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Mother-calf spatial relationships and calf development in the captive bottlenose dolphin (*Tursiops Truncatus*)

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Abstract

The development of two captive male bottlenose dolphin (*Tursiops truncatus*) calves, differing in age by a year, as well as changes in spatial relationships with their respective mothers were observed on five distinct occasions at roughly a month's interval. Recorded were the number of times each calf strayed from its mother, each mother retrieved its calf and vice versa, as well as how long each mother-calf couple engaged in swimming close together or over three metres apart. Data analyses indicated a shift in responsibility for proximity maintenance from mother to calf and for distance maintenance from calf to mother, a pattern consistent with Trivers' (1972) theory of parent-infant conflict, predicting disagreement between mother and infant over the amounts of investment to be given and received. Analyses of variance also showed significant differences through time over how long each couple spent swimming more than three metres apart ($P<0.01$) and a significant difference in this behaviour between the couples ($P<0.025$), as well as in the time spent swimming close together ($P<0.01$) and between couples ($P<0.05$). In addition the younger calf appeared to be more precocious than the older one, possibly because of the influence of an older and more developed calf present in the same pool 24 hours a day.

Introduction

Despite the existence of the well-established and ancient occupation of whaling, or perhaps even because of it, man has been in awe of cetaceans for centuries (Cousteau, 1974). Cetaceans—whales, dolphins and porpoises—are schooling, ocean dwelling, air breathing mammals, known to possess very large and convoluted brains (McBride & Hebb, 1947), with an apparently highly developed cerebral cortex (Kruger, 1959). Such factors are often believed to be indicative of high levels of intelligence and psychological development (McPhail, 1982) thus giving a considerable interest to the behaviour of these animals. In fact, 'no research on cetacea has attracted more public attention in recent years than work on their behaviour, communication and intelligence levels' (Gaskin, 1982, p. 112). Yet as Gaskin (1982) also states, prejudices, anthropomorphic influences, magazine and newspaper publicity and the preconceptions that popular books have the power to instill could easily bias our interpretations of cetacean behaviour, making it therefore imperative that it be examined '... in the strictest possible terms...' (Gaskin, 1982, p. 115).

Studies of mother-infant relationships among cetaceans both in their natural habitat (Norris *et al*, 1977; Taber & Thomas, 1982) and in captivity (McBride & Kritzler, 1951; Tavolga & Essapian, 1957), have emphasized the high degree of positive 'thigmotaxis' (Taber & Thomas, 1982, p. 1072), between infant and mother, referring to the close proximity maintained between the two. This was already a well-known phenomenon centuries ago, when whalers fired upon calves in the certainty that the mothers would remain near them and thus provide an easy target.

It is undoubtedly difficult for scientists to reliably measure behaviour, and to apply to behavioural observations any acceptable quantitative measurements. Studies of cetaceans in the wild are even more fraught with difficulties, including very basic ones such as unfavourable weather conditions and maintaining contact with the animals for extended periods of time. Studies conducted in captivity would therefore carry obvious advantages because of the confined and easily controllable environment it provides. Yet the complex and controversial question as to whether data gathered in captivity is reliable and valid obviously arises. It is highly likely that the captive environment, by placing different demands on the animals, distorts their behaviour. 'Among the important factors which may seriously distort the behaviour of captive dolphins can be included the size and shape of their pool and the psychological effects of close confinement which result...' (Gaskin, 1982, p. 116). Studies of animal behaviour carried out in the wild tend to be high in external validity in that the behaviours recorded would be those exhibited in a natural environment, not distorted by captivity, but nevertheless low in internal validity because of the increased difficulty of systematically gathering concise data. Studies carried out in captivity on the other hand are apt to be more accurate and systematic as far as the data-gathering process is concerned making them therefore high in internal validity, although such studies would be lower in external validity due to the probable behavioural changes captivity brings about. Nevertheless Gaskin (1982) concludes that when data from wild-ranging populations is available for comparison with that gathered from studies in captive colonies, the latter can be validated.

The aim of this study is to investigate in as systematic and scientific manner as possible, the behavioural development of two captive bottlenose calves (*Tursiops truncatus*), their spatial relationships towards their respective mothers, how these relationships may change through time reflecting the development of independence as well as attempting to provide a comparison of these factors between the two calves, one being a year older than the other.

The bulk of research so far carried out on mother-infant relationships and nurturant behaviour both in captivity and in the wild has yielded compatible evidence. The period of gestation in female bottlenose dolphins lasts eleven to twelve months. Birth, a process which usually lasts only a few minutes is by posterior presentation, the newborn calf immediately surfacing to breathe, often helped by the mother. Frequently, the pregnant female allows another female to swim with her during the period of gestation and assist her during parturition. These females, referred to as 'aunties', even though their exact genetic relationship to the mother is unknown, have been observed helping the mother to push stillborn calves to the surface, presumably to help them to breathe, and in captivity have sometimes been observed to take over and swim with the young calf while its mother is at the feeding platform. It has also been noted that straight after birth the mother and calf swim close together in what is termed 'echelon formation', where the calf, showing no swimming movements of its own, positions itself above and to one side of the mother 'perhaps riding the compression wave generated by the adult's swimming movements' (Norris & Prescott, 1961). During the first one or two months of life this position is maintained but 'gradually the baby then becomes accustomed to what the observers consider the typical rest position, under the mother's tail, with the top of its head lightly touching her abdomen' (Tavolga & Essapian, 1957, p. 21).

Most importantly, it has emerged that among cetaceans, 'epimeletic behaviour' (Scott, 1958), a term which indicates the giving of care and attention, is prolonged towards their young, and that 'close affiliation between the newborn and the mother continues for an extended period of time and dependency may persist even into adulthood' (Defran & Pryor, 1980). Typically, in the first few months of life the mother does not allow the calf to stray or leave her side. As the calf grows older though, its tendency to stray from the mother to explore its surroundings and presumably to engage in 'play' with other young animals increases.

Such increased exploratory behaviour has emerged in studies of mother-calf behaviour patterns in other mammals such as for example the moose (*Alces alces shirasi*) in which Altmann (1963) showed that increasing investigative behaviour is exhibited by the calf as a function of its development. Jay (1963) has shown that a langur calf (*Presbytis entellus*) will shift from initial stages of extreme discomfort if it is not in contact with its mother's body, to the stage when it is 1 month old when 'the infant moves freely within a radius of 3 to 5 feet of the mother, who frequently touches or looks at it but allows it to remain away as long as 4 minutes at a time' (Jay, 1963, p. 290). Similarly De Vore (1963) has shown how 3 month old baboons shift from straying very rarely from their mothers' arms to remaining 'away from the mother for longer periods of play and exploration' (De Vore, 1963, p. 318). In cetaceans too, the mother's tolerance to her calf straying increases with time, although maternal care is known to continue for a number of months or even years after birth.

Such intense caretaking behaviour on the part of the mother would appear to have very important survival value for the calf. In an instance reported by Tavolga & Essapian (1957), a female bottlenose dolphin, Spray, at Marine Studios, Marineland, Florida, gave birth to her first calf, Peggy, at 7 years of age. Spray appeared to show a 'distinct lack of care toward her infant' (Tavolga & Essapian, 1957, p. 22). 'She remained at the feeding platform throughout almost the entire feeding, returning to the calf only once or twice during this five or six minute period. The infant was alone during this time, except for the momentary visits of her mother' (Tavolga & Essapian, 1957, p. 23). Furthermore, Spray left the baby 'for unusually long periods of time, and failed to remove her from situations in which she might have been injured inadvertently by other animals' (Tavolga & Essapian, 1957, pp. 22–23). Although the reason for the mother's behaviour is not known, it resulted in the calf's death at 15 days of age.

Cetaceans are long-lived animals, the absolute lifespan among odontocetes (toothed whales) varying from about 13 to 16 years in the smaller species such as the common porpoise (*Phocoena phocoena*) 'to a maximum of about 50 years in the sperm whale *Physeter catodon*...(and)...25 years in *Tursiops truncatus*...' (Gaskin, 1982, p. 307). Thus, although the main initial aim of involved maternal care is undoubtedly the physical survival of the calf, it is possible that such care extends beyond the period of the calf's need for suckling and protection. Dr. Mike

Bigg of the Sea Mammal Research Programme of Vancouver's Pacific Biological Station has suggested that the reason why Killer whales (*Orcinus orca*), odontocetes of the Delphinidae family like Tursiops, stay with their mothers even into adulthood and don't move to any other pod is to allow a very long training period to take place, undoubtedly permitting the calf 'to survive better than had it stayed with its mother for a year or two and then had to live by itself' (Bigg, 1985). In a very cautious, (if not a timid manner), Bigg also suggested that by staying with its mother the calf is '... likely to learn the traditions of the mother, and so end up with cultures ... within pods or within the communites that would be unique to that group or community' (Bigg, 1985). According to Bigg, this phenomenon has all the makings of a culture transmission process. Because they are a very long-lived and intelligent animal 'they've got these long-term bonds so they can teach their young whatever lifestyle it is that that pod lives' (Bigg, 1985). This of course, has been suggested to be the case for other altricial and long-lived species such as humans.

In general then, the mothers keep calves close to their sides, retrieving them at once if they stray, they push the calves away from unusual or new objects and watch them constantly. It has been observed that when a calf repeatedly swims away from the mother the latter's actions tend to become more aggressive. As reported in one instance by Tavolga (1966)

> 'after such a series of flights by the young one, the mother swam over the young animal and pinned him down to the floor for some thirty seconds, effectively immobilizing him. She released him only when she rose to take a breath of air. On several occasions the mother swam under the young one on her back, and, catching him between her flippers raised him out of the water on her ventral side, holding him just above the surface of the water. He wriggled vigorously in the air. After a minute of this treatment, the baby was seen to swim quietly by the mother's side for a time, making no further efforts to get away'.
>
> (Tavolga, 1966, p. 721).

This type of maternal care is more frequently observed in the first few months of the calf's life and gradually decreases as the calf grows older. Nursing in captivity continues until about 18 months, and by then the calf spends more time away from the mother (Tavolga, 1966). Nevertheless, as Tavolga & Essapian (1957) noted '... mother-young pairs may persist on an intermittent basis for remarkably long periods. For example, in the Atlantic bottlenose dolphin the members of a mother-young pair may return to each other in time of stress for years after the young has reached adulthood' (Norris & Dohl, 1980, p. 229). Similarly, as reported by Essapian (1953) two 4 and 6 year old dolphins would look for their mothers and join them when they were frightened or sleepy.

In the wild, studies have also shown proximity/distance relationships between mother and calf to change through time. For example, on observing a resident pod of Killer whales (*Orcinus orca*) off the coast of Vancouver, Dr. Mike Bigg noted that the calf will stay very close to its mother and travel close behind her, although as years pass such proximity decreases. This is probably indicative of the gradual increase in the calf's independence. Taber & Thomas (1982) carried out a systematic study of calf development and mother-calf spatial relationships in Southern right whales (*Eubalaena australis*) in the wild, off the Argentine coast. They found that close proximity between mother and calf was maintained 90% of the time in the first few weeks of the latter's life. Many more leaves and approaches to and from the mother were later initiated by the calves, combined with farther strayings. In yearling calves though, mothers left calves more than they approached them, probably due to weaning processes taking place and the calves were then found to be more responsible for maintaining contact. Such data is consistent with Trivers' theory of parent-offspring conflict in which the mother would be expected to protect her investment initially '... and later, close to weaning, with increased demands on her personal fitness, to be inclined to spend less energy on the calf, and to hasten its weaning. The calf... would be inclined to remain dependent upon her for as long as possible' (Taber & Thomas, 1982, p. 1080).

With an aim similar to Taber & Thomas's (1982) study of following calf development in cetaceans, albeit captive ones, and the changes in mother-calf spatial relationships through time, this investigation aims to record patterns of bottlenose dolphin calves straying from their mothers, how tolerant the mothers are of this behaviour in terms of their retrievals, how often the mothers stray from their calves and how often the calves retrieve them, also including a data collection on the amounts of time each mother-calf pair engages in close swimming or swimming at more than three metres distant from each other.

According to past data on mother-infant behaviour patterns in cetaceans one would expect as the calf grows older a decrease in the amounts of time each mother-calf pair spends swimming close together and an increase in their swimming over three metres distant from each other. One would also expect increasing instances of calves straying from their mothers through time and an initial high level of calf retrieval on the part of the mothers which would presumably decrease as the calf grows older. Also expected are low levels of mothers straying from their calves during the latter's early months of life, but nevertheless increasing through time. In accordance with Trivers' (1974) theory of parent-offspring conflict we would expect at later stages of the calf's development, for the mothers to become primarily responsible for straying and the calves primarily responsible for retrieving, possibly because 'natural selection working on the mother favors her halting parental investment while natural selection acting on the offspring favors his eliciting the parental investment' (Trivers, 1974, p. 251).

Method

Subjects
The study was conducted at Windsor Safari Park Marineland on two bottlenosed dolphin (*Tursiops truncatus*) mother-infant pairs: Lulu, an 18 year old female and her male calf, Juno, born on the 8th June 1984, at 11.30 pm, and Honey, an 18 year old female and her male calf, Neptune, born on 22nd June 1985 at 6.20 am. Both calves were fathered by Smartie, a 22 year old male present at Windsor Safari Park since 1971.

Apparatus
Data was initially collected through the use of a microprocessor—the 'MORE-Data Collection Unit', making it possible to store data in the form of various numerically encoded behaviour patterns. Using the 'timed event mode', 'the observer enters events as they occur and the MORE automatically clocks and stores each event in sequence with its duration' (MORE-Data Collection Unit Manual p1-1). In later sessions weather conditions prevented the outdoor use of the MORE, thus data was collected by entering the behaviour codes as they occurred in a tape recording, to be then fed into the MORE under more favourable conditions.

It was therefore possible to obtain an accurate measurement of how many times a particular event like straying or retrieving occurred, which dolphin exhibited such behaviour, and how long a behaviour like the mother and calf swimming close together or far apart lasted.

Procedure

The two mothers and calves were kept in an oval-shaped back pool separate from the rest of the dolphins (*Tursiops truncatus*) and killer whales (*Orcinus orca*). This pool, measuring 26 metres at its longer axis, 12.5 metres at its shorter axis and 3.5 metres in depth, was built partly above the ground, with 7 portholes for underwater viewing and a bridge for public viewing above water. Observations were carried out from the surface as visibility from the portholes around the pool was often poor.

The first sets of data were collected on the 8th and 9th November 1985, when Juno was 17 months old and Neptune 5 months old, for 45 minutes in separate 5 minute sessions per mother-calf pair. The second set of data was collected on the 18th December 1985 for 15 minutes per mother-calf pair, also in 5 minute sessions. On the 11th February 1986, 18th March and 15th April, data was collected for 25 minutes on each of these dates per mother-calf pair, in 5 minute sessions. On the 15th April, when the final data collection took place, Juno was 22 months old and Neptune 10 months old.

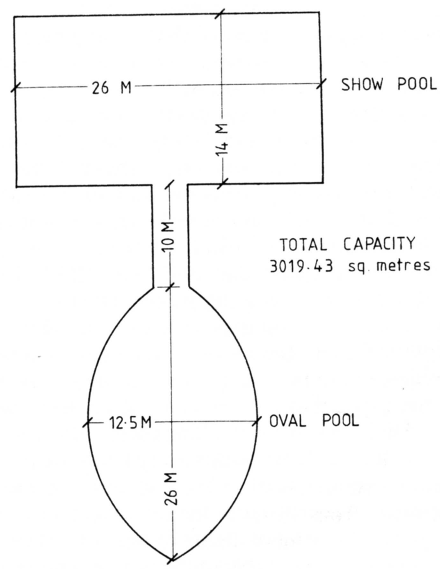

DIAGRAM OF POOL

Allowing an accurate time lapse of a month between the five separate occasions in which data was collected proved impossible due to adverse weather conditions and occasional technical problems. The number of five minute sessions on the different dates in which data was gathered also varied for the same reasons as above. The five minute sessions were alternated between mother-calf pairs, so that if for 5 minutes data was gathered for Juno and Lulu, for the next five it would be gathered for Neptune and Honey.

The behaviours observed and recorded consisted of straying and retrieving instances as exhibited by either one of the mothers or calves, for which different codes were given. Also recorded were the amounts of time mother and calf spent swimming close together or over three metres distant from each other.

The following table summarizes the codes given to the four different subjects exhibiting the behaviours in question.

Table A. Showing food intake of calves Juno and Neptune on the dates in which data was collected:

8 November 1985;	*first am; feed*	*10.30 am*	*13.30 pm*		*Total*
Juno	6.5 lbs + vits	3.5 lbs	3 lbs		13 lbs
Neptune	—	—	—		—
9 November 1985;			*14.20 pm*		
Juno	7 lbs + vits	3.5 lbs	3.5 lbs		14 lbs
Neptune	—	—	—		—
18 December 1985;			*14.30 pm*		
Juno	6.5 lbs + vits	3.5 lbs	3 lbs		13 lbs
Neptune	6	—	—		—
11 February 1986;		*12.00 pm*	*14.00 pm*	*15.00 pm*	
Juno	5.25 lbs + vits	4.5 lbs	0.25 lbs	0.5 lbs	10.5 lbs
Neptune	sprats	sprats	sprats	sprats	sprats
18 March 1986;	*first feed*	*second feed*	*third feed*		
Juno	2 lbs + vits	1 lb	1 lb		4 lbs
Neptune	sprats	sprats	sprats		sprats
15 April 1986;	*first feed*	*12.30 pm*	*16.30 pm*		
Juno	8 lbs + vits	4 lbs	4 lbs		16 lbs
Neptune	4 lbs + vits	2 lbs	2 lbs		8 lbs

Subject 1—Juno
Subject 2—Lulu
Subject 3—Neptune
Subject 4—Honey

Behaviour	*Code*
Swim close together	00
Juno strays from Lulu	10
Lulu strays from Juno	20
Swim over 3 metres apart	03
Juno retrieves Lulu	11
Lulu retrieves Juno	22
Swim close together	00
Neptune strays from Honey	30
Honey strays from Neptune	40
Swim over 3 metres apart	03
Neptune retrieves Honey	33
Honey retrieves Neptune	44

The records of fish intake of the animals kept at the dolphinarium by the trainers indicate, as expected, a gradual increase of fish intake on the part of the calves as a function of time. The table showing the fish intake of the calves on the dates in which data was collected shows no particular trend probably because the dates are too far apart from each other and are too few in number for any significant changes to be apparent. It appears nevertheless quite clear that the younger calf (Neptune) shifted from eating no fish at all, probably because he was still suckling, to eating sprats, and to eating 8 lbs of fish on the 15th of April 1986. What probably occurred between those dates was a gradual change in feeding habits, possibly characterized by decreasing suckling as a result of weaning and increasing fish intake.

The recorded fish intakes show quite a high level of variability from one day to the next in a few cases. One such case is apparent also in table A, being particularly noticeable in the case of the older calf (Juno). For example on the 11th February it is known that Juno ate 10.5 lbs of fish, only 4 lbs on the 18th March and 16 lbs on the 15th April. The reasons why on certain days the intake of fish is significantly lower than on others could be many and varied, but as indicated by the trainers it could be because initially the calves were not given a fixed amount of fish at each feeding, but rather, tended to each until satisfied, probably resulting in little appetite at the next feedings if not in the next days.

Of particular interest is the precocity of the younger calf (Neptune) with respect to Juno, which seems to have reflected itself also in the two calves' fish intake patterns. According to the records and the trainers' reports, Neptune started eating sprats at a much younger age than Juno had. This precocity factor is consistent with the true straying and retrieving patterns emergent from the data in which it appears that weaning and in dependence started to take its course earlier with Neptune than with Juno.

Results

Straying and Retrieving Patterns

Hinde (1974) in studying mother-infant interactions in Rhesus monkeys, and Taber & Thomas (1982) investigating mother-calf spatial relationships in Southern right whales, calculated a 'proximity quotient' to illustrate the calf's and mother's relative roles in maintaining proximity. In this study, a similar method was employed to calculate whether the mother or the calf was primarily responsible for retrieving the other when they had been swimming over three metres distant from each other. This

Table 1(a). Retrieval quotients for both mother-calf couples. Negative value = mother primarily responsible for retrieving. Positive value = calf primarily responsible for retrieving

S's 1+2 (Juno & Lulu) calf's age (weeks)	Retrieval quotient	S's 3+4 (Neptune & Honey) calf's age (weeks)	Retrieval quotient
74.0	−0.04	19.0	−0.07
79.6	−0.13	24.6	−0.07
87.3	0.08	32.4	−0.04
92.3	0.00	37.4	−0.16
96.3	0.08	41.4	0.12

Table 1(b). Straying quotients for both mother-calf couples. Positive value = calf primarily responsible for straying. Negative value = mother primarily responsible for straying

S's 1+2 (Juno & Lulu) calf's age (weeks)	Straying quotient	S's 3+4 (Neptune & Honey) calf's age (weeks)	Straying quotient
74.0	0.09	19.0	0.09
79.6	0.06	24.6	0.00
87.3	0.08	32.4	0.20
92.3	0.00	37.4	0.12
96.3	−0.04	41.4	−0.08

measurement is referred to as the RETRIEVAL QUOTIENT and is calculated by subtracting the proportion of retrieval instances made by the mother from the proportion of retrieval instances carried out by the calf on each of the five different dates in which data was collected. If the value obtained in the quotient is positive, then the calf was primarily responsible for retrieving, whereas if it is negative then the mother is primarily responsible. Following the same principle, a 'straying quotient' was calculated, a positive value in the quotient indicating that the calf was primarily responsible for straying and a negative one indicating that the mother was primarily responsible for doing so.

Table 1(a) summarizes the retrieval quotients and Table 1(b) summarizes the straying quotients for both mother-calf couples.

The retrieval quotients indicate that there was a shift from both mothers being primarily responsible for retrieving their respective calves to the calves retrieving their mothers. This shift occurred in subjects 1 and 2 when the calf in question, subject 1 (Juno), was 87.3 weeks old and in subjects 3 and 4 when the calf, subject 3 (Neptune), was 41.4 weeks old. Straying quotients show a similar shift in responsibility. Subject 2 (Lulu) became primarily responsible for straying from its calf (Juno) when the latter was 96.3 weeks old, whereas before that the calf had exhibited most of the straying patterns. In subjects 3 and 4 such a shift occurred when the calf was 41.4 weeks old. It should be noted however, that it would be inaccurate to claim the shifts in responsibility actually occurred at the ages stated. They may have occurred at any time between the previous data collection and the one where they were first observed. The age noted in relation to the responsibility shift is merely indicative of how old the calf was when that different pattern was observed for the first time.

Although there are distinct changes from positive to negative values in the case of straying, and from negative to positive in the case of retrieving, the magnitudes of the quotient values are not constant in the way they increase or decrease through time. This is apparent in figures 1 and 2.

Pearson's Correlation coefficient (r) was obtained to examine the degree of relationship between the age of each calf and the retrieval or straying quotients. The results were as follows:

1. There was no significant correlation between the age of subject 3 (Neptune) and the retrieval quotient ($r = 0.39$, $N = 5$, $r < 0.67$, $P > 0.05$ therefore NO SIGNIFICANT CORRELATION).

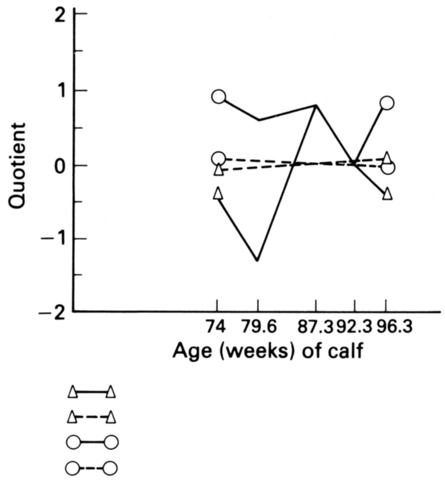

Figure 1. Subjects 1 and 2 (Juno and Lulu).
△——△ Retrieval quotient, △----△ Best fitting line through retrieval quotient data, ○——○ Straying quotient, ○----○ Best fitting line through straying quotient data.

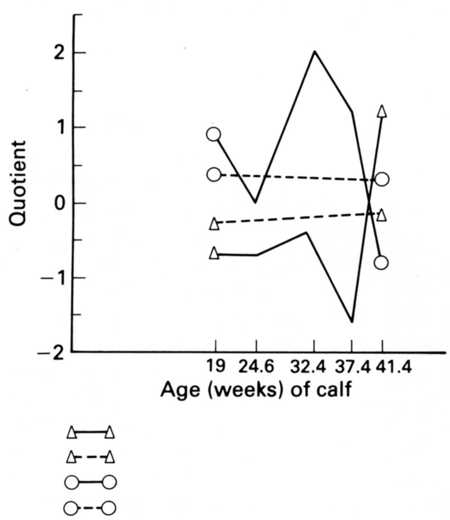

Figure 2. Subjects 3 and 4 (Neptune and Honey).
△——△ Retrieval quotient, △--- △ Best fitting line through retrieval quotient data, ○——○ Straying quotient, ○---○ Best fitting line through straying quotient.

2. There was no significant correlation between the age of subject 3 (Neptune) and the straying quotient ($r=0.21$, $N=5$, $r<0.67$, $P>0.05$ therefore NO SIGNIFICANT CORRELATION).
3. There was found to be a significant positive correlation between the age of subject 1 (Juno) and the retrieval quotient ($r=0.21$, $N=5$, $r<0.67$, $P<0.05$ therefore CORRELATION POSITIVE AND SIGNIFICANTLY DIFFERENT FROM ZERO).
4. There was found to be a significant negative correlation between the age of subject 1 (Juno) and the straying quotient ($r=-0.86$, $N=5$, $r<0.00$ $P<0.05$ therefore CORRELATION NEGATIVE AND SIGNIFICANTLY DIFFERENT FROM ZERO).

In addition, linear regressions were calculated to include best fitting straight lines to the retrieving and straying quotient graphs (Fig. 1 and 2).

Two-way analyses of variance (A1B1W) were carried out to test for possible significant differences between the 5 main dates in which data was collected (factor A), and between the two mother-calf couples (factor B). This was done separately for the two behaviour categories of mother and calf swimming more than three metres distant from each other (03) and mother and calf swimming close together (00). In these analyses of variance the method of unweighted means was employed because of the unequal numbers of five minute observational sessions on the different dates.

Analyses of the amounts of time mother and calf couples spent swimming over three metres distant from each other (03) resulted in a highly significant main effect in the five observation date sets (factor A, the repeated measures factor) [$F=4.444$, d.f. $(a)=4$, d.f. $\text{error}=43$, $P<0.01$], and a significant main effect in factor B, the two mother-calf couples [$F=3.502$, d.f. $(b)=1$, d.f. $\text{error}=43$, $P<0.025$]. There was no interaction between the two factors.

The second analysis of variance was carried out on the amounts of time mother-calf couples spent swimming close together (00). This resulted in a highly significant main effect in factor A, the 5 observation dates [$F=8.06$, d.f. $(a)=4$, d.f. $\text{error}=43$, $P<0.01$], and a significant main effect in factor B, the two mother-calf couples [$F=5.33$, d.f $(b)=1$, d.f. $\text{error}=43$, $P<0.05$].

Thus the amounts of time mother and calf couples spent swimming over three metres apart differ significantly through time at the 1% level, and there was a significant difference in this pattern between the two mother-calf couples at the 2.5% levels. In the times spent swimming close together there was a significant difference through time at the 1% level and a significant difference between mother-calf couples at the 5% level.

Figs. 3(a), 3(b), 4(a) and 4(b) summarize the mean amounts of time in seconds, mother-calf pairs spent swimming close together or far apart at the different ages of the calf in question.

Subjects 1 and 2 (Juno and Lulu) spent, through all 5 observations, a gross mean of 122.04 seconds in a 5 minute session swimming close together. The gross

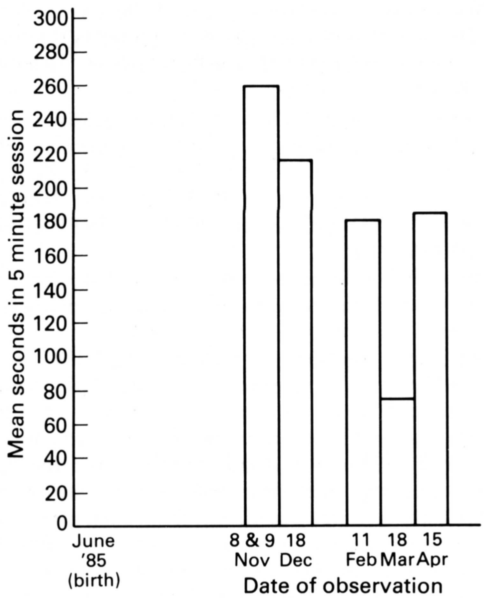

Figure 3(a). Graph showing mean amounts of time (in seconds per 5 min. session) subjects 3 and 4 (Neptune and Honey) spent swimming close together.

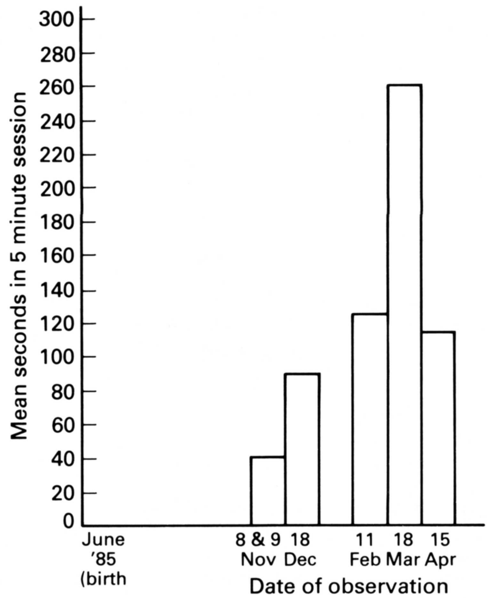

Figure 4(a). Graph showing mean amounts of time (in seconds per 5 min. session) subjects 3 and 4 (Neptune and Honey) spent swimming more than three metres apart.

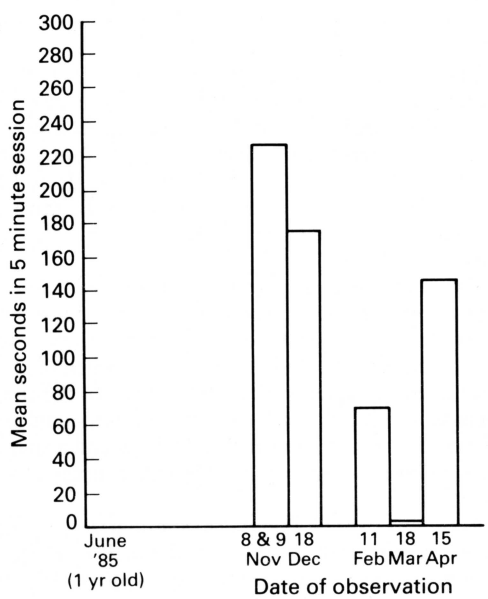

Figure 3(b). Graph showing mean amounts of time (in seconds per 5 min. session) subjects 1 and 2 (Juno and Lulu) spent swimming close together.

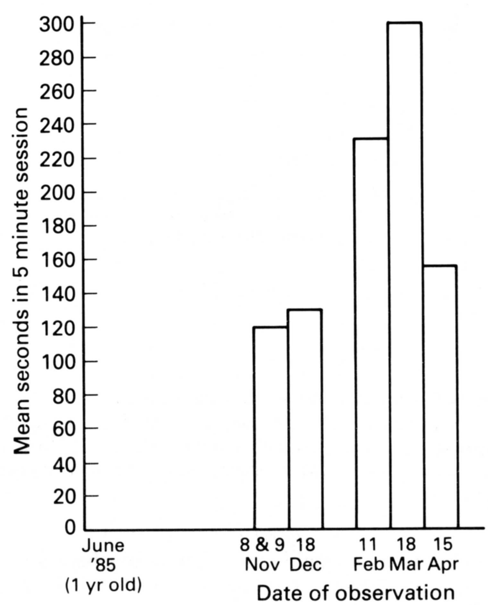

Figure 4(b). Graph showing mean amounts of time (in seconds per 5 min. session) subjects 1 and 2 (Juno and Lulu) spent swimming more than three metres apart.

mean for subjects 3 and 4 (Neptune and Honey) was 181.00 seconds. For the pattern of mother and calf swimming over three metres distant from each other, the gross mean for subjects 1 and 2 was 187.92 seconds and for subjects 3 and 4, 157.16 seconds.

Discussion

The data obtained from this study appears to conform to expectations of behavioural changes to be exhibited by captive bottlenose dolphin calves and the relationships with their mothers. From the data emerge patterns of behavioural development consistent with those obtained from studies of mother-infant interaction and infant development in other mammals, namely primates (De Vorr, 1963; Nash, 1978) and cetaceans (McBride & Kritzler, 1951; Tavolga & Essapian, 1957; Taber & Thomas, 1982).

The development of infant independence that can be expected to occur in most mammals, albeit at different ages, led to the prediction that the amounts of time the calves would spend swimming very close to their mothers, as well as the amounts of time they would engage in swimming more than three metres distant from them, would vary as a function of the calves' ages. Data analyses confirmed these predictions. It should be noted that although the first systematic observations were carried out on the 8th and 9th November 1985, when the older calf, subject 1 (Juno) was 74 weeks old and subject 3 (Neptune) was 19 weeks old, there are fairly accurate reports of each calf's earlier behaviour. For example, it is known that for about a month after birth the mother-calf pairs engaged in almost constant echelon swimming. On observing subjects 3 and 4 (Honey and Neptune) when the calf was 5 days old (27th June 1985) it was noted that throughout the day the mother and calf never left each other's side to the extent that at feeding time the mother would not stop at the feeding platform. As she swam by the platform with her calf, fish had to be thrown in the water before her, in order for her to eat. This is consistent with observations provided by various researchers including McBride & Kritzler (1951) and Essapian & Tavolga (1957) who noted that a calf will stay very close to its mother during the first month of life. Essapian and Tavolga (1957) also noted that 'special feedings are often provided for new mothers, who will accept fish thrown to them while swimming with the offspring after the regular feedings are over' (Tavolga & Essapian, 1957, p. 22).

Although in the case of both calves one would have expected a constant increase in independence, as measured by the calf swimming far from its mother, and a constant decrease in dependence, as measured by the calf swimming close to its mother, the data obtained showed these patterns not to be constant. As is apparent in figures 3(a) and 3(b) there is a decrease in the time both calves spent swimming close to their mothers up to the fourth set of observations which took place on 16th March 1986, and in both cases, a sudden increase in the same behaviour pattern on 15th April 1986. Similarly, the amounts of time both mother-calf couples spent swimming more than three metres distant from each other increased up to 18th March 1986, and then exhibited a marked decrease on 15th April. It is difficult to say what caused such changes in the April data, but because the phenomenon occurred in both mother-calf couples it is possible that it was caused by some external factor, or change, that affected them both.

Also confirmed was the prediction that the older calf, Juno, would be spending less time close to its mother than the younger calf, Neptune, at any point in time, and similarly, that Juno would engage in swimming far apart from his mother to a greater extent than Neptune. It is of interest that although this phenomenon was confirmed with high levels of significance, the younger calf appeared to exhibit marked increases in independence at an earlier age than Juno. For example, Neptune had reached a mean of 125 seconds per 5 minute session swimming far from its mother on 11th February 1986, when it was 32.4 weeks old, whereas Juno reached a mean of 129 seconds per 5 minute session in the same behaviour on 18th December 1985, when it was 74 weeks old. Although this is only one example, figures 3(a), 3(b), 4(a) and 4(b) clearly show that even though at any given date Juno showed significantly more independent and significantly more dependent behaviour patterns than Neptune, dependency patterns persisted with Juno until a later age than they did with Neptune, the reverse also being true, independent behaviour in Neptune beginning to emerge at an earlier age than it did with Juno. In studying mother-infant relationships in wild baboons (*Papio anubis*), Nash (1978) states that changes in such relationships 'must be understood in the context of the infant's interactions with others of its social group' (Nash, 1978, p. 746). This could perhaps imply that the younger calf started exhibiting more independent behaviour at an earlier age than Juno because of the presence of an older and thus already more independent calf that might have influenced it. Juno on the other hand had no older calves that might have influenced his development by accelerating it. It is therefore plausible to account for Neptune's precocious behaviour in the same way as it has been suggested that human children with older siblings are more 'adventurous' than an only or eldest child.

The records of fish intake of the animals kept at the dolphinarium by the trainers indicate, as expected, a gradual increase of fish intake on the part of the calves as a function of time. The table showing the fish intake of the calves on the dates in which data was collected shows no particular trend probably because the dates are too far apart from each other and are too few in number for any significant changes to be apparent. It appears nevertheless quite clear that the younger calf (Neptune) shifted from eating no fish at all, probably because he was still suckling, to eating sprats, and to eating 8 lbs of fish on the 15th of April 1986. What probably occurred between those dates was a gradual change in feeding habits, possibly characterized by decreasing suckling as a result of weaning and increasing fish intake.

The recorded fish intakes show quite a high level of variability from one day to the next in a few cases. One such case is apparent also in Table A, being particularly noticeable in the case of the older calf (Juno). For example on the 11th February it is known that Juno ate 10.5 lbs of fish, only 4 lbs on the 18th March and 16 lbs on the 15th April. The reasons why on certain days the intake of fish is significantly lower than on others could be many and varied, but as indicated by the trainers it could be because initially the calves were not given a fixed amount of fish at each feeding, but rather, tended to eat until satisfied, probably resulting in little appetite at the next feedings if not in the next days.

Of particular interest is the precocity of the younger calf (Neptune) with respect to Juno, which seems to have reflected itself also in the two calves' fish intake patterns. According to the records and the trainers' reports, Neptune started eating sprats at a much younger age than Juno had. This precocity factor is consistent with the straying and retrieving patterns emergent from the data in which it appears that weaning and independence started to take its course earlier with Neptune than with Juno.

Straying and retrieving quotients between each mother-calf couple, calculated to illustrate the mother and calf's relative roles in maintaining proximity or distance from each other, indicated that until 92.3 weeks of age Juno was primarily responsible for straying from Lulu and that until 37.4 weeks of age Neptune was primarily responsible for straying from Honey. Once again there appears to be an imbalance in age between the two calves in their roles in maintaining distance from their respective mothers. Data collected when Juno was 96.3 weeks old and Neptune 41.1 weeks old, showed that a reversal had occurred and that both mothers had by then become primarily responsible for straying from their calves. Until 18th December 1985, when Juno was 79.6 weeks old, Lulu had been primarily responsible for retrieving him. At 87.3 weeks of age, however, Juno was found to have become primarily responsible for retrieving Lulu. In the other mother-calf couple, Honey was observed to be primarily responsible for retrieving her calf until it was 37.4 weeks old. At 41.4 weeks of age, however, Neptune was found to be primarily responsible for retrieving Honey.

Analyses of these data indicated that there was no significant correlation between Neptune's age and the straying and retrieval quotients, but a significant, positive correlation was found to exist between Juno's age and the retrieval quotients and a negative, significant one between Juno's age and the straying quotients. Despite there being no significant correlation between Neptune's age and the two quotients the expected pattern of negative to positive retrieval quotient values and positive to negative straying quotient values nevertheless exists.

Once again, the quotient data has shown the same patterns occurring for both mother-calf couples at a much earlier age for the younger calf. In addition Honey seems to have started straying from Neptune earlier than Lulu started straying from Juno, as far as the calves' ages are concerned. If straying on the part of the mothers is regarded as being indicative of initiating attempts to wean the calf, then it is possible that Honey started weaning Neptune when the latter was younger than Juno, when Juno was being weaned, simply because of Neptune's precocity.

The pattern that also emerges from the quotient data is in fact consistent with Trivers' (1974) theory of parent-offspring conflict, which states that 'parent and offspring are expected to disagree over how long the period of parental investment should last (and) over the amount of parental investment that should be given . . .' (Trivers, 1974, p. 249). Offspring would thus expect more investment for longer, than the parent is prepared to give. The parent would initially place a high level of investment on its calf, yet as the calf grows older these levels would decrease, yet it would be in the calf's interest to seek to maintain them as high as possible. Translating this theory in terms of retrievals and strayings one would expect to find calves to increase straying from their mothers, mothers showing high levels of retrieval and later, mothers to initiate straying and calves increasing retrievals. 'Altmann (1980) and Hinde and his co-workers (Hinde and Atkinson, 1970; Hinde, 1974; Hinde and White, 1974), demonstrated that baboon (*Papio cynocephalus*) and rhesus (*Macaca mulatta*) infants initially increased the distance from their mothers, while mothers decreased that distance. In later months their dynamics were reversed, and mothers mainly increased the distance between themselves and their infants, while infants primarily decreased that distance. Several studies found that mothers were largely responsible for initiating infant independence and weaning through the use of rejection (Jensen et al, 1967; Rosenblum, 1968; Struhsaker, 1971; Hinde & White, 1974; Nash, 1978; Berman, 1980)'. (Taber & Thomas, 1982, p. 1081). Taber & Thomas (1982) found a similar pattern occurring in mother-calf groups of Southern right whales (*Eubalaena australis*).

In this study similar reversals were found to occur. Mothers initially retrieved more than they strayed from their calves and calves strayed more than they retrieved. As the calves grew older mothers began to leave their calves more than they retrieved them and calves became primarily responsible for attempting to maintain proximity between themselves and their mothers.

Thus, the data obtained in this study appears to be consistent with theories of mother-infant relationships in mammals, with studies of such relations in wild cetaceans and is supportive of inferences drawn from incidental observations of dolphins in captivity. Nevertheless, because of the extreme value of systematic studies of animal behaviour a much more detailed investigation of mother-calf relations is desirable. A replication of this study consisting of more frequent, if not daily observations of mothers and calves is needed to provide a clearer picture of calf development and the relationships with its mother.

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