

Mother–calf interactions and social behavior development in Commerson’s dolphins (*Cephalorhynchus commersonii*)

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Abstract Mother–calf interactions and the behaviors of mothers during separation from their calves were examined in four Commerson’s dolphin (*Cephalorhynchus commersonii*) mother–calf pairs. Four infants were observed: 56.8 h over 30 days from birth to 263 days of age, 36.9 h over 20 days from birth to 149 days of age, 10.4 h over 3 days from birth to 2 days of age, and 15.0 h over 3 days from birth to 2 days of age. All four pairs shared common characteristics in the rate and frequencies of mother–calf interactions and the behaviors of mothers during the first week of life. After the first week, individual differences in changes in the frequency of each behavior were observed. The three behaviors considered representative of maternal care (parallel swimming, synchronous breathing, and body-to-body contact) were frequently performed in the first week; thereafter, the frequencies declined. Separate behaviors of mothers were infrequent during the first week and increased with an increase in infants’ age. Bumping by infants increased with time, suggesting an increase in soliciting by calves and conflict between mothers and calves. The frequency of flipper-to-body rubbing also changed but in a complex manner, probably because the

calves needed to learn how to perform this behavior from their mothers and because initiator and recipient of this behavior can be changed quickly.

Keywords Commerson’s dolphin · *Cephalorhynchus commersonii* · Mother–calf interaction · Social behavior · Contact behavior · Synchrony · Behavioral development

Introduction

Stable social groups and relationships appear to be widespread among odontocetes (Connor 2002). In social groups, social behaviors play an important role in maintaining relationships between individuals. Mother and calf pairs of odontocetes engage in a variety of interactions (Mann and Smuts 1999; Connor et al. 2000; Whitehead and Mann 2000; Krasnova et al. 2006; Xian 2012), and such mother–calf interactions are considered to have two components. The first is maternal care behaviors and soliciting by calves, and they involve parent–offspring conflict (Trivers 1974). It has been predicted that mothers will attempt to decrease parental investment when the costs exceed the benefits to their lifetime reproductive success; on the other hand, the offspring will attempt to maximize paternal care to increase their own survival. The simplest predicted pattern is a steady decline in paternal care as the infants grow older. The second component of mother–calf interactions is providing the basis for the social interactions of the offsprings with other individuals after weaning. Such social interactions with other dolphins are required for their survival and/or reproduction. Synchronous swimming and breathing, flipper-to-body touching, and flipper-to-body rubbing have been suggested as social behaviors in other dolphin species (e.g., Connor et al. 2006a, b; Sakai et al.

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2006, 2010; Tamaki et al. 2006; Dudzinski et al. 2010). Adult Commerson's dolphins (*Cephalorhynchus commersonii*) also perform these behaviors (Johnson and Moewe 1999; Sakai, personal observation) and are considered as affiliative social behaviors.

Behaviors of dolphin calves have been described in captive bottlenose dolphins (*Tursiops truncatus*; Tavolga and Essapian 1957; Chirighin 1987; Eastcott and Dickinson 1987; Cockcroft and Ross 1990; Reid et al. 1995; Chechina 2009), wild bottlenose dolphins (*Tursiops* sp.; Mann and Smuts 1999), wild beluga (*Delphinapterus leucas*; Krasnova et al. 2006), captive Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*; Xian 2012), and wild Atlantic spotted dolphins (*Stenella frontalis*; Miles and Herzing 2003). Most studies have been conducted on bottlenose dolphins, and few studies have focused on the details of physical contact between the mother and her calf.

Commerson's dolphin is a small black-and-white dolphin found in the inshore waters of Argentina, in the Strait of Magellan, and around the Kerguelen Islands (Dawson 2009). They commonly form small groups of 2–10 individuals (Dawson 2009). Adult Commerson's dolphins have saw-toothed serrations on the leading edge of a pectoral fin, primarily the left fin (Goodall et al. 1988). Adult males tend to use the left flipper when touching the bodies of other individuals in an affiliative context (Johnson and Moewe 1999). There are some behavioral studies that have focused on pectoral fin touching (Johnson and Moewe 1999), resting behavior (Shpak et al. 2009), behavioral description during 2 weeks prior to parturition to 4 days postpartum (Joseph et al. 1987), reproduction, suckling, weaning and swimming behavior (Kastelein et al. 1993; Jingu and Nakata 2002), and behavioral description in the wild and in captivity (Gewalt 1990). However, there have been no continuous studies of mother–calf interactions in this species.

In this study, we focused on mother–calf interactions and the mothers' behaviors during separation from their calves. We obtained detailed quantitative behavioral data from birth to 263 days for one calf, from birth to 149 days of age for one calf, and from birth to 2 days of age for two calves. Here, we discuss parent–offspring conflict (Trivers 1974), which means trade-off of nursing cost, and the development of social behavior in this species.

Materials and methods

Facility and subjects

Observations and video recordings were made from an underwater observation window in front of an indoor pool (8.4 × 6.8 × 3.4 m, 194.2 m³ of water, water temperature

Table 1 Information of Commerson's dolphin (*Cephalorhynchus commersonii*) calves in this study

Name	Sex	Birthday	Mother
Peace	Male	4 July 2006	Laura
Toto	Male	27 July 2006	Lala
Riki	Male	7 October 2008	Lala
Lulu	Female	29 June 2011	Lala

14 °C). The mothers, Laura and Lala, were born in 1989 and 1991, respectively, at Matsushima Aquarium in Miyagi, Japan. Both have lived at the Toba Aquarium in Mie, Japan, since March 1996. Both the mothers were multiparous when starting this study. Table 1 shows the information of four calves.

The mother–infant pairs were observed or video recorded for 56.8 h over 30 days from birth to 263 days of age (Laura and Peace), 36.9 h over 20 days from birth to 149 days of age (Lala and Toto), 10.4 h over 3 days from birth to 2 days of age (Lala and Riki), and 15.0 h over 3 days from birth to 2 days of age (Lala and Lulu). During birth to 8 days of age, focal observations were made once or twice per day. Observation durations were ranging from 60 to 178 min in each day. In subsequent days, focal observation was made intermittently (see infant age in days in Fig. 2). Most focal observations lasted for 60 min, and only the days when focal observations were conducted for 50 min or longer were included in the analyses. During periods of no direct observation (days 0–14 for Peace; days 0, 1, and 20 for Toto; and days 0–2 for Riki and Lulu), data from video recordings were analyzed using the same protocols as were used for direct observations. Video data were collected in front of the underwater window and covered the entire area of the tank.

Behavioral data were collected by three observers for 93.5, 23.4, and 2.25 h, respectively. The observers were trained in the protocols required for video data collection and provided detailed definitions of each behavior to ensure interobserver reliability. After training, data collected by these observers from the same video were well matched.

Ethogram and sampling method

Mother–infant interactions and the separate behaviors of the mothers were assessed using focal follow sampling (Altmann 1974) (Table 2). A behavioral sequence in which a dolphin came in contact with and then separated physically from a subject/object was counted as one episode for each contact behavior (bumping, body-to-body contact, flipper-to-body touching, flipper-to-body rubbing, and self-rubbing). Parallel swimming was scored for each

Table 2 Ethogram for Commerson’s dolphins in this study

Behavior	Definition
Mother–calf interactions	
Parallel swimming	Mother and calf swim in parallel close (<0.5 m) to one another
Synchronized breathing	Mother and calf surface and exhale within 1 s of each other
Bumping	The calf comes into contact with the mother’s ventral side or genital area with its head or dorsal side. Nursing generally occurs after this behavior
Body-to-body contact	Mother and calf come into contact with each other via any body part except for the pectoral fins
Flipper-to-body touching	One dolphin comes into contact with another dolphin via its pectoral fin. The dolphin that uses the pectoral fin is designated the “toucher” and the dolphin that is touched the “recipient”
Flipper-to-body rubbing	One dolphin comes into contact with another dolphin via its pectoral fin and one or both dolphin swim along the partner’s body creating friction. The dolphin that uses the pectoral fin is designated the “rubber” and the dolphin that is contacted the “rubbee”
Separate behaviors of mothers	
Self-rubbing	The mother rubs its body against a wall or the base of the tank
Floating	Floating and resting at the water surface. A behavioral sequence in which a dolphin stops at the surface and then swims off again is counted as one episode

mother–infant pair at 5 min intervals by point sampling (Martin and Bateson 1986).

Statistical analyses

To evaluate the difference of behavioral development between two pairs observed for the longest period (Laura and Peace and Lala and Toto), linear regression and two-piece linear regression analyses were performed in the six mother–infant interactions (parallel swimming, synchronous breathing, bumping, body-to-body contact, flipper-to-body contact, and flipper-to-body rubbing) and for the two separate behaviors of mothers (self-rubbing and floating). First, a linear regression analysis and *F* test were used to analyze each of the eight behaviors to confirm whether or not the regression model was valid. Akaike’s information criterion (AIC) was then used to compare the fit of the linear regression and two-piece linear regression models. The model with lower AIC is more likely to be accurate and is therefore ranked higher. The AIC was calculated using the following formula where *n* represents the sample size, *S_e* represents the residual sum of squares, *P* represents the number of explanatory variables, and log represents the natural logarithm; *P* for the linear regression model was 3 (a gradient, an intercept, and a variance) and *P* for the two-piece linear regression model was 7 (two gradients, two intercepts, two variances, and a point of division).

$$AIC = n \left(\log \left(2\pi \frac{S_e}{n} \right) + 1 \right) + 2(P + 1)$$

If the AIC of the two-piece linear regression model was lower than that of the linear regression model, the *F* test was used for each of the regression lines. Biases in flipper-to-body touching and flipper-to-body rubbing exchanges

between a mother and her calf were evaluated using the Wilcoxon signed rank test. In all of the statistical analyses, *P* < 0.05 was considered statistically significant.

Results

Mother–calf interactions: parallel swimming

During the first week of life, three mother–infant pairs performed parallel swimming at most of the sampling points, but Lala and Lulu swam in parallel less frequently (Fig. 1a) than the other pairs. Table 3 shows both of the two pairs had the general trends of decline but there were differences between pairs in temporal changes in the parallel swimming rate. The parallel swimming rate of Laura and Peace declined monotonically. On the other hand, this rate of Lala and Toto decreased rapidly between days 14 (94.7 %) and 20 (72.2 %), i.e., during week 2.

Mother–calf interactions: synchronous breathing

Breathing frequency of the infants generally remained constant during the observation period at an average (±SD) of 3.8 ± 0.6 breaths per minute for Peace, 4.1 ± 0.5 breaths per minute for Toto, 4.0 ± 0.4 breaths per minute for Riki, and 3.9 ± 0.4 breaths per minute for Lulu. During the first week of life, 3 mother–infant pairs performed synchronous breathing with most of the infants’ breaths, but Lala and Lulu breathed in synchrony less frequently than the other pairs (Fig. 1b). Table 3 shows both of the two pairs had the general trends of decline but there were differences between pairs in temporal changes in the synchronous breathing rate. The synchronous breathing rate

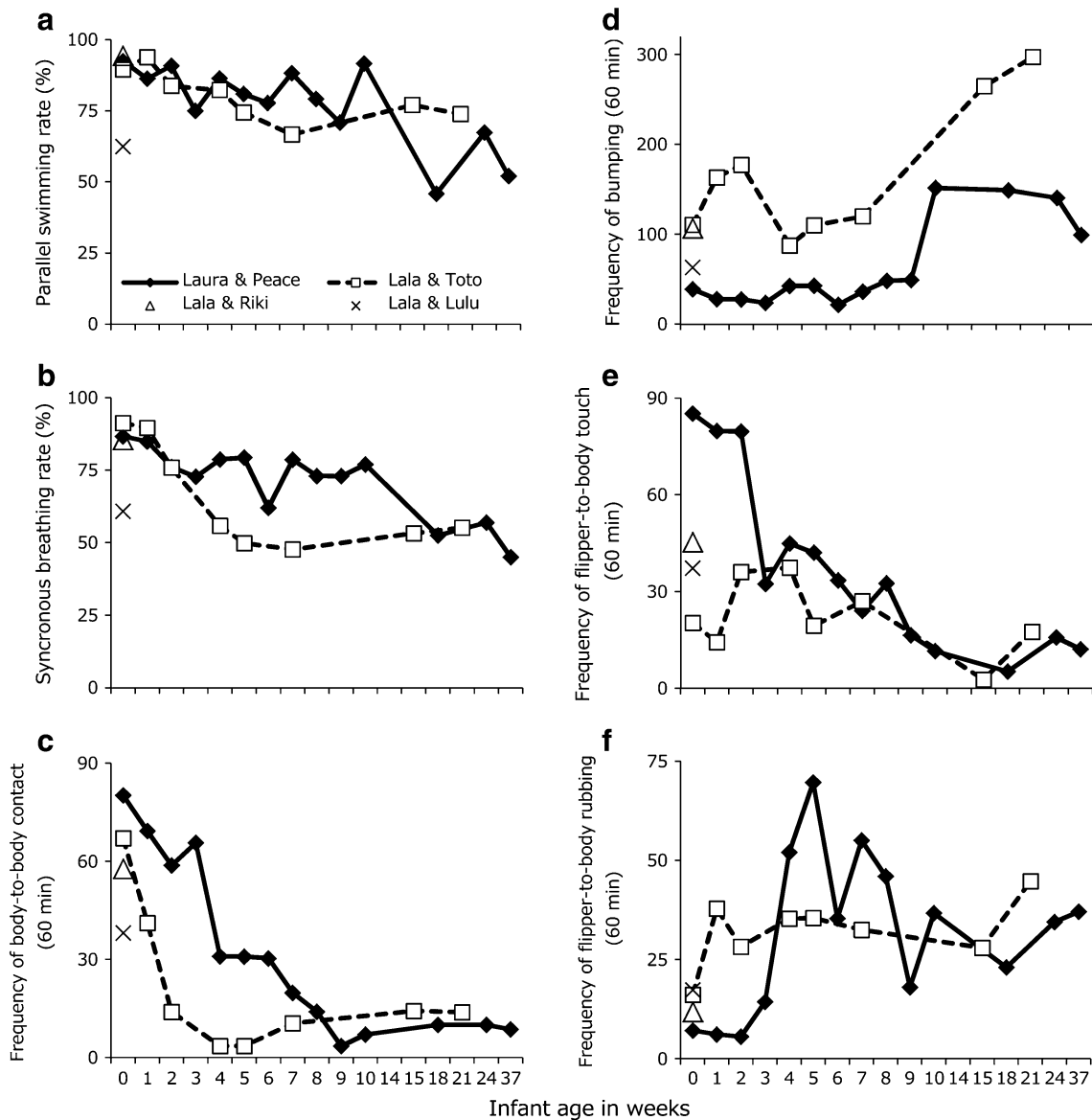


Fig. 1 Mother–calf interactions of Commerson’s dolphins (*Cephalorhynchus commersonii*) in relation to infant age in weeks

for Laura and Peace declined monotonically. On the other hand, this rate of Lala and Toto declined until day 35 (week 5), and thereafter, the rate was not related to infants’ age.

Mother–calf interactions: body-to-body contact

Body-to-body contact among the mother–infant pairs was more frequent during the first week of life than in subsequent weeks (Fig. 1c). Table 3 shows that both of the two pairs had the general trends of decline but there were differences between pairs in the point of changing frequency in body-to-body contact. The rate of body-to-body contact declined until day 35 for Laura and Peace and day 14 for Lala and Toto; thereafter, the rate was not related to

infants’ age in days and was generally constant for both pairs.

Mother–calf interactions: bumping

All infants performed bumping less frequently during the first week of life than in subsequent weeks (Fig. 1d). Table 3 shows that both of the two pairs had the general trends of increase but there were differences between the pairs in the changing frequency in bumping. The frequency of bumping by Peace remained generally constant from day 0 to day 63; thereafter, it increased rapidly on day 76. This frequency by Toto increased until day 14, decreased on day 20, and then increased once again.

Table 3 Statistical analysis of behavioral changes and infant age in days

	Laura and Peace			Lala and Toto		
	<i>F</i> test for linear model	Model with lower AIC	<i>F</i> test for each regression line in the TPL model	<i>F</i> test for linear model	Model with lower AIC	<i>F</i> test for each regression line in the TPL model
Mother–calf interactions						
Parallel swimming	↘**	L	–	↘*	TPL	NS (0–14) NS (20–149)
Synchronous breathing	↘**	L	–	↘**	TPL	↘** (0–35) NS (40–149)
Body-to-body contact	↘**	TPL	↘** (0–35) NS (37–263)	↘*	TPL	↘* (0–14) NS (20–149)
Bumping	↗**	TPL	NS (0–63) NS (76–263)	↗**	TPL	↗* (0–14) ↗* (20–149)
Flipper-to-body touching	↘**	TPL	↘** (0–43) NS (51–263)	NS	L	–
Flipper-to-body rubbing	NS	TPL	↗** (0–37) NS (43–263)	↗*	TPL	NS (0–4) NS (5–149)
Separate behaviors of mothers						
Floating	↗**	L	–	↗**	TPL	↗** (0–40) NS (53–149)
Self-rubbing	NS	L	–	↗**	TPL	↗** (0–7) ↗* (8–149)

The arrows indicates increase (↗) or decline (↘). Parenthetic numerals indicate the range of the infants’ age in days covered by the TPL regression line

NS not significant, *L* linear model, *TPL* two-piece linear model

* $P < 0.05$, ** $P < 0.001$ (*F* test)

Mother–calf interactions: flipper-to-body touching

All mother–infant pairs performed flipper-to-body touching more frequently during the first week of life than during subsequent weeks (Fig. 1e). Table 3 shows there were differences between two pairs in changing frequency in flipper-to-body touching. The frequency of flipper-to-body touching for Laura and Peace declined until day 43, and thereafter, the frequency was not related to infant’s age in days and remained generally constant. In contrast, this frequency for Lala and Toto was not related to infant’s age in days. The two infants more often assumed the “toucher” role than their mothers throughout the study period (Wilcoxon signed rank test: Laura and Peace: $R = 5.0, n = 30$ days, $P < 0.05$; Lala and Toto: $R = 0, n = 20$ days, $P < 0.05$; Fig. 2).

Mother–calf interactions: flipper-to-body rubbing

All mother–infant pairs performed flipper-to-body rubbing less frequently during the first week of life than during the subsequent weeks (Fig. 1f). Table 3 shows there were differences between pairs in temporal changes in the flipper-to-body rubbing frequency. The frequency of flipper-to-body

rubbing for Laura and Peace increased until day 37 (week 5); thereafter, the frequency decreased once and was not related to infant’s age in days and remained generally constant. On the other hand, this frequency for Lala and Toto increased significantly over time. This frequency of Lala and Toto changed between day 4 and day 5 (during week 0). Thereafter, the frequency of flipper-to-body rubbing was not related to infant’s age in days and generally remained constant. The two infants more often assumed the “rubbee” role than their mothers throughout the study period (Wilcoxon signed rank test: Laura and Peace: $R = 109.5, n = 30$ days, $P < 0.05$; Lala and Toto: $R = 21, n = 20$ days, $P < 0.05$; Fig. 3). The fluctuated changes in the frequency of assuming “rubber” role in each individual were observed (Fig. 3).

Separate behaviors of the mothers: floating

During the first week of life, the two mothers infrequently performed floating (Fig. 4a). Table 3 shows both of the two mothers had the general trends of increase but there were differences between individuals in temporal changes in the floating frequency. The frequency of floating by Laura increased monotonically. On the other hand, the rate of

Fig. 2 Flipper-to-body touching of mother–calf pairs in relation to infant age in days. **a** Laura and Peace, **b** Lala and Toto

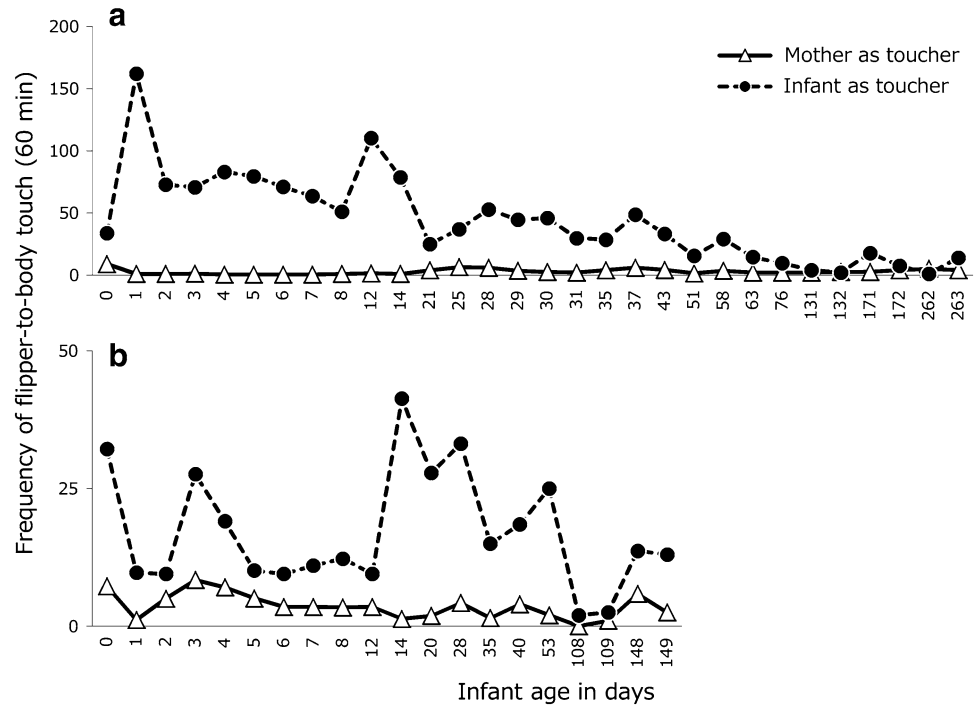
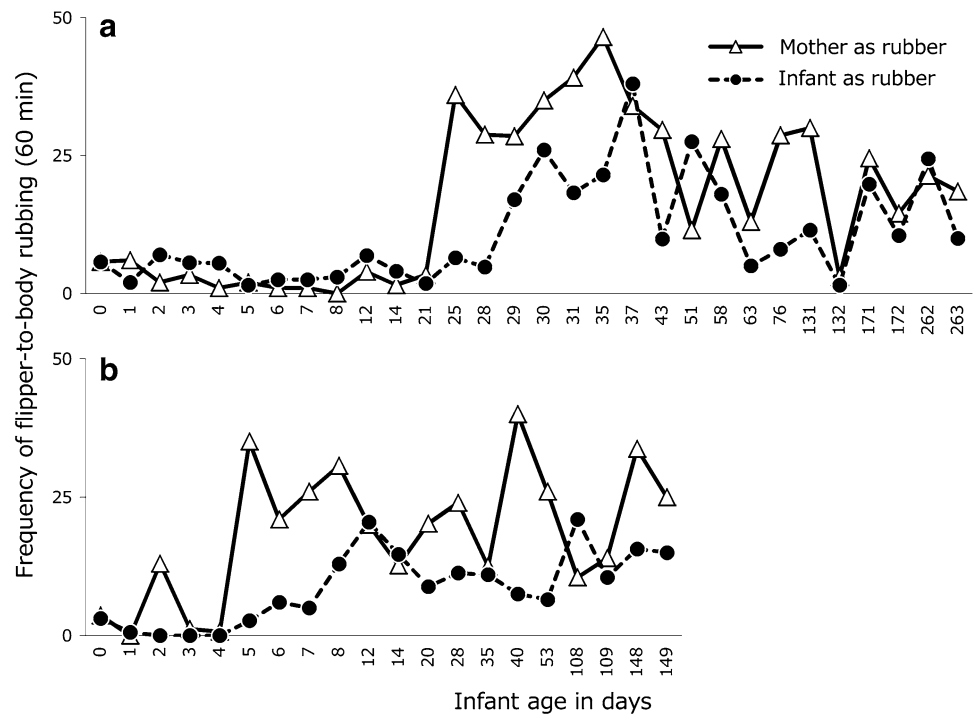


Fig. 3 Flipper-to-body rubbing of mother–calf pairs in relation to infant age in days. **a** Laura and Peace, **b** Lala and Toto



floating by Lala increased up until day 40; thereafter, the rate was not related to infant’s age in days.

Separate behavior of mothers: self-rubbing

During the first week of life, the two mothers infrequently performed self-rubbing (Fig. 4b). Table 3 shows

there were differences between mothers in temporal changes in the self-rubbing frequency. The frequency of self-rubbing for Laura was not related to her infant’s age in days. However, the frequency of this behavior for Lala increased rapidly up until day 7; thereafter, the frequency decreased once on day 8 and then increased again.

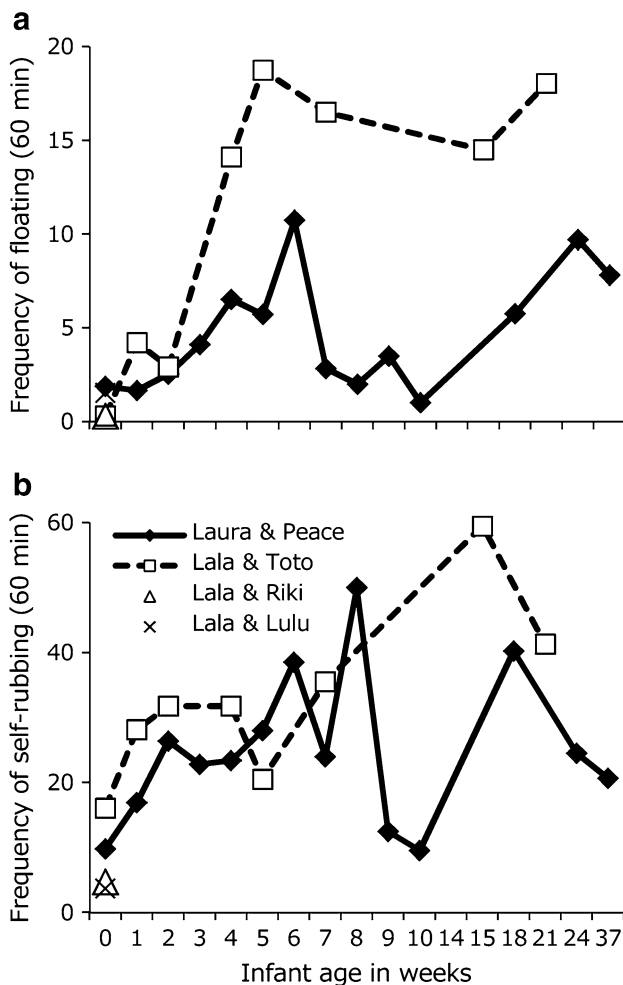


Fig. 4 Separate behaviors of mothers according to infant age in weeks

Discussion

Mother–calf interactions and maternal care

One of the functions of parallel swimming is considered to be a swimming cost reduction for infants. In captive bottlenose dolphins, there are clear hydrodynamic benefits for calves in the echelon position where the calves are in very close proximity to their mother’s mid-lateral flank and in the infant position when the calves swim very close to the mother underneath her peduncle (Noren 2008; Noren and Edwards 2011). We also observed that the infants stroked less frequently than their mothers when they were swimming in parallel. For maintaining proximity between the mother and her infant, they need to breathe synchronously. In general, a larger animal can dive for longer duration than a smaller animal because the larger animal has a lower oxygen consumption rate per unit body mass (Nielsen 1997). Therefore, mothers may shorten their breathing

interval to ensure synchrony with their infants. In addition, the drag when an animal breathes at the water surface is higher than that when it is submerged (Williams and Worthy 2002). Synchronous breathing would thus be a cost for mothers. Body-to-body contact occurred mainly in the following contexts; immediately postpartum, when the infants swimming skills were poorly developed and the infant occasionally hit the mother’s body, the mothers would push the infant’s body to prevent the infants crashing into walls. These interactions are considered representative of maternal care. Our findings support Trivers’ (1974) theory that parental investment declines as the infant grows older. Flipper-to-body touching generally occurred during parallel swimming. It appears that infants confirmed the distance between themselves and their mother by such touching, or occasionally they touched their mother because their swimming skills were still underdeveloped.

Lala and Lulu tended to perform these four behaviors less frequently than the other pairs. This might be due to kidnapping behavior by an adult female living in the same tank. This adult female repeatedly interrupted the parallel swimming by Lala and Lulu and tried to swim with Lulu. Lala tried to refuse this approach, but sometimes the adult female succeeded in swimming with Lulu. After this adult female was transferred to another tank, Lala and Lulu swam in parallel (90 %) and breathed in synchrony (81 %) more frequently.

During flipper-to-body rubbing, the “rubbee” is considered to receive some benefit (e.g., care of the body surface), and this was suggested as one of the calf-caring behavior by mothers in Indo-Pacific bottlenose dolphins (Sakai et al. 2006). Mothers tended to assume the “rubber” role in the present study (Fig. 3). Therefore, flipper-to-body rubbing in Commerson’s dolphins is also suggested to be one of the calf-caring behaviors. There were no simple changes in the frequency of this behavior, and this finding is discussed in more detail below.

Mother–calf interactions and soliciting by calves

Bumping has been reported to occur before nursing and has been suggested to occur in ungulates, elephants, and cetaceans when infants solicit nursing (Lent 1974; Langbauer 2000; Miles and Herzing 2003; Johnson et al. 2010). Such sudden changes in the frequency of this behavior might indicate a change in the supply of and demand for milk. Increasing bumping also suggests an increase in conflict between the mother and calf. Aquarium staff tried to give fish to Peace at day 85 (week 12), and Peace began to eat fish at day 92 (week 13). This was consistent with the report of several studies in which Commerson’s dolphins calves started to eat fish was ranging from day 73 to day

236 in 6 calves (Kastelein et al. 1993), ranged from day 95 to day 166 in 10 calves (Jingu and Nakata 2002), and was at approximately 2 months of age in one calf (Joseph et al. 1987). The result that bumping suddenly increased at day 76 (week 10) suggests his nutritional demands increased around that day, and the supply from milk could not cover his demands. Aquarium staff tried to give fish to Toto at day 154 (week 22), but he never ate fish and died at day 166 (week 23).

Mother–calf interactions and social behaviors

Parallel swimming, synchronous breathing, flipper-to-body touching, and flipper-to-body rubbing have been suggested as affiliative social behaviors in bottlenose dolphins (Connor et al. 2006a, b; Tamaki et al. 2006; Sakai et al. 2006, 2010). Although the functions of these behaviors in Commerson's dolphins remain unclear, pairs of adult Commerson's dolphin perform these behaviors frequently (Johnson and Moewe 1999; Sakai, personal observation). Such interactions by mother–calf pairs may facilitate social interactions with other individuals after weaning. Parallel swimming, synchronous breathing, and flipper-to-body touching were performed by all mother–calf pairs immediately postpartum. On the other hand, flipper-to-body rubbing was performed infrequently in the first week of life, and there was great variation in the subsequent frequency of this behavior. The calves more often assumed the role of “rubbee” than their mothers throughout the study period (Fig. 3). It may be more difficult for an immediately postpartum infant to perform flipper-to-body rubbing than flipper-to-body touching because they need to maintain the proper distance between themselves and their mother, and they need to swim alongside their mother while keeping physical contact. Further development of their swimming skills or lessons from their mother may be required for them to perform this behavior. Flipper-to-body rubbing in which the mothers assumed the “rubber” role increased before increasing this behavior in which calves assumed the “rubber” role (days 25–35 for Peace, days 5–8 for Toto; Fig. 3). These results suggest that the calves needed to learn how to assume the “rubber” role from their mother. In bottlenose dolphins, the “rubbee” is considered to receive some benefit from this behavior such as care of the body surface (Sakai et al. 2006). When calves are able to assume the “rubber” role (day 29 for Peace, day 8 for Toto; Fig. 3), the mother might receive some benefit by assuming the “rubbee” role. The fluctuating changes in the frequency of assuming the “rubber” role in each individual (Fig. 3) may be caused by this reciprocal characteristic. Further continuous studies are needed to reveal how mother–calf interactions influence the calves' social behavior, reproductive success, and survival rate as adults.

Separate behaviors of mothers

Floating and self-rubbing can be defined as behaviors performed by individuals alone. During the first week of life, the two mothers infrequently performed floating and self-rubbing. This was caused by the mothers caring for the infants constantly during this period. Subsequently, the frequencies of floating significantly increased for both mothers, and the frequency of self-rubbing also significantly increased for Lala. These results support Trivers' (1974) theory that maternal investment declines as calves grow.

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