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Underwater Sounds Produced by Neonatal Bottlenose Dolphins (*Tursiops truncatus*): II. Potential Function

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Abstract

Neonatal bottlenose dolphins (*Tursiops truncatus*) produce many sounds just after birth, including whistles and pulsed sounds. Herein, we report the possible function of the sounds produced by two captive-born, neonatal bottlenose dolphin as revealed by behavioural observations. Typical sucking sounds were observed during 71 to 81% of all suckling bouts. Since the neonates produced more sounds at the beginning of the suckling sequence than expected, it appeared that they might use the sounds as care-solicitation signals or begging signals. These sounds contained a higher proportion of whistles than sounds in other contexts, which implied that the proportions of sound types, especially whistles, were important for neonatal dolphins and their mothers to initiate the nursing sequence.

Key Words: bottlenose dolphin, *Tursiops truncatus*, neonates, vocalization, whistles, burst-pulse, begging, suckling behaviour, care-solicitation signals

Introduction

Morisaka et al. (2005) found that neonate bottlenose dolphins (*Tursiops truncatus*) produce sounds of various types and characteristics. Overproduced sounds can be costly in the wild for several reasons, including the restriction of respiration or by placing the neonates at predatory risk from killer whales (*Orcinus orca*) or false killer whales (*Pseudorca crassidens*). We hypothesized that the sounds produced by neonatal bottlenose dolphins may function as care-solicitation signals or begging signals. For neonates, care includes various classes and types of behaviour—for example, being protected from predators and being provided with food. Whistles, especially the signature whistles (Caldwell & Caldwell, 1965, 1968; Caldwell et al., 1990) of infant bottlenose dolphins, are thought to facilitate the reunion of a mother and her infant (Smolker et al., 1993). We also investigated another important care-solicitation function—the provision of nourishment.

The offspring of many animals beg for food from their parents by species-specific care-solicitation behaviours. Begging calls by altricial nestling birds—for example, wood warblers (Parulidae) (e.g., Haskell, 1999) and red-winged blackbirds (*Agelaius phoeniceus*) (e.g., Burford et al., 1998)—are well-studied care-solicitation signals. The offspring of altricial nestling birds produce loud sounds or begging calls to get food from their parents. Recently, most studies about begging signals have focussed on parent-offspring conflicts and honest signaling (Kilner & Johnstone, 1997). Not only altricial nestling birds but also precocial mammals—for example, domestic piglets (*Sus scrofa*) (Weary & Fraser, 1995), meerkats (*Suricata suricatta*) (Manser & Avey, 2000), and Grey seals (*Halichoerus grypus*) (Smiseth & Lorentsen, 2001)—are thought to have care-solicitation calls. The mothers of these mammals approach the calling infants to nurse them when care-solicitation calls are produced. Kilner & Johnstone (1997) provided a fine review of this topic.

If the sounds produced by neonatal dolphins function as care-solicitation signals, we expected that neonates would produce more sounds before the suckling bout than usual. We therefore investigated sounds and behaviours before suckling to determine whether the neonatal sounds functioned as care-solicitation calls.

Suckling behaviours in bottlenose dolphins have been described by many authors (Cockcroft & Ross, 1990; Eastcott & Dickinson, 1987; Jacobsen et al., 2003; McBride & Kritzler, 1951; Tavolga & Essapian, 1957; Triossi et al., 1998). The nursing bouts usually were initiated by the calf swimming underneath the mother and bumping the mother's mammary area with the top of its head (Cockcroft & Ross, 1990); however, no acoustical data were collected before or during suckling.

First, we made preliminary observations of suckling by each neonatal dolphin and its mother and determined the suckling bout lengths. Next, we investigated the relationship between sounds and the behaviours of the neonates before suckling to determine whether the sounds were used as care-solicitation calls.

Materials and Methods

Subjects

Two neonatal bottlenose dolphins were the subjects of this study. They were housed in an outdoor elliptic pool at the Suma Aqualife Park, Hyogo, Japan. The neonates were born from the same mother at 1657 h, 2 June 1999, and at 1242 h, 12 July 2000, so we refer to them as "neonate 99" and "neonate 00," respectively. Neonate 99 was a female, and neonate 00 was a male. Neonate 99 had been housed with her mother and two other adult females for 3.5 h after birth, but after that, she was housed only with her mother. Neonate 00 was housed with his mother and two other adult females. Neonate 99 died about 50 h after birth. The cause of death could not be determined by an autopsy, but there seemed to be no abnormalities in the facial-nasal region nor in the sound producing organs.

Data Collection

All underwater recordings were made with a fixed hydrophone (OKI ST-1020) connected to an amplifier (OKI SW-1020) through a 1 kHz high-pass filter. Sounds were recorded on a digital audiotape recorder (SONY TCD-D8). Each recording session was about 60 min. The sensitivity of the entire recording system was linear up to 24 kHz. Behaviours of the dolphins were recorded simultaneously with a digital video camera (SONY DCR TRV-900) through an underwater observation window, which provided a view of the entire tank.

We regarded teat lock-on and leakage of milk during the suckling bout as the first successful nursing. Neonatal dolphins have to seek the teats of their mothers to get milk, but they cannot suckle immediately after birth (Eastcott & Dickinson, 1987). We determined that neonate 99 had the first successful nursing at 14 h after birth, while it was 27 h after birth for neonate 00. We used the respective data after those times. The data periods from neonate 99 were 14-15 h, 17-18 h, 20-21 h, 23-24 h, and 26-27 h after birth. Although neonate 99 seemed to behave normally until about 40 h after birth, we excluded the data obtained from 28 to 50 h after birth so as to eliminate any effects from her impending death. The data from neonate 00 were obtained randomly from the age of 27 h to one month (27-28 h, 33-34 h, 44-45 h, 47-48 h, 50-51 h, 56-57 h, 68-69 h, 74-75 h, 92-93 h, 122-123 h,172-173 h, 291-292 h, 337-338 h, 602-603 h, 770-771 h). Neonate sounds were determined by bubble stream emissions from the neonate because these frequently occur simultaneously with sound production, especially in infants (McCowan & Reiss, 1995).

Sound Analysis

All acoustical data were analysed using *Avisoft-SASLab Pro for Windows*, *Version 4.0* (Avisoft Inc., Berlin, Germany, 2001). Spectrograms of whistles were generated with a sampling rate of 48 kHz, a high-pass filter of 1 kHz, FFT length of 512, frame size of 100%, and a Hamming windowing function, which resulted in an analysis frequency resolution of 93 Hz, and a time resolution of 5.3 ms. Sounds with good signal-to-noise ratio were used for the entire analyses. We categorized sounds as either burst-pulses or whistles. A few whistle-squawks (see Killebrew et al., 2001) were produced by the two neonates, which had characteristics of both frequency-modulated whistles and burst-pulse sounds. We treated whistle-squawks as whistles only when we were able to analyse the whistle component separately in the whistle-squawks. If we were not able to clearly separate them, we discarded the sounds.

Behavioural Analysis

Behavioural and acoustical data were collected using the focal-animal sampling method (Altmann, 1974).

Suckling Bout—An incidence of suckling behaviour starts when a neonate's rostrum contacts the mother's mammary gland (lock-on) and ends when the rostrum leaves the gland (lock-off) (Jacobsen et al., 2003; Triossi et al., 1998). Many studies revealed that the frequency of the odontocete calf being attached to the teat is not scattered randomly over time but is grouped into bouts of some teat attachments or lock-ons (see Jacobsen et al., 2003). Grouping suckling behaviour leads us to a more comprehensive analysis of nursing behaviour of odontocetes. To group suckling behaviour incidents into bouts, we determined bout criterion intervals (BCI) by $\log_e$ frequency analysis as suggested by Sibly et al. (1990) and Jacobsen et al. (2003) for each neonate. We only used the intervals when two suckling behaviour incidents were observed completely. The initial class width of the intervals for the analysis was set at one min. We discarded those suckling bouts which were 1 min between the beginning of the recording and the start of suckling bouts once suckling bout criterion intervals were determined.

To calculate the BCI for the neonates, we calculated a loge frequency plot and fit two regression lines, each viewed as a one-process distribution (Jacobsen et al., 2003). This method of fitting the two linear regression line model, is called a broken-stick regression model or breakpoint regression model. According to Sibly et al. (1990) and Jacobsen et al. (2003), the steeper regression line represents the fast process (f) (within bout intervals), and the slower regression line represents the slow process (s) (between bout intervals). The regression line of the simple one-process model can be represented by the following equation:

$$y = \log_e N\lambda - \lambda t \quad (1)$$

where, N = number of events, λ = number of events per unit time, and t = time.

The initial parameters, N_f and λ_f = N and λ for the fast process, and N_s and λ_s = N and λ for the slow process, were used to test the fit of the two-process model. The model is regarded as the most fitting one when the total of residual sum-of-squares (RSS) is minimum using a Visual Basic for Application (VBA) programme written by Shigenobu Aoki (Faculty of Social & Information Studies, Gunma University, Japan, 2003).

Then, according to Jacobsen et al. (2003), two different methods are conducted for the calculation of the BCI—one based on the minimizing of the total time misassigned (t_1), and one based on minimizing the total number of events misassigned (t_2) as follows:

$$t_1 = 1 / (\lambda_f - \lambda_s) * \log_e (N_f / N_s) \quad (2)$$

$$t_2 = 1 / (\lambda_f - \lambda_s) * \log_e (N_f\lambda_f / N_s\lambda_s) \quad (3)$$

Number of points misassigned when the bout criterion is t_c can be calculated by

$$N_f e^{-\lambda_f t_c} + N_s(1 - e^{-\lambda_s t_c}) \quad (4)$$

The criterion which has less misassigned points is chosen for BCI.

Suckling Sequence—We classified the position of the neonate with respect to the mother into two classes: (1) below the mother and (2) elsewhere. "Below the mother" was defined as *anywhere underneath the mother*, including the positions which other studies have designated as the infant position (Mann & Smuts, 1999) and as the P6 spatial states (Gubbins et al., 1999). "Elsewhere" was defined as *anywhere except underneath the mother*. This included the echelon position (Mann & Smuts, 1999) where the neonate is probably riding in the slip stream caused by the mother's body (Norris & Prescott, 1961), and thus, the calf maintains close contact in this position (Cockcroft & Ross, 1990; Norris & Dohl, 1980).

Our preliminary observations indicated that there might be a typical nursing sequence (Figure 1). Before the suckling bout, neonates always moved to a position below the mother from an elsewhere position and swam below the mother for a while until suckling behaviour started. We call this period the Below Mother Period (BMP). If neonates moved from the position below the mother to an elsewhere position to breathe, we regarded these two separate BMPs as one BMP. If they moved to another elsewhere position and did some other activity, excluding breathing or acting to avoid danger, such as socialising, we regarded the final period as a BMP.

Neonates often produced more than one sound before a BMP started. The period from the last sound which was produced within 10 min before the BMP to the beginning of the BMP was designated the Latency Period (LP). In other words, neonates produced no sounds and swam at the elsewhere position during the LP.

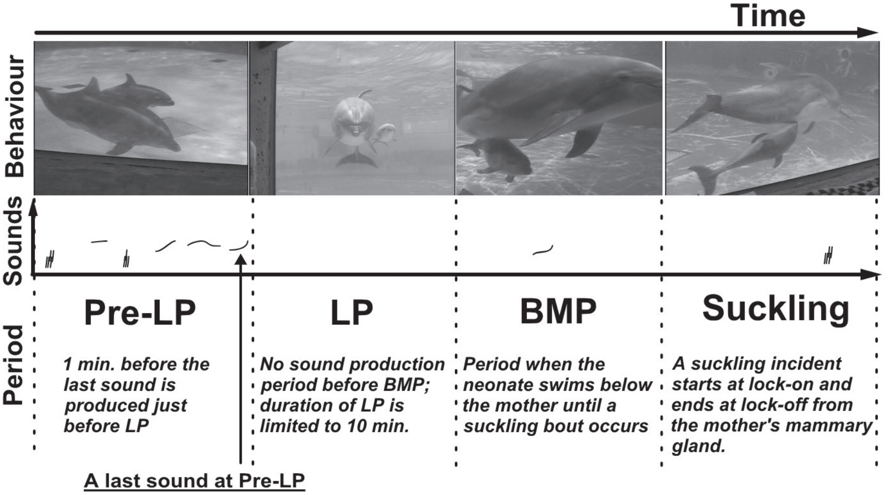

Figure 1. An example of a suckling sequence with sound production; examples of sound spectrograms of neonate sound are also shown (x-axis: Time; y-axis: Frequency).

We used a $\log_e$ frequency analysis suggested by Sibly et al. (1990) to determine the LP length criterion because a too long LP might have no meaning between the sounds before LP and BMP or the suckling bout. The data from both neonates were mixed because of the limited number of observations. The method was the same one that we used for suckling bout definition.

We then categorized the suckling sequences into two types: (1) the suckling sequence with a sound and (2) the suckling sequence without sounds. The former consists of the LP, BMP, and a suckling bout, while the latter consists of the BMP and suckling bout only.

Sounds Before LP—If the sounds which are produced before the LP have the function of a care-solicitation signal, neonates might produce sounds more frequently in this period than usual. The 1-min period before the LP was designated the Pre-LP. We compared the number of sounds produced by neonates in the Pre-LP (including the last sound) and the number of sounds expected during one min at that time. Also, if the sounds were to function as the care-solicitation signal, we expected that the sound type might differ from the sounds usually produced by neonates. We compared the sound types produced last in the Pre-LP and the sound types usually produced.

Statistical Analysis

JMP®, Version 5.0 (Sas Institute Inc., Cary, NC, 2002), was used for statistical analysis. We used the non-parametrical Wilcoxon rank-sum test to compare suckling bout duration, number of suckling behaviours within a bout, BMP duration, and LP duration between neonates. We used the one-tailed binomial test to reveal whether neonates tend to produce sounds during BMP and suckling bouts or not. The number of sounds produced by neonates in the Pre-LP and the number of sounds expected to be produced for a 1-min period in each recording session were compared using the non-parametrical Wilcoxon signed-ranks test. The expected number of sounds produced at the *t-th* recording session was calculated by the following equation:

$N_{texp} = N_t / D_t$ (5)

where, N_{texp} is the number of sounds expected to be produced during one min in the *t-th* recording session, N_t is the number of sounds produced by the neonate in the *t-th* recording session, and D_t is the duration of the *t-th* recording session (min).

The difference between the proportion of the sound types (whistles and burst-pulses) produced last by a neonate in the Pre-LP and that usually produced was tested by the Fisher exact test.

Results

We observed neonate 99 for 4 h 13 min and neonate 00 for 15 h 30 min. We identified 251 sounds from neonate 99 (whistles: 245, burst-pulses: 6) and 626 sounds from neonate 00 (whistles: 66, burst-pulses: 560).

Suckling Bout Definition

A total of 50 and 73 attempted suckling behaviour incidents were observed for neonate 99 and neonate 00, respectively. The data from both neonates were regarded as fitting a broken-stick model. For neonate 99, the initial parameter estimates for the fast process were $y = 4.63\text{-}1.32t$ ($R^2 = 1.00$, $n = 3$, $p = 0.02$), $\lambda_f = 1.32$ sucklings/min, and $N_f = 77.65$ sucklings. The initial parameter estimates for the slow process were $y = 0.23\text{-}0.01t$ ($R^2 = 0.03$, $n = 11$, $p = 0.63$), $\lambda_s = 0.01$ bouts/min, and $N_s = 203.62$ bouts. Two estimates of a BCI were then $t_1 = -0.73$ min (misassigned points: 203.62) and $t_2 = 3.35$ min (misassigned points: 5.11). Therefore, we regarded the suckling behaviours which have an interval within 3 min 21 s as one suckling bout for neonate 99.

For neonate 00, the initial parameter estimates for the fast process were $y = 5.12\text{-}1.55t$ ($R^2 = 0.95$, $n = 3$, $p = 0.15$), $\lambda_f = 1.55$ sucklings/min, and $N_f = 108.27$ sucklings. The initial parameter estimates for the slow process were $y = 0.42\text{-}0.01t$ ($R^2 = 0.06$, $n = 7$, $p = 0.90$), $\lambda_s = 0.01$ bouts/min, and $N_s = 153.40$ bouts. Two estimates of a BCI were then $t_1 = -0.23$ min (misassigned points: 153.40) and $t_2 = 3.06$ min (misassigned points: 5.56). Therefore, we regarded the suckling behaviours which have an interval within 3 min 04 s as one suckling bout for neonate 00. We thus observed 16 and 36 suckling bouts, respectively, from neonate 99 and neonate 00.

Behaviour Sequences Before Suckling

Thirteen and 25 suckling bouts, respectively, had more than one sound during the LP for neonate 99 and neonate 00. The $\log_e$ frequency distribution of LP length fit the single process model, which indicated these data did not need to be split into bouts (Figure 2). The parameters for the single process were $y = 2.63\text{-}0.31t$ ($R^2 = 0.89$, $n = 8$, $p < 0.001$), $\lambda = 0.31$ intervals/min, and $N = 45.04$ intervals since the x-intercept was 8.54.

Thirteen and 25 suckling sequences with one sound were obtained from neonate 99 and neonate 00, respectively, and 3 and 10 suckling sequences without sounds were also obtained (Table 1). One value from neonate 00 was discarded from further study because the sequence was less than 8.54 min from the beginning of the recording to the beginning of BMP.

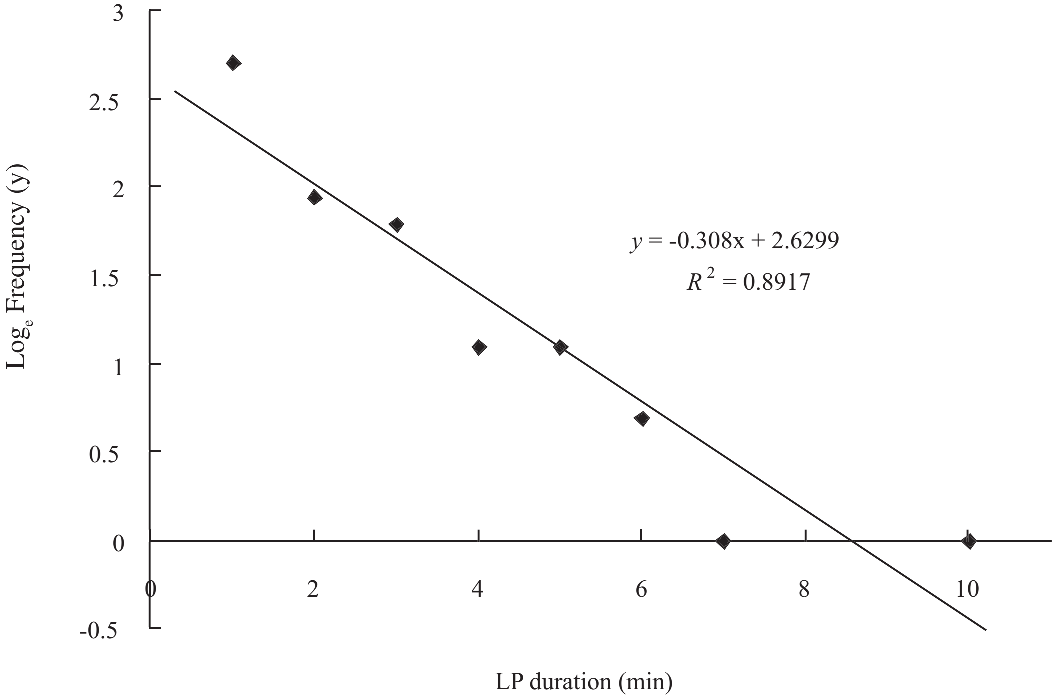

Figure 2. LP duration and log$_e$ frequency data; regression line represents the predicted single model.

Duration and Sound in Each Period

Table 1 summarizes these data. Average suckling bout lengths were 86.50 s (SD: 90.63) and 79.06 s (SD: 93.25) for neonate 99 and neonate 00, respectively. There was no significant difference between them (Wilcoxon rank-sum test: $z = -0.56$, $p = 0.57$). The average number of suckling incidents within a suckling bout was 2.63 (SD: 1.67) and 2.69 (SD: 2.01) for neonate 99 and for neonate 00, respectively. There was no significant difference between them (Wilcoxon rank-sum test: $z = -0.06$, $p = 0.95$). BMPs lasted 51.44 s (SD: 49.42) and 49.31 s (SD: 38.04) on average for neonate 99 and neonate 00, respectively. There was no difference in BMP duration between neonates (Wilcoxon rank-sum test: $z = -0.29$, $p = 0.77$). The mean LP was 104.85 s (SD: 164.85) and 134.36 s (SD: 107.44), respectively. There was no difference in LP duration between neonates (Wilcoxon rank-sum test: $z = -1.92$, $p = 0.054$).

Neonate 99 produced sounds in 2 BMPs out of 16, whereas neonate 00 produced no sounds in 35 BMPs. Neonates produced far less sounds during BMPs than at random (Null hypothesis is "neonates produce sounds at random (50%)." One-tailed binomial test: $p < 0.01$ and $p < 0.001$ for neonate 99 and neonate 00, respectively). Neonate 99 produced sounds in 3 suckling bouts out of 16, whereas neonate 00 produced sounds in 2 suckling bouts out of 35. Neonates produced fewer sounds during suckling bouts than at random (Null hypothesis is "neonates produce sounds at random (50%)." One-tailed binomial test: $p < 0.05$ and $p < 0.001$ for neonate 99 and neonate 00, respectively).

Neonate 99 averaged 4.85 sounds (SD: 4.12) during Pre-LP, whereas neonate 00 produced 3.52 sounds (SD: 3.29). Both neonates produced more sounds during Pre-LP than expected (Wilcoxon signed-rank test: $z = 2.80$, $p < 0.01$ and $z = 4.13$, $p < 0.001$ for neonate 99 and neonate 00, respectively).

The last sounds in Pre-LP from neonate 99 were 12 whistles and 1 burst-pulse, while the last sounds in Pre-LP from neonate 00 were 9 whistles and 16 burst-pulses. Neonate 99 tended to produce whistles more than usual, but did not significantly change her sound types compared to all sound types (Fisher exact probability test: $p = 0.30$), whereas the last sounds from neonate 00 contained more whistles than usual (Fisher exact probability test: $p < 0.01$). We did not observe that any typical sound was produced last in the Pre-LP.

Discussion

The results indicated that there may be a typical suckling sequence and that the neonatal sounds, especially whistles, may be important to start the

Table 1. Summary of data; values are means ± SD and *n* indicates the number of data used. One value of suckling bout number from neonate 00 was discarded (see "Results" section in the text).

Period	Parameters		neonate 99		neonate 00	
				n		*n*
Suckling sequence	No. of suckling bouts		16		35	
	Suckling bout duration (s)		86.50 ± 90.63	16	79.06 ± 93.25	35
	No. of suckling incidents within a bout		2.63 ± 1.67	16	2.69 ± 2.01	35
	No. of suckling sequences with one sound		13 (81%)		25 (71%)	
	No. of suckling bouts with sounds		3 (19%)	16	2 (6%)	35
Below Mother Period	Duration of Below Mother Period (s)		51.44 ± 49.42	16	49.31 ± 38.05	35
	No. of BMP with sounds		2 (13%)	16	0 (0%)	35
Latency Period	Duration of Latency Period (s)		104.85 ± 164.85	13	134.36 ± 107.44	25
Pre-LP	No. of sounds during Pre-LP		4.85 ± 4.12	13	3.52 ± 3.29	25
	Last sounds of Pre-LP	whistle	12 (92%)	245 (all)	9 (36%)	66 (all)
		burst-pulse	1 (8%)	6 (all)	16 (64%)	560 (all)

nursing. This is the first report on the possibility of care-solicitation signals or begging signals for cetaceans.

Suckling Bouts

Suckling bout lengths in this study were 79.06 and 86.50 s, respectively, on average, and there was no statistical difference between the two neonates. These differed from the length (107.7 s) calculated by Jacobsen et al. (2003) using the same method cited in Sibly et al. (1990). This may have occurred because our recording session was restricted to one h each time. Longer suckling intervals were excluded from our data. The suckling bouts per h, however, were 3.79 and 2.26, respectively, for neonate 99 and neonate 00, which are in the range of the studies by Reid et al. (1995) (0.96-3.99 bouts/h) and Jacobsen et al. (2003) (1.7-5.7 bouts/h) for bottlenose dolphins. Further research is needed to reveal the real suckling bout length of bottlenose dolphins.

Suckling Sequences and Sounds

This is the first study that revealed neonatal sounds preceding the suckling bouts. Cockcroft & Ross (1990) suggested that bumping, which is when the calf bumps the mammary area of its mother with the top of its head, marked the onset of the calf's initiation of suckling bouts, but bumping did not occur early in the calf's life (first 4 weeks). They also suggested that it was the mother rather than the calf that initiated nursing in the first four weeks. Our results suggested that not only after the first four weeks, but also during the first four weeks, neonates initiated the suckling sequence and indicated to the mother their need to nurse. Because we sometimes saw neonates bumping the mother's mammary gland in our observations, further study is needed regarding bumping in the first four weeks after birth. Successful suckling behaviour needs cooperation between the mother and calf because the mother swims slowly, stops fluke movements, and holds her peduncle high so it is easy for the neonates to suckle (Triossi et al., 1998). It must be important for the mother to know the milk needs of her neonates.

During LP, the mother sometimes presented her mammary area to her neonate and at other times did not allow her calf to move below her for a while because other dolphins were chasing them. LP is the period in which both neonate and mother, especially the mother, are waiting for a chance to start nursing behaviour. During BMP, neonates sometimes bump the mother's mammary area, which is thought to stimulate the "let down" of milk (Cockcroft & Ross, 1990). They also sometimes sought their mother's teat during this period. Although the reason why neonates produced hardly any sounds during these periods was not clear, it could be that sounds may have a large cost for neonates because of predation or restriction of breathing (see Morisaka et al., 2005). Sounds travel far away under water and are omnidirectional. Predators, such as killer whales and false killer whales, can easily find the bottlenose dolphins from detecting sounds. This may be the reason why neonates produce few sounds during LP, BMP, and suckling.

Possible Function of Neonatal Sounds as Care-Solicitation or Begging Signals

The neonates produced more sounds in the Pre-LP than usual. The results implied that the sounds produced by neonates in Pre-LP initiated the nursing behaviour sequence. Moreover, the whistle ratio of all sounds increased in the Pre-LP, which indicated that a higher proportion of whistles may function as one of the important care-solicitation signals or begging signals. Although we could not detect any statistically significant change between these sounds and the usual ones, neonate 99 tended to produce more whistles and produced few burst-pulses. It was very regrettable for us to lose this neonate, and further study is still needed to confirm our results. This will also reveal whether her imminent death had an effect on her sounds or not.

Whistles are thought to be used to maintain group cohesion (Janik & Slater, 1998) and to communicate over long distances (Janik, 2000). It is reasonable for neonates to use whistles as care-solicitation signals. Smolker et al. (1993) reported infant bottlenose dolphins produced whistles (signature whistles) when they were separated from their mother, which indicated that the whistles functioned to facilitate reunions of mother and infant. In our study, we sometimes observed that neonates produced sounds while separated from their mother.

The mother may determine the hunger condition of her neonate by its sounds, especially the high proportion of whistles, and then prepare to nurse it. No typical sounds were found among those sounds, which was not the same result as in the typical species-specific begging call of birds (e.g., Haskell, 1999). Further studies are needed to reveal whether these sounds really function as care-solicitation signals. Care-solicitation signals should be honest signals (Grafen, 1990; Kilner & Johnstone, 1997), and we hope to test three hypotheses by carrying out some playback experiments. From these experiments and other observations, we would expect to find that when we study care-solicitation signals (1) begging intensity should reflect infants' need; (2) parents should provide food for their young in relation to begging intensity; and (3) begging could be costly (Kilner & Johnstone, 1997).

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