



Daddy, daddy cool: stallion–foal relationships in a socially-natural herd of Exmoor ponies

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Abstract

Different forms of direct paternal investment have been described in mammals. One such species where paternal care was noticed, but remains poorly understood, is the horse (*Equus caballus*), where the male keeps a long-term relationship with several females and offspring. Therefore, the aim of this study was to analyse the interactions between the harem stallion and his foals. Two herds of Exmoor ponies living under semi-feral conditions in two separate reserves within Czech Republic were studied, each during one of the two consecutive breeding seasons (in 2016 and 2017). Both herds consisted of a stallion, 14 mares and their offspring (12 and 10 foals). The behaviour of all group members was recorded focusing on the stallion–foal interactions. The results show that the stallion receives more friendly interactions, snapping and playful behaviour from foals compared with adult mares. Furthermore, the stallion is more tolerant than mares, and actively plays with his offspring. There is no statistical difference in the sex of the foals in the stallion–foal interactions; however, male foals are more active than female foals in interacting with their father. The probability of a certain behaviour occurring between adult and foals changed over time. The stallion's presence might, therefore, be crucial for the physical and psychological development of the foals, especially the colts. These results may bring new insight into the common management of domestic horses, where stallions are usually kept separately and are not allowed to form natural groups.

Keywords Colt · Paternal care · Play behaviour · Snapping · Social behaviour

Introduction

According to Trivers (1972), parental care is “any investment by the parent in an individual offspring that increases the offspring's chance of surviving”. It can be divided into two types—direct and indirect paternal investment. Direct investment has an immediate physical influence on the survival of the offspring, including feeding, carrying, grooming and playing with the young. Indirect investment includes behaviour that does not require contact between father and

the young to increase the offspring survival, such as gaining and maintenance of resources, elimination of competitors or the harem defence (Kleiman and Malcolm 1981). In mammals, paternal care is typically recorded in monogamous species, e.g. bat-eared fox (*Otocyon megalotis*) (Wright 2006), California mice (*Peromyscus californicus*) (Gubernick and Alberts 1989), crested porcupine (*Hystrix cristata*) (Mori et al. 2016), red-bellied titi (*Callicebus moloch*) (Hoffman et al. 1995). Yet, polygamous males also provide their offspring with care or protection. This paternal behaviour is well studied in primates such as gorillas (*Gorilla beringei beringei*) (Rosenbaum et al. 2011), yellow baboon (*Papio cynocephalus*) (Buchan et al. 2003), hanuman langurs (*Presbytis entellus*) (Borries et al. 1999), common marmosets (*Callithrix jacchus*) (Zahed et al. 2008; Ziegler et al. 2017), and has also been described in canids (Moehlman and Hofer 1997), Galapagos sea lions (*Zalophus wollebaeki*) (Barlow 1972), killer whales (*Orcinus orca*) (Lopez and Lopez 1985) and striped mice (*Rhabdomys pumilio*) (Schradin and Pilley 2004). Mammalian paternal care could increase female

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productivity and thus positively affect the male's reproductive success (West and Capellini 2016).

Wild and domestic horses, *Equus przewalskii* and *E. caballus* (Groves and Grubb 2011), naturally live in harems. The typical composition of a harem under natural conditions consists of a stallion, a group of mares and their immature offspring (Berger 1977; Klingel 1982; Waring 2003). Occasionally, multi-stallion harems may occur in free-living horses (Feh 1999; Linklater and Cameron 2000; Linklater et al. 2013). Further than reproduction, the stallion's presence in the herd has also other purposes. Stallions protect their harems from the attack of predators and they also prevent other males from mating with mares in the group (Berger 1986; Klingel 1982; Zimmermann et al. 2009). Moreover, the presence of the harem male and his reproductive behaviour reduces the agonistic interactions between mares, according to Granquist et al. (2012) and Kolter and Zimmermann (1988). As a result, the stallion maintains the long-term stability and integrity of his group, on which his reproductive success depends (Kaseda and Khalil 1996; Kolter and Zimmermann 1988; Waring 2003).

However, does this social system influence the development of the foals, and thus the fitness of the stallion? Unfortunately, the relationship between foals and stallions hasn't been thoroughly studied yet. One of the already recorded interactions between stallions and foals, is the occurrence of infanticide (Boyd 1991; Feh and Munkhtuya 2008; Gray et al. 2012; Zimmermann et al. 2009). However, this infanticidal behaviour brings no advantage for neither the stallion nor the mare: killing the foal does not make the oestrus cycle shorter (Feh and Munkhtuya 2008), and the mare avoids the aggressive stallion (Zimmermann et al. 2009). Berger (1977, 1983) and Bartoš et al. (2011) also described frequent abortions (probably to prevent the possibility of infanticide later) of pregnant mares in contact with an unfamiliar male. There are also positive interactions between the stallion and his offspring mentioned in the literature. Directly after the birth of the foal, together with the mare, the stallion controls the interest of other herd members in the new-born foal (Feh 1999, 2005). Another supportive behaviour of the stallion is mentioned in Boyd's works () on Przewalski's horses living in captivity: the stallion was often within the proximity of orphaned foals and shared food with them by chasing the mares away from the food source.

First signs of foal's social interactions with the stallion occurs within the second to third week of the foal's life, approximately. These interactions consist mostly of sniffing, licking and naso-nasal contact, mostly initiated by colts (Crowell-Davis et al. 1985; Crowell-Davis et al. 1987; Feh 2005; Tyler 1972; Wells and von Goldschmidt-Rothschild 1979). Allogrooming between the stallion and foals was observed only by a few authors (Boyd 1991; Crowell-Davis 1986a, b; Feh 2005). Usual foal-initiated behaviours are

snapping, and also tooth-clapping or champing (Haupt and Wolski 1980; Zeeb 1959). These behaviours are more often aimed at the stallion than towards the mares (Crowell-Davis et al. 1985; Pařízek et al. 1974; Tyler 1972; Waring 2003). These behaviours are thought to be a form of submission, but according to its broad behavioural context, Crowell-Davis et al. (1985) suggest that snapping could be a displacement activity caused by emotional excitement of the foal, and could be "triggered by conflict of desire to approach a possible mother and the fear from possibly unfriendly animal".

Play behaviours of the stallion and his offspring are described insufficiently within the current literature. Bökönyi (1974) and Zharkikh (2009) observed Przewalski's horses under captive and semi-feral conditions, and both authors suggested that the harem stallions didn't play with their foals and treated them with indifference in general. On the other hand, studies with different breeds and breeding conditions, showed that the play behaviour of foals was at least tolerated by stallions, and occasionally the male actively joined the playful interaction (Berger 1986; Crowell-Davis 1986a, b; Feh 2005; Kolter and Zimmermann 1988; Tyler 1972; Wells and von Goldschmidt-Rothschild 1979). Berger (1986) also mentions considerable preference of stallions for playing with their sons, but these interactions were recorded in a bachelor group, where the colts disperse at the age of 2–4 years (Waring 2003). In contrast to the stallion's play behaviour mentioned above, the mares tolerate the play interactions of their foal and mostly do not participate in them (Baker 2008; Sigurjónsdóttir et al. 2003; Tyler 1972; Wells and von Goldschmidt-Rothschild 1979; Zharkikh 2009).

The aim of this study was to establish a deeper understanding on the occurrence, frequency and characteristics of the social interactions between stallions and their foals, by comparing them with their interactions between other group members, like their mothers and other mares in the harem. Due to the evidence of the foal's interest in a stallion within the current literature, and also in their playful behaviour (previously noted), it was hypothesised that the stallion would be the favoured recipient of friendly and playful interactions of the foals, and that the foal would display more submissive signals such as snapping. Due to the higher attention of colts towards the stallion (Tyler 1972) and the need for acquiring physical and social skills for the role of a harem stallion (Crowell-Davis et al. 1987; Groves 1974), the sex of the foal should affect stallion–foal interactions. It is also expected that ontogenetic changes would occur in the foal's behaviour towards the adults (i.e. decreasing frequency of play behaviour).

Materials and methods

Location and animals

The study was conducted within two herds of Exmoor ponies, living under semi-feral conditions in two separate reserves (Milovice and Traviny) within the Czech Republic.

Herd Milovice: this herd is kept in an area of 40 hectares in size, within a former military range Milovice–Mladá. In the foaling season, 12 foals were born: nine colts and three fillies. The horses share the reserve with back-crossed aurochs (*Bos taurus*). The harem male (8 years old during observation period) has been used as a breeding stallion or lived in groups of geldings (intact males) and foals (Dickson 2017, personal communication).

Herd Traviny: horses of this herd are grazing in a locality of 120 hectares which belongs to the Benátky nad Jizerou municipality. In the observed breeding season, ten foals were born: six colts and four fillies. The area of the reserve is shared with European bison (*Bos bonasus bonasus*). Before transport to the Traviny herd, the male (9 years old during observation period) had lived in bachelor groups only, and this was his first experience as a breeding stallion (Matravers 2017, personal communication).

The composition of the herds is comparable: one harem stallion, 14 mares of different age (6–17 years) and primiparous or multiparous as well as their offspring; no other horses are present in the reserves. Both herds were established approximately 1 year before the observation period started. During the conducted research, it was the first breeding season after introducing the stallions into the established groups of mares. Except for three foals, paternity of the offspring was certain; all were sired by the harem stallion. Three mares were gravid before introducing the stallions, and their foals have different sires (one filly in the herd from Milovice and two colts in the herd from Traviny). Because these animals did not reach 2 years of age, which is considered as mature (Berger 1986; Tyler 1972; Waring 2003), they were also included from the analysis. For the respective groups' composition and parentage of the foals, see Supplementary file 1.

Human interventions in both reserves are kept as minimal as possible. Animals graze on pasture mainly consisting of dry grass (Jirků and Dostál 2015) and the only other food supplements provided are mineral blocks. Water is available ad libitum in artificial and natural water troughs.

Observation

Observations of the herds were conducted between 16th April and 2nd October 2016 for the herd Milovice, and

between 26th March and 10th September 2017 for the herd Traviny. The observations were managed regularly, at fortnightly intervals. One observation block lasted 14 h and was divided into 2 days and four sessions (10.00–14.00, 16.00–20.00 h and 8.00–12.00, 14.00–16.00 h). The observation time changed slightly in some instances, due to extreme environmental conditions. In total, 357 h were recorded (180 h in Milovice herd and 177 h in Traviny herd). Each herd was involved in 13 observation blocks.

Data were collected by the “all occurrence sampling method” (Altmann 1974), by one observer. Horses could be approached on foot and observed without binoculars from approx. 5–10 m distance, due to the habituation of the horses to the presence of the observer from previous projects. All animals were recognized individually by their differences in colour, size, and markings or by branding marks on adults.

Recorded interactions were divided into four categories—agonistic (head-threat, kick-threat, kick, bottom pushing, chasing, displacement), friendly (nose-nose contact, sniffing, nibbling/licking, grooming), playful (sexual, locomotive, play-fighting) and snapping, compiled according to Araba and Crowell-Davis (1994), Christensen et al. (2011), McDonnell (2003). For ethogram used see Supplementary file 2. Initiators and recipients of all interactions were recorded.

Statistical analyses

The full dataset was divided into different subsets according to the needs for statistical analyses: Interactions initiated by the foal ($n = 1629$); Interactions initiated by the foal and received by an adult ($n = 641$); Interactions initiated by the foal and received by a foal ($n = 988$); Interactions initiated by the adult and received by a foal ($n = 860$).

Histograms were built for initial inspection of the data, and normality tests were conducted (both Shapiro–Wilk and Kolmogorov–Smirnov test were used according to the sample size available for each variable). Differences in the occurrence of the studied behaviours initiated by the foal and directed towards the stallion, the mother or any mare in the herd were tested for significance using one-way ANOVA testing. Levene's test was conducted to check for homogeneity of variances, and Tukey's test was used for post-hoc analyses. Discrepancies from the expected frequency of each behaviour for the different initiators and different target groups were tested through Chi-square.

A set of Generalized Linear Mixed Models (GLMM) were designed to test the variation of the studied social interactions between each foal and adult ponies for the first year of life of the foals. Sex of the foal, age (in days), type of receiver (stallion, mother or other mare), and the interaction ‘age*receiver’ were entered into the models as independent variables. Similar models were created

to understand the variation in time of the interactions between foals. Sex of the foal starting the interaction, sex of the receiver foal, age of the initiating foal, and the interaction ‘age*receiver’ were used as independent variables. For the categorical variables, ‘filly’ and ‘mother’ were used as categories of reference. Group and identity of the initiator of the interaction were entered as random factors. Each model analysed the effects of these factors on the probability of occurrence for each studied behaviour; for interactions initiated by the foal, target variables were snapping, friendly, and playing; for interactions initiated by the adult, target variables were agonistic and friendly. Agonistic initiated by foal (directed both towards adults or foals), and snapping and playing initiated by the adult, were not modelled because of their very low occurrence. Binary response (binomial distribution with logit function) was used. Final models were selected after a traditional stepwise backward selection procedure.

The threshold for significance was always considered as $P < 0.05$. All analyses were performed in IBM® SPSS® Statistics (version 25.0 for Windows; IBM, USA).

Ethical statement

This research was strictly observational. Sampling frequencies with no direct contact with the animals were designed to reduce the stress experienced by the animals, according to the European and Czech laws and current guidelines for ethical use of animals in research (“Guidelines for the treatment of animals in behavioural research and teaching” 2018).

Results

Social interactions involving foals are not constant over time: foal-foal, foal-adult, and adult-foal interactions increased as the foals grew, reaching a maximum when foals were approximately two months old, and decreased thereafter (Fig. 1).

The apparent similarity of these patterns (independently of who is the initiator or receiver of the interaction) concealed the high variability. From the 1629 interactions initiated by a foal that were recorded, playing accounted 42.0% of the observations, friendly behaviour for 30.8%, snapping for 16.3% and agonistic behaviour for 10.9%. Of the 674 interactions initiated by an adult and directed to a foal, agonistic behaviour accounted for 87.1% of the observations, friendly behaviour for 11.3%, playing for 1.3% and snapping only for 0.1% (just one observation).

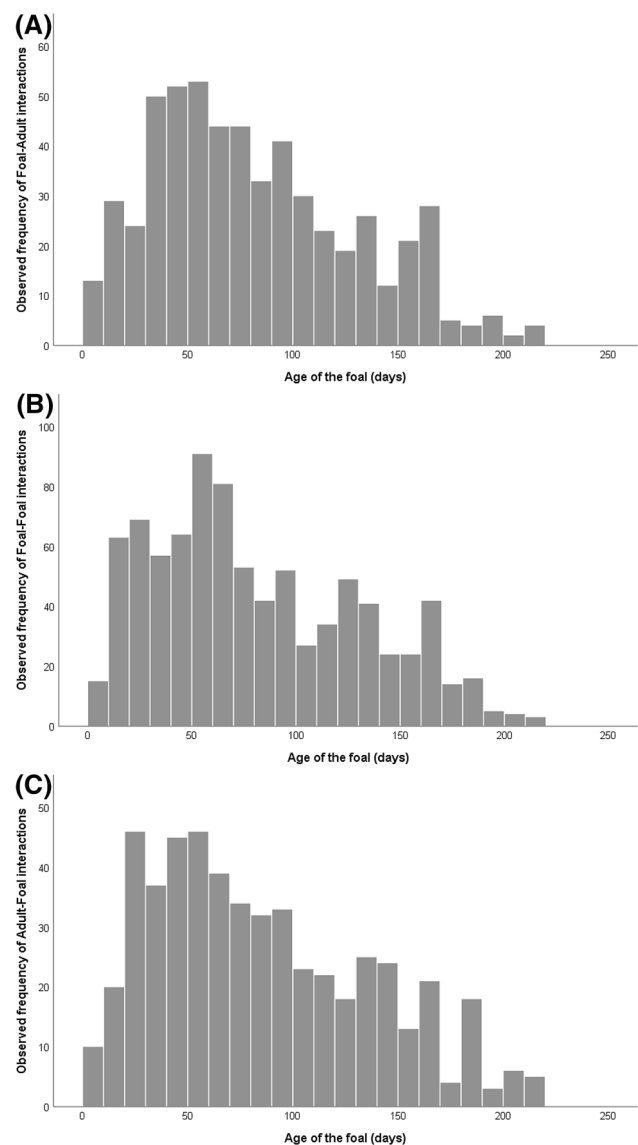
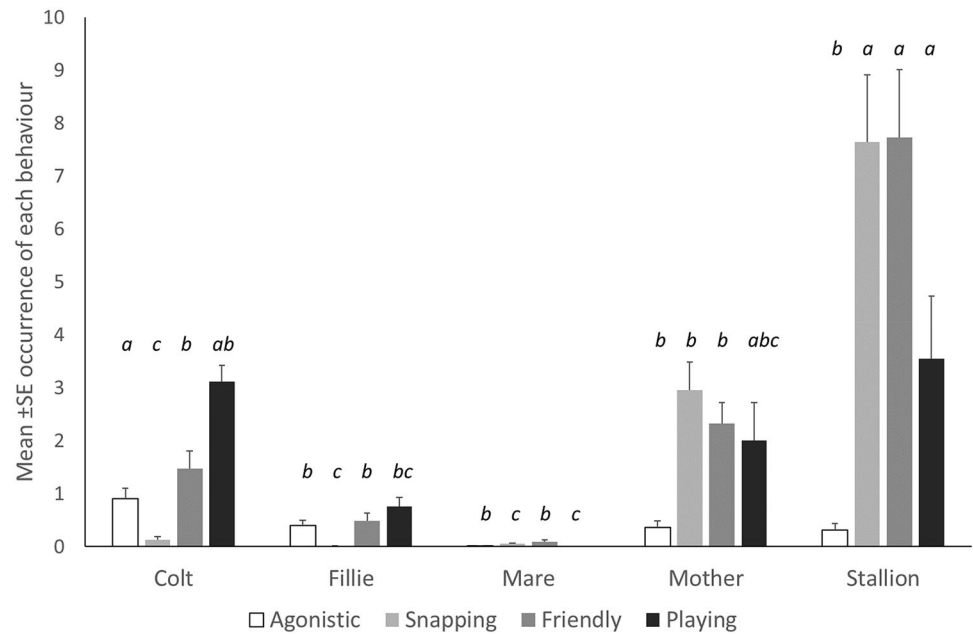


Fig. 1 Histograms showing the frequency of occurrence (total number of observations) of Foal–adult, Foal–foal, and Adult–foal interactions in ponies, within their first months of life

Behaviour of foals towards adults and other foals

The foals behave differently towards adults than towards other foals. According to the expectations after consideration of the observed ethogram (see Supplementary file 2), the foals direct more snapping to adults (38.9%) and friendly (38.9%) behaviours than expected, and less agonistic (10.9%) and playing behaviours (19.2%) ($\chi^2 = 332.597$, $P < 0.001$). Similar patterns were observed for the foal’s behaviour towards the stallion, mother and mares, individually (stallion: $\chi^2 = 243.477$, $P < 0.001$; mother: $\chi^2 = 67.486$, $P < 0.001$; mares: $\chi^2 = 40.229$, $P < 0.001$). Nevertheless, when foals initiate an interaction, the stallion is their

Fig. 2 Mean occurrence (number of observations) of each studied behaviour (agonistic, clap, friend, and play) directed by foals towards the colts, fillies, mares in the herd, the mother or the stallion. Superscripts indicate differences in the occurrence of each behaviour amongst the five types of potential receivers, after analysis using ANOVAs and Tukey's tests



favourite target for snapping ($F_{4,105} = 28.524$, $P < 0.001$), friendly ($F_{4,105} = 24.673$, $P < 0.001$), and playing behaviour ($F_{4,105} = 5.529$, $P < 0.001$). Only for agonistic behaviours, the favourite target is other foals (Fig. 2). Indeed, agonistic behaviour of foals towards adults is randomly targeted (i.e., not different to an expected 33% towards the stallion, the mother or another mare; $\chi^2 = 1.368$, $P = 0.504$), but higher than expected towards the stallion, and lower towards the mother and mares for snapping ($\chi^2 = 142.856$, $P < 0.001$), friendly ($\chi^2 = 138.104$, $P < 0.001$) and playing behaviours ($\chi^2 = 70.129$, $P < 0.001$). For illustrations of stallion–foal interactions, see Supplementary file 3.

A similar pattern was also supported by colts and fillies separately, with certain particularities. As observed previously, agonistic behaviour from foals towards adults was randomly targeted both for colts and fillies (colts: $\chi^2 = 0.400$, $P = 0.809$; fillies: $\chi^2 = 0$, $P = 1.000$), while snapping (colts: $\chi^2 = 102.408$, $P < 0.001$; fillies: $\chi^2 = 42.111$, $P < 0.001$) and friendly behaviours (colts: $\chi^2 = 122.755$, $P < 0.001$; fillies: $\chi^2 = 15.842$, $P < 0.001$) were higher than expected towards the stallion and lower towards the mother and mares. However, playing behaviour by colts is favoured towards the stallion, as expected towards the mother ($\chi^2 = 73.603$, $P < 0.001$), but negligible towards mares (only 1 observation). On the contrary, fillies do not play; only 4 observations were made, 2 targeted towards the mother, 2 towards a mare and none towards the stallion. This behaviour reflects a general greater shyness of fillies; each colt performed $1.75 \times$ agonistic, $1.70 \times$ snapping, $2.60 \times$ friendly and $18.81 \times$ greater playing behaviours towards adults than each filly. In addition, the behaviour of foals is different if the target is a colt or

a filly ($\chi^2 = 9.974$, $P = 0.019$); playing is favoured towards colts, while agonistic behaviour is preferred towards fillies. However, while colts behave rather similarly towards other colts than towards fillies ($\chi^2 = 6.480$, $P = 0.090$), fillies don't ($\chi^2 = 11.995$, $P = 0.007$); agonistic and friendly behaviour is favoured towards fillies, while snapping and playing behaviour is favoured towards colts.

Behaviour of adults towards foals

Compared to the ethogram shown at the beginning of the results, stallions, mother and mares behave differently towards the foals ($\chi^2 = 55.786$, $P < 0.001$). Mares and mothers perform agonistic behaviour towards foals more often than expected, while stallions exhibit a lower frequency (95.7%, 93.4%, and 78.3%, for mares, mother and stallion respectively). On the contrary, the stallion performs more friendly behaviours towards the foals than expected, while mares and mothers perform less (4.3%, 6.6%, and 18.1%). Even if extremely infrequent, it is remarkable that play behaviour was only initiated by stallions (0%, 0%, and 3.2%) and interestingly, all of them were directed towards colts.

The behaviour of adults is also different towards colts and fillies. Towards colts, the behaviour of adults is very similar to the pattern previously described ($\chi^2 = 43.265$, $P < 0.001$). With fillies, mares behave quite the same. Mother and stallion are less aggressive but more friendly (agonistic behaviour: 94.9%, 88.2%, and 71.2% for mare, mother and stallion respectively; friendly behaviour: 5.1%, 11.8%, and 28.8%; $\chi^2 = 12.046$, $P = 0.002$).

Ontogenetic changes in the foal–foal, foal–adult and adult–foal interactions

The interactions (and their variability) between foal–foal, foal–adult, and adult–foal within their first few months of life, were studied in detail using generalized linear mixed models for those behaviours exhibiting high enough frequencies to be included. After controlling for group, individual, sex of the foal and type of receiver within the model, the results confirmed that snapping, friendly and playing behaviour from a foal towards an adult changed with age of the foal in general, and/or linked to the type of adult (Table 1A). The probability of occurrence of snapping behaviour of the foal increased towards the stallion but decreased towards mother and mares (Fig. 3a). The probability of occurrence of friendly behaviour of the foal

increased towards males and mares but remains constant towards the mother (Fig. 3b). The probability of occurrence of playing behaviour increased for all categories of adults, but this increase shows a greater intensity towards the stallion (Fig. 3c).

Similarly, the probability of the most important behaviours initiated by the adults changed with foal age (Table 1B). The probability of occurrence of friendly behaviour decreased for the stallion and mares but remains constant for the mother (Fig. 4a). The probability of occurrence of agonistic behaviour increased for the stallion and mothers but decreased for the mare (Fig. 4b).

Between foals (Table 1c), friendly and playful behaviours decreased as the initiating foal got older, while agonistic behaviour increased (Fig. 5). Colts were significantly more playful with other foals than fillies but performed less friendly and agonistic interactions.

Table 1 Generalized linear mixed models showing the probability of occurrence of foal–adult, adult–foal and foal–foal interactions. Group and identity of the animal initiating the interaction were included as random variables

	Intercept	Sex of foal ^a	Receiver ^b	Age	Age*Receiver ^c
(A) Foal–adult interactions					
Snapping	$\beta = 0.213, P = 0.246$	Colt: $\beta = -0.420, P = 0.004$	Stallion: $\beta = -0.316, P = 0.066$	ns	Age*Stallion: $\beta = 0.002, P = 0.009$ Age*Mare: $\beta = -0.003, P = 0.024$
Friendly	$\beta = -0.838, P < 0.001$	ns	Stallion: $\beta = 0.605, P = 0.001$ Mare: $\beta = 0.639, P = 0.045$	$\beta = 0.004, P = 0.001$	Age*Stallion: $\beta = -0.004, P = 0.003$
Playing	$\beta = 1.150, P < 0.001$	Colt: $\beta = -0.936, P < 0.001$	ns	$\beta = 0.003, P < 0.001$	Age*Stallion: $\beta = 0.225, P = 0.091$ Age*Mare: $\beta = 1.078, P = 0.008$
(B) Adult–foal interactions					
Agonistic	$\beta = 0.559, P = 0.021$	Colt: $\beta = 0.458, P = 0.002$	Mare: $\beta = 0.979, P = 0.008$	$\beta = 0.005, P = 0.001$	Age*Stallion: $\beta = -0.003, P = 0.028$ Age*Mare: $\beta = -0.006, P = 0.002$
Friendly	$\beta = -1.055, P < 0.001$	ns	Stallion: $\beta = 0.558, P = 0.003$	$\beta = -0.002, P = 0.002$	Age*Mare: $\beta = 0.002, P = 0.048$
(C) Foal–foal interactions					
Agonistic	$\beta = -2.057, P < 0.001$	Colt: $\beta = -0.867, P < 0.001$	ns	$\beta = 0.012, P < 0.001$	Age*Colt: $\beta = -0.006, P < 0.001$
Friendly	$\beta = -0.093, P = 0.693$	Colt: $\beta = -0.876, P < 0.001$	ns	$\beta = -0.003, P < 0.001$	ns
Playing	$\beta = -0.281, P = 0.085$	Colt: $\beta = 1.194, P < 0.001$	ns	$\beta = -0.007, P < 0.001$	Age*Colt: $\beta = -0.005, P < 0.001$

Agonistic F-A, Snapping A-F, Playing A-F and Snapping F-F were not modelled because of low sample size

^aFillie as category of reference

^bMother as category of reference

^cAge*Mother and Age*Fillie as categories of reference

ns Not significant

Fig. 3 Probability of occurrence of **a** snapping, **b** friendly and **c** playing behaviour in foals during the first year of life. Solid lines indicate the interactions directed to the stallion; truncated lines indicate interactions directed to a mare; dotted lines indicate interactions directed to the mother

Discussion

The presented study is the first of its kind aimed solely at investigating the stallion–foal relationship in horses. The study focused on the comparison of foal–adult behaviour, the influence of the sex of the animals on their interactions, and the development of these interactions over time. The results clearly show that the stallion is the preferred adult recipient for snapping, friendly interactions and playful behaviour from the foals. The stallion is also the most tolerant adult compared with mares and the mothers of the foals, who in turn behave more aggressively to the young than the stallions do. Colts are generally more interested in the stallion, and the frequency of initiated interactions is much higher compared to that of the fillies towards the stallion. On the other hand, fillies are treated in a friendlier manner by adult horses than the colts. The relationship between foal and adults changes over time, with the peak of interaction frequency around the second month of the foal's life. The probability of occurrence of adult–foal interactions also changes over time, with different tendencies for the different initiators/receivers.

Foal–stallion relationship

The present results confirm the hypothesis that the stallion is the most frequent adult recipient of snapping, friendly and playful behaviour of the foals. The frequency of friendly behaviour of the foals correlates with the previous findings of the foal's interest towards stallions, mentioned in the introduction (Crowell-Davis 1986a, b; Crowell-Davis et al. 1985; Feh 2005; Tyler 1972; Wells and von Goldschmidt-Rothschild 1979). Interestingly, allogrooming between stallions and foals was not observed in the present research, unlike other studies (Boyd 1991; Crowell-Davis et al. 1986; Rho et al. 2007; Wells and von Goldschmidt-Rothschild 1979), probably because the foals had enough opportunities for allogrooming between their peers. Most of the friendly interactions observed in the present study consisted of investigative or greeting behaviours, including nose–nose contact, sniffing and licking, which corresponds with findings of Hoffman (1985) and Klingel (1974a).

Nevertheless, considering the greater aggressive behaviour of mares towards foals, and the stallion's higher tolerance in the present study (discussed below), the foal's preference for social bonding with the stallion is not surprising. The foal's interest might simply be a result of the stallion's

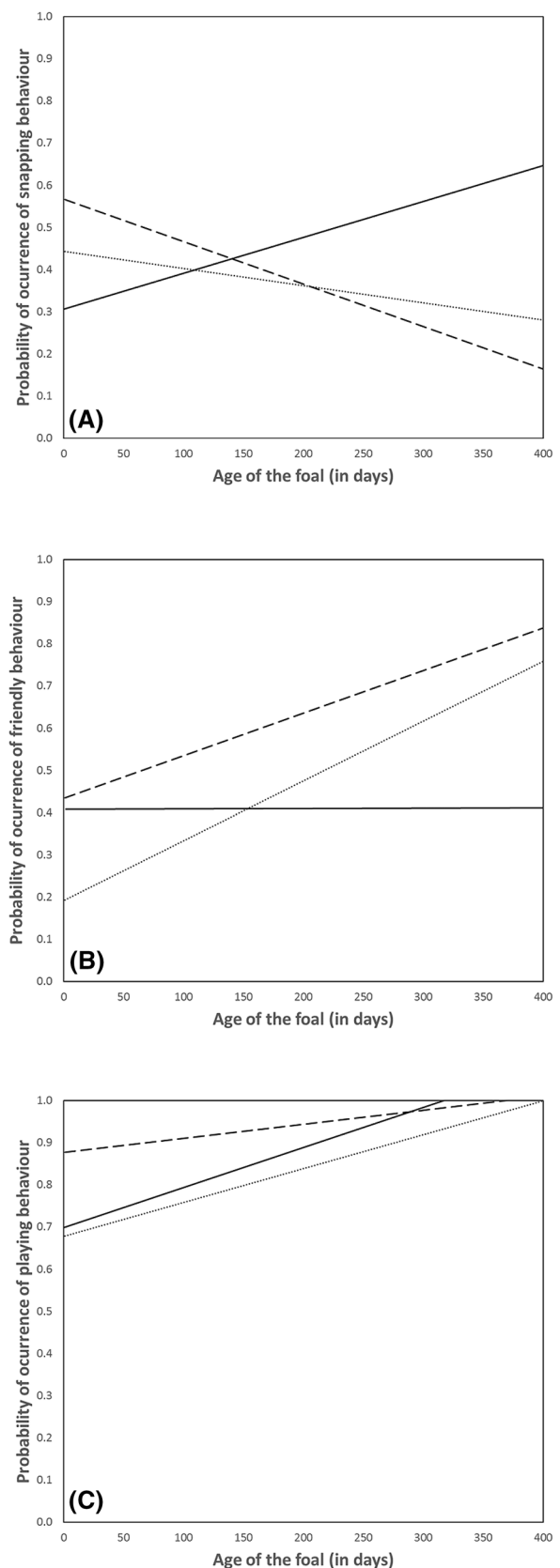


Fig. 4 Probability of performance of **a** friendly, and **b** agonistic behaviour from adults towards foals during the first year of life. Solid lines indicate interactions initiated by the stallion; truncated line indicates interactions initiated by a mare; dotted lines indicate interactions initiated by the mother

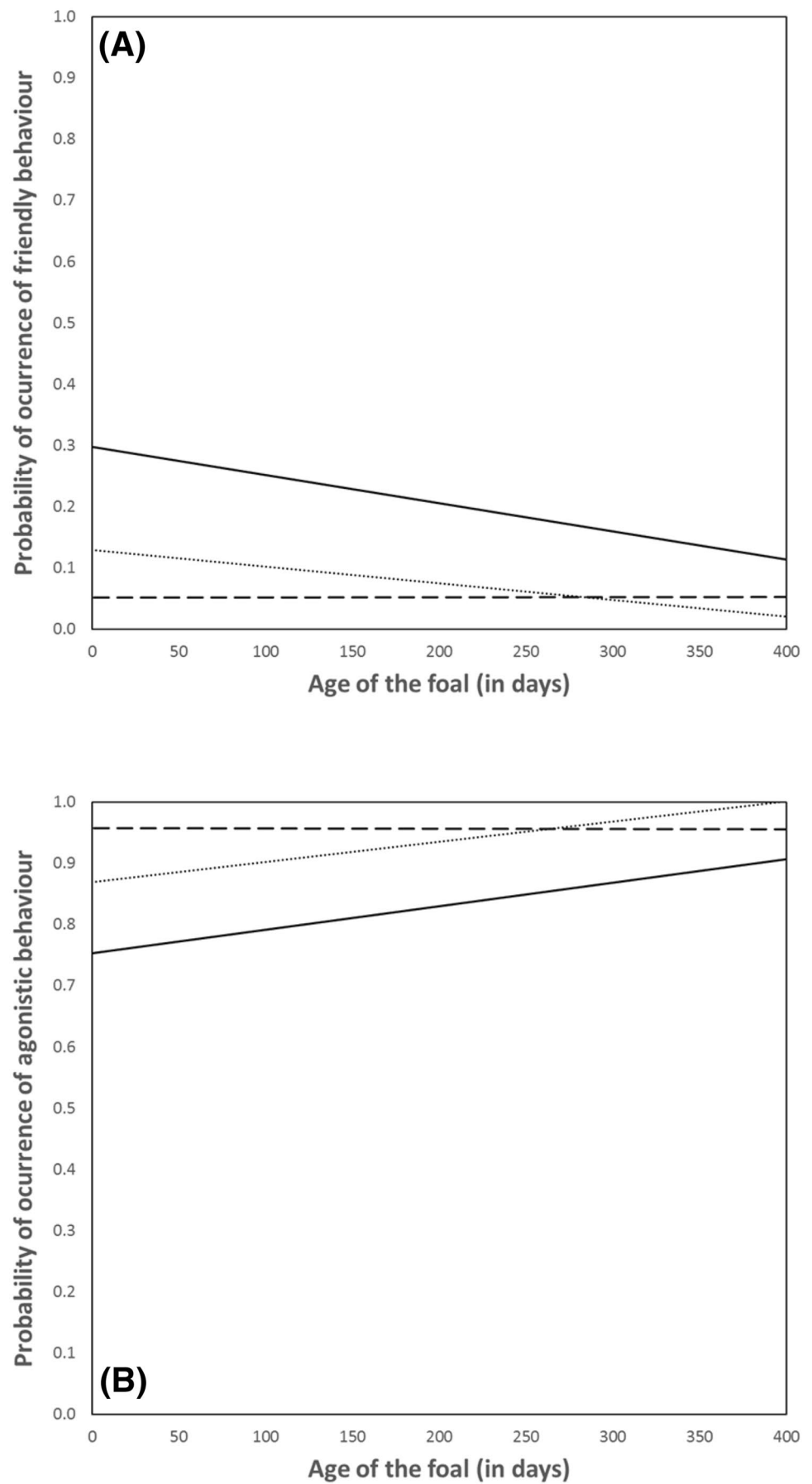
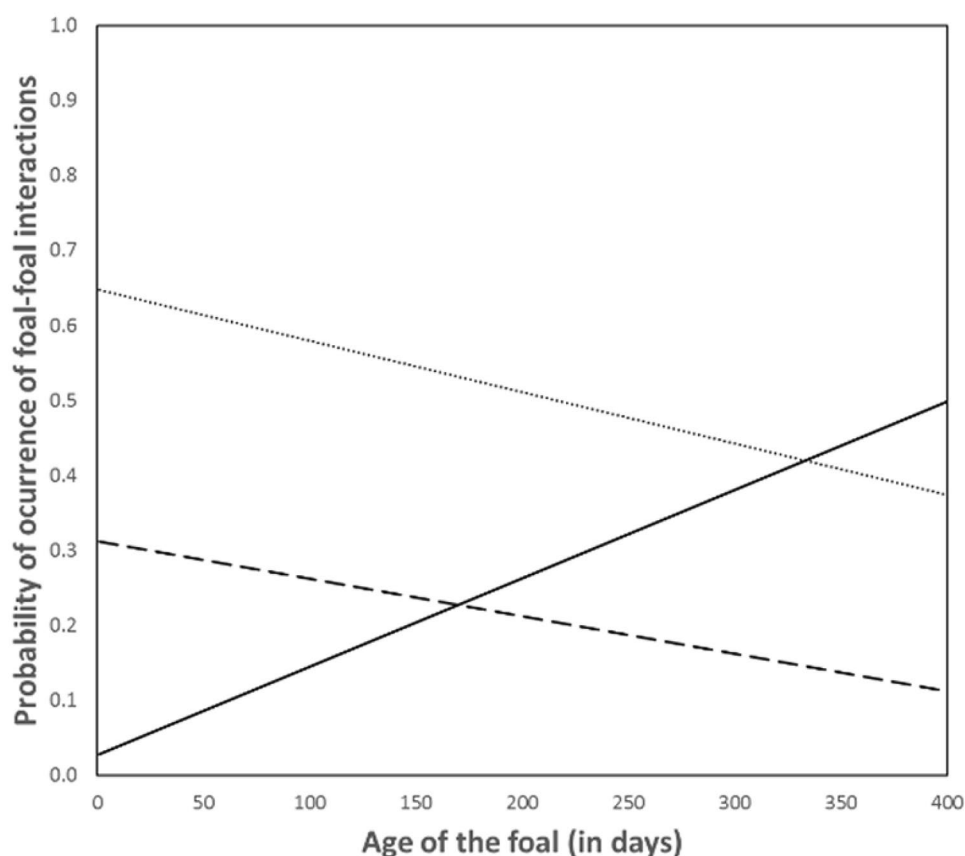


Fig. 5 Probability of occurrence of foal-foal agonistic (solid line), friendly (truncated line) and playing interactions (dotted line)



tolerance for their attempts to make a social contact, and the foals then only investigate the adult who allows them to.

Although the stallion is also the most frequent adult recipient of play behaviour, the most preferred partner for the foal's games are other foals, which is confirmed by Boyd (1991) and Crowell-Davis et al. (1987). Playing of the foal with the stallion could be explained by the theory of play as preparation for the unexpected (Held and Špinka 2011). In this theory, by playing with a bigger and stronger partner (the stallion) the foals have the opportunity to gain experience for unpredictable situations, and also to gain fighting skills for the colt's future lives (Crowell-Davis et al. 1987). Similar trends of the attraction of young to the adult male have been found in gorillas, where 2-year old animals prefer to spend their time in the proximity of high-ranking males (Rosenbaum et al. 2011). The age of these young primates could correspond well with the socialization period in foals (around 2–3 months) (Crowell-Davis 1986a, b). Both gorillas and foals are partially independent of their mother at this age, but they are still vulnerable to infanticide or predation, and, therefore, the presence of the male is advantageous for them (Rosenbaum et al. 2011).

High frequency of the foal's snapping towards stallion is mentioned quite regularly in literature (Crowell-Davis et al. 1985; Feist and McCullough 1976). During the

present study observation, snapping was connected to a wide variety of the stallion's (and other adult's) activities; for example, friendly interaction, proximity of an adult, or their reproductive behaviour, and was not connected strictly to the aggression or its prevention. This result is similar to work of Boyd (1988), Tyler (1972) and Wells and von Goldschmidt-Rothschild (1979). In this perspective, snapping could be considered a sign of high emotional excitation of a foal (Crowell-Davis et al. 1985; Tyler 1972) and not a submissive behaviour only (Feh 1990; Zeeb 1959).

As mentioned above, the reason for the foal's preference for the stallion could be a result of his tolerance of the foals' attempts to make social contact. This tolerance and occasional participation, or even initiating play, might be caused by the stallion's absence of maternal investment. Also, thanks to the lack of predation and competition in the study areas, the stallion can spend spared energy in the play with his offspring. This interpretation could be indirectly supported by results of other studies; active stallion–foal play was not recorded in free-roaming herds of Przewalski's horse (Christensen et al. 2002; Zharkikh 2009). It is probable that within such herds, the stallion must actively defend his harem against predation and other stallions. On the other hand, the play between stallion and foal was present mostly in herds living under semi-feral, domestic, or

captive conditions, where the defensive role of a stallion is not as essential (Crowell-Davis et al. 1987; Feh 2005; Kolter and Zimmermann 1988; Pařízek et al. 1974; Tyler 1972). An alternative explanation for the stallion's tolerance and active contact with foals could be the potential reproductive gain for the stallion. Harem males who are more affiliative towards their offspring could be more preferred by mares and thus more reproductively successful, as also found in primates and carnivores (Rosenbaum et al. 2018; West and Capellini 2016). The indirect evidence for this statement could be the avoidance of mares after infanticidal behaviour of the stallion (Feh and Munkhtuya 2008; Rubenstein 1986), but wider research under feral conditions are needed. Also, the higher attention of male paid towards the young could result in their better survival rates, similarly to common marmosets (Ziegler et al. 2017), but it is difficult to make conclusions with this sample size and within an area with no predation.

Foal–mother and foal–mares relationship

The foals perform more friendly behaviour towards their mothers than towards other mares, but less compared with the stallion. This result corresponds with the findings of Crowell-Davis (1986a, b) and Rho et al. (2007). The foals probably do not have to explore the mother as an unknown member of a group, and this friendly explorative behaviour might be replaced with nursing behaviour. Also, the play behaviour of foals towards their mothers is in lower frequency than towards the stallion, and active play of the mare with a foal was not recorded at all—mothers appear to simply withstand the games of their offspring. The unwillingness of adult mares to play was also described by Baker (2008), Sigurjónsdóttir et al. (2003), Tyler (1972) and Wells and von Goldschmidt-Rothschild (1979). The reluctance of mothers to play with their foals could also be the result of the transference of the play behaviour towards the stallion who is the only adult individual to actively participate in, or even initiate, play.

All recorded types of foal-initiated behaviours had the lowest frequency towards other mares. It is probable that mares are reluctant to invest any energy in other foals except their own, and that another foal's attempts are thus refused with agonistic behaviour. It is also possible that agonistic interactions of the mares are influenced by dominance rank (Weeks et al. 2000), which the analysis thereof was not included within this study.

Behaviour according to sex of the foal

The most significant difference between the sexes of the foals was their social activity; colts are considerably more

active in initiating interactions with the stallion and other herd members (Cameron et al. 2008; Crowell-Davis et al. 1987). Higher sociability of the colts indicates the importance of the early onset of their social behaviour for their future life, especially during setting and maintaining of their own harem (Rho et al. 2007). This could be parallel with the paternal influence observed in California mice pups, where higher paternal care resulted in higher territorial aggression in the offspring (Frazier et al. 2006). Higher sociability of young males has also been reported in premature bulls (*Bos indicus*) (Reinhardt et al. 1978).

Generally, adult horses behave in a friendlier manner towards fillies, than they do towards the colts. The aggression rate of mares in the present study is similar to that of Camargue horses, where the mares showed more aggression to non-related foals and young males (Wells and von Goldschmidt-Rothschild 1979). A similar trend was found in vervet monkeys (*Chlorocebus pygerythrus*), where mothers associated with and groomed their daughters more (Fairbanks and McGuire 1985). One explanation of such difference can be the parent–offspring conflict (Trivers and Willard 1973); sons of mares in good condition get more maternal care than fillies (Cameron and Linklater 2000) and that is why the mares are not willing to invest any other energy into the (un)related colts. The second possibility is the preference of mares to spend time with the sex that is likely to be a potential future ally (Pereira 1988); in horses, the daughters can serve as “aunts” for their siblings (Kolter and Zimmermann 1988).

Fillies never initiated play with the stallion in the present study. The difference in play behaviour of colts and fillies was also observed in the works of other authors; although, these studies were focused on play behaviour within a group of foals (Boyd 1988; Cameron et al. 2008; Crowell-Davis 1986a, b). However, the involvement in playful behaviour could have been affected by maternal investment and condition (Cameron et al. 2008). The higher interest of colts to play with the stallion was reported only by Crowell-Davis et al. (1987).

Snapping and friendly behaviour of foals towards adults is not influenced by the sex of the initiator. It is possible that the absent sex influence in friendly behaviour is related to the relatively small sample size of the analysed data; although, the same result was obtained in Camargue horses (Wells and von Goldschmidt-Rothschild 1979) and in gorillas (Rosenbaum et al. 2011). In contrast with the current results, literature indicates that snapping is mostly or exclusively performed by colts (Crowell-Davis et al. 1985; Feist and McCullough 1976; Wells and von Goldschmidt-Rothschild 1979; Zeeb 1959) but considering the higher sociability of the colts, this result could have also been affected by small sample size.

Time changes in adult–foal relationship

Frequencies of all types of the foal's behaviours changed over time. After the birth of the foal, the time frequency of interactions grows quite steeply, with the peak at around the second month of age. After this stage, the rate of interactions slowly decreases (Boyd 1988; Crowell-Davis et al. 1985; 1987; Tyler 1972; Waring 2003). The foal's behavioural development can be classified into three stages (Crowell-Davis 1986a, b; Tyler 1972). Initially, the low frequencies of interactions correspond with the foal's dependence on its mother. Then, the peak of the interaction frequency coincides with the main socialization period of the foals. Lastly, the interaction rate slowly decreases as the foal gains adult behavioural patterns. The third stage of development of foal's behaviour explains why the probability of a particular behaviour increases, but its frequency decreases in time. Considering the three-stage social development and the probability of friendly behaviour of mothers and stallion towards foals, this probability of occurrence of friendly behaviour decreases, whilst concurrently, the probability of occurrence of agonistic behaviour increases. On the contrary, in mares, the trend is slightly reverse. It is possible, that the foal is primarily socialized by its parents with more attention paid to the stallion, and subsequently, they develop advanced social skills through interacting with other adult herd members.

Conclusion

Within this study, the first complex research about the father–offspring relationship in equids is presented. The results demonstrate the foal's preference to socially interact with the stallion over other mares and even their mothers. In contrast with mares and mothers of the foal, who treated the young more aggressively, the harem male showed more tolerance towards the foals. The stallion is also the only adult individual who actively played with his offspring, preferentially with the colts, who are significantly more attracted to the male and are also more socially active in general than fillies. Through play behaviour and mild aggression towards colts, the harem male could pose as an important social model.

Nevertheless, results based on observation of two males interacting with their offspring could have been influenced by their different life history and previous experiences or personalities. Thus, further studies and comparison with herds without stallions are needed, as well as using other equids. This study may change the perception towards stallions in domestic breeding and zoological facilities, as often the stallions are isolated from the herd and their offspring, which can lead to social stress and reproductive disorders.

Keeping the stallion within the herd of mares and foals could help the colts become dominant males, who behave appropriately within the herd and are competitively strong. These features are crucial, especially in free-roaming equids, within reintroduction and rewilding projects.

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Author contributions KS and MK designed the study, KS carried out the observations and wrote the manuscript with support from MK and FC. FC processed the experimental data and performed the analysis.

Availability of data and material The data generated during this study are available from the corresponding author, upon reasonable request.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

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