

Behavioural responses of *ex-situ* captive hippopotamus (*Hippopotamus amphibius*) in lactation season: Maternal investment and plasticity of infant self-independence

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Abstract In order to promote hippopotamus management in the captive and *ex-situ* environment, especially the control of behavioural and physiological status during breeding and lactation seasons, we conducted a preliminary study on behavioural responses of a pair of hippos including both mother and infant in Hangzhou Wildlife Park, China. The study of the captive hippos for about 1-month in the lactation season was carried out during August and September, 2009. The behavioural patterns were identified by all occurrence sampling and instantaneous scanning sampling methods with 5–10 min intervals. As a result, mother-offspring conflicts and interactions did occur throughout the whole study period. Early maternal investment showed a positive trend in activity rhythms (slope = 0.0014, $Z = 0.3027$, $P < 0.001$) and a negative trend (slope = -0.0066 , $Z = 0.8807$, $P < 0.001$) in territorial occupation of water, all of which supported our hypotheses that the mother hippo might exert less care for the infant and cut down on her own obligations in nursing. For infant self-independence, during the whole lactation season, the primary trends of activities and territorial occupation dynamics of the infant hippo were slightly different from before, judging from linear models (slope = -0.0017 , $Z = 0.3309$, $P < 0.001$). However, the frequencies of activities were not stable, especially at around 12 days of age. The trends of territorial occupation (slope = -0.0071 , $Z = 0.904$, $P < 0.001$) also showed negative dynamics in water body occupation by the time the infant hippo grew up. The general trend (slope = -0.005 , $Z = 0.06$, $P < 0.001$) of suckling dynamics was

demonstrably negative, with an upwards fluctuation at period 3 (10–15th day). This also illustrated that as the infant developed, the dependency on the mother was reduced at the end of the lactation season. In addition, a sharp decline between P3 and P4 also supported the mother-offspring conflict theory. In general, time budgets of hippos in active behaviour were $(31.8 \pm 2.1)\%$ for the mother and $(32.1 \pm 2.6)\%$ for the infant. Spatial distributions in water within temporal limitations were $(80.1 \pm 2.7)\%$ for the mother and $(81.8 \pm 2.7)\%$ for the infant. Behavioural dynamics showed strong synchronous relations between maternal investment and infant independence. Our current short-term investigation proves to be a key in management and conservation of hippopotami during the lactation season.

Keywords hippopotamus (*hippopotamus amphibius*), behaviour, captive, maternal investment, infant independence, lactation season, zoo

1 Introduction

The hippopotamus (*Hippopotamus amphibius*) is one of the largest land animals in the world, with a round body, four short legs, and a big, broad head. Historically, this animal once occupied an extensive range of wetland ecosystems in Africa. However, gradually, the geographical distributions have shrunk significantly resulting in distributions occurring only in some middle and southern African countries (Eltringham, 1999). Due to habitat losses and commercial poaching, the population of wild hippos has decreased dramatically (McCarthy, 1998). Therefore, conservation management is strongly and urgently

recommended to save this famous and popular species. However, as we know, management is not possible without understanding a species' natural behaviours.

Some recent studies concerning hippos mostly focused on the natural population, reproductive physiology, environmental effects and molecular evolution (Laws and Clough, 1966; Dittrich, 1976; Marshall and Sayer, 1976; Smuts and Whyte, 1981; Bronson, 1989; Eltringham, 1999; Smith et al., 2000). However, studies related to lactational behaviour of hippos are still lacking. This is especially true in the case of maternal investment and infant independence during lactation season, which are key behaviours exhibited by females and are partially known to the scientific community.

In the present study, based on zoo conservation, we tested multiple behavioural dynamics, which means different targeting behaviours occurring independently within certain temporal sequences, of both mother and infant hippos during the lactation season. Because normally hippos give birth to one calf after an 8-month gestation period (Eltringham, 1999), there might be a potentially high risk of losing their infants in the natural habitat. Moreover, the infant hippopotamus is born underwater and the mother hippopotamus takes care of her calf, nursing it underwater although occasionally giving birth also on land (Laws and Clough, 1966). Due to the long duration of underwater activity, there is very little knowledge regarding the initiative actions of lactational behaviour as well as infant suckling behaviour. Thus, it is important to understand synchronous behaviours of both mother and infant during the infant's early development, which might later contribute to deep studies on how mother hippos invest their time and energy, and even genetic approaches in raising baby hippos. This study will also help those communities who work in wildlife reproduction and raising management.

To understand how behavioural patterns oscillate and the relationships between mother and calf, we designed this experiment to approach conservation of the hippopotamus (*Hippopotamus amphibius*) and explore more useful information in *ex-situ* conservation.

2 Materials and methods

2.1 Geographical and environmental information

The research was conducted at Hangzhou Wildlife Park (119°59'E, 30°09'N), Fuyang County, Hangzhou City, Zhejiang Province, China. The average temperature in this region is 16.2°C annually, with average temperatures of 28.6°C and 3.8°C in summer and winter, respectively. The average rainfall is 1435 mm per year. During the time of our research, the average temperature range was from 36.3°C to 42.4°C. The captive hippos were individually housed in a concrete enclosure with an area of 500 m² in

the open field and a 100 m² indoor room (80 m² water pool with slope and 0.5–1.0 m in depth). The water in the pool was changed every other day in the morning (8:00 am to 9:00 am). The hippos were fed twice a day with dry and fresh plants as needed at around 10:00 am and 3:00 pm. They were in good health, and the experimental protocol met the regulations of animal care and uses (Law of Wildlife Protection, China, 1988 and Regulations for the Administration of Affairs Concerning Experimental Animals, China, 1988), and also received approval from the Veterinary Committee of Wildlife Park.

2.2 Sampling and processing

A pair of hippos, both mother hippo (7 years old) and infant hippo (male), were observed in this study. During observation time, the observers usually hid in front of the enclosure, keeping a distance 10 m away; video recordings were also made and assisted with the final checking. The observation lasted 3 weeks, from 9:00 am to 5:00 pm daily (according to the regulations of the wildlife park, the calf should be separated from his mother and translocated to another room after it reaches 3 to 4 weeks old.) during August and September 2009. Moreover, Langer (2008) discussed the possible subdivision of the maternal investment period into three phases. Hence, special consideration was given to lactation and was divided into two phases. The first phase was the period when the offspring exclusively ingested milk and the second phase was the period when both milk and solid food were taken.

The behavioural frequencies were identified by all occurrence sampling and instantaneous scanning sampling methods with 5 min intervals from 9:00 am to 5:00 pm daily for 20 days. Each targeting behaviour was recorded by instantaneous scanning every 5 min.

Owing to the underwater suckling behaviour of the infant hippo and primary nursing behaviour always occurring in the calf in the lactation season, we gave much attention to the water body monitoring. The behaviours recorded in this study mainly included resting (in or out of the water body), feeding, which was strictly time-controlled (out of the water body), moving (in or out of the water body), and suckling behaviour (in the water body). Resting was defined as standing or lying quietly on the ground or in the water without moving or nursing. Feeding was defined as a parent initiatively eating fresh or dry grass on the ground. Moving was defined as walking or swimming in or out of the water without any other relevant target actions. Suckling behaviour primarily meant suckling milk from the mother hippo. Furthermore, activity rhythms were demonstrated by the difference between non-active and active behaviours. Non-active behaviour meant resting and active behaviour included feeding, moving, and suckling behaviours. Synchronous behaviour referred to the similarities of the two animals' initiative actions in certain time scales, and the similarities

are represented by the consistency of wave peaks in the curve models.

Maternal investment was revealed by activity budgets and temporal and spatial dynamics of infant territorial occupation. The processing of infant self-independence was tested through activity budgets and temporal and spatial dynamics of infant territorial occupation as well as suckling behaviour in the post-puerperal period. Due to impressionable disturbance of suckling behaviours caused by environmental influences, e.g. frequent fresh water changing (hippos prefer dirty water to stay in and lactate for safety purposes, but water was practically changed every other day in the wildlife park), mother's food quality (related to production of breast milk, but the quality of fresh grass could not be accordantly guaranteed), human disturbance (zoo setting makes human-induced stress unavoidable), etc, together with the properties of the suckling curve (wave crest and trough) and the baby's termination behaviour of suckling, the whole term of suckling behaviour was scaled into 4 parts (each period (P) covered 5 days). Period 1 (P1) represented the suckling acceptance period, Period 2 (P2) illustrated the suckling adaptation period, Period 3 (P3) showed the suckling habituation period, and Period 4 (P4) meant the developed post-suckling period. Synchronous behavioural dynamics were also put forward to demonstrate behavioural characteristics between maternal investment and infant self-independence. In order to study the different stages of synchronous behaviours, we scaled rhythms and territorial occupation into different parts through the variation of curve shifting positions as well as wave crests and wave troughs.

2.3 Data statistics and analysis

Data statistics and analysis were processed by statistical software R version 2.9.0 (www.r-project.org) and Microsoft Office Excel 2003. The total efficient data were 7680 sampling observations, including 3840 observations for behavioural patterns and 3840 observations for territorial preference. Behavioural data was calculated by temporal percentage of defined behaviour (resting, feeding, moving and suckling behaviour) within the observation period, which started from 9:00 am to 5:00 pm daily for 20 days; observations were taken at intervals of 5 min. The ratio (full ratio is equal to 1) of activity meant the occurring frequency of defined behaviour. The One-way ANOVA test was used to compare the mean activities in different days of each individual as well as in comparing behavioural differences in both adult and infant (Tables 1 and 2). We also plotted dynamic models of activity rhythms and territory occupation for both hippos based on mean ratio of active and non-active behaviours and percentages of territory occupation (Figs. 1 and 2). The generalized estimating equation approach was designed to achieve positive and negative trends in behavioural

dynamics. The significant level was set at 0.05. The data was represented as mean±SEM.

Table 1 General ratios of activity rhythms in both mother and infant hippos

	active behaviour	non-active behaviour
adult hippo	0.318±0.021	0.682±0.021
infant hippo	0.321±0.026	0.679±0.026
<i>P</i> value (* <i>P</i> < 0.05)	<i>P</i> = 0.829 > 0.05 (non-significant)	

Data are means±SE.

Table 2 General ratios of time budgets in territorial occupation in mother and infant hippos

	water territory	land territory
adult hippo	0.801±0.027	0.198±0.127
infant hippo	0.818±0.027	0.182±0.027
<i>P</i> value (* <i>P</i> < 0.05)	<i>P</i> = 0.107 > 0.05 (non-significant)	

Data are means±SE.

3 Results

3.1 Maternal investment

In Fig. 1, we defined activity patterns into 2 categories — active (resting) and non-active (moving, feeding, and suckling) behaviours — according to the status of body movement. The ratio of maternal active behaviour increased in the linear model (slope = 0.0014, *Z* = 0.3027, *P* < 0.001, sample size = 1920). On average, the ratio of active behaviour was 0.318±0.041 times and that of non-active behaviour was 0.682±0.021 times in the whole lactation period. However, during the period between the 8th and 12th days, there was a resilient oscillation to move back to the beginning pattern. After the 12th day, the trend changed upwards slightly until the end of the lactation season.

Figure 2A shows that the spatial occupation of the mother hippo territory in the water tended to decline where average temporal percentage of maternal territory occupation in the water was (80.1±2.74)% and the temporal percentage on the land was (19.8±5.75)%. The negative linear model (slope = -0.0066, *Z* = 0.8807, *P* < 0.001, sample size = 1920) suggested that the mother hippo might take less care of her infant (more active in general) and cut down on her own obligations in nursing (less active in the water).

3.2 The plasticity of infant self-independence

According to Fig. 1, the primary active behavioural trend of the infant hippo was consistently similar to that of the beginning of birth (linear model: slope = -0.0017, *Z* = 0.3309, *P* < 0.001, sample size = 1920). However, the behavioural dynamics changed more often and fluctuated especially before 12 days of age. The formation of

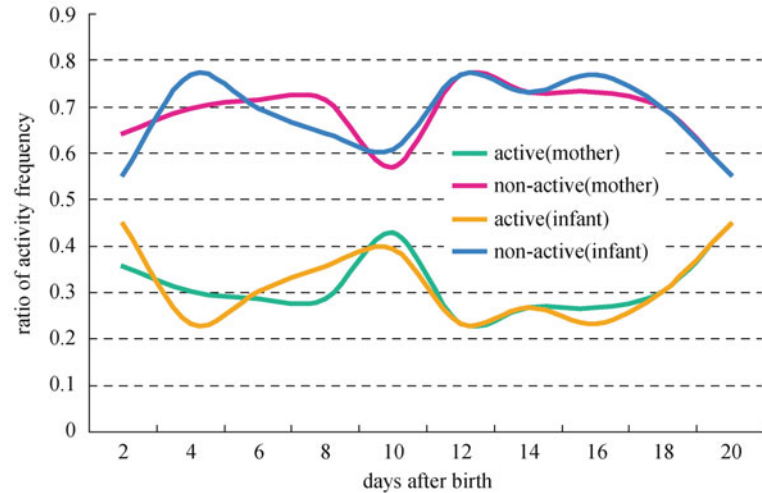


Fig. 1 Dynamic model of maternal and infant activity rhythms

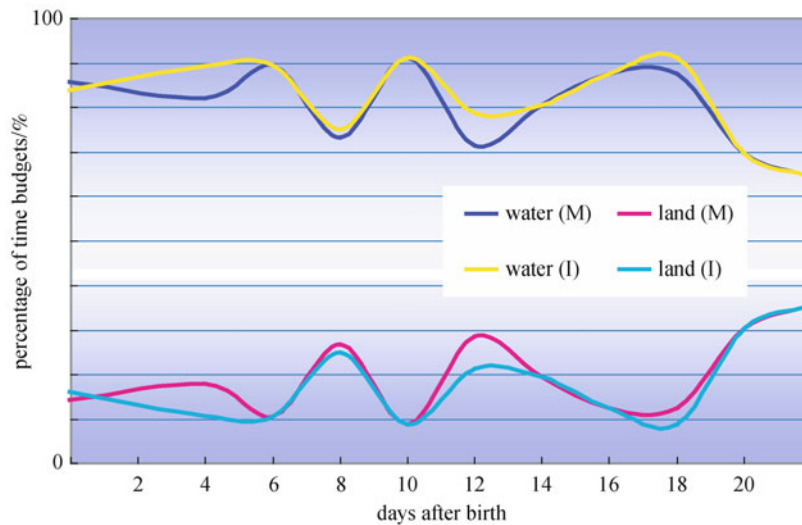


Fig. 2 Temporal and spatial dynamics of territorial occupations. Land (M) and water (M) were maternal territorial occupation of land and water body respectively. Land (I) and water (I) showed territorial occupations of infant hippo.

plasticity of infant self-independence after the 12th day moved up stably. In general, the percentage of active (moving) behaviour was 0.321 ± 0.026 times and that of non-active (resting) behaviour was 0.679 ± 0.085 times.

According to Fig. 2B, the spatial dynamics of infant territorial occupation showed a slight decrease in the water, and the infant spent relatively more time on the ground. The linear model indicated a negative trend of water territory occupation (slope = -0.0071 , $Z = 0.904$, $P < 0.001$, sample size = 1920). Moreover, on average, the percentage of territory in the water was $(81.8 \pm 2.74)\%$ and that on the land was $(18.2 \pm 2.74)\%$.

Due to the primary feeding habit, suckling was the most important behaviour during the physiological development of the infant. As demonstrated in the following graph (Fig. 3), the general trend (slope = -0.005 , $Z = 0.06$,

$P < 0.001$, sample size = 1920) of the suckling dynamic was negative with an upwards fluctuation at period 3 (P3), which also illustrates that as the infant grew up the mother-dependent behavioural dynamics gradually weakened at the end of the lactation season. Nevertheless, the reason for the suckling behaviour appearing to rise upwards between P1 and P3 can be explained as body growth processing, and it should also be detected in the future, and beginning from P4 independent processing was consequently shaped and dramatically decreased.

3.3 Synchronous behavioural dynamics

Maternal investment and infant self-independence were concluded as synchronous events in this study. The comparisons of behavioural differences and sequence

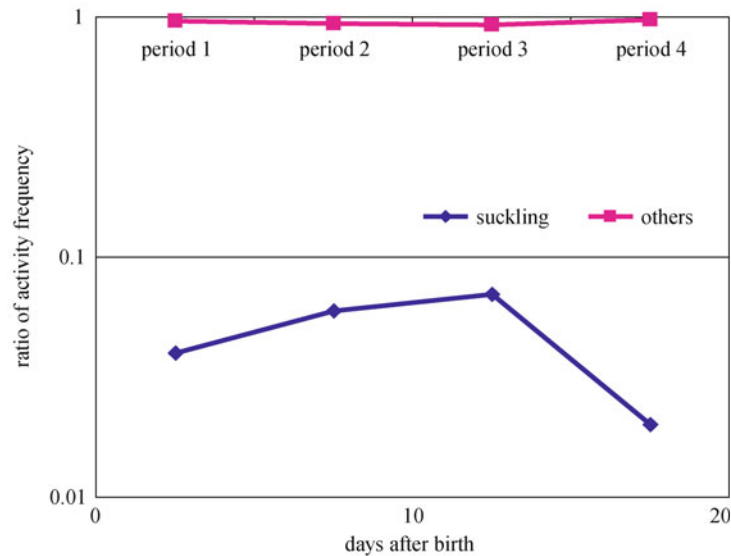


Fig. 3 Dynamic model of suckling behaviour

dynamics in the lactation season are revealed by the following results.

3.3.1 Comparisons of general behavioural differences in the lactation season

Our results indicated that adult and infant hippos displayed different behavioural budgets either in rhythm dynamics or in the temporal and spatial territorial occupations during the lactation season (Tables 1 and 2).

3.3.2 Synchronous behavioural analysis

Synchronous behaviours of maternal and infant active rhythms were generated through smooth curve models (Fig. 4). According to the degree of curve fluctuations, we scaled the whole curves into five synchronous foci and their related areas, e.g., A, B, C, D, and E, by means of wave crests and wave troughs which also elaborated shifting dynamics of behaviours. A strong synchronous time delay (distances between each nearby peak value) phenomenon occurred in the first 8–9 days of the lactation season (Fig. 4A). Then in the following 2–3 days, the time delay phenomenon (Fig. 4B) was reduced, and the wave length was much shorter than before (Fig. 4A). Compared to the first 10–11 days (Fig. 4A and B), the following periods (Fig. 4C, D, and E) were relatively and gradually decreased in their time delays and headed towards behavioural synchrony.

In general, synchronous behavioural patterns in territorial occupations of both maternal and infant hippos were strongly consistent in the lactation season. According to wave crests and wave troughs (arrows in Fig. 5), habitat preferences in temporal level were compared between

mother and infant, which indicated severe maternal-dependent synchronous behavioural trends throughout five scaled shifting periods according to behavioural shifting points simulated by wave crests and wave troughs (Fig. 5A–E). Before the 7th day (Fig. 5), behavioural changes in both mother and infant hippos were slightly different, but the water territory occupations were still mainly dominant within the lactation season. The fluctuations between the 6th and 15th days (Fig. 5B–D) were consistently strengthened judging from wave length shrink and wave amplitude enlargement comparatively. Later on, both hippos showed a trend of reduced occupation of water territory (Fig. 5E).

4 Discussion

Maternal investment is a classic subject of nursing behaviour. Currently, most theories concerning maternal investment strategies are to maximize fitness under adverse environmental conditions and predict sex-biased investment in offspring under certain circumstances. Sikes (1995) indicated that maternal investment strategies to food resources control in eastern woodrats (*Neotoma floridana*) were significantly related to the growth of youth. Gomendio (1991) demonstrated that between parent and offspring there were still some conflicts in suckling rejection in rhesus macaques (*Macaca mulatta*), which proved that the lesser the rejection of suckling, the lesser the failure of reproduction. Normally, after a long-term pregnancy, mothers are always strongly willing to take care of their babies not only in human society but also in the animal world as well, leading to successful breeding. However, until now, there are few relevant studies

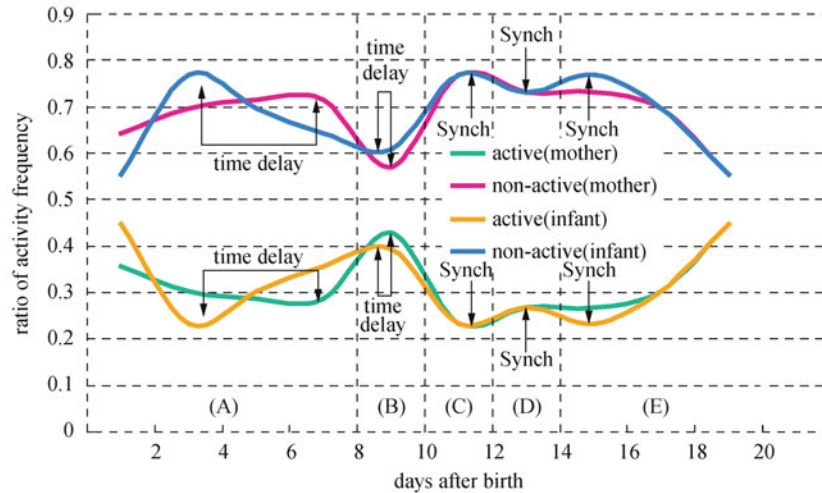


Fig. 4 Synchronous dynamic model of maternal and infant activity rhythms

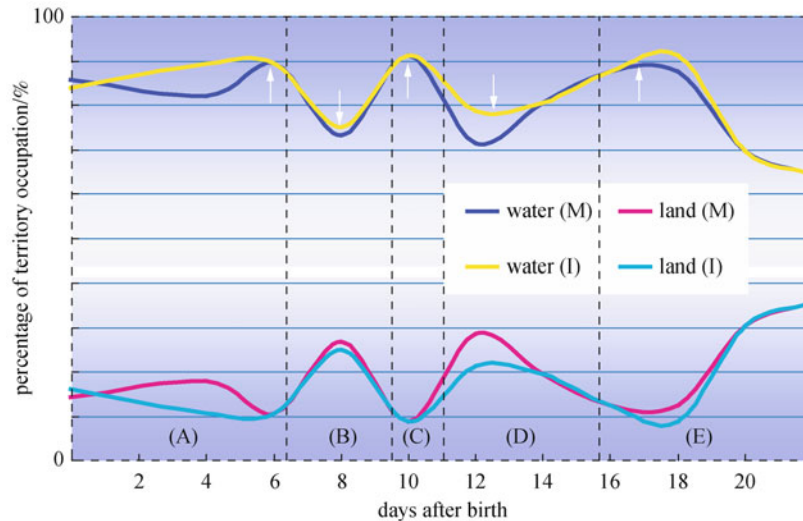


Fig. 5 Synchronous dynamic model of territory occupations. Land (M) and water (M) were maternal territorial occupation of land and water body respectively. Land (I) and water (I) showed territorial occupations of infant hippo.

regarding maternal investment and infant self-independence of hippos. Therefore, this study brings some fresh insight into the knowledge gaps.

Hippo lactational behaviours, especially suckling behaviour, always take place under the water because the water environment is the most preferred habitat for hippos in the reproductive season (Eltringham, 1999). Our results proved again that hippos were apt to stay for a longer time in water than on land in the lactation season (Table 1). The development of behavioural processing regarding the plasticity of infant self-independence of hippos is still unknown. This also needs to be addressed firstly for the purpose of behavioural developmental mechanism, especially due to the difficulty in monitoring and accessing of developmental behaviour underwater. According to our

pilot results, the processing of infant self-independence is generally much more related to maternal investment and its own physiological development. The consciousness of territorial occupation in female hippos was considerably affected by behavioural dynamics, particularly fierce in the reproductive season (Laws and Clough, 1966).

According to our observation (Fig. 1), maternal investment in hippos showed a positive trend in activity rhythms and negative dynamics (Fig. 2) in water territory occupation, all of which supported our hypothesis that mother hippos might take less care of the infant and cut down on her own obligations in nursing by the time the infant becomes more independent. The above conclusion is consistent with the study of Pluháček et al. (2010), which indicated that an increasing rate of suckling termination or

rejection by the mother would indicate a decreasing effort by the mother to invest in her offspring.

To infant self-independence, during the whole lactation season, the primary active action trend (Fig. 1) and water territory occupying dynamics of the infant hippo (Fig. 2) were both relatively consistent at the beginning of birth, based on linear models. However, the sequences of activities fluctuated, especially around the 12th day after birth. The trends of territorial occupation also showed relatively negative dynamics in water body occupation by the time the infant hippo matured. The general trend (Fig. 3) of the suckling dynamic was demonstrably negative with an upwards fluctuation at period 3 (P3), which illustrated that as the infant matured the mother-dependent behavioural dynamic gradually weakened by the end of the lactation season. As we assumed, and as also proved by previous modelling of maternal investment and parent-offspring conflicts (Trivers, 1972, 1974; MacNair and Parker, 1978; Parker and MacNair, 1978; Smith, 1980; Carlisle, 1982; Lee and Moss, 1986), mothers can either limit or change their investments to their offspring at any period of early development. However, either abiotic or biotic environmental factors might possibly dominate suckling behaviour dynamics as well (Pluháček et al., 2010).

General behavioural rhythms of both mother and infant hippos were tested firstly in this study and all of the results strongly illustrated synchronous relations between maternal investment and infant self-independence. According to Figs. 4 and 5, infant behaviours strongly relied on his mother's behaviours. Tables 1 and 2 apparently displayed the similarity of behavioural temporal distributions of both mother and infant hippos that also supported our hypothesis that time budgets for them did not have any significant differences.

Synchronous behaviours of maternal and infant active rhythms displayed differently during the whole lactation season. A strong synchronous time delay occurred in the first 8–9 days of lactational season, and in the following 2–3 days, the time delay was reduced, and the wave length was much shorter than before (Fig. 4A). Compared to the first 10–11 days (Fig. 4A and B), in the C, D, and E periods, time delays were relatively and gradually decreased and more synchronized phenomena appeared. Through this observation, we briefly concluded that the infant after birth might have to adapt to new environments. Meanwhile, imprinting behaviour could be generated and induced by co-accompanying activities with his mother.

In general, synchronous behavioural patterns in territorial occupations of both maternal and infant hippos were strongly consistent in the lactation season. However, behavioural fluctuations in the mid-lactational season were much fiercer at the beginning than later on (Fig. 5B–D). We assumed that mother-offspring conflicts might be strengthened in the beginning and later on. However,

the aspects of synchronous behaviour are still lacking and should be addressed in the future.

5 Conclusion

In this study, maternal investments in hippos proved to be synchronously and mutually responsive to infant self-independence during lactation season. We confirmed that strong mother-offspring conflicts did exist and they interacted during the whole study period. Activity rhythms were developed from a long time delay to a comprised time synch. Territorial occupations proved again that water territories were the most preferred habitat during lactation season. Suckling behaviours of hippos tended upwards from birth and turned downwards after the 12th–13th day. The result of this work will be helpful in the raising and reproduction management of hippos in *ex-situ* conservation.

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