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Seasonal reproduction of northernmost endangered forest musk deer (*Moschus berezovskii*) in China and the synchronization with climatic conditions

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Abstract: Reproductive rhythms, as a response to environmental seasonality, may maximize the survival possibility of both newborns and parents, which is vital for *ex situ* conservation and sustainable management in wildlife. Forest musk deer (*Moschus berezovskii*) is a critically endangered ungulate of China. In order to estimate its reproduction characteristics and performance in northern China, a historical distribution area, the parturition pattern of northernmost captive forest musk deer in Huailai Musk Deer Farm from 2017 to 2018 was analysed. We found that the parturition of forest musk deer was highly seasonal with a peak on May 27th, and 75% of parturitions were completed within 22 days from May to June, which could be an adaptation to the seasonality of local food resources. The parturition peak was four weeks before the best hydrothermal conditions when food resources were maximally provided. The time lag between parturition date and peak of food availability was affected by climatic conditions during lactation as warmer temperatures in the 4th and 5th week and heavier precipitation in 4th week of lactation shortened the time lag by five days ($P < 0.05$). The synchronization between parturition rhythms and seasonality of climatic conditions indicated that the forest musk deer could be farmed in Northeastern Taihang Mountains and northern China, where there is suitable climate for the musk deer reproduction. Sustainable musk production and musk deer release into the wild where there are suitable climatic conditions has been proved to be practicable, which can benefit the *ex situ* conservation of endangered forest musk deer and musk resources sustainability.

Keywords: *ex situ* conservation; parturition rhythm; reproduction characteristics; musk resources sustainability

In the temperate zone with high seasonal variation, the long winter with low temperature and reduced food availability has an important influence on the survival of females and newborns (Ptacek et al. 2017), and appears to be the main limitation of reproduction success and population growth in wild animals, especially for declining populations. This can further affect the performance of

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ex situ conservation and sustainable management (Whiting et al. 2012).

Seasonal variation in climate is the essential driver of fluctuation in food resources, and a major environmental factor influencing ungulate life-history events such as reproduction in temperate regions (Gustine et al. 2017). To synchronise with the maximum supply of food resources, the peak time of ungulate parturition usually occurs in late spring and early summer, namely three to four weeks before the environmental hydrothermal peak (Veiberg et al. 2016; Gustine et al. 2017). The time lag between parturition time and hydrothermal peak affects the food availability to females and newborns, which in turn affects their survival, reproduction and population growth (Post and Forchhammer 2008). Understanding reproductive rhythms in animals and their response to climatic conditions can help to reveal the adaptive strategies of animals in a seasonal environment, and the population dynamics in a continuous climate change (Gustine et al. 2017).

Reproductive rhythms have been reported in reindeer (*Rangifer tarandus*; Paoli et al. 2018), bighorn sheep (*Ovis canadensis*; Festa-Bianchet 1988), and Dall sheep (*Ovis dalli*; Rachlow and Bowyer 1991). Peek and Hershey (2002) reported that the parturition date of mule deer was affected by local climatic variations, while the seasonal response of elk (*Alces alces*) distributed in the same region was much weaker. Hass (1997) reported that the parturition timing of Canadian bighorn sheep varied among habitats; and the parturition rhythms of these sheep in mountain habitats were obviously influenced by seasonal variation of hydrothermal conditions, while the parturition seasonality for the sheep in desert habitats was weaker due to the warm winter and high uncertainty of plant phenology. Ungulates in seasonal environments have seasonal reproduction, however, their reproductive rhythms may depend on species, feeding habits, geographical and climatic features (Pettorelli et al. 2007).

Forest musk deer (*Moschus berezovskii*) is a small solitary forest ruminant with strong vigilance, and highly selective on plant food resources with preference to fresh young leaves of woody plants such as elm (*Ulmus pumila*) (Sheng and Liu 2007; Zhao et al. 2019). Musk produced by males is widely used in traditional medicine and perfumery, and due to the habitat degradation and overexploitation, musk deer are now endangered, and listed as CITES Appendix II species and priority for wildlife protection in China.

Reproductive rhythms of wild musk deer are hard to explore, and most studies on reproduction and related parameters of musk deer are based on captive population. Meng et al. (2003a; 2003b) showed that captive and wild musk deer in western China maintained similar reproductive rhythms, but the former had a relatively longer birth season with lower levels of synchronization with environments. Zhao et al. (2019) reported that captive musk deer gave birth before the arrival of environmental hydrothermal peak, and winter temperatures affected the parturition time of the next year. Sun et al. (2017) found that seasonal reproduction of captive forest musk deer was less synchronized with the increase of captivity time, and influenced by the variation of temperatures, precipitation and food resources. However, the response of reproductive rhythms in a quantitative approach to seasonality, and the time lag between parturition and hydrothermal peak are far less concerned.

Captivity is not only an effective way for *ex situ* conservation of endangered musk deer and sustainable musk production, but also a basis of future reintroduction. In 2016, Huailai Musk Deer Farm (HMDF), with an aim of breeding and *ex situ* conservation of forest musk deer, was established in the northeastern part of Taihang Mountain, which is a historical distribution area of forest musk deer in northern China. The forest musk deer in HMDF has become the northernmost population in China and around the world. In this study, we monitored the parturition timing and synchrony of the captive forest musk deer and analysed their responses to climatic conditions, with an attempt to understand the reproductive timing patterns in seasonal environments and assess the management performance of forest musk deer in northern China.

MATERIAL AND METHODS

Study area

The study was conducted in 2017–2018 at HMDF (established in 2016) of Hebei Province, which is located in the northeast of Taihang Mountain (N40°31'56.77'', E115°37'51.00''). The farm belongs to temperate and semi-arid regions, and has a typical

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temperate continental monsoon climate characterized by dry winters and wet summers, and large temperature differences between day and night. The farm is located at an altitude of 1 180 m above sea level with an annual average temperature of 4.6–6.5 °C, an extremely high temperature of 30.6 °C in the hottest month (July), and an extremely low temperature of –18.5 °C in the coldest month (January). The average diurnal temperature difference is 11.5–16.5 °C, and the average seasonal temperature difference is 20.5–25.5 °C. The mean annual precipitation is 396 mm, the average annual sunshine time is 3 027 h, and the frost-free period lasts for 149 days. The vertical hierarchy of vegetation is obvious, and there is a main distribution of deciduous broadleaved trees, such as elm, aspen (*Populus davidiana*), and apricot (*Armeniaca vulgaris*).

Musk deer farm and forest musk deer in captivity

The basic population of HMDF's captive forest musk deer comes from farms in Shaanxi and Sichuan Provinces. There are 40 enclosures in HMDF, and each consists of one 100 m^2 activity field and four to six 2 m^2 sub-enclosures. Two to four forest musk deer are kept in each enclosure. The activity field has a natural muddy basement covered with ground vegetation and 1–2 trees.

There were 150 musk deer in HMDF and all deer were around four years of age with similar body mass (10–15 kg). Full-time keepers were in charge of feeding and daily management. Deer were fed twice a day, at dawn and dusk, mainly with about 2 kg/head fresh leaves (in summer and autumn) or dried leaves (in winter and spring) of naturally growing elms, aspens, apricots collected from the natural habitats around HMDF, which includes food plant species for musk deer to some extent (Zhang et al. 2008), meeting deer's selection for food. Furthermore, the deer were provided with water *ad libitum*.

Statistical analysis

Data on parturition date and performance of each forest musk deer were collected in HMDF, and we calculated the length of birth season (the time span between first and last birth) and 75% of parturitions (the time span when from 10% to 85% of parturitions occurred; Meng et al. 2003a; Zhao et al. 2019). The climate data come from the NASA Power Global Meteorology (https://power.larc.nasa.gov/data-access-viewer/), including daily, weekly and monthly mean temperatures and precipitation. Parturition dates were converted into Julian dates, namely the days to January 1st of the year. The time lag between parturition and hydrothermal peak was the days from parturition date to July 1st, since the hydrothermal peak in HMDF occurred in July.

The data in 2017 and 2018 was compared by *t*-test, showing no significant difference between years (all $P > 0.05$), then the data was combined and analysed. The Kolmogorov-Smirnov test was used to assess the normality of parturition data. If the data sets were in normal distribution, *t*-test or ANOVA was used, otherwise the Kruskal-Wallis test was used. Stepwise regression analyses were used to examine the relationship between climatic parameters (average temperature and precipitation during 1st–12th weeks of lactation) and parturition time. Variance inflation factor (VIF) was used as one criterion to assess collinearity, and VIF > 2 means there is collinearity, and the goodness of fit (R^2) is smaller than 0.5. Besides, the eigenvalue around 0 and condition index over 10 also indicate collinearity (Jou et al. 2014). Partial correlation analysis was used to remove the effect of collinearity among climatic parameters, and select main climatic factors affecting the parturition time. The significance level was set at $\alpha = 0.05$. All the analyses were performed in SPSS v20.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Seasonal reproduction of captive forest musk deer

Thirty-one deliveries with 51 newborns of captive forest musk deer were recorded in HMDF, including 11 deliveries (18 newborns) in 2017 and 20 deliveries (33 newborns) in 2018. Parturitions occurred between May and June (Figure 1).

In 2017, the first parturition took place on May 18th, and the last on June 12th. The average delivery day was May 12th (131.39 ± 3.32, $n = 18$), the birth season lasted for 25 days, and 75% of parturitions were accomplished within 19 days (from May 20th to June 8th).

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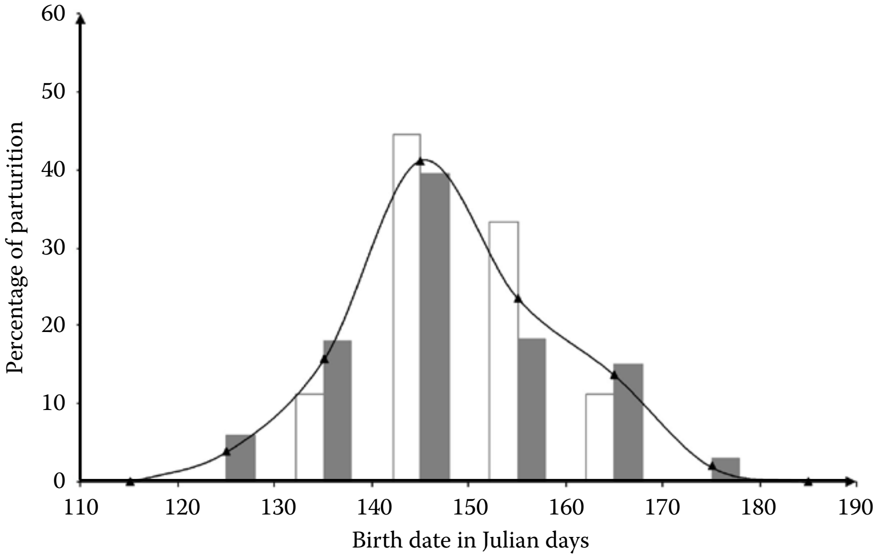

Figure 1. The parturition pattern of captive forest musk deer in Huailai Musk Deer Farm
The time interval is 10 days; open and solid bars indicate data of 2017 and 2018, respectively; the line with triangles indicates the average percentage of parturitions in two years

In year 2018, the first parturition took place on May 2nd, and the last on June 26th. The average delivery day was May 25th (144.88 ± 7.58, n = 33), the birth season lasted for 55 days, and 75% of parturitions were accomplished within 25 days (from May 11th to June 5th).

No significant differences were found in the parturition pattern between 2017 and 2018 (F = 0.542, t = 0.372, df = 29, P = 0.712), we therefore combined the 2-year data for subsequent analysis. Overall, the average parturition date of HMDF captive forest musk deer was May 27th (146.76 ± 10.97, n = 51), the birth season lasted for 40 days, and 75% of parturitions were accomplished within 22 days (May 15th to June 6th), which showed strong seasonality. Parturition dates were normally distributed (Z = 0.621, n = 31, P = 0.836), with kurtosis of 0.988 ± 0.821 and skewness of 0.330 ± 0.421, which indicated that the distribution was steep with long right tail, and 54.84% of deliveries occurred before the average parturition date.

Relationship between parturition timing and litter size in captive forest musk deer

The parturition date of female musk deer having singletons (May 27th, 146.75 ± 10.81 days) was slightly later than that of female musk deer having twins (May 26th, 145.67 ± 11.07 days), but the difference was not significant ($F_{(1, 28)}$ = 0.561, t = 0.265, P = 0.793).

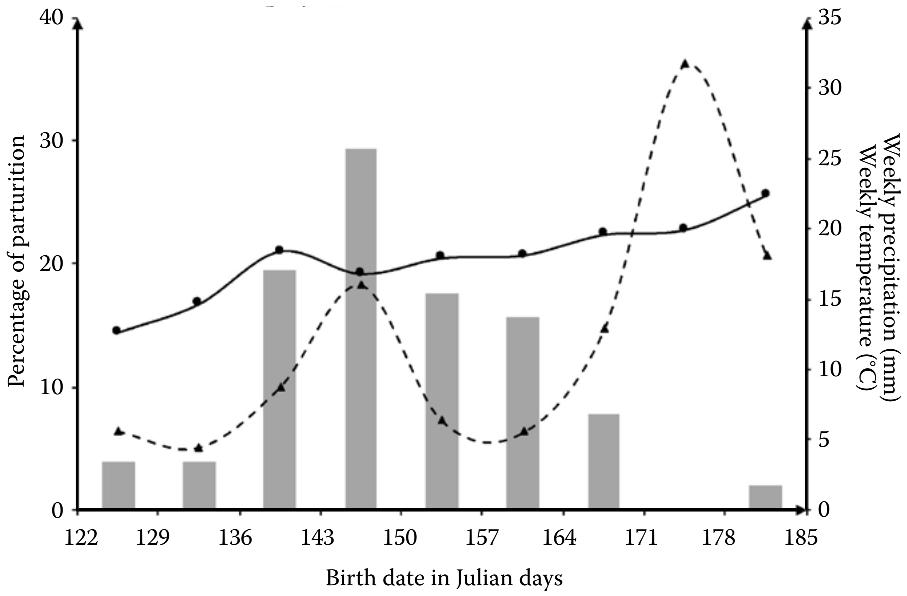

Figure 2. Dynamics of percentages of parturitions (solid bars) of captive forest musk deer and climate conditions in Huailai Musk Deer Farm
Average weekly temperature (solid line) was 17.83 ± 2.89 °C during the parturition season, and average weekly precipitation (dashed line) was 12.16 ± 8.84 mm; the peak of hydrothermal conditions in Huailai was in July, namely four weeks before the parturition peak

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Relationship between parturition timing and climatic conditions in captive forest musk deer

In 2017–2018, the average annual temperature in HMDF was 6.24 °C with average annual precipitation of 478.47 mm, and 86.05% of the precipitation occurred from May to September when the average monthly temperature was 18.51 °C. The hydrothermal peak occurred in July when the monthly temperature was 22.18 °C with the monthly precipitation of 153.55 mm.

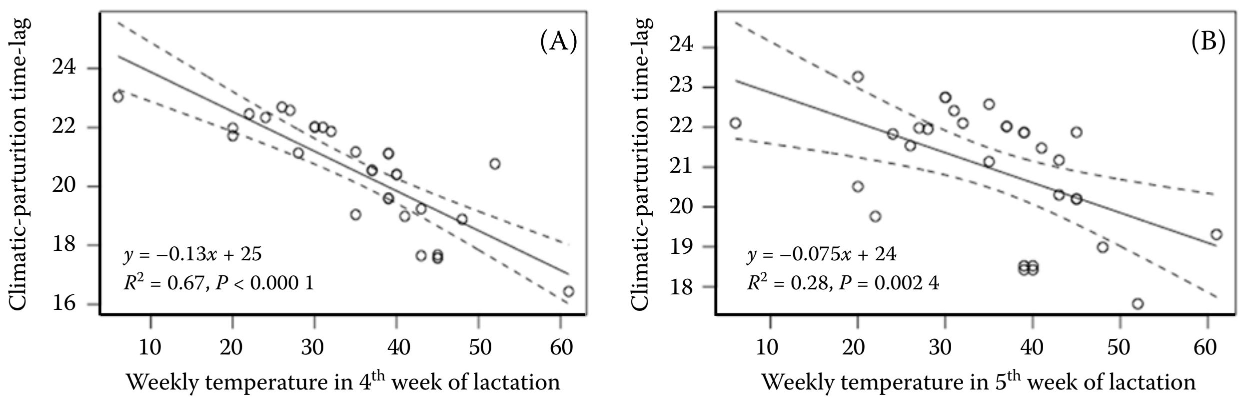
The parturitions of captive forest musk deer in HMDF began in May, and 75% of parturitions were accomplished before June 6th, nearly four weeks before the local hydrothermal peak (July 1st), when the weekly precipitation increased to 16.02 mm, exceeding the average weekly precipitation (9.20 mm) for the first time, and the temperature reached 16.80 °C (Figure 2).

The gradually fitted model between weekly temperature and precipitation of the 1st–12th week in the lactation period and the climatic parturition time lag showed that the weekly temperature and precipitation of the 4th week (wt4 and wp4) and weekly temperature of the 5th week (wt5) in lactation significantly affected the time interval between parturition and the hydrothermal peak when maximal food availability occurred (Figure 3). The final model after elimination of collinearity was obtained: climatic parturition time lag = 145.796 – 3.556wt4 – 0.229wp4 – 1.517wt5 (R^2 = 0.948, *df* = 30, $F_{(3, 27)}$ = 183.121, P < 0.001). With an increase of selected climatic parameters by one at each step, the time lag was shortened about five days (Table 1).

DISCUSSION

Parturition patterns of captive forest musk deer

To adapt to seasonal environments, animals in temperate zones usually reproduce seasonally. Parturition and lactation are periods with high demand for nutrition and energy; by occurring in a season with optimal food resources and climatic conditions, the winter survival and reproduction success in the following year can be guaranteed (Molik et al. 2017; Paoli et al. 2018; Zhao et al. 2019). Musk deer usually deliver in late spring



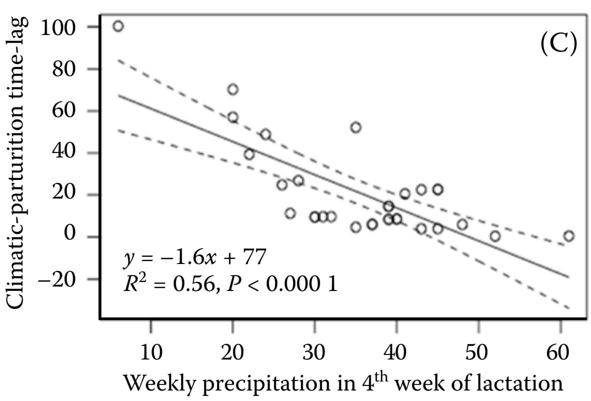


Figure 3. Relationships between weekly temperature and precipitation during lactation to the time lag between parturition date and peak of food availability
Weekly temperature of the 4th week in lactation (A) and that of the 5th week (B) is in °C, and weekly precipitation of the 4th week in lactation (C) is in mm
Circles indicate the data observed in a specific climatic condition; fitted lines (solid lines) as well as 95% confidence interval bands (dashed lines) are provided

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Table 1. Statistics of selected climatic parameters during lactation for assessment of the time lag between parturition date and peak of food availability

Model predictors	Unstandardized coefficients		Standardized coefficients	t	P	Collinearity statistics	
	beta	SE	beta			tolerance	VIF
Constant	145.796	7.477	–	4.976	< 0.001	–	–
wt4	−3.556	0.275	−0.586	12.908	< 0.001	0.841	1.189
wp4	−0.229	0.021	−0.483	10.667	< 0.001	0.845	1.183
wt5	−1.517	0.310	−0.218	4.895	< 0.001	0.878	1.139

VIF = variance inflation factor; wp4 = weekly precipitation of the 4th week; wt4 = weekly temperature of the 4th week; wt5 = weekly temperature of the 5th week

to early summer (Meng et al. 2003a), specifically from May to July, and the parturition peak occurs around mid-May (Sheng and Liu 2007).

With the decrease of environmental seasonal variation, the reproduction seasonality of animals tends to slack, for example, the birth of bighorn sheep in a weak seasonality environment is relatively weak in seasonality (Festa-Bianchet 1988). For animals in captivity, environmental seasonality is relatively weak, and the factors such as restricted movement, forage rationing and high population density also have impacts on the reproductive rhythm, resulting in a different reproductive pattern from that of the wild ones (Zhao et al. 2019). Seasonal breeding of the leaf-nosed bat (*Carollia perspicillata*) in captivity no longer exhibited the reproductive synchrony due to a lack of environmental reference cues (Stoner et al. 2016). In contrast, our study showed that the captive forest musk deer in HMDF delivered from May to June, 75% of parturitions were accomplished in 22 days, and their parturition timing and environmental synchrony were similar to those of wild populations (Sheng and Liu 2007). The *ex situ* conservation population in this study is aimed for reintroduction in the wild. The musk deer enclosure is designed to be a completely open environment without any temperature control facilities so that natural behaviours are maintained. Temperature and precipitation in HMDF are completely synchronized with climatic conditions of a natural habitat. In addition, the forage of captive forest musk deer was collected from natural habitats near the farm, including preferred leaves, ground plants and seasonal fruits and vegetables. Therefore, compared with wild forest musk deer, environmental factors and food resources for captive forest musk deer in HMDF still have strong seasonality, resulting in the reproductive rhythm being similar to that of the wild ones (Sheng and Liu 2007). Similar results were observed in captive alpine musk deer (*Moschus chrysogaster*; Meng et al. 2003a; 2003b).

Latitude and altitude directly affect the reproductive rhythm of wild animals. In general, their phenology showed a time lag in regions with higher latitude and altitude, the resources tended to be more concentrated in a shorter time period, and the later onset and peak of parturition had higher levels of synchrony with seasonal environments (Festa-Bianchet 1988; Stoner et al. 2016). Sun et al. (2017) reported that in the Maerkang musk deer farm of western Sichuan Province, which was at 10° lower latitude and 1 500 m higher altitude than HMDF, the captive forest musk deer gave birth from May to July, and 75% of parturitions were accomplished in 22 days with an average parturition date on May 25th, which was two days earlier than in HMDF. Compared with HMDF, the Shanghang Farm of Fujian Province is at 15° lower latitude and 200 m lower altitude, the parturition period of captive forest musk deer started there from May 3rd, and 87.5% of parturitions were accomplished in 16 days with an average parturition date on May 10th, which was 17 days earlier than in HMDF (Ge 2015). The Xinglongshan musk deer farm of Gansu Province (N35˚38'–35˚58'), which is 5° lower in latitude and 900 m higher in altitude than HMDF, had the captive alpine musk deer being physically larger with longer gestation period than the forest musk deer (Sheng and Liu 2007). Seventy-five percent of parturitions of captive alpine musk deer were accomplished in 27 days, and the birth season lasted for 54 days with an average parturition date on May 31st (Zhao et al. 2019), which was four days later than that in HMDF. The above-mentioned studies, as well as our present study, all show

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strong seasonality in the reproduction of captive musk deer, however, different latitudes, altitudes and species can generate a diversity of patterns in parturition timing and environmental synchrony in captive musk deer. Besides, the reproduction pattern in HMDF suggested that the northern part of China can be an additional place for forest musk deer captive management and *ex situ* conservation to restore the declining population.

Animal pregnancy and parturition are costly physiological processes, and the total energy consumption during reproduction is affected by litter size (Millar et al. 2004), while the litter type (i.e. litter size and sex ratio) is associated with parturition timing (Wolcott et al. 2015). In dioecious monogamous species, son-producing females gave birth later; while for polyembryonic species, the effect of litter size on parturition timing is also influenced by offspring sex. For example, for white-tailed deer (*Odocoileus virginianus*), females who had mixed-sex twins delivered significantly earlier than those that had single-sex twins or singletons, while the parturition timing of females with single-sex twins did not differ from those with singletons (Wolcott et al. 2015). Our study showed that in the captive forest musk deer of HMDF the parturition date of females who gave birth to singletons was slightly (i.e., 1-day) later than in those who gave birth to twins. Because of the lack of offspring sex information in this study, the interaction between offspring sex and litter size on parturition timing needs further research.

Effect of climatic conditions on reproductive rhythms in forest musk deer

Breeding, lactation and recovery of female ungulates in seasonal environments occur in the optimal season of food resources when temperature and precipitation are favourable for vegetation growth, so that the high energy demand matches with the seasonal food supply, which can maximize maternal and newborn survival, and continuing reproductive success (Broucek et al. 2004; Zhao et al. 2019). Musk deer are distributed in seasonal environments, and lactation lasts for three months after parturition. The later lactation stage (September to October) is just before the next oestrus of female musk deer, and also the beginning of food-deficient winters. Thus, adequate food resources during lactation can allow postnatal females to restore their reproductive energy and fat reserve, and ensure successful overwintering, thereby preparing for the forthcoming oestrus and increasing their reproduction success for the following year (Meng et al. 2003b). Similarly, through parturition timing and environmental synchrony, the breeding season (May–June) and the lactation season (May–September) of captive forest musk deer in HMDF coincide with optimal climatic conditions and maximal food resource availability in the region, which is beneficial to females' energy restoration and overwinter survival.

Temperature and precipitation are the main environmental cues and driving forces for plant germination and growth, and food resources for phytophagous ungulates accumulate with hydrothermal increases (Kawabata et al. 2001). Reindeer in the Arctic start the birth season two to four weeks before the hydrothermal peak (Tveraa et al. 2013), and mule deer tend to start about four weeks after plant germination (Stoner et al. 2016). Due to the phenological time lag between plant growth and animal reproduction in seasonal environments, there is an interval between the peaks of demand and supply (Post and Forchhammer 2008), and the longer lag or mismatch between food demand and supply is detrimental to the animal survival and reproduction (Gustine et al. 2017). Doiron et al. (2015) reported that body weights and sizes of goose (*Caerulescens atlantica*) decreased significantly when the gap between incubation period and the peak of environmental nitrogen supply was more than nine days. In Greenland, the increase of the interval between plant growing season and the reproduction season of reindeer directly led to the disturbance of parturition timing and survival rate decrease (Post and Forchhammer 2008).

As a concentrate selector, musk deer mainly feed on young leaves of shrubs and the surface vegetation with low fibre and high protein, and they are highly dependent on the plant phenology and environmental resources (Sheng and Liu 2007). Our results showed that the time interval between parturition and hydrothermal peak was affected by weekly temperatures of the 4th and 5th week, and weekly precipitation of the 4th week in lactation. Musk deer started lactation immediately after parturition, and the young began to feed on plants tentatively after two weeks, and then they became completely weaned and independent to feed on plants after 2–3 months (Sheng and Liu 2007; Wang et al. 2018). In HMDF, the young musk deer gradually ingested

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plants on their own in the fourth week after the parturition peak (June–July) when the region also entered the optimal climatic period with maximal food supply, and abundant plant resources provide sufficient high-quality food for newborns to be weaned gradually and for the recovery of females. Besides, under the circumstances of global climate change, with the continuous rise of temperature, it can be speculated that the reproduction peak of forest musk deer could advance, which however needs further investigation.

CONCLUSION

Being a northernmost forest musk deer population in China, though it has been in captivity for a few years, the parturition stage was timed so as to match to good forage under favourable conditions of temperature and precipitation in the 4^{th}–5^{th} week of lactation. The synchronization between reproductive rhythms and local climatic conditions indicated that North China, where once was the natural habitat of wild musk deer, could be a suitable place for developing *ex situ* conservation and further potential reintroduction. In addition, it is speculated that the time lag between parturition and hydrothermal peak could be reduced under the increasing temperature affected by the global climate change, which may arouse a new challenge in captive management and which needs further investigation.

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Conflict of interest

The authors declare no conflict of interest.

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