SHORT COMMUNICATION



Novel observation of play behaviour between a harem holder and a bachelor group of Przewalski's horses in the wild

Anna Bernátková¹ · Francisco Ceacero¹ · Ganbaatar Oyunsaikhan² · Dalaitseren Sukhbaatar² · Jaroslav Šimek³ · Martina Komárková¹

Received: 19 October 2022 / Revised: 28 March 2023 / Accepted: 23 April 2023 © The Author(s) 2023

Abstract

Przewalski's horses live in stable nonterritorial families (harem) of one or more harem stallions, several mares, and their offspring. The harem stallion typically behaves aggressively towards any male intruder approaching the harem. Play behaviour is frequently observed among the group members in horses. For stallions, the most common, well-known cases of play behaviour are found between members of bachelor groups (groups of young stallions) and between the harem stallion and his offspring. The play between the harem stallion and members of the bachelor groups is, on the other hand, seemingly much rarer as a description of such events in the literature is anecdotal. In this note, we present our observation conducted in the Great Gobi B Strictly Protected Area (Mongolia) and describe the play behaviour between a Przewalski's horse harem stallion and members of a bachelor group. The observation was done as a part of broader research during which selected Przewalski's horses' groups were located by binoculars in daily monitoring routines and filmed from a close distance (from 150 to 800 m). Behavioural Observation Research Interactive Software (BORIS) was used to extract data from the video recordings. The observation described in this note lasted for ~ 180 min, during which the horses engaged in three separate bouts of play and repeated inter-group association. During the whole study (241.5 h of video recordings), this was the only observation including inter-group interactions. We observed two other events during which two harems approached each other (but never merged). Our observation is the first video recording of such an event and raises the question of how prevalent this behaviour is in the Przewalski's horses' restored natural populations. We conclude that this behaviour is unusual or has not been sufficiently studied in wild or feral harems. Further technological advances may help reveal more information on this topic.

Keywords Equus ferus przewalskii · Gobi · Stallion · Social behaviour · Mongolia

Introduction

Since the earliest systematic studies of behaviour, the subject of why animals play has been a topic of discussion (Darwin 1871; Groos 1911). Play is mainly perceived as a tool by which young animals acquire skills (e.g. fighting, mating, social behaviour) necessary for their adult life (Martin and Caro

1985; Paquette 1994). However, the fact that play is observed in many species after sexual maturity suggests that it may be relevant for animals throughout their lifetime (Asensio et al. 2022; Beckel 1991; Bond and Diamond 2003).

Adult-only social play is typically observed among group mates and is mainly described as a mechanism for fostering social networks and encouraging collaboration among individuals. Adult play may provide a social bonding purpose similar to grooming, allowing animals to socialise. In other words, it enables animals to create and sustain social connections as well as restrain anger, lower tension, and enhance tolerance under challenging situations (Baldwin and Baldwin 1973; Enomoto 1990; Ferguson and Frankis 2001; Martin and Caro 1985; Merrick 1977; Norscia and Palagi 2011; Palagi et al. 2006).

Published online: 10 May 2023



Francisco Ceacero ceacero@ftz.czu.cz

Faculty of Tropical AgriSciences, Czech University of Life Sciences Prague, Prague, Czech Republic

² Great Gobi B Strictly Protected Area, Takhin Tal, Mongolia

Zoo Praha, U Trojského Zámku 120/3, Prague, Czech Republic

In horses, play is most common and noticeable in foals and yearlings, although it also occurs in adult individuals (McDonnell and Poulin 2002). Play is also frequently observed among the members of the horse bachelor groups (Feh 2005), including Przewalski's horses (Christensen et al. 2002). Play behaviour is believed to be essential in developing specific social skills (e.g. fighting) in young males compared to young females (Crowell-Davis et al. 1987; Rho et al. 2007). Indeed, it has been observed that colts (male foals) interact more actively with the harem stallion (their father) than fillies (female foals; Crowell-Davis et al. 1987; Šandlová et al. 2020). However, in adult stallions with their harem, observations of play with other mature stallions are very scarce (Berger 1986; McDonnell and Poulin 2002).

Przewalski's horses (*Equus ferus przewalskii*) live in stable, nonterritorial family units called harems (Bourjade et al. 2009) and exhibit female defence polygyny. The harems consist of one or more harem stallions (males), several mares (females), and their young progeny (King et al. 2015; Rubenstein 2011). When a colt or filly reaches reproductive age, typically between the ages of one and four, they separate from their family. While colts usually join a bachelor group until they can form their own harem, fillies typically join another stable family unit (Bahloul et al. 2001; Boyd and Bandi 2002; International Takhi Group 2021; King et al. 2015). Mature stallions form a new harem by taking over an existing harem or joining females dispersed from other harems. These stallions become harem holders and protect the mares and their offspring from other stallions and predators (Boyd et al. 2016). To guard the harem successfully, the stallion typically stays more vigilant, feeds less, moves more, and shows less behavioural synchrony than other harem members (King et al. 2016; Souris et al. 2007). As mares are generally protected from stallion harassment by the group structure, they are often in better condition, and their reproductive success is higher than in mares not bonded to a breeding group (Linklater et al. 1999). It was also hypothesised that affiliative interactions between mares and other mares or stallions might boost reproductive success by minimising harassment (Cameron et al. 2009; Linklater et al. 1999). Cases of two or more stallions defending the same harem have been reported (Linklater et al. 2013). Previously, it was suggested that these stallion alliances improve the ability of stallions to defend their mutual family group from other stallions (Boyd et al. 2016) and might increase the foal survival rate in their group (Feh 1999). However, removal experiments showed that the cooperative hypotheses do not appear to explain the existence of multi-stallion groups (Linklater et al. 2013).

It has been described that in free-roaming populations of horses, most stallions know each other and their relative fighting ability (Rubenstein and Hack 1992), and most encounters result in ritualised behaviours (Sigurjonsdottir et al. 2012). In this note, we provide a recording and description of the play behaviour between Przewalski's horse harem

stallion and members of a bachelor group in the Great Gobi B Strictly Protected Area (Mongolia) to raise the question of how prevalent and important this behaviour is in the Przewalski's horses' restored natural populations and to encourage future research on this topic.

Methods and results

This observation was conducted in July 2018 in the Great Gobi B Strictly Protected Area (GGBSPA), Mongolia, during broader research fieldwork (July 2018, May–June 2019, and September–October 2019) focusing on the behavioural ecology of Przewalski's horses. In the summer of 2018, two wild-born harems involving 21 adult horses were recorded. In spring 2019, three groups were recorded (two wild-born harems and one harem consisting of long-term reintroduced mares and a wild-born stallion) involving 25 adult horses. In autumn 2019, four groups were recorded (two wild-born harems and two harems consisting of long-term reintroduced mares and wild-born stallions) involving 27 adult horses (Bernátková et al. 2022).

During the whole study (241.5 h of recordings), we observed only one inter-group interaction (the one described in this short note). Once, two harems were observed feeding close to each other (~ 50 m) but never merged or interacted (one of these harems was Tsetsen, the one also involved in the observation described here). Two harems approaching each other (neither of which was Tsetsen) were also observed just once, but both groups stopped ~ 300 m from each other except for the harem stallions, who kept approaching each other, stopped ~ 50 m from each other, and returned to their group.

The GGBSPA, in SW Mongolia, is a reintroduction site for Przewalski's horse and an important refuge for several other endangered species (International Takhi Group 2021; Kaczensky et al. 2008, 2011). Since 2019, it has encompassed ≈18 000 km² of desert steppe and desert habitat (≈9 000 km² before the enlargement, International Takhi Group 2021). At the time of the research, there were 349 Przewalski's horses in 24 harems and 3–5 bachelor groups. The structure and number of the bachelor groups change frequently. During this research, the GGBSPA population comprised a maximum of 200 females and 149 males (GGB-SPA administration, personal communication). Fieldwork consisted of locating Przewalski's horses' groups with binoculars during daily monitoring routines. Once one of the target groups was localised, it was approached and filmed from a close distance without disturbing them (from 150 to 800 m) by a 4 K Panasonic VX1 video camera with a tripod. The ethogram consisting of 5 categories (feeding, locomotion, resting, social, and other) was used to categorise observed behaviours. Play behaviour was included in



the social category (Bernátková et al. 2022). Behavioural Observation Research Interactive Software (BORIS) was used for event logging, coding, and observation of the captured videos (Friard and Gamba 2016).

Play between harem stallions and members of bachelor groups has never been observed in the population of the GGBSPA (GGBSPA administration, personal communication). While observing one of the selected groups (a wild-born harem called Tsetsen harem), we noticed the nonagonistic social behaviour of the harem stallion towards a bachelor group which approached his harem. The Tsetsen harem consisted of 8 individuals: 1 harem stallion (Tsetsen, 7-year-old), three adult mares (2-, 5-, and 6-year-old), 2 2-year-old males, 1 1-year-old male, and 1 1-year-old female. The GGBSPA administration confirmed that none of the mares was in oestrus during the observation. Tsetsen was a harem holder for the first time in his life, and the harem was relatively new (it was formed just two months before our observation). All the breeding mares remained there until our following fieldwork one year later. Tsetsen established his harem by taking over half of the mares from his father's harem, in which all the mares of our study had been together since 2016. The bachelor group consisted of 5 stallions of various ages (3 3-year-old stallions, one 4-year-old stallion, and one 7-year-old stallion). The GGBSPA administration confirmed that the two oldest bachelor stallions were cousins (their mothers were sisters) of Tsetsen and had previously been together with Tsetsen in a bachelor group. However, each of these stallions had been born into a different harem (GGBSPA administration, personal communication).

The observation started on 18.07.2018 at 11.29; there were no water points or prime forage areas at a close distance (at least 5 km from the observation point). Two other harems were observed from our position (~ 1 km from the observation point). No interaction between them and the Tsetsen harem or between them and the bachelor group was observed. At the beginning of the observation, all members of the Tsetsen harem were resting. The bachelor group started approaching the Tsetsen harem and stopped relatively close to the Tsetsen harem (~ 40 m). Members of the Tsetsen harem became alert, looking toward the approaching bachelor group. After approximately 30 s, the harem stallion Tsetsen moved a bit forward (~ 5 m) in front of his harem in the direction of the bachelor group, standing in an alert position facing the bachelors. All the other members of the Tsetsen harem stood close to each other in a relaxed position, and none seemed to be alert anymore. After approximately 1 min, Tsetsen started running towards the bachelors, joined them, and the horses started to investigate each other mutually. The rest of Tsetsen's harem remained resting, paying almost no interest in the interactions between Tsetsen and the bachelors (video 1). After approximately 1 min, Tsetsen returned to his harem, and both groups stood approximately 20 m from each other. Eighteen minutes after our observation started, Tsetsen joined the bachelor group again. We observed mutual investigation and play behaviour (muzzle sniffing, slight rearing, head resting) between him and the stallions of the bachelor group. No direct aggression was observed (video 2). Twenty minutes after our observation started, one 2-year-old stallion from the Tsetsen harem approached the bachelor group and Tsetsen. The rest of the harem followed him. Both groups merged momentarily, but after a few mutual aggressive encounters started by the harem mares (kick threats, kicking), they split. At this moment, Tsetsen herded his harem and then chased the bachelors away. However, 25 min after the start of our observation, the Tsetsen harem and bachelor group merged again, and no aggressive behaviour, herding, or any other behaviour aiming to prevent this from the Tsetsen side was observed this time (video 3). We observed both groups merging and splitting away multiple times. During these events, Tsetsen mostly remained closer to the bachelor group than to his harem. The 2-year-old stallion from the Tsetsen harem was also observed joining the bachelor group and Tsetsen in the mutual investigation and play behaviour (video 4). Approximately 50 min after the start of our observation, the oldest mare of the Tsetsen harem led the harem away from the bachelors. Tsetsen followed his harem; however, he stopped in the middle between his harem and the bachelor group when his harem stopped. The 2-year-old stallion from the Tsetsen harem did not follow the harem but remained with the bachelor group and rested with them while the Tsetsen harem returned to Tsetsen. Afterwards, both groups (Tsetsen with his harem and the bachelor group with the 2-year-old stallion) rested approximately 80 m apart. Approximately 95 min after the start of our observation, the bachelor group with the 2-year-old stallion from the Tsetsen harem started running towards the Tsetsen harem. At first, Tsetsen tried to chase the bachelors away from his harem and the 2-year-old stallion, but after a moment, he stopped, showed no more aggression, and moved back towards his harem, followed by the 2-year-old stallion from his harem and the bachelors. Both groups merged again. When the groups split (~ 10-15 m apart), Tsetsen remained with the bachelors, and the 2-year-old stallion remained with the Tsetsen harem. Again, play behaviour was performed (nipping, slight rearing) between Tsetsen and three members of the bachelor group (video 5). Approximately 104 min after the start of our observation, the 2-year-old stallion from the Tsetsen harem moved towards the bachelor group (and Tsetsen). He was followed by the Tsetsen harem, except for the oldest mare and her 1-year-old daughter. Both groups merged again, and we observed aggressive mutual encounters between the mares of the Tsetsen harem and the members of the bachelor group, started by a kick from the 2-year-old mare from the Tsetsen harem towards the centre of the merged groups.

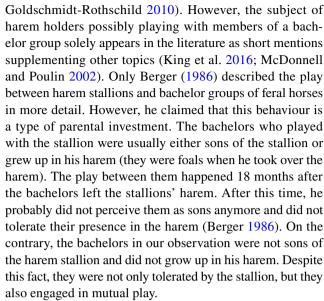


This lasted approximately 1 min, and all the members of the Tsetsen harem moved back to join the oldest mare and her daughter, except for Tsetsen. He was standing with the bachelors, pawing the ground. Afterwards, he started moving towards his harem and again stopped between the two groups (video 6). Both groups merged again after Tsetsen started moving back towards the bachelor groups (~ 108 min after the start of our observation) and was followed by his harem (video 7). After approximately 3 min, Tsetsen herded his harem to make the harem move a bit far from the bachelor group (~ 5 m). One of the adult mares kicked Tsetsen (video 8), the whole Tsetsen harem moved towards the bachelor group, and both groups merged again, with no more aggression observed (video 9). Approximately 114 min after the start of our observation, the oldest mare of the Tsetsen harem started leading the whole harem away from the bachelors. The Tsetsen harem stopped approximately 20 m from the bachelor groups. We observed both groups standing and resting. Approximately 118 min after the start of our observation, two members of the bachelor group started to walk away slowly. In contrast, the rest of the bachelor group (3 horses) remained. Both groups were resting apart from each other (~ 20–30 m), and no more interactions were observed between the two groups (video 10). We remained in the place until all the members of the bachelor group left the area and went out of sight (~ 180 min after the start of our observation). No more interactions between the Tsetsen harem and the bachelor groups were observed by us or by the rangers after this event.

As a context for this observation, we observed 429 play interactions among 9 harems during the entire study period, and just 22 of them (5%) involved the harem holder stallion. Three of the 9 harems were composed exclusively of the harem holder and mares (no other stallions were in the harem). The 6 other harems that included other stallions further than the harem holder displayed 274 play behaviours, 11 of them (4%) involving the harem holder stallion, and just one play interaction was observed involving the harem holder (not Tsetsen) and another stallion at the harem.

Discussion

This appears to be the first evidence showing the harem stallion (Przewalski's horse harem holder) tolerating his group to "spend time" with a group of bachelors and playing himself with the bachelor stallions. Numerous studies describing the play behaviour of young males and members of bachelor groups have been published (e.g. Christensen et al. 2002; McDonnell and Haviland 1995; Zharkikh and Andersen 2009). The presence and importance of play between the harem stallion and his foals have also been emphasised (Feh 2005; Šandlová et al. 2020; Wells and



We observed a young stallion (7 years old) who became a harem holder for the first time in his life. Tsetsen established his harem by taking over half of the mares from his father's harem. One year after the described observation (in 2019), we recorded that one 3-year-old stallion in the Tsetsen harem (the then 2-year-old described interacting with the bachelor group) was repeatedly mating with mares of the harem (i.e. both Tsetsen and this stallion were mating with the mares during this breeding season). Thus, we conclude that those two stallions formed an alliance that year (Boyd et al. 2016).

The harem stallion Tsetsen was probably not the father of any of the foals in the GGBSPA at the time of our observation (GGBSPA administration, personal communication). Therefore, we conclude that the play behaviour between him and the bachelor stallions should not be attributed to parental investment, as suggested by Berger (1986). However, it is important to state that due to the population's size and type (wild horses) and the area, the reproduction records of the GGBSPA are based on direct observations (GGBSPA administration, personal communication). Berger (1986) also described that familiarity, not the actual genetic relatedness, is the probable cause of harem stallion tolerance and play behaviour with bachelors. It has been proven that horses have a good memory (Hanggi and Ingersoll 2009; Lansade et al. 2020) and that familiarity, not relatedness, is the main factor in social relations between adult horses (Mendonça et al. 2021). Bachelor groups are generally less stable, and both intra- and inter-group play behaviours are prevalent (Feh 2005; King et al. 2016, 2022; McDonnell and Poulin 2002; Zharkikh and Andersen 2009). The GGBSPA administration confirmed that Tsetsen was in the same bachelor group as the two oldest stallions from the bachelor group, so they know each other very well. Therefore, he might have been able to assess their fighting ability (Rubenstein and Hack 1992) and not perceive them as competitors (Rubenstein 1994). He probably also knew the



other three stallions from the bachelor groups as in feral and wild horse populations; all the bachelors typically know each other (Feh 2005; Rubenstein and Hack 1992; Sigurjonsdottir et al. 2012).

Furthermore, no sexual behaviour was observed between the members of the bachelor group and the harem mares, and the aggressive behaviours between them were most probably caused solely by the increased proximity. For this reason, Tsetsen could use this opportunity to maintain social bonds with members of the bachelor group and possibly also to practice and improve his fighting skills, as frequently observed in bachelor groups (King et al. 2016, 2022; McDonnell and Poulin 2002; Zharkikh and Andersen 2009). Another reason for Tsetsen's tolerance and "friendliness" might be that he was an inexperienced harem holder (Boyd et al. 2016) and had limited control over his harem (Linklater et al. 2013), as he seemingly formed an alliance with a 3-year-old stallion (his half-brother) from his harem 1 year after this observation was conducted (Boyd et al. 2016).

In summary, our observation appears to be the first video record of a harem holder playing with sexually mature bachelors and tolerating their presence close to his harem. Although play behaviour is generally characteristic of immature animals, its presence in adults has also been revealed, and many of its functions are probably yet to be discovered. Our observation raises the question of how common this behaviour is in the reestablished natural populations of Przewalski's horses. Short events are challenging to monitor in the wild, but the development of technology (e.g. unmanned aerial vehicles; Schad and Fischer 2022) may help reveal the extent to which play between adult stallions occurs and its importance in inter-group relationships. The new technology might be beneficial in vast areas with large populations of wild horses, where most of the groups are too suspicious of human presence to be observed in person, such as the population in the GGBSPA or populations of free-roaming horses in Australia and the USA.

Acknowledgements We appreciate the permission to conduct our research and the support during the fieldwork by the management of the GGBSPA. The study was partially funded by the Faculty of Tropical AgriSciences (IGA-20223107), Prague Zoo, and Nadace "Nadání Josefa, Marie a Zdeňky Hlávkových".

Funding Open access publishing supported by the National Technical Library in Prague.

Declarations

Conflict of interest The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in

the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

- Asensio N, Zandonà E, Dunn JC, Cristóbal-Azkarate J (2022) Socioecological correlates of social play in adult mantled howler monkeys. Anim Behav 186:219–229. https://doi.org/10.1016/j.anbehav.2022.01.017
- Bahloul K, Pereladova OB, Soldatova N, Fisenko G, Sidorenko E, Sempéré AJ (2001) Social organisation and dispersion of introduced kulans (*Equus hemionus kulan*) and Przewalski horses (*Equus przewalski*) in the Bukhara reserve. Uzbekistan Journal of Arid Environments 47(3):309–323. https://doi.org/10.1006/JARE.2000.0714
- Baldwin JD, Baldwin JI (1973) The role of play in social organisation: comparative observations on squirrel monkeys (Saimiri). Primates 14(4):369–381. https://doi.org/10.1007/BF01731358
- Beckel AL (1991) Wrestling play in adult river otters, *Lutra canadensis*. J Mammal 72(2):386–390. https://doi.org/10.2307/1382111
- Berger J (1986) Wild horses of the Great Basin: social competition and population size. University of Chicago Press
- Bernátková A, Oyunsaikhan G, Šimek J, Komárková M, Bobek M, Ceacero F (2022) Influence of weather on the behaviour of reintroduced Przewalski's horses in the Great Gobi B Strictly Protected Area (Mongolia): implications for conservation. BMC Zoology 7(1):32. https://doi.org/10.1186/s40850-022-00130-z
- Bond A, Diamond J (2003) A comparative analysis of social play in birds. Behaviour 140(8–9):1091–1115. https://doi.org/10.1163/156853903322589650
- Bourjade M, Thierry B, Maumy M, Petit O (2009) Decision-making in Przewalski horses (Equus ferus przewalskii) is driven by the ecological contexts of collective movements. Ethology 115(4):321–330
- Boyd L, Bandi N (2002) Reintroduction of takhi, *Equus ferus przewalskii*, to Hustai National Park, Mongolia: time budget and synchrony of activity pre- and post-release. Appl Anim Behav Sci 78(2–4):87–102. https://doi.org/10.1016/S0168-1591(02)00088-6
- Boyd LE, Scorolli A, Nowzari H, Bouskila A (2016) Social organisation of wild equids. In J. I. Ransom & P., Kaczensky (Eds.), Wild Equids: ecology, management, and conservation. (pp. 7–22). John Hopkins University Press
- Cameron EZ, Setsaas TH, Linklater WL (2009) Social bonds between unrelated females increase reproductive success in feral horses. Proc Natl Acad Sci 106(33):13850–13853. https://doi.org/10. 1073/pnas.0900639106
- Christensen JW, Zharkikh T, Ladewig J, Yasinetskaya N (2002) Social behaviour in stallion groups (*Equus przewalskii* and *Equus caballus*) kept under natural and domestic conditions. Appl Anim Behav Sci 76(1):11–20. https://doi.org/10.1016/S0168-1591(01) 00208-8
- Crowell-Davis SL, Houpt KA, Kane L (1987) Play development in Welsh pony (*Equus caballus*) foals. Appl Anim Behav Sci 18(2):119–131. https://doi.org/10.1016/0168-1591(87)90186-9
- Darwin C (1871) The descent of man. Appleton
- Enomoto T (1990) Social play and sexual behavior of the bonobo (*Pan paniscus*) with special reference to flexibility. Primates 31(4):469–480. https://doi.org/10.1007/BF02382531
- Feh C (1999) Alliances and reproductive success in Camargue stallions. Anim Behav 57(3):705–713. https://doi.org/10.1006/anbe. 1998.1009



- Feh C (2005) Relationships and communication in socially natural horse herds. In: Mills D, McDonnell SM (eds) The Domestic Horse: The Evolution, Development and Management of its Behaviour. Cambridge University Press, pp 83–93
- Ferguson E, Frankis J (2001) Sex and sexual orientation. J Homosex 41(2):119–143. https://doi.org/10.1300/J082v41n02 07
- Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol Evol 7(11):1325–1330. https://doi.org/10.1111/2041-210X.12584
- Groos K (1911) The play of animals. Appleton
- Hanggi EB, Ingersoll JF (2009) Long-term memory for categories and concepts in horses (*Equus caballus*). Anim Cogn 12(3):451–462. https://doi.org/10.1007/s10071-008-0205-9
- International Takhi Group (2021) Save the wild horse. https://savet hewildhorse.org/en/
- Kaczensky P, Enkhsaikhan N, Ganbaatar O, Walzer C (2008) The Great Gobi B Strictly Protected Area in Mongolia - refuge or sink for wolves *Canis lupus* in the Gobi. Wildl Biol 14(4):444–456. https://doi.org/10.2981/0909-6396-14.4.444
- Kaczensky P, Ganbataar O, Altansukh N, Enkhsaikhan N, Stauffer C, Walzer C (2011) The danger of having all your eggs in one basket—winter crash of the re-introduced Przewalski's horses in the Mongolian Gobi. PLoS ONE 6(12):e28057. https://doi.org/10.1371/journal.pone.0028057
- King SRB, Boyd L, Zimmermann W, Kendall BE (2015) Equus ferus (errata version published in 2016). https://www.iucnredlist.org/ species/41763/97204950
- King SRB, Asa C, Pluhacek J, Houpt KA, Ransom JI (2016) Behavior of horses, zebras, and asses. In: Ransom JI, Kaczensky P (eds) Wild Equids: ecology, management, and conservation. John Hopkins University Press, pp 23–40
- King SRB, Schoenecker KA, Cole MJ (2022) Effect of adult male sterilisation on the behavior and social associations of a feral polygynous ungulate: the horse. Appl Anim Behav Sci 249:105598. https://doi.org/10.1016/j.applanim.2022.105598
- Lansade L, Colson V, Parias C, Trösch M, Reigner F, Calandreau L (2020) Female horses spontaneously identify a photograph of their keeper, last seen six months previously. Sci Rep 10(1):6302. https://doi.org/10.1038/s41598-020-62940-w
- Linklater WL, Cameron EZ, Minot EO, Stafford KJ (1999) Stallion harassment and the mating system of horses. Anim Behav 58:295–306
- Linklater WL, Cameron EZ, Stafford KJ, Minot EO (2013) Removal experiments indicate that subordinate stallions are not helpers. Behav Proc 94:1–4. https://doi.org/10.1016/j.beproc.2013.02.005
- Martin P, Caro TM (1985) On the functions of play and its role in behavioral development (pp. 59–103). https://doi.org/10.1016/S0065-3454(08)60487-8
- McDonnell SM, Haviland JCS (1995) Agonistic ethogram of the equid bachelor band. Appl Anim Behav Sci 43(3):147–188
- McDonnell SM, Poulin A (2002) Equid play ethogram. Appl Anim Behav Sci 78(2–4):263–290. https://doi.org/10.1016/S0168-1591(02)00112-0
- Mendonça RS, Pinto P, Inoue S, Ringhofer M, Godinho R, Hirata S (2021) Social determinants of affiliation and cohesion in a population of feral horses. Appl Anim Behav Sci 245:105496. https://doi.org/10.1016/j.applanim.2021.105496

- Merrick NJ (1977) Social grooming and play behavior of a captive group of chimpanzees. Primates 18(1):215–224. https://doi.org/10.1007/BF02382960
- Norscia I, Palagi E (2011) When play is a family business: adult play, hierarchy, and possible stress reduction in common marmosets. Primates 52(2):101–104. https://doi.org/10.1007/s10329-010-0228-0
- Palagi E, Paoli T, Tarli SB (2006) Short-term benefits of play behavior and conflict prevention in Pan paniscus. Int J Primatol 27(5):1257–1270. https://doi.org/10.1007/s10764-006-9071-y
- Paquette D (1994) Fighting and playfighting in captive adolescent chimpanzees. Aggressive Behav 20(1):49–65. https://doi.org/10.1002/1098-2337(1994)20:1%3c49::AID-AB2480200107%3e3.0. CO:2-C
- Rho JR, Srygley RB, Choe JC (2007) Sex preferences in Jeju pony foals (*Equus caballus*) for mutual grooming and play-fighting behaviors. Zoolog Sci 24(8):769–773. https://doi.org/10.2108/zsj.24.769
- Rubenstein D (2011) Family Equidae (horses and relatives). Handbook of Mammals of the World. (R. A. Mittermeier & D. E. Wilson, Eds.; 2nd ed., Vol. 2). Lynx Edicions
- Rubenstein DI (1994) The ecology of female social behaviour in horses, zebras and asses. (P. Jarman & A. Rossiter, Eds.). University Press.
- Rubenstein DI, Hack MA (1992) Horse signals: the sounds and scents of fury. Evol Ecol 6(3):254–260. https://doi.org/10.1007/BF02214165
- Šandlová K, Komárková M, Ceacero F (2020) Daddy, daddy cool: stallion–foal relationships in a socially-natural herd of Exmoor ponies. Anim Cogn 23(4):781–793. https://doi.org/10.1007/s10071-020-01388-x
- Schad L, Fischer J (2022) Opportunities and risks in the use of drones for studying animal behaviour. Methods Ecol Evol. https://doi.org/ 10.1111/2041-210X.13922
- Sigurjonsdottir H, Thorhallsdottir AG, Hafthorsdottir HM, Granquist SM (2012) The behaviour of stallions in a semiferal herd in Iceland: time budgets, home ranges, and interactions. International Journal of Zoology 2012:1–7. https://doi.org/10.1155/2012/162982
- Souris A-C, Kaczensky P, Julliard R, Walzer C (2007) Time budget, behavioral synchrony- and body score development of a newly released Przewalski's horse group *Equus ferus przewalskii*, in the Great Gobi B Strictly Protected Area in SW Mongolia. Appl Anim Behav Sci 107(3–4):307–321. https://doi.org/10.1016/j.applanim. 2006.09.023
- Wells SM, Goldschmidt-Rothschild B (2010) Social behaviour and relationships in a herd of Camargue horses. Z Tierpsychol 49(4):363–380. https://doi.org/10.1111/j.1439-0310.1979.tb00299.x
- Zharkikh TL, Andersen L (2009) Behaviour of bachelor males of the Przewalski horse (*Equus ferus przewalskii*) at the Reserve Askania Nova. Der Zoologische Garten 78(5–6):282–299. https://doi.org/10.1016/j.zoolgart.2009.10.005
- **Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

