

# Importance of the social environment for reproductive and general welfare of domestic horse (*Equus caballus*) stallions

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## ABSTRACT

The obligation to ensure the welfare of domestic horses is evident. Social bonds are an essential part of the daily life of feral horses. In human-controlled conditions, stallions usually live alone in a barren environment of individual boxes or paddocks with contact to conspecifics limited to visuals. Still, many stallions do not have regular access to paddocks and pastures. This provokes frustration and stress which has been shown to contribute to the development of stereotypies, self-mutilations, abnormal sexual behaviour and reproductive problems. This review highlights how domestic environments may negatively diverge from the natural conditions necessary for the healthy behavioural development of stallions. We address stallions' welfare and reproductive problems that may arise from their lack of social contact. These issues are discussed along the stages of a stallion's life under free ranging conditions. We postulate that today's breeding stallions must be enabled to enjoy the positive aspects of a bachelor stallion's life. This should include adequate consideration of the stallions' reproductive behaviour including contact with a sexually receptive mare. This will not only improve animal welfare but also ensure optimal semen quality and fertility.

## 1. Introduction

Motto: *The stallion is a horse like any other horse* (Briard et al., 2016).

Good reproductive performance does not necessarily reflect good welfare as has been demonstrated in cattle (Ritter et al., 2019). The obligation to ensure the welfare of domestic horses is evident. The five freedoms of welfare (Fig. 1), which have been defined by the Farm Animal Welfare Council (FAWC, 2012) are, however, not routinely provided to all breeding stallions (reviewed by De Oliveira and Aurich, 2021).

Similarly, a more recent approach to welfare issues, the Five Domains of Welfare theoretical construct (Mellor, 2017, Fig. 2), has been published. They involve not only the functional areas, i.e. survival-related factors of an animal's basic needs, but also the requirement that humans must ensure the environmental conditions which allow positive feelings, i.e. unimpaired cognitive, social and emotional functions of an individual in all aspects of life (Mellor and Beausoleil, 2015, Mellor, 2016, Mellor et al., 2020). This is, unfortunately, not true for all stallions. In this context, it must be accepted that normal reproductive behaviour of the stallion does not only relate to copulation and ejaculation, which is the final act of reproductive and

social facilitation under natural conditions. In horses, it involves intense and often long-lasting social interaction between the male and the female. In contrast, for human convenience and animal safety, in stallions used for semen collection, the interaction with females is often restricted and limited to as minimal interaction as necessary to stimulate the male's sexual arousal and the sexual response cycle, finally leading to ejaculation. This is highlighted by the fact that in well-trained, experienced stallions, the overall mean time they spend in the breeding barn for semen collection is less than 10 min (Pasing et al., 2013).

Horses are social animals that under wildlife conditions form groups (harems) consisting of at least one mature male (stallion), several or a dozen adult females (mares) and their offspring, usually up to two-years-old females (fillies) and males (colts). Migrating young females will soon be gathered by other harem stallions or young stallions that have been without mares to this point. Dispersing males usually form or join bachelor groups (bands) or, less often, join an existing harem (Feist and McCullough, 1975; McDonnell and Murray, 1995; Fig. 3). The social organisation of wild horses (Przewalski's horses, *Equus ferus przewalskii*) and feral domestic horses (*Equus caballus*), which is directly related to their reproductive biology, has been described in detail repeatedly (Feh, 1988; McDonnell, 2000; Boyd and Keiper, 2005). It must be concluded

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that all horses, irrespective of their sex, strive to live in groups. This feature is an intrinsic part of the equine temperament (Lansade et al., 2008). The only exception and voluntary abandonment of the group by individual horses is the migration of maturing subadults (Hoffmann, 1985), and the transient solitary stay of a young stallion preceding the acquisition of mares when establishing his own harem (Khalil and Murakami, 1999). It is important to note that both these conditions occur for very limited time periods. In conclusion, except for the latter cases, no stallion will stay alone on his own account.

The welfare of free-living stallions is continuously challenged due to numerous environmental issues like shortage of forage or water, high pressure from rivals and the huge threat by predators (Górecka-Bruzda et al., 2020; Harvey et al., 2023). In contrast, domestic stallions may enjoy a good life in abundance: shelter, vaccination, deworming, hoof trimming and production of offspring with many females. Under human-controlled conditions, however, stallions usually live alone in a barren environment of individual boxes, often without access to paddocks and pastures (De Oliveira and Aurich, 2021). Moreover, traditional husbandry practices involve early weaning of foals (Ladewig et al., 2005; Lansade et al., 2022) with a lack of comforting support from the social group. From weaning onwards, male horses are refrained from contact with adult females and the associated learning success regarding female reproductive behaviour (McDonnell, 2000), which is in stark contrast to the situation under natural conditions. To avoid problems because of aggressive behaviour among stallions after puberty, they are often kept individually from an early age. These artificial conditions of stallions will often cause frustration and stress, subsequently resulting in stereotypies, self-mutilations, abnormal sexual behaviour and reproductive problems (Kirkpatrick and Turner, 1986; McDonnell, 1992; 2000; Aurich et al., 2015; De Oliveira and Aurich, 2021).

In this review, we present evidence that the domestic environment can be a detrimental departure from the natural conditions of appropriate behavioural development of a stallion. We address the welfare and reproductive problems of stallions when they cannot fulfil the social role they evolved for. These issues are discussed with individual stages of the stallion's life under natural conditions. We hope that this review will contribute to a better understanding of stallions' basic needs from the scientific and practical perspective of equine breeders, keepers and veterinarians.

## 2. Material and methods

In our study, we focused exclusively on the social environment of the stallion. Other issues related to reproductive control and the welfare of horses are available in a recent review by Bechert et al. (2022). We searched for literature on domestic, feral and semi-feral stallions (i.e., free-roaming horses, living in natural groups in reserves, sanctuaries or being communally grazed), and, when needed, we referred to research on wild species (e.g., Przewalski's horses, *Equus ferus przewalskii*). We used Google Scholar, Pub Med and Scopus applying the keywords "stallion" and "feral", "social", "stress", "behaviour", "aggression", "abnormal behaviour", "self-mutilation", "welfare", "stabling", "keeping conditions", "weaning" and "fertility" alone or in combination. In addition, literature cited in previous studies and further references were retrieved using snowball sampling. Papers related to the keywords "heat" or "oxidative stress", and conference abstracts were excluded. Eventually, 110 references were analysed.

## 3. The male foal: natural vs. human-controlled environment

Under natural conditions, mares undergoing parturition will separate to a certain distance from other horses but deliver their foals in the proximity of their group (Crowell-Davies, 2005). It takes two to three days for the foal to form an attachment to its dam, and during this time the dam chases conspecifics away from her foal to ensure complete development of the mare-foal bond (Carson and Wood-Gush, 1983). Still, the newborn can join and become acquainted with the natal group members, protected by their mother (Ladewig et al., 2005), at an early age, ensuring that the foal will be easily accepted as a new member of its group. Taking this into account, under domestic conditions, most breeders separate the mare before parturition. Whereas in Europe, this separation takes often place in a single "foaling" box, for example in Australia, North and South America, depending on the breed and time of year, mares will foal outside in paddocks or yards. After foaling, the mare and her foal may stay separated from other broodmares and their offspring for a few days, but integration into the group is usually strived for very soon. The tendency of inexperienced breeders to delay re-integration for longer periods to avoid that the foal is hurt, threatens the socialisation of the foal and should be avoided. Male foals initiate the play and spend more time in mutual play than fillies (Carson and



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Specific requirements to ensure the Five Freedoms for breeding stallions:

- Provide regular opportunities for
  - free movement
  - pasture grazing
  - visible and physical (tactile) contact to conspecifics
- Ensure that management at semen collection or in-hand-breeding considers and respects the requirements of the stallion's reproductive behavior as far as possible

Fig. 1. Schematic representation of the Five Freedoms of Welfare and their specific relevance for horse stallions.

Wood-Gush, 1983; Crowell-Davies and Weeks, 2005; Šandlová et al. 2020), but irrespective of their sex, playing or interacting with group members will allow the foals to learn about their counterparts and adult horses' agonistic and affiliative behaviour (Tyler, 1987; Sigurjónsdóttir et al., 2003; Crowell-Davies and Weeks, 2005; Šandlová et al., 2020). There is, however, little aggression among foals (Carson and Wood-Gush, 1983; Tyler, 1987). When a domestic foal has no contact with other adult horses except its dam, the colt may turn into a pushy, aggressive, and dangerous stallion without the disciplinary presence of other adults or at least competent human handling (AGB, own observations). Even if raised with other mares and foals until weaning, the reduced time a domestic foal spends in the familiar group may affect the development of social competencies. This is indicated by the fact that weanlings raised in the presence of adults who were not their dams presented more appropriate social behaviours than their counterparts reared with companions of similar age only (Henry et al., 2012).

Under natural conditions, foals will stay in their natal group up to two years after their natural weaning and the birth of their younger siblings whereas under domestic, human-controlled conditions, foals are weaned much earlier, on average 4–6 months after birth (Carson and Wood-Gush, 1983). Abrupt weaning of young foals results in a pronounced stress response that affects their welfare for several days to weeks (Erber et al., 2012; Górecka-Bruzda et al., 2015; Wulf et al., 2018). To their caretakers, this procedure may seem not to affect a young horse's behaviour in the long term, however, yearlings experimentally reunited with their mothers and other familiar mares five months after weaning took place still chose to approach and stay in proximity of their dams (Lansade et al., 2022). Some sex-related differences in the stress response to weaning exist (Wulf et al., 2018). To the best of our knowledge, long-term effects on the social behaviour of early weaning to fillies and colts have not yet been determined.

According to the Five Domains of Welfare, the affective state of free-

living foals with respect to nutrition and health may be compromised due to potential food and water scarcity (Theunissen, 2019; Harvey et al., 2023) and the lack of protection against infectious diseases (Hain-Saunders et al., 2025), and predation, as foals are more frequently targeted than adults by cougars or wolves (Andreasen et al., 2021; Lagos & Bárcena, 2022). Despite these risks, the behavioural needs of free-living foals appear to be fully met, as young horses benefit from prolonged maternal care and the social company of both peers and adults. Conversely, while nutritional and health aspects are generally provided under human management, the behavioural domain is potentially less satisfied when foals may experience frustration, stress, and helplessness resulting from early maternal and social isolation.

#### 4. Bachelors: natural vs. human-controlled environment

In free-living horse populations, juvenile males are expelled from the natal group either by their sire, or his successor, or they may migrate voluntarily (Berger, 1986; Kaseda et al., 1997; Boyd and Keiper, 2005; Górecka-Bruzda et al., 2023). Dispersed young males, usually at the age of two years (range: 1–5 years; Klingel, 1975; Feh, 1999; Salter and Hudson, 1982; Berger, 1986), form or join already existing single-sex groups, called "bachelor bands", which may also include older stallions who have lost their mares (Boyd and Keiper, 2005). At this stage of life, young males often interact socially during play-fighting (Berger, 1986; Tilson et al., 1988; McDonnell and de Haviland, 1995; Khalil and Murakami, 1999; Christensen et al., 2002a; McDonnell and Poulin, 2002). Bachelor bands are socially unstable due to the rotation of males; while sub-adults join the group, mature males leave the band to gather a group of mares, i.e., their own harem. Despite its variable composition, members of a bachelor band establish mutual bonds and social rank (Berger, 1986; Tilson et al., 1988; Christensen et al., 2002a). Sometimes, sub-adult males do not leave the natal group. Such subordinate stallions

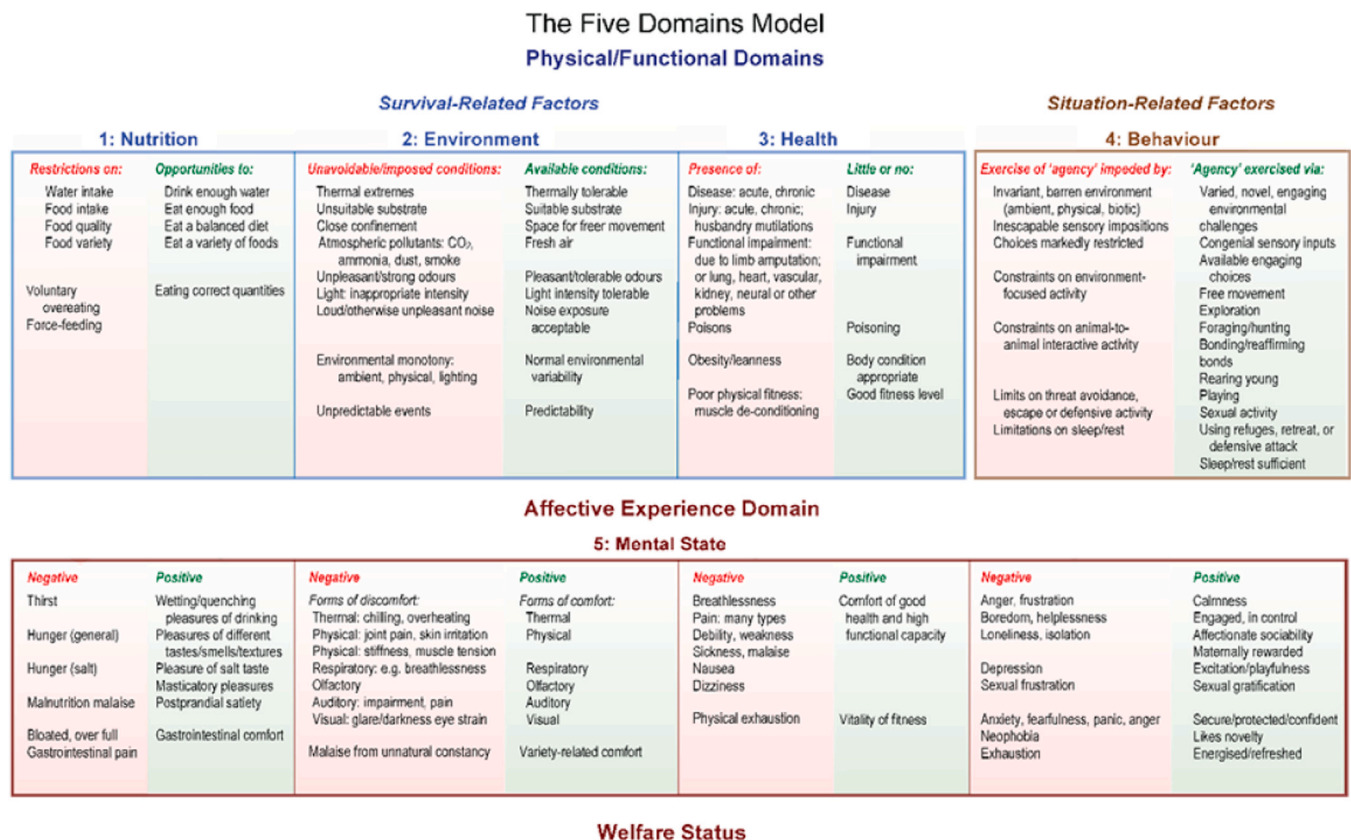


Fig. 2. The Five Domains Model (Mellor, 2017). The physical/functional Domains 1–3 are related to survival-related factors, while Domain 4 focuses mainly on behaviour, and external situation-related factors. Each of the Domains 1–4, with its negative or positive affective aspects, is relevant to Domain 5, the mental state.

(Fig. 4a) were occasionally identified in feral groups, evidencing the peaceful coexistence of two adult males even in the presence of mares (Feh, 1999; Linklater et al., 1999; Linnartz and Linnartz-Nieuwdorp, 2017).

Under domestic conditions, weaned colts are usually reared in groups of male foals of the same age; sometimes they are even accommodated in individual boxes (Christensen et al., 2002b; Søndergaard and Christensen, 2007). As they are much younger at weaning than migrating feral males and considering their need for a mother for much longer (Lansade et al., 2022), the presence of other immature males alone does not provide sufficient social support for weanlings. The presence of adult horses familiar to the group that stay with the weanlings when their dams leave the foals can reduce the stress response of the weaned horses (Erber et al., 2012). At this early stage, adult horses (Henry et al., 2012), especially the dams (Lansade et al., 2022), are beneficial for the appropriate behavioural development of foals. Individually housed colts, despite having visual and olfactory contact with conspecifics of similar age were not ready to associate with them when turned out in a group and exhibited more aggressive behaviour compared to their group-housed counterparts (Christensen et al., 2002). In contrast, individually housed foals presented more affiliative behaviour (grooming and playing) as a “rebound effect” when provided with social companions and the open space they were deprived of. When weaned colts were individually housed, they showed more motivation for physical contact, approaching and interacting with the trainer during training sessions (Søndergaard and Christensen, 2007). The authors suggested that single housing impairs the foals’ opportunity to practice their social skills with other young horses. It is important to note that a considerable percentage (67 %) of single-kept weanlings performed stereotypies at the age of two 2 years in comparison to their group-stabled counterparts (Visser et al., 2008). According to the Five Domains of Welfare, the affective state of free-living bachelors may appear to involve frustration, including sexual frustration, when they are unable to maintain their own harem or have constant contact to females. Although bachelor groups may be socially unstable, the presence of other horses is crucial for positive welfare within the affective domain, supporting engagement, playfulness, security, and affectionate stability (McDonnell and Murray, 1995; McDonnell and Poulin, 2002). In contrast, human-managed conditions, particularly the social separation and isolation of young stallions, may negatively affect the affective domain, leading to frustration, boredom, or loneliness.



Fig. 4. (a.) Two-year-old stallion with a mare and her foal – they all belong to a dominant stallion harem (picture taken April 2023, Popielno reserve, Poland). This stallion was still present in the same harem as a satellite stallion in 2025. Between 2022 and 2025, he changed his status several times by taking over some mares and losing them again and (b) The Konik polski dominant harem stallion resting in the proximity of his harem (including a satellite stallion from Fig. 4a) in the Popielno reserve, Poland (photo taken in July 2022). Photos by Michał Bruzda.

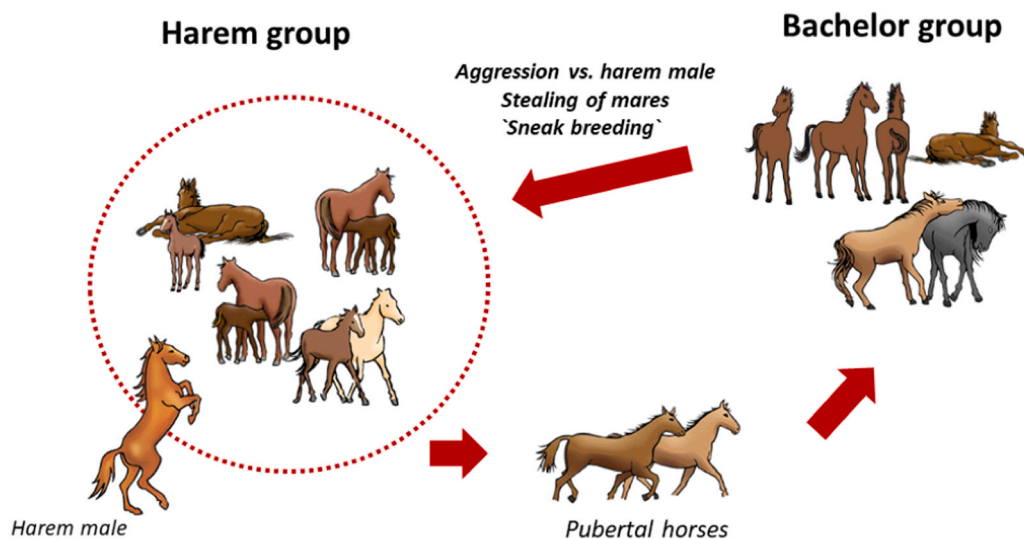


Fig. 3. Cartoon illustrating the social structure of horses living under wildlife conditions.

## 5. The behaviour of the free-roaming harem stallion and his social contribution

Social bonds are an essential part of the daily life of horses (van Dierenonck, 2006; Cameron et al., 2009; Hartmann et al., 2012). Horses recognise and accept members of their group but usually confront newcomers irrespective of their sex. Harem groups are important social subunits that are always clearly distinguishable even among large herds of up to 600 individuals (Ozogány et al., 2023). Social relationships of female horses are very stable and may last their entire lives (Jaworska et al., 2020). Also, stallions form established relationships with the mares of their harem that may last for up to ten years (Feh, 1999; Jaworska et al., 2020a). Harem members may disperse when grazing (Stanley et al., 2018), but they synchronise their locomotor activity and rest. In contrast to other equids like donkeys (*Equus asinus*) and Grevy's zebras (*Equus grevyi*) that are territorial, domestic and Przewalski stallions remain with their mares also beyond the reproductive season and regardless of the mares' reproductive status (Klingel, 1975; Crowell-Davis, 2007).

Bachelor stallions will usually form harems at the age of 4–6 years (Berger, 1986; Kaseda et al., 1997; Khalil and Murakami, 1999; Morel and Gunnarsson, 2000). Only stallions who can conquer, attract and defend their mares in the long term will achieve reproductive success reflected in the number of foals they produce (Klingel, 1982; Franke Stevens, 1990). Stallions that succeeded in harem formation at a lower age, i.e., the more dominant bachelor stallions (Boyd and Keiper, 2005; Bourjade et al., 2009) as well as sons of mares of high dominance (Feh, 1999) have been identified to have increased reproductive success.

In feral horses, the harem stallion has great importance regarding his social role in the group. Alongside his guarding behaviour, indicated by herding or snaking (Ginther et al., 2002), he assures the cohesion of his harem, usually during collective locomotion, but also in challenging situations like harassment by competitors (Linklater et al., 1999; Sigurjónsdóttir and Haraldsson, 2019) or threat from predators (Klingel, 1982; Lema et al., 2022). The presence of the stallion is beneficial for the harem by reducing inter-individual aggression (Granquist et al., 2012; Sigurjónsdóttir and Haraldsson, 2019), which results in stability and thus may increase reproductive efficiency (Linklater et al., 1999).

Stallions are less involved in affiliative interactions than females and juveniles (Feh and de Mazières, 1993; Kimura, 1998; Granquist et al., 2012). Yet, there are preferred mares to whom the stallion keeps a close distance (Kimura, 1998). Interestingly, stallions exchange more affiliative interactions with young foals than the harem mares (Šandlová et al., 2020). In young stallions, allogrooming bouts decline in the same male pairs with increasing age and generally disappear in four-year-old stallions (Hoffmann, 1985). Nevertheless, in spring, with the start of the breeding season, the allogrooming of mares with stallions increases, although there is no increased allogrooming with other mares (Heitor et al., 2006). This may indicate an increasing interest between male-female pairs, which positively stimulates the development of mutual social bonds.

Under feral conditions, the mare's interest in stallions and her pre-emptive behaviour in response to the sexual attractiveness of a stallion increases during oestrus. She actively seeks and approaches the stallion (Kaseda et al., 1997; McDonnell, 2000; Heitor et al., 2006; Crowell-Davis, 2007). The proximity of the stallion thus ensures optimal timing and frequency of mating, associated with high reproductive efficiency. Females appear to be attracted by the following stallion's behavioural features: dominance (Feist and McCullough, 1975; Berger, 1986; Monard et al., 1996), aggressive behaviour (Miller, 1981), or attentiveness to his mares (Rutberg, 1982). Interestingly, the vocalisation of males with high reproductive performance was more attractive to mares than that of less fertile stallions (Lemasson et al., 2015).

Stallions are, however, interested in all available females, taking over mares from other harems or incorporating dispersed fillies. The defensive capacity of a stallion is not unlimited, though. Harems with

more than 10 mares were rarely observed and only when the harem stallion experienced only weak harassment from other stallions (Pacheco and Herrera, 1997; Linklater et al., 1999). It has been proposed that pair selection in horses may be related to subtle biological communication, i.e., their types of the major histocompatibility (MHC) complex. In an experimental study, luteal phase but not oestrous mares preferred stallions with dissimilar MHC-type. Similarly, the total sperm number produced by a stallion was increased when an MHC-dissimilar mare but not an MHC-similar mare was present at semen collection (Burger et al., 2017). The MHC-directed pair selection was not confirmed in a study in semi-feral horses (Jaworska et al., 2020b), where an equal male/female ratio was, however, not assured.

The fertility of feral stallions is hard to assess due to difficulties in determining the parentage without genetic testing (Kaseda et al., 1997). In semi-feral Konik harem stallions, the siring rate per mare, confirmed by parentage testing, was very high (up to 89%; Górecka and Jezierski, 1997), including aged and sub-fertile mares. Acceptance of old and potentially not "useful" partners in the harem or in bachelor bands is one of the social specifics of equine groups and indicates the crucial importance of the presence of equine companions for the welfare of horses of both sexes. It was, however, observed that in the feral Assateague Island horse population, there is a tendency for increased foaling rates in older, more dominant mares (57%) than in younger, subordinate mares (46–53%; Keiper, 1985). This may suggest that the mating of younger mares by the harem stallion is prevented by older, more dominant mares. Dominant mares intervened in sexual encounters between the stallion and subordinate mares (Tarouco et al., 2018), but in other feral herds, mares presented high reproductive performance up to 84% (Wolfe et al., 1989).

Another characteristic of the natural reproductive behaviour described in free-roaming horses is the "sneak breeding" of stallions. As described in detail by McDonnell (2016), non-harem stallions benefit from occasionally mating with oestrous mares by the strategy to hide ostentatious male sexual behaviour. They are more inclined to breed dispersing females, so in cases of non-confirmed paternity, the fertility rate of harem stallions may not be as high as supposed.

Their various social functions and their almost constant vigilance and engagement highlight how important these activities are for a male horse. Stallions help maintain control over the environment and potential rivals, as well as support group cohesion, which contributes to a positive affective state of being in control of both him and the group. In the absence of strong harassment from other males, the harem stallion displays positive social behaviour and remains calm and sexually satisfied.

## 6. Behaviour of the stallion under domestic conditions

Under today's domestic conditions, free mate selection is often no longer possible. Stallions are selected not for their fighting and guarding qualities, but usually for their performance in racing or equestrian competitions or merely for body conformation (De Oliveira and Aurich, 2021). Behavioural characteristics that may be important for females to invest in their progeny are no longer considered. In this context, the ability of semi-feral Konik polski stallions that on the one side present a perfectly calm and friendly behaviour towards their harem, are on the other hand well capable to successfully guard the group from other stallions' harassment is of interest (AGB, personal observations, Fig. 4b).

In many domestic breeds, stallions used for breeding are usually kept isolated from mares (Hartmann et al., 2015). Their exposure to female visual, olfactory and tactile stimuli, which is considered important to stimulate male behaviour, is not provided or is limited to the short time needed for mating or semen collection (Guillaume et al., 2018; Jezierski et al., 2018; King and Gurnell, 2007). Semen collection in the presence of an oestrous mare increases the volume of the ejaculate (Jeannerat et al., 2018). In Europe, only in some pony breeds, pasture breeding is practised to a wider extent (Sigurjónsdóttir et al., 2012), which fulfils

the stallions' behavioural needs concerning their social environment but only during the reproductive season. Similar extensive breeding practices also exist in some equestrian cultures, such as ranch horses in the Americas and native breeding systems in Asia. In this context, it is important to note that the reproductive efficiency of stallions in pasture breeding is usually excellent (86 %, Hugason et al., 1985; up to 97 %, Bristol, 1987). When used for "in-hand" breeding or semen collection, instead of ten, the stallion may breed up to 200 (natural in-hand breeding, Walborn et al., 2017) or even 400 mares (artificial insemination, Palmer, Chavatte-Palmer, 2020). The reproductive behaviour of the "well-trained" stallion is therefore mostly reduced to quick and mechanical reflexes (Noue et al., 2001). The natural reproductive behavioural repertoire of both the mare and the male has been described in detail (McDonnell, 2000 and 2016). It involves unrestrained preceptive and receptive behaviour of the mare and a cautious stallion response. In short, the harem stallion is not ready to breed the mare before the investigation of her receptivity by naso-nasal inspection, approaching her without full erection and the initial non-receptive behaviour of the mare may enhance the libido of the male. In turn, the restriction of movement in the pair during mating or the training of the stallion to not approach the mare unless full erection is achieved is in contradiction to normal behaviour. Also, in connection with restricted stabling conditions, often associated with a lack of social contact, free movement, and grazing, the welfare of breeding stallions is considerably reduced, although they are considered very precious animals by their owners and stud personnel (De Oliveira and Aurich, 2021).

## 7. Other human interventions influencing the social and reproductive behaviour of stallions

As in other horses, restrained conditions of stabling incompatible with science-based welfare recommendations trigger behavioural problems like stereotypies, depression-like states and aggression (Ruet et al., 2019). Stallions are especially prone to developing aggression towards other horses and humans, together with other abnormal behaviours (Tadich et al., 2012). Most issues related to inadequate social environments or human interventions are based on the use of restrictive management practices in stallions (De Oliveira and Aurich, 2021). These are mainly a result of the sanitary regulations associated with breeding and artificial insemination or the desire to minimize the potential of a stallion to injure himself, other horses or humans (Burger et al., 2012; De Oliveira and Aurich, 2021).

Under natural conditions, stallions are exposed to the presence or the harassment of other males (Linklater et al., 1999). The close presence of stallions in the bachelor group decreases peripheral testosterone concentrations (McDonnell and Murray, 1995), but they are also reduced in sexually active compared to inactive stallions (Aurich et al., 1999). In breeding stallions housed in a barn without females, cortisol concentrations increased during the reproductive season, suggesting stressful challenges, most likely due to aggression among animals (Aurich et al., 2015). Interestingly, stallions kept under similar conditions also provided semen with improved sperm characteristics in comparison to males kept in proximity to female horses (Burger et al., 2015). Keeping stallions in male-only barns is therefore not automatically detrimental to semen quality although there may be negative effects on reproductive behaviour (McDonnell, 2016). While some stallions may have excellent libido, those with reduced sexual drive ("shy breeders" and "bird-watchers") may provoke irritation of their handlers. Stallion handling during breeding, therefore, requires a person who can judge and consider how to respond to the different behavioural patterns that exist among stallions to allow for successful semen collection.

In sexually experienced and well-trained stallions, the procedure of semen collection is perceived as a modest temporary stressor as indicated by only minor changes in heart rate and cortisol secretion (Pasing et al., 2013). It is important to note that heart rate increased already when the stallion was exposed to the teaser mare. This reflects emotional

stress stimulated by social interaction with the mare and can be interpreted as "eustress" (Pasing et al., 2013). To the best of our knowledge, there is no information on the stress-response of stallions when semen collection attempts are not successful, i.e., do not result in ejaculation, even if attempts are repeated several times. In healthy fertile stallions, such failure of ejaculation during semen collection or mating is often caused by an inadequate breeding routine including a lack of sexual stimulation, improper handling, punishment of undesired behaviour or disregard of the stallion's individual preferences as for example type or colour of the teaser mare. While the stallion will perceive successful ejaculation as a positive reinforcement, failure of ejaculation will result in frustration and may be a reason for the aggressive behaviour that some stallions present towards humans or the teaser mare at mating or semen collection. This clearly indicates non-fulfilment of the recommendations in the "Five Domains", as frustration, "anger", boredom, helplessness, loneliness due to isolation and sexual frustration are often observed in domestic stallions. Careful adjustment of the breeding routine to the stallion's demands and preferences will improve such situations (CA, own observations).

Under natural socially stable conditions, the competitive behaviour among stallions is mostly ritualised (McDonnell, 2016). Injuries are almost exclusively caused by more aggressive fights with other males during their attempts to gather mares into their harem (reviewed in Górecka-Bruzda et al., 2023). In domestic stallions, social isolation, together with a lack of stimulation by free movement and grazing in pastures or outdoor paddocks, may provoke self-mutilation (McDonnell, 2008). This behaviour in stallions may be associated with social, visual, or olfactory cues that elicit frustration or fear. Such responses may occur when stallions are exposed to the visual or olfactory presence of oily body secretions or faeces deposited by other males within confined environments, such as paddocks or transport trailers (McDonnell, 2008). The resulting self-injurious behaviour presents serious concerns for animal welfare, with potential adverse effects on both fertility and overall health.

Another aspect of breeding stallions' welfare is their participation in sporting events. According to the International Equestrian Federation, 66,018 stallions are commonly registered as competing worldwide in equestrian sports (<https://data.fei.org/Default.aspx>) and there are many more in other activities like horse racing. Participation in competitions exposes stallions to new environments, including novel social settings. Although the impact of physical exertion during training and competition on semen characteristics has been studied repeatedly, the results remain ambiguous (negative: Wilson, Twigg-Flesner, 2017 and Wilson et al., 2019; neutral: Lange et al., 1997; Hensel et al., 2023). No references were, however, found regarding the welfare implications of stallions' exposure to familiar and unfamiliar conspecifics during training and performance, respectively. This represents an important gap in the existing knowledge.

## 8. Options to improve social welfare for stallions

The observation of stallions living under wildlife conditions demonstrates that social satisfaction results in secure, confident males, as recommended by the Five Domains of Freedom. Innovative solutions improving social welfare in housing conditions of stallions have been reviewed by De Oliveira and Aurich, (2021) The "social boxes", i.e. facilities enabling physical contact between stallions through the opening in the partition between two boxes, ensure, at least in part, components of physiological behaviour. The strong vertical bars 30 cm apart allow insertion of the head, neck and leg into the neighbouring box, while the solid part of the partition assures privacy for the horse (Zollinger et al., 2023). Only minor injuries and little excitement occurred during the first days of interactions using the opening. Of all social interactions observed, 71 % were positive (Zollinger et al., 2023). The recent practical results from this type of stabling demonstrate that socially stabled stallions presented fewer unwanted behaviour when driven in pairs

compared to males stabled with solid walls between boxes (Gmel et al., 2022)).

Another approach to increase social welfare is pasturing stallions in groups in large enclosures after the breeding season which is practised in, for example, Switzerland, Austria, Romania and France (Briefer Freymond et al., 2013, De Oliveira and Aurich, 2021, Popescu et al., 2022, Flamand et al., 2025). Like the situation of stallions kept in social boxes, the stallions' behaviour was more alert during the first days after their release, and impressive encounters were observed. The stallions' initial excitement resulting from the freedom of movement and unrestricted social interactions is quickly redirected towards grazing if this is possible (Popescu et al., 2022). Aggressive behaviour may, however, always occur, so the progressive habituation of stallions to become familiar before the common turnout is highly recommended (De Oliveira and Aurich, 2021). This was confirmed by Flamand et al. (2025) who implemented a gradual 54-day socialisation protocol prior to the final release of six stallions into a common pasture. It must, however, be noted that one of the stallions was eventually excluded from the group, as he could not be resocialised (Flamand et al., 2025). These findings emphasize the importance of careful behavioural monitoring during such encounters to ensure animal safety.

In a worldwide survey on the situation regarding handling and housing of stallions used for breeding, responses from 115 horse breeding centres located in North America (12 %), South and Central America (37 %), Europe (41 %), Middle East (5 %), and Oceania (5 %) were collected. Interestingly, only 9 % of them reported that they keep stallions together in the same paddock or pasture and 24 % had experienced accidents when stallions were kept together (De Oliveira and Aurich, 2023). In this context, it is important to note that the formation of a stable hierarchy in a stallion group requires two to three months (Briefer Freymond et al., 2013). Beneficial effects of group housing may therefore not occur immediately (Kroschel et al., 2025). If the opportunity of keeping stallions in groups is not considered an option, providing a gelding as a companion to the stallion in the neighbouring paddock may be a successful method to resolve aggression problems. There are also anecdotal reports from owners referring to beneficial effects on the stallion's welfare when keeping him with pet animals like goats, sheep or donkeys to allow at least some kind of social interaction (CA, personal observation). To what extent social interaction of stallions to other horses during training or performance which is common in many parts of the world (De Oliveira and Aurich, 2023) contributes to the wellbeing of stallions requires further research.

## 9. Conclusions

Under the demands of today's horse breeding routine practiced in most sport horse and racehorse breeds, pasture breeding, which must be considered the only "natural" situation for a domestic stallion, will not be accepted by many stallion and mare owners. The monetary and sentimental value of their horses will prevent them from exposing their horses to potentially dangerous situations. These may occur when integration into a herd or mating between a male and a female unfamiliar to each other is initiated. On the other hand, some stallions are so popular that the demand to have mares bred to them can only be met by artificial insemination or well-managed "mating calendars". The findings of our review suggest that the situation of domestic stallions used for regular semen collection or in-hand breeding is most comparable to the situation of bachelor stallions. Like bachelor stallions, in most cases, they live together (in barns) but are separated from female horses. Their regular use for semen collection (i.e., in a stallion breeding via artificial insemination this ranges between three to five times weekly) is comparable to the occasional "sneak breeding" described in bachelor stallions. Wild bachelor stallions live in a natural and therefore acceptable situation under equine welfare considerations, therefore domestic "bachelors" may live a good life as long as all their requirements, including the positive social aspects of welfare, are considered. We,

therefore, suggest that today's breeding stallions can and must enjoy these positive aspects of a bachelor stallion's life to meet the recommendations of the "Five Domains". In this context, the management of semen collection or natural mating must consider and respect as many necessary stimuli of the stallion's physiological reproductive behaviour as possible. This should include contact with conspecifics, i.e., oestrous mares at semen collection to allow for display of sexual behaviour, which is necessary to provide optimal semen quality and fertility. Because horses are a domestic species, they adapt easily to human-provided conditions. With an appropriate approach to equine basic biological needs, the welfare and high reproductive efficiency of domestic stallions may be combined satisfactorily.

## CRedit authorship contribution statement

**Aleksandra Górecka-Bruzda:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Christine Aurich:** Writing – review & editing, Methodology, Conceptualization.

## Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Grammarly in order to correct the English spelling. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## References

- Andreasen, A.M., Stewart, K.M., Longland, W.S., Beckmann, W.S., 2021. Prey specialization by cougars on feral horses in a desert environment. *J. Wildl. Manag.* 85, 1104–1120. <https://doi.org/10.1002/jwmg.22087>.
- Aurich, C., Gerlach, T., Hoppen, H.O., Aurich, J.E., 1999. Sexual activity influences the secretion of reproductive hormones in the stallion. *Reprod. Domest. Anim.* 34, 405–441. <https://doi.org/10.1111/j.1439-0531.1999.tb01393.x>.
- Aurich, J., Wulf, M., Ille, N., Erber, R., von Lewinski, M., Palme, R., Aurich, C., 2015. Effects of season, age, sex, and housing on salivary cortisol concentrations in horses. *Domest. Anim. Endocrinol.* 52, 11–16. <https://doi.org/10.1016/j.domaniend.2015.01.003>.
- Bechert, U.S., Turner, J.W., Jr, Baker, D.L., Eckery, D.C., Bruemmer, J.E., Lyman, C.C., Prado, T.M., King, S.R.B., Fraker, M.A., 2022. Fertility control options for management of free-roaming horse populations. *Hum. Wildl. Inter.* 16, 179–216. (<https://www.jstor.org/stable/27316334>).
- Berger, J., 1986. *Wild horses of the great basin: social competition and population size*. University of Chicago Press, Chicago, IL, USA.
- Bourjade, M., Tatin, L., King, S.R.B., Feh, C., 2009. Early reproductive success, preceding bachelor ranks and their behavioural correlates in young Przewalski's stallions. *Ethol. Ecol. Evol.* 21, 1–14. <https://doi.org/10.1080/08927014.2009.9522507>.
- Boyd, L.E., Keiper, R.R., 2005. Behavioural ecology of feral horses. In: Mills, D., McDonnell, S. (Eds.), *The Domestic Horse: The Evolution, Development and Management of Its Behaviour*. Cambridge University Press, Cambridge, pp. 55–82.
- Briard, L., Deneubourg, J.L., Petit, O., 2016. L'étalon, un cheval presque comme les autres: Statut et comportement social de l'étalon vivant en groupe familial. 42ème Journée de la Recherche Equine, Paris, 17 March 2016, pp. 121–124.
- Briefer Freymond, S., Briefer, E.F., Niederhäusern, R.V., Bachmann, I., 2013. Pattern of social interactions after group integration: a possibility to keep stallions in group. *PLoS One* 8, e54688. <https://doi.org/10.1371/journal.pone.0054688>.
- Bristol, F., 1987. Fertility of pasture bred mares in synchronised oestrus. *J. Reprod. Fertil. Suppl.* 35, 39–43.
- Burger, D., Wedekind, C., Wespi, B., Imboden, I., Meinecke-Tillmann, S., Sieme, H., 2012. The potential effects of social interactions on reproductive efficiency of stallions. *J. Equine Vet. Sci.* 32, 455–457. <https://doi.org/10.1016/j.jevs.2012.05.076>.
- Burger, D., Dolivo, G., Wedekind, C., 2015. Ejaculate characteristics depend on social environment in the horse (*Equus caballus*). *PLoS One* 10, e0143185. <https://doi.org/10.1371/journal.pone.0143185>.
- Burger, D., Meuwly, C., Marti, E., Sieme, H., Oberthür, M., Janda, S., Meinecke-Tillmann, F., Wedekind, C., 2017. MHC-correlated preferences in diestrous female

- horses (*Equus caballus*). *Theriogenology* 89, 318–323. <https://doi.org/10.1016/j.theriogenology.2016.09.015>.
- Cameron, E.Z., Setsaas, T.H., Linklater, W.L., 2009. Social bonds between unrelated females increase reproductive success in feral horses. *Proc. Natl. Acad. Sci.* 106, 13850–13853. <https://doi.org/10.1073/pnas.0900639106>.
- Carson, K., Wood-Gush, D.G.M., 1983. *Equine behaviour: 1. A review of the literature on social and dam-foal behaviour*. *Appl. Anim. Ethol.* 10, 165–178.
- Christensen, J.W., Zharkikh, T., Ladewig, J., Yasinetskaya, N., 2002a. Social behaviour in stallion groups (*Equus przewalskii* and *Equus caballus*) kept under natural and domestic conditions. *Appl. Anim. Behav. Sci.* 76, 11–20. [https://doi.org/10.1016/S0168-1591\(01\)00208-8](https://doi.org/10.1016/S0168-1591(01)00208-8).
- Christensen, J.W., Ladewig, J., Søndergaard, E., Malmkvist, J., 2002b. Effects of individual versus group stabling on social behaviour in domestic stallions. *Appl. Anim. Behav. Sci.* 75, 233–248. [https://doi.org/10.1016/S0168-1591\(01\)00196-4](https://doi.org/10.1016/S0168-1591(01)00196-4).
- Crowell-Davies, S.L., Weeks, J.W., 2005. Maternal behaviour and mare-foal interaction. In: Mills, D., McDonnell, S. (Eds.), *The Domestic Horse: The Evolution, Development and Management of its Behaviour*. Cambridge University Press, Cambridge, pp. 126–138.
- Crowell-Davis, S.L., 2007. Sexual behavior of mares. *Horm. Behav.* 52, 12–17. <https://doi.org/10.1016/j.yhbeh.2007.03.020>.
- De Oliveira, R.A., Aurich, C., 2021. Aspects of breeding stallion management with specific focus on animal welfare. *J. Equine Vet. Sci.* 107, 103773. <https://doi.org/10.1016/j.jevs.2021.103773>.
- De Oliveira, R.A., Aurich, C., 2023. Stallion management on breeding facilities – a questionnaire. *J. Equine Vet. Sci.* 125, 11. <https://doi.org/10.1016/j.jevs.2023.104585>.
- van Dierendonck, M.C., 2006. The importance of social relationships in horses. PhD Thesis, Utrecht University, The Netherlands.
- Erber, R., Wulf, M., Rose-Meierhöfer, S., Becker-Birck, M., Möstl, E., Aurich, J., Hoffmann, G., Aurich, C., 2012. Behavioral and physiological responses of young horses to different weaning protocols: a pilot study. *Stress* 15, 184–194. <https://doi.org/10.3109/10253890.2011.606855>.
- FAWC, 2012. The five freedoms. (<http://www.fawc.org.uk/freedoms.htm>) (accessed 25 March 2025).
- Feh, C., 1988. Social behaviour and relationships of przewalski horses in Dutch semi-reserves. *Appl. Anim. Behav. Sci.* 21, 71–77. [https://doi.org/10.1016/0168-1591\(88\)90101-3](https://doi.org/10.1016/0168-1591(88)90101-3).
- Feh, C., 1999. Alliances and reproductive success in camargue stallions. *Anim. Behav.* 57, 705–713. <https://doi.org/10.1006/anbe.1998.1009>.
- Feh, C., de Mazières, J., 1993. Grooming at a preferred site reduces heart rate in horses. *Anim. Behav.* 46, 1191–1194. <https://doi.org/10.1006/anbe.1993.1309>.
- Feist, J.D., McCullough, D.R., 1975. Reproduction in feral horses. *J. Reprod. Fertil. Suppl.* (23), 13–18.
- Flamand, A., Eyraud, C., Llopis, V., Frantz, L., Cuir, F., Valençon, M., Petit, O., 2025. Pilot study on the resocialisation of stallions. *Appl. Anim. Behav. Sci.* 283, 106528. <https://doi.org/10.1016/j.applanim.2025.106528>.
- Franken Stevens, E., 1990. Instability of harems of feral horses in relation to season and presence of subordinate stallions. *Behaviour* 12 149–161. <https://doi.org/10.1163/156853990X00167>.
- Ginther, O.J., Lara, A., Leoni, M., Bergfeldt, D.R., 2002. Herding and snaking by the harem stallion in domestic herds. *Theriogenology* 57, 2139–2146. [https://doi.org/10.1016/S0093-691X\(02\)00702-1](https://doi.org/10.1016/S0093-691X(02)00702-1).
- Gmel, A.I., Zollinger, A., Wyss, C., Bachmann, I., Briefer Freymond, S., 2022. Social box: influence of a new housing system on the social interactions of stallions when driven in pairs. *Animals* 12, 1077. <https://doi.org/10.3390/ani12091077>.
- Górecka, A., Jezierski, T., 1997. Analiza wskaźników użyteczności rozplodowej kłaczy konika polskiego w latach 1956–1995. *Pr. Mat. Zoot* 51, 21–29.
- Górecka-Bruzda, A., Suwała, M., Palme, R., Jaworski, Z., Jastrzębska, E., Boroń, M., Jezierski, T., 2015. Events around weaning in semi-feral and stable-reared konik polski foals: evaluation of short-term physiological and behavioural responses. *Appl. Anim. Behav. Sci.* 163, 122–134. <https://doi.org/10.1016/j.applanim.2014.11.004>.
- Górecka-Bruzda, A., Jaworski, Z., Jaworska, J., Siemienuch, M., 2020. Welfare of free-roaming horses: 70 years of experience with konik polski breeding in Poland. *Animals* 10, 1094. <https://doi.org/10.3390/ani10061094>.
- Górecka-Bruzda, A., Jaworska, J., Stanley, C.R., 2023. The social and reproductive challenges faced by free-roaming horse (*Equus caballus*) stallions. *Animals* 13, 1151. <https://doi.org/10.3390/ani13071151>.
- Granquist, S.M., Thorhallsdottir, A.G., Sigurjonsdottir, H., 2012. The effect of stallions on social interactions in domestic and semi-feral harems. *Appl. Anim. Behav. Sci.* 141, 49–56. <https://doi.org/10.1016/j.applanim.2012.07.001>.
- Guillaume, D., Moussu, C., de Geoffroy, F., Chesneau, D., Keller, M., 2018. Olfactory stimulation or inhibition of sexual behavior of stallions in the non-breeding season. *Physiol. Behav.* 186, 1–9. <https://doi.org/10.1016/j.physbeh.2017.12.031>.
- Hain-Saunders, N.M.R., Knight, D.R., Harvey, A., Bruce, M., Hampson, B.A., Riley, T.V., 2025. *clostridioides difficile* in feral horse populations in Australia. *Appl. Environ. Microbiol.* 91, e02114-24. <https://doi.org/10.1128/aem.02114-24>.
- Hartmann, E., Søndergaard, E., Keeling, L.J., 2012. Keeping horses in groups: a review. *Appl. Anim. Behav. Sci.* 36, 77–87. <https://doi.org/10.1016/j.applanim.2011.10.004>.
- Hartmann, E., Boe, K.E., Christensen, J.W., Hyyppä, S., Jansson, H., Jørgensen, G.H., Ladewig, J., Mejdell, C.M., Norling, Y., Rundgren, M., Särkijärvi, S., Søndergaard, E., Keeling, L.J., 2015. A nordic survey of management practices and owners' attitudes towards keeping horses in groups. *J. Anim. Sci.* 93, 4564–4574. <https://doi.org/10.2527/jas.2015-9233>.
- Harvey, A.M., Beausoleil, N.J., Ramp, D., Mellor, D.J., 2023. Mental experiences in wild animals: scientifically validating measurable welfare indicators in free-roaming horses. *Animals* 13, 1507. <https://doi.org/10.3390/ani13091507>.
- Heitor, F., do Mar Oom, M., Vicente, L., 2006. Social relationships in a herd of sorraia horses: part II. Factors affecting affiliative relationships and sexual behaviours. *Behav. Proc.* 73, 231–239. <https://doi.org/10.1016/j.beproc.2006.05.005>.
- Henry, S., Zanella, A.J., Sankey, C., Richard-Yris, M.A., Marko, A., Hausberger, M., 2012. Adults May be used to alleviate weaning stress in domestic foals (*Equus caballus*). *Physiol. Behav.* 106, 428–438. <https://doi.org/10.1016/j.physbeh.2012.02.025>.
- Hensel, B., Jakop, U., Schmicke, M., Schröter, F., Jung, M., Schulze, M., 2023. Dual use of breeding stallions is possible without affecting the sperm quality. *Reprod. Dom. Anim.* 58, 691–698. <https://doi.org/10.1111/rda.14337>.
- Hoffmann, R., 1985. On the development of social behaviour in immature males of a feral horse population (*Equus przewalskii* f. *caballus*). *Z. Säugetierkunde* 50, 302–314.
- Hugason, K., Arnason, T., Jónmundsson, J.V., 1985. A note on the fertility and some demographic parameters of Icelandic toelter horses. *Livest. Prod. Sci.* 12, 161–167. [https://doi.org/10.1016/0301-6226\(85\)90088-0](https://doi.org/10.1016/0301-6226(85)90088-0).
- Jaworski, J., Jaworski, Z., McDonnell, S.M., Górecka-Bruzda, A., 2020a. Harem stallion changes are not associated with diminished reproductive performance of females in semi-feral konik polski horses (*Equus caballus*). *Theriogenology* 151, 1–6. <https://doi.org/10.1016/j.theriogenology.2020.03.033>.
- Jaworska, J., Jaworski, Z., Tobolski, D., Siemienuch, M., Janowski, T., Górecka-Bruzda, A., 2020b. Selection of reproductive partners in semi-feral horses (*Equus caballus*) is not influenced by major histocompatibility complex (MHC): a field study. *Appl. Anim. Behav. Sci.* 226, 104973. <https://doi.org/10.1016/j.applanim.2020.104973>.
- Jannarat, E., Marti, E., Berney, C., Janett, F., Bollwein, H., Sieme, H., Burger, D., Wedekind, C., 2018. Stallion semen quality depends on major histocompatibility complex matching to teaser mare. *Mol. Ecol.* 27, 1025–1035. <https://doi.org/10.1111/mec.14490>.
- Jezierski, T., Jaworski, Z., Sobczyńska, M., Ensinger, J., Górecka-Bruzda, A., 2018. Do olfactory behaviour and marking responses of konik polski stallions to faeces from conspecifics of either sex differ? *Behav. Proc.* 155, 38–42. <https://doi.org/10.1016/j.beproc.2017.09.015>.
- Kaseda, Y., Ogawa, H., Khalil, A.M., 1997. Causes of natal dispersal and emigration and their effects on harem formation in misaki feral horses. *Equine Vet. J.* 29, 262–266. <https://doi.org/10.1111/j.2042-3306.1997.tb03121.x>.
- Keiper, R., 1985. *The Assateague Ponies*, 1985. Tidewater Press, Cambridge, MD, USA.
- Khalil, A.M., Murakami, N., 1999. Factors affecting the harem formation process by young misaki feral stallions. *J. Vet. Med. Sci.* 61, 667–671. <https://doi.org/10.1292/jvms.61.667>.
- Kimura, R., 1998. Mutual grooming and preferred associate relationships in a band of free-ranging horses. *Appl. Anim. Behav. Sci.* 59, 265–276. [https://doi.org/10.1016/S0168-1591\(97\)00129-9](https://doi.org/10.1016/S0168-1591(97)00129-9).
- King, S.R.B., Gurnell, J., 2007. Scent-marking behaviour by stallions: an assessment of function in a reintroduced population of przewalski horses (*Equus ferus przewalskii*). *J. Zool.* 272, 30–36. <https://doi.org/10.1111/j.1469-7998.2006.00243.x>.
- Kirkpatrick, J.F., Turner, J.W., 1986. Comparative reproductive biology of north American feral horses. *J. Equine Vet. Sci.* 6, 224–230. [https://doi.org/10.1016/S0737-0806\(86\)80045-4](https://doi.org/10.1016/S0737-0806(86)80045-4).
- Klingel, H., 1975. Social organization and reproduction in equids. *J. Reprod. Fertil. Suppl.* 23, 7–11.
- Klingel, H., 1982. Social organization of feral horses. *J. Reprod. Fertil. Suppl.* 32, 89–95.
- Kroschel, L., Pilger, F., Aurich, J., Nagel, C., Aurich, C., 2025. Group housing increases alertness and social interaction compared to traditional single stabling in two-year old sport horse stallions during pretraining. *Animal* 19, 101584. <https://doi.org/10.1016/j.animal.2025.101584>.
- Ladewig, J., Søndergaard, E., Christensen, J.W., 2005. Ontogeny: preparing the young horse for its adult life. In: Mills, D., McDonnell, S. (Eds.), *The Domestic Horse: The Evolution, Development and Management of its Behaviour*. Cambridge University Press, Cambridge, pp. 139–149.
- Lange, J., Matheja, A., Klug, E., Aurich, C., Aurich, J.E., 1997. Influence of training and competition on the endocrine regulation of testicular function and on semen parameters in stallions. *Reprod. Dom. Anim.* 32, 297–302. <https://doi.org/10.1111/j.1439-0531.1997.tb01299.x>.
- Lansade, L., Bouissou, M.F., Erhard, H.W., 2008. Reactivity to isolation and association with conspecifics: a temperament trait stable across time and situations. *Appl. Anim. Behav. Sci.* 109, 355–373. <https://doi.org/10.1016/j.applanim.2007.03.003>.
- Lansade, L., Lévy, F., Parias, C., Reigner, F., Górecka-Bruzda, A., 2022. Weaned horses, especially females, still prefer their dam after five months of separation. *Animal* 16, 100636. <https://doi.org/10.1016/j.animal.2022.100636>.
- Lema, F.J., Ribeiro, S., Palacios, V., 2022. Observations of wolves hunting free-ranging horses in NW Iberia. *Carniv. Damage Prev.* 24, 1–10.
- Lemasson, A., Remeuf, K., Trabalon, M., Cuir, F., Hausberger, M., 2015. Mares prefer the voices of highly fertile stallions. *PLoS One* 10, e0118468. <https://doi.org/10.1371/journal.pone.0118468>.
- Linklater, W.L., Cameron, E.Z., Minot, E.O., Stafford, K.J., 1999. Stallion harassment and the mating system of horses. *Anim. Behav.* 58, 295–330. <https://doi.org/10.1006/anbe.1999.1155>.
- Linnartz, L., Linnartz-Nieuworp, E., 2017. The social organisation of natural herds of koniks (*Equus caballus*): subordinate stallions, rule or exception? *Lutra* 60, 27–42.
- McDonnell, S.M., 1992. Normal and abnormal sexual behavior. *Vet. Clin. North Am.* 8, 71–89. [https://doi.org/10.1016/S0749-0739\(17\)30467-4](https://doi.org/10.1016/S0749-0739(17)30467-4).

- McDonnell, S.M., 2000. Reproductive behavior of stallions and mares: comparison of free-running and domestic in-hand breeding. *Anim. Reprod. Sci.* 60, 211–219. [https://doi.org/10.1016/S0378-4320\(00\)00136-6](https://doi.org/10.1016/S0378-4320(00)00136-6).
- McDonnell, S.M., 2008. Practical review of self-mutilation in horses. *Anim. Reprod. Sci.* 107, 219–228. <https://doi.org/10.1016/j.anireprosci.2008.04.012>.
- McDonnell, S.M., 2016. Revisiting clinical stallion sexual behavior: applying ethology in the breeding shed. *J. Equine Vet. Sci.* 43, 18–22. <https://doi.org/10.1016/j.jevs.2016.06.070>.
- McDonnell, S.M., de Haviland, J.C.S., 1995. Agonistic ethogram of the equid bachelor band. *Appl. Anim. Behav. Sci.* 43, 147–188. [https://doi.org/10.1016/0168-1591\(94\)00550-X](https://doi.org/10.1016/0168-1591(94)00550-X).
- McDonnell, S.M., Murray, S.C., 1995. Bachelor and harem stallion behavior and endocrinology. *Biol. Reprod.* 52, 577–590. [https://doi.org/10.1093/bioreprod/52.monograph\\_series1.577](https://doi.org/10.1093/bioreprod/52.monograph_series1.577).
- McDonnell, S.M., Poulin, A., 2002. Equid play ethogram. *Appl. Anim. Behav. Sci.* 78, 263–290. [https://doi.org/10.1016/S0168-1591\(02\)00112-0](https://doi.org/10.1016/S0168-1591(02)00112-0).
- Mellor, D.J., 2016. Updating animal welfare thinking: moving beyond the “Five Freedoms” towards “a life worth living”. *Animals* 6, 21. <https://doi.org/10.3390/ani6030021>.
- Mellor, D.J., 2017. Operational details of the five domains model and its key applications to the assessment and management of animal welfare. *Animals* 7, 60. <https://doi.org/10.3390/ani7080060>.
- Mellor, D.J., Beausoleil, N.J., 2015. Extending the ‘Five Domains’ model for animal welfare assessment to incorporate positive welfare states. *Anim. Welf.* 24, 241–253. <https://doi.org/10.7120/09627286.24.3.241>.
- Mellor, D.J., Beausoleil, N.J., Littlewood, K.E., McLean, A.N., McGreevy, P.D., Jones, B., Wilkins, C., 2020. The 2020 five domains model: including human–animal interactions in assessments of animal welfare. *Animals* 10, 1870. <https://doi.org/10.3390/ani10101870>.
- Miller, R., 1981. Male aggression, dominance and breeding behavior in red desert feral horses. *Z. Tierpsychol.* 57, 340–351. <https://doi.org/10.1111/j.1439-0310.1981.tb01930.x>.
- Monard, A.M., Duncan, P., Boy, V., 1996. The proximate mechanism of natal dispersal in female horses. *Behav* 133, 1095–1124. <https://doi.org/10.1163/156853996X00611>.
- Morel, M.C.G.D., Gunnarsson, V., 2000. A survey of the fertility of Icelandic stallions. *Anim. Reprod. Sci.* 64, 49–64. [https://doi.org/10.1016/S0378-4320\(00\)00192-5](https://doi.org/10.1016/S0378-4320(00)00192-5).
- Noüe, P., Bernabé, J., Rampin, O., Vidament, M., Dumas, T., Palmer, E., Magistrini, M., 2001. Sexual behavior of stallions during in-hand natural service and semen collection: an observation in French studs. *Anim. Reprod. Sci.* 68, 161–169. [https://doi.org/10.1016/S0378-4320\(01\)00153-1](https://doi.org/10.1016/S0378-4320(01)00153-1).
- Ozogány, K., Kerekes, V., Fülöp, A., Barta, Z., Nagy, M., 2023. Fine-scale collective movements reveal present, past and future dynamics of a multilevel society in Przewalski’s horses. *Nat. Commun.* 14, 5096. <https://doi.org/10.1038/s41467-023-40523-3>.
- Pacheco, M.A., Herrera, E.A., 1997. Social structure of feral horses in the llanos of Venezuela. *J. Mammal.* 78, 15–22. <https://doi.org/10.2307/1382634>.
- Palmer, E., Chavatte-Palmer, P., 2020. Contribution of reproduction management and technologies to genetic progress in horse breeding. *J. Equine Vet. Sci.* 89, 103016. <https://doi.org/10.1016/j.jevs.2020.103016>.
- Pasing, S., von Lewinski, M., Wulf, M., Erber, R., Aurich, C., 2013. Influence of semen collection on salivary cortisol release, heart rate, and heart rate variability in stallions. *Theriogenology* 80, 256–261. <https://doi.org/10.1016/j.theriogenology.2013.04.003>.
- Popescu, S., Lazar, E.A., Borda, C., Blaga Petrean, A., Mitrănescu, E., 2022. Changes in management, welfare, emotional state, and human-related docility in stallions. *Animals* 12, 2981. <https://doi.org/10.3390/ani12212981>.
- Ritter, C., Beaver, A., von Keyserlingk, M.A., 2019. The complex relationship between welfare and reproduction in cattle. *Reprod. Domest. Anim.* 54, 29–37. <https://doi.org/10.1111/rda.13464>.
- Ruet, A., Lemarchand, J., Parias, C., Mach, N., Moisan, M.P., Foury, A., Briant, C., Lansade, L., 2019. Housing horses in individual boxes is a challenge with regard to welfare. *Animals* 9, 621. <https://doi.org/10.3390/ani9090621>.
- Rutberg, A.T., 1982. Inter-group transfer in assateague pony mares. *Anim. Behav.* 40, 945–952. [https://doi.org/10.1016/S0003-3472\(05\)80996-0](https://doi.org/10.1016/S0003-3472(05)80996-0).
- Salter, R.E., Hudson, R.J., 1982. Social organization of feral horses in Western Canada. *Appl. Anim. Ethol.* 8, 207–223. [https://doi.org/10.1016/0304-3762\(82\)90205-X](https://doi.org/10.1016/0304-3762(82)90205-X).
- Šandlová, K., Komárková, M., Ceacero, F., 2020. Daddy, daddy cool: Stallion–foal relationships in a socially-natural herd of exmoor ponies. *Anim. Cogn.* 23, 781–793. <https://doi.org/10.1007/s10071-020-01388-x>.
- Sigurjonsdóttir, H., Thorhallsdóttir, A.G., Hafthorsdóttir, H.M., Granquist, S.M., 2012. The behaviour of stallions in a semiferal herd in Iceland: time budgets, home ranges, and interactions. *Int. J. Zool.* 162982. <https://doi.org/10.1155/2012/162982>.
- Sigurjonsdóttir, H., Haraldsson, H., 2019. Significance of group composition for the welfare of pastured horses. *Animals* 9, 14. <https://doi.org/10.3390/ani9010014>.
- Sigurjonsdóttir, H., Snorrason, S., van Dierendonck, M., Þórhallsdóttir, A., 2003. Social relationships in a group of horses without a mature stallion. *Behav* 140, 783–804. <https://doi.org/10.1163/156853903322370670>.
- Søndergaard, E., Christensen, J.W., 2007. The effects of social environment on the behaviour of young horses. In: Hausberger, M., Søndergaard, E., Martin-Rosset, W. (Eds.), *Horse behaviour and welfare*. Wageningen Academic Publishers, pp. 71–77.
- Stanley, C.R., Mettke-Hofmann, C., Hager, R., Shultz, S., 2018. Social stability in semiferal ponies: networks show interannual stability alongside seasonal flexibility. *Anim. Behav.* 136, 175–184. <https://doi.org/10.1016/j.anbehav.2017.04.013>.
- Tadich, T., Smulders, J.P., Araya, O., Nicol, C.J., 2012. Husbandry practices associated with the presentation of abnormal behaviours in Chilean creole horses. *Arch. Med. Vet.* 44, 279–284. <https://www.redalyc.org/articulo.oa?id=173024970011>.
- Tarouco, A.K., Freitas, C.C., Neves, A.P., Gregory, R.M., Mattos, R.C., 2018. Sexual and social behaviors of pony stallions and mares. *Anim. Reprod. Sci.* 6, 535–535.
- Theunissen, B., 2019. The oostvaardersplassen fiasco. *Isis* 110, 341–345. <https://www.journals.uchicago.edu/doi/full/10.1086/703338>.
- Tilson, R.L., Sweeny, K.A., Binczik, G.A., Reindl, N.J., 1988. Buddies and bullies: social structure of a bachelor group of przewalski horses. *Appl. Anim. Behav. Sci.* 21, 169–185. [https://doi.org/10.1016/0168-1591\(88\)90106-2](https://doi.org/10.1016/0168-1591(88)90106-2).
- Tyler, S.J., 1987. The behaviour and social organization of the new forest ponies. *Anim. Behav. Monogr.* 5, 87–196. [https://doi.org/10.1016/0003-3472\(72\)90003-6](https://doi.org/10.1016/0003-3472(72)90003-6).
- Visser, E.K., Ellis, A.D., Van Reenen, C.G., 2008. The effect of two different housing conditions on the welfare of young horses stabled for the first time. *Appl. Anim. Behav. Sci.* 114, 521–533. <https://doi.org/10.1016/j.applanim.2008.03.003>.
- Walborn, S.R., Love, C.C., Blanchard, T.L., Brinsko, S.P., Varner, D.D., 2017. The effect of dual-hemisphere breeding on stallion fertility. *Theriogenology* 94, 8–14. <https://doi.org/10.1016/j.theriogenology.2017.02.003>.
- Wilson, M., Twigg-Flesner, A., 2017. A preliminary comparison of semen quality between competing and non-competing equine stallions. *J. Vet. Sci. Tech.* 8, 443. <https://doi.org/10.4262/2157-7579.1000443>.
- Wilson, M., Williams, J., Montrose, V.T., Williams, J., 2019. Variance in stallion semen quality among equestrian sporting disciplines and competition levels. *Animals* 9, 485. <https://doi.org/10.3390/ani9080485>.
- Wolfe, M.L., Ellis, L.C., MacMullen, R., 1989. Reproductive rates of feral horses and burros. *J. Wildl. Manag.* 53, 916–924. <https://doi.org/10.2307/3809588>.
- Wulf, M., Beythien, E., Ille, N., Aurich, J., Aurich, C., 2018. The stress response of 6-month-old horses to abrupt weaning is influenced by their sex. *J. Vet. Behav.* 23, 19–24. <https://doi.org/10.1016/j.jveb.2017.10.010>.
- Zollinger, A., Wyss, C., Bardou, D., Bachmann, I., 2023. Social box: a new housing system increases social interactions among stallions. *Animals* 13, 1408. <https://doi.org/10.3390/ani13081408>.