Aquatic Mammals 2012, *38*(2), 127-135, DOI 10.1578/AM.38.2.2012.127

The Development of Spatial Positions Between Mother and Calf of Yangtze Finless Porpoises (*Neophocaena asiaeorientalis asiaeorientalis*) Maintained in Captive and Seminatural Environments

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Abstract

For many toothed whales, two predominant and multifunctional spatial positions occur between a mother/calf pair after birth: (1) the echelon position and (2) the infant position. Other nonpredominant positions also have social and developmental significance for the calf. So far, the observational period of studies on the spatial positions tends to be too short, and the studies have primarily focused on the marine groups. Moreover, few, if any, studies examining spatial relations between mother/calf pairs have been conducted on endangered toothed whale species. The Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) is one endangered and freshwater toothed whale. We studied the development of echelon, infant, and other position(s) in one calf maintained in captivity and two in a seminatural enclosure up to 1 y after birth. Focal following and continuous recording methods were used. A total of 180.6 h of video were recorded for the captive calf during the first year after birth (1.8 ± 0.5 h/d; *n* = 99 d). For the two calves in the enclosure, a total of 254.9 and 479.9 h of visual observations were recorded between 12 to 109 d after birth (5.8 ± 0.9 h/d; *n* = 44 d) and during the first year after birth (5.9 ± 0.5 h/d; *n* = 81 d), respectively. Results indicated that time spent in echelon, infant, and other position(s) accounted for 24.6 ± 2.7%, 34.4 ± 8.1%, and 4.6 ± 2.2% (*n* = 3), respectively. As the calves grew, they decreased their time spent in the echelon position. In contrast, time spent in the infant position increased and decreased in a parabolic fashion. The peaks (40.2%, 47.8%, and 46.8%) were approached at 91, 62, and 62 d after birth for the three calves, respectively. At 245 d after birth for the captive calf and 187 d for the second seminatural calf, time spent in the infant position began a second increase. This increase continued until the end of the year. Other positions were assumed during a small amount of time and changed slightly over time. In regards to animal management and conservation, we should regulate human activities contributing to the separation of a mother and her calf, especially before 90 d after birth. In addition, we should eliminate fishing gears and other risky factors in the environment until at least 60 d after birth.

Key Words: conservation, echelon position, infant position, *Neophocaena asiaeorientalis asiaeorientalis*, management

Introduction

Spatial position influences animal relations and plays a role in protection, food capture and consumption, locomotive enhancement, etc. (Barnard, 2004). A typical example is found in the formations of birds, which can improve aerodynamic efficiency (Lissaman & Shollenberger, 1970). For many toothed whales, two predominant positions occur after birth between a mother/calf pair (e.g., Tavolga & Essapian, 1957; Miles & Herzing, 2003; Krasnova et al., 2006; Gero & Whitehead, 2007). The first is the echelon position, wherein the mother and calf swim side by side. This position provides the calf with a hydrodynamic boost and tight bonding with the mother (Gubbins et al., 1999; Weihs, 2004; Noren et al., 2006, 2008; Noren & Edwards, 2007). The second is the infant position, in which the calf swims under the mother's genital region. This position provides the calf with a hydrodynamic boost, milk, refuge (countershading), and a break from the mother (Gubbins et al., 1999; Noren & Edwards, 2011).

Compared with the infant position and other nonpredominant spatial positions, the echelon position helps the calf obtain more hydrodynamic benefits (Noren & Edwards, 2011). Other nonpredominant positions (e.g., swimming ahead of the mother or on her back; Tavolga & Essapian, 1957; Krasnova et al., 2006) also have social and developmental significance for the calf (Pilleri & Chen, 1979; Mann & Smuts, 1999; Krasnova et al., 2006). Because of a calf's growth, its time spent in the echelon position decreases with age while time spent in the infant position increases. Development of the calf's two primary spatial positions suggests that older and stronger calves prefer to obtain more and more social benefits from the infant position (such as camouflage to avoid predators) by gradually sacrificing the hydrodynamic benefits of the echelon position (Noren & Edwards, 2011). With regard to the development of other positions, these are rarely documented. In belugas (*Delphinapterus leucas*), the time spent in positions other than the infant or echelon positions changed little across time as the young aged (Krasnova et al., 2006).

Much research has been conducted on spatial positions among toothed whales (e.g., Gubbins et al., 1999; Miles & Herzing, 2003; Krasnova et al., 2006); however, there are still two major problems. First, the general developmental pattern of mammals indicates that calves will start to decrease the time spent in infant position with age (Gubbins et al., 1999). At the start, weaning process from the infant position begins (Martin, 1984). As soon as a calf's sibling is born, time spent by the older offspring in the infant position would decrease to its lowest level. At this point, the weaning process is complete. Thus, to describe the relationship between a mother and her offspring during a critical period of development, it is necessary to follow them for at least one inter-birth interval. Therefore, it could be suggested that the observational period of previous studies generally has been too short. For example, the inter-birth interval of bottlenose dolphins (*Tursiops* spp.) is 2 to 4 y (Perrin & Reilly, 1984; Mann et al., 2000), while researchers typically follow a mother and calf for up to 1 y (e.g., Gubbins et al., 1999). Thus, previous studies would only be able to depict a scenario of interaction between mother/calf pairs before the decrease of time spent in the infant position. Secondly, toothed whales include 10 families (Committee on Taxonomy of the Society for Marine Mammalogy, 2009), with species found from marine to freshwater niches. So far, studies on spatial positions have primarily focused on the marine groups, particularly bottlenose dolphins. Moreover, few, if any, studies examining spatial relations between mother/calf pairs have been conducted on endangered toothed whale species.

The Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) (Pilleri & Gihr, 1972; Jefferson & Wang, 2011) is endemic to the Yangtze River and some of its adjacent waters of China and is the only identified freshwater population of Phocoenidae (Gao & Zhou, 1995). Due to intensive human disturbance in this area, this subspecies is currently endangered (Baillie & Groombridge, 1996). To protect them, a series of rearing and breeding programs in captivity and seminatural reserves have been attempted since the 1990s. In 2005, breeding was successful at both facilities (Wang et al., 2005).

Previous studies indicate that the gestation period of Yangtze finless porpoises is 10 to 11 mo, the inter-birth interval is one to 1.5 y, and the nutritional weaning process happens early between 4 and 6 mo after birth (Chen et al., 1982; Zhang, 1992; Xia et al., 2005; Xian, 2010; Xian et al., 2011, first published online). Therefore, a year's observation after birth may be sufficient to describe the spatial relationship between a mother and her calf during the critical period of development. Following the successful birth of calves at captive and seminatural facilities, we observed three subjects to collect data on spatial positions for up to 1 y after birth. We believe this study will be helpful in (1) understanding the species' early life history, adaptation, and phylogeny; and (2) providing information for animal management and conservation (Gubbins et al., 1999).

Materials and Methods

Subjects

The first calf was Terry; he was the world's first captive born Yangtze finless porpoise calf (Wang et al., 2005). Terry was born on 5 July 2005 in the Baiji Dolphinarium, Wuhan, China. His mother was estimated to be 6.5 y old at the time (Zhang, 1992). Terry and his mother lived with three other porpoises, including the father (10.5 y old; Feng et al., 2009), an adult female (10.5 y old), and an adult male (6.5 y old).

The second and third calves were C06 and C07. They were maintained in the seminatural enclosure of Tongling Freshwater Porpoise National Nature Reserve, Tongling, China. C06 (male) was born on 13 July 2006 and died from entanglement on 29 October (109 d after birth). C07 (sex unknown) was born on 13 August 2007. The mothers of both calves were estimated to be 11.5 and 6.5 y old in July 2006, respectively. C06 and his mother lived with four other porpoises, including the father (13.5 y old; Feng et al., 2009), his full sibling sister (1 y old, died on 30 October 2006; Feng et al., 2009), the mother of C07, and one adult male (12.5 y old). C07 and its mother lived with the mother of C06 (died on 31 January 2008) and the same two other adult males (including the father, but paternity is still unknown). All of the animals could move within the enclosure freely.

Housing Facilities and Animal Management
In captivity, all five animals were maintained in a kidney-shaped pool (20 m × 8 m × 3.5 m) with a connected round pool (diameter 10 m, depth 3.5 m) (Liu, 1997). There were seven and one oblong portholes (2 m × 1.5 m each) on the walls of these pools, respectively. The portholes (4 ± 1.9 m apart from each other) enabled underwater viewing of about 95% of the entire underwater area. To avoid the males' sexual coercion towards the mother and aggression towards the calf, the pools were separated by a slotted metal fence between 15 March 2005 and 6 March 2006 (112 d prior to and 245 d after Terry's birth, respectively). Both adult males were held in the round pool, leaving the mother, calf, and the other adult female in the kidney-shaped pool. All animals could visually and acoustically interact with each other through the fence. The adult porpoises were fed four times a day at 0830-0900 h, 1130-1200 h, 1430-1500 h, and 1650-1720 h. To fulfill the mother's nutritional requirements, an additional meal was provided beginning 6 mo prior to the birth and during the year after birth. Each individual was provided with about 1 kg of fish in each meal. When the calf started to ingest solid food at 101 d after birth, he was fed in accordance with the mother's schedule and was provided 0.05 to 0.5 kg of fish. Training and other human-animal interactions were exclusively conducted during feeding. To reduce the animals' notice of observers, the observers were forbidden to attract, frighten, play with, or feed the animals throughout the study.

The seminatural enclosure is a former side-channel (30°48' to 30°49' N, 117°43' to 117°44' E) of the Yangtze River, which was completely enclosed in 1993. The enclosure (1,600 m × 80 m to 220 m × 3 m) has a flat and sandy bed. Although the porpoises could capture fish in the enclosure, additional food was regularly provided daily at 0900-0930 h and 1400-1430 h. In each meal, 2 kg of fish was provided to each individual except the calf. When C06 started to ingest solid food at 87 d after birth, he was provided with 0.1 to 0.2 kg of fish per meal. Between late January and early February 2008, a severe freeze struck the enclosure. During this time, all the animals were kept in a smaller area by net from 166 to 187 d after birth. Also, observers were forbidden to attract, frighten, play with, or feed these animals throughout the study.

Video Recording in Captivity
Terry was observed every Sunday and Wednesday during the first year after birth. A 10.5-min recording session was selected for each hour between 0500 and 1900 h. Some sessions were conducted at a fixed time for set hours (i.e., 0800-0811 h, 0920-1000 h, 1100-1111 h, 1220-1300 h, 1400-1411 h, 1520-1600 h, 1601-1630 h, and 1740-1800 h). During other hours, the sessions were selected randomly. This sampling schedule contributed to (1) minimizing possible disturbance of feeding on the reliability of observations, (2) equally using the length of daylight, and (3) collecting as much data as possible. For each day of observations, 60 to 160 min of data could be collected. From the portholes, the researchers conducted focal follows while continuously video recording Terry's behavior (Martin & Bateson, 1993; Lehner, 1996).

Cues for Underwater Spatial Positions
Due to poor underwater visibility (about 30 cm) in the enclosure, regular underwater observation of spatial positions between a mother and her calf was not often possible. Hence, it was necessary to find some behavioral cues on the surface that could reliably indicate underwater spatial positions. In captivity, Terry and his mother surfaced synchronously and side by side in the echelon position (echelon surfacing). In the infant position, soon after the mother completed surfacing, Terry moved to the surface and then returned to under the mother's genital region (infant surfacing). With regard to other positions, surfacing patterns between mother and calf were irregular (irregular surfacing). Therefore, we used the echelon, infant, and irregular surfacing(s) as the cue to underwater echelon, infant, and other spatial position(s), respectively. Similar methods have been applied to document spatial position between mother and calf in bottlenose dolphins (Mann & Smuts, 1999).

Visual Observations in the Enclosure
C06 was observed daily 12 to 18 d after birth, every other day between 19 and 76 d, and every 2 to 3 d between 77 and 109 d (C06's death). C07 was observed every 2 to 3 d between 1 to 255 d after birth and every 6 d between 256 and 364 d. A 2-h observation session was selected from each of the following periods each day: before 0830 h, 1000 to 1330 h, and after 1500 h. Also, this schedule contributed to the achievement of three goals of sampling in captivity (see above). On each day, about 6 h of data could be collected. From the adjacent river bank, which was 6 m above the water level, the observer focally followed the calf and continuously recorded events of echelon, infant, irregular, and other surfacing(s) (Martin & Bateson, 1993; Lehner, 1996). The calves were observed via naked eyes or binoculars (7 × 50 mm) depending on the weather and animal-observer distance. Observers were generally at a distance of 30 to 200 m from the focal animal to minimize disturbance yet maintain reliability in observations.

Data Analysis

In captivity, all videos were digitized and stored on a hard drive. Using the editing software *10Moons*© *DV 1-2-3*, each video record was manually played back at a speed of four times the real time until any of the three spatial positions was detected, then the video was manually played frame by frame to obtain the complete duration of the position (in s). The summed duration was divided by the total observation period (in s) each day to calculate a time percentage.

From the enclosure, the total number of events of echelon, infant, and irregular surfacing(s) was divided by the total number of surfacing events per day. Then, the calculated percentage was assumed to be approximately equal to time percentage of the corresponding underwater position. To compare with the data from previous studies (Mann & Smuts, 1999; Krasnova et al., 2006), the time percentages from months one and two after birth were also calculated. Since the start of the weaning process from the infant position was a milestone during the calves' behavioral development, it was important to define this time. As indicated above, following an increase since birth, time spent in the infant position begins to decrease, reaching the lowest level after weaning. Hence, it was applicable to fit this process by an exponential function composited with a quadratic function (Puppe & Tuchscherer, 2000). The function is expressed as

$$Percentage = a + b \cdot e^{-(c \cdot day - d)^2}$$

In this function, the peak (a + b) appears at d/c day after birth when the weaning process from the infant position has started. The parameters a, b, c, and d were estimated by the Levenberg-Marquardt method of nonlinear regression. All data were analyzed under *SPSS*® *13.0 for Windows* and were presented as mean ± SD.

Results

A total of 180.6 h of video were recorded for Terry during his first year after birth (1.8 ± 0.5 h/d, n = 99 d). For C06, a total of 254.9 h of visual observations were recorded between 12 to 109 d after birth (5.8 ± 0.9 h/d, n = 44 d). For C07, the value was 479.9 h during the first year after birth (5.9 ± 0.5 h/d, n = 81 d), excluding days 166 through 187.

During the study, time spent in echelon, infant, and other position(s) accounted for 24.6 ± 2.7%, 34.4 ± 8.1%, and 4.6 ± 2.2% (n = 3), respectively. Between months one and two, time spent in the echelon position was 44.6 ± 8.3% and 28.3 ± 1.9%, 34.1 ± 6.0% and 44.7 ± 4.5% in the infant position, and 3.9 ± 3.1% and 4.8 ± 3.9% in other positions (n = 3), respectively (Table 1). As calves grew, they decreased their time spent in the echelon position. The trend became irregular after 187 d for C07. In contrast, time spent in the infant position increased and decreased in a parabolic fashion. The peaks (40.2, 47.8, and 46.8%) were approached at 91, 62, and 62 d after birth for Terry, C06, and C07, respectively. At Terry's 245 d and C07's 187 d after birth, the amount of time spent in the infant position (about 20% of the time) began a second increase. This increase continued until the end of the year. Other positions were assumed during a small amount of time and changed slightly over time (Figure 1).

Table 1. Time spent in echelon, infant, and other position(s) of three Yangtze finless porpoise calves, Terry, C06, and C07, from birth to 1 y old

	Time percentage								
	Echelon position			Infant position			Other positions		
Subject	Month one	Month two	Year one	Month one	Month two	Year one	Month one	Month two	Year one
Terry	53.0±14.1 (n = 9)	28.1±8.4 (n = 9)	21.6±13.6 (n = 99)	27.2±6.8 (n = 9)	39.8±3.9 (n = 9)	28.4±9.9 (n = 99)	7.4±6.9 (n = 9)	9.1±4.8 (n = 9)	6.3±4.3 (n = 99)
C06	36.4±6.4 (n = 12)*	26.5±6.0 (n = 15)	25.2±10.0 (n = 44)**	37.4±8.8 (n = 12)*	48.7±10.3 (n = 15)	43.6±10.3 (n = 44)**	1.3±2.1 (n = 12)*	1.5±1.3 (n = 15)	2.1±1.8 (n = 44)**
C07	44.3±11.1 (n = 9)	30.2±5.6 (n = 9)	26.9±12.1 (n = 81)#	37.7±12.8 (n = 9)	45.6±4.1 (n = 9)	31.2±12.2 (n = 81)#	3.0±2.3 (n = 9)	3.9±1.1 (n = 9)	5.5±3.0 (n = 81)#

Note: For C06 and C07, time of echelon, infant, and other position(s) are indicated by a percentage of the number of events of echelon, infant, and irregular surfacing(s), respectively.

*Only including data between 12 and 30 d

**Only including data between 12 and 109 d

#Not including data between 166 and 187 d

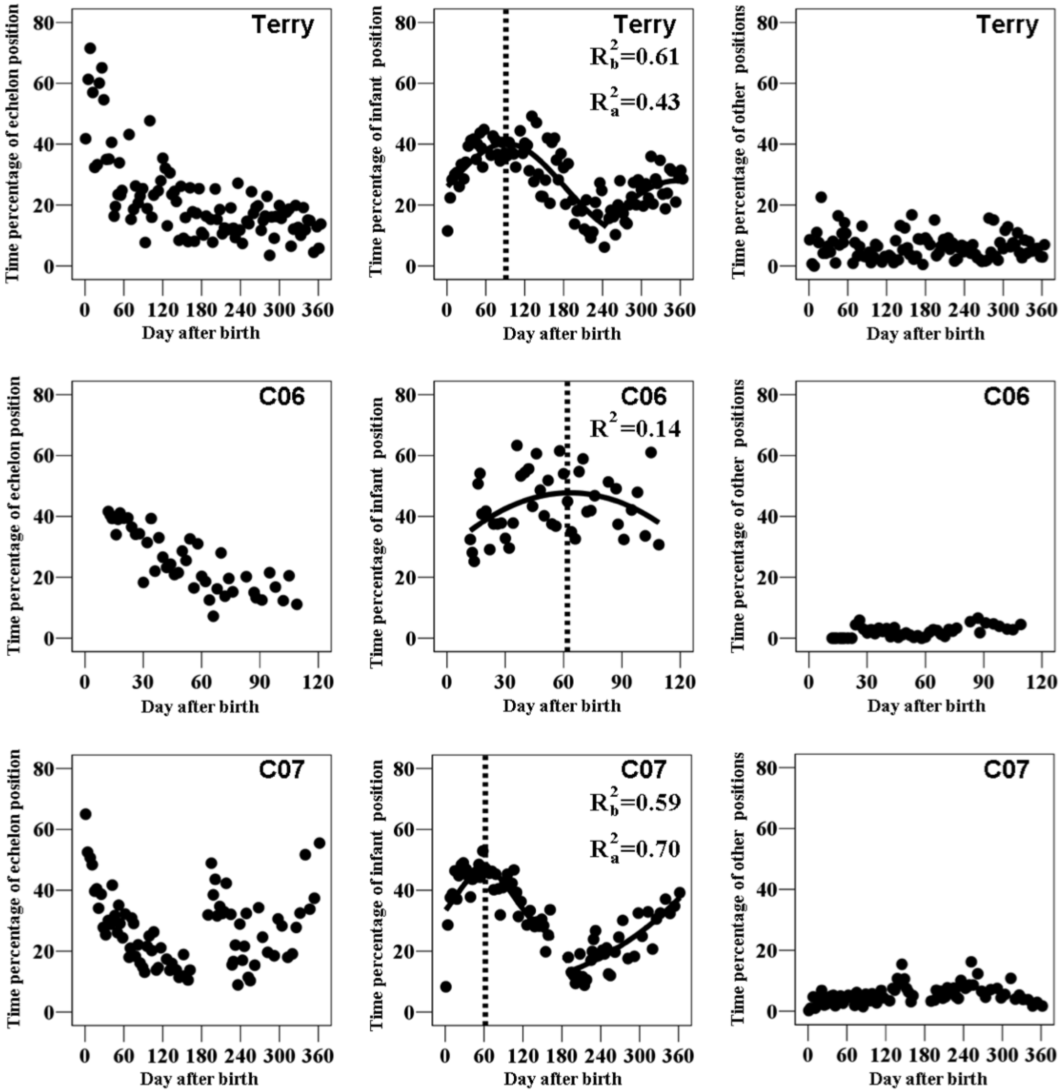

Figure 1. Development of echelon, infant, and other position(s) of three Yangtze finless porpoise calves, Terry, C06, and C07, from birth to 1 y old. For C06 and C07, time of echelon, infant, and other position(s) are indicated by a percentage of the number of events of echelon, infant, and irregular surfacing(s), respectively. Time percentage of the infant position of Terry before (b) and after (a) the pool connection (245 d after birth) is fitted independently by the same function. A similar method is also applied to that of C07 before (b) and after (a) the period when the animals were kept in a small area by nets (166 to 187 d after birth). The dash lines indicate the peak (40.2, 47.8, and 46.8%) at 91, 62, and 62 d after birth for Terry, C06, and C07, respectively.

Discussion

We only had the three calves for our subjects. Moreover, one calf, C06, died before completion of the study. Although these factors likely influenced the results, this study still has important theoretical and practical implications.

Comparisons with Previous Studies

The results obtained from three Yangtze finless porpoise calves are consistent with those of other odontocetes (Tavolga & Essapian, 1957; Gubbins et al., 1999; Mann & Smuts, 1999; Miles & Herzing, 2003; Krasnova et al., 2006; Gero & Whitehead, 2007)—that is, (1) the predominance of the echelon position and infant position between birth and at least 4 mo of age, (2) a decrease in time spent in the echelon position between birth and at least 4 mo of age, (3) an increase in time spent in the infant position between birth and at least 2 mo of age, and (4) a consistency in time spent in other positions between birth and at least 2 mo of age (Krasnova et al., 2006). This consistency suggests general characteristics of adaptation related to spatial positioning between mothers and their calves in toothed whales. Further, it provides evidence of phylogenetic conservation (Gubbins et al., 1999), regardless of taxonomy and niches (salt or freshwater).

There are two differences, however, between the present and previous studies. First, when comparing the time percentage of the echelon and infant positions between month one and two, our results (44.6 and 28.3% for the echelon position; 34.1 and 44.7% for the infant position) were similar to those of belugas (47.5 and 30.9%; 20.8 and 30.3%) (Krasnova et al., 2006), but different from those of bottlenose dolphins (69.3 and 10.6%; 7.7 and 18.0%) (Mann & Smuts, 1999). It seems that during the first month after birth, the swimming abilities of bottlenose dolphin calves are more vulnerable, so they need a greater hydrodynamic boost from the mother. As calves grow, they quickly develop swimming competency; meanwhile, they need more milk, social interaction, and other developmental benefits such as object and motor play (Mann & Smuts, 1999). As a result, they drastically decrease the time spent in the echelon position at month two after birth. With regard to the time spent in other positions, it seems that beluga calves (31.8% for month one and 38.8% for month two; Krasnova et al., 2006) are more sociable than the Yangtze finless porpoise (3.9 and 4.8%). Second, time spent in the infant position decreased at 91 d (in captivity) or 62 d (in the enclosure) after birth, much earlier than those of some dolphins and large toothed whales that generally occur 1 y after birth (reviewed in Tyack, 1986; Mann et al., 2000; Miles & Herzing, 2003). This difference is determined by the inter-birth interval of the species (see above).

Infant Position and Environmental Constraints

Previous studies indicated that, compared to in the wild, behavioral development in captive animals is characterized by quantitative rather than qualitative changes in the nature of responses; the captive environment can slow behavioral development (reviewed in Price, 1999). Our study found that the peak of infant position occurred at 91 d after birth in captivity and 62 d in the enclosure. This month's difference of peak may reflect environmental constraints on behavioral development. Our subjects lived in groups with a similar number of individuals, sex ratio, and age class. In captivity, however, the housing space was much smaller, and the mother did not need to forage and travel. Under this environment, Terry and his mother had more opportunities to form and sustain the infant position, so development of the infant position might have actually been slower. Still, this month's difference of peak may just be the result of sampling methods between the two environments in our study.

Explanations for the Second Increase of Infant Position

The time spent in the infant position increased again for Terry at 245 d and for C07 at 187 d after birth. We attributed this change to the effect of the breeding season of the species. In Yangtze finless porpoises, the breeding season ranges from spring to autumn (reviewed in Hao et al., 2006). This period overlaps that of the second increase of the infant position. Some behavioral observations indicated that the adult males in captivity and in the enclosure initiated energetic and aggressive copulation attempts towards the calves during the second increase in the infant position (Y. Xian, pers. obs., 12 August 2008; Xian et al., 2010). Since these activities are abusive to calves, the calves likely return to their mother and assume the infant position. This position represents a place of hydrodynamic boost, refuge (counter-shading), and rest as seen in bottlenose dolphins (Tavolga & Essapian, 1957; Gubbins et al., 1999).

Infant Position and Trivers' Two Theories

In ethology, the theory of parental investment (Trivers, 1972) and the theory of parent-offspring conflict (Trivers, 1974) are often adopted to interpret the relationship between mother and offspring (reviewed in Barnard, 2004). According to these two theories, the mother may increasingly invest resources, such as time and energy, into their offspring to ensure their survival. However, to prepare for her next birth, she would decrease investment in favor of the pending birth and new offspring. At this point, the current offspring is forced to be nutritionally and/or behaviorally weaned (Martin, 1984). From the offspring's side, it is advantageous for them to obtain as much benefit as possible from the mother. As a result, a conflict of interest between mother and offspring occurs. When the mother's investment decreases down a threshold, the offspring is stimulated to take behavioral and/or psychological measures to counter this decrease. For example, a bottlenose dolphin mother gradually decreases her responsibility for proximity maintenance with the calf; when the responsibility becomes equal between them, the calf starts to increase its responsibility in this relationship (Reid et al., 1995; Mann & Smuts, 1999). In our study, it seems that the theory of parental investment could explain the development of the infant position between birth and 245 d (in captivity) or 187 d (in the enclosure), and the theory of parent-offspring conflict could explain the offspring's development thereafter. The point is that both theories are based on the assumption that the mother strongly controls the relationship and proximity with her offspring. Our observations indicated that Terry and his full sibling (Xian et al., 2011, first published online) exclusively controlled the break and formation of the infant position (Y. Xian, pers. obs., 11 July 2007). Therefore, Trivers' two theories might not be suitable for interpreting the development of the infant position in our subjects. However, this topic needs further investigation since our sample size was limited.

Applications of Studies of the Infant Position

We found that time spent in the infant position started to decrease at 91 d (in captivity) or 62 d (in the enclosure) after birth. The decrease indicated the start of the weaning process from the infant position, one milestone during the calves' development. Thus, we recommend using the time of 90 or 60 d after birth to be a reference for decisionmaking regarding management and conservation of this species. First, we should regulate human activities contributing to the separation of a mother and her calf especially before 90 d after birth. Like other toothed whales (Jefferson & Curry, 1994; Richardson et al., 1995), boat traffic, fishery operations, sand mining, channel deepening, and other human activities are main factors disrupting the lives of wild Yangtze finless porpoises (reviewed in Wang, 2009). These factors may lead to the separation of a mother and her calf as seen in spotted (*Stenella attenuata*) and spinner dolphins (*S. longirostris*) (Noren & Edwards, 2007). If calves of Yangtze finless porpoise are orphaned, particularly before 90 d after birth, they would not survive on their own. Second, we should eliminate fishing gears and other risky factors in the environment as of 60 d after birth in particular. Young animals generally like to explore their environment and manipulate novel objects. This tendency contributes to their accumulation of experience useful for their future lives, but it also may lead to risks for survival (Barnard, 2004). In our study, the decrease of time spent in the infant position implies that the probability for calves to show such tendency would increase, which may account for the death of C06. On his 109th d after birth, C06 left his mother, searching along the bottom of the enclosure; he died after becoming entangled in discarded fishing gear (Y. Xian, pers. obs., 29 October 2006). In summary, in regards to the importance of infant position and its development in the management and conservation of Yangtze finless porpoises, it is necessary to increase our sample size in future studies.

Acknowledgments

We thank our colleagues for their assistance in animal husbandry. We thank Lijun Dong, Xinqiao Zhang, and Shouyue Dong for help in video recording. We thank Wuyi Wang and Bajin Zhang for their valuable instructions on visual observation in the enclosure. We thank Jiakuan Shu, a postgraduate of the School of Life Science at Anhui University, for sharing his helpful experience and findings with us. We also thank Dr. Xiulian Sun from the Insect Virus and Genetic Engineering Group, Wuhan Institute of Virology, Chinese Academy of Sciences, China; Dr. Jianqiang Xiao from the Psychology Department, Rutgers University, Piscataway, New Jersey, USA; and Dr. Armin Tuchscherer from the Research Unit Genetics & Biometry, Leibniz Institute for Farm Animal Biology for providing valuable instructions on statistics. This work was supported by grants from the Chinese Academy of Science (KSCX2-EW-Z-4), the National Natural Science Foundation of China (30730018), and the President Fund of the Chinese Academy of Sciences (220103).

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