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The Development of Mother-Calf Interactions During the First Year in Yangtze Finless Porpoises (*Neophocaena asiaeorientalis asiaeorientalis*)

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Ran Chen, Wenbo Li, Wenhua Jiang, Bangyou Zheng, and Jinhua Li (2018) Mother-offspring interactions are widespread in humans and other mammals, and play an important role in offspring survival and development. Mother-calf interactions have been described in a wide range of ocean cetacean species, but they have not yet been documented in freshwater cetaceans. In this study, we observed the behavior of two mother-calf pairs of Yangtze finless porpoises living in Tongling Freshwater Porpoise National Natural Reserve, China, to explore the maternal relationship between mother porpoises and newborn calves during the calves' first year. The results showed that mothers performed significantly more approach behaviors and fewer leave behaviors than calves during the lactation period, but performed significantly fewer approach and more leave behaviors than calves during the non-lactation period (starting from the seventh month after birth). The landmarks for maintaining intimate relationships within each mother-calf pair occurred within sixth months of birth. The duration of calf separations from their mothers increased with calf age.

Key words: Approach-leave behavior, Hinde Index, Mother-calf, Interactions, Yangtze finless porpoises.

BACKGROUND

Mother-offspring interactions are widespread in humans and other mammals (Trivers 1974; Taber and Thomas 1982; Olson et al. 1984; Szabo and Duffus 2008; Guarino et al. 2017), and play an important role in offspring survival (Xian et al. 2012a; Sakai et al. 2013). The offspring often benefits from its mother's vigilance and protection, and from the shelter of her den or burrow (Mann and Smuts 1999; Noren and Edwards 2011). On the other hand, the maternal care behaviors and soliciting by offspring involve parent-offspring conflict (Trivers 1974). Mothers may also suffer directly from the fitness costs associated with maternal care and a reduction in foraging efficiency (White and Berger 2001). It has been predicted that a mother will attempt to decrease parental investment when the fitness costs exceed the benefits to its lifetime reproductive success (Sakai et al. 2013). Mother-calf interactions have been documented in some cetaceans, including southern right whales (*Eubalaena australis*) (Taber and Thomas 1982), humpback whales (*Megaptera novaeangliae*) (Szabo and Duffus 2008), blue whales (*Balaenoptera musculus*), killer whales (*Orcinus orca*) (Smultea et al. 2017), wild beluga whales (*Delphinapterus leucas*) (Krasnova et al. 2006), bottlenose dolphins (*Tursiops truncatus*) (Noren 2008), and Commerson's dolphins

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(*Cephalorhynchus commersonii*) (Sakai et al. 2013). Unlike many other mammals, cetaceans may have precocious swimming proficiency, which allows newborn calves to be intimate with their mothers from the beginning of their lives (Mann and Smuts 1999; Xian et al. 2012a; Hill and Campbell 2014). In the early newborn calf stage, the mother-calf mutual relationship is predominantly maintained by the mother (Tavolga and Essapian 1957; Mann et al. 2000). As the calf grows, it becomes increasingly independent and begins to leave its mother, come in contact with other individuals (Mann and Smuts 1998), and explore natural environments to master its survival skills and benefit from rich social experiences (Mann and Smuts 1998). Although mother-calf interaction behaviors have been described in a wide range of ocean cetacean species, our knowledge of the presence and development of mother-calf interactions in freshwater cetaceans remains unclear.

The Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*), a subspecies of the narrow-ridged finless porpoise, is endemic to the middle and lower reaches of the Yangtze River and its two adjoining lakes (Poyang Lake and Dongting Lake), China (Gao and Zhou 1993). It is the only freshwater cetacean remaining in the Yangtze River following the presumed extinction of the baiji (*Lipotes vexillifer*) in 2006 (Turvey et al. 2007). Recent demographic trends highlight an accelerating decline of the Yangtze finless porpoise and indicate a high probability of extinction (86%) within the next 100 years (Mei et al. 2017). To protect them, a series of rearing and breeding programs in captivity and semi-natural reserves have been attempted since the 1990s. There are some behavioral studies that have focused on social sexual behavior (Xian et al. 2010), the development of spatial position (Xian et al. 2012a), suckling behavior (Xian et al. 2012b), maternal care behavior (Wu et al. 2015), and behavioral laterality (Platto et al. 2017); there are also some histological and reproductive biological studies on the finless porpoise (Guo et al. 2014; Zeng et al. 2015; Yu et al. 2016; Nabi et al. 2017). However, there have been no continuous studies of mother-calf interactions and development in Yangtze finless porpoises, and such studies may benefit this endangered species in the future. The current study provides the first evidence for mother-calf interactions (approach and leave behaviors) in Yangtze finless porpoises.

The purpose of the present study was to document mother-calf interactions and developmental changes between lactation and non-lactation periods. Previous studies indicate that the nutritional weaning process happens between four and six months after birth (Zhang 1992; Xian et al. 2010 2012b). Therefore, a year-long observation directly after birth might be sufficient to describe mother-calf interactions. We were specifically interested in (1) who maintains close proximity in mother-calf pairs during the lactation and non-lactation periods and (2) identifying the landmarks in maintaining an intimate relationship and the durations of calf separations from their mother. The present study will be helpful in understanding the role of mother and calf in maintaining an intimate relationship and parent-offspring conflict in this species.

MATERIALS AND METHODS

Study site and sampling

The study was conducted in a channel of the Yangtze River at Tongling Freshwater Porpoise National Nature Reserve (TLFPNNR), Tongling, China (30°48'- 30°49'N, 117°43'-117°44'E) (Fig. 1). The channel is approximately 1600 m long and 80-220 m wide, with a maximum depth of 5 m (Fig. 2), which is an ex-situ conservation site for Yangtze finless porpoises by TLFPNNR.

Eight porpoises lived in the channel during the study. Between 5 June 2014 and 26 June 2015, we systematically observed two mother-calf pairs of finless porpoises (Xiaoci-Xiaohei, XC-XH; Banban-Banqing, BB-BQ) (Table 1) to explore mother-calf interactions during the calves' first year. Although this species has no dorsal fin, we could identify porpoise individuals according to body size, body spots; *i.e.*, there were lots of spots BB's head (the red circle of the Fig. 3). Additionally, the mother and calf always occurred in pairs during the calves' first year (Fig. 3), so we could easily identificat with other members of the group. Between 5 June 2014 and 26 June 2015, we systematically observed the two pairs of mother-calf finless porpoises. On the shore side of the channel, observers (walking or riding a bicycle) were generally at a distance of 30-200 m from the focal animals to minimize disturbance. We used focal animal sampling (Altmann 1974) to follow the mother-calf interactions and separate behaviors via naked eyes or binoculars (OLYMPUS® 10 × 42) depending on animal-observer distance. We

defined three mother-calf interaction ethograms,as defined by Xian et al. (2010) (Table 2). Each day, a 10 min focal sampling session was selected from each of the following periods: 09:00-10:00, 10:00-13:30, and after 15:00; each mother-calf pair was sampled during each period.

Data analysis

The data were normalized prior to analysis. Differences in mother-calf interactions (the number of approach behaviors and leave behaviors per hour between mother and calf) observed

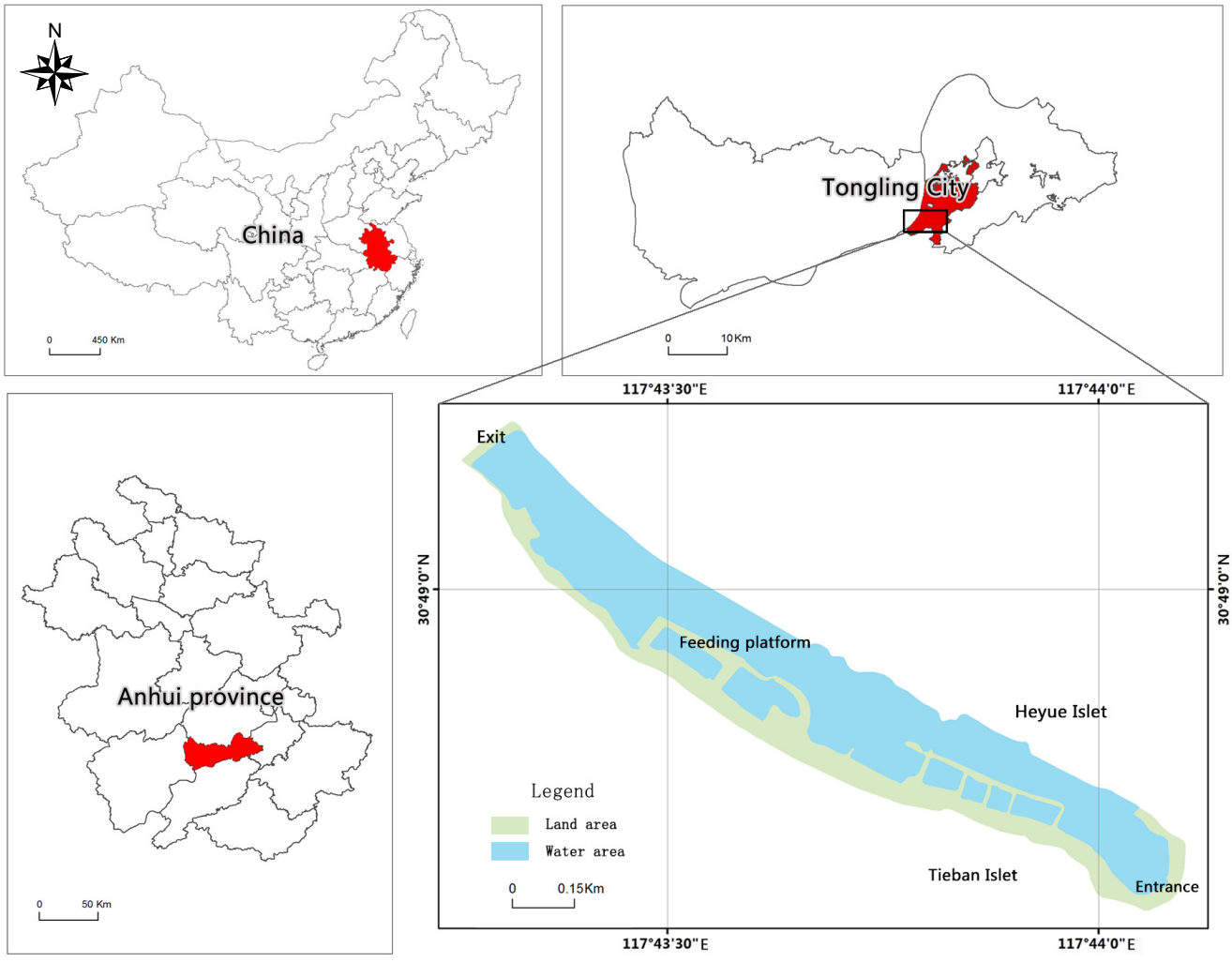

Fig. 1. Location and sketch map of the observation site.

Table 1. The subjects and their biological parameters in this study

Name	Mother	Mother	Calf	Calf
	Xiaoci (XC)	Banban (BB)	Xiaohei (XH)	Banqing (BQ)
Sex	Female	Female	Male	Male
Weight(kg)	33.6	27	Unknown	Unknown
Length(cm)	131	122	Unknown	Unknown
Age group	Adult	Adult	Infant	Infant
Birthday	-	-	June 10th, 2014	June 4th, 2014

between lactation and non-lactation periods were tested using one-way ANOVA and least-significant difference (LSD) test. A Wilcoxon test was used to analyze differences between mother and calf's approach and leave behaviors during the lactation and non-lactation periods. With reference to Zhang (1992), in this study we define the lactation period as the calf's first six months

Fig. 2. Aerial photograph of the observation site.

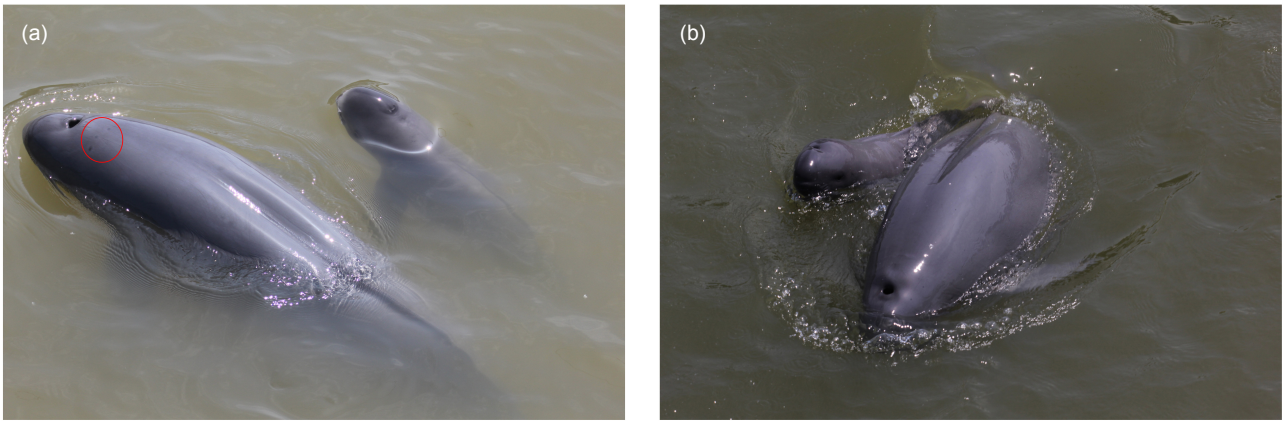

Fig. 3. Photo of mother and calf (a: Banban (mother) to the left, Banqing (calf) to the right, b: Xiaoci (mother) to the right and Xiaohei (calf) to the left). Note: Banban has many spots on head and body (circled in red) and this diagnostic feature allow it to be distinguished from Xiaohei.

Table 2. Ethograms of Yangtze finless porpoises in this study

Behavior	Definition
Approach	Animal swims to another for 2 m radius, and anther keeps relative stillness
Leave	Animal departs from another for 2 m radius, and anther keeps relative stillness
Calf separate mother	A calf stay alone or play with others departing from the mother

after birth and the non-lactation period as the calf's seventh month onward. The correlation between the mean duration of calf separations away from their mothers and the calf's age was evaluated using Pearson's correlation coefficient (r). In all of the statistical analyses, $p < 0.05$ was considered statistically significant. SPSS software was used for statistical analysis (SPSS 1997).

The Hinde Index (HI) was used to calculate who was responsible for maintaining proximity within each mother-calf dyad (Hinde and Atkinson 1970). The HI was determined by the proportion of approach (A) and leave (L) behaviors that are initiated by the mother (M) and calf (C): $HI_{c\text{-}m} = A_c / (A_c + A_m) - L_c / (L_c + L_m)$. The index ranges from -1, when the mother is totally responsible for maintaining proximity, to +1, when the calf is totally responsible for maintaining proximity. An index close to 0 indicates equal responsibility.

RESULTS

In total, we conducted 11950 min of focal samplings of XC-XH and 10670 min of focal samplings of BB-BQ (Tables 3 and 4).

Approach and leave behaviors

The two mother-calf pairs of porpoises performed approach and leave behaviors during both lactation and non-lactation periods (Tables 3 and 4). One-way ANOVA showed that both mothers ($F_{1, 23} = 88.157$, $p = 0.000$) and calves

Table 3. The approach-leave interaction frequencies and Hinde Index between Xiaoci and Xiaohei during the first year after birth

Age (month)	Obs. days	calf approach mother (times/h)	mother approach calf (times/h)	calf leave mother (times/h)	mother leave calf (times/h)	HI index
1	16	0.2 ± 0.98	0.78 ± 2.62	1.75 ± 2.64	0.47 ± 1.85	-0.58
2	22	0.67 ± 1.96	1.57 ± 3.65	1.71 ± 2.11	1.38 ± 1.69	-0.25
3	18	0.89 ± 2.12	1.3 ± 2.34	1.82 ± 2.28	1.21 ± 2.62	-0.20
4	21	0.89 ± 1.44	1.2 ± 2.48	1.43 ± 2.72	0.91 ± 1.17	-0.19
5	20	1.1 ± 1.82	1.22 ± 2.65	1.71 ± 2.53	1.22 ± 1.12	-0.11
6	24	0.89 ± 1.87	0.98 ± 1.78	1.6 ± 2.89	1.35 ± 1.98	-0.07
7	24	0.98 ± 2.32	0.31 ± 2.12	1.24 ± 1.56	2.2 ± 3.21	0.17
8	22	0.65 ± 2.75	0.43 ± 1.56	1.12 ± 1.91	2.32 ± 1.45	0.26
9	23	0.43 ± 1.87	0.32 ± 1.32	0.41 ± 1.45	1.89 ± 2.67	0.39
10	23	0.35 ± 1.12	0.18 ± 1.21	0.64 ± 1.87	2.17 ± 3.45	0.43
11	20	0.26 ± 1.38	0.24 ± 1.31	0.78 ± 1.45	1.78 ± 3.12	0.21
12	17	0.35 ± 1.32	0.12 ± 1.67	0.52 ± 0.35	1.67 ± 2.65	0.50

Table 4. The approach-leave interaction frequencies and Hinde Index between Banban and Banqing during the first year after birth

Age (month)	Obs. days	calf approach mother (times/h)	mother approach calf (times/h)	calf leave mother (times/h)	mother leave calf (times/h)	HI index
1	20	0.33 ± 1.34	0.77 ± 1.12	2.05 ± 3.12	0.4 ± 1.13	-0.42
2	22	0.41 ± 1.67	1.44 ± 2.01	2.4 ± 3.37	1 ± 2.11	-0.49
3	18	0.78 ± 1.14	1.2 ± 1.09	2.56 ± 3.14	1.94 ± 2.48	-0.18
4	21	0.78 ± 2.21	0.89 ± 1.78	2.5 ± 2.46	1.25 ± 1.89	-0.20
5	20	0.82 ± 1.53	0.97 ± 1.34	1.98 ± 2.45	2.14 ± 2.15	-0.03
6	24	0.84 ± 1.46	1.12 ± 1.06	1.2 ± 1.98	2.23 ± 3.12	-0.03
7	24	0.89 ± 1.12	0.53 ± 1.15	0.88 ± 2.16	2.36 ± 2.56	0.19
8	22	0.91 ± 1.34	0.52 ± 1.23	0.89 ± 2.87	2.1 ± 1.78	0.34
9	23	0.53 ± 1.09	0.46 ± 1.03	0.79 ± 1.78	1.98 ± 2.45	0.25
10	23	0.36 ± 1.56	0.24 ± 1.23	1.1 ± 2.13	1.87 ± 2.58	0.23
11	20	0.28 ± 1.45	0.18 ± 0.98	0.88 ± 1.45	1.69 ± 1.98	0.27
12	17	0.31 ± 1.39	0.16 ± 0.87	0.45 ± 1.98	1.56 ± 1.67	0.44

($F_{1, 23}$ = 5.679, p = 0.026) performed significantly more approach behavior during the lactation period than in the non-lactation period (Fig. 4a, b, Tables 3 and 4). During the lactation period, mothers (XC, BB) approached more frequently than calves (XH, BQ) did (Fig. 4a, b) (Wilcoxon test Z = -3.059, p = 0.002). However, during the non-lactation period, the frequency of the two mothers' approach behavior was largely decreased to less than that of the calves (Wilcoxon test Z = -3.059, p = 0.002).

One-way ANOVA showed that leave behavior of mothers (XC, BB) significantly increased across lactation and non-lactation periods ($F_{1, 23}$ = 6.665, p = 0.017), and the observed increase in leave behavior of calves (XH, BQ) was almost significant ($F_{1, 23}$ = 9.848, p = 0.05) (Fig. 5a, b, Tables 3 and 4). During the lactation period, mothers performed less leave behaviors than calves (Wilcoxon test Z = -2.981, p = 0.003). During the non-lactation period, mothers performed more leave behavior

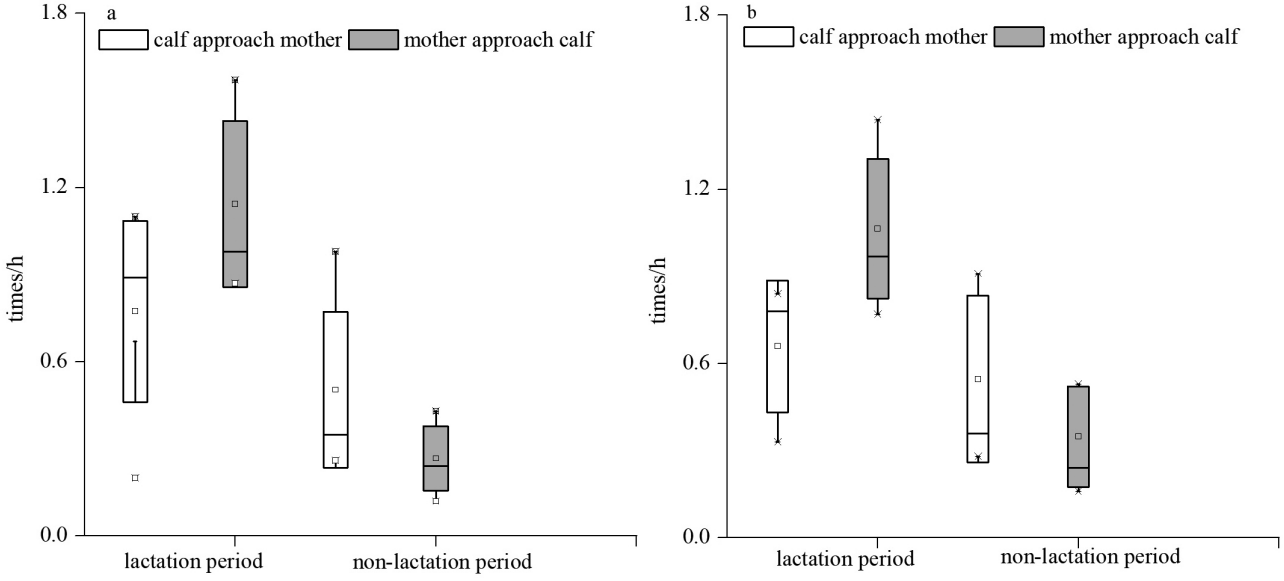

Fig. 4. The frequencies approach behavior between mother and calf during lactation and non-lactation period. (a: Xiaoci-Xiaohei pair; b: Banban-Banqing pair).

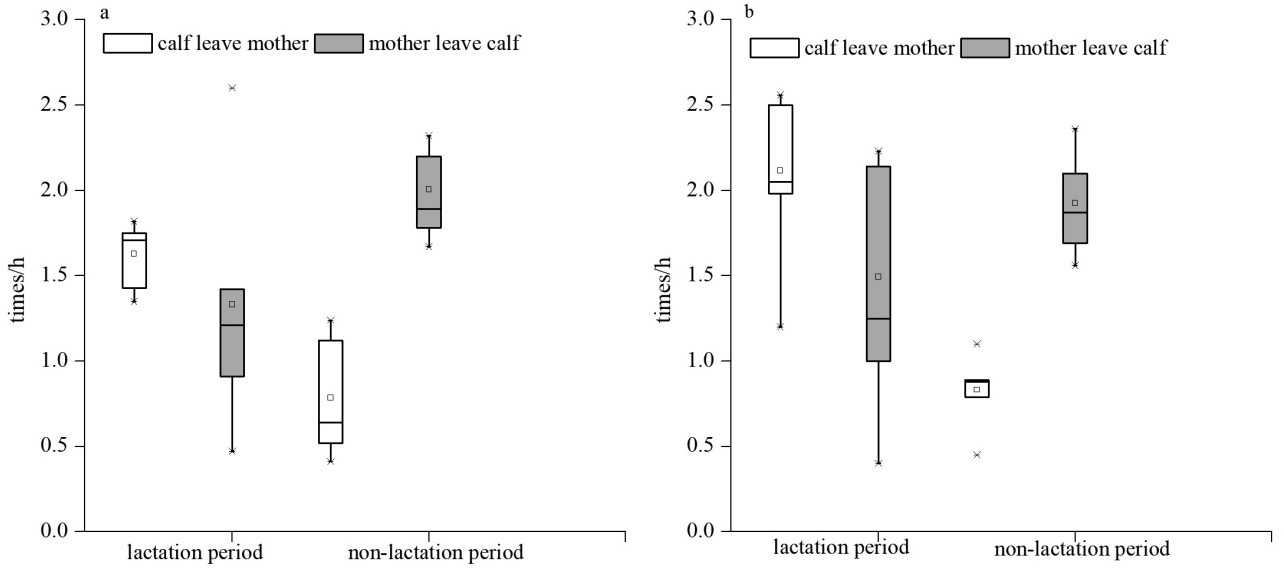

Fig. 5. The frequencies of leave behavior between mother and calf during lactation and non-lactation period. (a: Xiaoci-Xiaohei pair; b: Banban-Banqing pair).

than calves (Z = -3.061, p = 0.002).

Intimate relationship index

The HI index showed an intimate relationship between mother and calf. $HI_{c\text{-}m}$ revealed an increasing tendency from negative values to positive values, and a landmark occurs during the sixth month after birth, at the division between lactation and non-lactation periods (Tables 3 and 4). These results indicated that during lactation, mothers were mostly responsible for maintaining proximity, whereas calves took more responsibility during the non-lactation period.

Separation duration

The separation durations of calves from their mothers was positively correlated with the calves' age in months for both mother-calf pairs: N = 12, p = 0.00, r = 0.963 for XC = XH; and N = 12, p = 0.00, r = 0.969 for BB-BQ (Fig. 6).

DISCUSSION

We found that the interactions between mother finless porpoises and their calves begin directly after calf birth, just like in humpback whales (Szabo and Duffus 2008), killer whales (*Orcinus orca*) (Guarino et al. 2017), and Commerson's dolphins (*Cephalorhynchus commersonii*) (Sakai et al. 2013). Mothers seldom leave newborn calves during the first month (Tables 3 and 4). This might be because the calf's swimming skills are still unstable or because the mother and calf have not yet been able to initiate approach and leave interactions. The frequency of mother and calf approach-leave behavior becomes greater and greater as they grow older, this is like in some other cetacean species' behaviors. 1) Southern right whales (*Eubalaena australis*): During the first few weeks of a calf's life, mothers and calves were within close proximity over 90% of the time, and the mothers were responsible for maintaining contact with her infant. Later, calves strayed farther and initiated many more leaves and approaches than their quiescent mothers (Taber and Thomas 1982); 2) Humpback whales (*Megaptera novaeangliae*): As the season progressed, females became significantly less responsive to their offspring, at the same time, calves appeared to increase their role in maintaining proximity with the mothers increasingly often (Szabo and Duffus 2008); 3) Wild beluga whales (*Delphinapterus leucas*) the behavior of calves becomes more complex as they physically grow and develop, they become more independent (Krasnova et al. 2006);

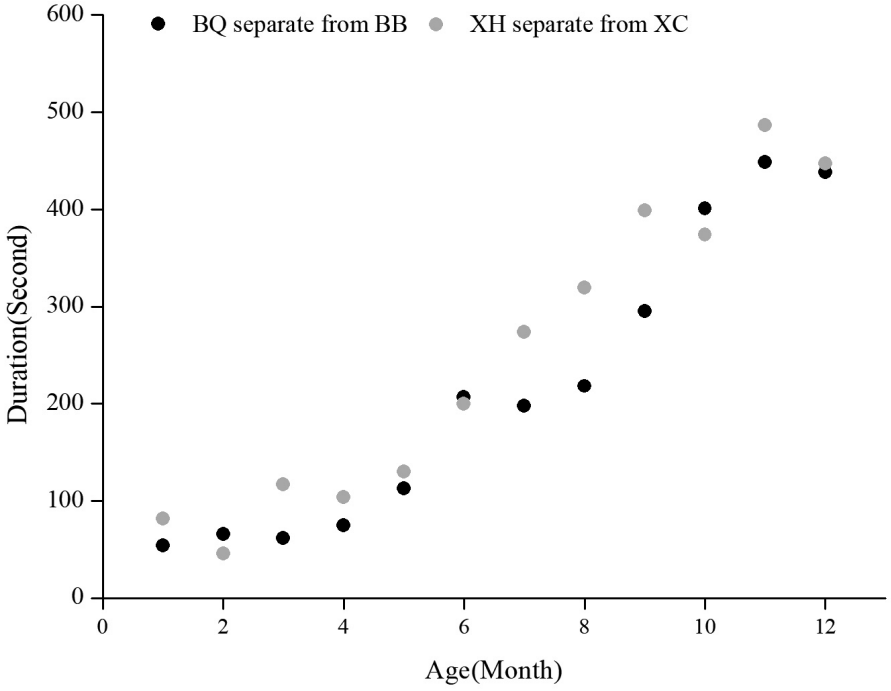

Fig. 6. The duration of calves' (Xiaohei, Banqing) separating from their mothers (Xiaoci, Banban).

4) Commerson's dolphins (*Cephalorhynchus commersonii*) separate behaviors of mothers were infrequent during the first week and increased with an increase in infants' age (Sakai et al. 2013) and bottlenose dolphins (*Tursiops truncatus*)as the same (Noren 2008). For calf dolphins, this may be because of a need to improve their sensory and motor abilities or for social interactions (Xian et al. 2012a; Mann and Smuts 1999).

Unlike many terrestrial mammals (*e.g.*, Florida panther, *Felis concolor coryi* (Maehr et al. 1989); spotted hyaena, *Crocuta crocuta* (Hofer and East 1993), whales are unable to hide their calf in open aquatic environments, and therefore mother and calf must be closely linked together. Mothers can maintain an intimate relationship to assist calves' swimming and protect them through approach and leave interactions. Leaving behavior could improve calves' sensory and motor abilities and increase opportunities for social interactions (Xian et al. 2012a). In addition to taking care of calves, mothers must also forage, therefore temporary separation is inevitable in mother-calf interactions. Maternal provisioning among mammals allows offspring to develop until they can independently acquire and process their own food (Pond 1977). With increasing calf age and improvement of their sensory and motor abilities, the mother leaves her calves more and more frequently.

The mother played the dominant role in maintaining mutual proximity between mother and calf during their calf's first six months of life, but the calf took over this role was taken over by the calf in the second half of its first year. After the landmarks at six months after birth, the calf became more independent in maintaining the intimate relationship within each mother-calf pair. This transformation was also reported for 1) Bottlenose dolphin (*Tursiops* sp.): Hinde Index declined significantly from month one to month two, indicating that maternal responsibility for proximity decreased over time (Mann and Smuts 1999); 2) southern right whales: yearling calves stayed close to their mothers when returning to their mothers' area, and few leaves and approaches by either pair member were recorded. The yearling calves were responsible for maintaining contact as the mothers left them more than approached them (Taber and Thomas 1982). One explanation for this shift comes from considering the energetics associated with lactation, because the demands of the offspring are reported to increase throughout lactation (Szabo and Duffus 2008; Sakai et al. 2013) *e.g.*, needing more milk (Mann and Smuts 1999) and the fat concentration in the milk rises (Oftedal 1997). However, maternal provisioning among mammals could not remain forever. As a result, mothers drastically increase leave behavior and calves increase separation duration. This could be viewed as not only mother-calf conflict but also dynamic balance. Mother finless porpoises reduce responsiveness to their calves, which represents a reduction in parental investment in favor of an increase in foraging efficiency and, potentially, the success of their future offspring. During this time, however, calves develop a series of sensory, motor, and foraging abilities and improved survival opportunity. The changing roles in proximity maintenance observed in cetacean mother-calf pairs can be viewed in more general parent-offspring conflict (Trivers 1974) terms. In natural settings, the theory of parent-offspring conflict is often evoked during instances where the mother rejects nursing solicitations by the offspring. In this study, we used the duration of calf separations away from its mother as an indicator of parent-offspring conflict. The observed increase in separation duration as calves grow may partially represent parent-offspring conflict. During this time, however, it is still in the calf's best interest to maintain proximity to its mother, for both the protection that this affords and the opportunity to nurse, and therefore the calf must become increasingly proactive in doing so.

CONCLUSIONS

The current study provides the first evidence for mother-calf interactions (approach and leave behaviors) in Yangtze finless porpoises. Our results indicate that mothers performed more approach behaviors during the lactation period and were mostly responsible for maintaining proximity in this period. Transitioning into the non-lactation period, calves played a larger role in maintaining proximity, and calves separated from their mothers for longer. The landmarks in maintaining intimate relationships within each mother-calf pair occurred during the sixth months after birth. Our results suggest that, considering the high demands during the first six months, an increase in the feeding of fish meals for adults may be helpful in maintaining the mother's energy and increasing care towards her calf. However, further research is warranted to shed light on how the social pressure between individuals of same group may influence

the outcomes of approach-leave behaviors in cetaceans. In addition, studies on environmental conditions and adaptation may also help us further understand the function of mother-calf interactions.

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Authors' contributions: Ran Chen and Wenbo Li performed the field work and statistical analyses and wrote the paper. Jinhua Li conceived and designed the research. Wenhua Jiang and Bangyou Zheng collected the sample data.

Competing interests: Ran Chen, Wenbo Li, Wenhua Jiang, Bangyou Zheng and Jinhua Li declare that they have no conflicts of interest.

Availability of data and materials: Observation data are presented in supplementary tables 1 and 2.

Consent for publication: Not applicable.

Ethics approval consent to participate: Data were collected with approval from the Tongling Freshwater Dolphins National Nature Reserve.

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Supplementary Materials

Table S1. Xiaoci (XC) and Xiaohei (XH). The first column are Observation dates. *e.g.*: 20140511 means May 11 2014, and that day we got 6 focal samplings (600 seconds). In a focal sampling, we record mother approach (leave) calf and mother approach (leave) mother total times, also record calf separate mother total duration (seconds). (download)

Table S2. Banban (BB) and Banqing (BQ). The first column are Observation dates. *e.g.*: 20140505 means May 11 2014, and that day we got 8 focal samplings (800 seconds). In a focal sampling, we record mother approach (leave) calf and mother approach (leave) mother total times, also record calf separate mother total duration (seconds). (download)