



Reproductive Characteristics and Musk Secretion of Captive Alpine Musk Deer *Moschus chrysogaster* Hodgson, 1839 (Artiodactyla: Moschidae)

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Abstract: Reproduction outcomes affect the population growth, especially for endangered species in *ex-situ* conservation. Alpine musk deer (*Moschus chrysogaster*) is an endangered ungulate that is well-known for the musk secreted by adult males. Despite being captive for years, the reproduction outcome and the musk production of captive populations are not well documented; moreover their growth seems to be declining. To understand the characteristics in reproduction and musk secretion as well as the influential factors, we studied the litter size, parturition date, weaning success and newborns' sex ratio of 897 deliveries in captive alpine musk deer from 2008 to 2018. Additionally, we assessed the relationships between these traits with age and stud's musk secretion using generalized linear mixed modelling. We found that the seasonal parturition lasted for 70 ± 17.86 days with a peak on June 22nd and there were more twins (49.3%) born than singletons (41%) with a female-biased secondary sex ratio. Twinning probability, weaning success and parturition date differed significantly among years, while female age affected positively both twinning probability and parturition date as senile females had late parturition with a tendency to have twins. However, age of males or musk secretion did not affect twinning probability or parturition date, studs with higher musk secretion contributed to a male-biased reproduction, resulting from better body condition and sexual attractiveness. The results enhance our zoological understanding of this endangered species, for which reproduction outcome can be predicted by monitoring maternal age and musk secretion of stud musk deer. Further, our findings have practical implications as they provide a basis for improving musk deer conservation and captive management.

Key words: alpine musk deer (*Moschus chrysogaster*), reproduction outcome, age, musk secretion, captivity

Introduction

Reproduction outcome is essential for population growth, affecting the conservation status of endangered animals, especially for species kept for

captive breeding, as they form a significant component of wildlife conservation (ASA et al. 2011, SWAISGOOD et al. 2006). Alpine musk deer *Moschus chrysogaster* Hodgson, 1839 is a small solitary forest ruminant, which once occurred in areas at el-

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evaluations 3000–4500 m a.s.l. across 13 countries in Asia and the east Russian Federation. Currently, it is classified endangered by the International Union for Conservation of Nature (IUCN). The species is facing a worldwide drastic decline due to over-exploitation of musk, secreted by adult males and extensively used in traditional Asian medicine and perfumery industry, coupled with habitat loss and degradation (GREEN 1986, MENG et al. 2006). The farming of alpine musk deer has been conducted since 1990 for *ex situ* conservation and sustainable musk production (HE et al. 2014). However, our understanding of their characteristics and the musk secretion remain poor, which impedes the captive management for restoring population growth (QI et al. 2011).

Previous researches on this species have shown that female musk deer generally give birth to singleton or twins, yet polyembryony or infertility did happen in both wild and captive populations (MENG et al. 2006, XU & XU 2003). The parturition normally occurs during late spring to early summer and is affected by environmental conditions (ZHAO et al. 2020). However, the other reproduction characteristics, such as weaning success and offspring's sex, have not been overall reported, except for an offspring's male-biased mortality found in a small captive forest musk deer (*M. berezovskii* Flerov, 1929) population (QI et al. 2011, XU & XU 2003).

The age affected reproductive success with a general pattern of an increasing reproduction investment of individuals with advancing age (HARSHMAN & ZERA 2007). LOISON et al. (1999) reported a decrease in semen quality and fertility with increasing age of males. Though MENG et al. (2003) reported that senile female musk deer entered estrus earlier and more synchronously than juvenile ones, the influential factors including parental age have not been validated on captive alpine musk deer and the males' roles were often neglected (MYSTERUD et al. 2009). Apart from age, as a unique mean of males' olfactory communication since the significant scented odour (DOTY 2012), musk is secreted by adult males (≥ 1 yr) annually before rutting season and it is costly to produce, given the accompanying drastic feeding and drinking reduction. Males with poorer body condition cannot afford the energy requirement for reproduction and are reported to perform poorly in terms of reproduction outcome (GOMENDIO et al. 2006). Besides, studies have shown that the musk odour affects females' ovulation, reproduction success and early life-stage survival to some extent (CARLSSON et al. 2000, COMFORT 1973). However, the impacts

of musk secreted by male musk deer on the reproduction outcome are far less explored and it is reasonable to expect that musk secretion plays a role in reproduction outcome.

In this study, we used long-term individual-based data from a known-age population with recorded musk secretion of alpine musk deer living in captivity in west China, which is among one of the main breeding centres of the endangered musk deer. Litter size, weaning success, parturition date and offspring's sex-ratio were used as measures of reproduction outcome in the population (CLUTTON-BROCK et al. 1986, GUINNESS et al. 1978, NEWBOLT et al. 2017). We hypothesised that the reproduction outcome of the population will be influenced by parents' age and the response will vary between males and females because of the different initial investment on offspring (MICHALCZUK & MICHALCZUK 2016). Secondly, we also predicted that musk secretion, the key olfactory sexual communicating way of the species (GREEN 1986), plays a role in reproduction outcome and is, therefore, useful for adjusting population growth. In this way, the overall reproduction characteristics of alpine musk deer in captivity for years can be assessed based on long-term data and the relationships with both parental age and musk secretion can be taken into account. These, in turn, will provide a reference for improving reproduction outcome of musk deer in general, and particularly for a more effective management of captive alpine musk deer.

Materials and Methods

Study site and populations

The data on male's musk secretion and females' parturition was collected from the Xinglongshan Musk Deer Farm (XMDF) in the western China (35°N, 104°E), situated at around 2000 m a.s.l., with typical continental climate, an annual precipitation 450 to 650 mm and average temperature between 3 and 7°C. In the farm, all musk deer are marked with ear tags at birth, making it possible to know individual traits and age. One to three males or five to seven females were kept separately in a mud-grounded enclosure, which consisted of a 10 x 10 m² outdoor square and seven lined brick cells, separated by iron-mesh fence, with a two meter-high ceiling above the floor. Forage, mainly consisting of fresh (in summer/spring) or dried leaves (in winter/autumn) collected from the nearby natural habitats of wild musk deer, was provided twice a day (around 5 minutes at dawn and dusk) by deer-keepers and water *ad libitum*.

Data collection and statistical analyses

We explored the alpine musk deer population in captivity from 2008 to 2018. We recorded 897 cases of deliveries by 363 females and with 175 copulation males involved. Age of females and the copulation males with known age, musk secretion and litter size (number of fawns produced), parturition dates (converted into Julian days since January 1st), weaning success (fawns survived until weaning occurring after 3 months, MENG et al. 2003) and offspring's sex ratio (sons out of fawns) were recorded for each of the deliveries. Three cases with barren females and seven cases with triplets were excluded from the analyses; another 23 cases in which no musk extraction on a certain year for males with diseases, were also excluded from the analyses.

For statistical analyses, Generalized Linear Mixed Model (GLMM) was adopted, using the lme4 package in R (R development Core Team, 2007). We included males' age and females' age and musk secretion as a fixed factors, while the identity of copulated musk deer was included as a random effect in all models. GLMM with a binomial distribution with the logit link was used to analyse the relationship between litter size and all predictors. GLMM was also used to analyse the relationship between parental age, musk secretion with parturition date, weaning success and offspring's sex ratio, respectively. Model selection was performed using Bayesian information criterion (BIC) and the model with the smallest BIC, as well as the models within a Δ BIC of 2 units were retained as competing models. Besides, because female age was reported to affect parturition date in a quadratic manner (SOLBERG et al. 2007), the relationship was also verified using quadratic models.

Results

Parturition date

Female musk deer mainly gave birth in June and the average parturition season lasted for 70 ± 17.86 days ($n=11$). The average parturition date was around June 22nd (171.86 ± 15.86 , $n = 864$) and it differed significantly among years ($\chi^2=47.98$, $df=10$, $p < 0.001$). Neither parental age nor musk secretion affected parturition date in linear models (Table 1), while female age significantly affected parturition dates in a quadratic manner (Fig 1; $\chi^2=10.82$, $df=2$, $p=0.004$; $\beta_{age} = -1.871 \pm 0.568$, $\beta_{age}^2 = 0.115 \pm 0.036$), suggesting juvenile and senile females gave births later than adult females and the earliest parturition occurred around 8 years.

Twinning probability and weaning success

From 864 deliveries included in our analysis, we had more twins (49.3%) than singleton (41%). Also, 73.6% (1026 out of 1394) fawns survived to weaning (i.e. after three-months), the weaning success rate for each individual included 0 (all dead), 0.5 (one out of two survived) and 1 (all survived), which accounted for 19.5%, 9.9% and 20.6%, respectively. Finally, 45.3% of fawns died in the first week of their life, including 11.4% on the parturition date for dystocia or deficiency.

Both twinning probability ($\chi^2=25.32$, $df=10$, $p=0.005$) and weaning success ($\chi^2=84.28$, $df=10$, $p < 0.001$) differed significantly among years. Female age significantly affected the twinning probability ($\chi^2=40.64$, $df=1$, $p < 0.001$) with a positive regression coefficient $\beta_{age} = 0.157 \pm 0.025$, suggesting the probability of giving birth to twins increased with female age (Fig 2). Weaning success was not affected by female age, male age or musk secretion (all $p > 0.05$; Table 1).

Offspring's sex and musk secretion

The musk secretion ranging from 0 to 19.00 g per head with an average of (7.43 ± 5.14) g per head. Fewer males were born as compared to females (291 out of 601) from 2008 to 2018, showing a female-biased reproduction with no variation in sex ratio among years ($\chi^2=4.81$, $df=10$, $p=0.85$). Musk secretion positively affected the offspring's sex ratio ($\chi^2=6.01$, $df=1$, $p=0.014$; $\beta_{musk} = 0.011 \pm 0.004$), suggesting studs who secreted more musk contributed to having more male newborns, while the sex ratio was not affected by female age ($\chi^2=1.08$, $df=1$, $p=0.29$) or stud age *per se* ($\chi^2=0.01$, $df=1$, $p=0.91$) (Table 1).

Discussion

The parturition of ungulates in temperate regions has strong seasonality and according to our study showed that female captive musk deer in XMDF mainly gave birth in June, the average parturition date was around June 22nd, which supported a previous study that alpine musk deer delivered in the late spring to early summer, specifically from May to July and the parturition peak occurred between June 4th and 24th (SHENG & LIU 2007).

As we firstly hypothesised, we found that a large proportion of the variations in litter size for captive alpine musk deer were explained by females' age, while males' age almost made no differences to them. Female age significantly affected

Table 1. Selection (using Bayesian Information Criterion, BIC) on mixed effect regression models assessing the effect of female age, male age and musk on twinning probability, weaning success, parturition date and offspring’s sex ratio. Female and male identities were incorporated as random effects; year was a fixed factor in all models. The most parsimonious model is shown in bold.

Response	Independent variables						BIC
	Female age	Male age	Musk secretion	Male identity	Female identity	Year	
Twinning probability				√	√	√	1247.107
	√			√	√	√	1213.223
	√	√		√	√	√	1219.983
		√	√	√	√	√	1258.911
			√	√	√	√	1252.179
	√	√	√	√	√	√	1226.071
Weaning success				√	√	√	1861.287
	√			√	√	√	1874.233
	√	√		√	√	√	1886.526
		√	√	√	√	√	1888.728
			√	√	√	√	1876.473
	√	√	√	√	√	√	1901.912
Parturition date				√	√	√	7044.139
	√			√	√	√	7051.993
	√	√		√	√	√	7058.067
		√	√	√	√	√	7059.483
			√	√	√	√	7053.506
	√	√	√	√	√	√	7067.368
Offspring’s sex ratio				√	√	√	608.269
	√			√	√		544.604
	√	√		√	√		558.145
		√	√	√	√		554.257
			√	√	√		540.697
	√	√	√	√	√		567.379

parturition dates in a quadratic manner and juvenile and senile females tended to give birth later than prime age females, which likely resulted from the late socially induced estrus and weak sexual stimulation. This concurs with the studies on red deer (*Cervus elaphus* L., 1758), reindeer (*Rangifer tarandus* L., 1758), moose (*Alces alces* L., 1758) and other populations reporting that reproduction trends are regulated by the female’s intrinsic factors (ANDERSEN & LINNELL 1996, GREEN et al. 2017, HOLAND et al. 2003). Factors such as the female’s sexual maturity, rank and endocrine responsiveness to social interactions between the same sex and opposite sex also directly affect the timing of estrus, mating and delivery (MENG et al. 2006, SOLBERG et al. 2007). In general, the response threshold of females at different age to initiate their estrus is different. The juvenile females, as well as primiparous females need more intense behavioural stimulation, longer time to initiate their ovulation and other physiological ac-

tivities, so they had later parturition date. The senile females are normally experienced in reproduction but are in poorer body condition, resulting in later births as well. Researches also reported that individuals in good physical condition had earlier birth than those in poor body condition (MYSTERUD et al. 2009, ZHAO et al. 2020).

The importance of the role of females in reproduction was substantiated by the fact that only maternal age was selected in litter size models, in which female age positively affected twinning probability. The probability of producing twins increased for adult females and this may be related to their body condition and accumulated parturition experience. In captivity, with sufficient food resources, maternal body condition of adults can be maintained with improved performance and bare intraspecific competition (ORO et al. 2014). Adult females are experienced in delivery and have large fat reserve, enabling them to invest more heavily in their prog-

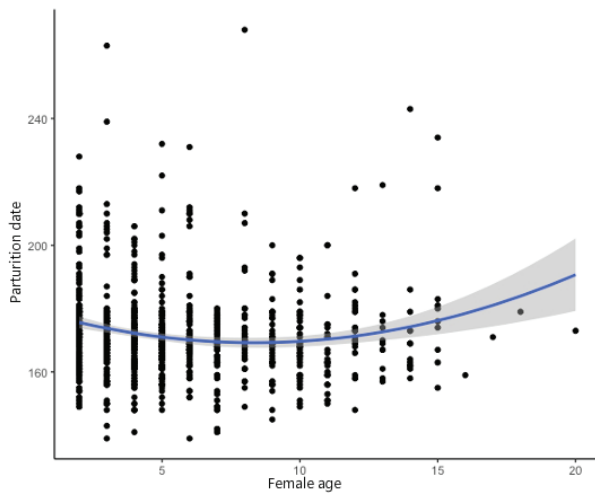


Fig. 1. Relationship between parturition date (in Julian day) and female age (years) in alpine musk deer of the Xinglongshan Musk Deer Farm. Dark dots indicate the parturition date for specific-age individuals. The 95% confidence interval band around the fitted line is provided.

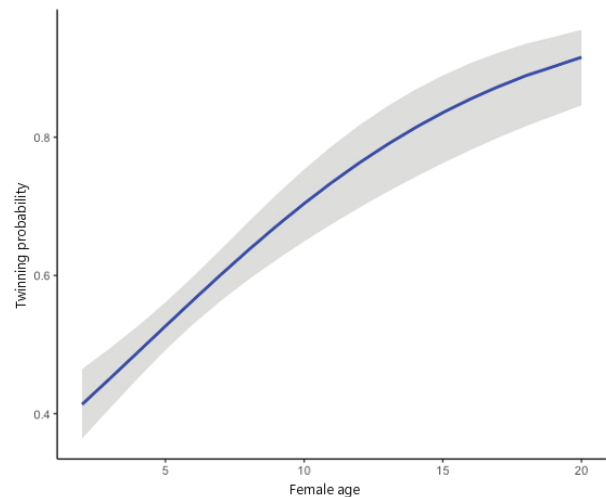


Fig. 2. Relationship between probability of giving birth to twins and female age (years) in alpine musk deer of the Xinglongshan Musk Deer Farm. The 95% confidence interval band around the fitted line is provided.

eny and more likely to produce a double egg during ovulation (SHARP & CLUTTON-BROCK 2010). The positive relationship between litter size and maternal age has been confirmed by a ten-year study on white-tailed deer whose litter size also increased with age (GREEN et al. 2017). However, in our study, weaning success was neither affected by female age, paternal age nor musk secretion, which may result from the extra care provided by deer-keepers. In order to obtain a maximum captive population, weaker newborns can obtain artificial suckling and timely treatment, which may increase the weaning success and reduce the impacts brought by parental body conditions (SWAISGOOD et al. 2006).

Although offspring's sex ratio of ungulates is involved in more than one mechanism across different environmental conditions (MYSTERUD et al. 2009), which could be concealed by stable food resource in captivity, males have enough sexual attractiveness and body condition does increase the males rate among newborns (GOMENDIO et al. 2006). This is in accordance with our result that the male musk deer secreting more musk contribute to a male-biased fertilisation, thereby supporting our second hypothesis to some extent. Musk secretion can be an indicator for the hormone cycle, triggering the initiation and end of the rut and copulation (CONNER et al. 2007), while acting as chemical communication in musk deer, which is regarded as a vital sexual trait for males (DOTY 2012, GREEN 1986). Moreover, musk secretion occurs before the rutting season, along with reduced foraging regime,

fewer motion and getting easily excited (MENG et al. 2006). Thus, males in better body condition can afford the costly energy consumption to obtain better olfactory sexual communication by producing more musk. By the time of the mating season, males who had restored better body condition with enough olfactory sexual attractiveness could enhance male-biased newborns. Similarly, studies in antlers, another significant sexual trait in ungulates, suggested that males with large antlers invest more in reproduction (CLUTTON-BROCK et al. 1986, MALO et al. 2005). The ratio of male to female newborns produced by dominant parents in better body condition, is significantly higher than that produced by subordinates (CLUTTON-BROCK et al. 1986, WAUTERS et al. 1995).

According SOLBERG et al. (2007), apart from the intrinsic factors, external factors also affect the population's reproduction characteristics. The interannual variations we found in litter size, weaning success and parturition date during the study period indicated that other external factors, such as year, also contributed to reproduction outcomes. Although interannual variation in sex ratio have not been found in offspring, as sex allocation studies are notoriously inconsistent among mammals (MERKLING et al. 2019), the result is in agreement with the six-year study on red deer (GUINNESS et al. 1978), seven-year study on roe deer (*Capreolus capreolus* L., 1758, see WAUTERS et al. 1995) and 11-year study on white-tailed deer (*Odocoileus virginianus* Zimmermann, 1780, see GREEN et al. 2017). Though this result was mostly explained by

food supply (NIELSEN & MØLLER 2006), which is artificially regulated in captive populations, climate changes can be the key ultimate factor in explaining the interannual variation for most populations (VISSEER et al. 2004). Factors such as higher temperature and lower precipitation or snow coverage have been associated with advanced parturition date, smaller litter size and reduced weaning success (LOISON et al. 1999, PAOLI et al. 2018). However, the interannual variances of reproduction outcome and the relationships with potential external factors, including climate changes, in captive alpine musk deer population need further investigations.

Conclusion

The twinning probability, weaning success, parturition date and offspring's sex ratio in alpine musk deer after being several years in captivity, were influenced to some extent by parental age and musk secretion. Faced with declining population growth, maintaining the population growth of captive musk deer is a challenge for sustainable musk resource. Our results suggest that within these captive populations, reproduction outcome can be predicted by and offspring's sex ratio can regulate through monitoring maternal age, musk secretion of stud musk deer and choosing the males with proper musk secretion as studs. These have important implications for the conservation of musk deer population and sustainable management of musk resources.

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Availability of data and materials: The information of all data used in the study is available in the Ecology Department, School of Environment and Natural Resources, Renmin University of China.

Consent for publication: This manuscript does not contain any individual person's data.

Ethics approval: In this work, all involved animals were observed in accordance with the guidelines established by the Academic Committee of School of Environment and Natural Resources, Renmin University of China.

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