.02**
2-10 m	7.49	4.31	17.84	11.85	**0.02**
> 10 m	2.07	1.99	3.64	3.62	0.19
Party composition					
Mother-Infant only	44.41	7.24	7.98	10.87	**0.03**
Female	45.82	5.92	80.13	17.07	**0.03**
Mixed	6.17	5.47	7.29	11.75	0.77
Mother, infant, immatures	1.51	1.19	0	0	–
Infant alone	1.36	1.08	0	0	–
Infant, ad. males	0.12	0.25	0	0	–
Infant, female	0.52	0.38	0	0	–
Infant, immatures	0.13	0.26	0	0	–
Party size					
1	0.88	1.17	0	0	–
2	45.99	8.46	7.98	10.87	**0.03**
3 to 5	25.97	11.81	39.21	14.22	0.10
6 to 8	18.88	13.86	49.34	17.53	**0.03**
9 to 12	5.13	4.48	3.47	4.51	0.93
> 13	2.10	2.15	0	0	**0.03**

All values represent % time engaged in the behaviour or in those types of groups.
– Too few data to run test.
Permutation tests are non-parametric to estimate probabilities of obtaining a particular distribution of ranks.

from the PA during the first two months of life (occupying on average 52.1% of the infant's time) but was not so prevalent in the provisioning area (x = 27.4%). Other infant behaviours did not differ significantly between the PA and non-PA.

Provisioning had obvious consequences for mother-infant proximity. Infants spent less time in close proximity (< 2 m) and more time further away (2-10 m) in the PA compared to non-PA (Table 3). In the provisioning area, mothers often stayed near the tourists standing in shallow water, while their infants circled several meters away in deeper water.

Differences in party composition must be considered in light of differences in definition of party composition in and away from the PA. In the PA, animals did not form tight, cohesive parties, thus we defined associates more broadly as including any animal observed within 200 m of the provisioning area. Based on these somewhat different criteria, associations between the mother-infant dyad and other dolphins differed in the two contexts. For example, mothers and infants were often alone when away from the PA (averaging 44.4% of the time), but infrequently so in the PA (averaging 8.0% of the time). Because feedings typically occurred in the morning, and the rangers waited until most of the regularly provisioned females showed up before feeding, all the provisioned females tended to show up around the same time, and all tended to leave right after the feeding. Thus, in the PA, 'female' parties (defined as mother, infant, and at least one adult female) were the norm (80.1% of the time, *vs* 45.9% of the time non-PA), and these parties often (45.9% of the time) included 6-8 individuals (3-4 provisioned mothers and their infants), whereas away from the provisioning area, parties of 6-8 occurred only 18.9% of the time. Very large groups (> 13 animals) were more common away from the provisioning area than in the provisioning area, despite the larger radius used to define party composition in the provisioning area.

The total number of associates differed significantly between the PA and non-PA (permutation test, p = 0.03). In the PA, infants had 7-19 associates in total during the first two months of life (N = 6), but away from the PA, infants had 29-37 in total (N = 4). Even though the provisioning data were collected over the course of four years, the same 24 individuals tended to visit the provisioning area, and they accounted for all associations in that area. During non-PA observations of newborns, however, we recorded 71 different associates over the course of two consecutive field season years.

Developmental changes

I. Locomotion, respiration and diving, and breathing synchrony
For the results described in this sub-section, only non-PA data were used with one exception. Exact respiration rates were observed for two mothers and their infants in the provisioning area.

Speed.   All infants were observed swimming rapidly (> 2 mph) with their mothers during the first two days after birth. By the third day, traveling was noticeably slower. From then on, infants and mothers tend to swim < 2 mph. Swimming speed (measured by the depth sounder log and parallel tracking) over the first eight weeks of life averaged 1.4 ± 0.15 mph for the four calves observed away from the provisioning area.

Respiration and diving.   During the first two days of life, newborns bobbed 'corklike' to the surface to breathe. By the third day, corklike surfacings were atypical, but still occurred (*ad libitum* notes). During the first 2-3 weeks of life, but rarely thereafter, newborns often surfaced with most of the torso clearing the water and with the jaw angled at roughly $30°$ or greater from the water surface; upon diving, the jaw slaps down against the water surface. In contrast, older infants and adults roll at the surface without bringing the jaw fully out of the water (*ad libitum* notes). We call these newborn surfacings 'chin-ups' to distinguish them from 'chin-slap' displays, which are more exaggerated, are not part of a breath series, and tend to appear in a social context.

The earliest dives were observed on days 5 and 7 (peduncle dives). No infants were observed doing tail-out dives before day 12. Most infants were not observed doing tail-out dives until the fifth week of life or later, even though their mothers were tail-out diving throughout the first month of infant life. One infant was never observed doing a tail-out dive. All infants did peduncle dives by the second week of life and regularly thereafter.

Not only are newborns buoyant, remaining at the surface more than their mothers, they also breathe more frequently. During deep water (> 5 m) non-PA observations of mothers and newborns (4 dyads), involving 930 surfacing bouts for mothers and 960 bouts for infants, $22.7 \pm 10.8\%$ of infant surfacing bouts were longer ($\geqslant 1$ s) than those of the mother, $70.0 \pm 10.72\%$ were of equivalent duration, and only $7.3 \pm 1.36\%$ were shorter. Infants surfaced and

TABLE 4. *Surfacing bouts*

	Mean (s)	SD
Mean surfacing bout duration		
Infant (all mos.)	35.29	40.23
Mother (all mos.)	33.31	39.70
Infant (mo. 1)	36.93	11.49
Mother (mo. 1)	34.70	14.10
Infant (mo. 2)	38.27	22.08
Mother (mo. 2)	36.92	21.57
% of surfacing bouts		
Infant = Mother (all mos.)	70.00	10.72
Infant > Mother (all mos.)	22.72	10.82
Infant < Mother (all mos.)	7.27	1.36
Infant = Mother (mo. 1)	69.56	11.71
Infant > Mother (mo. 1)	23.76	11.80
Infant < Mother (mo. 1)	6.67	2.24
Infant = Mother (mo. 2)	76.95	10.67
Infant > Mother (mo. 2)	10.46	12.12
Infant < Mother (mo. 2)	12.59	7.14

N = 960 infant bouts, 930 maternal bouts for 4 mother-infant pairs.
For 30 infant bouts, the infant surfaced and dove without overlapping with the mother.
Surfacing bout durations did not change significantly over time, but during month 1, infant bouts were longer than maternal bouts much more often than the reverse.
Mean interval between surfacing bouts (time submerged) = 65 s (SD = 30 s).

dove without their mothers on only 30 occasions. For all surfacing bouts of the same duration for mothers and infant, mother and infant surfaced and dove together, and only 3.1% of newborn surfacing bouts showed no overlap in time with the mother's time at the surface. No age changes were detectable in infant or maternal surfacing bout durations (Table 4). The mean interval between surfacing bouts was 65 ± 30 s, and the longest interval between surfacing bouts was 208 s. Breaths within a bout were typically 3-15 s apart.

Actual respiration rates were measured weekly for two infants (Rab, Nov) and their mothers during PA observations from birth to eight weeks of infant age (sampled for one 20 minute period each week for a total of 13 sampling sessions). Breaths were audible in air. For all sampling sessions (pooled data), newborns breathed more often than their mothers did (Wilcoxon matched pairs signed ranks: $p < 0.001$; each sample period is treated independently, N = 13). The average breath rate for infants was 3.8 ± 0.3 per minute; maternal breath rate was 2.6 ± 0.1 per minute.
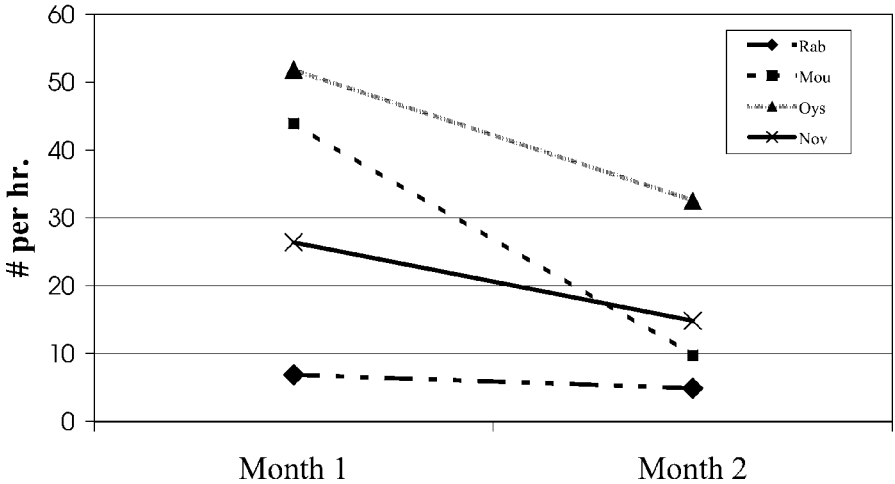
Mother-Infant Breathing Synchrony

Fig. 2.   This shows the rate of synchronous breaths between mothers and infants (N = 4 pairs). Each line represents one mother-infant pair observed away from the provisioning area. All dyads showed a decline in synchrony from month one to month two.

Breathing synchrony.   Exact breathing synchrony occurs when mother and infant break and/or submerge into the water in perfect unison — a more specific and fine-tuned measure than the comparisons of overlapping maternal and infant surfacing bouts, above. During synchronous breaths, the mother and infant are typically close (< 2 m), parallel or slightly staggered in position. All infants showed their highest rate of synchrony with the mother during the first week of observations (range = 9.0-54.1 times per hr). With breath rates of 3-4 times per minute, perfect synchrony occurred in 1/3 or fewer of all infant breaths. All four infants observed away from the PA showed a decline in breathing synchrony from month one to month two (Fig. 2). One infant (Rab) showed a very low rate of synchrony overall. His mother spent the most time foraging, a time when synchrony tends to be low.

II. Maternal and infant proximity and maintenance
PA and non-PA data were combined to examine developmental changes in mother-infant proximity. As expected, from week one to later, and from month one to month two, the proportion of time infants spent at close distances to their mothers gradually decreased and the proportion of time

TABLE 5. *Summary of findings*

Behaviour	Non-provisioned & provisioned combined		Provisioned only	
	Wk 1 *vs* Wks later	Mo 1 *vs* Mo 2	Wk 1 *vs* Wks later	Mo 1 *vs* Mo 2
Mother-infant proximity (% time)	(N = 6)	(N = 9)	(N = 5)	(N = 7)
≤ 30 cm	>[*]	>[*]	>[†]	>[*]
< 2 m	>[*]	>[*]	>[†]	>[*]
2-10 m	<[*]	<[*]	<[†]	<[*]
> 10 m	<[*]	<[*]	<[†]	<[*]
Separations				
Rate (# per hour)	<[*]	<[*](N = 7)	<[†]	<[*]
Mean bout duration	na	<[*](N = 7)	na	na
Infant behaviour				
Echelon	>[*]	>[*](N = 7)	>[†]	>[†](N = 5)
Infant position	<[*]	<[*](N = 7)	<[†]	NS
Social	<[*]	<[*](N = 7)	<[†]	<[*](N = 6)

[*] = $p < 0.05$, [†] = $p < 0.10$, NS = not significant; na = not applicable because no tests were done. We report significance levels of $p < 0.10$ because, due to small sample sizes, for some analyses 0.06 was the highest possible significance-level obtainable. All tests were Wilcoxon-matched pairs signed ranks test; '<' indicates direction of change from week 1 to weeks later or month 1 to month 2. Some infants were excluded because (a) they were not observed during the first week of life; or (b) relevant data were not systematically collected.

they spent at far distances gradually increased (Table 5). More specifically, the time spent next to the mother (≤ 30 cm) (Wilcoxon matched pairs signed ranks test, wk one *vs* later, $p < 0.04$; mo one *vs* mo two, $p < 0.005$) and the time spent at close distances from the mother (≤ 2 m) (Wilcoxon matched pairs signed ranks test, one wk *vs* later, $p < 0.04$; mo one *vs* mo two, $p < 0.005$) decreased over time. In complementary fashion, the time spent at moderate distances from the mother (> 2 m but ≤ 10 m) (Wilcoxon matched pairs signed ranks test, wk one *vs* later, $p < 0.04$; mo one *vs* mo two, $p < 0.005$) and the time spent at far distances from her (> 10 m) (Wilcoxon matched pairs signed ranks test, one wk *vs* later, $p < 0.04$; mo one *vs* mo two, $p < 0.005$) increased over time.

Proximity maintenance and the Hinde index. The mean rate of mother-infant separation (> 2 m apart) was significantly higher in the provisioning

area (14.3 ± 4.4 times per hr, range = 7.9-19.5) compared to the rate of separation away from the provisioning area (3.18 ± 1.22 times per hr, range = 2.21-4.91 times per hr, permutation test, $p < 0.03$). All infants observed in the PA had a higher rate of separation than all infants observed away from the PA.

The identity of who approached or left the other member of the pair was consistently scored during PA observations, but could only be recorded *ad libitum* during non-PA observations. For the two infants observed in both contexts, we combined their approaches and leaves. Infants rarely separated from their mothers during the first week of life, and two of five infants observed during the first week did not separate from their mothers at all during that time. By the second week, all infants separated from their mothers for brief periods (Mann & Smuts, 1998). Only one mother was observed leaving her infant during the first two weeks of life.

Infants were responsible for the majority of approaches (80.24%, range = 58.7-89.7%) and almost all leaves (96.5%, range = 93.4-100%). However, because the Hinde Index was positive (the proportion of approaches by the mother was greater than the proportion of leaves by the mother), mothers were technically more responsible than their newborns for maintaining proximity within the pair. The Hinde Index declined significantly from month one (0.28 ± 0.15) to month two (0.11 ± 0.09) (Wilcoxon matched pairs signed ranks test, $p = 0.03$), indicating that maternal responsibility for proximity decreased over time.

Separations from the mother. Away from the provisioning area, newborns spent an average of 8.14 ± 4.40% of their time separated (> 2 m) from the mother (range = 2.19-12.38). Infants were observed traveling to up to 100 m away from their mothers. At the provisioning area, infants were observed going even further, up to 200 m away. During the majority of non-PA separations, infants were alone (66.81 ± 17.58%, range = 47.54-83.33). Patterns of association during separations are examined in detail elsewhere (Mann & Smuts, 1998).

All four infants observed away from the PA spent more time separated from their mothers during month two (24.73 ± 12.97%, range = 6.12-35.99) compared to month one (2.50 ± 2.87%, range = 0.29-6.59). When the PA data are included, this pattern is significant (Wilcoxon matched pairs signed ranks test, $p < 0.04$, $N = 9$). Similarly, the rate of separation increased for

all infants from month one (non-PA 1.95± 1.72 per hour, range = 0.38-2.22) to month two (non-PA 7.78 ± 2.26 per hour, range = 5.81-10.91; Wilcoxon matched pairs signed ranks test, $p < 0.02, N = 7$). The mean bout durations of the separations increased as well from month one (38 ± 13 s, range = 2-307 s) to month two (133 ± 68 s, range = 2-1058 s, $N = 4$). If mean bout durations of separations are estimated for PA infants based upon the number of point sample intervals between approaches and leaves, then the combined data reach statistical significance (Wilcoxon matched pairs signed ranks test, $p < 0.02, N = 7$). In sum, as infants grew older, they were separated from their mothers more often and for longer periods of time.

III. Infant activity

Infant activities were collapsed into five main behavioural states: echelon swimming, infant position swimming, resting, traveling, and socializing. Infants did not forage (but see description of 'play snacking' below). Infants did not initiate or interact with people at the provisioning area until three or four months of age (unpublished data). Other infant activities were brief and are described as 'infant behaviours' (see below).

Echelon position.   All newborns decreased the time spent echelon swimming between wk one and later (Wilcoxon matched pairs signed ranks test, $p < 0.04, N = 6$), and between month one and month two (Wilcoxon matched pairs signed ranks test, $p < 0.02, N = 7$). During the first month, infants spent most of their time echelon swimming (69.3 ± 20.8%, range = 49.3-98.5%), but by the second month, this behaviour had decreased dramatically (10.6 ± 11.4%, range = 0-24.0).

Infants spent much less time swimming in echelon when close to people ($\leqslant 2$ m away) than when further from them (Wilcoxon matched pairs signed ranks test, $p < 0.04, N = 6$). Thus, the differences between animals within and away from the PA in time spent echelon swimming (see Table 3) may be attributable to the dyad's proximity to people.

Infant position.   During the first week of life, infant position was rare. The three infants observed away from the PA during the first week of life (Nov, Rab, Mou), were all observed in infant position, but never for longer than 74 s, and more typically for less than 30 s. Typically, the infant stayed in infant position long enough to nurse for several bouts (often nursing several

seconds on one side and then on the other). Of the 19 bouts of infant position observed in the first week, nursing (defined as infant rostrum to mother's mammary slit) definitely occurred during 17 bouts; during the other two cases, we were not close enough to document nursing or its absence. By the second week, infant position bout length increased and the infant remained there when not nursing, often for several minutes at a time (mean bout duration $= 61 \pm 72$ s, range $= 2\text{-}411$ s, $N = 60$ bouts, nursing observed in 9 bouts).

At the provisioning site, we did not see Rab and Nov in infant position until days nine and ten respectively despite intensive observations during that period, whereas several brief bouts of infant position were observed away from the provisioning area on days one and two. Most of the newborns who were observed only in the provisioning area spent very little or no time in infant position. Thus, none of the age changes for time spent in infant position were statistically significant at the provisioning area. However, when the time spent in infant position was examined as a function of location with in the provisioning area, and each sample week was treated separately, infants spent much less time in infant position when near people ($\leqslant 2$ m) than when further away (Wilcoxon matched pairs signed ranks test, $p < 0.04$, $N = 6$). In shallow water, infants cannot stay under their mothers, and it sometimes appeared as if mothers used the shallows to prevent their infants from gaining infant position contact.

Away from the provisioning area, age changes were more evident. During the first month of life, the four infants spent an average of $7.66 \pm 7.14\%$ of the time in infant position (range $= 0\text{-}13.6$), but by month two, they spent an average $18.0 \pm 6.07\%$ of the time in infant position (range $= 12.0\text{-}24.3$), twice as much time as spent in echelon position. When these data are combined with the PA data, newborns showed a significant increase in time spent in infant position from month one to 2 (Wilcoxon matched pairs signed ranks test, $p < 0.04$, $N = 7$).

Resting and floating. Resting is characterized by slow movement and occasional floating or hanging at the surface. During the first week, infants were not seen to stop moving for more than a few seconds, but older newborns often floated in place for up to several minutes. After the first week, infants in the provisioning area floated much more ($4.2 \pm 6.1\%$ of the time) than outside of the provisioning area ($0.1 \pm 0.22\%$), even though

time resting overall did not differ (Table 3). Away from the provisioning area, infants engaged in floating bouts at the rate of 0.3 per hour; these bouts were typically short, averaging only 8 ± 6 s (range = 2-28). Floating bouts were not timed in the provisioning area.

Traveling. During the majority of the mother's traveling, the infant swam with her in either echelon or infant position. We defined infant traveling as movement > 2 mph in a particular direction when not in echelon or infant position. Away from the provisioning area, all four infants increased the time they spent traveling from month one ($6.23 \pm 5.21\%$, range = 0-12.7%) to month two ($13.5 \pm 4.62\%$, range = 8.0-17.6%).

Socializing. The percentage of time that non-PA infants spent socializing increased from month one ($2.06 \pm 0.78\%$, range = 1.5-3.17) to month two ($26.4 \pm 20.1\%$, range = 6.76-47.73). With the PA data added, this pattern was significant (Wilcoxon matched pairs signed ranks test, $N = 7, p < 0.04$). Note that our method (predominant activity sampling during a 5-minute interval) is likely to underestimate the amount of time spent socializing because social bouts tended to be of short duration. Below, we include more detailed descriptions of social interactions.

IV. Infant behaviours
Rubbing and petting. Rubbing was the most common form of newborn socializing, beginning in the first days of life with the mother. Infants initiated virtually all (99.9%) rubbing interactions with their mothers. Typically, newborns rubbed their lateral side or full body on the mother's jaw or rostrum, sometimes near the melon or eye. Of 1,311 mother-infant rubbings observed during the first eight weeks of life (PA and non-PA), 48.0% focused on the mother's head area. The second most favored body part was the mother's lateral side (26.2% of all rubbings). Otherwise, newborns rubbed on their mothers' dorsal side (15.0%), or ventrum (10.2%), but rarely in her tail region (0.7%). A specific type of rubbing called a keel-rub, which is common between adult females and males, involves the actor (usually female) swimming belly-up under the recipient (usually male), and rubbing the base of the tail flukes vigorously across the recipient's chest or between the pectoral fins. Two newborn females were observed 'keel-rubbing' with older females on a

total of 5 occasions, but newborn males were never observed keel-rubbing. Newborns were never seen to rub or pet with subadult or adult males.

Sociosexual rubbing (rubbing involving the infant's genital area) is easier to detect among males than females because of the visibility of erections. Males were involved in sociosexual rubbing within the first two weeks of life. Rab's erection was first seen on day 9, and he rubbed his penis on his mother's dorsal side and peduncle multiple times on day 11. On day 17, he rubbed his penis on her peduncle, dorsal side and dorsal fin. Oys mounted his mother during the second month. Shd, Nak, and Pep were all observed rubbing their penises on their mothers during the first two months of life (*ad libitum* and focal observations). Older female infants have been observed rubbing their genital area on others, but we did not observe this behaviour among newborn females.

Petting occurs when the pectoral fin of the 'petter' is actively moving up and down on the body parts of another animal. This was seen only 26 times among newborns. In 22 of the 26 cases, the infant received petting; newborns played the active 'petter' role on only four occasions. Two cases involved the male infant Rab, who pet his mother twice on her blowhole area and melon on day 17 (earliest newborn petting observation). The other two instances involved the female, Nov, who pet an adult female on days 51 and 52.

Bonding.   During 'bonding', the 'bonder' swims alongside the 'bondee' but shifted back a little, so that the bonder's pectoral fin can rest on the bondee's posterior flank. Bonding is similar to echelon swimming, except that during echelon swimming, animals may or may not be in contact, and the infant's pectoral fin is placed either beneath the dorsal fin of the mother, or on the anterior flank of the mother. Bonding is a highly distinctive behaviour that occurs between two females, at least one of whom is typically cycling, in the presence of adult or subadult males (Richards, 1996). Although newborns occasionally swam echelon with other animals, only one clear case of bonding was observed. Nov, when 52 days old, swam 'bonded' to her 11 year-old sister Joy for approximately 7 minutes. During this time, Joy was being pursued by three subadult males, who displayed, mounted, goosed and swam in formation behind her. The mother of Joy and Nov was 20-50 m away throughout.

Social play.   Play is difficult to define in any species (Fagen 1981). We coded infant activity as play when the infant was involved in reciprocal chasing and/or displaying with another dolphin (Table 2). Social play was infrequent, so we describe the types of play and when they first occurred. Play was first observed at the end of the first week, but it was not common until after the third week. As early as the first month, reciprocal chasing occasionally involved objects. For example, when Rab was 4 weeks old, he and Sur (then a subadult female) played with the same piece of seagrass. Rab had the seagrass, Sur stole it and Rab chased her, snapping at the seagrass, but did not succeed in retrieving it. A week later, Rab and a one-year old male chased each other, each carrying seagrass in their mouths. Seagrass play continued to occur during the second month.

By the second month of life, nearly all newborns were involved in reciprocal chasing. At 6 weeks, Nov frequently played chase with an older male infant, her nephew. Pic and Shd chased one another during the second month of life, as did Oys and Mou. Infants appeared to 'invite' a chase by swimming past the target animal onside or belly-up, and veering away just as they reach the potential playmate. Mothers occasionally chased their infants and then would turn away, apparently 'allowing' their infants to chase them.

Displays infrequently occurred. We describe their first occurrences and the types of displays observed. Initially, infants sometimes engaged in displays without any clear social context, but by the third week, displays typically occurred during social interaction. Some displays occurred as early as the end of the first week of life. For example, Rab was first observed doing a 'face slap' (slapping the side of his face on the water surface) alone on day 6. By Day 18, Rab expanded his repertoire, doing spy hops, chin slaps, back slaps, and belly slaps. Shd began displaying spy hops and swimming belly-up in pursuit of playmates in his third week.

Displays that we interpret as aggressive among adults, jaw claps and head jerks (Table 2), were rare in the newborn period, but did occur during the 3rd and 4th weeks of life. Mou jaw clapped in week 3 and Rab clapped his jaw and jerked his head multiple times during the 4th week of life. All of the jaw claps and head jerks observed occurred when the infant was alone (> 10 m from others).

Play forage and object play.   Older infants (> 3 months) frequently engage in what we call 'snack' foraging, which involves chasing small fish belly-up

and trapping them at the water surface. The fish are often visible, jumping at the surface or causing small ripples in the water. Most infant foraging is of this type. We have not observed newborns catching fish, but behaviours that mimic snack foraging, which we term 'play snacking', were seen as early as the third week of life. Infants sometimes snapped at weed or repeatedly jaw clapped at the surface. Rab was the most precocious in this regard. For example, on days 21 & 22, Rab was observed swimming belly-up and snapping his jaw, as if snacking. On day 23, Rabble chased seagrass (*Amphibolis antarctica*) belly up and snapped at it as older calves do with fish. He would let the seagrass go, swim away, and then again chase after it belly-up, snapping at the same piece. Three calves were observed play snacking at 7 weeks of age (Nak, Hbt, Nov), but not earlier. Oys was never observed play snacking. Play snacking was not recorded for the other calves.

Object play was not common but was seen occasionally (*ad libitum*). Seagrass weed (*Amphibolis antarctica*) was the most common object used. Seagrass play occurred both alone and with partners. Rab carried seagrass around for long periods on day 18. On day 22, Rab again swam rapidly around with weed in his mouth. As mentioned above, seagrass can stand in for fish during play snacking. On day 22, Rab chased and 'goosed' a cormorant with his rostrum several times.

V. Maternal activity and behaviour

Outside of and in the provisioning area, maternal behaviours showed no significant changes from month one to month two. Thus, only overall patterns (months one and two combined) are summarized here (Table 3). Outside of the PA, mothers spent most of their time resting (48.5 ± 7.8%, range = 40.3-59.0) or foraging (27.5± 12.6%, range = 13.36-40.8). Resting included bouts of floating at the surface, and, although mothers floated much more often than their infants (2.5 bouts per hour *vs* 0.3 infant bouts per hour), it still made up a very small proportion of their time (0.74 ± 0.21%). The mean duration for all maternal floating bouts was 10 ± 10 s (range = 2-70). Traveling was the next most prevalent activity (19.2 ± 8.0%, range = 13.0-30.69). The two provisioned females begged from boats away from the provisioning area (1.99% and 7.6% of the time respectively). Mothers socialized an average of 2.4 ± 3.6% of the time (range = 0.36-5.43), much less than their infants. The proportion of time spent socializing is likely to be slightly underestimated by PAS sampling because bouts of social behaviour tend to be short.

Nursing.   The infant was considered to be nursing if the beak was in contact with one of the mother's mammary slits. We cannot reliably record every instance of nursing, nor estimate milk intake, but we often saw nursing during non-PA follows (see previous section on infant position swimming). In the provisioning area, calves apparently attempted to get into infant position by bumping or pushing under the mother, often accompanied by loud whistling (audible in air), but we did not see them nurse until after they left the shore area. Since visibility was better in the provisioning area than away from it, the absence of nursing in the provisioning area probably indicates that mothers did not allow infants to nurse or remain in infant position near people.

All newborns except for the two who were videotaped (Nak, Hbt) were observed nursing. During the first two months of life, all but three of the 58 observed nursing bouts involved the infant going belly-up or onside while the mother remained stationary or moved very slowly. Only one mother was observed turning on her side to let the infant nurse (3 nursing bouts). Infant 'beak to mammary slit' times ranged between 3-10 s, similar to values reported in captivity (*e.g.* Reid *et al.*, 1995).

Associations with others

As described earlier, dolphins did not form 'parties' near the provisioning area the way they did outside of it, and patterns of association differed dramatically between the PA and non-PA contexts. Here, we describe further the association patterns of the four newborns observed away from the provisioning area. The mean non-PA party size was 4 ± 2.8 (range 3-5, Table 3); thus, on average, mothers and infants were accompanied by two others. The minimum party size was one animal (infant alone), and the maximum was 14 animals. Large parties tended to be mixed, with both adult females and adult males present. Party size did not change from month one to two.

The most common, or modal party size was two animals, mother and infant. Thus, mother/infant pairs were more likely to be alone than with anyone else. Mothers and infants were alone together an average of $44 \pm 7.24\%$ of the time. Otherwise, they were usually in a 'female' group, defined as a party with at least one other adult female and no adult males ($45.8 \pm 5.92\%$). Mother/infant pairs were in mixed groups (groups containing

at least one other adult female and one adult male) an average of 6.17 ± 5.47% of the time (Table 3). Mothers and infants were never in parties with adult males only, but one infant associated with adult males away from his mother. Interactions between males and infants rarely occurred, but affiliative behaviours (petting and rubbing) between adult males and mothers occurred on several occasions (see Mann & Smuts, 1998, for more detailed analyses of patterns of association and allomaternal care over the newborn period).

Summary of developmental changes

Since we have described developmental changes for each behaviour separately, we conclude this section with a brief summary that provides a more integrated picture of developmental trends.

Virtually all patterns of infant behaviour, mother-infant proximity, and spatial relationships with the mother changed as a function of infant age. Maternal activity, however, did not change over time, except that mothers decreased their role in maintaining proximity to their infants from the first month to the second month of infant life.

Fetal folds (lumpiness) distinguished infants in the first week of life. During this time, infants swam rapidly and almost exclusively in echelon position. The infant adopted infant position only briefly, presumably just to nurse. Surfacings were 'corklike' and chin-up surfacings were common, as were synchronous breaths between mother and infant. Infants rarely remained still at the surface. Although week-old infants engaged in little social behaviour, they frequently rubbed on their mothers, especially around the head area. Rubbing continued to be the most common form of social activity for infants during the newborn period.

During the second week of life, the mother tolerated further and longer separations, and separations occurred more often. Infants engaged in prolonged (up to several minutes) bouts of socializing (either rubbing with their mothers, or turn-taking chase games with others). Synchronous breaths with the mother declined, but the overwhelming majority of mother-infant surfacings overlapped. Infants began to dive (peduncle and tail-out dives) and remained in infant position for several minutes (outside of the nursing context). They also began to float at the surface for several seconds at a time.

The frequency of separation from the mother, playing, and displaying all increased during the third and fourth weeks. Also, infants began to

pet with others, although this behaviour was not common any time in the first 10 weeks. Infants occasionally carried or played with objects such as seagrass. During the fourth week infants engaged in reciprocal chase games, occasionally involving objects. We first observed play snacking (practice foraging) during the fourth week, but it was not common at this age.

During the second month, fetal lines remained visible. Infants typically swam in infant position, and echelon position became uncommon. Infants sometimes spent 10 minutes or more over 20 m from their mothers, and the degree of coordination and synchronization between mother and infant declined relative to the first month. Play involving turn-taking and displays increased. Most infants engaged in play snacking by the end of this period.

Discussion

Young dolphins undergo dramatic developmental changes during the new-born period, with significant changes in proximity to the mother and activity over time. In contrast, maternal activity budgets changed little over the new-born period. These behavioral patterns are discussed in relation to (a) the effects of provisioning; (b) comparisons between captive and wild newborn dolphin behaviour; and (c) the life-history and ecology of delphinids and other cetaceans.

The effects of provisioning

Because over half of the observations reported here come from semi-provisioned dolphins, it is important to address the effects of provisioning and its implications of provisioning for ethological research. As the popular-ity of eco-tourism increases, so do the economic incentives of making large, social animals available for close viewing. Provisioning can often facilitate this process, and it too, is likely to become increasingly common. Because provisioned animals are easier to find and observe, researchers sometimes find them ideal subjects. The reverse situation also occurs when ethologists initiate provisioning to make observations easier and tourism develops later (*e.g. Pan troglodytes*, chimpanzees — Goodall, 1986; *Pan paniscus*, bonobos — Kano, 1982). Similarly, the success of tourism at Monkey Mia has been cited in support of the development of tourist oriented-dolphin provision-ing elsewhere in Australia and North America (Orams *et al.*, 1996; National

Marine Fisheries Service [US], 1994). Thus, increasingly, research on animals like dolphins and primates may involve subjects who are artificially provisioned and/or who have extensive contact with tourists (*e.g.* bottlenose dolphins — Orams *et al.*, 1996; bonobos — Kano, 1982; *Macaca* sp. — Oleary & Fa, 1993; Hill, 1994). These trends make research on the effects of provisioning on behaviour *and* the animals' well-being (*e.g.* health, mortality, stress) essential for those 'managing' artificial feeding and tourism, for those interested in conservation and well-being of wild populations, and for researchers interested in documenting natural behaviour and how it is affected by human intervention of this type.

Artificial provisioning of wild mammals in Shark Bay and elsewhere can facilitate research, but it also inflicts costs. The benefits include increased access to animals that are otherwise difficult to study (Connor & Smolker, 1985; Wrangham, 1974). For example, in the absence of the provisioning area, comparable data on newborns would have taken many years to obtain. The costs include distortions in behaviour and life histories (*e.g. Cercopithecus aethiops*, vervets: Lee *et al.*, 1986; *Macaca fuscata*, Japanese macaques: Sugiyama & Ohsawa, 1982; *Papio cynocephalus*, savanna baboons: Altmann & Muruthi, 1988). For example, female aggression was observed only once during 79 hours of non-PA observations of newborns, but occurred often (0.26 times per hour) in the provisioning area. For two reasons, we conclude that provisioning triggered aggression: (1) Since aggressive behaviours are fairly obvious, even away from the PA, it is unlikely that the higher rates of aggression in the provisioning area are solely attributable to the superior observation conditions there, and (2) Artificial feeding is associated with increased aggression among primates (*e.g.* Loy, 1970; Wrangham, 1974; Oleary & Fa, 1993) and other mammals (*Ursus* sp.: Herrero, 1985; bottlenose dolphins — Orams *et al.*, 1996;).

Although we were struck by how similarly provisioned females and non-provisioned females behaved when outside of the PA (*i.e.* the two provisioned female-infant pairs observed away from the PA never both ranked below or above non-provisioned female-infants pairs on any characteristic except for boat-begging and synchrony), provisioned females spent several hours per day near human activity, which altered activity budgets, association patterns, and maternal behaviour for substantial portions of the day. Data from Shark Bay indicate that calves of provisioned females experience greater mortality than calves of non-provisioned females

(Mann *et al.*, in press). While the exact causes of this difference remain a mystery, behavioural differences between provisioned and non-provisioned mother/newborn pairs may play a role. In the PA, mothers focused on humans, were less likely to forage or socialize, and had available only a limited number of potential social partners, compared to outside of the PA. Infants, in turn experienced reduced opportunities to be in contact with the mother, an increased frequency of separations from the mother, and reduced numbers of associates, compared to away from the PA. In the provisioning area, infants also incurred increased risks of becoming beached or entangled in fishing lines (Mann *et al.*, 1995). Increased proximity to fast moving boats may also be hazardous (Wells & Scott, 1997), but no infants have yet been harmed this way.

Although provisioning clearly influenced the frequencies of different behaviours, the order in which new behaviours appeared and the direction of developmental changes in infant behaviour were very similar within and outside of the provisioning area (see Table 5). For example, although infants separated more often from their mothers in the provisioning area than when outside of the provisioning area, the rate of separation increased in both contexts as infants aged.

Boat follows may also influence dolphin behavior. Janik & Thompson (1996) found that bottlenose dolphins in the Moray Firth, Scotland, dove for longer periods when being followed by a large tour boat than when boats were just passing by. In Shark Bay, the fact that dolphins regularly engage in intimate behaviors such as nursing, petting, and sexual interactions near our boats, but not near the people at the provisioning area suggests to us that the dolphins are well habituated to our boats. Calf mortality for focal animals (who were followed in boats) does not differ from mortality for non-focal calves who were only surveyed (unpubl. data). However, the effects of boat follows on dolphin behavior, their predators or prey, have not been systematically examined in Shark Bay.

Below we discuss major developmental trends documented in our study and compare them, when possible, with captive data. These comparisons are useful for managing captive dolphins, particularly during the vulnerable newborn period, and determining the external validity of captive studies.

Breathing synchrony, locomotor coordination, and mother-infant contact

The early breathing patterns of Shark Bay mothers and calves resemble those reported by for captive Indian Ocean *Tursiops* (Peddemors, 1990; Kastelein

et al., 1990). For example, mean breathing rates documented for two calves in the provisioning area were similar to those reported by Kastelein *et al.* (1990). However, maximum breathing intervals were much greater for Shark Bay newborns than for captive newborns (Peddemors, 1990), possibly because wild infants sometimes dove to greater depths than is possible in a tank. Alternatively, Peddemors recorded breathing rates during rest only, whereas the Shark Bay breathing data were derived from all behavioural states of mother and calf. With different behavioural definitions of rest, we cannot make direct comparisons.

Peddemors (1990) found that 90% of mother-calf respirations were synchronous, a much higher figure than we reported. However, this difference is likely attributable to differences in how synchrony was defined: it is unclear whether Peddemores' definition of synchrony refers to exact synchrony, overlapping breaths, or overlapping time at the surface during surfacing bouts. In Shark Bay, most (70%) of mother and infant surfacing bouts were the same length (70%), indicating a high degree of coordinated breathing, and 97% of infant surfacing bouts overlapped with those of the mother. These values did not change significantly from the first to second month of life, but the frequency with which mother and calf surfaced in exact unison did decline as the calf aged. Peddemors (1990) also reported that breathing synchrony declined over time, with most of the decline occurring after 60 days of calf age, beyond the newborn period of the current study.

During the first month of life, but not the second, a significant minority (about one-quarter) infant surfacing bouts were longer than those of the mother outside of the provisioning area, indicating that newborns may take more breaths than their mothers. This was the case during the first two months of life for two mother/infant pairs whose breathing rates were precisely documented in the provisioning area. Similarly, in sperm whales, *Physeter macrocephalus*, a species that dives deeply, immatures breathe more often than adults (Whitehead, 1996).

Motor patterns of surfacing and diving seem to be similar in the wild and in captivity. Wild newborns rarely showed the 'chin-up' surfacing pattern after week three; Peddemors, similarly, reported that "by the 25th day post partum the calves had all acquired the smooth roll which characterizes respiratory surfacing of the adult" (1990, p. 179). Thus, observations of the chin-up surfacing pattern may prove useful in estimating the ages of young calves in the wild.

Wild infants appeared to find diving difficult at first, but two infants were seen peduncle diving at the end of the first week, and all calves did so by the second week. Similarly, in captivity, infants can dive by the 6th day of life (Eastcott & Dickinson, 1987). (Determination of dives in their study was based on underwater observations of infant swimming near the bottom of the tank.) Most Shark Bay infants did not perform tail-out dives, which are typically deeper than peduncle dives, until after week five. The increase in time spent in infant position swimming during week two appeared to depend on the development of skillful swimming and diving, such that the infant could more easily remain beneath the mother.

Although dolphin calves clearly exhibit motoric precociousness, compared to, for example, nonhuman primates or terrestrial carnivores, several observations indicate that motor coordination improves with age. First, the decline in chin-up surfacings over the first few weeks corresponds with the development of epaxio-musculature (see Cockcroft & Ross, 1990) that enables the infant to smoothly break and re-enter the water surface. Second, the infant's increasing ability to remain in infant position, to dive to deeper depths, and to float relatively motionless at the surface suggest steady improvements in physical and respiratory competence. Third, most infants of provisioned females became beached accidentally during the first week, but none did so after this time. Fourth, the increasing distances and durations of separations from the mother exemplify the infant's growing competence in negotiating the marine environment and finding the mother rapidly. Fifth, the declining breathing synchrony (Fig. 2) between mother and infant may reflect the fact that the infant has achieved respiration/diving competence sufficient to guide its own surfacing and diving patterns, independent of the mother.

Several studies of captive *Tursiops* have described developmental shifts in patterns of mother-infant contact. During the first weeks of life, infants tended to swim in echelon formation (also called contact swimming) (*e.g.* Tavolga & Essapian, 1957; Chirighin, 1987; Eastcott & Dickinson, 1987; Reiss, 1988; Cockcroft & Ross, 1990; Reid *et al.*, 1995). In captive studies and our field study, echelon swimming declined rapidly in the first few weeks of life, but for some infants, continued into the second month of life.

Echelon swimming may benefit the infant by aiding in swimming. When in echelon position, the infant is essentially led alongside the mother and thus reaches the surface to breathe around the same time she does. Almost

certainly, this helps the newborn coordinate movements, breathing, and diving patterns with the mother. In contrast, when in infant position, the infant must briefly break the position to surface alongside of the mother to synchronize breaths. Norris & Prescott (1961) proposed that echelon swimming gives infants a hydrodynamic boost, but this hypothesis has not been tested.

In both captivity (Tavolga & Essapian, 1957; Cockcroft & Ross, 1990; Reid *et al.*, 1995) and in the wild, infants gradually spend less time in echelon position and more time in infant position, in contact under the mother's abdomen, where nursing takes place. This early shift from the mother's head area to the abdomen reflects the changing abilities of the newborn, who must first be able to stay with her, and learn how to use and respond to sound. Once motor ability has improved, the calf switches to infant position. After the newborn period, Shark Bay infants maintained infant position roughly 30-40% of the time until weaning (Mann, 1997). In terms of coordination or effort, infant position may be more challenging than echelon swimming, but it provides easy access to the mammary slits and the tactile stimulation may enhance milk production. Little is known about the possible hydrodynamic benefits of infant position swimming or the energetic costs this position may carry for the mother.

Fast-swimming is characteristic of newborn dolphins and their mothers during the first two weeks, both in this sample and in captivity (Tavolga & Essapian, 1957; Amundin, 1986; Eastcott & Dickinson, 1987). Right whale (*Eubalaena australis*) calves studied in the wild also go through a period of fast-swimming soon after birth (Thomas & Taber, 1984). Thomas & Taber (1984) propose that rapid swimming is an anti-predation strategy that also helps the calf stay buoyant to breathe.

Shark Bay newborns performed the majority of approaches and leaves that occurred between mother and infant, but, since their mothers were typically more likely to approach than to leave them, mothers were more responsible than were infants for maintaining proximity. Consistent with studies of proximity maintenance in captive Tursiops (Chirighin, 1987; Reid *et al.*, 1995) and free-ranging right whales (Taber & Thomas, 1982), we found a decline over time in the mother's responsibility for maintaining proximity to her infant.

Maternal behaviour

Some maternal behaviours reported in captivity or elsewhere in the wild have not been seen in Shark Bay. These include calf tossing/lifting, calf pinning, and maternal ventral present during nursing. We discuss each in turn.

In the wild (dos Santos & Lacerda, 1987; Shane, 1990) and in captivity (Caldwell & Caldwell, 1972; Thurman & Williams, 1986; Cockcroft & Ross, 1990) mothers (or presumed mothers) have been seen lifting or propelling their infants clear out of the water. This 'calf tossing' behaviour is distinct from supporting behaviour, in which another animal gently pushes a calf to the surface. We never observed calf tossing, but once a mother briefly swam belly-up at the surface with her calf between her pectoral fins. Cockcroft & Ross (1990) interpreted similar behaviour in captive dolphins as maternal discipline.

Captive studies have yielded several reports of mothers pinning young infants to the bottom; these were interpreted as cases of maternal punishment or aggression (*e.g.* Tavolga, 1966; Caldwell & Caldwell, 1972; Thurman & Williams, 1986; Cockcroft & Ross, 1990). Marine trainers have also observed this behaviour soon after parturition (Amundin *et al.*, 1989; N. Hecker, pers. comm.). Although in Shark Bay we can often see clear to the bottom, we have observed calf-pinning only once when, following a shark attack, a mother pushed her dead offspring to the seafloor and held her there (Mann & Barnett, 1999). This occasion was of particular interest because the mother supported her dead calf for roughly half an hour before she pinned her. It is possible that pinning is an attempt to revive, not punish, the infant, and its physiological underpinnings should be investigated (Amundin *et al.*, 1989).

Early nursing behaviour in captivity is characterized by the mother turning on her side while the infant nurses (Essapian, 1953; Caldwell & Caldwell, 1972; Cockcroft & Ross, 1990). For example, Cockcroft & Ross (1990) report that all suckling during the first 4 weeks occurred in that fashion. During the second month, the infant turns on her side and the mother remains upright. We observed 58 nursing bouts during the first weeks of life, and only one mother showed this pattern three times. In general, from birth on, the infant, not the mother, turned on his/her side to nurse. It is possible that the different subspecies of *Tursiops* studied in captivity and in Shark Bay show different nursing styles.

Developmental trends and milestones

In aquaria, bottlenose dolphin calves typically take fish between 6-12 mos. (Essapian, 1953; Caldwell & Caldwell, 1972; Amundin, 1986; Chirighin, 1987; Cockcroft & Ross, 1990). In our study, infants did not catch small fish until they were between 4-6 months old. Prior to this time, infants 'practice' forage. The onset of regular practice foraging during the second month coincides with the timing of the apparent development of echolocation skills among captive newborns (Reiss, 1988). The distinctive belly-up 'snacking' that Shark Bay infants engage in may enhance sensory integration of visual and echolocation skills because infants can visually track the backlit fish (or seagrass) at the surface, while receiving acoustic information on the stimulus.

Erections have been observed in captive dolphins at two days of age (McBride & Kritzler, 1951) and during the 3rd week of life, when they have become more socially active (Reiss, 1988). Caldwell & Caldwell (1972) reported that all male calves mount their mothers within the first 3 weeks of life, but no specifics were given. We observed erections and occasional mountings (rubbing the penis on the mother's genital area) by newborn males, but relative to later periods of development, little sexual behaviour takes place during the newborn period. At older ages, infant males mount a variety of males and females ranging from peers to older adults. Older male infants were often seen mounting and even achieving intromission with their mothers (JM, pers. obs.).

Social interactions and relationships

Newborns engaged in a variety of affiliative behaviours such as rubbing and petting, primarily directed to their mothers. Newborn play was characterized by chasing and displays, and involved very little body-to-body contact. This strikes us as different from older-infant play, which tends to involve extensive contact (unpubl. data).

In Sarasota, Florida (Wells *et al*., 1987), the size of the parties in which infants were found declined with infant age. Shark Bay calves are in larger groups during the newborn period compared to all other ages pre-weaning (Mann *et al*., in press). However, party size did not decrease from month one to month two during the newborn period. Our party sizes were considerably smaller than those reported in Sarasota, possibly due in part to different

definitions of a group. We used a 10-meter chain rule, whereas in Sarasota, animals within 100 m radius were considered part of the same group (Wells *et al.*, 1987).

Shark Bay mothers and infants associated most often with other mother-infant pairs and adult females. Adult and subadult males were rarely present, showed no interest in calves, and interacted with a newborn only once. However, males occasionally engaged in affiliative interactions (petting and rubbing) with mothers (Mann & Smuts, 1998). Multiparous females rarely interacted directly with infants, but females inexperienced in parenting often did (Mann & Smuts, 1998). Infants (newborn and older) also showed considerable interest in young calves and engaged in numerous chase bouts with them. The fluidity of dolphin parties provides the young animal with frequent and diverse social stimulation, typically involving 30 or more animals during the first months of life.

The motor play of wild newborns resembled patterns reported in ungulates (*e.g.* Cuvier's gazelle — Gomendio, 1988). Different types of play may have different adaptive functions (Bateson & Young, 1981; Martin & Caro, 1985; Gomendio, 1988), and following their view, motor play may suit the immediate needs of newborns, who must learn to negotiate the marine environment, and in particular, avoid large sharks and find their mothers quickly. Both reciprocal chase play and the frequent approaches and leaves with the mother characteristic of newborns may enhance sensorimotor skills necessary to survive this critical period. But why chase others and leave the mother at such an early age? Why don't infants remain close to their mothers and avoid risky separations and play bouts with others until the newborn period is over? Newborns must learn to separate and rejoin with their mothers early on, because maternal foraging activities guarantee frequent separations. Thus, given that the infant cannot always stay close to the mother, learning to locate and return to the mother is of utmost importance.

Integration of complex sensorimotor tasks seems especially critical for newborn mammals in a marine environment. Following an initial focus on swimming, breathing, and synchronizing with and identifying the mother, newborns begin to dive and negotiate brief separations with the mother. By the end of two months, infants regularly socialize with others and practice foraging skills. Such precociousness appears to be paradoxical when contrasted with their long period of dependency (median age at weaning is 4 yrs, range = 2.7-8, Mann *et al.*, in press). By the end of the newborn period,

infants have developed many of the skills necessary for maneuvering in a marine environment. However, establishment of social bonds in a fission-fusion society and refined foraging skills may take many more years to develop.

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