IMPACT OF THE CONFLICT INTERACTIONS AND SOCIAL LEARNING ON THE HIERARCHY STRUCTURE IN CAPTIVE MALES OF *MOSCHUS CHRYSOGASTER* (MOSCHIDAE)

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Moschus chrysogaster (hereafter – musk deer) is an endemic to the Qinghai-Tibet Plateau and surrounding areas in China. Due to historical overutilisation and habitat degradation and loss, the musk deer is endangered and faces serious threats to its survival. Besides *in situ* conservation, musk deer farming is an important and effective means for *ex situ* conservation and sustainable supply of musk resources. Wild musk deer are solitary and highly territorial, but in captivity they are subjected to intensive farming practices that confine them to a limited space, leading to the development of a hierarchy structure. This study was carried out from January 2021 to December 2023 at the Musk Deer Farm in Zhuanglang County, Gansu Province, China. Focal sampling and all-occurrence recording were used to measure conflict behaviour of captive musk deer. Social network analysis was used to study the relationships between social conflict and social learning within the captive community. Our finding revealed a significant positive correlation between the hierarchy rank of the conflict initiator and the receiver, and individuals tended to initiate conflict against individuals close to their ranks, which reflected the individual identification of the hierarchy within the community. The social learning behaviour of musk deer in various ranks was significantly different. The social learning behaviour of middle rank (40.7%) was significantly higher than that of high rank (14.5%) and low rank (14.0%). Compared with the social learning behaviour of musk deer before conflict (37.9%), the social learning behaviour of musk deer after conflict (62.1%) was significantly increased, but there was no significant difference in non-social learning behaviour before conflict (46.7%) and after conflict (53.3%). This research reveals the majority of conflicts unfolding among the higher ranks of the captive population. To improve musk deer farming, it is imperative to assess the conflict potential and sociality of individuals within the broader hierarchy. In addition, we found a significant surge in socially learning behaviours among musk deer post-conflict, indicative of the essential spread of information on individual rank and fighting capabilities within the captive population. Recognising the pronounced social learning in captive individuals with middle ranks, managers should focus on these key members. The alleviating conflict level by rationally translocating individuals while maintaining a hierarchical structure within the group is critical to the successful musk deer conservation and farming.

Key words: Alpine musk deer, *ex situ* conservation, hierarchy structure, non-social learning behaviour, social learning behaviour, social network

Introduction

Hierarchy is a common inter-individual dominance-subordination relationship structure in animal communities (Leimar & Bshary, 2022). It is considered a group-level attribute that arises from the aggression of individual animals (Hobson & DeDeo, 2015). Hierarchy structures are believed to have an impact on population dynamics and individual fitness (Ellis, 1995). However, most studies focus on the orderliness of social hierarchy or the influence of individual phenotypic characteristics on hierarchy structure (Shizuka & McDonald, 2012; Weidling et al., 2024). This narrow scope, however, inhibits a holistic understanding of the multifaceted processes at work within hierarchical structure. For instance, a dominant animal is often faced with physical challenges from subordinates, whereas other lower ranked individuals of similar rank tend to receive submissive gestures (Dey & Quinn, 2014). In a group with a clear hierarchy, individuals tend to interact primarily with others of similar rank (Rat et al., 2015), although they may also interact randomly with other members of the group regardless of rank (Silk et al., 2019). Rowell (1966) astutely observed that the overt aggression of dominant animals, while instrumental in preserving their status, is but one piece of the puzzle. It is the less conspicuous behaviours (subordinate submission and the learning that occurs through observation) that are particularly crucial for the long-term stability of the hierarchy (Kaufmann, 1983). The expression of submission is not merely a response to dominance; it is a behaviour intertwined with the development of individual recognition and social learning within the community. These mechanisms have a significant impact on conflict interaction and can significantly mitigate the costs associated with them (Rowell, 1974).

Social learning refers to learning influenced by observation of, or interaction with, another (typically a conspecific) animal (Box, 1984). In contrast, non-social learning encompasses behaviours that evolve independently of social exchange (Heyes, 1994). Social learning will be favoured when the cost of animals directly obtaining individual information within the community becomes expensive (Rieucau & Giraldeau, 2011). Since the establishment and maintenance of hierarchy structure in animal communities is dynamic, social conflict through aggression or attack is an important way for animals to obtain social information such as individual competition or resource-holding potential, but direct participation in social conflict leads to time and energy consumption and increased risk of injury. Therefore, individuals adopt behavioural strategies such as social learning to mitigate these conflict-driven costs (Rieucau & Giraldeau, 2011). Social learning necessitates a shift from an egocentric perspective, enabling animals to assess interactions in which they are not directly involved (Seyfarth & Cheney, 2015). In captive settings, conflicts within animal communities are seldom isolated events, offering bystanders the opportunity to obtain information about other individuals through social learning (Abril-de-Abreu et al., 2015). As social conflict is related to hierarchy structural establishment, the emergence of winners and losers in the outcome of conflict interactions provides social information on competitiveness, which allows bystanders to assess potential competitors' resource-holding potential and to adopt appropriate behaviour patterns without direct participation in the conflict (Braga Goncalves & Radford, 2022).

Animal social network analysis serves as a powerful tool for understanding the social hierarchy structure and behavioural characteristics of animal communities. It employs a suite of key network indicators that offer a quantifiable measure of an individual's social attributes. The In-degree and Out-degree reflect the number of individuals being selected by others or actively choosing to interact with others, respectively. These metrics can be further weighted by frequency of interactions, a refinement known as Weighted degree. This approach provides a more detailed understanding of an individual's status within a social network (Deng et al., 2019). A plethora of studies has delved into the social network analysis within wildlife populations. For instance, a social network analysis on *Gorilla beringei graueri* Matchie, 1914 found that female individuals were the most socially centered individuals in the group (Leeds et al., 2024), and a study on *Suricata suricatta* Schreber, 1776 found that age and weight are pivotal determinants of an individual's social status, with younger and lighter individuals typically exhibiting a higher degree of social engagement than their older, heavier counterparts (Pacheco, 2020). In a study combined with non-injury sampling, it was found that preferential leaders in *Bison bonasus* Linnaeus, 1758, i.e. the older and more dominant individuals, which are more central ones, are less stressed compared to other group members (Ramos et al., 2022). To date, the application of social network analysis has predominantly concentrated on highly social species. However, there is a lack of relevant research on mammals that are more solitary by nature, especially within the confines of captive environments. The impact and efficacy of their behaviours and ecological adaptability within the social networks of captive groups remain largely unexplored.

The wild *Moschus chrysogaster* (Hodgson, 1839) (hereinafter – musk deer), which is native to the Qinghai-Tibet Plateau and surrounding areas in China, plays an important role in traditional medicine and the perfume industry, owing to the musk secreted by adult males. However, due to historical overutilisation and habitat degradation, the musk deer is listed as an Endangered (EN) taxon on the IUCN Red List (Harris, 2016), Appendix II species in CITES and a first-grade protected animal in China (Geng & Ma, 2000). In order to effectively protect the musk deer populations, both *in situ* and *ex situ* conservation measures are used (Jiang et al., 2020). These measures encompass the protection of wild populations and their habitats, alongside artificial captive breeding. The latter offers a conservation avenue by translocating endangered animals from their natural habitats to controlled, optimal artificial environments, with the ultimate aim of reintroducing captive-bred individuals to restored habitats (Lv et al., 2023). However, musk deer are small, solitary forest-dwelling ungulates, with minimal social interactions between individuals and loose social ties between groups in the wild. In limited captivity environments, high density of individuals and lack of escape space for subordinates promote the formation of hierarchy structure and strengthen its influence (Kaufmann, 1983). In these captive settings, certain social networks of conflict and hierarchy structure are established, which influences the dominance relationships between individuals and profoundly shape the behavioural patterns of musk deer (Meng et al., 2012a). With the emphasis on conservation and sustainable utilisation of wild animals, the *ex situ* conservation of musk deer has attracted much attention, and social network analysis provides a powerful tool for understanding the social dynamics of the musk deer in captivity. While prior research hints at a connection between conflict interactions and the recognition of individual hierarchy ranks (Meng et al., 2012b), a comprehensive understanding of the social networks among captive musk deer remains largely unexplored. It has not known whether musk deer adaptively collect and use relevant information from interactions of other individuals in their social learning behaviours. Given this gap in knowledge, there is an urgent need to better understand the relationships between the conflict social network and hierarchy structure of musk deer.

Therefore, by sampling the behaviours of captive musk deer, we analysed differences in conflict rivalry and social learning of individuals with various hierarchy ranks of the conflict social network. The primary objectives of our research encompass the following. 1) we aim to discern whether a correlation exists between the hierarchy rank of the conflict initiator and the receiver in order to support the individual recognition ability of the musk deer. 2) We seek to evaluate the impact of varying hierarchy ranks on the propensity of captive musk deer to initiate or receive in conflicts within the social network. 3) Our analysis aimed to determine if distinct patterns of social learning behaviours emerge among musk deer of various ranks during times of the conflict. 4) We intend to scrutinise the variations in social and non-social learning behaviours among individuals of varying ranks, both preceding and succeeding conflict interactions. We anticipate that the findings of this study will enhance the management and conservation strategies of captive musk deer, fostering the sustainable development of musk deer breeding initiatives, and also contribute new insights to the development of the field of wildlife captive breeding research.

Material and Methods

Research area and experimental animals

The study was performed at the Musk Deer Farm in Zhuanglang County, Gansu Province, China, situated in the eastern extension of the Qilian Mountains and the western foothills of the Liupan Mountains, at an altitude of 1800 m a.s.l. The average annual temperature is around 8°C, with the highest temperature in July and the lowest in January. The annual precipitation is 489 mm, mostly concentrated in summer (July – September). The average annual frost-free period is 142 days.

The layout of each enclosure was similar, consisting of an area of 100 m^2, with a natural soil substrate and a central shelter for rest (Fig. S1). All musk deer were provided with sufficient drinking water and fed twice daily (05:00 h, 17:00 h) the same diet, which included artificial fodder (20% wheat bran, 20% soybean, and 60% alfalfa) and wild-collected leaves (e.g. *Berberis kansuensis* C. K. Schneid., *Hippophae rhamnoides* L., *Armeniaca vulgaris* Lam., *Prunus salicina* Lindl.). Enclosures were cleaned daily at 17:00 h during the feeding time and were otherwise undisturbed by keepers. For identification, each musk deer had a numbered plastic ear tag.

Definition and sampling of musk deer behaviour

We observed the behaviour of 52 healthy musk deer from 13 musk deer enclosures in the musk deer farm, each containing six adult males (older than three years old). Behavioural sampling was conducted during the peak periods of musk deer activity (06:00–08:00 h, 17:00–19:00 h) using focal behavioural sampling and all-occurrence recording methods (Altmann, 1974). Two behavioural samples were collected each day for musk deer individuals, and the behavioural sampling was made for two days per week. We conducted a total of 120 days of behavioural sampling and 480 hours of total observation time. The conflict behaviours and definitions (see Meng et al., 2012a,b) are shown in Table 1. The unique ear-tag of musk deer and the individual body characteristics were used for quick individual identification. Tag numbers of individuals engaged in fighting and the outcome of the fight were recorded.

Table 1. The conflicting behaviours and definitions according to Meng et al. (2012a,b), and the types and definitions of social/non-social learning according to Heyes (1994), Hoppitt & Laland (2008)

Type of behaviours		Definitions
Conflicting behaviour	Attacking	Physical contact aggression by mouth or hoof against other individuals
	Chasing	Conflict occurs when the inferior individual flees and the superior individual pursues and continues to attack the fleeing individual
	Displacing	Individuals tend directly to other individuals and take their place
	Threatening	The individual's neck is erect, head is held high, and upper canine teeth are displayed, accompanied by lip twitching and a puffing sound, while the back of the body is twisted and moved closer to the threatened individual
	Fleeting	Inferior individuals in a conflict flee the scene of the conflict
	Evading/Retreating	Individual leaves its location when other individuals are approaching it
Non-social learning	Lying down	Individuals are lying down with limbs curled up underneath the body in a sleepy state
	Ingesting	Feeding on feed troughs or nibbling on blades of grass in the activity yard
	Environmental sniffing	Individuals perceive environmental information with the nasal muzzle
	Defecating/Urinating	Individual animals excreting feces or urine
Social learning	Standing and gazing	Individuals are awake and upright, with eyes gazing at a fixed point in front or above them
	Defensive gesture	Individuals stand in a tense state and gaze at other individuals
	Vigilance	Individuals with increased sensitivity and showing signs of nervousness, such as standing with head up, auricular rotation, looking around the room

In addition to the conflict behaviours, we also recorded the behaviours of bystanders at the time of the conflict (Table 1). Depending on whether an individual's behaviour is directed towards other individuals or not, we recorded behaviours that pointed to others, namely (i) standing and gazing, (ii) defensive gesture, (iii) vigilance. We defined them as social learning behaviours (hereinafter – SL), whereas behaviours that only involve the animal itself, namely (i) lying down, (ii) ingesting, (iii) environmental sniffing, (iv) defecation/urinating were classified as non-social learning behaviours (hereinafter – NL) (Heyes, 1994; Hoppitt & Laland, 2008). For the sake of avoidance of ambiguity, it is hereby clarified that NL in this paper are the opposite of SL, and are only used to differentiate between the behaviours of bystanders, and that such behaviour should not be regarded as a type of learning behaviour.

Hierarchy structure

In conflict interactions one party was defeated and fled, so that it was considered the loser of the conflict interaction, and vice versa, the other one the winner of the conflict. The hierarchy rank was determined according to the David's score (D_S) of all individuals. The higher the score, the higher the order rank. The procedure for calculating the D_S of each individual in a group of N individuals on the basis of the observed numbers of dyadic wins and losses is as follows. First, the dyadic proportions of wins are calculated. The proportion of wins by individual *i* in its interactions with another individual *j* (P_{ij}) is the number of times that *i* defeats *j* (s_{ij}) divided by the total number of interactions between *i* and *j* (n_{ij}), i.e. $P_{ij} = s_{ij}/n_{ij}$. The proportion of losses by *i* in its interactions with *j* (P_{ji}) equals $1 - P_{ij}$. If $n_{ij} = 0$, then $P_{ij} = 0$ and $P_{ji} = 0$ (Gammell et al., 2003):

$$D_s = w + w - l - l_2 ,$$

Here *w* represents the sum of *i*'s *Pij* values, i.e.:

$$w = \sum P_{ij} (j = 1...N; j \neq i) ,$$

while w_2 represents a weighted sum of *i*'s P_{ij} values (weighted by the *w*-values of its interactants), i.e.:

$$w_2 = \sum w_j P_{ij} (j = 1...N; j \neq i) .$$

Similarly, *l* represents the sum of *i*'s *Pji* values, i.e.:

$$l = \sum P_{ji} (j = 1...N; j \neq i) ,$$

and l_2 represents a weighted sum of *i*'s *Pji* values (weighted by the *l*-values of its interactants), i.e.:

$$l_2 = \sum l_j P_{ji} (j = 1...N; j \neq i) .$$

Social network analysis

Social conflicts between each musk deer individual were converted into a binary matrix, and the data were imported into Gephi 0.10.1 (Bastian et al., 2009) for conflict social network analysis. Conflict social networks were constructed by assigning edge weights to the frequency of conflict interactions and calculating in/out and the weighted degree for a node (Sosa et al., 2021). The in/out-degree separately indicates the number of incoming/outgoing edges for a node, i.e. the number of partners, with which a musk deer received/initiated an interaction. The weighted in/out-degree indicates the sum of incoming/outgoing edge weights for a node, i.e. the sum of interactions, which a musk deer received/initiated (Foris et al., 2019).

Statistical analysis

We conducted Shapiro-Wilk tests to assess the normality of the data. Spearman correlation analysis was used to investigate the correlation between hierarchy rank of conflict-initiating individual and the rank of the conflict-receiving individual. Pearson's Chi-squared test was used to analyse the differences in the social learning behaviours of different hierarchy ranks of musk deer at the time of conflict. The Kruskal-Wallis test analyses whether there is a difference in the weighted degree of individuals with different hierarchy ranks. The Wilcoxon signed rank test was used to analyse the differences in social learning behaviours of musk deer before and after the occurrence of conflict. Non-normally distributed data were expressed as median (interquartile range), and data analyses were conducted with the SPSS 29.0 (Armonk, NY: IBM Corp), using two-tailed probability, with a significance level of p = 0.05. Statistical tests involving two-by-two comparisons were adjusted for significance values (Meng et al., 2012a,b).

Results

Relationships between hierarchy structure and conflict interaction

In the conflict social network (Fig. 1), we found that the rank of the parties to the conflict interaction was close. The data of individual hierarchy ranks were normally distributed. We found a significant positive correlation between the hierarchy rank of the conflict-initiating individuals and the rank of the conflict-receiving individuals (Pearson, r = 0.440, p = 0.003). With the hierarchy rank of the conflict-initiating individual as an independent variable (*x*) and the rank of the conflict-receiving individual as a dependent variable (*y*), the equations $y = 0.347x + 2.357$ (p = 0.005) could indicate the relationship between the hierarchy rank of the initiating and receiving the conflict interactions of musk deer.

Depending on the individual's D_S, the individuals in each enclosure were categorised as high-rank group (rank = 1–2), middle-rank group (rank = 3) and low-rank group (rank = 4–6) (Meng et al., 2012a,b). The data of the in/out and weighted degree were non-normally distributed (Table S1), and expressed as median (interquartile range) (Table 2). There was no significant difference in the out-degree (Kruskal-Wallis test: H = 0.740, p = 0.390) and in-degree between individuals of different ranks in the conflict network (Kruskal-Wallis test: H = 0.740, p = 0.390). But individuals in the high hierarchy rank had the highest weighted out-degree of 67.5 and initiated conflict most frequently, and there was a significant difference in the weighted out-degree of individuals in the three hierarchy ranks (Kruskal-Wallis test: H = 8.605, p = 0.014), with significantly higher weighted out-degree of individuals in the high hierarchy rank of the musk deer (67.5) than those in the middle rank (57, Kruskal-Wallis test: H = 2.111, p = 0.017) and a low hierarchy rank (35, Kruskal-Wallis test: H = 2.393, p = 0.035), whereas there was no significant difference in the weighted out-degree of low and middle hierarchy rank musk deer (Kruskal-Wallis test: H = 0.104, p = 0.907).

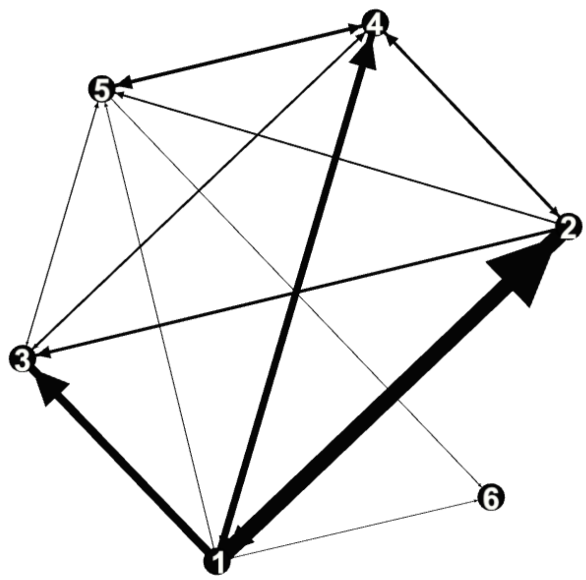

Fig. 1. The conflict social network of musk deer (*Moschus chrysogaster*) at the Musk Deer Farm in Zhuanglang County, Gansu Province, China, where the numbers indicate various ranks. The direction of arrows indicates the direction of the conflicting behaviour and the thickness indicates the frequency of the conflicting behaviour.

Similarly, in the conflict social network, a high hierarchy rank musk deer had the highest in-degree of 70 and the highest frequency of receiving conflicts. There was a significant difference in the weighted in-degree of individuals in the three hierarchy ranks (Kruskal-Wallis test: H = 6.410, p = 0.041), with the weighted in-degree of individuals in the high hierarchy rank significantly higher than that of individuals in the low hierarchy rank (41, Kruskal-Wallis test: H = 2.472, p = 0.013).

Relationships between hierarchy rank and social learning

The frequency data of SL and NL of various ranks of musk deer were non-normally distributed (Table S2). In order to reflect more intuitively the differences in social learning behaviours of individuals at different ranks, we calculated the frequency of SL and NL as a percentage of the total frequency for each rank separately (Table 3). Then we used cross-table Chi-square test. The results showed significant differences in social learning behaviour types at different levels ($p < 0.001$). Pairwise comparisons (with an adjustment level of 0.0167, $\alpha' = 0.05/(k(k–1)/2)$) were then used and the results (Table 3) showed significant differences between the social learning behaviours of high and middle hierarchy ranks of musk deer ($\chi^2 = 10.843$, $p < 0.001$), between the social learning behaviours of individuals in middle and low hierarchy rank ($\chi^2 = 0.005$, $p = 0.002$), and no significant difference was found in social learning behaviours between high and low hierarchy rank ($\chi^2 = 10.027$, $p = 0.942$).

Relationship between hierarchy rank and social learning behaviours before and after conflict interactions

The frequency data of SL and NL of different ranks of musk deer were non-normally distributed. In order to more intuitively reflect the differences in individual social learning behaviours before and after conflict interactions, we calculated the SL and NL frequencies as a percentage of the total frequencies for individuals of each rank before and after conflict, respectively (Table S3, Table S4). The social learning behaviours and non-social learning behaviours of musk deer before and after conflict interactions were non-normally distributed. Based on the Wilcoxon test, there was a significant difference in social learning behaviours before and after conflict (Z = -4.681, $p < 0.001$). After conflict, the social learning behaviour of musk deer was significantly increased, while there was no significant difference in nonsocial learning behaviours (Z = -1.293, p = 0.196).

Table 2. The in/out and weighted degree and pairwise comparisons of different ranks of musk deer (*Moschus chrysogaster*) in conflict networks. Significance values have been adjusted by Bonferroni correction method

Hierarchy rank	High (H) rank (n = 26)	Middle (M) rank (n = 13)	Low (L) rank (n = 13)
Out-degree	2 (0.75)	2 (1)	2 (1)
Weighted out-degree	67.5 (112)	57 (59)	35 (74)
Kruskal-Wallis test	H-M: H = 2.111, p = 0.017	H-L: H = 2.393, p = 0.035	M-L: H = 0.104, p = 0.917
In-degree	2 (0)	2 (1)	2 (2)
Weighted in-degree	70 (132)	54 (35)	41 (97)
Kruskal-Wallis test	H-M: H = 1.680, p = 0.093	H-L: H = 2.472, p = 0.013	M-L: H = 0.561, p = 0.575

Table 3. Pairwise comparison of social learning behaviour differences among different hierarchy ranks of musk deer (*Moschus chrysogaster*)

Hierarchy rank	Social learning	Non-social learning	Pearson's Chi-square test
High (H) rank (n = 26), %	14.5	85.5	H-M: $\chi^2 = 10.843$, $p < 0.001$
Middle (M) rank (n = 13), %	40.7	59.3	H-L: $\chi^2 = 0.005$, $p = 0.942$
Low (L) rank (n = 13), %	14.0	86.0	M-L: $\chi^2 = 10.027$, $p = 0.002$

Table 4. Pairwise comparison of social learning behaviours of musk deer (*Moschus chrysogaster*) before and after conflict

Hierarchy rank	Social learning			Non-social learning		
	Before conflict (%)	After conflict (%)	Wilcoxon test	Before conflict (%)	After conflict (%)	Wilcoxon test
High rank	19.6	29.6	Z = -2.865, p = 0.004	22.4	27.9	Z = -1.499, p = 0.134
Middle rank	10.7	19.1	Z = -1.823, p = 0.003	15.0	16.8	Z = -0.352, p = 0.725
Low rank	7.6	13.4	Z = -1.740, p = 0.036	9.3	8.6	Z = -0.229, p = 0.819
Total	37.9	62.1	Z = -4.681, p < 0.001	46.7	53.3	Z = -1.293, p = 0.196

Discussion

Conflict interaction is pivotal in the establishment of social hierarchy structures, with the combative prowess of both parties significantly influencing the course and outcome of such encounters (Bubak et al., 2016). In group-living species, the behavioural patterns adopted by animals are often contingent upon the hierarchical standings of their conspecifics (Hobson et al., 2021). Consequently, the capacity for individual's status recognition is of paramount importance. A study of *Cervus elaphus* Linnaeus, 1758 revealed that some individuals tended to keep in proximity with others, while others consistently avoided the rest of the herd. It was also observed that some animals would repeatedly attack other members of the group, while others were never seen attacking any other musk deer over the course of the entire period of observation (Esattore et al., 2020). Indeed, we found that individuals exhibit equivalent in-degree and out-degree within the conflict networks. But our findings also corroborate the notion that conflicts are more probable between individuals with similar hierarchy ranks than across vastly different ranks. The first content of our study can be used as an evidence for the rank recognition ability of the musk deer. Parallels can be drawn to research on captive *Gazella dorcas* Linnaeus, 1758, where individuals were found to prefer socialising with individuals of analogous social and hierarchical status (Cortés et al., 2024). It might be that when the level gap between the two sides is small, the ability of the two sides is close, and the possibility of winning the conflict interaction is similar. Therefore, the individuals of the lower rank were more motivated to challenge the individuals of the higher rank (Dey & Quinn, 2014). This phenomenon is congruent with theoretical models predicting the evolution of aggressive behaviour based on the costs and benefits of conflict (Parker, 1974).

The hierarchy rank is inextricably linked to the allocation of critical resources such as mates, territory, and access to food. Previous theoretical models have suggested that conflict interactions should be the greatest in dominant individuals because of the higher benefits of obtaining rank, and social conflict can be used to maintain dominance, for example, threatening or aggressive behaviour (Silk et al., 2019). Our second key finding aligns with this perspective. In the confines of a captive environment, we observed that musk deer leverage their hierarchical status to secure access to food resources. Individuals of higher rank regard their peers, particularly those with ranks closely matched to their own, as formidable rivals in the contest for dominance. Consequently, they are more prone to instigate conflict with these rivals, while simultaneously circumventing interactions with those of significantly lower rank. This type of conflict avoidance between individuals of higher and lower ranks is very common in social animals, where the cost for conflict is minimised by the deliberate avoidance of confrontations between vastly disparate ranks (Senar et al., 1990; Cortés et al., 2024). Lower rank individuals through recognition of hierarchy rank within the community and social learning from the conflict interactions of other individuals, seldom initiate conflict. Instead, they exhibit submissive behaviours, by opting to flee or yield when faced with higher-ranking counterparts. This strategic choice mitigates their exposure to injury and conserves valuable time and energy that would otherwise be expended in futile confrontations.

Social learning represents a critical phenomenon within animal societies, enabling individuals to leverage observations from social encounters, to modulate their behaviour accordingly (Hobson & DeDeo, 2015). For example, *Astatotilapia burtoni* Günther, 1894 can infer social rank by observing the outcome of conflict interactions with other individuals (Grosenick et al., 2007). In instances of the conflict, bystanders are not merely passive observers. They actively monitor the progression and outcome of these interactions. By doing so, they glean insights into the dominance hierarchy and subsequently utilise this social intelligence to inform their own behaviour, thereby circumventing the potentially substantial costs associated with direct conflict engagement (Mesterton-Gibbons & Heap, 2014; Tibbetts et al., 2022). This process underscores the survival value of social learning in minimising risks and optimising social status within the community.

In wild animal groups, the hierarchical relationship of middle rank individuals is the most difficult to predict and relatively unstable, and conflict interactions are essential for them to rise to higher hierarchy rank (Silk et al., 2019). Conversely, our research observed that middle rank musk deer in captivity engage in less conflict interactions, yet they exhibit a marked propensity for social learning behaviours, surpassing those of both higher and lower rank individuals. Middle rank individuals play an important role in connecting individuals of high or low ranks in the enclosure, have to interact with individuals of different ranks and face complex behavioural strategies. Consequently, they need to cultivate robust social learning ability and this enables them to assimilate novel adaptive strategies through social learning (Leimar & Bshary, 2022). For high-rank individuals, as previously noted, conflict interactions were predominantly instigated by those already entrenched in positions of dominance. Their focus is directed towards the preservation of their current resources and hierarchical status. Whereas, for lower-ranked individuals, similar to the Grooming for commodity hypothesis (Bagnato et al., 2023), they mostly adopt avoidance strategies to show compliance, and this simple behavioural pattern that basically allows them to maintain their survival in the captive environment. Therefore, all of this leads to a lack of social learning among these individuals.

It can be speculated that the significantly higher social learning of middle rank musk deer than that of other ranks may reflect their adaptability and flexibility in learning strategies in complex social environments, and that this behavioural pattern may help middle rank musk deer to better adapt to different stressful contexts and improve their chances of survival and reproduction. Previous research have indicated that male musk deer in middle ranks tend to secrete more musk than those in higher and lower ranks. This phenomenon arises from the distinct energy allocation strategies and varying degrees of social stress experienced at different hierarchical ranks (Meng et al., 2011). Individuals of the higher rank must allocate increased time and energy to preserve their status, while those of lower rank face increased aggression from their superiors, which in turn restricts their access to essential resources like food and shelter, thus negatively affecting their musk secretion (Meng et al., 2011). The significant social learning capabilities observed in middle rank musk deer may be an adaptive response, reflecting their capacity for agility and adaptability within the complex social conditions. This enhanced learning acumen could equip middle rank individuals with a versatile repertoire of strategies to navigate the intricacies of social dynamics.

Finally, we explored the potential shifts in the social learning behaviours of individuals following conflict interactions. Our findings indicate a notable escalation in social learning behaviours among musk deer subsequent to conflict episodes, while non-social learning behaviours remained relatively unchanged. Conflict interactions serve as a pivotal mechanism for the preservation of hierarchical standings within the community. They facilitate not only the exchange of information between the parties involved but also, through their outcomes, demonstrate the hierarchy, enable the displacement of rivals, and secure resources. This process, in turn, stimulates social learning among onlooking community members (Tibbetts et al., 2022). Bystanders, having witnessed the conflict, are often better positioned to anticipate the behaviours of other individuals (Yang et al., 2023). Moreover, it has been observed that within animal communities, individuals may engage with a third party following a conflict, either to mitigate the negative repercussions or to seek indirect reconciliation (Yu et al., 2005). In such instances, individuals are likely to become more attuned to the behaviours and standings of their conspecifics, thereby enabling them to adopt suitable behavioural responses, including the enhancement of social learning.

Conclusions

The establishment of a hierarchy rank offers a dual advantage within the musk deer community. It does not only consolidate the position of those at the top but also shields lower rank individuals from the risks of conflict-related injuries. Our study reveals that the hierarchy structure significantly influences the nature of conflict interactions among individuals. Dominant individuals are more prone to direct their aggression towards those in close proximity to their own rank, with the majority of conflicts unfolding among the higher ranks of the captive population. In light of these findings, it is necessary for managers to closely monitor the hierarchical structure and to be mindful of the evolving dynamics within the community. By reasonable captive group mobilisation, it is possible to diminish the likelihood of conflict, thereby fostering a more stable and balanced hierarchy. Such measures are instrumental in enhancing the survival and reproductive prospects of the musk deer in captivity.

Our research has also uncovered a significant relationship between the hierarchy structure and the social learning behaviours of the endangered musk deer. Individuals of the middle rank exhibit the most pronounced social learning behaviours, necessitated by their frequent interactions with both higher and lower rank individuals. As such, they must employ adaptable learning strategies to navigate the complexities of the captive environment. Furthermore, our findings indicate that the social learning behaviour of musk deer experiences a notable upswing following conflict interactions, which may serve as a conduit for the dissemination of social information, critical for preserving the integrity of the hierarchy structure. Consequently, it is essential for managers to focus on individuals who exhibit robust social learning capabilities, particularly those in the middle ranks, and to intensify post-conflict monitoring of the musk deer. This vigilance will ensure the re-establishment of harmonious internal relationships within the community and uphold the stability and well-being of the musk deer population.

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Supporting Information

Additional data to the paper of Wang et al. (2024) may be found in the **Supporting Information**.

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ВЛИЯНИЕ КОНФЛИКТНЫХ ВЗАИМОДЕЙСТВИЙ И СОЦИАЛЬНОГО ОБУЧЕНИЯ НА СТРУКТУРУ ИЕРАРХИИ У САМЦОВ *MOSCHUS CHRYSOGASTER* (MOSCHIDAE), СОДЕРЖАЩИХСЯ В НЕВОЛЕ

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Moschus chrysogaster (рыжебрюхая кабарга) является эндемиком Цинхай-Тибетского нагорья и прилегающих территорий в Китае. Из-за чрезмерной эксплуатации в прошлом, а также деградации и уничтожения мест обитания, *Moschus chrysogaster* находится под угрозой исчезновения и сталкивается с серьезными угрозами своему выживанию. Помимо сохранения in situ, разведение *Moschus chrysogaster* является важным и эффективным средством сохранения ex situ и устойчивого снабжения ресурсами мускуса. В дикой природе *Moschus chrysogaster* ведут одиночный образ жизни и очень территориальны. Однако в неволе они подвергаются интенсивному воздействию методов ведения сельского хозяйства, которые ограничивают их распространение небольшими пространствами, что приводит к развитию иерархической структуры их сообществ. Исследование проводилось с января 2021 г. по декабрь 2023 г. на ферме по разведению *Moschus chrysogaster* в уезде Чжуанлан провинции Ганьсу, Китай. Для изучения конфликтного поведения содержащихся в неволе особей *Moschus chrysogaster* использовались фокусная выборка и регистрация всех наблюдений. Анализ социальных сетей использовался для изучения взаимосвязи между социальным конфликтом и социальным обучением особей в неволе. Полученные результаты выявили значительную положительную корреляцию между иерархическим рангом инициатора конфликта и его получателя, а также то, что особи были склонны инициировать конфликт против других особей, близких к их иерархическому рангу, что отражало индивидуальную идентификацию иерархии в сообществе. Социальное поведение особей *Moschus chrysogaster*, относящихся к разным иерархическим рангам, значимо различалось. Социальное поведение обучения у особей среднего иерархического ранга (40.7%) было значимо выше, чем у особей высокого (14.5%) и низкого (14.0%) рангов. По сравнению с социальным поведением обучения оосбей *Moschus chrysogaster* до конфликта (37.9%), их социальное поведение обучения после конфликта (62.1%) значимо возросло, но в несоциальном поведении обучения до (46.7%) и после (53.3%) конфликта значимых различий не было отмечено. Это исследование показывает, что в условиях неволи большинство конфликтов разворачивается среди особей высшего иерархического ранга в сообществе. Для улучшения разведения *Moschus chrysogaster* крайне важно оценить конфликтный потенциал и социальность особей в рамках более широкой иерархии. Кроме того, мы обнаружили значительное повышение социального обучающего поведения среди *Moschus chrysogaster* после конфликта, что свидетельствует о существенном распространении информации об индивидуальном ранге и боевых возможностях среди особей популяции в условиях неволи. Признавая выраженную склонность к социальному обучению у особей среднего иерархического ранга в неволе, сотрудникам ферм следует сосредоточиться на этих ключевых членах сообщества. Снижение уровня конфликта путем рационального перемещения особей при сохранении иерархической структуры внутри группы имеет решающее значение для успешного сохранения и разведения *Moschus chrysogaster*.

Ключевые слова: иерархическая структура, несоциальное поведение обучения, рыжебрюхая кабарга, социальная сеть, социальное поведение обучения, сохранение *ex situ*