Identifying personality traits and their potential application to the management in captive forest musk deer (*Moschus berezovskii*)

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Abstract

Since the 1950s musk deer (Moschidae) are kept in captivity for the production of musk, a glandular secretion used in Chinese traditional medicine and as an ingredient in cosmetics. Most recently, forest musk deer (*Moschus berezovskii*) raised in captivity were reintroduced into the wild to augment depleted wild populations. The most prominent behavioral and social characteristics of musk deer are anxiety, a timid, solitary lifestyle and territoriality, making musk deer difficult to breed. Individual differences in the personality of captive male musk deer could allow breeders to sort bold individuals that are suitable for commercial farming from those with a shy and more timid personality suitable for reintroduction. We attempted to identify what behavioral variables and what novel stimulus tests are the most effective to characterize whether an individual is bold or shy. To measure boldness in 31 adult males, we used a two-step approach: i) using a Principal Component Analysis to identify reference behaviors that are indicative of either a shy or a bold personality, and ii) to establish individual boldness scores based on those reference behaviors and compare them between four novel stimuli. Two 'bold PCs' with high axis loadings from behaviors that are typical for curiosity, territorial marking or that represent the ordinary daily activity of a ruminant were obtained, as well as three 'shy PCs' that obtained high axis loadings from behaviors that are typical for anti-predator responses, intimidation or displacement behavior.

Although all tested stimuli were verified suitable, the unfamiliar human being was the strongest stimulus to test boldness, followed by leopard feces, the beach ball and the leopard dummy. Using cluster-analysis, nearly three quarter of tested individuals were identified as shy, while only one quarter was classified as bold. Previous studies on poultry and domestic ungulates, demonstrated that through continued selective breeding for boldness, the overall personality in the population is driven towards a calm temperament in the majority of the individuals. This might be beneficial for musk production but will have adverse effects on successful reintroductions due to reduced individual fitness and domestication effects.

Key words: boldness–shyness continuum; novel stimuli test; commercial farming; reintroduction, boldness score

Introduction

The consistency of individual behavior differences across time or context is a phenomenon commonly described as an individuals' personality or temperament (Dall et al., 2004; Reale et al., 2007; Hedlund and Lovlie, 2015). Animal personalities play an important role in population ecology as well as in evolutionary and ecological processes (Wolf et al., 2007; Sih et al., 2012; Wolf and Weissing, 2012). Empirical data revealed that individual personalities are closely related to an individual's life-history (Dammhahn, 2012; Guenther, 2018), its reproductive success (Armitage and Van Vuren, 2003; Reale et al., 2009) and overall fitness (Bremner-Harrison et al., 2004; Greenberg and Holekamp, 2017). Recently, an increasing number of studies have investigated animal personalities (Perals et al., 2017) and swift progress has been made, not only in theory but also in the application of personality traits in animal welfare and conservation (Bremner-Harrison et al., 2017). Five major metrics are frequently used to describe the consistency of personality in animals, i.e. boldness *vs* shyness (caution), exploration *vs* avoidance, activity, aggressiveness, and sociability (Reale et al., 2007). The boldness–shyness continuum (Wilson et al., 1994; Reale et al., 2007) represents the fundamental axis of behavioral variation(Wilson et al., 1994) and its study became increasingly popular in recent years, including a wide array of animal taxa such as insects (Schuett et al., 2018; Tan et al., 2018), fish (Jolles et al., 2015; Jolles et al., 2016; Nielsen et al., 2018), amphibians (Kelleher et al., 2018), reptiles (Ward-Fear et al., 2018), birds (Williams et al., 2012; Cole and Quinn, 2014) and mammals (Noer et al., 2015; Greenberg and Holekamp, 2017; Bubac et al., 2018; Myers and Young, 2018; Santicchia et al., 2018; Breck et al., 2019). Novel stimuli tests are hereby a commonly used method to determine the degree of an individuals' boldness or shyness (Bremner-Harrison et al., 2004; Sinn et al., 2014; Blaszczyk, 2017; Myers and Young, 2018).

Musk deer (Moschidae) are small forest-dwelling ruminants, endemic to central and East Asia. Illegal poaching for musk and habitat loss have reduced wild musk deer populations to only 3 to 5% of their historical population size in the 1960s (Sheng, 1996; Yang et al., 2003). Counteracting this dramatic decline of wild musk deer and reducing the human pressure on wild populations, China has instigated the captive breeding of musk deer (Meng et al., 2006). The most commonly bred species is the forest musk deer (*Moschus berezovskii*; hereafter referred to musk deer), with currently about 20,000 individuals in captivity (Hu pers. com.). According to the conservation objectives formulated by the Chinese government (He et al., 2014b; Wang et al., 2019), farmed musk deer should not only be kept to expand the captive stock for musk production and to satisfy ever increasing consumer demands (Li et al., 2012), but also to provide founder animals for reintroduction and to augment depleted wild populations.

Musk deer are solitary, territorial, small-sized, browsing ungulates that are highly susceptible to stress and stress-related illnesses, a suite of characteristics that make captive breeding challenging (Meng et al., 2006; Wu and Wang, 2006; Sheng and Liu, 2007; Jiang et al., 2012). Musk deer are particularly prone to disturbance, which causes stress, physical tension and suppressed immunity (He et al., 2014a), restraining thus the development of captive populations (Li et al., 2012; He et al., 2014b). Attempts to improve captive breeding included different aspects of the species' biology, such as behavior (Wang et al., 2016a), nutrition (Wang et al., 2013; Wang et al., 2015), reproduction (Lang et al., 2012; Wang et al., 2016b), or disease control

(Hu et al., 2016; Wei et al., 2016; Hu et al., 2018). Despite intensive research and management, the desired success to reduce stress responses and thus improve breeding conditions failed. Individual differences in the personality of captive musk deer will determine the animals' ability to adapt to the condition in captivity, with artificial, selective pressures favoring bold individuals with traits more suited to captive conditions than shy individuals (McDougall et al., 2006). Vice versa, animals with a shy and timid personality are less well adapted to anthropogenic disturbance in captivity but are more suitable for the release into the wild with higher survival rates than bold individuals (Bremner-Harrison et al., 2004). Retaining the natural behavior and social organization of endangered species kept in captivity is an essential prerequisite for successful reintroduction programs (IUCN/SSC, 2013). However, the gradual process of habituation and domestication in captive stock bred for reintroduction is detrimental for a successful reintroduction (He et al., 2014a). Research on personality traits of musk deer in captivity is therefore fundamental for the establishment of scientific conservation programs and successful reintroductions, but also for refining breeding success and musk production. In our study we therefore attempted to design an easily applicable method to find what behavioral variables and which novel stimuli are the most effective to characterize whether an individual is bold or shy. This will enable musk deer breeders to separate individuals with a bold personality, suitable for captive breeding, from those that are rather shy and timid, and thus suitable for reintroduction. In our two-way approach, we first defined behaviors that are characteristic for bold and shy personality in male forest musk deer, using Principal Component Analysis (PCA) on four novel stimuli. In a second step we used individual boldness scores to develop an easy applicable method for breeders to distinguish bold from shy individuals.

Material and methods

Study site and test animals

Our study was carried out in Shaanxi Pien Tze Huang Forest Musk Deer Breeding Center, located in Fengxian County in Shaanxi Province, China (34˚16′40.16″N, 106˚47′03.08″E). The center comprises 80 breeding units and retains a total of about 400 musk deer. Each unit consists of a communal outdoor activity space (4×10 m) and five retreat compartments to isolate individuals (each 2×2 m). Each unit was fenced by a 2.5 m high fence to prevent escape. Novel stimuli tests (see below) were conducted in the outdoor activity space, an area where mating takes place and in which musk deer are permitted to move freely once a week (Fig. 1A). Test individuals were therefore familiar with, and well habituated to this activity space. Since only sexually mature males produce musk (Wu and Wang, 2006; Sheng and Liu, 2007), we selected only individually identifiable, adult males, aged three to six years for our experiments. Moreover, to increases the survival rate of musk deer in captivity, young musk deer remain with their mothers beyond weaning age, i.e. until they have reached their reproductive age. Female musk deer usually deliver twins and separating the subadults from their kin would cause additional distress which would bias the testing of suitable for personality traits. During the test period, diet was provided according to standard protocol, i.e. food and water were put on the ground allowing the test individuals to feed ad libitum (He et al., 2014b). Diet comprised mainly of fresh leaves from local trees and shrubs, such as trident maple (*Acer buergerianum*), chinaberry *(Melia azedarach*), mulberry leaf (*Morus alba*) and elm (*Ulmus pumila*). Prior to each test, test animals were not fed for 12 hours.

Novel stimulus tests

Four separate stimulus tests were conducted with four novel stimuli located in the center of the activity space. Stimulus 1: a 1.5 m long leopard dummy (Fig. 1B), stimulus 2: a beach ball (1 m diameter, colorful; Fig. 1C), stimulus 3: fresh leopard feces (collected from Beijing Zoo and cryopreserved), and stimulus 4: an unfamiliar human being sitting immobile on a chair in the center of the activity space. The person was not a member of staff of the breeding center and thus unknown to the test animals. Moreover, the person was dressed in different color clothing compared to that commonly used by members of staff. None of these stimuli was ever presented to musk deer before the tests were carried out. The order of the four tests was random and changed throughout the study period.

Experimental procedures

Tests were carried out from 20th July to 10th August 2015 (first round: R1) and from 30th August to 15th September 2015 (second round: R2). During this time of the year, female musk deer are either pregnant or lactating, i.e. they are together with their last off-spring, and males have accumulated enough musk in their musk pouch to be harvested (Mengyuan et al., 2018). We chose 31 adult males as our test subjects, originating from nine different breeding units. In total we carried out 248 tests (31 animals × 4 stimuli × 2 rounds) in the activity space of the respective breeding unit. To ensure that behavioral observations were representative, tests were conducted from 6:00 to 9:00 and from 16:00 to 20:00, i.e. at dusk and dawn when musk deer are most active (Wu and Wang, 2006; Sheng and Liu, 2007). Each activity space was monitored by video cameras surveying the whole area. After completing the test set-up (see above), the test individual was released from its retreat compartments into the activity space and the door was closed immediately to prevent the animal from returning to the compartment. After the individual arrived at the activity space, a three minutes acclimatization period elapsed before recording was started. This relatively long acclimatization period was necessary, due to the timid and skittish character of musk deer, making them easily stressed and prompting them to perform fiercely during first three minutes after release from their retreat compartments. This was also the reason why each stimulus test lasted for 60 minutes. A shorter test period would be insufficient to identify the personality because the performances of different individuals would be biased towards behaviors indicating stress and anxiety, such as wall-jumping, urination and walking forth and back. All four stimulus tests were carried within one day, but each test individual was subjected to only one test series per day. Once the test subject was released into the activity space, it had no visual contact with any other FMD. Experiments were temporarily stopped during inclement weather conditions such as rain or temperatures below 20°C.

Behavioral records

Video recordings were analyzed off-site using a personal computer and either the frequency or duration of each behavior was determined for each individual during each test. In total 15 behavior variables were distinguished (Table 1). Apart from three behaviors that were measured as frequencies (pawing, wall jumping, snorting), all others were established as durations. At the end of the experiments, we determined the shortest distance observed between the test individual and the stimulus during each test using marks on the ground for orientation.

Statistical Analysis

Prior to our statistical analyses, durations (or frequencies) of all 16 behaviors and the distance to the stimulus were z-transformed to standardize data dimensionality (mean = 0, SD = 1). Subsequently, the durations (or frequencies) were condensed trough a factor reduction procedure (i.e. principal components analysis based on a correlation matrix) using the varimax rotation option. The resulting principle components (PCs) with an eigenvalue > 1.0, were used as explanatory variables to test for statistical differences among the four stimuli (leopard dummy, beach ball, fresh leopard feces, unfamiliar human being) using a Kruskal-Wallis one-way ANOVA. Dunn's multiple pairwise comparisons adjusted by Bonferroni correction, were applied to test for pairwise difference of each behavior between stimuli.

Previous studies using stimulus tests in mammalian species (ungulates: Romeyer and Bouissou, 1992; Bergvall et al., 2011; MacKay et al., 2014), primates: Carter et al., 2012; Blaszczyk, 2017 or carnivores: Bremner-Harrison et al., 2017; Myers and Young, 2018) recommended three major reference behaviors (i.e. feeding, sniffing towards the stimulus, and approaching the stimulus) and the distance to the stimulus to be indicative for a bold personality. These recommendations were further supported by the results of our principal component analysis (see below), and therefore used as reference behaviors to assign boldness scores. Individual boldness scores were calculated for each reference behavior and for each novel stimulus, using the following formula: ($B_s = (D – min) / (max – min) / N$), whereby B_s represents the boldness score, D the mean duration (or frequency), min the lowest duration (or frequency), max the highest duration (or frequency), and N the total number of individuals. The resulting values were rounded up to integers and averaged across all reference variables to obtain one boldness score for each male and each novel stimulus. Thereby, we considered the variance in the population, allowing an animal to be ranked differently for a set of reference behaviors and ensuring the top score and the bottom score to be statistically different (Vandenheede and Bouissou, 1993a; b). Boldness scores were tested for differences between novel stimuli using a Kruskal-Wallis ANOVA. Dunn's multiple pairwise comparisons adjusted by Bonferroni correction, were applied to test for pairwise difference of each behavior between stimuli. To test for repeatability, boldness scores were further evaluated using Kendall's coefficient of concordance (Siegel, 1956) determining whether coherence of individual behaviors prevailed between novel stimuli tests.

To test whether behavioral PC values obtained from Principal Component Analysis and boldness scores corresponded, we used a Spearman rank correlations independently for each stimulus. Based on individual boldness scores, we conducted a hierarchical cluster analysis to visualize the grouping patterns obtained from hierarchical clustering (dendrogram) and to partition the boldness scores of 31 male musk deer into two clusters (i.e. bold and shy). To test for differences between groups obtained from cluster analysis we used a Mann-Whitney *U* tests. Apart from hierarchical cluster analysis (performed using the 'factoextra package' in R), all other statistical analyses were conducted using SPSS version 22.

Ethics approval

This study was approved by the Ethics Committee of Beijing Forestry University, Beijing, China; Pien Tze Huang Pharmaceutical Corporation, Zhangzhou, China; and Pien Tze Huang Forest Musk Deer Breeding Center, Shaanxi, China. This study was also carried out in accordance with the recommendations of the Institution of Animal Care and the Ethics Committee of Beijing Forestry University. All test procedures were performed with the help of an expert veterinarian, and all efforts were made to minimize suffering. All procedures were reviewed and approved by the State Forestry Administration of China and were performed in accordance with the US Animal Welfare Act.

Results

Behavioral responses

Fifteen behavioral responses, observed in 31 male musk deer, were established as mean durations, mean number of events, as the mean shortest distance to the stimulus object and as percentage proportion for each of the four stimuli (Table 2). Behaviors that were performed in less than 50% of all males, included tail rubbing, ruminating, wall-jumping, urination, walking forth & back, pawing and snorting, the latter two only in the stimulus test using an unfamiliar human being.

Identification of behaviors indicative for bold or shy personality

The five resulting principle components (PCs) with an eigenvalue > 1.0, explained 62.41% of the total variance (Table 3). PC1 received high positive factor loadings from approaching, sniffing, tail rubbing, defecation and a negative factor loading from distance to the stimuli (Table 3). These behaviors are characteristic for a bold personality as they stand for the curiosity of an individual and its requirement to mark the territory. PC2 received high positive factor loadings from misgiving, walking for & back, urination, wall-jumping, snorting and a negative loading from resting (Table 3). These behaviors are characteristic for a shy personality as they stand for anxiety and a pronounced flight response. PC3 received high positive factor loadings from staring & gazing, urination, pawing, misgiving and urination, also indicating a shy personality (Table 3). PC4 received high positive factor loadings from ruminating, feeding, resting and comfort behavior (Table 3). These behaviors are characteristic for a bold personality as they indicate relaxation and comfort. Lastly, PC5 received high positive factor loadings from staring & gazing, again a behavior that is indicative of fear and carefulness (Table 3).

Testing reference variables between stimuli

A Kruskal-Wallis one-way ANOVA revealed a strong significant difference between novel stimuli for all PCs (PC1: $H = 19.01$, $N = 124$, $P < 0.001$, PC2: $H = 13.13$, $N = 124$, $P < 0.001$, PC3: $H = 4.48$, $N = 124$, $P = 0.21 > 0.05$, PC4: $H = 20.45$, $N = 124$, $P < 0.001$, PC5: $H = 26.35$, $N = 124$, $P < 0.001$). For PC1, a post-hoc multiple comparison procedure showed that an unfamiliar human being (mean ± SE: -0.51 ± 0.12) triggered significantly fewer bold responses (approaching, sniffing, tail rubbing, defecation) and larger distances to the stimulus than a leopard dummy (mean ± SE: 0.24 ± 0.26) or fresh leopard feces (mean ± SE: 0.37 ± 0.14; Fig. 2A). All other pairings did not show significant differences. For PC2, the post-hoc test revealed an unfamiliar human being (mean ± SE: 0.76 ± 0.30) to trigger significantly more shy behaviors (walking for & back, wall-jumping, snorting) than the leopard dummy (mean ± SE: -0.27 ± 0.09) or a beach ball (mean ± SE: -0.27 ± 0.07; Fig. 2B), while all other pairings did not show significant difference. For PC3, the post-hoc analysis demonstrated that and the unfamiliar human being (mean ± SE: 0.59 ± 0.33) triggered stronger responses of shy behavior (pawing, misgiving and urination) than all other stimuli (mean ± SE leopard dummy: -0.16 ± 0.04, beach ball: -0.26 ± 0.05, fresh leopard feces: -0.17 ± 0.04; Fig. 2C). For PC4, the post-hoc analysis revealed fresh leopard feces (mean ± SE: -0.34 ± 0.11) and an unfamiliar human being (mean ± SE: -0.38 ± 0.12) to trigger significantly less bold behavior (ruminating, feeding, comfort behavior and resting) than the leopard dummy (mean ± SE: 0.45 ± 0.25) or the beach ball (mean ± SE: 0.27 ± 0.16; Fig. 2D). No significant differences were detected between the other pairings. For PC5, the post-hoc analysis indicated an unfamiliar human being (mean ± SE: 0.67 ± 0.26) and fresh leopard feces (mean ± SE: -0.59 ± 0.08) to trigger significantly stronger shy responses (staring and gazing) than the leopard dummy (mean ± SE: -0.07 ± 0.14) or the beach ball (mean ± SE: -0.02 ± 0.12; Fig. 2E), while all other pairings did not show significant differences.

Boldness scores

Mean (± SE) individual boldness scores were 9.91 ± 0.69 for the leopard dummy, 10.30 ± 0.57 for the beach ball, 12.01 ± 0.71 for fresh leopard feces, and 8.41 ± 0.74 for the unfamiliar human being. Overall, mean (± SE) boldness scores showed a statistically significant difference between the four novel stimuli tests (One-way ANOVA: $F = 4.73$, $N = 31$, $P < 0.01$). A post hoc pairwise comparisons procedure (LSD; $P < 0.05$) revealed the leopard dummy to be significantly different from a strange human being and from fresh leopard feces (Fig. 3). Kendall's coefficient of concordance ($W = 0.468$, $\chi^2_{30} = 80.37$, $P < 0.01$), indicated a coherence between individual boldness scores i.e. the individual boldness ranking of each of the 31 males remained the same, regardless of which stimulus test was used.

Spearman rank correlations between PC values obtained from Principal Component Analysis and the corresponding boldness score revealed significant positive relations for all variables included in PC1 (sniffing, approaching, tail rubbing, defecation and the nearest distance to the stimulus) across all novel stimuli (Table 4). By contrast, the second PC indicating a bold personality, i.e. PC4 (ruminating, feeding, comfort behavior, resting) did not reveal any correlation with the corresponding boldness score (Table 4).

Based on individual boldness scores (established for each stimulus), hierarchical cluster analysis grouped the tested musk deer into two categories. The smaller group consisted of seven males that behaved more boldly, i.e. had higher boldness scores, and a large group with 24 individuals, i.e. that had a rather shy personality and lower boldness scores. A dendrogram, based on hierarchical cluster analysis, was created to visualize grouping patterns (Fig. 3). Across all four stimuli, individuals contained in the bold group had higher boldness scores than those grouped into the shy group (Fig. 4). A Mann-Whitney U test revealed, the two groups (bold, shy) obtained from cluster analysis to be significantly different for all four stimuli (leopard dummy: $Z = -2.339$, $P = 0.019$; beach ball: $Z = -2.315$, $P = 0.021$; fresh leopard feces: $Z = -3.757$, $P < 0.001$; unfamiliar human being: $Z = -3.024$, $P < 0.002$).

Discussion

In our study, we defined behaviors that were characteristic for a bold or shy personality in male forest musk deer and tested the results for differences between four novel stimuli. Our PCA of behaviors observed during this study, revealed five PCs, of which two (PC1 and PC4) were indicative of a bold personality, while the other three (PC2, PC 3 and PC5) were indicative for a shy personality. The 'bold PCs' included behaviors that express curiosity (approaching, sniffing, short distance to the stimulus), that are typically performed during territory marking (e.g. tail rubbing, defecation) or that represent the ordinary daily activity of a ruminant such as feeding, ruminating, resting and comfort behavior (Sheng and Liu 2007). The 'shy PCs' included behaviors that are usually performed as an anti-predator response (e.g. wall-jumping, snorting, staring and gazing), as a threat (e.g. pawing), or as a combination of both, i.e. a displacement activity as a result of a behavioral conflict between escape and threat (e.g. misgiving, urination, walking for and back). This result was not unexpected since numerous studies reported on behaviors, such as approaching, sniffing, feeding, ruminating and resting, to be indicative of boldness (Fraser et al., 2001; Bremner-Harrison et al., 2004; Brown et al., 2007; Biro et al., 2010; Eriksson et al., 2010; Chapman et al., 2011). Likewise, physical contact with, or close proximity to a stimulus object—in our study represented by the nearest distance to the stimulus—was also described by several studies to indicate boldness (Bergvall et al., 2011; Verdolin and Harper, 2013; Sinn et al., 2014; Blaszczyk, 2017).

Testing the 'bold PCs' between different novel stimuli revealed that unfamiliar human being and leopard feces (at least in PC4) triggered significantly fewer bold responses and larger distances to the stimulus than a leopard dummy or a beach ball. Leopard dummy and beach ball carried most likely the smell of humans and were not considered a threat since visual and olfactory cognition did not match. By contrast, fresh leopard feces carry the odor of the main natural predator (Wu and Wang, 2006; Sheng and Liu, 2007), while a living human being emanates the odor of a predator and appears like a predator, posing a severe threat to a musk deer and therefore causing the lowest number of bold responses. Vice versa, testing the 'shy PCs' between different novel stimuli revealed that unfamiliar human being and leopard feces (at least in PC5) triggered significantly higher rates of shy behaviors than the leopard dummy or the beach ball. This general pattern indicates that the unfamiliar human being (and to a certain degree also fresh leopard feces) had the strongest impact on the behavior of musk deer, and thus making it the most suitable stimulus to distinguish between a shy and a bold personality. Many personality studies on larger mammal species used a human being as the main stimulus (Romeyer and Bouissou, 1992; Vandenheede and Bouissou, 1996; Vandenheede et al., 1998; Janczak et al., 2003; Sibbald et al., 2009; Valsecchi et al., 2009; Meagher et al., 2016; Pierard et al., 2017; Neave et al., 2018; Shahin, 2018). However, most of these studies were carried out on domestic livestock or pets, making a strong stimulus imperative. By contrast, musk deer are very timid and skittish, and a human being represents the most invasive stimulus object, unreasonably stressing the test individual (Wang et al., 2016a). Moreover, testing hundreds of musk deer using unfamiliar human being would be neither time- nor cost-efficient. Since fresh leopard feces also differed significantly from other stimuli, they were also considered suitable to test for boldness (low factor loadings in PC4 and PC5). They could be used as an alternative stimulus, but the obligation to constantly pursue fresh feces from captive leopards appears to be rather challenging. We therefore recommend the use of beach ball, leopard dummy or any other novel object to identify the shyest individuals by focusing on 'shy PCs' (high factor loadings in PC2, PC3 and PC5), or on 'bold PCs' (high factor loading in PC1 and PC4) to identify the boldest individuals, i.e. those musk deer that keep on feeding, ruminating, sniffing or approaching despite the presence of the novel object.

In our second approach, we attempted to establish individual boldness scores as a simple method for breeders to distinguish bold from shy personalities. First, we proofed a high coherence of individual boldness since the individual ranking of each male remained the same, regardless of which stimulus test was used. Only if stimulus tests were coherent among each other, repeatability could be confirmed and respective boldness score could be used to indicate boldness (Bremner-Harrison et al., 2004). This was demonstrated by Kendall's coefficient of concordance, indicating that individuals referred to as being bold when exposed to one stimulus were also classified as bold when exposed to another stimulus and thus reflecting the repeatability of each variable (Bremner-Harrison et al., 2004; Bremner-Harrison et al., 2017). Subsequently, a Spearman rank correlation confirmed a strong correlation between the behavioral PC values of PC1 and the corresponding boldness score for each stimulus, suggesting that behaviors contributing to PC1 are particularly suited to establish the boldness scores.

Hierarchical cluster analysis grouped boldness scores obtained from reference behaviors (i.e. behaviors contributing to PC1 and PC4) into two groups, a shy group, and a bold group. Across all four stimuli boldness scores were significantly higher in the bold group than in the shy group, thus confirming the grouping pattern suggested by the cluster analysis. The visualization of our data using hierarchical cluster analysis has been proven as a useful tool for musk deer and livestock breeders (Wesley et al., 2012), to easily identify individuals suitable for reintroduction or production. Based on both cluster-analyses, nearly three quarter of tested individuals were regarded as shy, reflecting the nervous and timid character of musk deer. Vice versa, only one quarter of tested male musk deer was classified as bold. Through continued selective breeding towards increased musk yields (i.e., towards bold personalities), this ratio is supposed to be shifted towards bolder individuals with increasing time in captivity. This might be beneficial for musk production but will have adverse effects on successful reintroductions due to reduced individual fitness, inbreeding and domestication effects (McDougall et al., 2006). To avoid such domestication effects (Trut, 1999; Trut and Dugatkin, 2017) and their negative impact on the captive population, it is imperative that a certain number of shy individuals will be included in the commercial breeding of captive stock and only the shyest will be considered for release into the wild.

Declarations of interest

None.

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Tables

Table 1. Definition, coding, and type of measure of behaviors observed in male forest musk deer during this study.

Behavior	Measure	Definition
Feeding	Duration	Feeding on artificial (pellets) or natural diet (leaves and herbs) offered on the ground, drinking water
Sniffing	Duration	Olfactory sensing of external environment (directed towards the stimulus object or any other direction or object)
Approaching	Duration	Coming closer or near the stimulus object
Resting	Duration	Lying down, bedding, always without rumination
Defecation	Duration	Excretion of feces, digging and scratching to cover feces
Tail-rubbing	Duration	Rubbing the tail on the ground or on the surface of walls or door frames, often accompanied by sniffing, sometimes accompanied by digging soil
Ruminating	Duration	Regurgitation and repeated chewing of partly digested food
Comfort behavior	Duration	Combing or grooming with mouth or hoofs, stretching, yawning, jittering, or shaking
Staring & gazing	Duration	Standing still and staring at the stimulus object for a long time, sometimes with ears rotating, but without ruminating or any other obvious behavior
Pawing	Frequency	Single or repeated stamping toward the stimulus object or pawing with the foreleg
Wall-jumping	Frequency	Repeated violent jumping from the ground onto the wall whereby starting and landing point are the same without any horizontal movement; creates significant fatigue and shortness of breath
Urination	Duration	Urination in short time intervals after stimulation at a casual micturition location; without sniffing or burying behavior
Misgiving	Duration	Hesitant movements, stop-and-go, dragging the front feet
Snorting	Frequency	Sudden and abrupt pressing of air through nostrils, occurs usually as an alert when unsuspected abnormal stimulus occurs, produces a brief but loud wheeze or sneeze, together with standing-still and staring
Walking forth & back	Duration	Individuals walk uniformly back and forth without performing any other behavior, start and turning point are relatively fixed
Distance	Distance	Shortest distance observed between the animal and the stimulus object

Table 2. Mean (± SE), range and proportion of 15 behaviors and the nearest distance to the stimulus, observed in 31 male forest musk deer during four novel stimulus tests.

Behavior code (unit)	**Leopard dummy**				**Beach ball**				**Fresh leopard feces**				**Unfamiliar human being**			
	Mean	SE	Range	%	Mean	SE	Range	%	Mean	SE	Range	%	Mean	SE	Range	%
Feeding (sec)	208.10	52.90	0-3000	56.46	14.94	35.73	0-1085	58.06	147.31	30.12	0-936	58.07	45.58	18.62	0-946	19.36
Sniffing (sec)	29.44	5.86	0-285	79.03	19.58	5.00	0-193	67.74	38.53	4.94	0-143	91.94	6.04	2.52	0-145	40.33
Approaching (sec)	30.63	4.47	0-167	83.88	17.79	3.34	0-133	74.20	23.48	3.17	0-106	83.87	11.32	3.71	0-125	35.49
Resting (sec)	945.58	145.93	0-3600	56.45	933.16	126.81	0-3211	64.52	384.53	80.23	0-2606	45.16	201.90	68.00	0-2203	16.13
Defecation (sec)	51.11	8.91	0-305	53.23	57.47	7.63	0-231	67.75	69.34	9.73	0-393	70.97	32.09	7.98	0-437	46.78
Tail rubbing (sec)	10.74	3.68	0-119	16.13	5.37	1.95	0-70	14.52	5.15	2.31	0-112	11.29	1.32	1.32	0-82	1.62
Ruminating (sec)	62.60	29.99	0-1695	14.52	50.95	20.94	0-841	14.52	6.77	4.84	0-250	3.23	-	-	-	-
Comfort behav. (sec)	30.82	6.04	0-332	93.55	19.55	3.02	0-108	90.33	21.40	5.58	0-343	95.16	17.95	4.12	0-195	80.65
Staring (sec)	660.63	75.22	22-2557	100.00	722.42	67.19	60-2459	100.00	247.66	25.60	20-994	100.00	1279.82	117.22	0-3600	98.39
Pawing (sec)	-	-	-	-	-	-	-		-	-	-	-	3.35	1.41	0-61	14.52
Wall jumping (No.)	0.45	0.27	0-15	8.07	0.73	0.31	0-14	14.52	0.92	0.74	0-45	6.46	20.71	6.03	0-317	46.78
Urination (sec)	1.95	0.88	0-38	9.68	2.94	1.33	0-64	9.68	1.26	0.77	0-40	4.84	22.23	6.05	0-288	43.55
Misgiving (sec)	6.32	1.30	0-46	58.07	5.03	1.20	0-55	59.68	3.71	0.80	0-37	51.61	42.18	7.42	0-278	82.26
Snorting (No.)	-	-	-		-	-	-		-	-	-		39.55	9.67	0-380	66.13
Walking f & b (sec)	5.47	3.85	0-182	3.23	4.95	3.85	0-236	8.06	4.66	2.77	0-140	8.06	60.08	15.07	0-557	38.71
Distance (m)	2.71	0.32	0.1—8	100	3.21	0.28	0.1-8	100	2.11	0.27	0.1-8	100	6.37	0.23	0.4-8	100

Table 3. Results of Principal Component Analysis of 16 behavioral variables obtained from 31 adult male forest musk deer. PC loadings > 0.45 are shown in bold font type.

Variable	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Eigenvalue	4.11	2.26	1.36	1.20	1.06
% of variance	25.66	14.15	8.49	7.49	6.62
Approaching	**0.81**	-0.07	-0.04	-0.11	-0.11
Sniffing	**0.71**	-0.19	-0.07	-0.10	-0.15
Tail rubbing	**0.71**	0.07	-0.06	0.31	0.19
Distance to the stimuli	**-0.65**	0.36	0.12	-0.04	0.42
Defecation	**0.64**	-0.01	-0.09	0.08	-0.10
Walking for & back	-0.12	**0.88**	0.00	-0.09	-0.11
Wall-jumping	-0.09	**0.73**	0.26	-0.03	0.20
Snorting	-0.23	**0.51**	**0.46**	-0.13	-0.20
Pawing	-0.09	-0.03	**0.88**	-0.01	0.03
Misgiving	-0.14	0.41	**0.76**	-0.10	-0.04
Urination	0.00	0.21	**0.60**	-0.06	**0.51**
Ruminating	0.00	0.00	-0.10	**0.73**	0.20
Feeding	0.29	-0.04	-0.08	**0.53**	-0.23
Comfort behavior	-0.02	-0.10	0.08	**0.50**	-0.25
Resting	-0.32	-0.39	-0.20	**0.47**	-0.12
Staring & gazing	-0.32	-0.11	-0.01	-0.17	**0.80**

Table 4. Spearman rank correlations between behavioral PC values obtained from Principal Component Analysis (PCA) and the corresponding boldness score for each novel stimulus test.

Behavior PC	**Leopard dummy**	**Beach ball**	**Fresh leopard feces**	**Unfamiliar human being**
PC1	0.215*	0.258**	0.243**	0.182*
PC2	0.02	-0.08	-0.16	-0.04
PC3	0.09	0.237**	0.14	0.12
PC4	0.09	0.09	0.00	0.09
PC5	0.05	-0.191*	-0.09	-0.13

*: $P \leq 0.05$; **: $P \leq 0.01$.

Figure captions

Fig. 1. Experimental set-up in the activity space

Experimental set-up in the activity space of a musk deer breeding unit at Pien Tze Huang Forest Musk Deer Breeding Center, Shaanxi Province, China (A), a male musk deer test individual with two novel stimulus objects, i.e. a leopard dummy (B), and a beach ball (C).

Fig. 2. **Results of five Principal Components**

Results of five Principal Components (median ± interquartile range) obtained from 16 behavioral variables presented for four novel stimulus tests (stimulus 1: leopard dummy, stimulus 2: beach ball, stimulus 3: fresh leopard feces, stimulus 4: unfamiliar human being).

Fig. 3. Dendrogram obtained from cluster analysis

Dendrogram obtained from hierarchical cluster analysis of individual boldness scores obtained from 31 captive male musk deer, using average linkage (between groups) and combined rescaled distance clusters.

Fig. 4. Individual mean boldness scores obtained from cluster analysis

Individual mean boldness scores of two groups of captive male musk deer (bold and shy) obtained from cluster analysis (see Fig 3) and established for each novel stimulus test (leopard dummy, beach ball, fresh leopard feces, and unfamiliar human being).