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Evaluation of harem stability in wild and feral horses

BACHELOR'S THESIS

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Declaration

I hereby declare that I have done this thesis entitled Evaluation of harem stability in wild and feral horses independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague 18. 4. 2024

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Lucie Mojžíšková

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Abstract

Wild and feral horses form relatively stable groups called harems, with strong long-term bonds between the members. Occasionally the stability is disturbed by individual horses changing bands. The thesis aims to provide a comprehensive review of existing literature on harem stability, to evaluate the main factors that have an impact on the rate of the changes and to extract and evaluate numerical data through a meta-analysis.

The research shows several mutually interconnected factors, that affect harem stability to different levels. The factors were divided into two categories. First category covered the external factors, which include environmental and seasonal changes, and human intervention in the form of fertility control via immunocontraceptions and surgical sterilizations. Second category covered the individual factors, that arose from the band itself, including behavioural aspects and hierarchical structure of the band.

The secondary aim to conduct meta-analysis to analyse rates of harem stability was unsuccessful, as existing numerical data regarding changes in the structure of bands are incomparable. The formula for calculating the rate of stability was different for each study and neither the criteria, on which the calculations were based (age of horses, sex of horses, time period during which changes in harems occurred) were not set up in a unified manner, therefore no statistical analysis could have been drawn from the review.

The different methodologies of harem stability calculations included counting individual horses that left the band, ratios of horses that left to horses that stayed with the band, or simple observation, whether the mares are still seen with the same stallion. Some researchers set up more complex formulas with specific time-binding and other criteria, to calculate the rate of harem stability.

Further research on harem stability of individual horse populations, as well as unification of the calculations will be necessary to ensure proper management and successful reintroduction projects.

Key words: Environmental effects; Individual effects; Meta-analysis; Reproduction; Social organization; Structure changes

1. Contents

List of tables

List of figures

List of the abbreviations used in the thesis

GnRH	Gonadotropin releasing hormone vaccine
PZP	Porcine Zona Pellucida
RCES	Rachel Carson Estuarine Sanctuary

2. Introduction

Dating back thousands of years, wild horses roamed vast territories across continents, their presence shaping ecosystems and influencing human cultures. With its ancestors of the *Equus* genus originating presumably from the plains of Northern America (Naundrup and Svenning 2015), the closest ancestor of the modern horse *Equus caballus* has dispersed over all continents except for Australia and Antarctica.

Currently, there are two subspecies of horse living in wild conditions, the domesticated horse (*Equus caballus*) and the Przewalski's horse (*Equus ferus przewalskii*). The Przewalski's horse, also known as takhi is believed to be the only wild subspecies of the horse, never domesticated unlike its' relative *Equus caballus*. The free roaming populations of *Equus caballus* not living under human care are known as feral, horses with domesticated ancestors which were released or escaped from horse keeping facilities and over the time formed aggregation, that are now being managed as wildlife (The Wildlife Society 2012).

Horses are harem forming species, aggregating themselves in generally stable, but still dynamic groups (Keiper 1986). In certain situation some rate of instability will occur in the harems, defined as emigration of breeding mares to different harems. There are many factors that can influence how stable the harems are and the cohesion of the group then impacts the movement, behaviour, and reproductive success of individual horses (Kaseda et al. 1995).

The relationship between these factors should be studied and understood to ensure proper management of the populations, as with constant landscape changes and shrinking of ecosystems, the large mammals increase the pressure put on the carrying capacity of their habitats, as well as create competition for resources with domestic animals.

3. Aims of the Thesis

The main objective of this study is to summarize the existing knowledge about harem stability in wild and feral horses worldwide. Furthermore, the aim is to evaluate the influence of environmental and individual factors on the social stability in horses, the implications of changes in social structures and to provide a comprehensive overview of the scientific literature dealing with this topic. Final aim is to evaluate the rates of harem stability through meta-analysis.

4. Methodology

The topic of the thesis was evaluated through comprehensive literature review of published books, scientific articles, and reports. The data was collected through available scientific databases, namely Science Direct, JSTOR, Scopus, PubMed etc. Other sources of information included government and research group webpages, such as U.S. Department of the Interior, National Park Service, or the International Takhi Group. For the meta-analysis numerical data were extracted from the scientific articles.

Keywords used for the research were: harem stability, band fidelity, consort relationship, feral horses, wild horses, horse behaviour, social organisation in horses, structure changes, reproductive success.

5. Literature Review

5.1. Ecology of wild and feral horses

Fig. 1 Feral horse (*Equus caballus*) (National Park Service).

Fig. 2 Przewalski's horse (*Equus ferus przewalskii*) (Prague Zoo).

5.1.1. Population dynamics

The horse is a species of the genus *Equus*, among asses and zebras and their respective subspecies. Equids are highly social animals found in two basic structures; harem-forming groups and territorial groups (Boyd et al. 2016). Horses similarly to plains zebra (*Equus quagga)* or mountain zebra (*Equus zebra)* form stable units called bands or harems, consisting of one dominant adult male, one or more adult females, not yet dispersed colts and fillies, and foals (Linklater 2000). In some harems subordinate males can be present, adult stallions which are permanent members of the group, however not related to the other harem members and prevented from siring any foals by the dominant male (Franke-Stevens 1990). On the other hand, arid-adapted equid species like Grevy's zebra (*Equus grevyi*), wild asses (*Equus africanus* and *Equus hemionus*) and the kiang (*Equus kiang*) form unstable groups where aggregation of adult individuals is rather temporary, with long-term bonds occurring only between an adult female and her current foal (Rubenstein 1986). Males of this type of social systems are highly territorial.

5.1.1.1. Harems

Horses have evolved to live in harem herds, also referred to as bands. This social organisation has a clear hierarchical system, in which each individual has its rank

(Keiper 1986). The ranking in females appears to be based on age and experience rather than aggression, as seen in mares making decisions for the band or even in individual lower-ranking horses, who show deference rather than fear towards the dominant animal. Other deciding factor might be genetics, as offspring born to higher ranking mares tend to be higher-ranking later in life (Houpt et al. 1978). Stallions may break into fights over dominance when defending females of their harem (Klingel 1974).

Herd formation is a survival strategy of many ungulates, it provides protection against predation, harsh environmental conditions, and even other members of own species (Rubenstein 1986). In wild and feral horses, the size of the herd is relatively small to moderate compared to other open habitat dwelling ungulates, with maximum of 9-21 members (Boyd et al. 2016; Széman et al. 2021). For comparison in black wildebeest (another grassland dwelling species), the maximum group size can be around 32 members (Richter 1971).

Harems consist of one or more stallions, one or more mares, young animals of both sexes called fillies (females) and colts (males), and foals. As in other group-living mammals a process of natal dispersal with the aim to breed occurs, during which young animals leave their natal group to join another group. In mammals it is more common for males to disperse than females (Greenwood 1980), however in case of horses, dispersal occurs for both fillies and colts (Monard et al. 1996; Górecka-Bruzda et al. 2023).

The age of dispersal ranges from 1 to 5 years in both males and females (Feh 1999; Monard et al. 1996; Górecka-Bruzda et al. 2023), with the average timing being around 2 years of age. Mares care about their offspring, forming strong attachment with their foals. Research on Misaki horses in Japan shows, that the mare's attachment with her first foal is stronger in males, as young stallions tried to return to their natal group multiple times after dispersal (Khalil and Kaseda 1997). With each subsequent foal a mare has, the attachment becomes shorter resulting in sooner emigrations of young horses (Khalil et al. 2010).

Research suggest that fillies are less likely to be driven out of their natal groups than colts are, that are experiencing more aggression from the harem stallion as they age (Monard et al. 1996; Górecka-Bruzda et al. 2023), disagreeing with Klingel's (1972) research on another harem forming equid, the plains zebra (*Equus quagga*), in which he

argues there is no evidence of stallions chasing their sons out of the natal group. On the other hand, there is a proposition that the relationship between mares and their adolescent sons can prolong the colt's stay with his natal herd (Stanley and Schultz 2012).

5.1.1.2. Bachelor groups

Horses do not like being on their own and prefer living amongst others of their kind, so when young colts leave or are driven out of their natal herd by the dominant stallion, they tend to group with other young colts and form so called bachelor bands (McDonell and Murray 1995). This type of social organisation is relatively stable. There are various ways in which the young stallions acquire mares and form a new harem. They can obtain young mares which have dispersed from their natal band (Keiper 1986) or unguarded older mares that wander away from their harem stallion (Khalil and Murakami 1999). Other option is to fight the harem stallion for all the mares or raid the band and steal some of them (Boyd et al. 2016). If the male has not dispersed, but stayed with his natal group, it is also possible for him to inherit the harem after the death of the dominant stallion (Roelle 2010).

5.1.2. Distribution

In present days, feral horses can be found on every continent with the exception of Antarctic in varying abundance (Petersen et al. 2023). Some of the countries of the studied populations include Canada (Salter and Hudson 1982) and numerous states of the U.S. (Berger 1977; Franke-Stevens 1990; Nuñez et al. 2009) in North America, Argentina (Scorolli and Lopez Cazorla 2010) and Venezuela (Pacheco and Herrera 1997) in South America, England (Tyler 1972), France (Feh 1999) and Portugal (Mendonca 2022) in Europe, Namibia (Greyling et al. 2007) in Africa, Japan (Kaseda 1995) in Asia or New Zealand (Linklater 2000) in Australia.

The Przewalski's horse distribution is much less widespread and highly dependent on reintroduction projects. Currently the subspecies can be found free ranging in Mongolia, China, Russia, Kazakhstan, and Ukraine (Equid Specialist Group 2018).

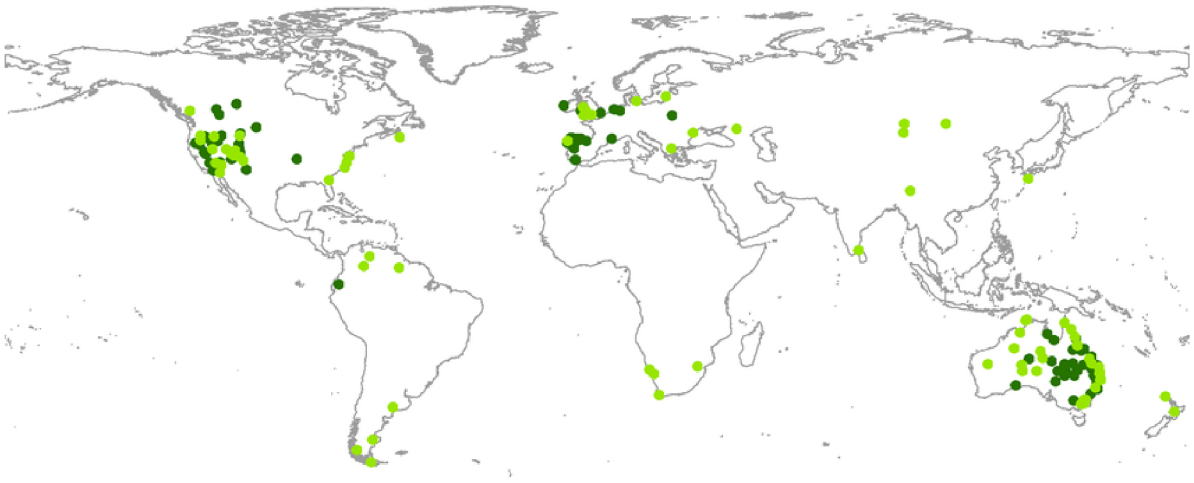

Fig. 3 Current distribution of wild-living horses (extracted from Naundrup and Svenning 2015). Colour of displayed data is not relevant for this thesis.

5.1.3. Habitat selection

Horses are large herbivores with modified monogastric digestive system. They are predominantly grazers, but may occasionally also eat various herbs, shrubs or even tree bark and leaves. Despite not belonging to the ruminant group, horses are able to digest large amounts of cellulose containing grasses, due to their enlarged cecum where fermentation occurs (Geor et al. 2013). Their jaws, flexible lips and hypsodont teeth are also helpful in the process. Horses are non-selective grazers, meaning they consume close to any forage regardless to species. Thanks to this adaptation, horses mainly inhabit open grasslands across the continents, but can be found on shrublands, deserts or even in coniferous forests as well (Girard et al. 2013).

The use and range of habitat is dependent mainly on availability of forage. In the arid Grand Canyon region of North America's Arizona, the range of local bands of feral horses decreases in size during the summer months presumably due to drought and scarce resources (Berger 1977). In Alberta, Canada, the range of local bands remains the same throughout the year. The habitat consists of mostly forested vegetation of mixed woods, with numerous meadows and shrublands (Salter and Hudson 1982). In New Zealand, the population of approximately 1500 Kaimanawa horses can be found in the Auahitotara ecological sector, a place with varying topographical features and vegetation. At this site, the horses favour tussock grasslands and depressed mesic grassland flush zones over high altitudes, slopes, and forested areas (Linklater et al. 2000).

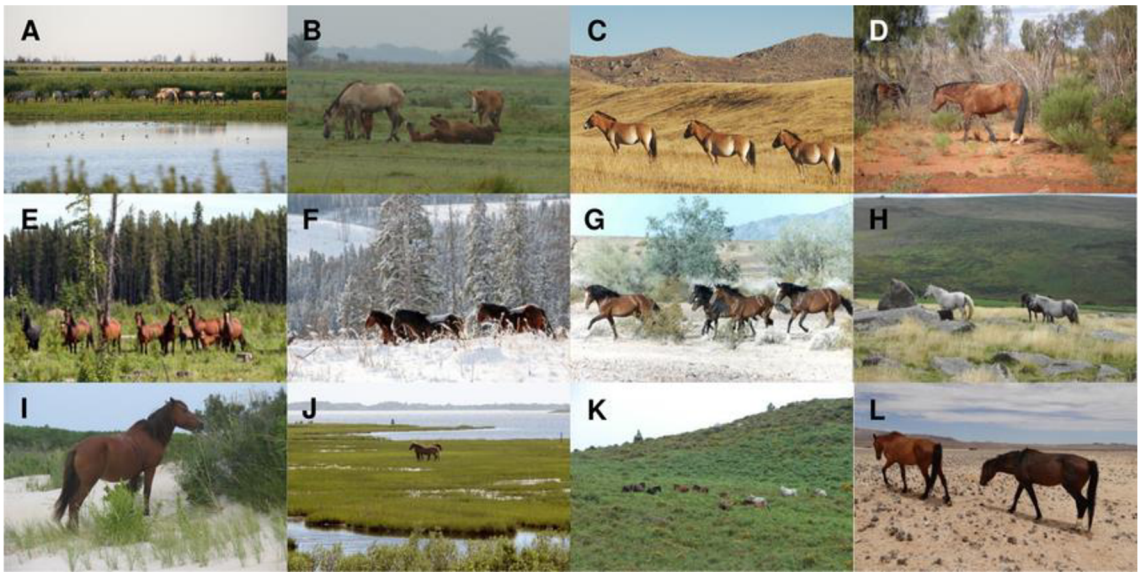

Fig. 4 Feral horses in different habitats (Naundrup and Svenning 2015).

5.2. Harem stability

Harem stability was first studied by Klingel in 1967, when he observed exceptional stability in social organizations of the plains zebra in Tanzania, where majority harems had no changes in membership whatsoever during the 2.5-year duration of the study (Boyd et al. 2016). In general harem stability describes the movement of individuals between bands and the affiliative bonds between mares and their harem stallion. The changes in band composition of harem-forming equids are rather infrequent, as the bonds created between the individual animals are long-lasting (Rubenstein 1986), however they are not completely absent.

The causes and frequency of harem changes should be known to the people and institutions managing the horse population, in order to successfully maintain the species, while conserving the land and other natural resources used by the animals to prevent degradation at the same time. The next chapters of the thesis will focus on an overview of different elements that influence harem stability in wild and feral horses, namely external factors like environmental and seasonal changes or human intervention in the form of fertility control, and internal factors, considering the herd structure and behaviour.

5.3. Effects of environmental factors on harem stability

In environmental causes, the stability correlates with the abundance of resources in relation to seasonal and climatic changes. In 1990, Franke-Stevens described the effect of scarce forage during winter months on the herd fidelity of feral horses of the Rachel Carson Estuarine Sanctuary (RCSE) in North Carolina. The reserve, located south of Beaufort is composed of two islands with diverse coastal habitats, including salt marshes, sand dunes, tidal flats, or shrub thickets, and at the time of the study held 12 bands of feral horses. During the study, Franke-Stevens reports one of the biggest harem instabilities ever observed, with 30% of adult females of the whole population changing bands. Most of the movement occurred during the winter months, when the abundance of forage is low and individual horses graze in far proximity of each other, in order to sustain themselves with sufficient food. The increased instability is attributed to two factors affected by the seasonal challenges, one being increased difficulty for harem stallions to guard their mares with the increased distances between individual animals, causing more frequent changes in the harem structure. The second factor affecting the affiliative relationships in the herd caused by competition for scarce food resources, is more frequent occurrence of stress induced aggression between females. The aggressive behaviour with the combination of lower frequencies of positive interactions between individual horses due to more time spent grazing, can therefore also be a driving factor for mares when changing bands.

Bernátková (et al. 2022) supports the claim with research on influence of weather on the behaviour of Przewalski's horses in the Mongolian Gobi Desert, which reports increased social interactions during sunny and warm weather, compared to feeding behaviour, which increased with cloudy and windy weather. It can be argued that since the behaviour can be notably altered by changes in weather only, then more intense environmental changes, such as periodic resource scarcity will have more severe effects on the social activities of horses.

Another supportive argument comes from Rubenstein's (1981) study, where he describes the relationships of another North Carolina population of horses, depending on richness and patchiness of forage. The horses inhabiting Shackleford Banks Island were seen forming different aggregations based on the vegetation zones. On the eastern side of the island, where continuous swale of grassland is growing, the groups of mares

were permanent with strong affiliative bonds. On the western side the aggregations were very loose and temporary. The habitat is mostly covered by sand dunes with small patches of vegetation, merging with dense maritime forest. According to Rubenstein, the size of the group was very dependent on the size of the grassland patch, operating on fission-fusion dynamic as the horses moved across the habitat, splitting apart when moving to smaller patches and fusing at large patches.

The feral horses of the Grand Canyon in Arizona are another group submitted to notable seasonal changes to the abundance of local resources, in this case water (Berger 1997). During the hot summer months, the ranges of the 4 harems present decreased to a common area with more abundant water springs in the dry season. Despite the close interband interactions caused by the changes in the horse's environment, the harems remained stable over the whole season. Berger reports strong agonistic behaviour, including 11 fights between stallions during interband encounters, but most importantly a tendency to mutually avoid any encounters if the necessity to use a common resource is not present. This factor might suggest the significance of intraband influences and decision making on the stability of horse harems being greater than the effect of environmental changes.

5.4. Effects of human intervention on harem stability

When managing wildlife populations, some of the tools include invasive methods. Historically it was common to use lethal methods to regulate the abundance of large ungulates, such as culling of individual animals (Wright 1999). Nowadays, the managers have shifted towards other methods, as a mean to respond to negative public opinions on animal hunting. Currently, the wide array of wild species is managed by fertility control, executed through immunocontraception or surgical sterilization (Fagerstone 2002; Bonaffini et al. 2023).

5.4.1. Immunocontraception

For the last fifty years, fertility control vaccines have been used to regulate populations of feral horses. Two types are currently in use, Gonadotropin releasing hormone vaccine (GnRH) and Porcine Zona Pellucida vaccine (PZP) (Kirkpatrick et al. 2011). The advantages of the vaccine are that there is no need for manipulation with the animal, as it can be administered remotely with the use of darts and that the contraceptive effects are temporary, the duration of contraceptive action being roughly one year (Powell and Monfort 2001; Kirkpatrick et al. 2011). It has been proven effective in inhibiting conception, however its influences on the animal's behaviour had only been studied recently.

During research on Shackleford Banks Island feral horses (Nuñez et al. 2009), mares who have been administered the PZP vaccine in the past years have been observed to change groups significantly more than unvaccinated control mares. The contracepted mares were also seen visiting other groups in comparison to control mares. This behaviour can be problematic for the population management, as the spike in harem infidelity can disturb relationships not only in the female's original group, but might also induce aggressive behaviour among other bands, caused by frequent interactions with stranger animals (Monard et al. 1996). The loosened intraband relationships caused by increased aggression can damage the entire hierarchy of a herd, as well as the mare's fidelity towards their harem stallion and prompt further harem instability.

The same population of horses was studied by Madosky (2011) who reports that 70.9% of mares treated with the PZP vaccine changed bands between two breeding seasons. The percentage of instability is almost equal to Klingel's (1967) findings on equid harem stability, where he reports 70% of studied individuals had not changed harems at all during the 2.5 years of study. With the time duration in which the changes in social organizations have occurred also taken into consideration when comparing Madosky's and Klingel's results on the matter, it can be argued that the PZP immunocontraception has one of the most severe effects on harem stability. Moreover, the vaccine seems to be affecting the females' behaviour years after the first administration (Nuñez et al. 2017), with band changes still more frequent than in untreated mares.

Fig. 5 Injection of PZP dart (Salt River Wild Horse Management Group n.d.).

Further research on PZP immunocontraception in Little Book Cliffs Wild Horse Range in Colorado, McCullough Peaks Herd Management Area in Wyoming and Pryor Mountain Wild Horse Range on Montana-Wyoming border suggests effects on horse behaviour, namely reproductive behaviour, which is closely linked to changes in band structures (Ransom et al. 2010).

The alternative to the Porcine Zona Pellucida is the Gonadotropin releasing hormone vaccine, which is widely used on different animal species, such as white-tailed deer, swine, as well as horses (Miller et al. 2008; Kirkpatrick et al. 2011). The effects of this type of vaccine had been tested on 16 bands of horses in the Theodore Roosevelt National Park in North Dakota. In contrary to the horse population treated with the PZP vaccine, which exhibits one of the largest harem instabilities recorded, the results of the study in North Dakota show band fidelity increase in comparison with past years (Ransom et al. 2014). However, in this case the use of GnRH vaccine has been supplemented with non-lethal culling practice or removing of specific individuals from the population. Because of the removal, the population dynamics have changed, instigating that the causes of higher stability in the bands might have been more of a social factor rather than direct effect of the GnRH vaccine administration.

5.4.2. Surgical sterilization

Other method of population control tool used in wild and feral horses is surgical sterilization, in form of castration or vasectomy in males and spaying in females. Unlike immunocontraceptions, surgical sterilization is permanent and cannot be reversed if the need arises (Kane 2018), therefore it is not a very sustainable method for fertility control. It has been deemed ineffective in reducing the populations to a notable extent in horses and other wildlife (Eagle et al. 1993; Boulanger and Curtis 2016) In addition to that, surgical treatments of wildlife can be seen as unethical by the public, making it less desirable than other methods of contraception.

The effects on horse behaviour caused by surgical fertility control have not been studied excessively, therefore not many conclusions can be drawn on the topic. Asa (1999) suggest correlation between vasectomy treatment, harem stability and reproductive success of stallions, however there was no direct indication that vasectomy would cause higher or lower stability in harems.

This claim is supported by a more recent study conducted on a population of Utah feral horses, which appears to show a more direct link between surgical sterilization and changes of stallion behaviour being observed (King et al. 2022). Over time, some of the castrated males tended to lose their harem maintaining behaviour and their harems reduced in size. However, the authors argue that the changes in organisational structures of the bands were more likely female dependent, rather than due to changes in the male's behaviour, as the castrated males did not lose their reproductive or agonistic behaviour or interest in mares. It therefore seems that in comparison with immunocontraception, the surgical sterilization method has less significant effect on harem stability.

Fig. 6 Harem tending behaviour (stallion positions himself between his mares and a stranger stallion) (Ransom and Cade 2009).

5.5. Effects of social structure of herds on harem stability

Horses are social animals with strong interindividual bonds, forming cohesive groups. Living in groups provides certain benefits, including predation risk mitigation or improved access to resources (Mendonca et al. 2021), but the dynamic environment also affects each individual member in various ways. According to available literature on the topic of harem stability, organisational structures and their variables are one of the most diverse factors that have an impact on the rate of changes in the bands.

5.5.1. Intraband relationships

One of the basic levels of evaluating harem stability based on social structures, is through the relationships between individual animals within a band. Familiarity between horses seems to be a crucial factor when talking about the cohesion of their group. It can be seen for example during natal dispersal of young mares, who tend to base their choice of band based on their familiarity of resident females (Monard and Duncan 1996). The fidelity of older mares appears to be influenced in the same manner, as familiar individuals tend to spend time in close proximity and do not move far from the herd (Mendonca et al. 2021). The same individuals spend more time performing affiliative behaviour, such as grooming, resulting in strengthened bonds within the group. This argument is supported by research on feral horse population on Cumberland Island, Georgia (Goodloe et al. 2000), where the great instability of local bands is attributed among other factors to lose bonds between the females.

A specific relationship, that directly effects stability in horse social organisations is the consort relationship between a mare and her harem stallion. The consort relations are important in the context of harem forming species, as in most cases only the harem stallion is breeding with the mares of his band (Boyd et al. 2016), therefore maintaining the reproductive success of the population. There is a strong correlation between the strength of a bond a mare has with her consort stallion and the mare's tendency to change harems (Kaseda et al. 1995).

5.5.2. Subordinate stallions

In case the band is not a single male, but has other permanent male members, the dynamics can be changed significantly. Males not in the position of dominant harem stallion, but who are permanent members of a band are called subordinate (Franke-Stevens 1990). These stallions usually do not breed with females, as that right is exclusive to the harem stallion (Górecka-Bruzda et al. 2023), instead they seem to be of use in other ways. Research suggest that subordinate males can help with guarding of the females and warding off intruders (Feh 1999). In some cases, higher harem stability has been attributed to the presence of subordinate stallions, such as in Franke-Steven's (1990) research, in which she states a clear link between subordinate males in a harem and number of females leaving, as of all mares changing bands during the period of study, none were from multi-male bands. The proposed link is supported by Miller (1981), who states that dominant stallions benefit from the presence of subordinate males when defending their females from being taken by males from other groups. He claims multi-male groups to be both more stable and bigger than those of a single stallion tenure.

On the other hand, more recent studies have shown little to no effect of subordinate stallions on harem stability. There is a consensus that subordinate stallions can affect the aggression levels and harassment towards females in a band (Miller 1981; Linklater et al. 2013; Pinto et al. 2022), however their presence does not necessarily mean greater harem stability. During an experimental removal of subordinate males in New Zealand Kaimanawa feral horse population (Linklater et al. 2013), the bands were observed if any changes in composition or behaviour would occur. Results of the study show, that during the time spent without the presence of other stallions, the composition of the harems has not changed and in addition to that the aggressive behaviour towards mares was reduced. This case suggests that multi-male bands are unnecessary in context of harem tending, even counter-productive in certain settings.

The research done on a population of feral horses in northern Portugal diversifies the results even more, as local single-male bands had more females than multi-male bands and that harem stability was not dependent on the number of males per band (Pinto et al. 2022). It therefore appears that although subordinate stallions do

influence their bands to some level, there are factors with greater impact on the stability of the groups.

5.5.3. Hierarchy

Hierarchies are an important aspect of equid social organisations and can have an effect on their stability. There are two types of dominance compositions in horses, the intraband hierarchy regarding individuals within a single band, and the interband hierarchy regarding the ranking between different bands (Boyd et al. 2016). Interband hierarchy considers the ranking of a band as a whole based on the ranking of its harem stallion and determines the band's access to resources shared withing a population of horses (Berger 1977).

In a population of Camargue horses in France, it was observed that higher ranking stallions were able to hold a harem on their own, whereas low-ranking stallions had to form alliances with other males, in order to guard their females (Feh 1999). In this case, such composition was beneficial for the low-ranking stallions, as they had a chance at holding mares against more dominant males, with the subordinate stallions assisting in fights and guarding. However, this might not be applicable to all feral horse populations, as in numerous instances harem stallions have no issue maintaining their bands on their own regardless of their rank (Linklater et al. 2013; Pinto et al. 2022).

Although fights between males of different ranks are common, hierarchical system does not always result in aggressive behaviour. In horses of the Grand Canyon region, a clear interband hierarchy was observe, during the bands' encounters and priority access to a water stream (Berger 1977). Despite number of fights occurring between the stallions when defending their harems, a common decision when meeting another band was to avoid it completely. All the bands were stable over the time of the study.

A specific type of hierarchy that might have a greater impact of harem stability, is the intraband hierarchy or ranking of animals within the harem. Usually, the older animals are higher on the rank, and the stallion is not necessarily the most dominant individual (Houpt and Keiper 1982). In some studies, it was reported that more aggressive animals were more dominant (Houpt et al. 1978), some argue that aggression

has no direct impact on ranking (VanDierendonck et al. 1995). The daughters of dominant mares are also often dominant (Houpt et al. 1978).

In past studies it was believed that animals of the same rank form closer affiliative bonds and direct their aggression towards lower ranking individuals (Briard et al. 2015). Boyd (1991) reports such behaviour in Przewalski's horses, where 55% females of the study directed aggression towards horses just below their rank. The females at the very bottom of the hierarchy then showed most aggression towards newcomers in the group. Mendonca (et al. 2021) disagrees with the claim, as in her study stronger affiliative (friendly) behaviour between horses of the same rank can only be seen in newly formed groups, where the hierarchy was not very apparent yet. In stable groups, animals of different ranks spent more time in close proximity, without the higher-ranking animal exhibiting aggressive behaviour towards the other. The proximity strengthens the relationships between the individual, resulting in stable harems.

To broaden the idea of intraband hierarchy having an impact on harem stability of horses, the stability of the hierarchy itself can be taken into consideration. In newly formed harems, where the hierarchy is still not clearly established, the aggression rates are higher compared to stable harems (Granquist et al. 2012). The relationship between harem stability and hierarchy stability can be double-sided, as instability in one can cause instability in the other and vice versa.

5.5.4. Presence of foals in the bands

Amongst the more commonly observed organisational factors mentioned above, there is a number of solitary influences of the harem stability, that might be specific for certain populations or have not been widely studied. One of the factors is the presence of foals in the band. In a study done on multiple populations of the northern U.S. it was found that the presence of foals in a band was directly linked to the mare's fidelity to the harem stallion (Ransom et al. 2010). In general, both pregnant mares and mares with foals tend to change or visit groups less than mares without foals (Nuñez et al. 2009). Despite this factor, Khalil et al. (2010) report number of mares in Japanese population of feral horses changing bands very shortly before parturition, therefore while pregnant. However, only young mares leaving their natal bands were considered, making up a small portion (14%) of all mares changing bands during the study. Additionally, the

number of times a mare was pregnant in the past seems to correlate with the strength of her harem fidelity, as they change groups less than mares with lesser years of pregnancy (Nuñez et al. 2009). This claim is supported by Berger (1983), who attributes harem instability to low foaling rates.

On the other hand, in research conducted on feral horses in predator abundant area of Serra d'Arga, Portugal, where foaling rates were consecutively low, the high instability of the harems was not attributed to this factor, as no significant correlation was found, but rather to the disappearance of the harem stallion (Mendonca et al. 2022). During a short period of time between 2017 and 2021, almost two thirds of all individuals disappeared, most probably due to predation and illegal human interventions. Approximately 76% of all remaining mares changed bands following the disappearance of their harem stallion. This highlights the grand importance the dominant stallions have in tending to their harem mares and maintaining stable groups, as well as pointing out the significance of structural changes based on outer influences.

In feral horses, living on Misaki Island in Japan, it was found that harem stability is something that transcends generations. In this population of feral horses the females, whose mothers had high stability were also generally very stable (Khalil et al. 2010). The tendency to stay with one harem stallion was passed from mother to daughter, presumably through observation of the mother's reactions towards the harem stallion and her behaviour in relation to other members of the band.

5.6. Effects of horse behaviour on harem stability

The stability of harem is greatly influenced by behaviour of each individual, as both affiliative (or friendly) and agonistic (aggressive) acts can be deciding factors if a member of a band will stay or leave. The behaviour of each horse within a band is conditioned by different aspects,

5.6.1. Herding or aggression?

As stated in the chapter that explores the influence of band structure on harem stability, the presence of a dominant stallion is crucial for the organisation to remain stable (Mendonca et al. 2022). The mission of the stallion is to guard his females from other males, look for lost animals and guide them back to the herd and reproduce. To accomplish this, the stallion behaves in specific ways. One of the major behaviours observed in harem stallions is herding or driving behaviour. Herding behaviour serves as a tool to move females into desired direction. The stallion assumes a threatening pose, lays his ears back and drops his head downwards while stretching it out (Feist and McCullough 1976). The intensity of the signal is determined by how low the stallion carries his head and by the speed he approaches the mares. This behaviour aids harem stallions in keeping the mares in close proximity, mitigating the threat of abduction by stranger males.

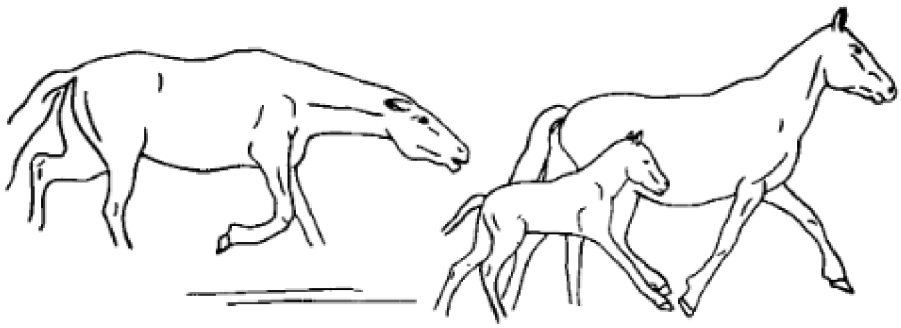

Fig. 7 Stallion herding a mare and her foal (Feist and McCullough 1976).

Franke-Stevens (1990) supports the argument with her research on the RCSE population of horses, where poor environmental conditions in winter months caused individual members of a band to graze in far proximity from each other. The increased distances between mares made herding more demanding, and the stallions were rarely

observed exhibiting such behaviour in comparison to other seasons, resulting in greater instability. Ransom (2010) describes herding as the most common intraband social behaviour observed in horses of northern United States.

Miller (1981) argues that in his study herding was not interpreted as a movement inducing behaviour, but rather as aggression towards the mares, either direct or redirected in response to other male's aggressive behaviour. This understanding of herding behaviour would have a completely different impact on harem stability, as intraband aggression can be the reason for some mares to emigrate.

The indications are the same for the small population of feral horses on Santa Cruz Island, located of the southwestern coast of California. Over the course of the study which took 5 years in total, only two females were seen changing bands (Blumenshine 2002). One of the moves involved a filly, for which it could be argued it was more of a case of natal dispersal. However, the second female changing bands bore clear marks of aggression in the form of hair loss caused by bites.

Madosky (2011) researched direct link between intraband harassment and harem instability. Her findings show strong correlation between both harassment rates from males and harassment rate from females and the harassed mare's tendency to change harems. Madosky also proposes a two-way relationship, as according to her findings, harassment can drive mares to change bands, but also that mares who changed bands are experiencing aggression more frequently, than stable mares. This claim can be explained by the animals' distrust towards horses they have not formed bonds with. According to the literature, it can be therefore said that if an individual is feeling uncomfortable or threatened in its' original band, it will seek other groups to reside in.

5.6.2. Fighting, posing, defending

A different behaviour exhibited by the harem stallion, are various forms of agonism towards other males in close proximity of the band. If multiple bands inhabit a common area, resources such as water streams or vegetation rich belts (common in island populations (Rubenstein 1981)) usually must be shared, causing inevitable encounters between the groups. When coming across stranger horses, the harem stallion uses vocalization to alert the other males of his presence. He then assumes a behaviour called 'posturing', a set of prefight agonistic movements (Berger 1977). These include

head bowing (rapid raising and lowering of head), prancing (quick repetitive steps with the front legs) and stomping. In some cases, posturing is where the interaction between the stallions end, in other the males break into physical fight, which includes kicking with both front and hind legs, biting and rearing on hind legs. Some fights are terminated by either the winning or the dominant animal chasing the other away, while attempting to bite at the rump of the escaping horse (Feist and McCullough 1976).

Fighting off rival stallions has direct effect on harem stability, as one of the female acquiring strategies used by males is raiding the harem and stealing portion of mares or defeating the harem stallion and taking over the whole band (Boyd et al. 2016). In Camargue feral horses in, as mentioned lower ranking stallions were seen forming alliances with subordinates to stand a chance against stallions higher up in the hierarchy when defending their harems (Feh 1999). It was argued that the alliances were not that important, regarding only social structure as a cause for harem stability, however considering other aspects, like ranking of the males and the behaviour they needed to form these alliances for, it appears as a more significant concept. These stallions benefited from the subordinate's assistance in fights, which they had to endure more frequently in comparison to higher ranking stallions and would have most probably lost (with the majority or all their mares) if they were on their own.

5.6.3. Affiliative behaviour

As an opposite to agonistic behaviour there is affiliative or friendly behaviour, that strengthens the bonds between the horses. It is mostly exhibited by the proximity in which the individuals stand and graze and through mutual grooming (King et al. 2016). Number of studies propose that the familiarity and positive relationships between horses can influence the stability of their groups.

Cameron (et al. 2009) reports that positive social interactions can lower the rates of harassment in the band, which is one of the reasons females change bands. Grooming occurs in both same sex and different sex individuals, giving the mares an opportunity to maintain bonds not only with the other females of the band, but also the harem stallion (Mendonca et al. 2021), which can result in stronger consort relationship and greater harem stability.

5.7. Implications of harem stability

Horses exhibit complex social behaviours and hierarchical relationships within their groups. Over the many years of research, their social organisations have been described as stable, with occasional changes usually caused by one or more of the factors illustrated in the previous chapters. The stability of these groups plays a crucial role in the horses' survival strategy, shaping their behaviour both as a group and as individuals, reproduction rates and habitat use.

5.7.1. Foaling rates and infanticide

The most studied effect of harem stability on the wellbeing of the band, is through foaling rates and reproductive success of the adult horses. Mares who are fully integrated into the band with stable relationships with the harem stallion had greater reproductive success, than mares with loser bonds (Cameron et al. 2009). The number of years a mare stays bonded to one stallion also positively correlates with her foaling rates (the frequency at a mare gives a birth to foals), giving her strong reproductive advantage against unstable females (Kaseda et al. 1995).

When discussing the structure of the bands, in some cases the presence of subordinate stallions was seen as an advantage (Franke-Stevens 1990; Feh 1999), in other as a neutral nuisance or direct disadvantage (Linklater et al. 2013). In the case of foaling success, the multi-male bands can pose a threat, as there is a risk of foal infanticide (Cameron et al. 2009). In case mares breeds with other than the harem stallion they sometimes change bands, which can result in an injury or death caused by the aggressive behaviour of the harem stallion towards the unrelated foal (Gray et al. 2012). The claim is supported by Ryder and Massena (1988), who report infanticide by a new harem stallion in a group of Przewalski's horses.

5.7.2. Movement of the band

The other implication of the rate of harem stability and social behaviour of the horses was the movement of the whole band. It was shown that a lot of decision making is done by the harem stallion, for example when steering his band in an attempt to avoid another stallion (Berger 1977). Females with higher fidelity towards the harem stallion

are more likely to stay in close proximity of him (King et al. 2016), therefore moving as one cohesive group. The stable relationships between mares acquired through mutual affiliative behaviour is also one of the impactful factors, as the familiar animals do not resort to aggression between each other, which would cause the group to be more dispersed across their home range (Madosky 2011).

Controlled use of the habitat is crucial for the reintroduction projects of Przewalski's horses, for which stable herds are desired in order to maintain stable foaling rates and increase the species' number in wild. By observing the movement patterns in Przewalski's horses caused by the dynamics in their harems, the project managers can determine the sites for reintroduction, which would be most suitable for the animals, and at the same time minimize contact with domestic horses of the local pastoralists (Kaczensky et al. 2007).

5.8. Meta-analysis

One of the aims of the thesis was to conduct a meta-analysis on the overall rate of harem stability if possible. After the extraction and evaluation of numerical data regarding movement of members between bands available it was apparent, that the meta-analysis will not be possible. Despite of every study researching the same concept of harem stability, which is considered to be a part of understanding the basic social structure of equids, the data were very varying and incomparable.

There was no common way of calculating the rate of stability, as each researcher used their own method that roughly described changes in band structure. In some cases, the stability was express as a ratio (Blumenshine 2002; Khalil et al. 2010; Scorolli and Lopez Cazorla 2010), in others as a simple number of females changing (Asa 1999). Some authors created a more complex formula to try and contain multiple aspects of harem stability in one calculation (Mendonca et al. 2021, Bernátková et al. 2022, Pinto et al. 2022).

Problematic were also the criteria set up for the harem stability calculations, as neither this factor was unified. Firstly, in most studies only mares were considered in as the variables in how stable the harems are; however, some have also included male transfers (Salter and Hudson 1982; Mendonca et al. 2021). In the case the study only focused on female transfers, the age of the mares was the limiting factor, as in most cases the mares were only considered in the stability calculation after reaching certain age, which was different for different studies.

The time period during which the stability was evaluated was also not consistent, as some changes were observed over the course of 1 year, some between breeding seasons, therefore over the course of few months, some during breeding season. Other were comparing the change of two breeding season. In one case the whole life of the mare after the age of 2 was considered (Kaseda et al. 1995), working with the concept of lifetime stability, rather than changes in annual or another short-term period.

Tab. 1 Methods of evaluating harem stability in literature.

Location	Calculations	Criteria	Source
Argentina	Percentage of all females that changed harems within a year.	Age 3 years and older	Scorolli and Lopez Cazorla 2010
Canada	Only those animals absent during at least two consecutive observations of original group and/or joining another group after initial description were considered to have left.	Categories considered: *Subordinate adult male* *Adult female with foal* *Adult female without foal* *Two-year-old male* *Two-year-old female* *Yearling male* *Yearling female* *Unidentified yearling* *Foal*	Salter and Hudson 1982
Japan	Seen with the same stallion on every observation during the breeding season of one year.	Age 2 years and older	Kaseda et al. 1995
Japan	Ratio of the number of years in which the mare has a stable consort relationship with the harem stallion to the total number of years after 2 years of age.	1. Age 2 years and older 2. Stable if a particular mare was seen with the same stallion at least eight times in the breeding season of one yearfrom early April to late August	Khalil et al. 2010
Mongolia	Number of mares present in the herd during the previous and the observation year, divided by the number of mares present in one or another year.	Breeding mares	Bernátková et al. 2022
Portugal	PT: The proportion of individuals that left the group was calculated by dividing the number of individuals that transferred/ disappeared during the interval between the two breeding seasons by the number of individuals existing in the group in the previous breeding season. PI: The proportion of individuals that integrated into the group was calculated by dividing the number of individuals that immigrated into the group during the interval between the two breeding seasons by the number of individuals existing in the group during the observed breeding season.	1. Males and females 2. For a group to be considered "stable", the proportion of individuals who transferred/disappeared or integrated into the group had to be ≤0.5	Mendonca et al. 2021
Portugal	1. Number of join events between consecutive field seasons. 2. Number of leave events between consecutive field seasons. 3. (mares joined - mares left)/0.5(final mare group size + initial mare group size)	1. Breeding females aged 4 years and older 2. Young females 2-4 years old	Pinto et al. 2022
U.S. (California)	Percentage of all females that changed harems within a year.	Age 3 years and older	Blumenshine 2002
U.S. (Nevada + Oregon)	Gained and lost members within a year and between years.	x	Asa 1999

As shown in the table, the methodology greatly varies. In more recent studies a tendency to set up more complex formulas that would better grasp the concept of harem stability and all the variables (Bernátková et al. 2022; Pinto et al. 2022), however neither of the studies provide results that can be statistically compared.

6. Conclusions

The aim of this thesis was to evaluate harem stability in wild and feral horses and summarize the factors influencing the changes in their social organisations. From a comprehensive review of existing literature on the topic it can be deduced, that the movement of horses between bands is usually caused by combination of factors that are closely interlinked, like forage scarcity and lack of affiliative behaviour or changes in band structure and aggression.

The aim to conduct a meta-analysis to determine the general rate of harem stability was not achieved, as the numerical data was not consistent. It appears that despite harem stability being widely studied by researchers in various populations across the world, the concept is yet to be explicitly defined. There was little to no consensus on what factors should be included when researching the changes in bands. The proposition is therefore to agree, whether changes in both male and female members should be considered, or if only mares should be applicable. Furthermore, future research should have unified criteria set up for determining the stability, like the age of the mares, time period during which the changes occur, or considering both animals that leave and animals that integrate into the group.

The goal for the future would be to quantify harem stability in individual bands. To make the result more transparent in the field of equine research, that already takes place on different sites across the world, the proposition is to create a unique formula, that would take into consideration the criteria mentioned above and determine the rate of harem stability in a way that is comparable for different horse populations.

Finally, as argued through the literature review, the factors affecting harem stability are in some cases universal, but often very population specific. It is therefore advised for the managers to keep records on the stability of bands in local populations, as the knowledge can play a crucial part in successfully executing reintroduction projects. Comprehensive data allows for comparison between populations with similar traits and external conditions (e.g. environment and climate) and understanding of the behaviour of managed groups.

The specific case in equine world would be the Przewalski's horse reintroduction efforts, for which stable foaling rates which are directly affected by

harem stability are desired, as well monitoring of the horses' movement across the area, to ensure best management practices, prevent conflicts with local rural communities and their livestock, and minimize the interactions between wild and domestic horses.

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