Natal attraction: allomaternal care and mother–infant separations in wild bottlenose dolphins

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Abstract. To determine whether allomaternal care occurs among bottlenose dolphins, we examined patterns of association and mother–infant separations for eight infants (164.4 focal h) during the first 3 months of life. During the first week of life, three inexperienced females (nullipara and mothers of infants that did not survive the newborn period) attempted to take infants from their mothers 13 times. Mothers responded by rapidly retrieving the infant and threatening the female. By the second week, mothers consistently allowed the same females to escort their infants to tens of metres away from them, suggesting that such separations were no longer risky, possibly because infants had imprinted on their mothers. To determine whether escorts benefited mothers after the first week, we compared maternal behaviour when infants were away from their mothers, but alone (solitary separations), to when infants were away, but with escorts (social separations). Mothers were less likely to forage and were more likely to engage in non-foraging activities (socialize, rest or travel) when infants were with young escorts (other dependent infants) compared with when infants were alone. When infants were with older (juvenile or adult) escorts, maternal activity did not differ significantly compared with when infants were alone. This result suggests that escorts did not benefit mothers by allowing them to forage. Inexperienced females that never raised an infant were more likely to escort newborns than were parous experienced females, supporting the 'learning to parent' hypothesis.

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Association and/or interaction between infants and non-mothers, termed allomaternal behaviour, is widely reported in social mammals (reviewed in Hrdy 1976; Reidman 1982; Gittleman 1985). Allomaternal behaviour can vary considerably, both within and between species, in the form that it takes and the consequences that it has for infants, mothers and allomothers. Hrdy (1988, page 105) suggested that it would be useful to classify allomaternal behaviour according to 'the sort of behaviour at issue, be it allomaternal care, abuse, or indifference.' Although it may be appropriate to label allomaternal behaviour as care or abuse when the functional consequences are clear-cut (e.g. care when the infant is carried away from danger or abuse when the infant is injured), these

consequences are not always obvious, perhaps especially when allomaternal behaviour entails neither overt aggression nor maternal behaviour such as nursing, but involves mainly association between the allomother and the infant. In this study, we investigated such associations between wild newborn dolphin infants and non-mothers and consider their possible functional significance. Our main goal was to clarify whether the allomaternal behaviour we observed benefits the infant or mother, thus fitting Hrdy's definition of allomaternal care.

Descriptive accounts of allomaternal behaviour abound in captive and wild cetacea (e.g. bottlenose dolphins, *Tursiops truncatus*: Tavolga & Essapian 1957; Gurevich 1977; Leatherwood 1977; Wells 1991; sperm whales, *Physeter macrocephalus*: e.g. Best 1979; Whitehead 1996; spinner dolphins, *Stenella longirostris*: e.g. Johnson & Norris 1994; killer whales, *Orcinus orca*: e.g. Haenal 1986; harbor porpoises, *Phocoena*

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phocoena: e.g. Anderson 1969). Most of these studies assumed that whenever an infant associated with a conspecific away from the mother, this constituted allomaternal care. With the exception of Whitehead (1996), these studies did not quantify the behaviour involved or carefully consider the costs and benefits of these acts to mother, infant or allomother. Several studies of captive delphinids documented aggressive as well as neutral or affiliative allomaternal behaviour toward newborns (e.g. Thurman & Williams 1986; Johnson & Norris 1994). Such aggression could be typical of conspecifics under natural conditions, or it may be the result of social or physical constraints of captivity. In the wild, bottlenose dolphins live in fission–fusion societies (Wells et al. 1987; Smolker et al. 1992), in which individuals change associates on a fluid basis, possibly allowing mothers to avoid unwanted associates during the postpartum period.

Infant–allomother associations often involve two variables: the interaction with the allomother and the separation from the mother. These variables are typically confounded because solitary infant separations are rare or are not considered relevant (i.e. when offspring are cached). For example, when maternal foraging efficiency increases during allomaternal care, it is difficult to know whether this effect is due to the care per se or the fact that the infant is simply out of the mother's way. Similarly, maternal distress during her infant's association with an allomother could reflect mother–infant separation rather than maternal concerns about the allomother harming the infant. Bottlenose dolphins are an excellent species for clarifying such issues because, compared with other mammals with prolonged mother–infant association and allomothering (e.g. chimpanzees, *Pan troglodytes*: Nishida 1983; elephants, *Loxodonta africana*: Lee 1987), newborn bottlenose dolphins frequently separate from their mothers (see Results), and during these separations, infants may be alone (solitary separations) or with others (social separations). By allowing a comparison between social and non-social separations, our data help to distinguish between the effects of association with others and the effects of maternal–infant separation. We first review the kinds of costs and benefits associated with allomaternal behaviour in other species and consider which of these might apply to the dolphins we studied.

Costs and Benefits to Infant

The costs of allomaternal behaviour to an infant depend on the parameters used for comparison. For example, allomaternal association might be costly to an infant compared with association with the mother, but beneficial to an infant compared with being alone. Potential costs of allomaternal association include increased probability of disease or ectoparasite transmission, or increased chance of attracting predators. Costs would also be associated with unskilled allomaternal care or allomaternal abuse. Infant injury and death through allomaternal mishandling or abuse are, for example, well documented in primates (e.g. Silk 1980; Goodall 1986; Shopland & Altmann 1987).

Potential benefits to dolphin infants of association with non-mothers may include hydrodynamic advantages of echelon (i.e. close, roughly parallel) swimming (Norris & Prescott 1961). Social separations, compared with solitary separations, may deter predation (either through detection, defence or decreased probability of predator attack). This benefit could be important, but such predation attempts are rarely observed and are difficult to quantify. Allomaternal nursing, although rare in mammals, provides obvious benefits (Packer et al. 1992). Other benefits may include varied social experience leading to short- or long-term gains in skills and the development of social relationships, including the possibility of adoption if the mother dies. Given that a dolphin infant is much more likely to die than the mother, and that infants normally nurse for several years postpartum, the promise of adoption is unlikely to offer mothers or infants substantial benefits in terms of fitness.

Costs and Benefits to Mother

Mothers and infants share many of the costs and benefits of allomaternal care. Harassment or abuse of infants and well-intentioned but unskillful care obviously decrease the mother's fitness. Agonistic interactions between mothers and would-be allomothers are interesting for two reasons: (1) maternal reactions to attempts by others to take offspring might reliably indicate the cost to her fitness; (2) the agonism itself may inflict costs. The potential benefits to mothers include respite from caregiving duties, more efficient foraging (e.g. capped langur monkeys, *Presbytis pileata*:

Stanford 1992), reduced need for vigilance and reciprocal benefits, such as grooming or petting by the allomother in exchange for infant access (e.g. patas monkeys, *Erythrocebus patas*: Muroyama 1994).

Costs and Benefits to Allomothers

The main costs to allomothers are probably those associated with changes in activity (energetic investment) and, potentially, agonistic interactions with the mother or others that might defend an infant, such as adult male associates of the mother (i.e. savanna baboons, *Papio cynocephalus*: Altmann 1980). The benefits to allomothers of association with infants probably vary with the allomother's age and sex class. For example, immature or nulliparous females might benefit by gaining mothering skills (Fairbanks 1993), and infants might derive benefits from playing with one another.

In this study, we investigated some potential benefits to mothers and infants of allomaternal behaviour by examining whether (1) mothers receive more petting and rubbing from allomothers than non-allomothers and (2) maternal foraging differs during infant social separations compared with solitary separations. Increased maternal foraging during social separations might suggest that allomothers provide increased safety to the infant compared with solitary separations.

To examine the potential costs and benefits of allomaternal behaviour for the allomothers, we focused on adult and juvenile females (we excluded males because adult and juvenile males rarely associated with infants; Mann & Smuts, in press). To examine possible costs to allomothers, we evaluated aggression between mothers and would-be allomothers. Possible benefits to allomothers include (1) parenting experience, (2) developing a relationship with an infant (future ally), (3) cultivating a relationship with the mother (current or future ally), (4) inclusive fitness gains (helping kin), and (5) increasing the allomother's competitive ability by harassing or harming the infant (e.g. Hrdy 1976; Nicolson 1987; Fairbanks 1993). Alternatively, the 'cute' or reproductive-error hypothesis suggests that natal attraction by non-mothers is a by-product of selection for attraction which, under most conditions, favours maternal behaviour towards one's own offspring (Quiatt 1979).

These hypotheses are not mutually exclusive. Hypothesis 1 has received the most support in primate studies (e.g. Epple 1978; Fairbanks 1993). Several patterns are consistent with hypothesis 1 (reviewed by Hrdy 1976; Fairbanks 1993). (a) Females with little infant experience, such as nulliparous (juvenile or adolescent) females, or those with no surviving offspring, are particularly attracted to infants. (b) Primiparity is associated with higher infant mortality than multiparity, or there are clear differences in maternal care as a function of parity. (c) Females are attracted to very young infants, which have the highest mortality, thus enhancing the chances that the female can guide her own infant through this vulnerable period. (d) Females with prior allomaternal experience have higher infant survivorship compared with females without such experience. None of these predictions is necessarily consistent with hypotheses 2–5.

To test hypothesis 1, we consider the distribution of allomothers across different age/sex classes and review the evidence for a–d. For hypotheses 2 and 3, we would expect allomothers to continue to associate preferentially with the mother or infant after the newborn period and possibly beyond infancy. We could not test these two hypotheses because (1) not enough infants survived (five of nine died by the seventh month of life), and (2) females were not followed after losing their infants. Although we present data on kinship between infants and allomothers, we cannot adequately test hypothesis 4 because we knew only a limited number of kin relationships. We addressed hypothesis 5 by examining allomother–infant interactions and maternal reactions to social separations. The 'cute' or reproductive-error hypothesis suggests that all females, regardless of age or reproductive state, would exhibit natal attraction (a misdirected proximate mechanism). Thus, an age or reproductive state bias in natal attraction (measured by likelihood of being an escort) would be inconsistent with this hypothesis.

METHODS

Study Site and Subjects

Our study site incorporated a 130 km² 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 study was established in 1984, and the mother–infant study was initiated by the authors in 1988. Following methods developed by Würsig & Würsig (1977), we used photographs to identify fins by shape, nicks and other natural markings. By 1994, well over 400 dolphins were identified, and roughly 100 animals were sighted regularly.

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 two to three feedings, most of which occur in the morning. In the afternoon, occasional feedings occur, but the dolphins spend less time near the beach in the afternoons (W.A. Conservation and Land Management, unpublished data). Dolphins occasionally receive handouts from fishers, although this practice is strongly discouraged.

Because several dolphins come near the shore almost daily, we conducted observations from the beach that the provisioned animals visit or from a nearby jetty. These we term onshore focal observations. For the mother–infant study as a whole, we collected most observations during offshore focal observations, which involved following individual animals in small boats (4–5 m dinghies equipped with 6–15 hp motors) for up to 10 h at a time (Smolker et al. 1993; Mann & Smuts, in press). More than half of the data presented here, however, were derived from onshore observations (Table I). We included onshore observations because data on newborn dolphins are difficult to obtain in the wild because we must see the female just before and just after parturition to know the date of birth. Daily observations of provisioned mothers and their infants allowed us to record neonatal behavioural and physical developments almost as often as one could in aquaria. Absolute behaviour rates of provisioned mothers and their infants differed from those of non-provisioned mothers and infants but developmental changes in behaviour did not differ between groups. Behaviour of provisioned dyads away from the beach was indistinguishable from that of non-provisioned dyads, with one exception:

Table I. Summary of focal observations

Infant	Mother	Sex	Ages observed (weeks)	Observation time (min)
Rab*	Nic	M	1–8	3164
Nov*	Hol	F	1–10	3174
Hbt	Hol	F	3–8	80
Nak	Nic	M	2–8	90
Pic	Puc	F	1–10	1142
Shd	Sur	M	1–8	571
Oys†	Alg	M	≤2–≤5	450
Mou†	Min	?	1–8	1190
Total				9861

Fifty-two per cent of observations occurred during the first 4 weeks of infant life. Nov and Pic were observed for 10 h during weeks 9 and 10, leaving 154.4 h of observation for the first 8 weeks.
*Infant observed both in the provisioning area and offshore, where there is minimal human disturbance, Rab: 1110 min (18.5 h) offshore; Nov: 1968 min (20.1 h) offshore.
†Infant observed offshore only; mothers of Oys and Mou were never provisioned. Oys' exact date of birth was not known.

provisioned females, but not non-provisioned females, occasionally chased and begged from incoming fishing boats (Mann & Smuts, in press).

This study, conducted between 1990 and 1994, incorporated 164.4 h of focal observations on eight infants born to six mothers. We observed two of these infants both onshore and offshore, two were observed offshore only, and four were observed onshore only (Table I). Of four provisioned adult females (Nic, Hol, Puc, Sur) that regularly visit the Monkey Mia campground, we observed three with two newborn infants (i.e. six infants). For all but one infant (Oys), the date of birth was known within 2 days. Oys' mother, Alg (one of the non-provisioned females), was last seen 2 weeks before Oys was first sighted. This allowed us to classify the first 2 weeks of observations of Oys–Alg as occurring during the first month of life, but later observations could have fallen at the end of the first month or the early part of the second month of life. We classified our later observations of Oys as occurring during the second month because this method underestimates age effects (comparing month 1 to month 2). All females except one (Sur) were multiparous. Due to paucity of data, we excluded observations during the third month of life from most of the analyses (see Table I).

Offshore Focal Observations

We collected all data using a focal-animal sampling procedure, including continuous, instantaneous and predominant activity sampling (Hutt & Hutt 1970; Altmann 1974). We used instantaneous sampling of spatial relationships and activities to determine party composition, mother–infant distance, nearest neighbours, and other information. Predominant activity sampling (i.e. activity must occur for a minimum of 50% of a predefined interval to be considered a predominant activity) was used to assess infant activity and maternal activity at regular intervals and during separations. We recorded exact durations (onset and offset) of social events when observation conditions permitted. Every 5 min, party/group composition was determined using a 10-m chain rule (also see Smolker et al. 1992). Any animal that was within 10 m of an animal within the party was considered a party member and infant associate.

We defined mother–infant separations as greater than or equal to 2 m. Such short distances defined separations because mothers reacted strongly to these separations during the first week but not the second week of infant life (see Results). Thus, we considered this distance biologically significant to the dolphins. Mother–infant separations were of two types: (1) solitary separations, when the infant was alone (≥ 2 m from any individual throughout $\geq 90\%$ of the separation); and (2) social separations, when the infant was accompanied (<2 m) by another dolphin (the escort) during most of ($\geq 90\%$) the separation. We classified all separations into one of these two categories. During separations, we scored maternal, infant and escort activities, maximum distance during the separation and identity of escort(s) that remained less than 2 m from the infant during the separation. The primary escort was defined as an escort that accompanied the infant during at least 50% of social separations for a given focal observation period.

Infant and maternal activities included the following: (1) infant position swimming (infant only: swimming under the mother in contact with her abdomen); (2) echelon swimming (infant only: swimming alongside the mother, roughly parallel, just above her midline); (3) slow-travel/resting (<2 mph, frequent floating at the surface, frequent direction changes); (4) travelling (straight direction, ≥ 2 mph); (5) foraging/hunting (rapid surfaces, echolocation clicks heard, frequent direction changes, fast swims, fish chases, observations of fish catches); (6) socializing, including mounting, chases, genital inspections, pokes, play, bonding (pectoral fin of one non-infant animal resting on another) and displays in the presence of others (spy hops, leaps, slaps with tail, face, jaw, belly, dorsal side). Socializing also included two types of generally mutual physical contact: petting (pectoral fin actively moving on other's body part) and rubbing (body contact not involving obvious movement of pectoral fins).

We divided maternal activity states into two classes: non-foraging and foraging. Non-foraging included maternal resting, socializing and travelling. Maternal foraging also included begging (from boats or <2 m from people onshore).

Onshore Focal Observations

We observed six infants from the beach when their mothers came close to shore to accept fish and interaction from humans. Observations of infants typically started soon after the mother and calf came into the provisioning area. We never started observations during feeds or right after feeds because the dolphins typically left the provisioning area immediately following feeds. Onshore focal observations typically lasted 30 min, although some were shorter if the dolphins left the provisioning area. Focal observations less than 10 min long were excluded. We used a combination of instantaneous sampling, event and continuous sampling to record maternal and infant activity and the identity of individuals that approached and left the infant from a 2-m radius. We scored all animals in the vicinity (<200 m from the beach) as present and potential associates of the infant during each sample. For two infants (Nak, Hbt), behaviour and distance from the mother were coded from videotapes.

For most of the onshore data collection, we used 30-s instantaneous samples to assess mother–infant distance, activity and neighbours. All mother–infant approaches and leaves (within a 2-m radius) were identified within 30-s blocks. This enabled us to classify the durations of separations as greater than or less than 30-s for logistic regression analyses. For onshore observations, we defined the escort as any individual less than 2 m from the focal infant at each 30-s instantaneous

sample when the infant was greater than 2 m from the mother. Maximum distance of each separation was recorded. Protocols for data collection onshore and offshore were similar unless otherwise indicated.

Age/Sex Classifications and Definitions of Terms

We classified animals by known sex (views of genital area or birth of calf) and age approximations, based on ventral speckling, which typically begins around the time of sexual maturity (Ross & Cockcroft 1990; Smolker et al. 1992). To test the 'learning to parent' hypothesis for allomaternal behaviour, we defined two classes of females: (1) experienced females were those that had successfully reared an infant through the first 3 months of life (the period of greatest infant mortality); and (2) inexperienced females were those that had not done so over the last 6–10 years, either because they were still reproductively immature, or because all of their newborns died. Five of the eight inexperienced females were immatures. We considered animals to be 'infants' if they were still dependent on the mother, nursing and swimming in infant position. All infants in this study were less than 4 years of age.

Two behaviour patterns were common in the first week of infant life. 'Chasing' refers to rapid accelerations by the mother to retrieve a straying infant. 'Bolt with infant' refers to instances in which another animal (not the mother) suddenly accelerated and rapidly swam directly towards and then next to (<1 m) the infant, causing the infant to veer away from the mother and follow the animal. Infants appeared to have a strong following response during the first month of life, which others can exploit by accelerating near the infant. Mothers always responded by immediately chasing and retrieving the infant with the same technique.

To distinguish between animals that associated with the mother from those that may have an interest in the infant independent from the mother, we use the term 'associate' to refer to conspecifics that spent time close to the dolphin infant, regardless of mother–infant proximity, and the term 'escort' to refer to animals that spent time with the infant when s/he was away from the mother. All escorts were associates, but not all associates were escorts.

Descriptive Data and Quantitative Analyses

We pooled behaviour durations, frequencies and instantaneous samples across weeks or months and converted these to rates or proportions for each infant. We used non-parametric tests (two-tailed) for all comparisons. For some comparisons, we combined offshore and onshore mother–calf data to increase the sample size. However, proportions or rates are presented separately for these two groups because the offshore data represent natural behaviour better. When offshore and onshore data were combined, Rab and Nov onshore data were excluded and their offshore data were used. Means and standard deviations for the offshore data, but not the provisioning data, are presented for descriptive purposes.

Because of our interest in maternal responses to allomaternal behaviour, we wanted to determine whether maternal behaviour during separations varied as a function of whether or not the infant was with an escort. To investigate this question, we needed to determine first whether solitary and social separations differed in terms of any other variables, such as distance or duration of separations, or age of infant, likely to influence maternal behaviour. To obtain large enough sample sizes to address this question statistically, it was necessary to pool separation data either across or within infants. Because there was so much variation among infants, we chose to pool data within infants and run multiple logistic regressions for each infant, treating each separation as independent. Although this analysis violates the assumptions of independence, we include the results here because they are the best evidence available indicating that it is valid to ignore separation duration, distance and age of infant when comparing solitary and social separations.

RESULTS

Maternal Chases, Bolting and Early Separations

We recorded maternal chase rates and 'bolt with infant' rates for five newborns, both in the provisioning area and offshore (Fig. 1). We observed 14 'bolt with infant' instances involving four of these five infants, all during the first week of life. During week 1, 38% of all chases involved bolting with infant attempts. No bolting attempts
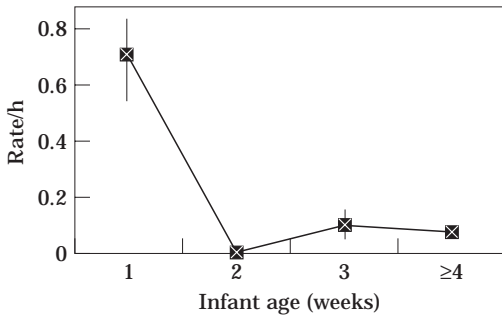
Figure 1. Mean ± SE rate at which mothers chased their infants (*N*=5 infants, 44 chases). Chase rates were calculated using 147 h of focal observations, including 44 h during the first week of infant life.

occurred after week 1. All chases during week 1 were in response to infant straying, either with or without a bolter. Chases and bolting attempts occurred offshore and onshore, but were more common onshore. Bolting with infant attempts occurred 3.8 times more often onshore than offshore. Those that attempted to bolt with infants included three inexperienced females and one male infant. The male infant was the nephew of the female newborn he attempted to bolt with. The male infant made one bolting attempt, and the females each made more than one, typically on the same day. Mothers responded to bolting attempts by rapidly chasing and retrieving their infants, and on six of the 14 occasions, the mother charged or threatened the individual. The most severe maternal aggression involved a charge, head jerk and jaw clap near the eye of the dolphin that had tried to bolt with the newborn six times. The female continued to try to bolt with the infant on subsequent days. Bolters did not show aggression toward infants or mothers. In five of the

bolting attempts, mothers responded so rapidly that infants were never more than 2 m ahead of their mothers before being successfully retrieved (thus, these events did not qualify as social separations). Similarly, on 15 occasions during the first week of life, mothers chased their infants when the infant began to stray alone (infant initiates leave) but retrieved them before the infant wandered more than 2 m away. After the first week of life, we never observed bolting attempts or maternal chases in response to infant separations (either social or non-social), although mothers did chase their infants seven times in contexts other than separations.

Table II summarizes maternal responses to social and non-social separations in the first 2 weeks of life. Offshore, mothers never tolerated the few social separations that were attempted in the first week of life (i.e. mothers chased in all instances). Similarly, in the provisioning area, where separations occurred at higher rates (Mann & Smuts, in press), mothers never tolerated social separations during days 1–3, but did tolerate some social separations as early as days 4 and 5. When we pooled onshore and offshore separations for five infants, mothers tolerated 93.3% of solitary separations and 0% of social separations during days 1–3; they tolerated 94.0% of solitary separations and 80.0% of social separations during days 4–7; during days 8–14, they tolerated 100% of both solitary and social separations (Table II). Thus, mothers generally tolerated solitary separations, even during the first days of life, but showed a distinct shift, around the end of the first week, from complete intolerance of social separations to frequent and subsequently complete tolerance. This shift is highlighted by the fact that, on 24 occasions during the second week, mothers permitted their infants to stray with three of the

Table II. Total number of separations, social and solitary, observed during the first 2 weeks of infant life

Infant age (days)	Hours observed	Total no. separations	No. of solitary separations	No. of social separations	Solitary separations involving maternal chases (%)	Social separations involving maternal chases (%)
1–3	22.3	17	15	2	6.7	100.0
4–7	22.1	145	110	35	6.0	20.0
8–14	23.0	134	98	36	0	0

Data are pooled for five infants. Note that the majority of solitary separations were tolerated (mothers did not chase), but social separations were not tolerated by the mother until the fourth day of infant life.
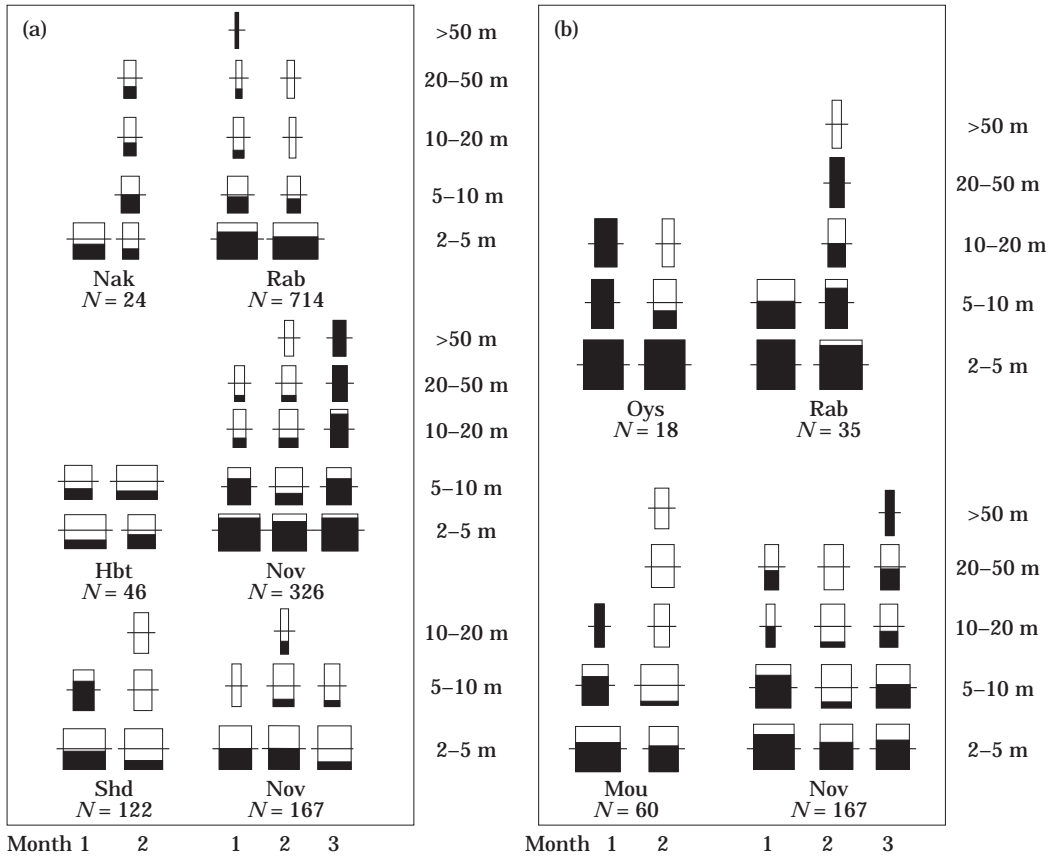
Figure 2. Rectangles show the relative proportion of separations that infants spent at different distances with another animal (social separations, □), or alone (solitary separations, ■) at 1, 2 and 3 months of age (a) separations onshore; (b) separations offshore. The height of each rectangle remains constant and the width is adjusted using a square-root transformation of the proportion of separations within each age class. This transformation permits viewing of small proportions in the sample. The wider the rectangle, the greater proportion of separations that occurred at that distance for a given age. Midlines mark 50% of the separations at a given distance (Dunn 1987). *N*=number of separations observed for each infant.

four individuals that attempted to bolt with the infant and provoked chasing the week before.

Description of Separations by Month

During the first 3 months, we recorded 1432 separations in the onshore provisioning area (Fig. 2a) and 280 separations offshore (Fig. 2b). From month 1 to month 2, infants showed significant increases in the rate, proportion, mean bout duration and distance of separations (Mann & Smuts, in press). Rate of separation, proportion of time spent separated, and proportion of separations with and without an escort were calculated for

each offshore infant (*N*=4) for the first 2 months only. The mean ± SD rate of separation per hour was 3.2 ± 1.2 (range=2.2–4.9). The mean bout duration of separations was 47 ± 151 s (range=2–1058). The mean rate of separation increased from 2.0 ± 1.7/h (range=0.38–2.2) during the first month to 7.8 ± 2.3/h (range=5.8–10.9) during the second month. The proportion of time that infants spent separated from their mothers across the first 2 months was 8.1 ± 4.4% (range=2.2–12.4), and increased from a mean of 2.5 ± 2.9 (range=0.3–6.6) during month 1 to a mean of 24.7 ± 13.0% during month 2 (range=6.1–36.0). The maximum distance of separations was about

Table III. Mean ± SD percentage of separations that infants were alone and with different age/sex classes of escorts

Age/sex of escort	Onshore	Offshore
Alone	43.3 ± 16.9	66.6 ± 17.9
Escort–infant	40.3 ± 23.7	15.0 ± 10.4
Escort–inexperienced female	9.0 ± 7.5	19.1 ± 19.2
Escort–experienced female	11.1 ± 8.9	2.4 ± 2.8
Escort–adult/subadult male	0.02 ± 0.1	1.4 ± 1.6

Means were calculated across infants rather than pooling across all separations. More than one escort could have been present per separation. These data are descriptive, presenting the proportion of time infants were escorted by members of a given age/sex class, not controlling for the proportion of time that associates of a given age/sex class were available to act as escorts. For example, experienced females were present in the provisioning area (associates) for an average of $80.1 ± 17.1\%$ of observations ($N=6$), but in only $43.0 ± 9.7\%$ of offshore observations ($N=4$). $N=1432$ separations for six infants observed in the provisioning area and 223 separations for four infants observed offshore (total $N=1655$ separations). Only the first 2 months of data are included.

100 m, but one infant did not venture past 20 m. During $66.6 ± 17.9\%$ of separations, infants were alone (i.e. no others within 2 m). In 73.2% of these solitary separations ($N=168$ separations), no dolphins besides the mother were in the same party as mother and infant.

To determine whether escort and non-escort separations were related to these variables, we ran multiple logistic regressions for each infant in which duration of separation (< or ≥ 30 s), maximum distance of separation (short: 2–5 m; moderate: 5–10 m; far: 10–100 m) and age of infant (1, 2 or 3 months) were the dependent variables used to predict the likelihood of a solitary versus social separation. Offshore and onshore data were run separately, and a quadratic model was applied for Pic and Nov, both of which were also observed in the third month, to determine whether distance or duration of social and solitary separations could be predicted over 3 months. Only three regressions showed significant patterns. Far separations predicted social separations for Nov onshore (distance coefficient ± SE$=1.4 ± 0.31$, $N=326$ separations, $P<0.001$, linear model), but longer separations predicted social separations for her offshore data (duration coefficient$=1.6 ± 0.5$, $N=167$ separations, $P<0.001$, quadratic model). When only the first 2 months of Nov's offshore data were used, longer separations no longer predicted social separations (linear model). Longer separations onshore predicted social separations for Rab (duration coefficient$=1.5 ± 0.2$, $N=714$ separations, $P<0.001$, linear

model), but no significant results emerged for his offshore data. When we compared social and solitary separations in subsequent analyses, for Rab and Nov we included only offshore data for the first 2 months of life, thereby eliminating from the analysis the only separations in which distance, duration or infant age were significantly related to presence and absence of escorts. Thus, the statistical results described below (comparing maternal behaviour for social and solitary separations) are unlikely to be confounded by other variables that might influence maternal behaviour.

Social and Solitary Separations and Age/Sex Class of Escorts

Table III shows the average proportion of separations that infants spent alone and with different types of escorts, both offshore and onshore. In general, solitary separations were the most common, followed in turn by separations with another infant, inexperienced females and experienced females. Males rarely escorted infants. Offshore, experienced females rarely escorted newborns. Thus, when newborns were accompanied during a separation, the escort was typically an inexperienced female or another infant.

Escorts and Associates

To determine whether inexperienced females were more likely to escort infants than
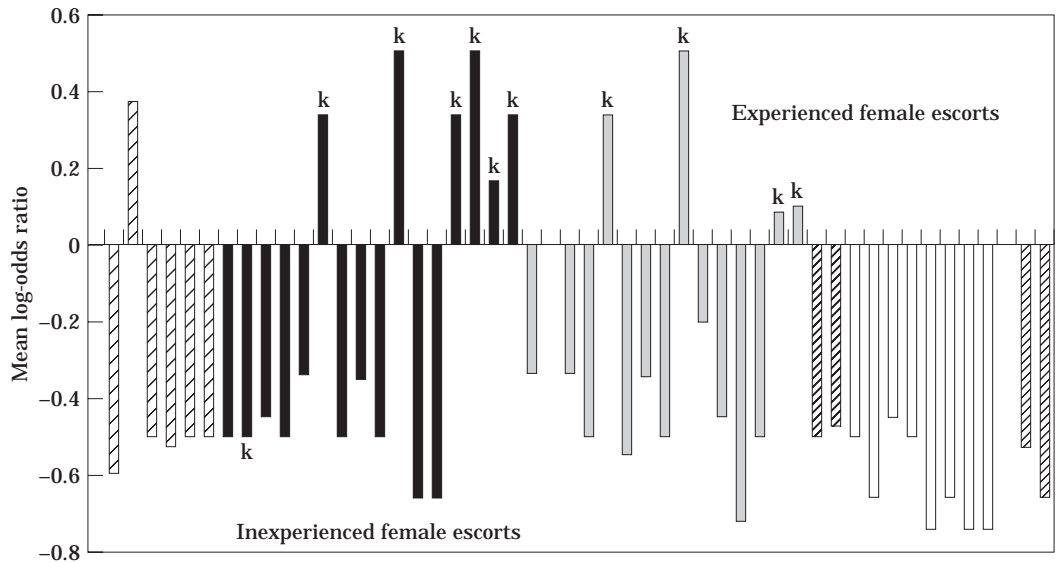
Figure 3. Distribution of the mean log-odds ratio of experienced and inexperienced female escorts for six infants across 50 days of observation. Each infant is represented by different bar patterns. Negative values indicate that inexperienced females were more likely to escort infants than experienced females. Positive values indicate that experienced females were more likely to escort infants than inexperienced females. A primary escort was defined as an escort that accompanied the infant during at least 50% of social separations for that day. If the primary escort was kin ($r > 0.25$), then the ratio is marked with a 'k'.

experienced females, we controlled for the number of animals available by creating a separate database containing all instances in which both inexperienced and experienced females were simultaneously associates of mothers and newborns. Two infants did not have both age classes of females simultaneously available during any separations and were not included. For six infants, totalling 50 observation days and considering each day of observation as independent, we calculated a log-odds ratio based on the number of inexperienced and experienced females available per separation and number of escorts per separation. Ratios for each separation were averaged for each infant for each day (Fleiss 1981; Fig. 3). On 37 days, inexperienced females were more likely to escort newborns than were experienced females (positive ratios); on only one of these days was the primary escort a related female. On 11 days, experienced females were more likely to be escorts than inexperienced females; on 10 of these days, the primary escort was an experienced female kin (one sister and one grandmother). If we removed female kin from analysis (because kin were not equally available to all infants), then,

with one exception (one separation for one mother–infant pair), experienced females were never more likely to escort newborns compared with inexperienced females ($\chi^2 = 33.1$, $P < 0.001$). On 2 days, the log-odds ratio was zero. The influence of kinship requires further investigation.

Escort Behaviour

Escorts were never observed to harm or threaten infants, although mothers threatened some escorts during the first week. Infants typically swam in echelon position or actively played with escorts. Occasionally they engaged in prolonged petting or rubbing bouts with escorts. Three female escorts were observed herding infants away from boats or people in the provisioning area. One newborn briefly assumed infant position with two different young female escorts for less than 1 min. No allomaternal nursing was observed. Although nursing is difficult to detect in the wild, we could easily observe infant position, during which all observed bouts of mother–infant nursing occurred. Of 1679 h of observations of dolphin infants (0–4 years of age),

infants spent 30–45% of the time in infant position with mothers, but less than 13 min (0.01%) in infant position with non-mothers (*N*=14 events). During three of these events, we observed infants attempting to nurse. It is unlikely that infants acquired milk from escorts, because infants were never observed in infant position with mature females that had dependent young. In one of the three nursing attempts, a 1.5-year-old infant attempted to nurse from an adult female that had lost her calf 6 weeks earlier.

Are Escorts Likely to Pet with Mothers?

Mothers of newborns engaged in very little social activity overall. Offshore, mothers spent an average ± SD of 2.4 ± 3.6% of their time socializing (*N*=4), and they spent even less time socializing near the provisioning area (mean=0.3 ± 0.5%, *N*=6). Near the provisioning area, mothers were never observed petting or rubbing with anyone except their infants (Mann & Smuts, in press). Offshore, rubbing bouts were observed between mothers and infants and between infants and others, but not between mothers and others. All four mothers engaged in petting bouts with other dolphins. We observed 20 petting bouts involving four mothers with seven partners, at a mean ± SD rate of 0.43 ± 0.72 times/h (range=0.05–1.5). Of these 20 bouts, six involved two old males (very heavily speckled ventrums), 11 involved four juvenile/adolescent males (very few speckles) and three involved one juvenile female. In one case, the juvenile female pet with the mother twice before escorting her infant. In the other case, the same juvenile female pet with a different mother when her infant was 4 days old, but she did not escort the infant. None of these males escorted infants. Thus, in general, escorts did very little petting with mothers. Ninety-five per cent of all petting was with males (old adults and immatures), which spent only about 6% of their time with mothers and newborns offshore (Mann & Smuts, in press).

Do Escorts Provide Allomaternal Care?

To determine whether escorts provided care to infants and offered respite from caregiving duties to mothers, we examined maternal activity as a function of all offshore separations (social and solitary). First, we compared rates of separation during four maternal states: rest, travel, forage and socialize. Infants were least likely to separate from their mothers during resting. On average ± SD, infants separated 2.1 ± 2.2 times/h during maternal resting (range=0–5.1), 3.0 ± 2.4 times/h during maternal travelling (range=0–5.5), 5.2 ± 2.5 times/h during maternal foraging (range=3.8–9.0), and 5.4 ± 4.9 times/h during maternal socializing (range=0–12.0). With only four offshore infant–mother pairs, we could not determine the significance of these differences, but all infants separated relatively often during maternal foraging. When we pooled across infants, infants separated at a rate of 5.1 times/h during foraging, 4.2 times/h during travelling, 4.0 times/h during socializing and 2.6 times/h during resting.

Second, we investigated whether mothers were more likely to forage (or beg in the provisioning area) for fish during social and solitary separations. For each separation, we classified maternal behaviour as forage and non-forage. We included four offshore and four different onshore mother–infant pairs in this analysis. For this analysis, we excluded all onshore separations where both mothers and infants were within 2 m of people, leaving only separations in which the infant travelled at least 5 m distance from the mother (132 onshore separations). We excluded the short-distance separations, because under these circumstances, infant proximity to people could influence maternal behaviour independent of the presence or absence of an escort.

We contrasted the proportion of time that each mother engaged in foraging during solitary separations with the proportion of time that the same mother foraged during social separations. For all infants except one (Rab), mothers were less likely to forage during social separations (with escort) than when infants were alone (Wilcoxon signed-ranks test: Z=2.38, P<0.02). During social separations, the average percentage of time mothers foraged was 55.2 ± 33.9% (median=68.9, *N*=8); during solitary separations, the average was 72.7 ± 20.3% (median=77.4, *N*=8).

Escorts include animals of all age classes that associated with infants away from the mother. We separated escorts into two classes: 'old', which included juveniles (weaned) and older animals, and 'young', which included all dependent infants (≤4 years). If newborns had more than one escort and at least one was 'old', we used the older age class. All but one of the old escorts were females.

Young escorts included both sexes. Two infants were never escorted by old escorts and one infant was never escorted by a young escort; these cases were excluded from the analyses. We contrasted social separations involving 'old escorts' with solitary separations and found no significant differences in maternal foraging behaviour (average percentage of time mothers foraged during social separations with old escorts $=63.4 \pm 34.8$, median $= 60.7$; Wilcoxon signed-ranks test: $Z=1.48$, $N=6$, $P=0.14$), although four of six mothers still foraged less during social separations with old escorts compared with solitary separations. When we contrasted social separations involving young escorts with solitary separations, all seven mothers were less likely to forage when their infants were with other infants than when their infants were alone (Wilcoxon signed-ranks test: $Z=2.37$, $N=7$, $P<0.02$; average percentage of time mothers foraged during social separations with young escorts $=47.0 \pm 33.4$, median $=55.0$). Thus, the first result, with all escorts combined, could be attributed largely to young rather than old escorts.

DISCUSSION

Our results present a complex picture of bottlenose dolphin mother–infant associations, separations and relationships with others during the newborn period. During the first few days of life, mothers resisted all attempts by others to swim with their newborns, and they occasionally showed aggression towards potential escorts. In contrast, during this same period, mothers tolerated the vast majority of solitary separations. By the second week, mothers permitted their infants to stray with the same individuals that had provoked an aggressive interaction the week before. After the first week, infants separated from their mothers often (2–3 times/h), typically alone, or, less often, with an escort. Escorts were most likely to be other infants or inexperienced females. Mothers were less likely to forage when their infants were with young escorts compared with when their infants were alone, but maternal foraging behaviour did not differ significantly when infants were with older escorts compared to when they were alone. Compared with inexperienced females, experienced females were unlikely to escort newborns unless they were kin.

We found no evidence that mothers benefit from allomaternal behaviour via increased forag-

ing or increased affiliative behaviour (i.e. petting or grooming), as demonstrated for some non-human primates (Stanford 1992; Muroyama 1994). However, maternal tolerance of escorts after the first week suggests that the costs to her of allomaternal behaviour are minimal. It is possible infants receive benefits from escort behaviour (e.g. social experience and/or reduced predation risk) that result in benefits for the mother through increased infant survival or reproduction. Escorts, in turn, may benefit from association with newborns by gaining social experience (young infant escorts) or by gaining parenting experience (inexperienced, older female escorts). The social and developmental significance of these patterns are discussed below.

Evidence for Imprinting?

Mothers shifted from complete intolerance to tolerance of infant social separations towards the end of the first week of life. We hypothesize that this shift reflects a 'sensitive period' for infant–mother recognition, or imprinting, during the first few days after birth. Bottlenose dolphins are highly social and have precocious locomotion at birth; both patterns are associated with imprinting in other species (Lorenz 1937; Bateson 1991).

An infant may rapidly learn the mother's identity by her signature whistle. Captive data (P. Tyack, J. McIntosh and K. Fristrup, unpublished data) indicate that mothers markedly increase whistling just prior to and after parturition. The hypothesis that infants imprint on maternal whistles predicts a rapid decline in maternal whistling around the time that mothers begin tolerating social separations; we have no data to evaluate this hypothesis. An alternative explanation for the shift in maternal tolerance of escorts is that, after the first few days of life, infants have developed sufficient locomotor ability and whistling skills to facilitate reunions with their mothers. This hypothesis, however, does not explain why mothers tolerate solitary separations prior to tolerating social separations. Although the imprinting hypothesis is speculative, we include it to stimulate researchers to document maternal and infant whistling during the newborn period, especially in captivity where these behaviour patterns can be closely monitored.

Is 'Bolting with Infant' a Form of Female–Female Competition?

The strong and rapid following response of newborns may be adaptive, allowing the infant to follow the mother closely under dangerous conditions (i.e. shark approach), but this response may cost the mother and infant by making the infant vulnerable to following non-mothers, especially when they attempt to bolt with the infant as described above. We did not observe successful 'kidnappings' such as those reported in primates (e.g. Silk 1980; Shopland & Altmann 1987), so it is unknown whether newborn following of non-mothers entails costs, including infant death. In captivity, newborns can become disoriented, swim into tank walls and be fatally injured when others interfere with mother–infant echelon swimming (Thurman & Williams 1986).

Primate infant kidnapping by females may be viewed as a form of female–female competition. In some studies, experienced and inexperienced females appeared to be equally interested in kidnapping, harassing or associating with infants. For example, multiparous and nulliparous females were equally likely to kidnap infant bonnet macaques, *Macaca radiata* (Silk 1980). In contrast, Nishida (1983) found that the majority of chimpanzee infant interactions with unrelated, lactating females were abusive, but unrelated nulliparous females were typically solicitous and caring towards infants. Thus, in the same population, nulliparous chimpanzee females may 'practice mothering' while lactating females may be competitive.

Although bottlenose dolphin infants are vulnerable to following others during the first week, some evidence suggests that attempts to bolt with infants do not reflect female–female competition. First, no experienced females attempted to bolt with infants, although several associated with newborns during the first week. If resource competition is the primary explanation for attempted boltings in the provisioning area, then experienced provisioned females should also bolt with infants. Second, three of four 'bolters' associated with and escorted the infants after the first week of life without interference from the mother. Third, infants never received aggression/abuse from bolters or escorts during the entire newborn period. In primate kidnappings, kidnappers are often dominant to mothers (or come from dominant matrilines), and can forcibly restrain infants, preventing mothers from retrieving infants. In contrast, all bolters in our study were smaller and younger than the mothers, suggesting that they were unlikely to be dominant to mothers. Fourth, in the wild, the risks of following others may not be that great compared with captivity because mothers can retrieve infants quickly.

Did Escorts Help Newborns or Mothers?

Some studies of allomaternal behaviour or helpers at the nest have shown that alloparents help (e.g. birds: Komdeur 1994; Mumme 1992; primates: Fairbanks 1990; ungulates: Hass 1990) or hinder the reproductive success of mothers (e.g. birds: Komdeur 1994; primates: Silk 1980; Shopland & Altmann 1987). In this study, some evidence suggests that: (1) escorts did not directly help mothers; (2) benefits to the infant may explain maternal tolerance of escorts; and (3) escorts did not appear to impose serious costs on mothers or infants.

As noted above, our analysis provided no evidence that mothers were able to forage more during social compared to solitary separations. Furthermore, social and solitary separations did not differ in duration, distance, or as a function of infant age, suggesting that infants did not take advantage of the potentially greater safety of social separations by travelling further away from the mother or by staying away for longer periods. Still, mothers tolerated social separations after the first week of life, and infants willingly left the mother to associate with others, suggesting that both mothers and infants may derive benefits from escorts.

Why do newborn infants separate from their mothers at all? Infants were particularly likely to leave during maternal foraging, suggesting one possible benefit of mother–infant separations: as in some non-human primates (Stanford 1992), mothers may forage more efficiently when the infant is not 'underfoot'. Mothers foraged the same amount when the infant was with an older escort and when it was alone, suggesting that both situations were equally conducive to maternal foraging. In contrast, mothers foraged less when the infant was with another infant, possibly because infants in the presence of other infants more easily lose track of their mothers' whereabouts compared with infants that are alone or

infants with a potentially vigilant older escort. As in other precocial mammals, bottlenose dolphin young take considerable responsibility for following the mother, initiating and terminating the majority of mother–infant separations (Mann & Smuts, in press). Thus, the infant's ability to monitor the mother (either directly or with the help of an older escort) may influence the mother's willingness to engage in an activity that reduces her vigilance compared with when she is resting or travelling. If so, then infants may tend to associate with other infants when their mothers can most afford it, such as when they are resting and can monitor infants.

During the majority of social separations, infants engaged in social interactions (playing, rubbing, petting) or simply swam with escorts. The clearest cases of caregiving, where the escort seemed to take a more protective role (i.e. when the infant assumed an infant position with the escort and when the escort herded the infant away from people who were at shore or in boats), all of these cases involved older escorts. In all of the instances in which escorts herded infants away from people, however, the mothers were also with people. Thus, escorts could be keeping infants away from their own mothers. It is difficult to document benefits to infants of associating with other infants, but opportunities to develop bonds with peers are likely to be important in such a social species. One pair of males, for example, frequently separated from their mothers to play and swim together when they were a few months old. They continued this preferential association for at least 5 years, 2 years after their mothers died (J. Mann, unpublished data). Such early male–male bonds may develop into the alliances that are so critical to adult males (Connor et al. 1992).

Escort associations that benefit the infant do not necessarily benefit the mother. In particular, interactions with other infants could impose a net cost on the mother (e.g. forcing increased maternal vigilance that, in turn, reduces maternal foraging) while offering a net benefit to the infant, because the infant is expected to devalue the costs to the mother by some fraction (reflecting the expected degree of relatedness between the infant and future siblings; Trivers 1974). Mothers and infants may thus experience conflict over the infant's associations with others, a possibility rarely considered in studies of infant associations with non-mothers.

Did Escorts Benefit?

Benefits to allomothers, particularly improved survivorship of their first-borns, are well documented in non-human primates (e.g. Epple 1978; Fairbanks 1990). Our results are most consistent with the 'learning to parent' hypothesis. Captive subadult females have been described as taking an interest in infants (e.g. Tavolga & Essapian 1957; Amundin 1986). Similarly, in this study, inexperienced females showed a strong interest in newborns compared with experienced adult females. Although inexperienced females may benefit from practicing mothering skills, this is difficult to quantify, because we cannot determine how much practice young females get in the wild, and how this affects their reproductive success. High mortality associated with captive first-borns (Cornell et al. 1987) suggests that practice does have some effect.

The main potential costs to escorts are probably opportunity costs, because they could be engaged in other valuable activities. During the first week, escorts may incur a cost for bolting with infants, because in 43% of the attempted bolts, the mother charged or threatened the bolter.

Experienced females that did associate with infants tended to be kin. With such a small sample all within one matriline, we could not test for effects of kinship on infant association and social separations, but in 9 of the 10 days during which experienced females associated with newborns more than inexperienced females did, the experienced females were kin. This result suggests that kinship influences escort identity.

Separations and the Behavioural Ecology

One of the notable features of Shark Bay dolphin infants was the fluidity with which they separated and reunited with the mother, thus starting to emulate, in the first few weeks of life, the fission–fusion nature of the society at large (also see Smolker et al. 1992, 1993). Most of these separations occurred during maternal foraging, when the mother repeatedly accelerated to chase and capture prey. Thus, faced with frequent separations, the infant must learn quickly to negotiate the marine environment. Infant-initiated departures from the mother are likely to provide the infant with opportunities to develop these essential survival skills. Other precocial mammals with

a long dependency period do not show such patterns (e.g. elephant calves: Lee 1987; humpback whales, *Megaptera novaeangliae*: Tyack & Whitehead 1983; southern right whales, *Eubalaena australia*: Taber & Thomas 1982). Species differences in maternal foraging behaviour could help to explain these patterns. Like other baleen whales, humpback and right whale females do not feed during the early stages of lactation. Thus, these mothers have no conflict between foraging activities and maternal care. Elephant calves may hinder their mothers' foraging, but mothers rarely accelerate and separate from their calves in order to feed.

Trade-offs between maternal foraging and vigilance are evident in toothed whales. Bernard & Hohn (1989) examined the stomach contents of female spotted dolphins, *Stenella attenuata*, in different reproductive states and suggested that lactating spotted dolphins feed on less desirable prey (flying fish, *Exocoetidae* sp.) so that they can remain near the surface with their infants, while pregnant females eat the preferred diet of squid (*Ommastrephidae* sp.), found at lower depths. Allomaternal care may be important for cetacean species in which mothers dive for long periods, thus leaving their infants, which are less proficient divers, at the surface (Papastavrou et al. 1989). Sperm whales are likely to decrease their dive synchrony if an infant is present, suggesting that non-mothers may alter their behaviour to the benefit of infants (Whitehead 1996). For deep-diving animals such as sperm whales, allomaternal care may be critical to the protection of infants and may be an important selection pressure favouring matrilineal group living (Whitehead 1996).

Although sperm whale units are stable and maintain continuous contact, bottlenose dolphin groups change composition frequently. Co-operative defence of offspring against predators may be critical for sperm whales (Arnbom et al. 1987), but less important for dolphins, which may primarily rely on detecting and out-manoeuvring their main predator, sharks (e.g. Corkeron et al. 1987; Cockcroft et al. 1989). Escorts neither provide obvious benefits nor impose obvious costs on mothers and infants. Future research dedicated to detailed acoustic recording and behavioural observations of mothers, infants and escorts during separations may help to identify who monitors whom across different contexts, and what age and sex class of escorts are preferred by mothers and infants. At this point, escorts should not be considered helpers, aunts, caregivers or babysitters. We may consider escorts afflicted with natal attraction, a condition that is likely to favour behaviour patterns that enhance their social and parenting skills and reproductive success.

REFERENCES

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49,** 227–267.

Altmann, J. 1980. *Baboon Mothers and Infants*. Cambridge, Massachusetts: Harvard University Press.

Amundin, M. 1986. Breeding the bottlenosed dolphin at the Kolmården Dolphinarium. *Int. Zoo Ybk*, **24/25,** 263–271.

Anderson, S. 1969. Epimeletic behavior in a captive harbour porpoise, *Phocaena phocaena*. In: *Investigations on Cetacea. Vol. 1* (Ed. by G. Pilleri), pp. 203–205. Berne: Braine Anatomy Institute.

Arnbom, R., Papastavrou, V., Weilgart, L. S. & Whitehead, H. 1987. Sperm whales react to an attack by killer whales. *J. Mammal.*, **68**, 450–453.

Bateson, P. 1991. Are there principles of behavioural development? In: *The Development and Integration of Behaviour: Essays in Honour of Robert Hinde* (Ed. by P. Bateson), pp. 19–39. Cambridge: Cambridge University Press.

Bernard, H. J. & Hohn, A. A. 1989. Differences in feeding habits between pregnant and lactating spotted dolphins *Stenella attenuata*. *J. Mammal.*, **70**, 211–215.

Best, P. B. 1979. Social organisation in sperm whales, *Physeter macrocephalus*. In: *Behavior of Marine Animals. Current Perspectives in Research 3* (Ed. by H. E. Winn & B. L. Olla), pp. 227–289. New York: Plenum Press.

Cockcroft, V. G., Cliff, G. & Ross, G. J. B. 1989. Shark predation on Indian Ocean bottlenose dolphins *Tursiops truncatus* off Natal, South Africa. *S. Afr. J. Zool.*, **24**, 305–310.

Connor, R. C. & Smolker, R. A. 1985. Habituated dolphins *Tursiops* sp. in Western Australia. *J. Mammal.*, **662**, 398–400.

Connor, R. C., Smolker, R. A. & Richards, A. F. 1992. Dolphin alliances and coalitions. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 415–443. Oxford: Oxford University Press.

Cornell, L. H., Asper, E. D., Antrim, J. E., Searles, S. S., Young, W. G. & Goff, T. 1987. Progress report: results of a long-range captive breeding program for the bottle-nose dolphin *Tursiops truncatus* and *Tursiops truncatus gilli*. *Zool. Biol.*, **6**, 41–54.

Corkeron, P. J., Morris, R. J. & Bryden, M. M. 1987. Interactions between bottlenose dolphins and sharks in Moreton Bay, Queensland. *Aquat. Mammal.*, **13**, 109–113.

Dunn, R. 1987. Variable-width framed rectangle charts for statistical mapping. *Am. Statist.*, **41**, 153–156.

Epple, G. 1978. Reproductive and social behavior of marmosets with special reference to captive breeding. *Prim. Med.*, **10**, 50–62.

Fairbanks, L. A. 1990. Reciprocal benefits of allomothering for female vervet monkeys. *Anim. Behav.*, **40**, 553–562.

Fairbanks, L. A. 1993. Juvenile vervet monkeys: establishing relationships and practicing skills for the future. In: *Juvenile Primates: Life history, Development and Behaviour* (Ed. by M. E. Pereira & L. A. Fairbanks), pp. 211–227. New York: Oxford University Press.

Fleiss, J. L. 1981. *Statistical Methods for Rates and Proportions*. New York: John Wiley.

Gittleman, J. L. 1985. Functions of communal care in mammals. In: *Evolution: Essays in Honour of John Maynard Smith* (Ed. by P. J. Greenwood, P. H. Harvey & M. Slatkin), pp. 187–205. Cambridge: Cambridge University Press.

Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Harvard University Press.

Gurevich, V. S. 1977. Post natal behaviour of an Atlantic bottlenose dolphin calf. In: *Breeding Dolphins: Present Status, Suggestions for the Future* Report No. MMC-76-/07 (Ed. by S. H. Ridgway & K. Benirschke), pp. 168–175. Washington D.C.: U.S. Marine Mammal Commission.

Haenal, N. 1986. General notes on the behavioural ontogeny of Puget Sound killer whales and the occurrence of allomaternal behaviour. In: *Behavioural Biology of Killer Whales* (Ed. by B. C. Kirkevold & J. S. Lockard), pp. 285–300. New York: Alan Liss.

Hass, C. C. 1990. Alternative maternal-care patterns in two herds of bighorn sheep. *J. Mammal.*, **71**, 24–35.

Hrdy, S. B. 1976. Care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Adv. Study Behav.*, **6**, 101–158.

Hrdy, S. B. 1988. Skeptic amidst the converted. *Am. J. Primatol.*, **14**, 103–106.

Hutt, S. J. & Hutt, C. 1970. *Direct Observation and Measurement of Behavior*. Springfield, Illinois: Charles C. Thomas.

Johnson, C. M. & Norris, K. S. 1994. Social Behavior. In: *The Hawaiian Spinner Dolphin* (Ed. by K. S. Norris, B. Würsig, R. S. Wells & M. Würsig), pp. 243–286. Berkeley, California: University of California Press.

Komdeur, J. 1994. Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*. *Behav. Ecol. Sociobiol.*, **34**, 175–186.

Leatherwood, S. 1977. Some preliminary impressions on the numbers and social behaviour of free-swimming bottlenose dolphin calves. In: *Breeding Dolphins: Present Status, Suggestions for the Future* Report No. MMC-76-/07 (Ed. by S. H. Ridgway & K. Benirschke), pp. 143–158. Washington D.C.: U. S. Marine Mammal Commission.

Lee, P. C. 1987. Allomothering among African elephants. *Anim. Behav.*, **35**, 278–291.

Lorenz, K. Z. 1937. The companion in the bird's world. *Auk*, **54**, 245–273.

Mann, J. & Smuts, B. B. In press. Development and behaviour among wild bottlenose dolphin newborns (*Tursiops* spp.). *Behaviour*.

Mumme, R. L. 1992. Do helpers increase reproductive success? An experimental analysis in the Florida scrub jay. *Behav. Ecol. Sociobiol.*, **31**, 319–328.

Muroyama, Y. 1994. Exchange of grooming for allomothering in female patas monkeys. *Behaviour*, **128**, 103–119.

Nicolson, N. 1987. Mothers, infants and adult females. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. Struhsaker), pp. 330–342. Chicago, Illinois: University of Chicago Press.

Nishida, T. 1983. Alloparental behaviour in wild chimpanzees of the Mahale Mountains, Tanzania. *Folia Primatol.*, **41**, 1–33.

Norris, K. S. & Prescott, J. H. 1961. Observations on Pacific cetaceans of California and Mexican waters. *Univ. Calif. Publs Zool.*, **634,** 291–402.

Packer, C., Lewis, S. & Pusey, A. E. 1992. A comparative analysis of non-offspring nursing. *Anim. Behav.*, **43,** 265–281.

Papastravrou, V., Smith, S. C. & Whitehead, H. 1989. Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. *Can. J. Zool.*, **67,** 839–846.

Quiatt, D. 1979. Aunts and mothers: adaptive implications of allomaternal behavior in non-human primates. *Am. Anthropol.*, **81,** 310–319.

Reidman, M. L. 1982. The evolution of alloparental care and adoption in mammals and birds. *Q. Rev. Biol.*, **57,** 405–435.

Ross, G. J. B. & Cockcroft, V. G. 1990. Comments on Australian bottlenose dolphins and taxonomic status of *Tursiops truncatus* Ehrenberg, 1832. In: *The Bottlenose Dolphin* (Ed. by S. Leatherwood & R. R. Reeves), pp. 101–128. New York: Academic Press.

Shopland, J. M. & Altmann, J. 1987. Fatal intragroup kidnapping in yellow baboons. *Am. J. Primatol.*, **13,** 61–65.

Silk, J. 1980. Kidnapping and female competition among captive bonnet macaques. *Primates*, **211,** 100–110.

Smolker, R. A., Richards, A. F., Connor, R. C. & Pepper, J. W. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, **123,** 38–69.

Smolker, R. A., Mann, J. & Smuts, B. B. 1993. Use of signature whistles during separations and reunions among wild bottlenose dolphin mothers and calves. *Behav. Ecol. Sociobiol.*, **33,** 393–402.

Stanford, C. B. 1992. Costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). *Behav. Ecol. Sociobiol.*, **30,** 29–34.

Taber, S. & Thomas, P. 1982. Calf development and mother-calf spatial relationships in southern right whales. *Anim. Behav.*, **30,** 1072–1083.

Tavolga, M. C. & Essapian, F. S. 1957. The behaviour of the bottle-nosed dolphin *Tursiops truncatus*: mating, pregnancy, parturition and mother-infant behaviour. *Zoologica*, **421,** 11–31.

Thurman, G. D. & Williams, M. C. 1986. Neonatal mortality in two Indian Ocean bottlenose dolphins bred in captivity. *Aquat. Mammal.*, **123,** 83–86.

Trivers, R. L. 1974. Parent-offspring conflict. *Am. Zool.*, **14,** 249–264.

Tyack, P. L. & Whitehead, H. 1983. Male competition in large groups of wintering humpback whales. *Behaviour*, **83,** 1–23.

Wells, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: *Dolphin Societies: Discoveries and Puzzles* (Ed. by K. S. Norris, B. Würsig, R. S. Wells & M. Würsig), pp. 199–225. Berkeley, California: University of California Press.

Wells, R. S., Scott, M. D. & Irvine, A. B. 1987. The social structure of free-ranging bottlenose dolphins. In: *Current Mammalogy. Vol. 1* (Ed. by H. H. Genoways), pp. 247–305. New York: Plenum Press.

Whitehead, H. 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol.*, **38,** 237–244.

Würsig, B. & Würsig, M. 1977. The photographic determination of group size, composition, and stability of coastal porpoises *Tursiops truncatus*. *Science*, **198,** 755–756.