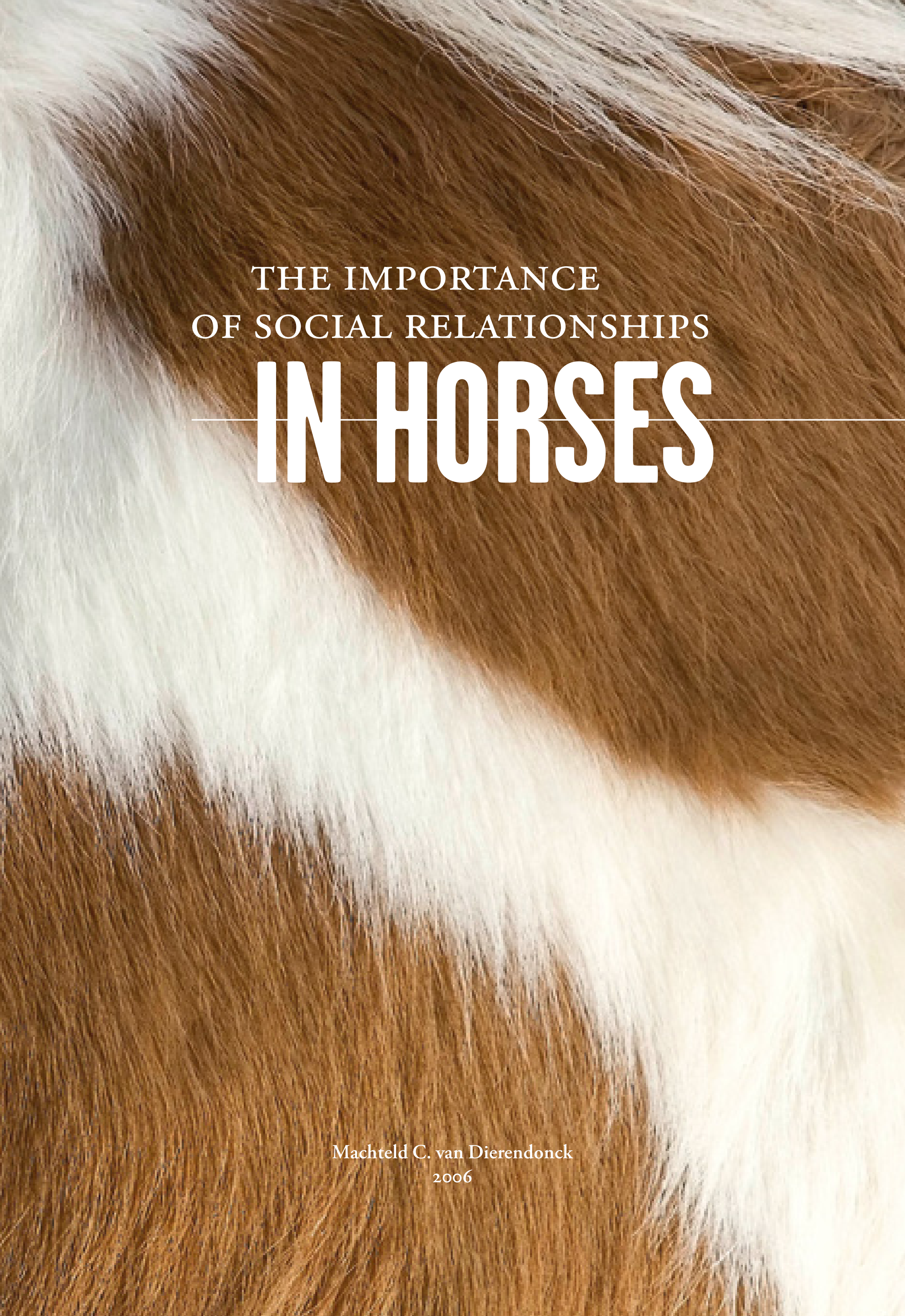

THE IMPORTANCE OF SOCIAL RELATIONSHIPS IN HORSES

Machteld C. van Dierendonck
2006

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THE IMPORTANCE OF SOCIAL RELATIONSHIPS IN HORSES

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CHAPTER 1

General Introduction

INTRODUCTION

The evolution of the horse covers more than 60 million years. During this period the fox sized, solitaire, browsing forest dweller on three digits adapted into a 13-14 hand (130-140 cm at the withers), social, steppe dwelling animal moving around on one digit and being able to thrive on low quality forage by the development of hypsodontic molars as well as by evolutionary adaptations to the digestive tract. The species has adopted early predator detection and flight as its primary defence mechanisms, thus rely on survival strategies centred on the formation of cohesive social bonds within stable bands (Mills and Nankervis 1999) (figure 1). For domestic horses much of their species specific behavioural and physiological capacities are based on the results of these millions of years of evolution directed to grazing and to optimal adaptation to unpredictable situations in a steppe environment.


PHOTO: MACHTELD VAN DIERENDONCK

Figure 1 Przewalski horses in Hustain Nuruu, Mongolia.

Horses were domesticated around 4000 BC, which may, in comparison with other domestic animals, be considered late (Levine 2005). According to Hale (1969) characteristics that facilitate domestication of certain species are 1) a social organisation with a clear dominance hierarchy, 2) a promiscuous reproductive strategy or a harem system, 3) offspring is precocial and stays for a relatively long period of time with one or both parents (so socialisation is required), 4) an absence of a strong flight reaction and 5) a high level of pliability towards diet and environmental stressors (see also Mignon-Grasteau et al. 2005). Most likely, 6000 years ago, wild horses scored relatively high on all of the above mentioned parameters, except for the fourth one. As in all domesticated species artificial selection changed, among many other aspects, also behavioural aspects in the horse. Changes can be found in terms of decreased reactivity, decreased flight distance, increased neoteny (juvenile characteristics like play, easy learning or decreased sexual foreplay), increased adaptation to human husbandry systems and increased physiological features which represent a higher economical value (Price 1999). However, although response thresholds at which animals show their defence mechanisms or stress reactions may change, studies on domestication show that the basic organisation of behaviour often remains relatively unchanged (Price 1999, Mills and Nankervis 1999). Indeed, in domestic horses, it has been shown that they de-domesticate relatively easily (Koene and Gremmen 2002), and evidence suggests that in horses species specific behavioural and physiological characteristics have remained relatively unchanged.

During evolution, sociality has developed as a trait associated with increased reproductive success in many species. In social mammals, the need to behave socially has become a prerequisite for survival of the offspring. It has been suggested that the execution of behaviours which are essential for the reproductive success of a species, became rewarding. Indeed, model studies in the rat indicate that the execution of social behaviour itself could be rewarding for the animal, not by restoring an internal physiological variable but by the performance itself (Spruijt et al. 2001). Social behaviour is also important for horses, but evidence that the physical execution of social behaviour in horses is rewarding in itself is lacking until now. (Nicol 1995, Nicol 1999, Weeks et al. 2000). The number of studies "looking from the mares or geldings own social perspective" concerning their social motivations and maintaining the social network in domestic horses is limited. Deprivation studies in horses are not easy to accomplish which made field studies an excellent alternative. Field studies provide indispensable information about natural incentives to animals and are essential in hypothesis generation for experimental studies.

In this thesis, social structure, social strategies and social interactions are investigated in groups of horses kept in captivity and in (semi)natural environments. Thereby, it is investigated whether individual horses use interventions as an instrument to influence their social network. Finally, the importance of these social interactions as an ethological need in mare–gelding herds are evaluated. The results of this thesis provides science based arguments to predict the horse's possibility to cope with the social factors in modern husbandry systems (isolation or overcrowding) in order to improve optimal welfare of horses in captivity.

SOCIALITY IN FERAL HORSES

Feral horses can be regarded as social animals. Sociality is an adaptive behavioural strategy, promoted when the costs (reduced availability of resources such as food and/or sexual partners) outweigh the benefits (e.g. increased defence mechanisms against predator attacks and decreased scanning time) (reviews by Mendl and Held 2001, Boyd and Keiper 2005). Sociality also increases intra-group competition and conflicts, disease transmission and entails a higher risk to attract predators. Since horses are prey animals and flight is their prime defence mechanism it is advantageous to spot potential predators as early as possible. Thus, shared vigilance (thereby increasing feeding time), concerted actions of group members during flight, and the associated communicative skills that are required for such actions are of primary importance for the members of each group. The key consequences of group life in horses have been the development of (ritualised) social interactions and social structures as a result of these interactions.

In social networks, social coherence can be described by a 'horizontal component' defined by affiliation and/or kinship, as well as by a 'vertical component', defined by dominance (Harcourt and de Waal 1992). In most species, possibly including feral horses, these two components do not much interfere with each other. In horses the two major affiliative behaviours performed are allogrooming (performed by all sexes and ages) and play (mainly performed by younger animals) (Tyler 1972, McDonnell and Poulin 2002, Waring 2003).

Worldwide, some feral horse populations range without any management practice, but in the majority of populations animal numbers are controlled by human interference. Such management is done by influencing sex ratios (via removing stallions or sub-adults (Boyd and Keiper 2005)) or by using contraceptives (decreasing fertility while safeguarding the social structure (Turner et al. 2002).

There is conclusive evidence that feral horses are truly social: e.g. life histories of the majority of feral horses seldom include periods of social isolation, (Linklater 2000, Waring 2003) except for a few weeks for bachelors in their pre-harem formation stage (Khalil and Muraka-

Figure 2. Two allogrooming horses. Note the anti-parallel position and the preferred grooming location.

PHOTO: MACHTELD VAN DIERENDONCK

mi 1999). Feral horses are also organised in discrete, long term stable, non-territorial reproductive associations with the characteristics of a female defence polygyny. This reproductive strategy results in two types of family bands: either harems (one adult stallion with several adult mares and their offspring) or multiple male bands (a few adult stallions: usually one breeding stallion and several peripheral younger stallions; adult mares and their offspring) (Linklater 2000). Apart from these family bands, which are skewed towards mares, the more loosely organised, male skewed, bachelor bands also exist in unmanaged populations. In addition, also multilevel societies (herds) have been observed in feral horse populations. In such herds breeding units (the family bands) and bachelor bands are organised as discrete social bands, while the herd as a whole shows social facilitation as well as coordinated flight for sudden dangerous environmental stressors (Schimmel 1914, Wernicke and VanDierendonck 2003, Waring 2003). Within each family band, adult mares form a long term (>10 years) stable nucleus, while the breeding stallion is regularly replaced (Linklater 2000). Furthermore, adult animals have strongly preferred associates both of affiliative nature and with regards to proximity (Duncan 1992, Kimura 1998, Feh 1999). In horses affiliative behaviour mainly consists of play and allogrooming in the latter two animals stand anti-parallel (figure 2) and gently nuzzle, nip or rub each other with their teeth (review by McDonnell 2003). Unlike grooming in primates, this behaviour almost exclusively takes place in a dyadic interaction, in which animals allow each other to come within their individual space and also increase safety by their position allowing a 360 degrees anti-predator vision. Contrary to primates, horses almost never show a passive and an active role, instead both groom simultaneously at approximately a similar spot. The function of allogrooming is among other things, to promote seasonal shedding and social bonding. Allogrooming originates from self grooming. Via de-arousing and reassuring behaviour in a mother-offspring relationship, allogrooming has evolved to a similar function in adult mammals (Spruijt et al. 1992, Mench and Sheamoore 1995). It has a calming and stress reducing effect, as reflected by lower heart rates and cortisol concentrations in the peripheral circulation when grooming at a preferred site close to the withers (Feh and Mazieres 1993, McBride et al. 2004).

Finally, analysis of cooperation in social interactions within herds of feral horses, underlines the relatively high level of organisational complexity of the group structure. Feral stallions for instance, use their social position to form alliances and coalitions which in turn enable them to try to gain better access to fertile females (Berger 1986, Kaseda and Khalil 1996, Feh 1999, Linklater and Cameron 2000, Linklater 2000). It is unknown whether this organisational complexity is also present in domestic mare–gelding herds where reproductive competition is absent. Only a few studies have been reported on triadic social interactions in other non-primate species (with intact males), e.g. interventions in zebra (Schilder 1990), coalitions and alliances among feral horses (Linklater 2000), within-group alliances among dolphins (Connor et al. 1992), and after-conflict affiliation in spotted hyena's (Hofer & East in Schino 2000). In general the cognitive capacities of a species are considered to be quite advanced when such a complex social organisation exists.

DOMESTIC ANIMALS AND WELFARE PROBLEMS

Modern husbandry systems sometimes induce problems in domestic animals because the limits of adaptive abilities of a species are exceeded (Spruijt et al. 2001). Wiepkema (1985, 1987) states that when a real value of a certain parameter ('actual value') is too much out of balance with a desired value ('expected value'), an animal has to take action. In case the action to be taken is chronically impossible - so the animal does not succeed in altering the actual value to approach the expected value - stress may emerge. This is also the case when two or more motivations are in conflict with each other due to incompatibility of required actions (Fraser and Broom 1990). In most species, including the horse, such conflicts are associated with food and foraging needs, locomotory requirements, exploratory or social needs, or a combination of these factors (Zeitler-Feight 2004, McGreevy 2004). In case of social conflicts numerous components can play a role; for example: overcrowding, isolation, dominance problems, unpredictable variability in social companions, early and/or abrupt weaning and physical obstruction to perform or finish normal (ritualised) social communication (Fraser and Broom 1990).

DOMESTIC HORSES AND WELFARE PROBLEMS

Most feral horses are descendants from domestic horses which have been released, or escaped, decades or even centuries ago (Boyd and Keiper 2005). All feral horses in the USA for instance are descendants of domestic horses shipped to the USA by Columbus or his successors. The relative ease with which domestic horses de-domesticate (Koene and Gremmen 2002), i.e. quickly form social bands (harems, multiple male bands or bachelor bands), show both male and female dispersal, survive, show appropriate social skills and produce fertile offspring, shows that selection during domestication has had little influence on the species specific characteristics of their social organisation.

During the last decades the use of horses changed from predominantly labour, to sports, leisure and pleasure. For the latter purposes humans selected horses to go fast, jump high, make beautiful movements. Although the financial investments and human emotions associated with this new use of the horse have changed husbandry and management practices considerably, it has not always been done in line with the (behavioural) needs of the horse and in particular these changes have not not always been in line with its social needs. Already in 1839 Holmes (1839) stated that "*racehorses and hunting horses of rich clients*" (Holmes 1839 p 168 L36-37) were "*fed very regular and with the best of provender*" (Holmes 1839 p 169 L6-7), but "*put in a stable, which is a prison to him… There he stands perhaps for 23 out of 24 hours or sometimes for weeks or month….*" (Holmes 1839 p 170 L5-8). These horses were much more prone to develop "*crib-biting*" (Holmes 1839 p 168 L39) than "*the cart-horse with the worst of provender*" (Holmes 1839 p 169 L7-8). Holmes stated "*I believe, then, crib-biting to be a habit which takes place in the consequences of the change which is produced in the animal when brought from a state approaching that of nature to an artificial one,- a state of domestication.*" (Holmes 1839 p 169 L38-41). He was way ahead of his time since most of his colleagues were convinced cribbing was a pathology of unknown origin. Even in those days the discrepancies between the human desires (economic, ergonomic, physical health, aesthetic, performance) and the evolutionarily rooted needs of horses were evident.

Conventional husbandry and behavioural aspects

Figure 3. Socially isolated and confined horses in their stables.

In most horse husbandry systems horses are kept confined and solitary: confined for up 23 hr/day (or even days) and solitary with social-contact-at-a-distance for years (for some even for a lifetime after weaning), figure 3. Many horse owners, keepers and veterinarians consider these husbandry systems as optimal in order to assure physical health, to prevent injury, to allow exact individual monitoring and to adjust individual health management. However, the very same systems often ignore some basic needs of the horse (e.g. social contact, foraging and locomotion needs), often resulting in abnormal behaviour (Vervuert and Coenen 2002, McGreevy 2004). Abnormal behaviours are also induced by inconsistently applying conditioning and positive or negative reinforcements, inappropriate training methods or distorted views on the physical and mental capacities of a horse (McGreevy 1997, McGreevy 2004). Such behaviour may be stereotypic, hyper-reactive or hypo-reactive to environmental variables (Fraser and Broom 1990, Mills 2005). The start of stereotypic behaviour usually is related to chronic stress due to mal-adaptations to cope with the environment (Spruijt et al. 2001, Mills 2003, Broom and Zanella 2004). The incidence of abnormal behaviours in the horse population varies between 7% (Vecchiotti and Galanti 1986), and 20 - 30% depending on the sport discipline or stable design (McGreevy et al. 1995, Boonstoppel and Schilder 1996).

Prevention of the development of stereotypic behaviour should be based upon a combination of the following three factors: 1) housing and management conditions which allow tactile contact with other horses (e.g. allogrooming), 2) daily free movement and 3) the provision of high amounts of roughage (Bachmann et al. 2003). This is in line with previous studies e.g. in race horses (McGreevy et al. 1995) in which abnormal behaviour was associated with time spent in the stable, type of stable bedding other than straw and box designs that minimised contact between neighbouring horses. In addition, management conditions around weaning appeared of crucial importance for the risk of the development of abnormal behaviour later in life. In a retrospective study of young horses (1-4 years) weaning by confinement, feeding concentrates after weaning and housing in barns after weaning were associated with an increased rate of development of abnormal behaviour, especially cribbing (Waters et al. 2002). Modern equine behaviour handbooks all describe social factors in the aetiology, treatment and prevention of abnormal behaviour (Mills and Nankervis 1999, Zeitler-Feight 2004, McGreevy 2004). Moreover, treatment of stereotypes also includes social factors for example by providing direct contact with neighbours or by equipping the stable with a mirror (Cooper et al. 2000, Mills and Davenport 2002).

Group housing and behavioural aspects

Figure 4. Group housing

As can be deducted from the above paragraphs, changes in feeding, husbandry and weaning practices, with a special emphasis on social contact, are likely to decrease the development of abnormal behaviours. By allowing more contact between individually housed horses or group housing systems an increase in welfare is to be expected. Group housed horses, however, usually live in relatively small areas and may have limited access to water, salt, food, social partners and resting or hiding sites, figure 4. Competition for scarce resources in a relatively limited area may lead to unwanted side effects like increased aggression (Mills and Nankervis 1999) and thus a decrease in welfare instead of the opposite.

Group husbandry systems usually consist of either single sex or mixed 'sex' (mare–gelding) groups. A limited number of studies have been performed on the social relations in mare–gelding groups. Group housed horses experience less stress during weaning (Heleski et al. 2002), are easier to handle (Christensen et al. 2002, Sondergard and Halekoh 2003), pass more pre set stages during training in a fixed training period (Sondergard and Ladewig 2004), have less respiratory problems and stronger bones (Vervuert and Coenen 2002) compared to individually housed horses. Major drawbacks however, are the increased risk of spread of infectious diseases (Vervuert and Coenen 2002) or individually acquired pathologies compared to individually housed horses. Other risks are decreased resting times (Zeitler-Feicht and Prantner 2000, Fader and Sambraus 2004) and reduced feeding times for low ranking horses compared to higher ranking horses (Zeitlerfeicht 1996). Thus, the welfare of domestic horses in modern group husbandry systems is not always guaranteed and more insight is required. Interestingly, hardly any information is available on aggression and aggressiveness, although dominance is the most important attribute determining resting and feeding time. Unfortunately, there is scientific disagreement on how dominance should be determined and which behaviours should be included to reflect dominance reliably. Some authors include in their dominance reflection analyses both offensive and defensive behaviours (Houpt and Wolski 1980) while others insist on using offensive behaviours only (Wells and von Goldschmidt-Rothschild 1979, Schilder 1988, Feh 1988). Submissive behaviour was considered to be of high importance in dominance evaluation according to some authors (Schilder 1988), while other authors did not include submission in their dominance analyses (Miller and Denniston 1979, Houpt and Wolski 1980, Roberts and Browning 1998). A study was set-up to solve this controversy.

Sociality as an ethological need: to what extend is this important in domestic horses?

In the previous paragraphs sociality in the horse in different environments is discussed from a evolutionary, proximate and an ultimate point of view. The indispensability of social behaviour can also be explained from a neurobiological, mechanistic point of view. This could possibly add a valuable extra dimension to the understanding of the importance of social relationships and the development of abnormal behaviour. This mechanistic approach is extensively (experimentally) studied in primates and rats (and humans), but still speculative for other social species including the horse.

In the mechanistic explanation, sociality is an 'ethological need' for social species. An 'ethological need' can be defined as: "a specific behaviour pattern that should be performed irrespective of the environment even when the physiological needs, which the specific behaviour serves, are fulfilled" (Jensen and Toates 1993). A behaviour may be regarded as an 'ethological need', if it has short term rewarding consequences irrespective of its long term consequences in a reproductive sense (Spruijt et al. 2001). Examples are rooting of pigs, exploration of predators like canines or bears, reproductive behaviour, social behaviour and dust bathing of poultry. One of the characteristics of an 'ethological need' is that the execution of this behaviour itself has rewarding properties rather than its direct consequences like physiological satisfaction when feeding. This mechanism is most likely mediated by neuro-endocrine pathways resulting in rewarding the execution of the behaviour in the brain, for instance by activating meso-limbic dopaminergic pathways during agreeable physical contact (van Ree 1985, Mench and Sheamoore 1995). Directly after birth the first strong rewards are experienced, when mother and offspring display different forms of affiliative behaviours and attachment. Nelson and Panksepp (1998) concluded that agreeable social contact in primates and rats is an ethological need (or even an addiction) due to the release of opioids. Since execution of behaviours which are 'ethological needs' apparently is essential for the animal, prevention of its display is stressful (Spruijt et al. 2001). For welfare there has to be a balance between the stress of the need to perform a behaviour and the reward of the execution of that behaviour. Absence of rewarding behaviours disturbs this balance, may result in chronic stress and can lead to stereotypic behaviours. For domestic horses it is not generally accepted whether or not the performance of affiliative social interactions is an 'ethological need'.

In modern horse husbandry systems there can often be too little or too much social contact (overcrowding). Both may lead to physiological and ethological stress behaviours. Deprivation studies (bottom-up approach) in horses are not easy to accomplish which makes field studies an excellent alternative (top-down approach).

Why Icelandic horses and why around parturition?

In order to study the mare–gelding social dynamics with minimal human influences, a homogenous population, living permanently outside in an enriched area, needed to be selected. The habituated individuals under investigation should know each other for a considerable amount of time, should have (known) different degrees of kinship and had to be born and raised in a mare–gelding herd, figure 5. These essential conditions reduce the number of confounding variables such as weaning procedures, socialisation and upbringing circumstances of the individuals. Preferably the individual life-histories should be known. The social dynamics were mainly assessed by studying interventions -

Figure 5. Birth of an Icelandic foal

and since these are low in frequency - a natural period of increased social dynamics was required for the study periods.

Most of the above mentioned factors were fulfilled in Icelandic horse herds during the foaling period when social dynamics were increased naturally. This study area had an additional advantage of 24 hour daylight during the observation period, enabling permanent observations.

AIM OF THE THESIS

This thesis focuses on the determination of different aspects of social relationships between domestic horses in mare–gelding herds. To evaluate the relative importance of social relationships in such herds, intervention patterns are analysed. Interventions are the horse's own 'instrument' to influence interactions between others. Fundamental knowledge on the social relations and social dynamics within social groups of animals without male reproductive competition will be an important result of the studies. Based on the findings, arguments and recommendations are provided to adapt husbandry systems such that the welfare of the horses may be improved.

After this general introduction (**chapter 1**), a review is presented about sociality among feral horses and the role of social bonds in different feral equine social organisations (**chapter 2**). The cultural differences in the human – horse relationship and their impact on husbandry and management are reviewed from a historical perspective. Subsequently, the possible consequences of sociality in feral horses based on the human - horse relationship type for modern domestic horse husbandry are assessed. Possible behavioural and physical consequences of modern husbandry for the health and welfare of domestic horses are evaluated. Preventive and curative solutions, including group housing are proposed.

In group housing, many problems are related to dominance. No clear guidelines were available how to reliably reflect and evaluate dominance in horses. A study was designed to determine a set of behaviours which could reliably be used for the assessment of dominance (**chapter 3**). Behavioural elements expected to be related to dominance, are analysed to find the most reliable candidates to reflect dominance. The behaviours which positively correlated with the required criteria are subsequently internally validated. After linearity checks, correlations with possible determinants of individual ranking are evaluated.

In mare–gelding herds, there is almost no male reproductive competition. These herds are also often much larger than feral bands or multiple male bands. The consequences of these two factors for the social relationships and spatial distribution are studied in a domestic herd on Iceland. In **chapter 4**, the social structure and its possible underlying forces in a mare–gelding herd are compared with feral bands in which reproductive adult stallions were present. The relative importance of affiliative and dominance relations, kinship and proximity are discussed for each sex-age class.

In the chapters 2-4 it is shown that adult mares play a crucial role in the stability and social dynamics in both feral and domestic herds. To analyse which factors within the adult mare subgroup determine the various roles an adult mare can have in a mare–gelding herd, data on the social and spatial dynamics of pregnant and non pregnant mares in a mare–gelding herd are evaluated (**chapter 5**). Changes in social behaviour, preferred partnerships, rank and proximity between pregnant and post partum adult mares are investigated in relation to those in non-pregnant control mares.

The stability and social dynamics of triadic equine social systems has only been addressed in feral studies in relation to coalitions and alliances of stallions. In the study it is analysed if such triadic dynamics in domestic mare–gelding herds exist (**chapter 6**). The importance of social relationships in different social situations is evaluated by studying intervention patterns. It is assessed whether and to what degree and with what possible aims an animal invests time, energy and takes risks to try to alter an ongoing interaction between two other animals.

In the summarizing discussion (**chapter 7**) the results of the different aspects of the above studied social dynamics within mare–gelding herds are integrated, evaluated and discussed. The complexity and the natural regulation are evaluated. The question is raised and explored whether affiliative social behaviour can be classified as an 'ethological need'. Direction of solutions for different husbandry problems and human–horse relationship problems based on the presented studies are proposed and remaining gaps in our knowledge requiring further study are defined.

* * *

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CHAPTER 2

Social contact in horses: implications for human-horse interactions

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ABSTRACT

The ancestors of the domestic horse were important prey species for many predators, including humans. Equids possess few physical defence mechanisms, relying on survival strategies centred on the formation of cohesive social bonds within stable groups. Mutual grooming is common between these individuals, maintains bonds and can be a source of reassurance following social conflict. Disruption of these bonds is associated with great social stress. Social isolation is uncommon in natural horse society.

Around 6000 BP the history of human-horse interactions began to change as the Eurasian wild horse population dwindled, threatening an important food resource. Early domestication processes began with human groups maintaining associations with free-ranging groups of mares and geldings, that were ridden, herded and harvested as meat, milk and hides. Cultural differences in approach to the human-horse relationship have been evident from ancient and classical history. These differences persist to the present day. There are two main approaches, a co-operative approach based upon understanding the behaviour of the horse, and an alternative approach based on human dominance and equine submission. Social interactions and contact between humans and horses have reflected these differences in approach.

Current management practices for horses are driven by human requirements and costs limitations, but often ignore basic equine needs. Intensive management of performance and leisure horses is frequently associated with social isolation, considerable alterations of feeding and foraging practices and confinement. These have behavioural and physical consequences for the health and welfare of horses. Preventive and curative behavioural solutions offer welfare, practical and financial advantages.

Keywords

Horses; social behaviour; human-horse interactions; domestication; husbandry practices.

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1 SOCIAL BEHAVIOUR OF ANCESTRAL, FERAL AND FREE-RANGING HORSES

1.1 Social organisations in feral horses

Feral equids are adaptable, ranging from high to low altitudes and inhabiting northern boreal plains, temperate forest, semi deserts and salty ocean shores. Despite this large variety, the social and spatial organisation of all studied feral populations are remarkably similar. Feral equid societies are mainly large, homomorphic and polygynous. Linklater (2000) compared the social and spatial organisation of 19 feral populations. He concludes, that, in areas with an unmanaged sex ratio, horses are generally organised in discrete, long term stable, non territorial reproductive associations. These usually comprise one (or occasionally a few) stallion(s), several adult mares and their offspring. These groups are referred to as harems, multiple male or family bands (Linklater et al. 2000, Berger 1986). In most cases there is a skewed, mare biased, sex ratio within a reproductive band, resulting in surplus stallions who often congregate in less stable bachelor bands (Duncan 1991, Linklater 2000, Waring 2003).

Occasionally authors describe the aggregation of family and bachelor bands into multilevel societies (herds). These do not only exist among zebra (sub) species (*Equus quagga spp*) but also occur within several feral domesticated horses (Wernicke and VanDierendonck 2003, MvD *pers. obs.*: Mongolian ponies). It is likely that herds were the predominant social organisation of Eurasian feral horses, since older textbooks refer to ‘aggregation of family bands into herds of 600-1000 horses’, possible due to large predation threats (Schimmel 1914). Within these herds there is clear interaction between bands, as well as coordinated escape in predation attacks. Both inter and intra band spatial and dominance relations occurred. Variations of these social organisation develop in areas where humans manage sex ratios (Linklater 2000).

1.2 Social life history of feral horses

Horses are precocial developers and thus develop rapidly during their first few hours and days of life. Within hours they perform a range of instinctive and learned behaviours, which they need to successfully bond with their dam and learn to recognise other natal band members. Within days foals assimilate with their natal band and interactions increase with their peers, siblings and other herd members (Waring 2003, Weeks et al. 2000, Houpt 2002, VanDierendonck unpub. data). They learn the social codes, develop physical abilities and explore their physical environment (Mills and Nankervis 1999). Approximately a month before the birth of a new sibling the dams gradually wean their foals (Waring 2003, Apter and Householder 1996). In temperate areas, most mares are seasonal breeders typically producing 4 foals in 6 years (Tyler 1972) (depending on the quality of the habitat).

Contrary to many species, in equids both sexes usually disperse between 1 and 3 years of age (Monard et al. 1996, Khalil and Kaseda 1997). To avoid inbreeding, juvenile mares prefer to move to groups with familiar residential mares but no familiar stallions, while juvenile stallions prefer bands with unfamiliar conspecifics (Monard and Duncan 1996). A bachelor unit facilitates a second phase of physical and social development of young stallions in a socially ‘less-serious’ environment (Hoffman 1985 in Waring 2003). Stallions gain their own mares by several strategies, including abduction and duelling, and start establishing heterosexual relationships when approximately 5-7 years (Kaseda et al. 1997). Feral horses are seldom solitary during their life neither during a change of band, nor when aging, but social isolation is always associated with social stress.

1.3 Social and physical contact in feral horse societies

Social behaviour is essential to minimise conflict and in promoting stability within a group (Goodwin 2002). An equine social unit can only act cohesively when individuals recognise each other and have predictable responses during social interactions, reducing the risk of injury through affiliative and agonistic (offensive, defensive and submissive behaviours) communication (Tyler 1972, VanDierendonck et al. 1996).

Social relations can be characterised in relation to areas of personal space that individuals perceive around themselves (Rees 1984, Mills and Nankervis 1999). The flight zone is that distance an individual actively maintains between itself and a perceived threat. In cases when there is neither a strong positive nor negative relationship, individuals are tolerated within another’s tolerance zone. Personal space differs from the flight zone and tolerance zone in distance and, social function. Generally, lower ranking animals respect the personal space around a higher-ranking individual, while preferred partners often associate within each other’s personal space. During affiliative interactions, individuals are actively encouraged to enter each others’ personal space.

1.4 Social positive (affiliative) relations

Social affiliation is essential to keep a social society together (Lindberg 2001). Preferred attachment between certain individuals is recorded in almost all systems at various levels, not only between dam and foal, but also among peers of all ages, genders and between species. During the first years of the reintroduction of Takhi (Przewalski’s horses: *Equus przewalskii*) in Hustain Nuruu, Mongolia, the first born colt foal had no peers nor siblings. He was the first to disperse but, as being the first, there were no equine bachelors to associate with. For several weeks at a time, he was recorded as within a herd of young red deer (*Cervus elaphus*). Only a year later, when younger peers also dispersed they formed a bachelor group together (MvD pers. obs.). It is interesting to note that until the present, this stallion has not been able to control his own mares, in contrast to many of his younger peers or siblings, possibly because he has not adequate learned the essential social skills for this task. Social facilitation / group living gives young animals social models, first from the dam then peers and other group members, that help to learn appropriate behaviour for each role (Dumont and Boissy 1999).

Equine affiliative relations are mainly evidenced by three reciprocal behaviours: allogrooming, social play and anti-parallel standing rest / mutual insect pest control (McDonnell 2003). Allogrooming does not only have a function in cleaning, removing hairs or relieving an itching skin, but when directed at certain locations it lowers the heart rate and cortisol levels (Feh and Mazieres 1993, Haverbeke et al. 2002). In this respect it is assumed to reduce social tension between group members and is used as a source of reassurance following social conflict.

For many years researchers could not agree whether spatial relations were an active process between individuals, similar to allogrooming relationships, or they were simply tolerating each other. VanDierendonck et al. (submitted) have shown that preferred social relationships are also the result of active individual initiatives. Moreover, spatial relationships are not only between individuals of the same sex-age, but also are related to the reproductive state of adult mares (barren, pregnant or lactating).

Social play is mainly performed between two or more foals, juveniles, bachelors or sometimes stallions. Play across these lines is also not uncommon. In the domestic setting, play is performed between adult geldings up to ages of great maturity (Sigurjonsdottir et al. 2003). Play is usually characterized as activities having no immediate use or function and involves a sense of pleasure (McDonnell and Poulin 2002). However, social play also serves a range of adaptive functions including musculo-skeletal development and maintenance, cardiovascular fitness, practicing reproductive and survival skills and building social and communication skills (McDonnell 1999, Zharkikh 1999, McDonnell and Poulin 2002, Brama et al. 2001).

1.5 Social negative (dominance) relations

In general if an animal ignores subtle offensive signals when within the personal space of another, and the other horse is dominant, there is often an offensive response towards the intruder causing the intruder to quickly leave the personal space of the dominant (Mills and Nankervis 1999, VanDierendonck et al. 1995). In free ranging horses, unsettled dominance relationships are usually only found between young horses, thus in a feral society, dominance mainly seems to control space and avoid conflicts (Goodwin 2002). Stallions especially, have a large range of ritualised behaviours assessing each others strength and avoiding direct contact and thus risk on injury.

A dominance relationship between two individuals is always a dynamic process, but not always clearly visible for the human eye. VanDierendonck et al. (1995) statistically analysed interactions within domestic herds to determine which behaviours would best characterise a dominance relation between two individuals. One of their conclusions was that care should be taken to distinguish between offensive and defensive behaviours. In general, offensive behaviours are performed with the head, while threats with the hindquarters can be used both offensively as well as defensively. Thus, threats with the hindquarters are less suitable for determining a dominance relation. This agrees with the suggestion by Fraser (1992) that avoidance is a better measure of individual position in a social system, than aggression. VanDierendonck et al. (1995) concluded that the combination of a few specific offensively used behaviours combined with submission give the best characterisation of a dyadic dominance relationship.

All dyadic dominance relations together can be used to construct a rank order of the whole band/herd. It is not clear whether such a rank order means something for a horse, or whether he only judges its own position towards other herd members. Rank orders within feral horses may be linear, at least at the top or bottom end, though they are also frequently circular. In general the position of the (α) stallion is context dependant: in case of male-male competition or predation he is dominant over all other band members, while in other situations e.g. food, water, saltlicks he can be submissive towards some mares (Houpt and Keiper 1982). A rank order often correlates with several factors, including; age, residence time, weight and aggressiveness, although there is some disagreement in the literature. This disagreement can largely be attributed to the difference in methods and whether or not the rank order is tested for linearity before testing co-factors. Mares are often ranked according to age or residence time. Interestingly there are indications that the top ranking mares are not the oldest, while these oldest mares are ranked just below (VanDierendonck et al. submitted).

2 HISTORY OF HUMAN – HORSE INTERACTIONS

The earliest evidence that we have of the importance of horses to human culture in Eurasia comes from faunal remains and cave paintings around 15,000 years ago from the South of France and Spain (Clutton-Brock 1992). Faunal assemblages of equids at Solutré, in the Mâcon region of France, indicate three separate populations of horses were predated by humans, but at very different times: Aurignacian, Upper Perigordian and Magdalenian periods (Levine 1983, 1979, 2002 pers comm.). At this site wild equids were hunted co-operatively by humans and in large quantities, though kills were probably of small bands or groups driven into a geographical cul-de-sac on the site. They were then skinned and some butchered on site (Olsen 1989). By 9000 years ago a combination of climatic change and an expanding human population appears associated with a reduction of the numbers of equids in the faunal record. There is a complete absence of equids at this time at sites associated with humans.

The first evidence of domestication of sheep, goats and cattle appears around 9000 years ago. The first indication of horse domestication does not appear until around 6000 years, ago at a small number of sites in the Ukraine, Western Europe and Asia. However, the domestication process probably proved problematic due to the difficulty of restraint and captive breeding. For example, recent evidence (Levine 2002) suggests that the horses at Dereivka in the Ukraine and Botai in Kazakhstan were probably tamed captives rather than truly domestic. At these sites most of the horses died during their most productive years, which is considered evidence of hunting. The presumed difficulty of keeping horses captive limited their early use in human culture and so Levine suggests that taming was probably a bi-product of hunting. Foals orphaned during the hunt could have been raised as pets and later found to be capable of functions other than food. The development of horse handling skills does not appear to have begun to influence human social culture until some time between the Neolithic and early Bronze age (Levine 2002). Evidence from the Plains tribes of 18th Century North America that capturing wild horses and stealing tamed or domestic ones was considered preferable to breeding them supports this argument (Levine 1999a). There could, therefore, have been a relatively long period during which horses were captured by chasing, driving and trapping as documented from Mongols and Plains Tribes (Levine 1999a).

There is some historical evidence that 'wild' horses were widespread in Eurasia until the Middle Ages (Levine 2002 pers.comm), though whether they were really wild, feral or a mixture of both is unclear. Recent mDNA sequencing data suggests that several distinct populations were involved in the domestication of the horse (Jansen et al. 2002).

2.1 History of social horse management

Due to the difficulty of keeping horses captive and breeding from them, and the difficulty of distinguishing domestic, tame and wild horses morphologically it is very difficult to postulate how early populations were managed. Evidence from Dereivka suggests that mares and castrated males may have been herded by riders mounted on tamed individuals (Levine 1999b), however, mares may have been covered by wild stallions (Levine 2002 pers comm.). Evidence that the broodmare was the foundation of Eurasian horse culture can be gained from classical through to recent history in Celt, Basque, Mongol, Bedouin, Khazakh and Gypsy sources. Here the bloodline of the mare is most highly regarded, as it was they and their foals that had to be lived with and that remained with nomads and farmers (Bennett, 1992).

The horse has been domesticated in China since approximately 3000BC. They were highly prized and some were obtained by brute force from outside China, e.g. the Ferghana horses that were derived from the Tarpan and prized for 'sweating blood' (producing sweat that was blood coloured), though this is probably evidence of infection with Parafilaria multipapillosa (Epstein 1969). There is limited information about how they were managed, though evidence from Chinese Bronze Age burials indicate a gradual increase in height from 133 cm to 149 cm at the withers (Ben-Shun 1989).

The Sythian horse cultures used their understanding of horse behaviour, gleaned from their nomadic existence with their horses, to become feared horsemen in conflicts throughout Eurasia from 1000 BC to the middle ages. Their horses were their most treasured possessions, they were furnished with gold inlaid saddles and bridles, had their tails plaited and were sacrificed and interred as grave goods of the nobility (Clutton-Brock 1992). The Sythian horse culture was probably the origin of the Greek myth of the Centaur. Unusually in the Classical world, the Sythians castrated their male horses to make them easier to manage. Consequently these geldings grew approximately 10 cm taller than the rest of the population and were used exclusively by the nobility (Rudenko 1970).

2.2 Cultural differences in approach to the human-horse relationship

2.2.1 Horses in European/Western societies

There appear to have been two main approaches to the horse-human relationship since the Classical period. One is based on co-operative understanding of the behaviour of the horse, the other based on human dominance over the horse (Goodwin 1999). Barclay (1980) considered that these differences originated in the type of mounted combat that different cultures employed. Both approaches were probably used then, as now, to different extents depending on the trainer and the purpose of the mount. For example, a war-horse is required to be obedient to his rider and suspend intra-specific agonistic interactions in order to mount an effective cavalry charge. It is, however, unlikely that all Roman cavalrymen were skilled horsemen (Hyland 1990), though many of the tribes they engaged in combat, including the Celts and Huns, were part of ancient horse cultures and so were likely to have become adept horsemen during childhood.

Early handling and training in the Classical world was described by the writings of the Greeks Simon and Xenophon, and although the Romans employed some of these principles there is no corresponding work in Latin on horsemanship (Hyland 1990). However, there are guidelines on housing horses in the Roman period attributed to Pelagnious, who paid particular attention to housing horses in dry stables with good floors to avoid problems associated with infections of thrush in the feet. Pelagonius and Columella both recommended keeping sick animals on deep beds of straw or chaff. Stabling at the Roman estate described by Varro comprised separate stalls for mares and in cold weather stables were shut and a brazier lit for warmth. At Pompeii stables with four stalls each with masonry partitions have been excavated and at sites in Syria stables have been located with tie rings and mangers. Several methods of housing horses indoors were evident from Latin texts which included references to loose boxes, stalls and racing stock housed in groups of hundred. Cavalry horses at temporary camps were tethered in picket lines as today. The Roman authors Pelagonius, Varro and Columella also described horse management requirements, handling skills and measures ensuring that horses did not become ill through unreasonable and avoidable stresses (Hyland 1990).

As in Classical times a range of horse-human relationships exist in current society, from lifelong companion to sporting utility vehicle (Endenburg 1999). This is accompanied by a spectrum of attitudes regarding these interactions ranging from co-operation to dominance/submission (Goodwin 1999). Even within equestrian disciplines that may appear as superficially similar as Classical Dressage and Competition Dressage, the attitude to the horse and the means of accomplishing results may be diametrically opposed (Odberg and Bouissou 1999).

2.2.2 Horses in nomadic societies

There is evidence of strong feelings of identity with horses in many nomadic societies, ranging from the Mongols to North American Plains Indians (Lawrence 1988). These nomadic peoples often consider their fate intertwined with their horses (Robinson 1999). Many of the horse cultures have been characterised as proud, defiant and aggressive when challenged. The horses of North American Crow Indians were highly esteemed and represent measurements of wealth and prestige (Robinson 1999), as did ancient Sythians (Clutton-Brock 1992). A wealthy North American Blackfoot named Many Horses (circa 1900) was reported to be able to describe a missing horse in great detail to boys sent to find it, though there may have been thousands of horses around the encampment (Ewers 1955). Though Blackfoot owners of large herds were able to identify individuals by markings and colour, they generally only named their horses when they were trained to be ridden plus a few prized mares and stallions. Blackfoot Chiefs selected campsites based on the abundance of species of grass that their horses preferred, however, individual families tended their own herds (Ewers 1995). In Blackfoot families care of the horse herds was entrusted to young adolescents. Their duties included driving the horses from their overnight pasture to water at daybreak and then driving them to new pasture near camp before breakfast. The owner of the horses would then select his mount(s) for the day. These buffalo hunting, war or racehorses were picketed (tethered) by the neck or foreleg close to the tipis overnight, where the wives were expected to keep watch over them. At midday the boys drove the herds to water again. The watering process was repeated a third time in early evening before driving them to their scattered night pastures, whereupon the lead mare was hobbled by the forelegs to prevent straying overnight (Ewers 1995) and the lads returned to camp. The Cree tribe practiced winter hobbling by the hind legs, leaving the front legs free to dig for grass through snow, though the Blackfoot did not hobble in winter. The horses received no supplementary feed and no hay was provisioned in winter prior to the establishment of Reservations. When grass in the vicinity of winter camps was consumed the camp was moved a few miles to new pasture. In severe snowfalls Cottonwood bark was stripped and fed to the horses (Ewers 1995).

2.3 Working horses and human interactions

In many cultures, those who work with horses develop a close bond and affinity with them based on mutual regard. This relationship is frequently functional, though open to abuse when economic drives combine with the less talented/empathetic members of human society. American mounted police officers report a close relationship with their horses based on spending many hours a day together. They consider this essential to developing mutual trust and being able to predict how their horses will behave in most situations (Lawrence 1988).

The ability to work with horses has frequently been ascribed mystical, occult or religious connotations in many societies throughout history. In Celtic nations this is often associated with the pagan horse cult and Epona, the goddess of the horse and fertility, from the pre-Roman period till present. In the UK and particularly in England and Scotland a secret society of horsemen, akin to Freemasonry, exist(ed), members included farriers, carters, ploughmen and ostlers (grooms caring for horses at inns). Initiation ceremonies were associated with pagan rituals that included the preparation of frog breast bones (symbolic of the frog in a horse's hoof) and communication of the 'Horseman's Word'. This was said to endow mystical powers over horses when whispered into the horse's ear and is probably the source of the term for Natural horsemanship trainers as Horse Whisperers. The collection of narratives, by oral historian George Ewart Evans (1960), from elderly horsemen who had worked the land prior to mechanisation described rituals and many traditional practices employed by men who had lived with, worked with and had taken great pride in their horses. Many folk remedies and control techniques appeared centred around detailed knowledge of the horse's olfactory preferences and responses to dietary supplements. Evidence that the relationship was not always unidirectional was provided in several accounts of draft horses successfully negotiating busy London streets to return an unconscious driver to the Brewery; First World War soldiers being saved from drowning by their mounts and of a horse lying down next to his collapsed groomsman overnight to keep him warm until help arrived (Denham 1970).

2.4 Social interactions and contact between humans and horses

Though the number of people currently interacting with horses professionally and recreationally is large, the variety and disparity of these interactions has rendered them easily overlooked. Consequently the contribution to the economy is also often ignored (Suggett 1999) and there has been little scientific enquiry into the nature of the relationship (Endenburg 1999, Robinson 1999).

Endenburg (1999) considers that the importance of the horse to many private owners is more emotional than economic, and that the attraction and attachment to horses is linked with the large number of voluntary workers in this sector. Many private individuals report a close relationship and bond with their horse and report great distress during illness and grief over the death of the horse (Lawrence 1993). In this respect the relationship with the horse can be compared to that between humans and dogs. However, it also differs in some respects, for example horses rarely share our homes and unlike the dog the bond may often not last for the lifetime of the horse, if the horse is outgrown, physically or aspirationally. The relationship between some riders and competition horses may be one that is deliberately held at a distance by the rider to enable them to push the animal to perform at its maximum potential, or due to the requirement to continually change mounts. However, even amongst sport horses close human relationships may develop, and these are not only limited to that between a horse and its groom.

Riding has been linked with human social status throughout history, and for some the horse is seen as a passport to a social group that might otherwise be unattainable (Robinson 1999). There appears an interesting dichotomy between human genders and their interactions with horses in current society. Most leisure and amateur riders are female, whilst most professional riders are male. The relationships reported between men and women and their horses also vary. Robinson (1999) reports that women are frequently more affectionate with their horses, while Brown (1984) described men as more punitive with their horses than with dogs and postulated that this was due to a greater perceived dominance threat from a larger animal.

Unlike to human-cattle handling (Grignard 2001) and perhaps due to its diversity and complexity current research in human-horse relationships is scarce but would benefit from further enquiry, particularly in terms of cost-benefit analysis and effects of the relationship on human and equine health. The research can be subdivided into a) indirect handling: husbandry and management, b) direct handling: training methods; and c) research related: to early handling or imprint training and the assessment of temperamental traits. The assessment of temperamental traits is only just starting to give insights in the mechanisms which could be used for better matching between horse-rider-discipline-level thus limiting mismatches and therefore welfare issues (Visser 2003).

In an excellent recently presented review book (Waran 2002) human horse conflicts in different life stages are reviewed. Unfortunately, many social conflicts arise from handling, usually due to misunderstanding the horse's behaviour and during social isolation though individual confinement.

3 BEHAVIOURAL AND PHYSICAL CONSEQUENCES OF SOCIAL ISOLATION AND CONFINEMENT

3.1 Theory and practice concerning equine abnormal and redirected behaviour

Current management practices for horses are driven by human requirements and costs limitations, but often ignore basic equine needs. In developed countries most performance and leisure horses are intensively managed. They are predominantly confined and socially isolated in a stable. Compared to the feral situation three aspects are altered:

Socially:

- most domesticated horses are either socially isolated, or have very limited possibilities for social contact using only a few senses.

Locomotory behaviour:

- most domesticated horses are confined to their stable for more than ¾ of the day

Feeding and foraging practices:

- quantitatively
  - batch feeding 2-3 times a day (instead of 24 hr ad libitum feeding)
  - use of bedding which does not allow foraging behaviour
- qualitatively
  - limited amounts of roughage combined with relatively high amounts of concentrates (instead of large quantities of low quality roughage).

Feral horses spend approximately 60-80% a day on feeding, during which they walk 5 -10 km a day. In stabled horses this are both significantly reduced (Waring 2003, Mills and Clarke 2002, Sweeting et al. 1985, Vervuert and Coenen 2002). When there is a high motivation for a stabled horse to perform behaviours, but expression is restricted due to environmental factors this can lead to frustration and hence to abnormal behaviour (Mills and Clarke 2002, Rushen et al. 1993).

Though some papers focus on the impact of alterations in feeding, foraging and confinement on behaviour (Mills and Clarke 2002, Davidson and Harris 2002, Goodwin et al. 2002), there is less literature specifically about the desirability of social contact. For example, there are currently no consumer demand studies about the desirability of social contact between horses. However, many indirect results indicate the high motivation for physical social contact of horses, leading to the supposition that social contact is a highly motivated behaviour within domestic horses (Mills and Clarke 2002, Cooper and McGreevy 2002).

Abnormal behaviour can be categorised in four major groups: pathologies, stereotypes, learned behaviours and dietary deficiencies (Marsden 2002). Between 10 and 40% of stabled horses perform a stereotypic behaviour pattern e.g. box walking, weaving, crib-biting, tongue play, self mutilation, (Nicol 1999 in Cooper and McGreevy 2002). Performing stereotypic behaviour is often regarded as a way of coping with the environment, since it has been shown that both opiate and super sensitisation of dopaminerge systems are involved in the performance of a stereotypy. In stereotypic horses a decrease in heart rate, heart rate variability, respiration rate and cortisol levels as well as an increase in β endorphin levels have been identified (Lebelt et al. 1996, Pell and McGreevy 1999, Bagshaw et al. 1994, Marsden 2002, McBride and Cuddeford 2001, Rendon et al. 2001, McGreevy and Nicol 1998, Gillham et al. 1994, Bachmann et al. 2003).

Since feral as well as domestic horses live in a continually changing environment, they are capable of learning in many contexts. Moreover domesticated horses are artificially selected to be able to learn stimuli given by a handler quickly and to learn the desired response (Mills and Clarke 2002). Therefore, they are also capable of quickly learning behaviours to temporarily relieve highly motivated desires.

4 WELFARE ISSUES OF PREVENTIVE MEASURES

In horses emphasis is traditionally given to physical, chemical or surgical interventions - not alterations of the human behaviour - to extinguish undesired behaviour (Waring 2003, Mills and Nankervis 1999, Cooper and McGreevy 2002). Physically preventing a stereotypic behaviour may, in itself, lead to increased stress reactions (McGreevy and Nicol 1998, Cooper and McGreevy 2002), because the stereotypic behaviour is either a general coping response or its prevention frustrates a highly motivated response to specific challenges encountered in the domestic environment (Cooper and McGreevy 2002, pg 117). When preventive measures alone are taken, other stereotypic behaviours frequently emerge in order to cope with the environment. There is currently no scientific evidence indicating that horses can learn from observational learning (Lindberg et al. 1999), thus social isolation of a stereotypic horse - because of a perceived high possibility of mimicking by other horses - can be considered detrimental to the welfare and possibly even contra-productive to the affected horse. Many authors currently argue that the best prevention and treatment of undesired behaviours is to adapt the management, housing, training, feeding and foraging practices to enable the horse to react to the underlying social, locomotory or dietary motivations. Stereotypic behaviour has never been observed so far in feral or free ranging horses.

5 SOLUTIONS ACCOMMODATING EQUINE SOCIAL REQUIREMENTS

5.1 Pragmatic solutions: advantages and points of attention

Several solutions have been proposed that deal with the social requirements of horses without actually increasing physical social contact between horses, these include the use of mirrors (Mills and Davenport 2002, Cooper et al. 2000, McAfee et al. 2002, Cooper and McGreevy 2002). However, these are unlikely to prove a universal panacea and ethical judgement is required regarding the use do these devices. There are indications that abnormal behaviours also can be prevented by husbandry systems which provide extensive possibilities for social contact and free ranging activities (e.g. Cooper et al. 2000, McBride and Long 2001, Bashaw et al. 2001, Lebelt 1998, McGreevy 1997). However, loose house as well as pasture systems also require welfare considerations e.g. increased risk of spread of infectious diseases, increased risk of individually acquired pathologies, as well as risks related to increased social contact at a small open area. These can include injury from aggression due to changes in social composition and/or overcrowding, food restriction or reduced resting times for subordinate individuals (Zeitler-Feicht and Prantner 2000, Mills and Clarke 2002, Vervuert and Coenen 2002). VanDierendonck et al. (submitted) have shown that in mixed sex-age domestic herds natural (feral) social processes take place, without any indication of a deviation of the natural behaviour even around parturition of new born foals.

Unfortunately, there is limited research on innovative stable / paddock designs or combinations of solitary housing with periods of social interaction in pastures or paddocks, thus incorporating the advantages of the loose house systems, while decreasing some if its disadvantages. Innovations in stable designs include half stable walls or partitions that allow more physical contact within individual stables; outside stable feeding systems allowing more natural feeding postures combined with more natural horizons and parallel contact with neighbours; loose house systems with adjustable barriers, allowing physical isolation of lower ranking/injured individuals at periods for additional rest or feeding (Vervuert and Coenen 2002, Ventorp and Michanek 2001). Technological approaches are currently emerging (Vervuert and Coenen 2002, MvD unpublished results) in which housing and feeding management are supported by computer technology, in so called 'social-locomotion stables' or 'multi-room-group-stabling' systems.

6 ENHANCED HUMAN–HORSE RELATIONSHIPS

Since recent research (Sondergard and Halekoh 2003) reveals that the social environment affects the way horses react to humans in their home environment, but not in a novel environment, handling and husbandry practices can not be considered independent of each other. Therefore: regular handling is necessary to avoid potential dangerous situations.

In order to bridge the gap between traditional horse husbandry and training practices on one side and the evolutionary needs of horses on the other, the following issues are highlighted:

- Knowledge of species specific, highly motivated behaviours
- Knowledge of important transition periods in horse life histories
- Knowledge of the causative factors of performed undesirable behaviours
- Knowledge of learning theories and learning capabilities of horses
- Openness to innovative practices in management, housing, and training

From the above requirements, an action plan can be constructed for those seeking to develop more welfare centred human - horse interactions that could also achieve better performance at lower costs.

- horses are kept in stable social and challenging environments throughout life
- horses are managed more in accordance with their evolutionary needs
- adoption of adaptive feeding and foraging practices
- improved socialization of horses, both towards conspecifics and humans,
- handlers acquire knowledge of species specific behaviour
- handlers understand ways that horses communicate
- handlers acquire better knowledge of learning processes
- handlers are open minded towards innovation in husbandry and training techniques

Human culture has benefited greatly though its interactions with horses over the last 6000 years, and our history would have been very different without them. We are now developing knowledge to eliminate some of the detrimental consequences that domestication has imposed on the horse. The horse is powerless to implement these advances, that responsibility is entirely ours.

◆

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CHAPTER 3

An Analysis of Dominance, Its Behavioural Parameters and Possible Determinants in a Herd of Icelandic Horses in Captivity

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ABSTRACT

The applicability of the concept of dominance was investigated in a captive herd of 26 Icelandic horses and 5 ponies of different breeds. Eight out of 20 behaviours possibly related to dominance occurred frequently enough to be investigated in detail. For these eight agonistic behaviours the coverage, the unidirectionality in the exchange, and the degree of transitivity (Landau's linearity index) were calculated. Four offensive behaviours, together with avoidance, were suitable for further analysis with regard to dominance. The patterns of asymmetries with which these behaviours were exchanged were sufficiently similar as to justify the application of the dominance concept and to construct a (nearly) linear dominance hierarchy. The rank order of the castrated stallions was completely linear, the hierarchy of the mares was almost completely linear. The results suggest that offensive and defensive aggressive behaviours should be treated separately and that the concept of dominance is applicable. However, ritualized formal dominance signals between adult horses appear to be (almost) absent. The rank positions of the individuals were correlated with age and residency in the herd but not with height. Middle ranking horses tended to be more frequently in the close vicinity of another horse than high ranking or low ranking horses. Over and above this correlation at the individual level, it was found that pairs of horses close in rank to each other were more often also spatially close to each other. Being in oestrus did not influence the dominance relationships between mares. For castrated stallions the rank positions were correlated with the age at which they were castrated. This suggests that in male horses experience prior to neutering influences the behaviour afterwards.

Key words
Dominance; rank order; horses; Icelandic horses.

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INTRODUCTION

Dominance relationships constitute a major aspect of the social structure of some socially living animals. Often, however, dominance rank orders are constructed without prior investigations as to whether the concept of dominance is valid. This is the case for most of the studies of horse social organization. Following (Hinde 1974) our understanding of the concept of dominance is that if the main directions of asymmetries in the exchange of a number of behaviours within dyads are identical, the intervening variable 'dominance' can be used to summarise these asymmetries. Subsequently, it is often possible to rank individuals so that a more or less linear rank order results. This constitutes the second aspect of the dominance concept. Thirdly, a formal dominance signal can be assumed to exist when the exchange of this behaviour within each dyad is unidirectional for 100 % and if the coverage (the percentage of non-zero dyads) is high enough (cf. (van Hooff and Wensing 1987).

Many studies have examined the dominance relationships in both domestic horses (Grzimek 1944, Hechler 1971, Houpt et al. 1978, Sereni and Bouissou 1978, Houpt 1979, Asa et al. 1979, Houpt and Wolski 1980, Houpt and Keiper 1982, Arnold and Grassia 1982, Wood-Gush and Galbraith 1987 and feral horses (Ebhart 1954, Tyler 1972, Clutton-Brock et al. 1976, Feist and McCullough 1976, Berger 1977, von Goldschmidt-Rothschild and Tschanz 1978, Wells and von Goldschmidt-Rothschild 1979, Miller 1981, Houpt and Keiper 1982, Berger 1986, Keiper and Sambraus 1986, Rutberg and Greenberg 1990). Keiper and Receveur (1992) investigated dominance in Przewalski horses. Almost all authors describe a hierarchy in one way or another; only Berger (1986) found hardly any stable dominance hierarchy in his feral horse herds, while Feist and McCullough (1976) and von Goldschmidt-Rothschild and Tschanz (1978) could only detect a rank order between the males.

Several authors (Grzimek 1944, Houpt et al. 1978, Sereni and Bouissou 1978, Asa et al. 1979, Houpt and Wolski 1980, Houpt and Keiper 1982) used the rivalry around limited and monopolisable resources to establish the dominance-subordination relationships by using (paired) feeding tests. In such tests a possible influence of other herd members is excluded. Houpt et al. (1978) used paired feeding tests to show that in small herds (up to 9 animals) strictly linear hierarchies were found, while in larger herds (10-11 animals) also triangular relationships were formed. However, dominance relationships found in this way may differ from those found in a free roaming situation and during a longer period of observation.

Unfortunately, authors do not fully agree with regard to the behaviours they use to construct rank orders. For example, Houpt and Wolski (1980) used a mix of offensive and defensive aggressive behaviours. On the other hand, Feh (1988) and Wells (1978) explicitly state that these two classes of behaviour must be treated separately and Schilder (1988) found the same in a detailed analysis of dominance relationships in plains zebra stallions. Many authors (Grzimek 1944, Hechler 1971, Tyler 1972, Wells and von Goldschmidt-Rothschild 1979, Houpt et al. 1978, Houpt 1979, Houpt and Wolski 1980, Miller 1981) did not use avoiding behaviour, whereas this was useful in zebras (Schilder 1990). Since aggressive behaviours may well be used by lower ranking individuals against higher ranking ones, the use of aggressive behaviours only in investigating dominance may render an unclear or even invalid picture. This was the reason why in zebra stallions (Schilder 1988) and wolves (van Hooff and Wensing 1987) aggressive behaviour could not be used to construct a rank order.

To investigate which individual factors might be correlated to the rank position an animal has in the dominance hierarchy it is required that the rank order is (nearly) linear. Landau's linearity index (see Martin and Bateson 1993) can be used to assess the degree of linearity in a set of dominance relationships. If the value of this index exceeds 0.9 the linearity of the hierarchy is sufficiently strong to obtain meaningful correlations between rank positions and individual factors like weight or age. The weaker the linearity of the rank order the less these correlations can be meaningfully interpreted. This problem is encountered in Keiper and Receveur (1992).

What different types of individual factors could determine (partially) the rank position in a dominance hierarchy? In the literature the following findings have been reported. Some authors reported that dominance rank correlated with the height of the individuals (Hechler 1971, Clutton-Brock et al. 1976, Rutberg and Greenberg 1990). Weight correlated positively with rank in some studies (Hechler 1971, Clutton-Brock et al. 1976), but not in others (Grzimek 1944, Houpt et al. 1978, Houpt 1979, Houpt and Wolski 1980, Houpt and Keiper 1982). Sometimes no correlation with physical characteristics could be shown (Arnold and Grassia 1982). Concerning the aspect of age, adult horses are nearly always dominant over immature horses (Hechler 1971, Clutton-Brock et al. 1976, Houpt et al. 1978, Houpt 1979, Arnold and Grassia 1982, Keiper and Sambraus 1986). Also, in many studies (Grzimek 1944, Hechler 1971, Clutton-Brock et al. 1976, Wells and von Goldschmidt-Rothschild 1979, Keiper and Sambraus 1986), the age of adult horses correlated positively with their rank position. In the study of Houpt et al. (1978) age was correlated with rank in 6 out of 9 herds. However, age was not correlated with rank in the studies of Feist and McCullough (1976), Houpt and Keiper (1982) and Arnold and Grassia (1982). In the last study a group of horses was introduced into the herd during the study. All these new horses, irrespective of their ages, figured in the bottom part of the rank order. This suggests that residency in the herd could also be a determinant of rank position.

A last factor that might influence rank position is castration. Line et al. (1985) showed that there is a minimal difference in the effect of pre (<3 yr.) and post (>3 yr.) pubertal castration in male horses on their sexual and aggressive behaviour. But the total frequency of these behaviours is much lower when castrated. Since pre-castration experience may influence later behaviour, the age at which the stallions were castrated may determine the amount of experience and therefore, may influence the position in the rank order.

In the present study we begin with analysing the patterns of asymmetries in behavioural exchanges with the aim to detect behaviours that represent dominance at the dyadic level and whether dominance can be used as an intervening variable. Subsequently, we investigate for each of these behaviours how far it allows the construction of a linear rank order. To this end we calculate for each of the dyadic interaction matrices the Landau's linearity index, a directional consistency index, the number of tied dyads and the coverage. Using the behaviours that satisfy these criteria, a highly linear dominance rank order among 21 horses (excluding the juveniles, one deviant mare and the non-Icelandic horses) can be constructed. Finally, we investigate if and to what degree the factors age, sex, height, residency in the herd, age at castration, oestrus of a mare and the possession of a young foal are related to the rank position attained or to changes therein. We also investigate whether rank and rank difference correlate with kin, proximity and mutual allogrooming.

MATERIALS & METHODS

The study group

The herd was established in 1971 and contained all sex-age classes except for an intact stallion. There were 26 Icelandic horses (6 castrated stallions (geldings), 16 mares, 2 juvenile stallions and 2 juvenile mares) and 5 ponies of different breeds (table I). Many of these horses were kin. They lived at the 'Breidablik' farm, Tilburg, the Netherlands. The horses in the herd were living together outside, 24 hours a day the whole year round. The herd could always use a shed (20 X 20 m) and a transition corridor (400 X 8 m). They had (sometimes limited) access to a pasture (140 X 100 m) depending on the food availability. There were five of these pastures in a row, each used in turn for 1-3 weeks. The total area was 6.3 hectare. The herd had always free access to running water provided by automatic drinking bowls. It also had free access to extra mineral supplies. The water bowls and mineral supply could be monopolized.

The observations were made when the herd was allowed to graze in one of the pastures and had done so for at least an hour. The behaviour of the animals was sampled between April 1984 and September 1984 during 433 hours of observation. Some of the adult animals were irregularly used for riding, or were absent for some weeks for breeding purposes. The presence and absence due to riding, out of sight in the shed, breeding, etc. of the animals was registered. In all dyads the data have been corrected for temporary absence of individuals. Data concerning the vegetation composition was also collected.

In order to obtain a homogeneous sample the five non-icelandic ponies were excluded from the analyses. Observations on the juvenile animals were not used for the analyses because we were especially interested in dominance, its behavioural parameters and its possible determinants in adult horses. It has been shown by many horse ethologists that adult horses are (nearly) always dominant over immature horses (Hechler 1971, Clutton-Brock et al. 1976, Houpt et al. 1978, Houpt 1979, Arnold and Grassia 1982, Keiper and Sambraus 1986). This was confirmed in the present study (data not published). We also excluded one adult Icelandic mare (v), because she was very probably suffering from a hormone disorder since she was the only mare not seen in season during the study period. Moreover, she had experienced a false pregnancy during the first three months of this period. Her illness also caused deviant behaviour in different respects, for instance a high frequency of being solitary.

Table I

Attributes of the horses in the study group

Sex	Code	Breed*	Age (yrs)	Residence (month)	Height (cms)	1st order relative in herd**	Dam of ad., yl.,f.***	Age at castration
Castrated	D	I	20	104	131	No	-	5
Stallions	C^	S	±20	150	94	No	-	1
	H	I	18	61	136	No	-	?
	F	I	14	86	128	No	-	3
	B	I	12	143	133	Yes	-	7
	S	I	9	108	135	Yes	-	5
	O	I	6	72	138	Yes	-	1
Juvenile	M	I	1	13	-	Yes	-	-
Stallions	T	I	Foal	2	-	Yes	-	-
Mares	s	I	22	138	132	Yes	Ad. r, yl. M	-
	l	I	22	141	127	No	No	-
	b	I	19	152	129	Yes	Ad. B, ad. M	-
	K	I	19	155	125	Yes	Ad. k. fl G	-
	U	I	19	124	130	Yes	Ad. O	-
	v^	I	19	144	123	No	No	-
	f	I	18	61	135	No	No	-
	P	I	18	155	131	Yes	Ad. d, yl. g	-
	e^	NF	18	137	130	No	No	-
	p	I	15	114	133	Yes	Ad. S	-
	a^	C	15	13	146	Yes	Yl. A	-
	c^	S	13	120	95	No	No	-
	d	I	12	143	133	Yes	Ad. o	-
	k	I	9	109	128	Yes	No	-
	t	I	8	97	136	Yes	Fl. T	-
	m	I	7	85	134	Yes	No	-
	E	I	5	61	132	Yes	No	-
	r	I	5	61	136	Yes	No	-
	o	I	5	61	136	Yes	No	-
Juvenile	A^	NF	1	13	-	Yes	-	-
mares	g^	I	1	12	-	Yes	-	-
	G^	I	foal	1	-	Yes	-	-

* I = Icelandic horse; S = Shetland pony; NF = New Forest pony; C = Connemara pony

** This includes son, daughter, mother, brother and/or sister

*** mother of an other adult (ad), yearling (yl) or foal (fl), e.g. ad r in the row of mare s means that s is the mother of the adult mare r

^ not used for dominance analyses

Data sampling and analysis methods

The main body of data was collected using focal animal sampling: 100 * 10 minutes per animal or less according to its presence, and additional data were collected using ad lib sampling (Altmann 1974). The data were collected at randomly distributed times during the daylight period. The order of focal animals to be observed changed every day at random. The ad lib data sets included many aggressive and affiliative encounters. The focal animal and ad lib data sets were compared by calculating the rank correlation coefficient between the individual behavioural frequencies (corrected for presence and absence of each horse) found in each data set. This was done for a number of behaviours relevant to this study. The result was that the two data sets resembled each other so much that they could be lumped and treated as one.

For the analyses concerning linearity of rank orders and the influence of possible influential factors the data set was split as follows:

* Data sampled on days during which a young foal (0-3 weeks) was present (foal-days, N= 28) (Note: Three weeks is the mean time that the young foal moves more than two horse lengths from its dam (Tyler 1972, Crowell-Davis 1985); also in 75% of the cases its mother is its nearest neighbour (Crowell-Davis 1985).

* Data sampled on days during which at least one mare was in season (oestrus-days, N=52).

* The days without any of these special features were called normal-days (N=29).

A mare was considered to be in season when she displayed at least twice that day one or more of the following behaviours: Presenting: standing in the neighbourhood of a male with straddled hind legs, lifted tail, ears sideways, sometimes with winkling and loss of small amounts of urine (Tyler 1972, Asa et al. 1979, von Goldschmidt-Rothschild and Tschanz 1978, von Goldschmidt-Rothschild and Glatthaar 1983); Winkling: opening and closing of the labia major exposing the clitoris and the vulva, often with loosing urine (Waring 1983). Further, a mare was considered to be in season if she was sexually mounted by a juvenile stallion or a gelding.

The analysis of dominance

Out of the 127 behavioural elements that were recorded, we selected 20 elements that were possibly related to dominance (see Table II). Descriptions of these behavioural elements are given in von Goldschmidt-Rothschild and Glatthaar (1983) and Waring (1983). Next, we counted for each behaviour the number of relationships covered by that behaviour (the coverage). If the coverage of a behaviour was less than 15 % of all possible dyads this behaviour was excluded from further analyses. This left us with 8 behaviours (all with a coverage of at least 30 %) for further analysis (Table II). These behaviours were: attack: fast movement in the direction of an opponent, with ears flattened; bite: bite or bite attempt, followed by chase in some cases; threat to bite: movement of the head with flattened ears towards the other animal, usually head and neck in one line; approach with ears flattened and head held high or horizontally; threat to kick; kick: kicking back with one hind leg; buck: kicking back with both hind legs; avoidance: moving away from an other individual after being approached.

Table II

The coverage (% of non-zero dyads) of 20 behaviours possibly related to dominance

Behaviour	Coverage	Used in dominance analyses
Approach with ears flattened	61	X
Threat to bite	55	X
Bite	54	X
Attack	39	X
Fight	2	
Chase	5	
Drive	6	
Threat tot kick	35	X
Kick (kicking backwards with one hindleg)	32	X
Buck (kicking backwards with two hindlegs)	32	X
Push	5	
Head on back	3	
Walk backwards#	9	
Avoid	87	X
Tooth clapping##	10	
Roll over	1	
Urinate over^	<1	
Defecate over^	2	
Non-sexual mount	4	
Rearing	2	

only performed by 8 mares
only perfomed by the 5 juveniles
^ only performed by the geldings

For each of these eight behaviours the interaction frequency matrix was investigated with regard to the following properties (see table III):

I The coverage, i.e. the number of dyads with non-zero exchange of the behaviour.

II The number of tied dyads, i.e. the number of dyads with equal exchange of the behaviour.

III The directional consistency, i.e. the total number of instances the behaviour was performed in the main direction within each dyad divided by the total frequency of the behaviour. This Directonal Consistency index (DC-index) ranges from 0 (completely equal exchange) to 1 (complete unidirectionality) (see van Hooff and Wensing 1987). An equivalent index, namely a direction inconsistency index, has been used by Noë et al. (1980) and Schilder (1988).

IV The degree of linearity, measured by Landau's linearity index h (see Martin and Bateson 1993).

For the properties I and III we devised the criterion that the value a behaviour has for that property should be higher than the average value of that property averaged across the eight behaviours (cf. Schilder 1988). Similarly, for the property II, the criterion was that the value a behaviour has for this property should be lower than the average value. In table III the values reaching this criterion are underlined. For property IV the criterion was that Landau's linearity index should be statistically significant (Appleby 1983, De Vries et al. 1993). Only if a behaviour satisfied at least two criteria was the behaviour considered to be a possibly suitable indicator of dominance. This was the case for five behaviours: bite, threat to bite, attack, approach with flattened ears, and avoid. If the separate rank orders for these behaviours correlate sufficiently, the relationships between the animals can be summarised in a single hierarchy.

Table III
Properties of eight different dyadic interaction frequency matrices

Behaviour	Total frequency	Coverage (non-zero dyads)	Number of tied dyads	Directional Consistency Index	Landau's linearity index h	
						significance
Bite	351	119	5	0.72	0.30	P<.01
Threat to bite	334	128	0	0.90	0.46	P<.01
Approach with ears flattened	452	146	2	0.90	0.50	P<.01
Attack	239	96	4	0.95	0.30	P<.01
Threat tot kick	185	90	11	0.64	0.12	n.s
Kick	182	75	17	0.49	0.06	n.s
Buck	158	70	13	0.52	0.07	n.s
Avoidance	1423	201	6	0.92	0.86	P<<.001

Total number of dyads for each matrix: 210

We also investigated the similarities between the patterns of asymmetries in the eight behaviours mentioned in table III by means of two different asymmetry measures for each pair of horses. The first asymmetry measure is defined as: the number of times a behaviour was performed from A to B (f_{AB}) minus the number of times this behaviour was performed from B to A (f_{BA}). By dividing this difference by the sum of f_{AB} and f_{BA} a normalised index of asymmetry is obtained ranging between -1 and +1 (cf. Schilder 1988). We can call this the degree of asymmetry between A and B. A second measure, that only takes the direction of the asymmetry into account but not the degree, is obtained by taking the sign of this magnitude of asymmetry, that is: $\text{sign}(f_{AB} - f_{BA}) = 1$ if $f_{AB} - f_{BA} > 0$; $\text{sign}(f_{AB} - f_{BA}) = 0$ if $f_{AB} - f_{BA} = 0$; $\text{sign}(f_{AB} - f_{BA}) = -1$ if $f_{AB} - f_{BA} < 0$. Next, for each of these two asymmetry measures, a principal components analysis (PCA; see e.g. Tabachnik and Fidell 1987) has been done with the eight behaviours as variables and the 0.5N(N-1) dyads as cases. Because the asymmetry between A and B is the opposite of the asymmetry between B and A, each dyad is represented only once in the data table (that is: if (A,B) is a case in the data table then (B,A) is not). Table IV presents the results of the PCA based on the signs of the asymmetries. The PCA based on the asymmetry degrees rendered highly similar results and is not shown.

Construction of the final rank order

The following procedure was used to construct the rank order using the five agonistic behaviours that met the above stated criteria.

1) The outcome of the PCA above shows that the four aggressive behaviours (bite, threat to bite, approach with ears flattened and attack) all have high and quite similar loadings on the first factor. This means that these four behaviours all show a similar pattern of asymmetry across the dyads. Therefore, we decided to add, for each dyad, the frequencies of these four aggressive behaviours. Since we are interested in the dominance relationships

as such rather than the strength of these relationships, we converted this frequency matrix into a binary relationship matrix. That is, for each dyad, the animal that showed the highest frequency was given a one and the other animal was given a zero. The matrix that contains the avoidance frequencies was also converted into a binary relationship matrix, but now for each dyad the animal with the lowest frequency was given a one rather than the animal with the highest frequency, in order to make this matrix compatible with the binary aggression matrix. We decided to multiply this binary avoidance matrix by two, because avoiding behaviour is in principle a much better parameter for representing the dominance-subordinate relationship than the aggressive behaviours are. This is so, because by giving way to another approaching animal the avoiding animal acknowledges the other's dominance, whereas aggressive behaviour is not necessarily an expression of one's dominance over another animal (van Hooff and Wensing 1987, Schilder 1988). This is in accord with the fact that the avoidance matrix has the highest value of Landau's linearity index and a high directional consistency index (table III).

Table IV
Factor loadings resulting from a Principal Component Analysis based on the signs of dyadic asymmetries in 8 behaviours

Behaviour	Factor 1	Factor 2	Communality
Bite	54	-17	.33
Threat to bite	73	4	.54
Approach with ears flattened	77	8	.60
Attack	65	-13	.43
Threat tot kick	7	71	.51
Kick	-3	76	.57
Buck	-21	82	.71
Avoidance	-67	2	.45
Variance explained	30%	21%	

2)The two relationship matrices thus constructed were added. This combined relationship matrix has the advantage that one can easily see which dyads have a clear or less clear dominance relationship (see Fig. 1). The matrix contains the scores 0, 1, 2 and 3. A score of 3 means that in that dyad the dominant individual was dominant on basis of two behavioural parameters: aggression given and avoidance achieved. A score of 2 means that the dominant individual was only dominant on basis of avoidance achieved. In this matrix the horses were ordered according to the number of dominated animals. If, however, in the order thus obtained, the dyadic relationship between two adjacent individuals did not agree with this order then these two individuals were reversed (the "flipping heuristic", (Roberts Jr. 1990, De Vries et al. 1993). The result of this rearrangement procedure is a matrix in which the sum of scores below the diagonal is approximately minimized (cf. Schein and Fohrman 1955). This rendered the final rank order. All different steps in this procedure were done using MatMan, a program for the analysis of sociometric matrices (De Vries et al. 1993).

In this way, rank orders were constructed for the complete group as well as for males and females separately (see Figures 1, 2 and 3). Finally, a rank order for the complete group was constructed using the method of (Clutton-Brock et al. 1986), which excludes the influence of age.

The relationship between rank and other factors

Because of the different types of data and the constraints of some statistical tests, a number of different tests had to be used to detect relationships between dominance rank position and several factors that may influence that position. First, all rank orders were tested for linearity by a test proposed by Appleby (1983) using the MatMan program (De Vries et al. 1993). Correlations between the positions held in these rank orders and the factors age (expressed in years), height (in cm at the withers), residency in the herd (in months) and the age the geldings had at castration were calculated. For these comparisons the Spearman rank correlation coefficient (R_S) was used (Lee and Lee 1982). We wanted to know whether having a new-born foal influenced the rank of the mother and the occurrence of aggressive behaviour. To investigate the latter we calculated a relative aggression score (= Number of aggressive acts/observation time) for the normal-days and for the foal-days and compared these. Another question to be answered was whether the rank positions of the adult offspring were correlated with those of their mothers. For comparisons between rank position and the relative aggressiveness of (adult) offspring (N=9) and their dams (N=8) the linear Pearsons correlation coefficient (R_P) was used (Lee and Lee 1982).

The relationships between rank differences and social or kin bonds were analysed using matrices of allogrooming, proximity and kinship. Allogrooming was defined as mutual interactive nibbling between two horses, mainly at each others mane, withers, back and tail base. This behaviour occurred between almost all animals of all sex-age classes. When two animals were within two horse lengths from each other they were considered to be in each other's proximity. Proximity between each pair of horses was recorded every half hour by a scan sample. Kinship was defined as a familiar relationship an animal could have knowledge of: mother-offspring, grandmother-grandchild, brother-sister via the mother. Stallion offspring relationships were not included. The correlation between the rank differences between each pair of horses and the social or kin bonds between them is assessed by means of the Mantel test (Schnell et al. 1985). To obtain the significance probabilities we employed a permutation procedure which respects the interdependencies of the values within rows and columns of these matrices. The dual normalization procedure described in Freeman et al. (1992) was used to correct for individual variation in the tendency to allogroom or to be in the proximity of any other horse. We used the program MatMan (De Vries et al. 1993), to calculate dually normalized matrices and subsequently perform permutation Mantel tests.

RESULTS

Applicability of the concept of dominance

According to the first criterion stated in the previous section, eight behaviours occurred sufficiently often to be used for assessing dominance. The values the four parameters (coverage, number of ties, directional consistency and linearity) took for the eight selected behaviours as described above are shown in table III. Five behaviours satisfied, at least in two cases, the criterion that a value for a behaviour should be better than the average value for that specific property. None of the behaviours showed a Landau's $h > 0.9$, which is generally taken to denote a strongly linear hierarchy (Martin and Bateson 1993). On the other hand, application of the linearity test (Appleby 1983) showed that for five behaviours there was a significant deviation from non-linearity. Avoidance showed the strongest linearity. The results of the Principal Components Analysis (table IV) clearly showed that two groups of behaviours emerge: offensive aggressive behaviours (bite, threat to bite, approach with ears flattened and attack) and avoidance on the one hand, and defensive aggressive behaviours (kick, buck and threat to kick) on the other hand. The first group of aggressive behaviours are considered to be of an offensive nature, because of the strong approaching tendencies involved. This group is negatively correlated with avoidance. The second group of aggressive behaviours is considered to have a more defensive nature, because these behaviours may be shown while retreating. This is in line with observations made by Wells (1978), Wells and von Goldschmidt-Rothschild (1979), Feh (1988) and Rutberg and Greenberg (1990). Retreating is almost impossible in biting attempts, because these include necessarily a forward movement. Moreover, when using the hind legs the horse already is in a favourable position to withdraw. With regard to the contexts in which aggression occurred, we can say that aggression occurred on the pasture but was more common around the drinking bowls, the mineral supply and in the transition corridor. These last three situations have in common that there is limited availability in the sense that only one

	f	P	b	I	K	D	P	s	B	d	U	S	k	F	m	t	O	o	r	E	H
f	*	3	3	2	3	3	3	3		3	3	3	3	3	3	3	3	3	3	3	3
P		*	2	3	2		3	3	3		2	2	3	3	3	3	3	3	2	3	3
b			*	2	3	2	3	2	2	2	3	2	3	2	3	2	3	3	3	3	3
I	1		1	*	3	1	1	1	3	1	3	1	3	3	3	1	3	3	3	3	3
K					*	3	3		3	3	2	2	3	2	3	3	3	3	3	3	3
U			1	2		*	1			3	3	3	3	3	3	3	3	3	3	3	3
p							*	3	3	3	3	3	3	3	3	3	3	3	3	3	2
s					3			*	2		3	2	3	2	3	3	3	3	2	2	3
B	2					3			*	3	1		3	3	3	3	3	3	3	3	3
d			1	2				3		*		3	3	3	3	3	3	3	3	3	3
U										2	*	3	3	3		2	3	2	2	3	2
S												*	2	3	3	3	3	3	3	3	3
k													*	2	3	3	3	3	3	3	3
F													1	*	3		3	3	3	3	3
m															*	3	3	3	3	3	3
t														2		*	3	2		2	3
O																	*	3	3	3	3
o																		*	3	3	3
r																			*	2	1
E																			1	*	3
H																					*

Figure 1. Dominance relationship matrix for 21 male and female horses based on offensive aggressive behaviour and avoidance behaviour. The individuals are arranged in hierarchical order. The geldings are underlined. 3: the row individual is dominant over the column individual on the basis of aggression given and avoidance achieved. 2: the row individual is dominant over the column individual on the basis of avoidance achieved. 1: the row individual is dominant over the column individual on the basis of aggression given.

animal at a time could use the supply, or, in case of the corridor, could use the space.

The separate rank orders for these five behaviours correlated significantly with each other (table V), so that the use of dominance as an intervening variable (cf. Hinde 1974) is justified and one hierarchy can be constructed, using the combined relationship matrix as described in the methods section above. Figure 1 presents this relationship matrix based on the dyadic aggression and avoidance relationships. This combined relationship matrix contains only 28.75 circular triads out of the maximum of 385 circular triads possible in a matrix of size 21. This corresponds to a highly significant Landau's linearity index h of 0.925 (p << 0.01). There were only 5 blank relationships. Because of the strong linearity present in this set of relationships, we may conclude that a (nearly) linear rank order indeed exists among the 21 Icelandic horses and it is therefore justified to construct this (nearly) linear rank order. In the matrix of Fig. 1 the animals have been arranged according to this (nearly) linear rank order following the procedure described above in the Methods section. For the dominance relationships among the mares, the value of Landau's linearity index turned out to be also very large, namely 0.95 (n=15; p << 0.01). The rank-ordered dominance relationship matrix for the mares is presented in Fig. 2. For the geldings even a strictly linear hiearchy was found (Landau's h = 1; n = 6; p = 0.022). The dominance matrix for the geldings is presented in Fig. 3. These three (nearly) linear hierarchies will be used in the subsequent analyses, where we investigate which factors might be related to these rank orders.

	f	P	b	1	K	p	d	s	U	k	m	t	o	r	E
f	*	3	3	2	3	3	3	3	3	3	3	3	3	3	3
p		*	2	3	2	3	2	3	2	3	3	3	3	2	3
b			*	2	3	3	2	2	3	3	3	2	3	3	3
1	1		1	*	3	1	1	1	3	3	3	1	3	3	3
K					*	3	3		2	3	3	3	3	3	3
p						*	3	3	3	3	3	3	3	3	3
d			1	2			*	3		3	3	3	3	3	3
s					3			*	3	3	3	3	3	2	2
U									*	3		2	2	2	3
k										*	3	3	3	3	3
m											*	3	3	3	3
t												*	2		2
o													*	3	3
r														*	2
E														1	*

Figure 2. Dominance relationship matrix for 15 female horses based on offensive aggressive behaviour and avoidance behaviour. Same legend as Fig. 1.

	B	D	S	F	O	H
B	*	3	3	3	3	3
D		*	3	3	3	3
S			*	3	3	3
F				*	3	3
O					*	3
H						*

Figure 3. Dominance relationship matrix for 6 male horses based on offensive aggressive behaviour and avoidance behaviour. Same legend as Fig. 1.

Table V
Spearman rank correlations between five rank orders

Bite	Bite				
Threat to bite	0.85	Threat to bite			
Approach with ears flattened	0.84	0.92	Approach		
Attack	0.84	0.92	0.87	Attack	
Avoidance	0.87	0.93	0.94	0.87	Avoid

All correlations are highly significant ($p<0.01$)

Factors related to rank

Rank and sex

The top five places of the rank order of the complete group were taken by older mares; the first gelding (D) takes the 6th place. The rank positions of the males are interspersed with those of the females. It is noteworthy that the relative number of circular triads is highest (i.e., Landau's $\underline{h}$ is smallest) when the intra-sexual dominance relationships of the females (Fig. 2) and the males (Fig. 3) are combined with the inter-sexual relationships into one set (Fig. 1). This means that some intersexual dominance relationships are not transitive. Note, for instance, the remarkable subordinate position of the top ranking female f to the top ranking male B (top ranking in the male hierarchy, that is). Note also that the α and β male B and D in the male hierarchy have reversed rank positions in the complete hierarchy. This is due to the fact that there are two mares (p and s) who dominate B but not D, and there is also one mare (l) who is subordinate to D but not to B. It is evident that the dominance relationships between the top ranking males and the high ranking females are not transitive.

Rank and age

Age correlated positively with rank in the linear rank order of the complete group ($n = 21$) and in the rank order of the females ($n = 15$; see table VI). However, age was not correlated with rank in males. A female rank order constructed excluding the influence of age (see Clutton-Brock et al. (1986) for methods) showed a different picture. This rank order was not significantly correlated with the linear rank order ($\underline{R}_S = 0.15$, $\underline{n} = 21$, n.s.). Thus, age is an important rank determining factor, at least for the females.

Rank and height

Height correlated negatively with the linear rank order of the complete group (21 horses). So, the smallest horses were highest in rank. On the other hand, height correlated negatively ($\underline{R}_S = -0.60$, $\underline{n} = 21$, $\underline{p} < 0.01$) with age also. That is, younger animals are larger than the older ones. Height did not correlate significantly with rank in the separate female and male rank orders.

Rank and residency

Rank position was correlated positively with the time of residence in the herd.

Rank and relative aggression and relative submission

The rank position in the hierarchy was, surprisingly, not or very weakly correlated with the relative aggressiveness of the individuals. This means that not the overall amount of aggressive acts performed determines the rank of an individual, but rather to whom this aggression is directed. Relative submissiveness, on the other hand, correlated significantly with rank.

Rank and age at castration

The male rank order was correlated with the age at which they were neutered ($\underline{R}_S = 0.97$,

n=6, $p < 0.05$). That is to say, the older a male was when being neutered the higher his rank position. Below, we will show that age at castration in our study herd is strongly related to the amount of sexual experience and to the possibilities to develop male displays towards other (castrated) stallions. Therefore, we can say that not the castration age as such determines the rank order among the castrated males, but rather that the amount of socio-sexual experience of a castrated stallion determines its rank.

Icelandic horses are, in this herd but also on Iceland and at other studs, always living outside in a group. From this herd all sexual experiences of all males are known. The gelding that ranked highest in the male hierarchy (B) was castrated when 7 years old and had for two years his own herd of mares. He sired four of the other herd members. The second ranking gelding (D), who has a higher rank position in the full herd but is dominated by B, has only little sexual experience: as a five year old he had one mare for a few weeks. None of the other geldings have had any sexual experience. All Icelandic horses, except H and F, have lived in 'free roaming' batchelor herds until 5 years old. From H is only known that he was castrated on Iceland, most likely as yearling. He lived mainly in a small mixed herd. F and C were kept in mixed herds after neutering. So in this herd, age at castration is strongly related to the amount of socio-sexual experience.

Rank and being in oestrus and/or having a foal

Two foals were born during this study. Their dams climbed respectively one and three places in the rank order while their foals were less than three weeks old. This provided us with not more than a weak indication that dams temporarily rank higher when having a newborn foal. The relative aggression scores of both dams increased slightly after giving birth to a foal: for one dam from 1.13 to 1.57 and for the other from 0.72 to 1.00. The mean relative aggressiveness (n=21), on the other hand, decreased from 1.71 to 1.14. No influence of oestrus on the rank position of the mares concerned was evident.

The rank positions of a mare and her adult offspring

The rank positions of mares correlated positively with those of their adult offspring (R_p= 0.88). The relative aggressiveness of the dams and those of their adult offspring was also correlated (R_p= 0.75, n=8, $p < 0.05$). Since there is no correlation between age of dams and age of their offspring nor between age and relative aggressiveness in the group of adult animals, the possibility of the former correlation being due to the latter is unlikely.

Rank, kinship and social bonds

An interesting question is whether the difference in rank positions between each pair of horses is related to the social bond, measured as the frequency of allogrooming interactions between the two horses or as being in each other's proximity. It is also interesting to investigate the possible relation between rank difference and kinship. To this end we constructed the following dyadic matrices: (1) a kinship matrix: this is a 0-1 matrix, where a 1 means kin (via the mother) and a 0 means not kin; (2) a matrix of rank differences, which indicate how many horses separate any given pair in the hierarchy (see the lower triangular half of the matrix presented in Fig. 4), (3) a frequency matrix of mutual allogrooming, and (4) a proximity matrix, which contains for each pair of horses the frequency with which these two horses were within two horse lengths from each other (see the upper triangular half of the matrix presented in Fig. 4). All matrices are symmetric. For each pair of these matrices we calculated the Pearson's correlation and its statistical significance, using a permutation test which respects the interdepend-

	f	P	b	l	K	D	P	s	B	d	U	S	k	F	m	t	O	o	r	E	H	Total
f	*	0.5	2.0	1.0	0.0	0.0	2.0	1.5	3.5	0.5	0.0	1.5	1.0	2.0	0.0	1.0	1.5	2.5	0.5	0.0	1.5	22.5
P	0	*	1.0	1.5	2.0	1.5	1.5	3.3	2.0	1.1	1.0	1.8	4.3	1.8	1.7	1.0	2.5	0.8	1.0	0.8	0.5	31.5
b	1	0	*	2.5	1.8	0.8	5.0	5.3	2.5	3.8	2.0	0.8	10	1.0	4.0	1.8	2.3	2.0	2.0	2.3	1.0	54.2
l	2	1	0	*	1.5	0.5	4.0	3.0	2.0	5.5	1.5	3.5	2.5	4.0	3.5	3.5	3.0	4.0	2.5	2.0	1.0	52.5
K	3	2	1	0	*	3.3	0.5	2.7	1.0	2.3	6.5	1.5	2.3	0.5	2.3	3.3	0.3	1.3	0.5	1.0	0.5	35.1
U	4	3	2	1	0	*	2.3	0.3	4.0	1.3	0.5	5.0	1.0	5.8	1.7	0.8	2.8	0.8	0.8	0.5	1.0	37.5
p	5	4	3	2	1	0	*	4.0	8.0	5.8	3.0	8.3	4.3	3.5	2.3	0.8	3.0	1.0	1.0	1.3	0.5	62.1
s	6	5	4	3	2	1	0	*	2.3	3.0	4.0	0.7	5.3	0.7	0.3	2.3	4.3	1.0	3.0	1.3	0.0	48.3
B	7	6	5	4	3	2	1	0	*	6.3	1.5	9.0	5.3	5.0	2.3	1.5	9.5	1.5	1.3	0.8	1.0	70.3
d	8	7	6	5	4	3	2	1	0	*	4.5	5.0	6.3	1.0	2.7	0.8	4.0	2.5	1.8	2.3	1.5	61.9
U	9	8	7	6	5	4	3	2	1	0	*	1.0	1.0	0.0	0.5	3.0	1.5	3.0	0.0	2.0	0.0	36.5
S	10	9	8	7	6	5	4	3	2	1	0	*	2.7	3.3	4.7	0.3	11	4.0	1.0	0.5	1.0	66.9
k	11	10	9	8	7	6	5	4	3	2	1	0	*	1.0	7.3	3.0	6.3	1.3	3.0	3.0	1.5	72.7
F	12	11	10	9	8	7	6	5	4	3	2	1	0	*	2.7	1.0	5.3	2.0	1.5	1.5	1.5	45.1
m	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	4.3	6.7	4.0	1.3	2.3	0.5	55.1
t	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	1.3	2.5	2.0	2.5	0.5	37.2
O	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	4.0	2.5	1.5	2.0	75.6
o	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	5.3	5.5	1.5	50.5
r	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	8.8	1.0	40.8
E	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	0.5	40.4
H	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	18.5
tot	190	171	154	139	126	115	106	99	94	91	90	91	94	99	106	115	126	139	154	171	190	

Figure 4. This figure shows two triangular halfs of two symmetric matrices.
Below the diagonal: matrix of rank differences (i.e., the number of individuals in between each two rank positions).
Above the diagonal: matrix of proximity frequencies.
The column totals give the marginal totals of the full matrix of rank differences. The row totals give the marginal totals of the full matrix of proximity frequencies.

encies of the values within rows and columns of these matrices. The MatMan program (De Vries et al. 1993) was used to perform these permutation Mantel tests.

The upper panel of table VII shows the results of these tests. It turns out that kinship is not related in any way to difference in rank positions or to one of the social bond measures proximity and allogrooming. Rank difference, on the other hand, is strongly correlated with proximity ($\underline{r} = -.290$, $\underline{p} < .001$), that is: the closer two horses are in rank to each other the more frequently they are in each other's proximity. For the correlation between rank difference and allogrooming not more than a weak trend was found ($\underline{r} = -.117$, $\underline{p} = .09$). Not unexpected, proximity and allogrooming were strongly correlated ($\underline{r} = .491$, $\underline{p} < .001$).

Horses may differ in their tendencies to get involved in allogrooming interactions with any of the other horses. Similarly, they may differ in their propensities to be in the proximity of any of the other horses. A disadvantage of the Mantel test is that it does not take this individual variation into account. For instance, the correlation between rank difference and proximity obtained above by the Mantel test could be the result of a correlation between an animal's deviation from the mean rank position and its tendency to be in the proximity of any of the other horses. To overcome this problem (Freeman et al. 1992) suggested the use of an iterative proportional fitting procedure (Bishop et al. 1975, pp. 97-101) to fit homogeneous margins to observational data matrices like the proximity and allogrooming matrices. By this procedure the matrices are dually normalized; that is, for each pair of horses a value is obtained that represents the number of allogrooming acts (or being in proximity) they would be involved in if all the marginal totals were equal. Subsequent Mantel tests using these normalized matrices are thus corrected for individual variation in behavioral tendencies. To eliminate non-diagonal zero cells a constant of 0.25 was added to these cells before the iterative proportional fitting procedure was applied, as suggested by Freeman et al. (1992). The dually normalized matrices were calculated by means of a specially written extension of the program MatMan (De Vries et al. 1993).

Table VI
Spearman rank correlations between rank positions in the hierarchy and six individual factors

Feature	group	Rs	n	p
Age	Complete group	0.74	21	0.002
	Mares	0.75	15	0.002
	Geldings	0.09	6	n.s
Height	Complete group	-0.54	21	0.002
	Mares	-0.45	15	n.s
	Geldings	-0.54	6	n.s
	Complete group	0.70	21	0.002
Residency	Mares	0.65	15	0.02
	Geldings	0.94	6	0.01
Rel aggressiveness	Complete group	0.36	21	n.s
	Mares	0.42	15	n.s
	Geldings	0.83	6	0.05
Rel submissiveness	Complete group	-0.89	21	0.002
	Mares	-0.80	15	0.002
	Geldings	-0.94	6	0.01
Castration age	Geldings	0.97	6	0.01

n = number of individuals; p = probability

The lower panel of table VII presents the results of the Mantel test using these normalized matrices. The correlations between kinship and the other variables as well as the correlation between proximity and allogrooming did not change much. However, the correlation between rank difference and proximity dropped from a highly significant value of -.290 (p < .001) to a just significant value of -.143 (p = 0.04). This decrease is apparently due to the strong negative correlation of -.637 that existed between an animal's total sum of rank differences (indicating its deviation from the mean rank position) and its tendency to be in the proximity of any of the other horses (i.e., the correlation between the column totals in fig. 4 and the row totals in fig. 4). In other words, top ranking and bottom ranking horses stayed less frequently in the close vicinity of another horse than middle ranking horses did. "It's lonely at the top as well as at the bottom." There is one clear exception, namely the mare U, which occupied the middle rank position 11 (marginal total of 90), but at the same time had a very low frequency of being in another horse's neighbourhood (marginal total of 36.5).

The already rather weak correlation between rank difference and allogrooming (r = -.117) decreased to an insignificant value of -.045 when we performed a Mantel test using the dually normalized matrix of allogrooming. The difference between these two correlation values is not quite understandable to us, because the correlation between an animal's deviation from the mean rank position and its general tendency to be involved in allogrooming interactions is only -.031. However, there existed large differences between individuals to get involved in allogrooming, and therefore we felt that the application of the normalization method by which this individual variation is taken into account was required. Anyway, the conclusion can be drawn that rank difference and allogrooming are not significantly correlated.

Table VII

Matrix correlations between kin, rank difference, proximity and social bond

		Correlation r	p-value^	
Kinship	Rank difference	.063	>.25	n.s
Kinship	Proximity	.061	>.25	n.s
Kinship	Allogrooming	.041	>.40	n.s
Rank difference	Proximity	-.290	<.001	**
Rank difference	Allogrooming	-.117	.09	Tr
Proximity	Allogrooming	.491	<.001	**
Kinship	Rank difference	0.63	>.25	n.s
Kinship	Proximity	-.003	>.40	n.s
Kinship	Allogrooming	0.82	>.25	n.s
Rank difference	Proximity	-.143	0.04	*
Rank difference	Allogrooming	-.045	>.40	n.s
Proximity	Allogrooming	.468	<0.001	**

Upper panel: the dyadic frequency matrices (proximity and allogrooming) are not corrected for individual differences in their propensities for each of these social behaviours.

Lower panel: the proximity and allogrooming matrices are dually normalized by means of fitting the homogeneous margins to these matrices (Freeman et al. 1992), thereby correcting for individual differences.

^ The p-values are two tailed and based on a permutation test in which the rows and columns of one of the two matrices are simultaneously permuted 10.000 times.

Tr = trend .05 < p < .10; * = 0.01 < p < 0.05; ** =P < .001

DISCUSSION

The applicability of the dominance concept

In this paper we started with analysing what behavioural exchanges reflect dominance relationships in horses. The results demonstrate that only a very limited number of behaviours reflected dominance in such a way that they could be used to construct a rank order. An important result is that we were unable to construct a (nearly) linear rank order when defensive aggressive behaviours (threats or kicks with the hind legs) and offensive aggressive behaviours (threats or attacks with the head) were combined. This result is in line with those of Wells (1978), Feh (1988) and Rutberg and Greenberg (1990) on horses and of Schilder (1988, 1990) on zebras. It suggests that the habit of combining behaviours of an offensive nature with those of a relatively more defensive nature is unjustified. This conclusion is reinforced by the results of a PCA of the asymmetries in the exchange of eight behaviours, in which the factor loadings of the offensive and defensive behaviours are high on two different factors. The fact that kick and buck show a low degree of transitivity and a relatively low directional consistency suggests that they were used defensively against higher ranking opponents as well as (offensively?) against lower ranking opponents. On the basis of these results we recommend to keep aggressive behaviours involving the head and those involving the rear separated, and to take into consideration avoidance behaviour when investigating dominance in horses.

Just as with zebras (Schilder 1988), the conclusion can be drawn that the concept of dominance is applicable to a certain degree. Also comparable to zebras is that horses do not appear to use formal dominance signals as has been shown for chimpanzees (Noë et al. 1980) and wolves (van Hooff and Wensing 1987). These two species use highly ritualized displays which are (almost) completely unidirectionally exchanged within each dyad and are being shown in a large number of dyads. Such displays could therefore be considered as indicators of a formal status rank order. In horses toothclapping and ceremonies involving defecating/urinating over faeces/urine of other individuals could be regarded as dominance related ritualized displays. However, in our study group toothclapping was only performed by the juveniles, which is in agreement with other observations (Waring 1983). Defecating/urinating ceremonies were almost exclusively performed by adult stallions and were for that matter almost absent in this study (see Table II). Therefore, these behaviours could not be used in investigating dominance between adult horses. None of the other behaviours showed sufficient unidirectionality and high enough coverage to be designated as a formal dominance signal. In fact, the behaviour which reflects best the dominance relationship between two horses is avoidance. This is completely in line with the finding that the more two horses are separated in rank the less frequently they are within two horse lengths from each other. This means that if subordinate non-juvenile horses get involved in a conflict with a higher ranking horse, they can only give ground or defend themselves, but are unable to present a display (with the possible exclusion of tooth-clapping) by which they acknowledge the dominance status of the other thereby possibly reducing its aggression.

Rank and its possible determinants

The hierarchy of the horses does not consist of two disjunct parts, in which all males or all females would occupy the higher positions and the horses of the other sex would occupy the lower rank positions. In the (nearly) linear rank order of the complete group the rank positions of males and females are interspersed (Fig. 1). It turned out that the few triangular dominance relationships that existed involved intersexual relationships. The hierarchies of the males and females separately were more linear than the combined hierarchy (Figs. 2, 3).

In general, the rank position in the dominance hierarchy correlated strongly with the factors age, residency and castration age and less with the factor height. This can be interpreted by saying that the rank position of an adult horse appears to be determined by the amount of social experience acquired by the horse, rather than by its actual physical strength/height. This interpretation is strengthened by the fact that the rank of the castrated stallions was not correlated with age but with the age at which they were castrated. That is, geldings with a relatively high age at castration have a high rank. This could be a result of differences in the remaining hormone levels due to differences in surgical techniques, but these differences are usually very minor (Voith 1979). More likely it is an effect of the differential behavioural experiences the animal had before castration. For horses there are no specific reports on this issue available. Line et al. (1985) state that there is no difference in sexual and aggressive behaviour in pre- and post pubertal castrated male horses, but he does not refer to behavioural experiences. A study by Hart and Hart (1985) showed that about 50 % of the dogs that were neutered because of excessive aggression towards other dogs continue to attack dogs after castration. This suggests that experience may play a role here also. For the horses in the present study, hormones as well as the possibilities to mate influenced the socio-sexual experiences of the castrated stallions. This in turn determined strongly the rank order among the castrated males.

We were amazed by the fact that an effect of residency was still detectable, although the mean time of residency was 9.5 years (range: 5 - 12 years). Residency was, however, in most individuals related to age. The use of the ranking method developed by Clutton-Brock et al. (1986) could be a solution to separate these effects. Unfortunately, this method resulted in a lot of ties, which made this rank order unfit for further analysis.

Our results possibly can best be compared with studies involving groups of horses that are together for at least several years (for example Berger 1986 and Keiper and Sambraus 1986) rather than with studies in which horses do not know each other for a long time (as for example in the studies of Houpt et al. (1978) and Houpt and Keiper (1982). The reason for this is that the influence of the factor 'social experience' may be different.

Obviously, hormones also influence the social behaviour of both females and males in times of oestrus. However, in this study, being in oestrus did not have an observable effect on the rank of the female.

The rank positions of dams and their mature offspring were correlated and both correlated with relative aggressiveness. No correlation was found between age of dams and their offspring nor between age and relative aggressiveness. Therefore, the high rank positions of offspring of an aggressive mother are most likely due to aggressiveness of the offspring itself. Some other authors (Tyler 1972, Wells and von Goldschmidt-Rothschild 1979, Houpt 1979, Houpt and Wolski 1980) also showed a relationship between the rank position of dams and their adult offspring. Beaver and Amoss (1982) described cases in which aggressive behaviour was correlated with naturally elevated serum testosterone in mares. If there are hereditary factors involved, this would explain why foals tend to be as aggressive as their mothers. But, of course learning factors may be involved too (Houpt 1981).

Finally, we found that rank strongly influenced the proximity structure of the horses. At the individual level, it turned out that horses with a rank position close to the mean rank tended to stay more frequently in the proximity of other horses than high ranking or low ranking horses did. Over and above this effect at the individual level, we also found that pairs of horses close in rank to each other tended to stay close in each other's physical proximity. We did not find that rank or rank difference influenced the allogrooming relationships between the horses. Neither did we find any correlation between kinship and rank difference or kinship and the social bond measures (proximity and allogrooming). We conclude that rank and rank difference have a strong direct effect on the interindividual distances between the horses, but probably not on the social bonds between them.

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CHAPTER 4

Social relationships in a group of horses without a mature stallion

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ABSTRACT

1. The social relationships in a group of Icelandic horses without a mature stallion were studied. The horses were all familiar to each other. Mutual grooming and play relationships, spatial associations, dominance- subordinate relations and the effect of kinship on these relationships were analysed.
2. The social structure was clearly dominated by the behaviour of the adult mares. The horses preferred to form bonds within their social class (sex/age) and they kept close proximity with their friends. The group was effectively divided into two social subgroups, adult mares as one group and adult geldings and sub-adults as another group. The sub-adults and adult geldings formed associations, which were based on mutual grooming and play, while the adult mares did not play. Differences between the sexes were evident. Males played more than the females, had more playing partners and were more popular as playmates.
3. Aggression rates were low. The dominance hierarchy was linear. Adult mares ranked higher than adult geldings, sub-adults and the foals. Rank was significantly correlated with age. The closer the adult mares were in rank, the more they groomed with each other. Such relationships were not found amongst the other social group.
4. Kinship was calculated between all pairs of animals for up to 4 or 5 generations. Allogrooming and play frequencies and proximity were all positively correlated with kinship. Adult mares, which were close in the dominance hierarchy, were more related than those further apart.
5. The social relationships in the Icelandic herd were, to some extent, different from relationships reported from unmanaged and feral horse-herds with mature stallions and bachelors. Our results suggest, that adult mares groom more in groups without a stallion. Furthermore, they have more preferred partners than in natural harems and their partners are other adult mares, not their weaned offspring as seems to be the case in feral herds. The sub-adults also seem to be more socially active in the absence of stallions. Interestingly, in the Icelandic group, the adult mares showed stallion like behaviours, like mounting and protecting foals. Only by studying the behaviour and the nature of the relationships of horses in groups of different compositions, can we expect to gain a comprehensive understanding about individual social strategies and cognitive capabilities of the species. Such knowledge is valuable for management and welfare of the horse.

Key words:
Social relationships; Icelandic horses; kinship; dominance hierarchies; suppression.

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INTRODUCTION

For a variety of reasons the domestic horse is an ideal species to study bonding in social groups. Unlike in most mammals, where the sexes only maintain bonds during the breeding season (Clutton-Brock 1989), dominant males stay with their group all year, thereby forming strong bonds with the adult females that make up their harem (Rees 1993, Waring 2003). The domestic horse is non- territorial like the plains zebra, the mountain zebra and the Przewalski horse, and this is thought to have contributed to a more complex social organization than that seen in territorial equids, like the Grevy´s zebra and African wild asses (Klingel 1975 in Carson and Wood Gush 1983). Under feral and semi-feral conditions, both sexes disperse from their natal group and dispersal coincides with age at first reproduction (Rutberg and Keiper 1993, Linklater 2000). The organisation of horse groups into harems or family bands, (dominant male(s) and (un)related mares with their immature offspring) and bachelor groups, is generally considered to be remarkably similar across different breeds and populations of feral horses (McCort 1984, Linklater 2000, Boyd and Keiper 2002, Feh 2002). The same group types have developed in a small population of Przewalski horses under natural conditions (Feh 2002).

Many researchers have studied relationships between individuals in horse groups, especially dominance–subordinate relations (see Rutberg and Greenberg 1990, VanDierendonck et al. 1995), but in order to get a deeper understanding of the social structure, affinitive relations have to be known as well since they may form the basis for bonding among individuals of a group (Hinde 1976). Bonding is a very strong feature of the social life of horses (Rees 1993, Waring 2003). The long term bonds between stallions and their harem mares may have evolved due to predator pressure from cooperative hunting predators (Feh 2002) or be a manifest of a male strategy protecting the mares against harassment from other stallions as well as reducing inter-mare aggression (Linklater et al. 1999). Social attachment or bonding is indicated in various ways, e.g. by individuals taking part in interactive behaviours like mutual grooming and social play and tolerating the close presence of each other.

Mutual grooming or allogrooming is a very common behaviour in primates (Cheney and Seyfarth 1990, Dugatin 1997) and in some ungulates (cattle: Clutton-Brock et al. 1976 the impala: Hart and Hart, 1992 in Dugatin 1997). Apart from removing parasites, dead skin and excessive hairs, allogrooming is thought to cement the relationship between individuals (Feist and McCullough 1976, Dugatin 1997). In horses it is known that allogrooming lowers the hart rate and calms the animals (Feh and Mazieres 1993). Social play is generally considered to play an important role in the social development of young animals (Feist and McCullough 1976, Bekoff and Allen 1998, Waring 2003). Data on play relationships in mixed herds of feral horses is limited. Play is probably most common within peer groups and foals often play with foals of their dam's most preferred partner (Wells and von Goldschmidt-Rothschild 1979, Araba and CrowellDavis 1994, Weeks et al. 2000, Waring 2003).

Inevitably, bonding and affinitive behaviour between individuals are often strongly correlated with their relatedness, e.g. in family groups (parents and offspring, siblings). Nepotism is a widespread phenomenon amongst animals which seem to have various means to recognize related individuals, even without social learning (Sherman et al. 1997, Heth et al. 1998, Petrie et al. 1999). A preference for females to bond more with near kin than other individuals is seen in many social mammals (Cheney and Seyfarth 1990, Emlen 1997) including horses (see Wells and von Goldschmidt-Rothschild 1979, Berger 1986, Duncan 1992, Monard et al. 1996, Weeks et al. 2000). In a more general sense, however, the effect of relatedness on the behaviour of horses is not well documented.

Among horses the stallions play a central role in the structuring of bands and herds by controlling the movements of harem members (Feist and McCullough 1976, Miller 1981, Stevens 1990, Monard et al. 1996, Waring 2003). In this way the stallions minimize the risk of extra group fertilizations, future male coalitions and straying of the harem mares. Because they vigorously strive to keep the mares and their juvenile associates in an ordered and thereby defendable group, their behaviour (actively) and presence (passively) is significantly influencing all members of the group. This suggests that interactions among individuals and social structure in groups without a stallion could be significantly altered from the natural state. In 1976, Feist and McCullough suggested that the presence of stallions in feral groups might cause the mares to form less stable bonds and have a more poorly developed social hierarchy than in groups without stallions. Thus the mares might be more socially active when the dominant stallion is not around and even show stallion like behaviours (Tyler 1972, Waring 2003). In terms of behavioural strategies this phenomenon can be seen as a conflict between stallions and other group members where the stallions have the upper hand.

The compositions and husbandry of managed horse herds are quite varied. In Iceland the most common composition of herds is several adult mares, foals, yearlings, a few adult geldings and unbroken sub-adults. Colts are most often castrated at one year of age. The horses are kept outside all the year and many herds roam free in natural habitats during the summertime but are kept close to the farm during winter, and fed silage to compliment winter grazing. They are only rounded up for necessary treatments, when the mares are taken to a stallion in the summer or for training. In this paper, we present a detailed study of social interactions and social structure in such a semi-wild Icelandic herd, without a stallion present. Our study involves observations of affinitive and aggressive interactions and measurements of proximity. We analysed the effects of dominance rank, age, sex, and relatedness on the relationships. By comparing our results to results on social relationships to other studies on herds with stallion (s) present we can shed a light on how and to what extent the presence of a stallion can modify or change the behaviour of other individuals in a herd. Specifically, we address the suggestion that stallions subdue affinitive interactions among other group members and that the absence of stallions may reveal some underlying and interesting aspects of female and sub-adult behaviour.

STUDY GROUP

The research took place at Skáney Farm, W. Iceland in 1997. The composition of the study group was typical for Icelandic horse herds (see above). Most of the mares had been trained, but after being judged when they were five-six years old they were kept as breeding mares only. The herd, from which the study group was taken, was kept outside all the year and the horses mostly roamed free in a 200 ha enclosure in a hilly area. At the time of the study 34 horses; 12 pre- partum mares, five barren mares, two adult geldings and 15 yearlings and sub-adults were in the group and 8 foals were born (of which one died soon after birth). The yearlings were still suckling their mothers (See Table 1.).

METHODS

Fieldwork

During the observations, the horses were kept in an eight ha unmanaged field and were given supplementary silage on a daily basis. The observation period lasted five weeks, starting the 6th of May. After the birth of the first foal the groups were observed throughout the 24 hours. At this time of year, light conditions in Iceland allow observation throughout the night. A handheld computer pre-programmed by the Observer® software was used to collect data on social interactions between the horses, categorized in some pre-defined behaviours (see below). The behaviour of the adult mares was also recorded by focal sampling for 15 minutes each in random order, to collect data on frequencies of some of the behaviours and to calculate time-budgets (manuscript in preparation). The horses were monitored from an observation hut or outside and care taken not to interfere with them. In this study we focused on two types of friendly behaviour; allogrooming (i.e. two horses stand head to tail and scratch each other's skin) and play (i.e. two or more horses run after each other in a friendly fashion or play fight) eight types of aggressive behaviour; bite threat, bite, chase, attack, ears laid back, kick, threat to kick, and three types of submissive behaviour; move slowly away from threatening horse, flee and teeth clapping. (For descriptions of the behaviours, see (McDonnell 2003).

To assess which horses were preferred associates, judged from spatial positions, a map was drawn every half hour on which the positions of all the individuals with respect to each other were plotted. For each animal a circle was drawn including all the horses, whose head or tail were within two horse lengths. That distance represents the personal space and the individual flight zone of an individual (Cameron et al. 1999, Mills and Nankervis 1999).

Data treatment and analysis

In total, behavioural data from 488 hours were analysed and 534 of the maps were analyzed for spatial positions (maps, which were drawn while the horses were eating silage, were not included). The foals were only included in the analysis of data on play frequencies.

Matrices were made which showed how often each pair of horses (a dyad) had an interaction (allogrooming, playing, agonistic interactions). For the agonistic interactions it was recorded which horse was the initiator of an act and which was the receiver. A friendly relations matrix based on allogrooming and play was made for the sub-adults and the gelding group (=Gsa) by adding the two together. Because three of the sub-adults were introduced to the groups few days after observations started, the raw frequency data had to be corrected for each pair of animals. A proximity matrix was generated from the map data, showing for all dyads, how often a horse was within two horse lengths to another (data was transferred to percentages).

For most of the horses the pedigrees for five generations were known, so it was possible to calculate the genetic relation between all animals. The method used was to calculate the inbreeding coefficient, F, between all the dyads (Hartl and Clark 1997). The horses were all related to varying degree with two exceptions. One mare (code: J) had no genetic relation with 11 horses and her offspring (code:w) had no genetic relation with two horses. All the horses were familiar with each other prior to the study and the adult mares had been together for most of their lives.

The Observer®, Systat, Sigmastat and MatMan® softwares were used for data analyses. For the statistics the following statistics were used: Chi squares (for preferred associates), Mann-Whitney U tests, t-tests (when conditions for normality were fulfilled), Kruskall Wallis test for group comparisons, Spearman's rho correlations coefficients: permutation τ_{rw} Kr and partial $\tau_{rw,XY.Z}$ Kr correlations (for matrix comparisons); and Landau's H for dominance (Sokal and Rohlf 1981, Lee and Lee 1982, Siegel and Castellan 1988). Preferred associates or partners were those individuals with whom a horse interacted (allogroomed or played) significantly more often than expected if they had interacted equally with all horses (expected frequencies for each dyad were standardized with respect to time spent together in the herd). To calculate which horses were preferred as allogrooming partners the whole group was used, but only the geldings and the sub-adult group when play partners were identified since play amongst the adult mares was almost non-existent. Correlations were run between the matrices showing frequencies of allogrooming, play and proximities or values for relatedness between all dyads and between these matrices and test matrices. One test matrix showed rank distance between all dyads. Another one showed if the two horses in a dyad were of the same sex and in the same age-class (5 classes) (code = 1) or not (code = 0). The τ_{rw} Kr permutation test (Hemelrijk 1990) was employed to test for correlations between matrices. In some cases partial correlations ($\tau_{rw,XY.Z}$) were run to control for the effect of being in the same age-group.

Rank-order of individuals was found by using the MatMan software, which works with both aggression and submission matrices and adds them together (see VanDierendonck et al. 1995). The aggression and submission matrices were based on the total frequencies of aggressive acts and submissive responses caused by these aggressive acts. The horses were ranked according to the number of dominated individuals and if the order did not agree with the relationship between two adjacent horses the two individuals were reversed (De Vries 1993). The improved method of De Vries (1995) was used to find Landau´s linearity of each dominance hierarchy that was calculated (the whole group, the adult mares as a group and the Gsa as another group).

RESULTS

Allogrooming

All the horses, except the youngest foals (less than seven days old), were frequently seen allogrooming. On average an individual (foals excluded) took part in allogrooming 0.24 times per hour (range: 0.05-0.39). Overall, the horses preferred to allogroom with others of their same sex and age group ($\tau_{rw} = 0.41$, $n = 34$, $p < 0.001$). Nevertheless, some allogrooming occurred between horses of different sub-groups so allogrooming preferences were calculated for the whole group. All individuals had one or more preferred partners (see Table 1). No significant differences were between the five subgroups (adult mares, adult geldings, sub-adult geldings, colts, sub-adult mares), with respect to number of partners (Kruskall Wallis: $H = 6.897$, d.f. = 4, $p = 0.141$. The adult mares had other adult mares as preferred partners - the exceptions were one adult gelding, which was a partner of one adult mares, and three of the suckling yearlings which were partners of their mothers. Within the sub-adults and the adult geldings group (=Gsa), only two yearlings and one adult gelding had an adult mare as a preferred partner. The yearlings preferred other yearlings ($\chi 2 = 18.49$, d.f. = 1, $p < 0,001$), the sub-adult geldings allogroomed significantly less with the colts than expected ($\chi 2 = 5.76$, d.f. = 1, $p = 0.016$), while the sub-adult mares and the adult geldings chose more randomly ($\chi 2 = 1.50$, d.f. = 3, $p = 0.68$ and $\chi 2 = 4.72$, d.f. = 3, $p = 0.193$, respectively)

Some individuals were much more popular to have as a friend than others (see Table 1). Popularity was not related to rank amongst the mares (Spearman´s rho for mares: -0.154, n = 17, p = 0.546), nor amongst the geldings and the sub-adults (Spearman’s rho = 0.239, n =17, p = 0.346). There was no correlation of popularity with age in the two social groups (the adult mares: Spearman’s rho = 0.125, n = 17, p = 0.625; Gsa: rho = -0,031, n = 17, p = 0.898). The sexes were equally popular in the Gsa group (t = 0.484, d.f. = 15, p = 0.635).

Play

During the study period, 728 playing sessions were recorded. The adult mares were only involved in 11 sessions and are not included in the analyses reported below. On average the sub-adults (males and females), adult geldings and the five foals that reached at least the age of one week during the observation period, played 0.121 times per hour. The frequencies for the four sub-groups differed (Kruskal Wallis: $H = 16.6$, d.f = 3, $p < 0.001$). The sub-adult males played most or on average 0.215 times per hour. The sub-adult females played on average 0.031 times per hour which was significantly less than the value for males (Mann –Whitney U, T = 21, p = 0.001). The five foals played with others on average 0.106 times per hour (means for two colts is 0.16 and for three fillies is 0.07). Overall the horses preferred to play with others of the same sex and in the same age group ($\tau_{rw} = 0.331$, $n = 17$, $p < 0.001$). More detailed analyses showed that the sub-adult geldings and the yearlings showed preference for their own class ($\chi 2 = 22.8$, d.f. = 1, $p < 0.001$ and $\chi 2 = 9.53$, d.f. = 1, $p = 0.022$, respectively). The sub-adult mares and the adult geldings chose playing partners more randomly ($\chi 2 = 1.51$, d.f. = 3, $p = 0.680$ and $\chi 2 = 3.44$, d.f. = 3, $p = 0.328$, respectively). Both the sub-adult geldings and the colts played significantly less with the sub-adult mares ($\chi 2 = 5.62$, d.f. = 1, $p = 0.017$ and $\chi 2 = 4.69$, d.f. = 1, $p = 0.030$, respectively) than the other groups.

There was a significant difference in number of preferred playmates between the subgroups (Kruskal Wallis: H = 8.961, d.f. = 3, p = 0.03). The main difference was between the sexes; the males had significant more play partners than the sub- adult mares (t = 3.99, d.f. = 15, p = 0.001, means: 1.83 and 3.91, respectively). Some individuals were also more popular than others as playmates (see Table 1). Males were significantly more popular than females (t = 3.92, d.f. = 15, p = 0.001). There was no correlation between popularity and rank position nor between popularity and age (Spearman's rho = 0.261, n = 17, p = 0.307 and: rho= -0.019, n = 17, p = 0.936).

The allogrooming matrix for the Gsa group was significantly correlated with the play frequency matrix (τ_{rw} = 0.207, n = 17, p < 0.001). Consequently a combined positive relations matrix was constructed by adding the two together (see Table 3).

Table 1

Names, code, age (years), classification, which horses are half siblings through a mother, which are offspring of a mare, dominance rank of individuals horses in the study and identities of preferred partners (play partners in italics and bold).

Horse	code	age	group	sibling to:	off-spring of:	rank order	Preferred grooming and *play* partners of subject	Individuals pre-ferring the subject as grooming- or *playing* partner
Bylgja*	Y	19	pm			7	B,J,,o,F,	B,J,F,o,
Blída	B	18	pm			6	Y,T,x,I,	Y,T,R,x,I
Stjarna	S	18	pm			17	K,H,J,P,G	J,H,K,P,G
Rönd*	R	18	pm			3	H,T,G,B,i	G,H,
Gerdur*	G	16	pm			9	J,D,I,R,S	R,D,J,I,S,F
Drífa*	D	16	pm			11	K,J,P,T,G,a,q	G,J,T,K,P,a,F
Sjöfn*	J	15	pm			12	Y,G,D,S,	Y,S,G,D
Hvida*	H	15	pm			10	S,T,R	S,R,T,i
Tilraun*	T	12	pm			4	B,H,D,x,I,	B,D,H,R,x,I
Freyja*	F	11	pm			13	Y,K,G,D	Y,
Blika**	K	11	pm			15	P,D,S,i, a,	S,D, P,i,a,F
Perla*	P	9	pm			19	K,D,S	S,K
Rispa	i	20	bm			5	K,I,I	Kx,I,I
Stroka	o	17	bm			8	Y,x,I,O	Y,I,O,x
Faxa	x	15	bm			2	B,T,i,o,I	B,T, o,I,
Glæda	l	13	bm			1	B,T,G,i,x,o	B,G,T,i,o,x,
Pipa	a	10	bm			14	K,D, A	D,K,A
Geysir	q	10	g		R	18	D,z,m,n,c,C,N-***I,X,O,n,m,w***	D, N,C,z,u,n,m,-***n,I,O***
Tumi	u	.9	g			16	v,q,m,M-***m,N,v***	w,m,c,M,v-***N,M***
Vari	v	4	g	e		25	u,N,z- ***X,z,w,m***	z,- ***w,z,m,X***
Losti	w	4	g	n	J	22	z,u,n,m,C,M,c- ***v,m***	z,u,n,C,-***v, m,c,q***
Bliki	z	4	g	M	K	24	L,v,w,q,m,c,M,w,n- ***X,v,n,m***	L,v,w,q,n,m,c,M-***v,n,u,m,X***
Birna	N	3	sm		T	23	n,m,q-***u,m***	v,q,m-***u***
Mjöll	M	3	sm	z	K	20	z,C,c,N,u,n-***u***	w,z,u,n,C,c,-***A***
Týr	n	2	g	w	J	32	w,q,c,e,m,C,M,z-***L,z,q,m***	q,z,w,M,m,C,e,c,N-***z,m,L,q***
Safír	m	2	g		P	33	I,u,q,c,N,L,n,C,z-***L,w,n,v***	I,L,u,n,c,-***q,u,v,w,z,N,n,X,L***
Albína	C	2	sm	A	a	27	I,L,m,c,M,q,n,e.A- ***L,e***	X,L,q,n,m,c,e,I,M,w-
Þrista	e	2	sm	v		21	X,c,L,n,A-***X,L,c***	L,n,C,c-***C,c***
Kría	c	2	sm	X	x	34	L,z,w,q,n,C,e,M,m-***e,w***	z,w,n,m,C,e,M-***e***
Mosi	I	1	c		i	29	m,A,L,C,i-***X,O,L,q***	L,A,O,,m,C,i-***q,O,***
Blakkur	X	1	c	c	x	30	I,L,C,,A,O-***O,L,z,v,m***	OL,A,e-***q,v,z,e,I,O,L***
Blesi	O	1	c		o	31	A,I,X,L,O-***I,X,q***	X,L,A,o,-***q,I,X***
Tígull	L	1	c		l	28	X,z,m,C,e,I,z-,***X,n,m***	X,m,e,I,O,C,c-***n,m,C,e,I,X***
Blesa	A	1	sm	C	a	26	I,X,a,O,-***M***	I,X,O,a-

pm=pregnant, bm=barren mare, sm= sub-adult mare, g=gelding;, c=colt

* these mares gave birth

** the foal died 20 minutes after birth

Proximity

The horses stayed close to others of similar age and same sex (τ_{rw} =0.25, n = 34, p < 0.001). Furthermore, they tended to allogroom with the same individuals as they were spatially associated with (whole group: τ_{rw} = 0.39, n = 34, p < 0.001). This relationship is not confounded by being in the same age-group as results from partial correlations show (whole group: $\tau_{rw, XY.Z}$= 0.33, n = 34, p < 0.001; the adult mares as a group: $\tau_{rw, XY.Z}$ = 0.35, n = 17, p < 0.001; Gsa as a group: $\tau_{rw, XY.Z}$ = 0.34, n = 17, p < 0.001).

The adult geldings and the sub-adults were also spatially associated with their playmates (τ_{rw} = 0.29, n = 17, p < 0.0005).

Table 2

Linearity of the dominance hierarchy as measured by Landau's improved h'.

Group	Landau's h'	Chi	df	p	% blank	% one way
Whole group	0.717	309	39.9	0.001	16	83
Mares only	0.638	82	24.1	0.001	10	87
Geldings and sub-adults	0.532	64	24.1	0.001	30	68

The blank relationships are the percentage of dyads where there were no interactions recorded and one- way relationships are those in which the submission and the aggression results point in the same direction.

Agonistic behaviour

The calculated dominance rank order for the whole group was based on 1372 threatening and 1497 submissive acts. The frequencies of the aggressive acts (0.08 per horse per hour) are minimum values for the group as a whole because some of the more subtle acts have probably been overlooked. The higher number of submissive acts is also an indication of an underestimation of recorded aggressive acts. The value for the adult mares is 0.135 per hour or higher, and is more accurate because only the adult mares were observed by focal sampling.

The rank orders were significantly linear in the whole group and also within the two main social groups (See Table 2). The rank order was significantly related to age in the study group (Spearman's rho = 0.882, n = 34, p < 0.001). The two year-old geldings and one two year-old mare had the lowest ranks. This suggests that the yearlings, which were still suckling, had some benefit of their mother's social status.

The adult mares groomed more with those which were closer in rank (Spearman's rho= 0.22, n = 136, p = 0.018), while no such correlation was found amongst the Gsa group (Spearman's rho= 0.089, n = 136, p = 0.300).

Other behaviours

On 47 occasions, adult mares, five pre-partum and two barren, were seen mounting barren mares when they were on heat and in 26 of these cases this was done by the same pregnant mare. Interestingly, being very close to having a foal, did not seem to preclude this behaviour. Higher ranking mares were not more likely to show this behaviour than lower ranking ones.

Interventions, where horses prevented others in taking part in allogrooming or play, or actively prevented others from approaching a mare with a young foal occurred quite often.

Such behaviour was recorded on average every other hour in the study group. Six adult mares and all the sub-adults and geldings intervened in allogrooming. Two mares and 14 of the 17 sub-adults and geldings intervened in play. Protecting a mare and/or a foal characterized certain individuals. Two adult mares, one pregnant and one barren, and one two-year-old mare, exhibited this behaviour quite frequently or in 55% of all cases. (Manuscript in preparation.)

Kinship

Correlation between affinitive behavioural matrices (allogrooming, playing, friendship) and the genetic relation matrix showed that relatedness had a significant positive effect on frequency of affinitive interactions, both within the adult mares group and the adult geldings and the sub-adults group (Table 3). Although, rank distance and relatedness was not correlated in the whole group, splitting the group showed that amongst the adult mares the correlation was negative, while that was not true for the Gsa. Also, the horses tend to associate spatially more with the more related individuals. (Table 3.)

Table 3

Results from correlations (A) between (x) kinship (based on five generations) and several social matrices (y) and (B) partial correlations between the same matrices, controlling for (z) age-groups (5 age-classes).

Matrix (y)	**(sub) group**	τ_{rw} **(A) or** $\tau_{rw, XY.Z}$ **(B)**	**n**	**P**
Allogrooming				
A	All	0.081	34	0.001
B		0.076	34	0.002
A	Mares	0.142	17	0.003
B		0.138	17	0.001
A	Gsa	0.142	17	0.005
B		0.090	17	0.032
Play				
A	Gsa	0.206	17	0.002
B		0.191	17	0.001
Play + allogrooming (friendship)				
A	All	0.070	34	0.001
B		0.070	34	0.005
A	Gsa	0.200	17	0.0005
B		0.170	17	0.0005
Rank distance				
A	All	0.016	34	0.674
B		0.005	34	0.550
A	Mares	0.090	17	0.049
B		0.100	17	0.041
A	Gsa	0.022	17	0.375
B		0.030	17	0.301
Spatial association				
A	All	0.12	34	0.0005
B		0.12	34	0.0005
A	Mares	0.19	17	0.0005
B		0.18	17	0.0005
A	Gsa	0.23	17	0.0005
B		0.18	17	0.0005

Gsa: Geldings and sub-adults.

DISCUSSION

Allogrooming and play

Horses took part in mutual grooming on average 0.24 times per hour in this Icelandic herd. In two other Icelandic groups without stallions, which were composed of: (1) 30 adult geldings and adult mares and (2): a mixed group of 28 sub-adults and adults, allogrooming frequencies were 0.28, and 0.16 times per horse per hour, respectively, in December – April (H.B. Ingolfsdottir & H. Sigurjonsdottir, in prep.). Scottish Highland ponies (14 adult mares and three 1-2 year old sub-adults) groomed more often or on average 0.65 times per hour in July-September (Clutton-Brock et al. 1976). When compared with groups with a stallion these values are relatively high. Thus, in a group of Camargue horses (one stallion, eight mares, five foals and 12 1-2 year old sub-adults) the horses only allogroomed 0.06 (mares and yearlings) and 0.13 (males) times on average per hour in March till June and in November (Wells and von Goldschmidt-Rothschild 1979). And in one family of eight in a herd of Przewalski horses in France, allogrooming in September occurred infrequently or on average only 0.07 times per horse per hour when the two foals are excluded (unpublished results- the group was observed for 40 hours by the first author in 2000). In that study, the stallion and one of the adult mares were never seen to allogroom while the other adult mare allogroomed with her three offspring. The intensity of allogrooming is influenced by many factors such as season (winter coat shedding), weather, parasites and flies (Wells and von Goldschmidt-Rothschild 1979) as well as social factors, such as the existence of newcomers in a group and importance of establishing bonds. Therefore, it is necessary to know the number and the identity of partners to understand the nature of grooming relationships.

In most published studies, where relationships have been studied in details, the number of preferred partners is 0-3 (Tyler 1972, Clutton-Brock et al. 1976, Monard et al. 1996, Kimura 1998). In our study, the horses had more partners. When looking at the frequency of allogrooming and the identity of the preferred partners it seems that the presence or absence of a stallion could make a difference. Thus, mutual grooming seems to be more common in groups without stallions. Also, in the groups that did not have stallions the adult mares preferred to groom with other mares of similar age (Tyler 1972, Clutton-Brock et al. 1976, this study), while they tended to groom with their 0-3 year old offspring when in a harem (Feist and McCullough 1976, Wells and von Goldschmidt-Rothschild 1979, Przewalski horses pers. Obs.). It is more difficult to see the effect of the stallion on the preferences of the sub-adults. In Wells & van Goldschmidt-Rothschild´s study (1979), most mutual grooming occurred within the family but the yearlings and the foals also preferred to groom with their peers. After immigration, sub-adult mares quickly established bonds with mares of similar age (Monard et al. 1996). It is interesting that in the no-stallion Icelandic herd, the sub-adults (2-4 year olds) did not associate much with their mothers; instead they bonded with their peers and the adult geldings. In Clutton-Brock et al. study (1976), the sub-adult mares preferred to bond within their age group.

On the whole there was a good correlation between allogrooming and play preferences within the group of sub-adults and geldings, which supports the common notion that the horses play with the ones they associate mostly with. Data on play frequencies in natural herds is, however, very limited. Young dispersing males in the Camargue herd played 0.25 times per hour prior to emigration (Monard et al. 1996), which is similar to what we found for the sub-adult geldings in our study. Since dominant stallions are less protective of the dispersing daughters than other members in their band (Waring 2003), the young mares may in effect be more socially active than the other sub-adults. Feist and McCullough (1976) reported that the stallions in their study allowed the foals to play with foals from other groups but prevented other members in the harem to join other groups. In a herd of Przewalski horses in France the stallion acted in the same way. The only inter group social interaction that the stallion tolerated was play amongst the foals, which was rare (four foals and sub-adults played on average 0.04 times per hour) (H. Sigurjonsdottir, pers. obs.).

Not only did the males play more in our study, they also had more preferred playmates than the females. The young males preferred their own sex-age class, while the sub-adult mares played with both sexes. Monard et al. (1996), found that prior to emigration dispersing sub-adult Camargue mares preferred to play with immatures of both sexes and the stallion in their natal groups. As Wells & van Goldschmidt-Rothschild (1979) argue, all the sub-adults like to mingle with their peers. Differences in popularity amongst group members were striking (see Table 1). Popularity as a playmate was not related to rank position, instead individual temperament may be more important.

Dominance relationships

Aggression rates were lower in the Icelandic group than reported from other studies - only 0.17 per hour on average amongst the adult mares. Monard et al. (1996), Stevens (1990) and Rutberg and Greenberg (1990), who were all studying females in natural harems, reported aggressive rates of 0.3-0.5, 0.24 and 0.9-3.6, respectively. In Clutton-Brock et al. study (1976), mean aggression rate was 1.9 per hour. The differences between the groups may be due to different levels of competition for resources and age of the mares, since younger mares tend to be more aggressive (Rutberg and Greenberg 1990). Newly dispersed females also receive more aggressive acts than other mares and aggression is more frequent between females during male competition for mates (Linklater et al. 1999). Clearly, more factors need to be controlled for before the effect of stallions on female aggressiveness can be revealed. A clear and linear dominance hierarchy was found to characterize the group, where adult mares dominated the sub-adults. This finding is in an agreement with some studies (Houpt and Keiper 1982, Jezierski and Gebler 1984, Keiper and Sambraus 1986, Rutberg and Greenberg 1990, VanDierendonck et al. 1995), while in others the linearity was much less clear (Schoen et al. 1976, Feist and McCullough 1976). For the group as a whole there was a significant correlation between rank and age. The adult geldings were relatively young compared to the adult mares so it is not possible to reveal whether sex was more important than age. The top ranking mares were, however, not the oldest in the group (see Table 1). The same pattern was found to characterize the dominance hierarchy amongst the Exmoor ponies (Wood-Gush and Galbraith 1987). Positive correlation between age and rank has been found in a study on the Przewalski horse (Feh 1988, Keiper and Receveur 1992) and in the domestic horse, both feral and domestic groups (Clutton-

Brock et al. 1976, Keiper and Sambraus 1986, Rutberg and Greenberg 1990, VanDierendonck et al. 1995, Kimura 1998). Other studies on the domestic horse have not shown a significant correlation between age and rank, (Houpt et al. 1978, Houpt and Keiper 1982) although adults were dominant over juveniles. In some studies, offspring of dominant mares achieve a higher rank (Araba and CrowellDavis 1994, Weeks et al. 2000) but in others they do not (Keiper and Sambraus 1986). In our study, the five yearlings which were still suckling their mothers, ranked higher than some of the two and three year old subadults, so it seems that they benefited from their mother's presence in the group.

As Houpt et al. (1978), Houpt (1982), Berger (1977) and Weeks et al. (2000) point out, many factors influence dominance relations. It could be aggressiveness, weight, residence time or some other attribute. The longer a horse stays in a group, the more time he has to bond and gain social experience, which is likely to be the basis for strategic planning. Residency has been shown to influence rank among horses (Clutton-Brock et al. 1976, VanDierendonck et al. 1995, Monard et al. 1996). The social structure of horse groups is, without any doubt, much influenced by dominant/subordinate relationships between the horses since the dominant horses can choose which they want to associate with. Earlier findings, (Clutton-Brock et al. 1976, Wells and von Goldschmidt-Rothschild 1979, Ellard and CrowellDavis 1989, Monard et al. 1996, Kimura 1998), where individuals of similar rank form affinitive relationships, are supported in this study. Interestingly, although found amongst the adult mares, such a relationship was not apparent amongst the immatures. That is not surprising since they are probably still forming bonds and their preferences are less clear than the mare's.

Although the dominance status of the stallions in natural herds is clear when they herd their harems it is not necessary so in other contexts, like access to drinking or in aggressive encounters within the harem (see Waring 2003). For this reason the nature of affinitive relationships within a harem could be dependent on the dominance status of the stallion. The social structure of groups without a stallion could therefore be more like that of harems with a low ranking single-stallion. More research is clearly needed in this area.

Kinship

The horses preferred to have positive social relations (allogroomed, played and stayed close to) within their social groups with the more related individuals. This is an important finding, that has not been described before for horses except in the context of close kin preferences within harems (in the Camargue see Wells and von Goldschmidt-Rothschild 1979). Also, the more the adult mares are related, the closer they are in rank. A possible explanation for this is that relatives share genes, which influence the outcome of agonistic interactions and thus determine their rank positions in the hierarchy.

Kin recognition is a widespread phenomenon (Parr and de Waal 1999, Tang-Martinez 2001) and in some cases animals are able to discriminate between unfamiliar kin and non-kin (Sun and Muller-Schwartze 1997, Heth et al. 1998, Petrie et al. 1999). Little is known about kin discrimination in horses since familiarity is generally a confounding factor. Horses recognise herd members by sight, sound and smell (Feist and McCullough 1976, Waring 2003) and learning is definitely important. In tight family bands grooming occurs mostly within the family (Tyler 1972, Feist and McCullough 1976, Wells and von Goldschmidt-Rothschild 1979, Houpt 1982). Monard et al. (1996) showed that before dispersal, young mares reject the sexual advances of familiar males in their natal groups. That their mothers often interfered when close kin males were involved could be evidence of kin recognition. Preference for related individuals outside the family group as reported for the New Forest ponies herd, especially amongst the sub-adults (Tyler 1972) is probably another example. Although kinship relations might not be as important for the individuals in female - emigrating mammalian species as in female - resident species, (see Monard et al. 1996), it can nevertheless be a good strategy to form relationships with related individuals when young if it can raise inclusive fitness later on. In general young females in female-emigrating species form strong relations with members of their matrilines – a behaviour which could later facilitate integration into new harems (Monard et al. 1996). Such an argument is supported by the findings of Monard et al. (1996) who showed that dispersing mares approached groups in which there was a familiar and related young mare. Less is known about the males. Feh (1999) showed that the subordinate stallions that formed an alliance and kept a harem together had been close associates in their natal group, but they were not of close kin. It would be interesting to study the genetic relations between young dispersing males and associates in the new groups, which can be of different compositions (see Khalil and Kaseda 1998 for explanation).

In the Icelandic herd, all the horses were familiar to each other so it is not possible to assess if they would prefer unfamiliar individuals with common genes (through the father line). The correlation between relatedness and affinitive relationships was not due to bonds between siblings through the mother line nor between mothers and daughters (see Table 1). What is of special interest is the fact that within both social groups, the horses chose to associate with more related horses of similar age. That is an interesting finding which might be a consequence of stallion absence. Therefore the question of kin recognition abilities and nepotism among horses is unanswered until more horse groups of different compositions are studied.

SUMMARY AND CONCLUSIONS

The relationships that characterized the group in Iceland were dominance of the adult mares over the adult geldings and the sub-adults, mutual grooming bonds between the adult mares and mutual grooming and play relationships amongst the other horses. Horses that were close in age formed affinitive relationships. So did adult mares also, which were close in rank. The more the horses are genetically related, the more they attach socially. Compared to groups including a stallion, the relationship pattern differ mostly in how much the adult mares bond with other adult mares and how little they associate with their sub-adult offspring (the exception being bonds between three mothers and their suckling yearlings). As a consequence of the adult mares' dominance and preferences, the herd was in effect divided into two social groups the adult mares on one hand and the sub-adult plus adult geldings on the other. Interesting differences were found between these two social groups, reflecting more stable social structure in the adult mare group. For instance, the adult mares allogroomed with other adult mares of similar rank while no such correlation was found within the other group. Also, only within the adult mare group was there a positive correlation between relatedness and being close in the dominance hierarchy.

Our finding that kinship affects bonding within a group of horses outside the family unit has, to our knowledge, not been reported before. Both adult mares and the sub-adults and the adult geldings are more likely to be spatially associated with more related peers and they also allogroom and play (i.e. the sub-adults and the geldings) more with more related individuals.

There was a good agreement between standing close to each other and affinitive relationships, which is in agreement with many other studies (Clutton-Brock et al. 1976, Jezierski and Gebler 1984, Wood-Gush and Galbraith 1987, Whitehead and Dufault 1999).

Adult mares (pregnant and barren) showed a typical stallion-like behaviour when they mounted other mares. Such a behaviour has rarely been described for adult mares among horses (Feist and McCullough 1976, Waring 2003) but seems to be common in female donkeys, which by the way do not form permanent bonds with the males (McDonnell 2000). The mounting behaviour might be a sign of dominance as was witnessed amongst the stallions in Wyoming when they mounted immature stallions (Feist and McCullough 1976). Protection of a post-partum mare and her new born foal by another mare is another unusual behaviour. Perhaps, the herd members take up the protective role of the stallion in his absence.

Some new and some unusual findings emerged in this study. Our results suggest that stallions may suppress adult mares in natural bands by preventing them to move between bands and hence disrupt their allogrooming preferences. It is also likely that stallions suppress the youngsters in their group by intervening in play and allogrooming with youngsters from other harems and even within their own harem. More research is needed in this area; especially studies on play preferences amongst sub-adults in groups of different compositions and on stallion interventions in allogrooming and play.

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◆

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CHAPTER 5

Differences in social behaviour between late pregnant, post-partum and barren mares in a herd of Icelandic horses

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ABSTRACT

Group dynamics and the social behaviour of mares were investigated in the periods before and after foaling during 2 non-consecutive years, in a herd of Icelandic horses consisting of adult mares and geldings and juvenile fillies, geldings and colts. The horses were observed 24-hours a day for 5-6 weeks; i.e. a total of 1483 hours. There were significant changes in the social behaviour and interactions of mares after foaling, compared both to their own behaviour pre-partum and to that of barren control mares. While the frequency of allogrooming dropped during the study period in all mares, it dropped significantly more in foaling than in control barren mares. However, while the absolute allogrooming frequency was strongly correlated with reproductive state, it was still remarkably consistent within an individual adult mare between the study years. After foaling, mares with foals separated off into a distinct subgroup, whereas barren control mares increased interaction with the rest of the herd; it is presumed that separation served to keep the foals at a safe distance from the more boisterous geldings and sub-adults; alternatively, it could have been the result of mutual attraction between the foals. In general, the linear dominance order was correlated strongly with age, and the top-ranking mares were older mares that had not yet begun a senescent loss of physical condition which resulted in a later slight drop down the hierarchy. There was no consistent relationship between dominance rank and the pattern of preferred recipients of affiliative interactions, while familiarity was a more important determining factor than kinship in the selection of a preferred partner for affiliative interactions. The preferred partner for proximity was often the same individual as that for allogrooming, suggesting that proximity was a result of an active process rather than of passive acceptance. The presence of adult geldings in the herd did not seem to change the social behaviour of mares as compared to that described for feral horses, and did not appear to negatively affect behaviour during parturition, mare-foal bonding or subsequent maternal care. In short, maintenance of breeding mares in a herd of mixed age and sex did not interfere with normal species-specific behaviour or with the development of the stable, long-lasting mare-mare bonds that are central to maintaining a stable herd. It is concluded that such a system could be a welfare-friendly alternative to typical modern husbandry systems, as long as adequate space is available.

Keywords
Horses; social behaviour; parturition; allogrooming; mares; foals; geldings.

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INTRODUCTION

In many equine husbandry systems, the behaviour of horses is influenced negatively by the absence of opportunities for social contact, unhindered locomotion or foraging, and this is confounded by inappropriate feeding (Mills and Clarke 2002). In principle, abnormal behaviours could be prevented or ameliorated by the adoption of more "natural" husbandry systems, such as keeping mares and geldings in groups rather than individually. However, while group housing systems provide extensive opportunities for social contact and free locomotion (Mcgreevy 1997, Lebelt 1998, Mcbride and Long 2001), imposed and unstable social grouping can lead to problems such as extreme submission and/or aggression possibly leading to injury (Kolter 1984, Zeitler-Feicht 1996, Zeitler-Feicht and Prantner 2000, Bachmann and Stauffacher 2002, Mills and Clark 2002). However, these domesticated groups still differ markedly from the natural forms of social organisation, namely harems, multiple male bands or bachelor bands, described in the literature (Klingel 1975, Linklater 2000). In general, domesticated or managed groups of horses consist either of broodmares (and their foals), young stock (usually in year cohorts) or adult mares plus adult castrated males (geldings). And while extensive research has been performed on the behaviour of individuals in both breeding mare and young stock groups (Estep et al. 1993, Barber and CrowellDavis 1994, Weeks et al. 2000, Christensen et al. 2002a, 2002b), little data is available on complex groups with both (sub)adult geldings and breeding and non-breeding mares (Sigurjónsdóttir et al. 2003).

Important parameters for evaluating the stability and structure of an equine social group include aggression, dominance, allogrooming and proximity. Allogrooming seems to be a very useful behaviour to strengthen the bond between individuals, especially mares (Feist and McCullough 1976, Kimura 1998, Feh 1999), since it may help to reduce tension between animals (Spruijt et al. 1992, Feh and Mazieres 1993) as well as being a way of 'cleaning' or 'scratching'. The relationship between close proximity and allogrooming is, however, still under debate (Clutton- Brock et al. 1976, Jezierski and Gebler 1984, Wood-Gush and Galbraith 1987, Kimura 1998, Roberts and Browning 1998, Sigurjónsdóttir et al. 2003). Close proximity could be the result of individual initiatives such as allogrooming, or of passive acceptance. Proximity is usually defined in terms of 'nearest neighbour' scores, but occasionally as distances between individuals (Linklater et al. 2000). Every individual has a 'flight zone' and a 'personal space'; the area immediately around the horse in which only close companions are tolerated (for review see Mills and Nankervis 1999). For the study of proximity relationships, biologically meaningful information can best be obtained by evaluating which individuals are within a short distance (personal space) of each other, and less meaningfully by nearest neighbour scores.

In addition to allogrooming and proximity, dominance plays an important role in the social organisation of equine groups (Rutberg and Greenberg 1990, Vandierendonck et al. 1995, Roberts and Browning 1998, Sigurjónsdóttir et al. 2003). Often, similarly ranked animals form especially close social bonds (become 'preferred partners') (VanDierendonck et al. 1995). However, while rank and age are important to subgroup formation within a feral population (Kaseda et al.1995, Kimura 1998), duration of co-residence (VanDierendonck et al. 1995), familiarity and kinship (Roberts and Browning 1998) are also major factors contributing to strengthened social relationships between horses (Sigurjónsdóttir et al. 2003). Certainly, mares tend to have stronger bonds with familiar individuals or close kin (Estep et al. 1993, Barber and CrowellDavis 1994). It follows that a given individual will usually allow others with specific characteristics with regard to kinship, familiarity, duration of residence and sex within its flight or personal space.

The relationship between geldings and, in particular, foaling mares has not been examined extensively (Wood-Gush and Galbraith 1987, VanDierendonck et al. 1995, Asa 1999). In the closest feral counterpart of this type of herd, the multiple male band, mares are more frequently harassed and have less resting time, and therefore tend to be in poorer body condition than mares in harems (Linklater 2000). The breeding performance of mares in multiple male bands is also worse than in herds with a single harem stallion. However, it is not known if the presence of adult geldings has a similar detrimental effect.

Parturition and suckling are associated with short and long-term physiological and behavioural changes, related primarily to the demands of caring for a foal. These behavioural changes can also profoundly affect the dam's relationship with other group members. Self-imposed social isolation of the dam and her newborn foal serves to prevent others from interfering with the process of bonding between the newborn foal and its dam in the first few days after birth (Klingel 1975). Indeed, within a herd of broodmares, mares that foal are more likely to make changes in their affiliative relationships after foaling than before and, after foaling, mares are generally less affiliative with other herd mates (Estep et al 1993).

In the current study, which is part of a larger study (Sigurjónsdóttir et al. 2003), the behaviour of adult mares around the time of parturition was observed in a group of domestic horses that also included sub-adult (1-4 year old) mares, yearling stallions and sub-adult and adult geldings (but no adult stallions). This husbandry system has been used extensively for many centuries in Iceland, but is virtually unheard of in mainland Europe and has not been studied in great depth. In order to better understand the desires/needs of parturient mares and to determine the basic requirements of such a group management system during the foaling season, changes in the social behaviour of mares before and after parturition and differences to barren control mares were investigated.

ANIMALS, MATERIALS AND METHODS

During the foaling periods (April to mid-June) of 1997 and 1999, social behaviour was studied in pastured groups of Icelandic horses. The studied groups comprised adult mares (pregnant and non-pregnant) and geldings, sub-adult mares and - geldings (1-4 year olds) and yearling stallions (Table 1). Eighteen individuals (including 11 of the adult mares) were observed in both of the study years.

Table 1
Sex, age and reproductive status of the horses in the study groups.

	1997 n	1999 n	1997 mean ± sd age (years)	1999 mean ± sd age (years)
Pregnant mares*(≥ 6 yrs)	12	14	14.8 ± 3.3	16.4 ± 3.7
Post partum mares*	7	13**	13.9 ± 3.6	16.5 ± 3.8
Barren control mares (≥ 6 yrs)	5	4(5)**	15.0 ± 3.8	16.0 ± 7.0
Adult Geldings (≥ 4 yrs)	5	4	6.2 ± 3.0	13.5 ± 3.1
Sub Adult Males (1-4 yrs)	6	5	1.3 ± 0.5	2.8 ± 1.3
Sub Adult Females (1-4 yrs)	6	4	2.2 ± 0.8	3.3 ± 1.0
Foals	7	13		

* During the observation periods of 1997 and 1999, 7 and 14 mares foaled, respectively
** One foal died soon after birth and its dam was, therefore, moved from the pregnant group to the barren (no foal) control, instead of the post-partum, group after parturition

The animals studied were part of a herd of 80-100 horses that was free-ranged all year round in a mountainous, river-dense area exceeding 1200 hectares in Southeast Iceland. In winter and spring, supplementary silage was provided once daily. During the observation periods only, the animals under study were corralled within an 8-hectare sub-enclosure, to facilitate detailed observation. Shelter within the sub-enclosure was more than adequately provided by landscape elements.

In 1999, 8 animals (including 4 adult mares) from two neighbouring farms were added to the group observed in 1997, with the aim of introducing familiarity as a variable to the social interactions. Seven foals (2 colts and 5 fillies) were born in 1997 and 13 (5 colts, 8 fillies) in 1999. All horses, except one from 1997 and the 8 animals introduced in 1999, were born in the herd and all adult mares were multiparous. The degree of kinship between pairs of animals was calculated by means of co-ancestry over 5 generations, as described by Hartl and Clark (1997).

Observation and recording of behaviour patterns

The observation methods consisted of All Occurrence (AO) observations of 99 predefined behavioural elements, which included affiliative and dominance elements. In addition, in 1997, the AO observations were alternated every half hour with 15-minute focal animal (FA) observations of adult mares, and spatial scan (SS) samples. If a foal was born, preference was given to collecting FA and AO samples rather than SS samples. The ethogram used was described by Schilder (1990) and modified according to McDonnell and Haviland (1995). The FA and AO data were recorded on a Psion handheld computer(s) using 'The Observer' software®, and transferred daily to a laptop computer. Since there was 24-hour daylight in Iceland, the data were collected continuously, 24 hours a day. To prevent any structural bias in recordings, the observers worked in 8-hour shifts with one overlapping hour at each shift change, so that shift changes were not at the same time of the 24 hr clock every day. Each observer covered day and night periods equally. Some observation time was lost due to unfavourable weather conditions or human body maintenance requirements. Regular inter-observer reliability sessions were performed. In both years, the first foal was born 5 days after starting the baseline observations. Observation was continued for a total of 488 hours in 1997 and 828 hours in 1999, and 666 spatial samples were recorded.

Data analyses

The data from the adult breeding mares was analysed with respect to reproductive status, i.e. pregnant versus post-partum. In addition, a barren mare was assigned randomly to each foaling mare, as a control. The social interactions of the control mare were then grouped according to the pre and post-partum periods of the associated foaling mare, to control for the effect of season; these mares will be referred to accordingly as pre-foaling controls and post-foaling controls. Because foals were born at different dates, mares were observed for different lengths of time in the post-partum period. For this reason, all behavioural dyadic interactions were recalculated from absolute values to comparable frequencies per 24 hours per individual (or dyad) per period. When analysing the proximity samples, the observations made when the animals were feeding on silage were not included because the supplementary feeding enticed the animals into closer proximity than when grazing; as a result only 534 out of the 666 spatial samples were analysed. The proximity data were expressed as a percentage: the number of recordings divided by the number of opportunities (which was not the same for all dyads because of the different foaling dates) that individuals of a given dyad were within 2 horse-lengths of each other.

Dominance relationships and rank orders were determined on the basis of five behavioural elements, namely submission and 4 offensive behaviours (ears back, threat to bite, bite, and attack), as described by VanDierendonck et al. (1995). Relative aggressiveness of an individual was calculated as the frequency of the four offensive behavioural elements per 24 hours.

Data was analysed using a combination of MatMan® (DeVries et al. 1993), The Observer® (both from Noldus Information Technology, Wageningen, The Netherlands) and MVSP® software (Kovach Computing Services, Pentraeth, Wales). Statistical analyses were performed using the following tests: (partial) row-wise tau matrix permutation test (2000 permutations) for matrix comparisons (DeVries 1993), Wilcoxon signed ranks test for related samples, Mann-Whitney U test for unrelated samples, Spearman's Rank Correlation (Rho) and Pearson's correlation coefficients for rank correlations, Landau's 'h' (DeVries 1995) for linearity, Preferred partners were identified using Standardised Residuals (Siegel and Castellan 1988).

The small number of samples from individuals that performed less than [the mean minus the standard deviation] amount of a particular behaviour were excluded from the analysis of that behaviour.

The proximity results were plotted after a Principal Components Analysis (PCA: Manly 1994) of the standardised residual (SR) results per dyad. These SR results were expressed as the percentage of the highest value in each matrix of standardised residuals. Each individual was considered to be a single case.

Hypothesis matrices were all corrected for structural zeros and constructed for sex and age, mare reproductive state, kinship, familiarity (based on the place where the animals were located before joining the herd) and dominance rank distance.

RESULTS

Dynamics of allogrooming

Frequencies

Allogrooming was performed an average of 2.6 ± 0.83 times per individual adult mare per day in 1997 and 4.8 ± 2.03 in 1999 (mean ± standard deviation). The allogrooming frequency decreased significantly after the time of parturition in both foaling mares and in their control (barren) herd-mates (Fig 1a, b); the decrease was however significantly greater for the former (Table 2). In addition, while the allogrooming frequency of pregnant mares did not differ from that of the pre-foaling controls, that of post-partum mares was significantly lower than for post-foaling control mares (Table 2: Mann Whitney U test 1997: $p < 0.003$; 1999: $p < 0.05$).

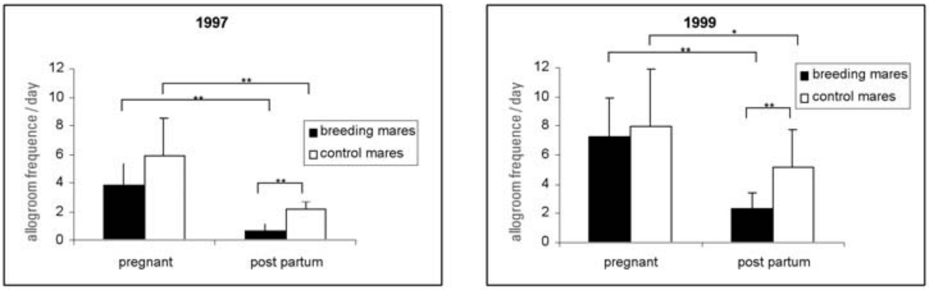

Figure 1a,b: Daily allogrooming frequencies for individual, adult breeding and control (barren) mares (mean ± sd) in 1997 (1a) and 1999 (1b).
*, ** indicates where frequencies differ significantly (* $p< 0.05$; ** $p<0.01$) (dependent subgroups via Wilcoxon's Signed Rank test; independent subgroups via the Mann Whitney U test).

Table 2
Comparison of allogrooming frequencies in pregnant, foaling and barren mares 1997 and 1999

			1997			1999		
		Tests*		**p**	**n1, n2**		**p**	**n1, n2**
Pregnant mares vs	**Post-partum mares**	**WSR**	-2.37	0.02	12, 7	-3.18	0.001	14, 13
Pre-foaling controls vs	**Post-foaling controls**	**WSR**	-2.03	0.04	5, 5	-1.83	ns (0.07)	4, 5
Pregnant mares vs	**Pre-foaling controls**	**MWU**	17	ns	12, 5	22	ns	14, 4
Post-partum mares vs	**Post-foaling controls**	**MWU**	0	0.003	7, 5	12.5	0.05	13, 5

Barren control mares were classified as pre-foaling controls and post-foaling controls, respectively, before and after the time of foaling in their matched foaling mare.
*tests: WSR = Wilcoxon Signed Ranks test; MWU = Mann Whitney U test

The allogrooming frequency of specific mares was similar in both years, as long as they were in the same reproductive state (Wilcoxon Signed Ranks test Z = -1.60, n = 9, p = 0.11). Allogrooming was performed preferentially between mares of the same reproductive status (pregnant, post-partum or barren: Kendall row-wise correlations for 1997: $\tau_{rw} = 0.16$, n = 29, $p < 0.001$; 1999: $\tau_{rw} = 0.13$, n = 36, $p < 0.001$).

Preferred allogrooming partners

All mares had at least one preferred allogrooming partner. The preferred partners for each individual were identified from their individual allogrooming frequencies and defined as a dyadic relationship with a Standardised Residual of >1.96, provided the analysed mare had an overall allogrooming frequency exceeding [the group mean – 1 sd]. In 78% of cases in 1997 and 75% in 1999, both members of such a dyad were each other's preferred partner. Preferred partnership was fairly consistent over the 2 study years, indeed of the 23 partnerships identified in 1997 ($N_{max} = 110$), 21 (= 91.3%) were still partnerships in 1999.

Dynamics in Proximity

Overall proximity frequencies

Proximity occurred preferentially among mares of the same reproductive status (pregnant, post-partum or barren: Kendall row wise correlation for 1997, $\tau_{rw} = 0.34$ (n = 29, $p < 0.001$). In control mares, the frequency of proximity decreased significantly during the foaling season (Mann Whitney U test for pre- vs post-foaling control mares: U = 2.02, $p < 0.03$); by contrast no such post-parturient decrease was observed for foaling mares. However, although the frequency of proximity to another animal was higher for foaling than barren mares after the time of parturition (Mann Whitney U = -2.68, $p < 0.001$), the foaling mares maintained proximity only with their own foal, and their distance from other adult mares actually increased (Fig. 2: "proximity to animals other than own foal"; for pregnant vs post-partum, Wilcoxon Signed Rank = 2.37, $p < 0.02$: for post partum vs control, Mann Whitney U = -2.84, $p < 0.003$).

For parturition itself, most mares separated themselves from the group by at least 50-100 meters, but within 4-8 hours of the birth of the foal they had returned to the periphery of the herd.

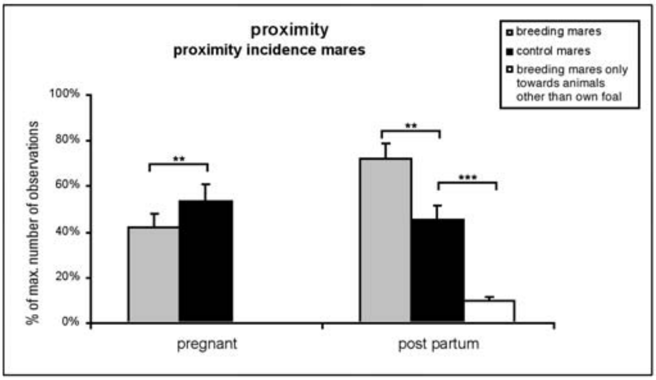

Figure 2: Mean (± sd) frequencies with which adult breeding and control (barren) mares were within 2 horse lengths of each other (proximity scores). For foaling mares, the additional column represents the frequencies that a mare was proximate to an animal other than her own foal.
, * indicates significant differences between proximity frequencies within a group of mares (** $p < 0.01$; *** $p < 0.001$) (dependent subgroups compared using Wilcoxon's Signed Rank test; independent subgroups using the Mann Whitney U test).

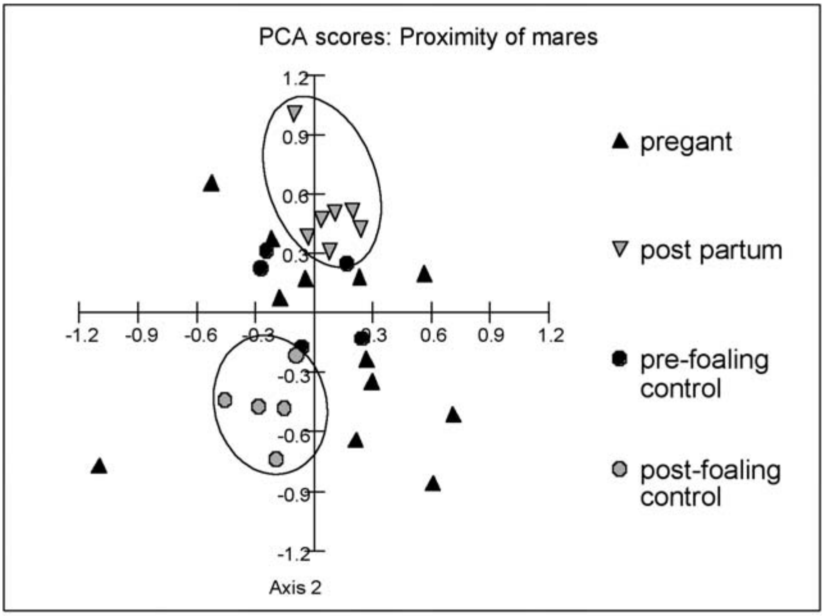

Figure 3: Principal Component Analysis to compare proximity scores between individual adult breeding and control (barren) mares. The clustering of mares indicates the clear spatial separation of the mares with foals from the barren mares, after the time of foaling. Prior to foaling, the barren and pregnant mares were intermingled.

Preferred proximity partners

All mares had at least one preferred partner with whom they had a close spatial partnership. In 59% of cases, there was a clear reciprocal proximity relationship between dyads of mares that were each other's preferred partner. There was no distinction between pregnant and barren mares with regard to the formation of preferred partnerships in proximity. Following parturition, however, there was a spatial separation between the mares with foals and the barren controls (Fig. 3), i.e. the foaling mares and the barren controls separated into sub-groups (indicated by the large circles in fig 3). With the first two axes 35.2% of the variance was explained, with the first three, 44.8%. Since all cases are individuals, the axes represent the spatial distribution.

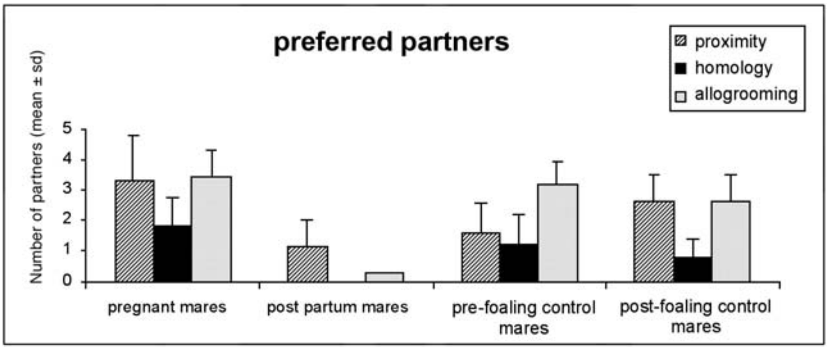

Figure 4: The relative number (mean ± sd) of preferred partners for allogrooming or proximity. Homology was when the same adult mare was the preferred partner for both allogrooming and proximity.

Comparison of allogrooming and proximity results

Dyadic proximity frequencies and allogrooming frequencies overlapped significantly (τ_{rw} = 0.32, n = 29, p < 0.001). For pregnant and pre-foaling control mares, there was considerable homology of the preferred partner for allogrooming and proximity (55.0% and 75.0%, respectively). By contrast, for foaling mares and post-foaling control mares, respectively only 0 and 30.8% of the proximity and allogrooming dyads were the same (fig 4).

Kinship and familiarity

Allogrooming and proximity were significantly related to kinship (allogrooming 1997, τ_{rw} = 0.17, n = 29, p < 0.001; 1999, τ_{rw} = 0.28, n = 36, p < 0.001: proximity 1997, τ_{rw} = 0.19, n = 29, p < 0.001). However, because there were no unfamiliar individuals in 1997, familiarity could only be investigated in 1999: in fact, familiarity had a stronger impact on the dyadic allogrooming relationships than kinship (partial Kendall row wise correlation between kinship and allogrooming frequency controlled for familiarity ($\tau_{rw;XY.Z}$) = -0.03, n = 36, p < 0.84: partial correlation between familiarity and allogrooming frequency controlled for kinship $\tau_{rw;XY.Z}$ = 0.38, n = 36, p < 0.001).

Dominance

Rank order

For all mares, the position in the dominance hierarchy was remarkably consistent across the 2 study years (comparing those animals present in both years: n = 21, Spearmans Rho = 0.958, $p < 0.002$). However, the position of individuals in the dominance hierarchy often changed in the period immediately after foaling, but there was no consistency in the direction of change in the dominance rank (from 5 ranks lower to 6 ranks higher than the position during pregnancy; n = 20). Possibly because the mares tended to become more aggressive at this time (Wilcoxons Signed Ranks test Z = -1.9, n = 20, p = 0.052).

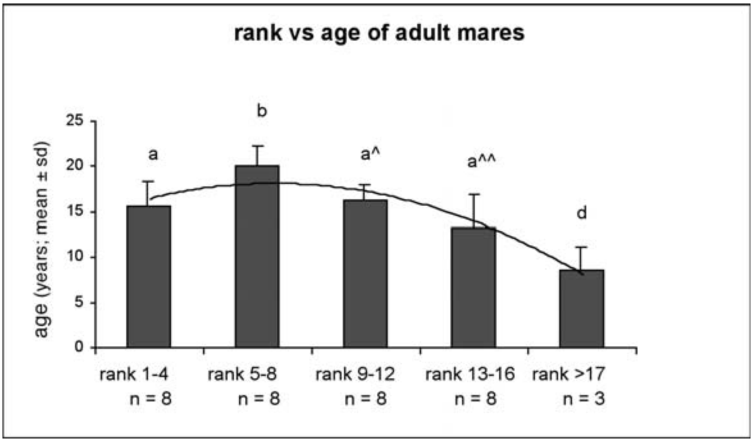

Figure 5. Age of adult mares (mean ± sd) in the various dominance rank categories. $^{a\text{-}d}$ Different letters indicate columns with mean ages that differed significantly ($p < 0.05$: Mann Whitney U test). a^ and a^^ indicate groups that tended to differ (a versus a^^, $p < 0.09$; a^/a^^, $p < 0.06$). The line of best fit was expressed by the quadratic regression $y = -1.3x^2 + 5.8x + 11.9$ ($R^2 = 0.54$, df = 32) and indicated a dominance hierarchy with the form: older mares > oldest mares > younger mares.

The calculated linear rank order (DeVries 1998) that fitted best the dominance relationships observed had only 9 inconsistencies with a strength of 58 and a linearity index (Landau's 'h') of 0.638 in 1997, and 12 inconsistencies with a strength of 69 and a linearity index 'h' of 0.814 in 1999. The rank positions were significantly related to age, irrespective of reproductive stage (Rho = 0.47, df = 22, $p < 0.02$: combined over the 2 study years). Relative aggressiveness was inversely related to dominance order among mares in 1999 (Rho = -0.42, n = 32, $p < 0.02$) but not in 1997 (Rho = 0.1165, df = 24, ns) and rank order was unrelated to the number of foals produced in a mare's lifetime. Although the linear rank order was strongly correlated with age, the top ranking mares were not the oldest (Fig. 5.). In fact, a regression analyses revealed that the data were better represented by a second-degree curve with a peak at around 14-15 years old and a slight decline thereafter, rather than a straight line.

In both study years, closely related horses (as calculated via co-ancestry) were significantly closer in dominance rank than horses with a lower degree of co-ancestry (1997 $\tau_{\rho\omega}$ = 0.219, n = 24, $p < 0.001$ and 1999: $\tau_{\rho\omega}$ = 0.300, n = 32, $p < 0.001$, no control for seasonality). However, closeness in dominance rank was not related to allogrooming frequency, spatial proximity or reproductive state.

DISCUSSION

In the observed herd of adult and sub-adult mares and geldings, and yearling stallions, mare-mare relationships were very stable and involved long lasting bonds that persisted after foaling and across the non-consecutive study years. There was a stable individual characteristic of the frequency of expression of various social behaviour elements and on dominance rank position over the years, although absolute frequencies of social behaviour and rank of a broodmare were also influenced strongly by its reproductive state. In general, frequencies of social interaction with other herd members decreased markedly in the period following parturition. Age, kinship and familiarity were also important factors that influenced the choice of partners for social interaction. These results suggest that, within a large mixed-sex domesticated herd, mare–mare dyadic relationships play a critical role in maintaining the intra-band bonds that help ensure the long term survival of the band, as has previously been reported for feral horses (Linklater 2000; Wernicke and VanDierendonck 2003), thus irrespective of the presence of castrated or intact stallions.

Allogrooming

Daily allogrooming frequency per individual mare did not differ between the study years, as long as the mares were compared in the same reproductive state in both years. Furthermore, while there was a seasonal effect on the frequency of allogrooming, the decrease noted across the observation period was considerably more marked in foaling than in control mares. As previously reported, the seasonal decrease of the allogrooming frequency coincided with the shedding of the winter coat (Tyler 1972, Kimura 1998). During the period of observation after foaling, the breeding mares did not return to their pre-partum allogrooming frequencies, but they did remain faithful to their preferred allogroom partners. This contradicts previous studies in which broodmares were reported to return to their pre-foaling allogrooming rates already within 3-4 weeks after parturition, but with different partners (Estep et al. 1993). The differences between these brood mares and the studied herd observations could be explained by differences in the sex-age composition of the herd, breed- and climate differences, or how the potentially confounding seasonal factors were dealt with during the observations and analysis of the different studies. Finally, although allogrooming behaviour of adult mares was similar over the study years, the absolute frequency was strongly influenced by reproductive state, a finding that should be taken into account when comparing allogrooming behaviour between situations.

Proximity

Following parturition, dams and their foals formed a distinct subgroup that was separated spatially from both post-foaling control mares and the remaining pregnant mares; by contrast the pregnant and pre-foaling control mare subgroups overlapped considerably. Furthermore, the mares and their foals had very different spatial patterns in relation to other herd members as well as those of barren control mares. Specifically, the barren mare, but not the dam and foal, subgroup overlapped spatially with the geldings and sub-adults. The increased interaction with males was emphasised by the more frequent recording of oestrous behaviour in the control mares during the period after foaling of the broodmares, than either earlier in the year or in the recently foaled mares themselves (unpublished observations). Klingel's bonding theory (Klingel 1975) may explain why pregnant mares separate themselves from the herd for a period of several hours around the time of parturition, namely to allow the foal to recognise and 'imprint' on its dam. In addition, sub-group formation by the foaling mares could be a means of avoiding the often boisterous activities of the subadults and geldings. In this respect, sub-adult males played more than once an hour, while adult mares did not play at all (Sigurjónsdóttir et al. 2003), and adult mares displayed threat behaviour towards geldings and sub-adults 5 times more often than towards other adult mares (unpublished observations). All of this suggests that the biological function of the sub-grouping of dams and foals is to facilitate protection of those foals; alternatively, it is possible that sub-group formation is stimulated by a mutual attraction between the foals.

Overlap between allogrooming and proximity results

There was a considerable overlap between the allogrooming interactions and proximity, in terms of both frequency and preferred partnerships. Up to 75% of preferred partners were the same for both allogrooming and proximity, suggesting that proximity was a result of active individual action rather than passive acceptance as also found by Kimura (1998).

Dominance

Increasing age was significantly correlated to dominance ranking. However, in contrast to the studies that have postulated a linear relationship between age and dominance (Van-Dierendonck et al. 1995, Kimura 1998), the dominance hierarchy was best described as; older mares > oldest mares > younger mares. Interestingly, previously high-ranking mares seemed to retain "respect" from most other herd members even when they had passed into a senescent physical decline. The negative relationship between relative aggressiveness and dominance rank suggested that high ranked mares don't need to perform visible acts of aggression to maintain their position, this echoed previous observations in feral horse groups (Rutberg and Greenberg 1990).

Mares tended to become more aggressive after parturition, as recorded previously for mares in feral groups (Rutberg and Greenberg 1990) but contrary to previous reports for domesticated horses (Estep et al. 1993). In the current study, the increase in aggressive behaviour was primarily in the form of 'interventions', during which dams defended their foals or other mares appeared to try to prevent the approach of herd members towards a very recently foaled dam. Future analysis of acts of 'intervention' may help to clarify the significance of this behaviour.

Social relationships, kinship and familiarity

Allogrooming frequencies between dyads of mares were correlated strongly with kinship. However, when unfamiliar animals were introduced into the group, familiarity was a more powerful predictor of the frequency of affiliative interactions than kinship. This supported previous observations that mares in particular are more attracted to familiar than to related herd mates (Monard et al. 1996, Linklater 2000). The significance of kinship versus familiarity regarding mare partnership preferences could be studied in more depth by observing further changes as the residence time of the introduced animals increases. Interestingly, mares of similar dominance position were usually more closely related than those that were further apart in rank.

In contrast to previous reports (Monard and Duncan 1996, Monard et al. 1996, Roberts and Browning 1998, Kimura 1998), there was no relationship between dominance rank and other social preferences. In particular, the studied Icelandic horse mares did not form subgroups based on rank or age, as was reported for mares in the feral Yururi herd (which also included geldings: Kimura 1998). In addition, although the presence of adult geldings and sub-adults did appear to influence the spatial and aggregative behaviour of the broodmares, there was no evidence to suggest that the mares formed bonds specifically to reduce direct aggression or harassment by male animals, as has been postulated by Linklater et al. (1999). The long-term stability of both affiliative social behaviour and dominance order was reminiscent of the important role of mare-mare bonding in harem stability in feral horse herds (Feist and McCullough 1976), and was not noticeably influenced by the presence of adult geldings. Furthermore, there were no ethological or physical indicators of a detrimental effect of the presence of geldings on the welfare of either the broodmares or their foals (e.g. no stereotypic behaviours, extreme aggressive or submissive behaviour, injuries or attempts at infanticide).

CONCLUSION

Parturition and motherhood changed temporarily the nature and frequency of social interactions between a mare and other herd members. However, there was no evidence that any other group members (other mares, geldings or youngsters) consistently harassed or disturbed mares or their foals either during or in the period after parturition. On the other hand, since mares with foals chose to separate off into a distinct sub-group after parturition, space is an important requirement when mares are expected to foal within such a complex social group. Nevertheless, maintenance of domestic horses within these mixed herds during the foaling season did not prevent the expression of characteristic species-specific behaviour, and it allowed the development of long-term stable relationships suggesting that, given sufficient space, this system represents a welfare friendly alternative to modern horse husbandry systems. By extrapolation, it is concluded that maintaining horses in mixed groups at pasture or in loose yards could provide a relatively natural social environment in which those horses could adequately express normal species-specific patterns of behaviour (Brambell 1965). Most modern husbandry systems entail a high degree of social isolation, whereas the results of this study and those of Bachmann et al. (2003), Cooper and McGreevy (2002), Christensen et al. (2002a) emphasise the significance of stable social contact.

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CHAPTER 6

Interventions in social behaviour in a herd of mares and geldings

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ABSTRACT

Feral horses are social animals and in feral bands, social stability is assured by affiliative and kinship relationships as well as by dominance, with the stallion playing an important role. However, because domestic herds often include castrated males (geldings) rather than intact stallions, differences in reproductive competition and different social dynamics are likely. The importance of these differences for modern, domesticated horse husbandry systems has been unclear: to what extent are social relationships important to the horses themselves and what instruments do domestic horses use to maintain social cohesion. We studied these social dynamics by analysing social interventions within groups of horses consisting of adult females, their offspring, adult geldings and sub-adults. In 1997 and 1999 the animals were observed continuously 24hr/day for a total of respectively 488 hr and 828 hr. All relevant dyadic and triadic social interactions, from initial behaviours to outcome, were recorded. Two unfamiliar small groups were added to the herd in 1999 order to introduce 'familiarity' as an additional variable.

The role of interventions in social dynamics was assessed to test whether domestic horses do use interventions to safeguard their social network. Of the 824 interventions analysed, a third occurred in affiliative interactions. Horses were significantly more likely to intervene in allogrooming or play interactions when at least one of the original partners was a preferred partner of the intervener. The stronger the preferred association in allogrooming between the intervener and a member of the initial dyad, the higher the chance the intervener would displace one initial member and continued allogrooming with the other, probably reconfirming their pre-existing relationship. Interveners from the smaller unfamiliar groups intervened significantly more often when a familiar group member allogroomed with an unfamiliar horse. In play, no difference in outcome or correlation with familiarity was found. During oestrus, interventions occurred both in courtship and in curiosity interactions. Several times, pregnant mares exhibited stallion-like behaviour, including mounting. These pregnant mares also intervened in the courting of mares in oestrus. Overall, the intervening horse stopped more than half of initial allogrooming interactions, and a third of all interactions; this excludes cases where the intervener continued the activity with one or both of the initial partners. Maintaining good relationships with preferred partners is apparently very important for horses and needs to be taken into account in management and husbandry.

Keywords
Horses, social relationships, interventions, mares, geldings, social network, pleasure.

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INTRODUCTION

Feral horses *(Equus caballus)* are social animals, however, in most modern husbandry systems they are kept confined and solitary (Holmes 1839, Schimmel 1914, Waring 2003, VanDierendonck and Goodwin 2005). These husbandry systems are often regarded as a better way to assure physical health and to allow exact individual monitoring and adjusted management, but they ignore the basic (social) needs of the horses, often resulting in abnormal behaviour. As more knowledge about the social behaviour of horses is gained, some of the shortcomings of these systems become apparent. There is a trend in western countries to move towards more natural husbandry systems, facilitating social contact.

Performance of any social behaviour is driven both by social and physical factors within and around two individuals (a dyad) as well as by individual internal motivations at any specific moment (Waring 2003, Houpt 2005). In horses affiliative as well as agonistic behaviours within dyads or triads (three individuals) occur. Social cohesion involves 'horizontal components' defined by affiliation and/or kinship, or 'vertical components', defined by dominance (Harcourt and de Waal 1992). 'Horizontal' interactions are frequent among horses however, it is unlikely that horses recognise kinship since feral horses use familiarity as a approximation (Monard and Duncan 1996). The two major equine affiliative behaviours are allogrooming (performed by all sexes and ages) and play (mainly performed by younger animals) (McDonnell and Poulin 2002, Waring 2003).

Interventions in dyadic behaviours are an intriguing aspect of social life. An animal may actively interfere with an ongoing interaction between a dyad with the apparent aim of altering the interaction. This interference may be a deliberate strategy to gain an advantage or resource. Studies on interventions by animals have predominantly considered non-human primates, concentrating on coalitions, alliances and (re)conciliation (Harcourt and de Waal 1992, Aureli and De Waal 2000). References to non-primates are sparse and focus, for example, on interventions in zebra (Schilder 1990), coalitions and alliances among feral horses (Berger 1986, Linklater and Cameron 2000), within-group alliances among dolphins (Connor and Whitehead 2005) and after-conflict affiliation in spotted hyena's (Hofer & East in Schino (1998)). Handbooks on horse behaviour (Mills and Nankervis 1999, McDonnell 2003, McGreevy 2004, Zeitler-Feicht 2004, McGreevy 2004) hardly refer to intervention related behaviours.

The importance of social relationships in domesticated horses in modern husbandry systems is still unclear: we lack fundamental knowledge concerning the extend to which certain social relationships are important to the horses themselves and whether domestic horses actively maintain their social network. Given the trend towards more natural housing for domestic horses, fundamental knowledge of their relationships and the maintenance of their network is needed. It is important to understand why certain individuals are more likely to accept each other and form durable units. Such knowledge can be used to improve animal welfare and minimise the risk of injury. Although various aspects of the relationships between horses in a domestic setting have been studied intensively (among others: Waring 2003, Sigurjonsdottir et al. 2003), investigations on interventions in domestic horses are lacking. There only is one report (Schilder 1990) on equine interventions (other than coalitions) and that concerns zebra in semi-captivity. Reproductive and food competition were important in that study, while in socially housed domestic horses, these factors are of minor importance.

Here we report on the role of interventions in the social behaviour in two groups of domestic horses. Formation of new relationships may threaten existing relationships, so if horses have preferred partners, interventions in allogrooming and playing dyads involving that preferred partner are to be expected. Thus the main question was: do domestic horses use interventions as a social instrument to maintain their own bonds within a network? Further, if domestic horses use interventions, in which circumstances do they use them and do they perform the behaviour in a systematic manner? The results extend our knowledge on what matters to horses with respect to their social environment and guide us to identify factors to be taken into account for stress reduction in horse husbandry and management.

ANIMALS, MATERIALS AND METHODS

Study site and period of study

During the foaling periods, from the beginning of May to mid-June 1997 and 1999, social and intervention behaviour was studied in a pastured group of Icelandic horses. The animals under observation were part of a herd of 80-100 horses that was normally free-ranged all year round in a mountainous area exceeding 1200 hectares at the farm Skaney in southwest Iceland. In winter and spring, supplementary silage was provided once daily. To facilitate detailed observation, during the observation periods the animals under study were corralled within an 8-hectare sub-enclosure. Shelter within the sub-enclosure was more than adequately provided by landscape elements; daily mean temperatures ranged between 4 - 10°C. Since there was almost 24-hour daylight in Iceland during the observation period, data were collected continuously 24 hours a day weather permitting. During the first days of the observations, there was no observation for approxamately 1-4 hr, due to dimlight conditions. Observations covered 488 hours in 1997 and 828 hours in 1999.

Animals

In both years half of the group consisted of breeding mares (pregnant and non-pregnant) and the other half a combination of adult geldings, sub-adult mares, sub-adult geldings and yearling stallions. During the study, 7 foals were born in 1997 and 13 in 1999. In total 47 different individuals of 1 year and older were observed, of which 18 individuals (including 11 of the adult mares) were observed in both years (VanDierendonck et al. 2004). In 1999, 8 animals (including 4 adult mares) from two neighbouring farms were added to introduce ‘familiarity’ as a variable in social interactions. All horses, except one in 1997 and the eight animals introduced in 1999, were born in the resident herd and all adult mares were multiparous. The degree of kinship between pairs of animals was calculated by means of co-ancestry over 5 generations, following the methods of Hartl and Clark (1997).

Observation methods

Due to the relative low frequency of interventions the observation method consisted of All Occurrence (AO) observations of predefined behavioural elements, which included affiliative, dominance and intervention elements. A modified ethogram was used (Schilder 1990, McDonnell 2003). All data were recorded on a Psion handheld computer using 'The Observer®' software, and transferred daily to a laptop computer. Regular inter-observer reliability sessions were performed. To prevent any structural bias in recordings, the observers worked in 8-hour shifts with one overlapping hour at each shift change, so that shift changes gradually permutated over time. Some observation time was lost due to weather conditions (i.e. fog) or computer failure.

For each intervention the animals and their roles were registered. The animal taking the initiative - with the apparent aim altering the behaviour of an interacting dyad (initial animals) - was defined as 'intervener'. If the intervener aimed its behaviour clearly towards one of the two initial animals involved in an interaction with a direction, that animal was called the 'target' and the other one the 'recipient' (Schilder 1990). Interventions by a dam to stop other animals in approaching her just born foal were not recorded. The main elements of the ethogram describing intervention behaviours are presented in Table 1; in analysis, choosing and keeping interposition were combined.

Table 1
Description of intervention behaviour elements

Intervention behaviour	Description
choose interposition	An animal positions itself between two or more animals
keep interposition	An animal keeps itself between 2 or more moving animals
push in between two animals	An animal pushes itself between two individuals standing close to each other
intervention via any other behaviour	Any other action than above that 1) prevents an interaction between two other animals from starting, continuing or 2) changing its character

For analyses, social behavioural elements were categorised in six mutually exclusive groups (Schilder 1990) as illustrated in table 2.

Table 2
Categories of social behavioural elements, with certain specific items.

Category	Behaviours
Affiliative	(initiate) allogrooming; nose play, (initiate to) play, take over play
Agonistic	Attack, threat with ears flat, (threaten to) bite, (threaten to) kick, fight, chase, herding
Curiosity/meeting	Approach, follow, nose-to-nose, nose-to-side, inspect foal, stand alert
Sexual	Nose-to-genitals, (attemp to) mount, present mare, winking, intromission
Neutral	Leave, stand, suckle, blocking mare, vocalise,
Unspecified	Unspecified

Data analyses

All behavioural dyadic interactions were recalculated from absolute frequencies to comparable 24-hour frequencies per dyad (VanDierendonck et al. 2004). For each intervention the sex, age, sex-age class and familiarity of the animals were registered as well as their specific role (initial animal, intervener, recipient, target). Interactions with foals as intervener were excluded from the analyses.

An initial behaviour was considered to be 'taken over' when one of the initial animals was displaced and the intervener continued the initial behaviour with the other animal. An intervention was considered to have 'stopped' the initial behaviour when one of the following behavioural elements was recorded and the initial behaviour was not 'taken over': stop allogrooming, stop play, supplant.

The mares were considered to be in oestrus when at least two of the following behaviours occurred within 24 hours: sexual mounting, winking, presenting or copulation. The oestrus was considered to end on the last day one of these behaviours was recorded.

Kinship was calculated for each dyad in the intervention. In addition, for each intervention for each of the dyads involved the strength of the association (SR) in allogrooming, playing and proximity was determined as described by Schilder (1990) and VanDierendonck et al. (2004). Dyads with a SR>1.96 were considered preferred partners. For each intervention, the rank order position of each animal was noted (VanDierendonck et al. 1995).

Per intervener the total relative frequency of allogrooming, play, nose-to-nose contact and mounting, of preferred partners was calculated. This provides the total number of opportunities to intervene that this individual had, in relation to the total remaining frequency of all other interactions of all non preferred animals. For each intervener the proportion of interventions, i.e. the 'number of interventions / total frequency in which an intervention could take place' was calculated.

To express the relative contribution by a particular sex-age group in each of the roles to the total amount of interventions the following deviation measure was used: z = (observed frequency – expected frequency) / √ expected frequency.

Data concerning triads in which at least one of the participants was in oestrus were analysed separately, since it is unclear whether the intervention was induced by reproductive or other factors (Schilder 1990).

Data was analysed using the software programs MatMan® (de Vries et al. 1993) and The Observer® (Noldus Information Technology, Wageningen, The Netherlands) and SPSS® (v11.5). Statistical analyses were performed: the Wilcoxon signed ranks test for related samples (WSR), the Mann-Whitney U test for unrelated samples (MWU) and the Monte Carlo procedure with a Bonferroni-corrected critical significance level of 0.005 was used for the familiarity comparison in allogrooming interventions. The Chi2 goodness-of-fit test was used in cases of non-parametric group comparisons in which expected values could be calculated. All tests were two-tailed with the critical level of significance α set to 0.05.

RESULTS

Initial behaviours and intervener distribution

Over both years, adults and sub-adults intervened 824 times. Interventions were most frequent in affiliative interactions (36%), followed by curiosity/meeting interactions (28%) and neutral (15%) or unspecified initial interactions (13%). Agonistic interactions were hardly ever intervened (2%). In 138 interventions, at least one of the participants was in oestrus. Interventions unaffected by oestrus behaviour (n=686) took place in allogrooming (162x), play (105x), while in 317 cases the interventions were directly related with the birth of a foal.

The initial interaction was completely stopped by the intervener and not 'taken over' in 35% of the cases (n=292). In interventions in allogrooming and play (not during oestrus nor related to the birth of a foal) (n=267) the interaction was altered e.g. by 'taking over' (28% of the cases).

The interveners were not randomly distributed over the different sex-age classes: in general, adult mares intervened relatively infrequently compared to the other three groups. However, around parturition, the relative intervention participation of all groups of animals drastically reversed (figure 1) (for all comparisons $182.8 > \text{Chi}^2 > 13.5$; df = 3; $p < 0.01$).

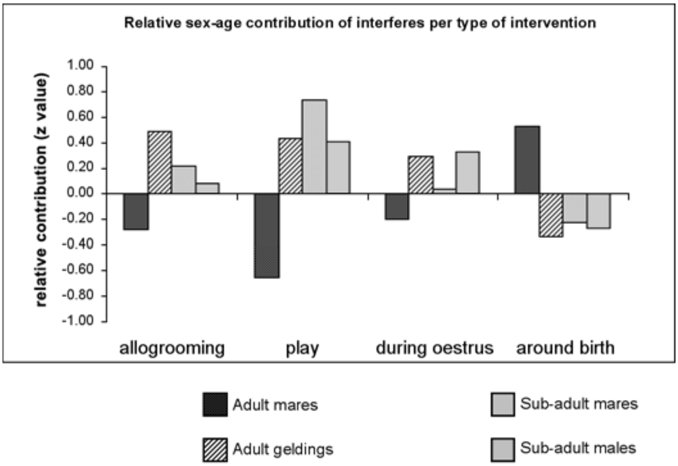

Fig. 1. Relative contribution of the different sex-age groups of the interveners to interventions in allogrooming, play, during oestrus and around birth in 1999 as an example of the differences between the relative contributions of the adult mares compared to the other subgroups. Bar above horizontal: involved in interventions more than expected; bar below horizontal, involved in interventions less than expected.

Interventions in allogrooming

Of the 37 different interveners involved in the 162 interventions in allogrooming, nine did so only once. An intervener was significantly more likely to intervene in allogrooming dyads which included at least one preferred partner of the intervener: (Wilcoxon signed ranks test z = -5.21, n = 37, p = 0.0001). Mares intervened significantly less than other sex age groups (1997: Chi2 = 37.3, df = 3, p < 0.001; 1999 Chi2 = 49.7, df = 3, p < 0.001), while there was minor difference between the adult geldings and the sub-adults (1997: Chi2 = 5.7, df = 1, ns; 1999 Chi2 = 13.8, df = 1, p < 0.02).

Results of interventions in allogrooming

In 29.8 % of the interventions in allogrooming, the intervener displaced one of the initial dyad members and continued allogrooming with the other (take over allogrooming). In 15.2 % the initial animals continued allogrooming while in 46.6 % the allogrooming was stopped entirely by the action of the intervener (in the remaining 3.9 % the horses changed to play interaction while in 4.5 % the result was unspecified).

Presence of a preferred partner of the intervener in the initial dyad positively influenced the proportion of interventions per intervener per end result only for 'stopped' compared to 'continuation by original dyad' (Wilcoxon signed ranks test, z = 2.12, n = 31, p = 0.034). However, allogrooming was taken over significantly more often when one of the initial actors and the intervener were more strongly preferred partners than when this partnership relation between intervener and initial actors was less tight ([a]Mann-Whitney test, $n_1 = 22$, $n_2 = 31$, z = -2.14, p = 0.03) (Table 3).

Table 3

Differences between registered end results of the interventions in allogrooming in the mean strength* of the association between the intervener and the initial actors.

Outcome of intervention	n	# interveners	Mean strength* mean ± sd
Taken over	50	22	14.1 ± 11.6 a
Continued	25	16	9.9 ± 9.3
Stopped	80	31	7.4 ± 6.7 a

*mean strength = mean Standardized Residual (SR) of intervener with both the initial animals. An individual is considered a preferred partner when SR>1.96 (VanDierendonck et al. 2004). [a] Values differ significantly p = 0.03

Does dominance influence interventions in allogrooming?

Irrespective of the outcome, more interventions in allogrooming took place when the initially interacting animals were both higher in rank than the intervener: $Chi^2 = 7.65$, df = 2, p < 0.05. 'Taking over allogrooming' was significantly observed more often when both initial animals were ranked higher than the intervener ($Chi^2 = 6.28$, df = 2, p < 0.05). Rank did not influence whether the intervention was 'stopped' or the initial dyad continued allogrooming ($Chi^2 = 5.64$, df = 2, p < 0.1, $Chi^2 = 1.0$, df = 2, p < 0.7 respectively).

Does familiarity influence interventions in allogrooming?

In table 4 the actual and the expected frequency distribution of the origin of the intervener in relation to initial dyads involving familiar, mixed or unfamiliar allogrooming animals are presented. For each of the nine different situations a Monte Carlo procedure was used to test whether the observed and expected frequencies differed from each other. To control the type I error rate over this set of nine tests a Bonferroni-corrected critical significance level of 0.005 was used.

In the two introduced (smaller) groups L and B a significantly higher frequency of interventions was observed when one of the initial dyad members was familiar and the other unfamiliar (Table 4, grey columns LL- and BB-). In group B interventions in pairs of familiar animals occurred significantly more often than expected by chance (column BBB). No relation between the tendency to intervene and kinship relationships were found for any sex-age class or role.

Table 4
Observed and expected frequencies of interventions when the initial allogrooming animals are both familiar, both unfamiliar or one familiar and one unfamiliar to the intervener.

Familiarity is represented by the home farm of the animals (>1 year):
Skaney (S (n =22) the residential herd), Litla Berg (L (n=3)) and Birkihlið (B (n=5)).

SSS / LLL / BBB	all three animals familiar
SS- / LL- / BB-	intervention in a familiar and unfamiliar pair
S-- / L-- / B--	intervention in pairs of unfamiliar animals

	SSS	SS-	S--	LLL	LL-	L--	BBB	BB-	B--	Ntot
Observed frequency	40	14	4	1	5	10	6	13	11	104
Expected frequency	51.7	20.7	3.0	0.03	0.8	9.7	0.3	4.3	13.5	104
P value*	0.03	0.11	0.77	0.10	0.001	1.00	0.0001	0.0001	0.56	

* The critical significance level is set to 0.005 (Bonferroni procedure for multiple tests).
In grey: combinations in which an intervener is familiar with one animal.

Interventions in play

In 24.5% of the interventions in play (n = 105), the intervener displaced one of the initial dyad members and started to play with the other (take over play), while in 25.5% the initial animals continued playing. In 32.1% the play was stopped by the intervention (17.9% unspecified). Of the 24 different interveners only 3 were adult mares (with a total of 5 interventions). There was no difference between adult geldings or sub-adults as interveners in play (1997: $\text{Chi}^2 = 0.05$, df = 1, ns; 1999 $\text{Chi}^2 = 2.9$, df = 1, ns)

Of the 105 interventions, 77 took place when at least one animal was a preferred partner in play of the intervener (n=28) (mean ± sd: 0.20 ± 0.42 interventions per animal per day), a much higher frequency than for allogrooming (0.049 ± 0.037 interventions per animal per day). Twenty eight interventions took place in dyads in which neither animal was a preferred partner of the intervener (n=15) (0.02 ± 0.03 interventions per animal per day). There was a significant preference to intervene in initial play dyads in which at least one animal was a preferred partner in play of the intervener: Wilcoxon signed ranks test, z = -3.89, n = 24, p = 0.0001.

Influences of rank and kinship on interventions in play

The strength of association between the intervener and either of the other animals was much lower in play than in allogrooming (play: mean SR = 3.21 ± 2.62; allogrooming: mean SR = 8.27 ± 6.38). Dividing up the play interventions according to the end result did not reveal any significant relation.

Contrary to interventions in allogrooming, neither rank ($Chi^2 = 2.55$, df = 2, p = 0.28) nor unfamiliarity ($Chi^2 = 0.3$, df = 2, p = 0.98) influenced intervention preferences. Males played significantly more than mares: up to 38.9% of the interventions were performed by mares interrupting play-dyads which in 91.6% of the times included at least one male.

Interventions just after the birth of a foal compared to other interventions

Interventions (317) in which a dam and her just born foal were recipients of an intervention directed towards animals in their direct vicinity mainly took place in the first few hours after the birth. Characteristics of the triads in these interventions differed significantly from chance ($176.7 > Chi^2 > 20.7$; df = 3; $p < 0.001$) for all sex age classes for all three roles (fig 1). Interventions related to births also differed in the initial type of behaviour. For comparison, table 5 gives the relative proportion of the various categories of initial behaviours around birth, during oestrus, and initial behaviours unrelated to oestrus, allogrooming, play or birth.

Table 5

Distribution of initial behavioural categories during birth of a foal and during oestrus.

Intervention frequencies*:		**Initial behaviour categories****					
	n	Affiliative	Aggression	Curiosity/ meeting	Sexual	Neutral	Unspecified
Around birth	317	0.0%	1.6%	49.9%^	0.9%	24.6%	23.0%
During oestrus	138	19.6%	1.4%	33.3%	23.9%	8.0%	13.8%
In other initial behaviours	102	0%	10.8%	25.5%	10.8%	12.8%	40.2%

*Around birth = interventions just after foaling, directed towards animals in the immediate vicinity of the dam and new born animal

*During oestrus = interventions while at least one partner was in oestrus

*Other initial behaviours = all initial behaviours not related to oestrus, allogrooming, play or to the birth of a foal

Interventions around birth differed strongly from the other interventions in frequency, sex-age distribution of the interveners, distribution of the initial behaviours, as well as the specific situation under which they occurred. These results will be fully discussed in a different paper (VanDierendonck et al. in prep).

Interventions during oestrus

Most of the 138 initial interactions which occurred when at least one of the partners was in oestrus, could be categorised either as curiosity/meeting initial interactions (33.3%) or sexual interactions (23.9%) (table 5). Of these interventions, 26 (18.8%) were performed by pregnant mares (9th-11th month). Only 7 of the 24 adult mares and 6 of the 8 sub-adult mares participated during their oestrus in any of the 3 roles in intervention. The adult mares in oestrus were in the majority of cases only a recipient, while the sub-adult mares in oestrus were involved in all roles. Of the 7 adult oestrus mares in oestrus who did intervene, a very skewed distribution emerged: three of them performed 78.9% of the interventions in this catagory. Three mares (two acted also as interveners) were members of 69.6% of the initial dyads in which an oestrus adult mare was involved.

In both years, when mares were in oestrus, not only (some) males 'mounted' the oestrus mares, but also mounting by females was regularly observed. In 1997 6.5 % (41) of the sexual 'mounting' attempts were performed by 4 of the pregnant mares, in 1999 5 pregnant mares performed 28.4% (38) of these 'mountings'. Two of these mares were the same over both years. Two barren mares in 1997 (3x) and one adult barren mare in 1999 (24x) also exhibited mounting behaviour.

Adult geldings were responsible for 13.8 % of the interventions, were the recipient in 10.2 % of the target in 29.9%. Distributions of intervention frequencies over both geldings and sub-adults were very skewed: among the adult geldings one gelding was target in 67.7% of all interventions where an adult gelding was the target; one yearling stallion was responsible for 63.8% of the interventions by sub-adult males, while the same yearling plus another yearling (out of 5 yearlings) were targets in 44.6% of the interventions in which a sub-adult males figured as target (table 6).

Table 6
Number of interventions during oestrus (n) and number of mares in oestrus for each of the three roles in an intervention. Number of geldings and sub-adult males involved in interventions in which at least one mare was in oestrus

	Intervener n (# animals)	Recipient n (# animals)	Target n (# animals)	Total n
Adult mares in oestrus (8/24)*	19 (4)	69 (7)	5 (3)	93
Sub-adult mares in oestrus (6/8)*	18 (5)	17 (4)	13 (6)	48
Adult geldings (5/8)*	12 (4)	9 (4)	31 (5)	52
Sub-adult males (8/8)*	47 (7)	16 (5)	56 (8)	119

*Number of intervening animals / total number of animals in that sex-age class

There was no correlation between the proportion of a sex-age group that intervened and the type of behaviour being interrupted (yearling stallions were a separate category in these analyses) Chi^2 test: interventions in sexual interactions vs curiosity interactions $\text{Chi}^2 = 6.14$, df = 4, p = 0.19; 'sexual interactions' vs 'affiliative interactions' $\text{Chi}^2 = 5.28$, df = 4, p = 0.26; 'curiosity interactions' vs 'affiliative interactions' $\text{Chi}^2 = 2.46$, df = 4, p = 0.65. Thus with an oestrus mare involved there was no preference to intervene in an initial dyad which had at least one preferred (allogrooming) partner: Wilcoxon signed ranks test z = -1.49, n = 12, p = 0.136. In contrast, in interventions in allogrooming and play (no oestrus mare involved), preferred partners were of major importance.

In 34.8 % of the cases the interventions stopped the initial interaction and the outcome in only 3.6% of the cases was a sexual interaction (either by the original mounting animal or the intervener). The intervener continued the affiliative interactions with one of the initial dyad in 8.0% of the interventions.

Interventions in aggressive or curiosity/meeting interactions

Interventions in aggressive initial behaviours

Rarely (n= 11) interventions took place in aggressive interactions, unrelated to foaling. In aggressive interactions familiarity did not increase the number of interventions ($Chi^2 = 2.57$, $df = 2$, $p = 0.28$). Rank also had no significant influence ($Chi^2 = 0.18$, $df = 2$, $p > 0.9$). Given their frequency (n = 11) these results are not further discussed.

Interventions in curiosity and meeting behaviours

Interventions in meeting interactions (not during oestrus or around birth) mainly took place when the behaviours 'approach', 'nose-to-nose' and 'nose-to-side' were performed. Initial behaviours without direction, like nose-to-nose, drew more interventions when non-familiar animals were involved ($Chi^2 = 7.2$, $df = 2$, $p < 0.05$), and directed behaviours (like 'approach' and 'nose-to-side') did not ($Chi^2 = 1.18$, $df = 2$, $p = 0.55$). Intervention was more likely if all three animals were of the same sex (undirected: $Chi^2 = 6.98$, $df = 2$, $p < 0.05$; or the initial dyad was of the same sex (directed: $Chi^2 = 7.00$, $df = 2$, $p = 0.03$).

DISCUSSION

Interventions were a fairly regular component of the social dynamics in the herd, taking place in affiliative interactions, around oestrus and foaling. The interventions frequently altered ongoing or beginning interactions, especially when preferred partners were interacting, or when familiar individuals were interacting with unfamiliar ones.

Preferred partnership in allogrooming, play and during oestrus and familiarity

In affiliative interactions with strong individual preferences, like in allogrooming, play but also nose-to-nose contacts, the interveners interrupted significantly more often when a preferred partner of the intervener was part of the initial dyad as found in zebra's (Schilder 1990). This contrasts to interventions in allogrooming and play during oestrus, which were not influenced by the presence of a preferred partner. Thus, interveners might be actively safeguarding their own social relationships (Schilder 1990), especially in those in which they earlier invested (Sigurjonsdottir et al. 2003, VanDierendonck et al. 2004). In allogrooming, significantly stronger preferred partnerships between the intervener and one of the initial members correlated with 'taking over' the allogrooming compared to the less strong (but still significant) partnerships in which the initial allogrooming was completely 'stopped'. Interventions have a corrective or preventive function as suggested earlier by Schilder (1990): when an individual notices a preferred partner allogrooming or playing with another animal, this interaction may influence the relation between the observing individual and the preferred partner. The observing individual may then influence the interaction by interfering and thus prevent a potential weakening of its bond with that preferred partner. In zebra only 11.4 % of the interveners 'took over' allogrooming, but in this species the harems are small compared to the herds in the present study. Additional factors to explain differences between the results in this study and that of Schilder (1990) could be: the lack of stallion control in the present study, a different competition regime or an increased need to reduce stress for the introduced animals.

In several social mammalian species (rats, primates, humans), and probably also in horses, the execution of behaviours which have only 'long term benefits' (e.g. social behaviour, reproduction or rooting in pigs) is self-rewarding in the brain (Spruijt et al. 2001). It induces a state which in humans coincides with 'pleasure'. The 'pleasure' experience is caused mainly by opioids and dopamine (Mench and Sheamoore 1995, Nelson and Panksepp 1998, Van Ree et al. 2000). Regular display of these behaviours becomes guaranteed because the animals every time experience this 'pleasure' when, for instance, allogrooming or playing. The characterization of social behaviour as a natural addiction is in line with this reasoning (Nelson and Panksepp 1998) while preventing the execution of this type of behaviours will induce chronic stress as shown in rats (Spruijt et al. 2001). Following the same reasoning: it is then logical to assume that a horse feels more 'pleasure' when allogrooming with a preferred partner, since in the past the horse has been rewarded for this interaction. This 'pleasure' experience may partly explain the cause of an intervention, not its function.

So far it seems as if the intervener intentionally intervenes to protect its relationships etc. The behaviour may have this function, but to what extent the intervener is aware of this remains to demonstrated. Another mechanism guaranteeing the occurrences without relying on the interveners intention, which assumes insight in consequences of the behaviour of others can be mentioned.

In several social mammalian species (rats, primates, humans), it has been shown that behaviours which have only 'long term benefits' (e.g. social behaviour, reproduction or rooting in pigs) are self-rewarding (Spruijt et al. 2001). In contrast to motivational systems such as eating which is governed by the direct physiological consequences of food intake, indispensable behaviours with long term functional benefits are regulated by short term rewarding properties of the display. Thus, regular display of these behaviours is guaranteed because of its direct rewarding consequence and does not rely on the animals insight in the functional consequences of its behaviour. Pigs root, predators explore because they like doing that not because they 'know' this will result into finding food. The rewarding properties are due to the involvement of opioids and dopamine (Mench and Sheamoore 1995, Nelson and Panksepp 1998, Van Ree et al. 2000). The characterization of social behaviour as a natural addiction is in line with is reasoning (Nelson and Panksepp 1998).

In horses, courtship, allogrooming and play have 'long term benefits', and probably are rewarding as well. Although there are no neuroendocrine data available from allogrooming and play in horses, the role of reward systems in other vertebrates in these behaviours is so evident there is no reason to suggest otherwise in case of horses.

The question arises now: do horses intervene because of they have insight in the social implications of social behaviours of other animals or, alternatively, does seeing allogrooming by associative learning elicit their reward seeking and approaching the grooming dyad with disturbance of this dyadic interaction as an unforeseen and unintentional consequence. The fact that they not always get engaged in grooming after terminating the ongoing interaction of the others cannot be explained by this proposed underlying mechanism of intervention. Moreover, such a mechanism can neither explain interventions by pregnant mares in courtship behaviours towards oestrous mares (this study), nor interferences by foals in the courtship behaviour by their father towards their dam (Schilder 1990). It seems more likely that stopping an unwanted interaction is rewarding by itself.

Differences between the horses in this study and other mammals which are recorded to use interventions are expected in interventions in courtship interactions, since there is no male reproductive competition in the herds under investigation. Nevertheless, oestrus mares were of particular interest to the yearling stallions and some geldings, although, mounting was not only recorded by yearling stallions (259x) but also by the other animals (304x). Interestingly highly pregnant mares not only mounted (79x) but also intervened during courtship (26x, by 7 different adult mares). The mounting of adult mares could not have been confused with dominant mounting (Feist and McCullough 1976), since the mounting was preceded and followed by typical courtship like behaviours like flehmen, nose-to-genitals, foreleg strike with squeal and neck biting. Dominant mounting is normally preceded by aggressive interactions and ’head-on-hindquarters’. Data on female mounting in non-pregnant mares is scarce (Feist and McCullough 1976, Asa et al. 1979, Waring 2003), but it seems more common in jennies (McDonnell 1998).

All adult mares were multiparous, therefore they had experienced breeding with a free running stallion, a normal breeding practice in Iceland. This might explain the sometimes persistent interest a mare might have for the gelding of her choice, provoking courtship. In the zebra population with its stallions, courtship was perceived as threat towards the mare by interfering youngsters who tried to ‘protect’ their kin from the perceived threat (Schilder 1990). In the present study the majority of the interventions around an oestrus mare was directed either towards animals observing the courtship actions or towards the courting animals. During ‘courtship’, yearling stallions were never seen courting their own (lactating) dam, but very frequently courted other oestrus mares.

Partnerships for allogrooming, play and proximity occurred within the adult mare group or within the ‘adult gelding-sub-adult’ group (Sigurjonsdottir et al. 2003). In the present study, adult geldings and sub-adults were more active in all three intervention roles than were adult mares, confirming the different social dynamics between these two groups. Sub-adult animals are more flexible in forming social relations and developing preferred partnership relations than adult mares are.

Although adult mares intervened relatively infrequently, however, this does not contradict with the observed ‘leading’ role of older mares (Linklater 2000, Waring 2003). Leadership among horses is poorly defined. Researchers often include behaviours like taking initiative to translocations, walking in front of a group specially when herded by a stallion and start feeding and /or resting periods. The animals that act conform this description are often older mares. This often coincides with the alpha position. Analyses at an individual level (data not shown), did reveal that participation of individual adult mares was skewed towards some older higher ranking individuals (VanDierendonck et al. 1995, 2004). These same individuals often initiated translocations (unpublished data), while other adult mares did not intervene or led the way at all. These older, intervening, relative higher ranking mares might be indeed referred to as 'leading' mares.

Consequences of results for horse husbandry

The above results suggest that physical interactions with preferred partners are of great importance for horses. Facilitation of the development and maintenance of these relationships should improve the welfare of (solitary) housed horses.

For group housed horses it is shown that (affiliative) relationships are not only a one-to-one issue, but may be influenced by the presence of another animals. Triadic interactions facilitate the stability of mare–gelding groups. Socially housed horses will form allogrooming relationships with preferred partners, and will benefit from these social interactions and from free locomotion. However, occasionally this may pose a practical problem since a few horses can become hyperattached to each other. Subsequently, when these horses are used individually this temporary separation may lead to separation anxiety (Zeitler-Feicht 2004). It therefore important to recognise the development of strong relationships at an early stage. Preventive conditioning of these individuals to temporary separation would prevent hyperattachment.

Based on this study it is recommended to first familiarise new horses to each other, or a single new horse to some resident horses before introducing a new horse / new horses in a resident group.

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CHAPTER 7

General Discussion

Feral horses are social animals, which have adopted early predator detection and flight as their prime defence mechanisms. They rely on survival strategies centered on the formation of cohesive social bonds within their family or bachelor bands. Many problems in the husbandry of social animals are due to the fact that the limits for social adaptive abilities are exceeded (Spruijt et al. 2001, Mignon-Grasteau et al. 2005). It is likely that adaptation abilities of domestic horses have been changed during domestication and the following selective breeding. However, it is unknown whether these abilities are sufficient to cope with the modern husbandry practices in which many horses are confined and kept solitary, sometimes with social-contact-at-a-distance for long periods. The social adaptability of domestic horses, their social needs and whether or not the horses actively defend their social network were studied in field studies in this thesis. Field studies provide an excellent way to study the social life and social cohesion of horses with the least possible human influences and confounding variables. From these studies we conclude that domestic horses live in a complex social organisation, with both dyadic and triadic interactions (figure 1). This complex organisation can be described by dominance and affiliative relationships and their determinants. Dominance relationships can be reliably characterized by just five behaviours. Equine affiliation is especially expressed by allogrooming and play. All individuals had at least one significantly preferred partner (friend) in allogrooming and play to whom they were consistent in their 'friendships' over the years. In play the preferred partnerships were the same as in allogrooming. Most horses used social interventions (approaching and trying to alter an ongoing interaction between two other animals) to defend their social network. Interventions especially took place when one or more preferred partners were involved in an initial affiliative interaction.

Figure 1 Start of intervention in play.

This general discussion will firstly integrate and discuss the results of the field studies. Secondly, underlying mechanisms of affiliative social behaviour will be discussed. It will also be explored whether physical affiliative behaviours (allogrooming, play) may be defined as an 'ethological need'. Subsequently, consequences for husbandry systems will be presented. Finally, directions for future research will be given.

AFFILIATIVE BEHAVIOUR, DOMINANCE AND INTERVENTIONS IN MARE–GELDING HERDS

The social structure, social strategies and social interactions were investigated in mare–gelding herds (24 hours per day for several weeks). The herds consisted of all sex-age classes, including several pregnant mares, excluding mature stallions but including several adult geldings. To introduce familiarity as a social variable, two small groups of animals were introduced in a resident group (chapter 4, 5, 6). This type of field studies in (semi)natural environments is an excellent way to study the social life of horses. They may provide the scientific knowledge necessary to elucidate on the social needs of domestic horses.

Dominance can be assessed relatively easily

Despite the low aggression rates in the groups studied, clear and linear rank orders could be constructed in each of the herds and often also within a sex-age group, like adult mares, adult geldings or sub-adults (chapter 3, 4, 5). These rank orders can be optimally constructed by using a cluster of five behaviours: four offensive threats with the head, and one submissive behaviour: avoidance (chapter 3). Avoidance appears to be the best predictor of a relationship, while they are optimally reflected by using all five. The results clearly show that the separation of offensive and defensive aggression is a prerequisite to arrive at a reliable rank order since aggression with the hind legs was used both offensively and defensively and thus context dependend. These hind leg threats appeared therefore, to be unreliable as a parameter for dominance relationships. These results are important since they contrasts strongly with indiscriminately mixing defensive and offensive behaviours as described in the literature (Houpt and Wolski 1980, Roberts and Browning 1998). Secondly, it is shown that the use of submissive behaviours as a rank order criterion is essential, despite this, some authors did not use submission in their analyses (Houpt and Wolski 1980, Roberts and Browning 1998).

Both the assessment of equine dominance and a proper understanding of the principles underlying equine dominance are relevant for social housing issues in sports and leisure horses. In general, least dominance disputes are to be expected in mixed sex mixed age groups, where the individuals have most varied interests and motivations (see below). Also for the selection of founding horses which are used in reintroduction or dedomestication projects, group compositions with the lowest possible risk of dominance conflicts are important (VanDierendonck and WallisDeVries 1996). However, if dominance problems do emerge, a proper assessment of equine dominance relationships is crucial for finding optimal solutions.

Familiarity more important than kinship

Recognising kinship is important to avoid inbreeding, since in feral horses both sexes disperse between 1.5 and 3 years of age and a mechanism must be present to avoid that the dispersing siblings merge in the same group (Rutberg and Keiper 1993, Monard et al. 1996, Khalil and Kaseda 1997, Linklater et al. 1999). However, since kinship is difficult to asses, it was shown by above authors that familiarity could be a good approximation, as in most herds familiarity will also mean kinship. Indeed, in feral horses fillies tend to join family bands with familiar mares but unfamiliar stallions, while colts tend to join bands with unfamiliar other stallions (Monard and Duncan 1996). Interestingly, in mountain zebra – who have a social system comparable to domestic horses - the tendency is that the young stallions join non-breeding groups with familiar stallions (and the young mares disperse to non-breeding groups with unfamiliar males) (Rasa and Lloyd 1994). It is unknown whether kinship and familiarity are recognised in domestic horses.

In this thesis a correlation between the strength of affiliative relationships and kinship was shown (chapter 4 & 5). However, it was investigated in chapter 5 whether preferred relationships between the adult mares were based on kinship or rather on familiarity. Using partial matrix correlations corrected for familiarity, the kinship–allogrooming matrix correlations disappeared. Conversely, when this was calculated between allogrooming and familiarity the matrix correlation remained after correction for kinship. Similar results were obtained for the other sex-age groups (unpublished results). Thus, familiarity was more important than kinship. It could therefore be concluded that horses select affiliative partners on the basis of familiarity rather than kinship.

Play: favourite and functional also for adult geldings

In all herds, not only all foals and sub-adults played, but also the adult geldings played until old age. In contrast, adult mares almost never played. Play is regarded as an important ontogenetic activity, allowing an animal to develop motor and cognitive skills and accelerate development, social functioning and anti-predatory behaviour. Play may also enhance the animal's behavioural flexibility and adaptive capacities in captivity (Vinke et al. 2005, Goodwin and Hughes 2005). Implications for play and in particular play by adult geldings, in husbandry systems will be discussed later on.

Interventions: a useful tool for a horse to maintain a social network

A natural period of increased social dynamics in permanent outdoor living herds is the spring time when foals are born. During that time, many interventions took place. However, in contrast, almost no interventions took place in agonistic interactions. The latter contrasts with the only other study on intervention behaviour in equids: a study on zebra in which about a third of the interventions occurred in aggressive encounters (Schilder 1990). Both in the zebra study and in the present study almost all animals (even the young foals) intervened apparently to safeguard their social network. In both species, especially the interaction of preferred partners was altered. In feral horses, triadic interactions have only been described for feral stallions who formed alliances and coalitions (Feh 1999, Linklater and Cameron 2000). Interventions have been reported in primates and among other mammals i.e. dolphins (Connor and Whitehead 2005), spotted hyena's (Hofer & East in Schino 1998) and feral goats (Schino 1998, 2000). However, it is unknown whether the paucity of data on interventions in other species is caused by lack of scientific interest or because that they simply only occur in a limited number of species which are characterized by a highly complex social organisation.

In general, the interventions were very successful in horses (chapter 6): over 80% of the interventions in allogrooming or play interactions resulting in stopping the interaction completely, or were taken over by the intervener (i.e. the intervener displaced one of the initial animals and continued allogrooming or playing with the other).

In zebra and primates, kinship plays an important role in interventions (Schilder 1990). In the zebra, a relatively large proportion of the interventions was performed by foals/yearlings in relation with direct kin and was often done in courting or aggressive interactions, while in our study kinship played no role. Two explanations are possible: since only animals older than one year were analysed the foals were excluded, while they intervened a lot in zebra and / or there was no male reproductive competition. Based on the intervention results presented in this thesis combined with the observations that allogrooming has a calming effect, (re)-conciliation is expected to occur after a conflict. Unfortunately, the frequency of (re)conciliation was too low to analyse this type of behaviours.

Mounting

One very curious but repeated observation remains to be mentioned: in all three herds stallion-like behaviour including 'mounting' of oestrus mares was performed particularly by pregnant mares. These pregnant mares not only mounted but also intervened between the oestrus mares and interested geldings. The 'mounting' behaviour could not be mistaken for dominant mounting. Data on female mounting in non-pregnant mares is scarce (Feist and McCullough 1976, Asa, Goldfoot, and Ginther 1979, Waring 2003) but it seems more common in jennies (McDonnell 1998). We do not know however, what function this mounting behaviour may have in establishing or maintaining relationships in groups of horses.

SOCIAL NEEDS AND WELFARE OF HORSES

Is affiliative behaviour essential for welfare of domestic horses?

In the present studies, a complex social structure was shown. In affiliative relations, the frequencies of allogrooming and play were relatively high – as compared to feral horses – and the animals defended their social network. Therefore, it is highly likely that the social needs of domestic horses in non-social husbandry systems are incompatible with either long term social isolation or social-contact-at-a-distance. This will be evaluated by taking into account the results of the field studies as well as results of other studies, in order to estimate the social adaptability of the domestic horse. This approach includes the following steps:

- Explanation of affiliative behaviours and interventions at an underlying mechanistic level, involving reward systems which also play a role in indispensable behaviours,
- Discussion whether allogrooming and play can be considered as true 'ethological needs',
- Discussion on the consequences of the results combined with the result of the 'ethological need' evaluation for the housing of horses,
- Provision of guidelines to prevent and to treat behaviour problems in group housed horses.

Importance of allogrooming and play interactions in the domestic setting

Neurobiological explanation of the need of social behaviour

Social processes as ethologically described in the above studies can also be explained from a mechanistic point of view. During domestication only a limited number of genes are involved and these affect a limited number of behavioural features leaving the 'original natural behaviour' mainly intact (Mignon-Grasteau et al. 2005). Indispensable behaviours are deeply anchored in the brain and are basically not altered due to selection during domestication. Short term needs like the need to eat or flight in case of a sudden appearance of a predator, have immediate physiological consequences (eating results in increased blood glucose concentrations). Such consequences occur when a concerted action of physiological and behavioural responses leads to a direct fulfilment of this need, i.e. these consequences are monitored in the brain and provide direct (physiological) feed-back (Mench and Sheamoore 1995, Van Ree et al. 2000, Spruijt et al. 2001). The occurrence of behaviours that can be monitored on a short term by their consequences such as in case of food intake, drinking etc. is regulated by those consequences.

However, behaviours with long term consequences such as exploration, courtship and grooming, lack direct physiological feedback regulatory mechanisms (Spruijt et al. 2001). For instance, the long term consequence of affiliative behaviour is beyond the scope of short time interest of the animal: social cohesion, higher level of safety, more feeding time due to shared vigilance, 'cultural transmission' of known locations of saltlicks etc. These long term consequences can not be directly estimated by the animals. Evidence is now emerging that for a guaranteed regular display of those behaviours with 'long term benefits' reward systems play a pivotal role as extensively shown in rats, primates and humans (Spruijt et al. 2001). Opioids and dopamine are involved in reproductive behaviour, play, grooming, exploration etc. These behaviours induce a state which in humans coincides with 'pleasure'. In short, such behaviours have a strong rewarding consequence and the animals display such behaviours probably because of their rewarding consequence. If such behaviours are highly rewarding and if welfare is defined as the balance of stress and reward (chapter 1), then the absence / deprivation of such behaviours has a major impact on the balance between stress and reward and results in chronic stress. The characterization of social behaviour as 'a natural addiction' is inline with this reasoning (Nelson and Panksepp 1998).

Courtship, allogrooming and play in horses have 'long term benefits', and should be self-rewarding. Although there are no neurophysiological data available associated with the display of allogrooming and play in horses, the pivotal role of reward systems in other vertebrates in this respect is so evident that there is no reason to suggest otherwise in the case of horses.

Are allogrooming and play 'ethological needs'?

An 'ethological need' is "*a specific behaviour pattern that should be performed irrespective of the environment even when the physiological needs, which the specific behaviour serves, are fulfilled*" (Jensen and Toates 1993). According to most authors, an 'ethological need' is not only a behaviour of which the expression is rewarding in itself (Spruijt et al. 2001), but it has to fulfil other criteria as well (Vinke 2004), some of which will be discussed for horses below.

Allogrooming and play are regularly performed by all animals

Affiliative social behaviour should be regularly performed by all individuals of the species under various environmental conditions. This is indeed confirmed for the horse in this thesis (chapter 3-6) as well as in many other studies (see chapter 2). Foals start allogrooming and playing within the first or second week of age (Waring 2003), unpublished results). Moreover, in this thesis it is even shown that all individuals have at least one preferred partner with whom they allogroom, play or stand within 2 horse length significantly more often than expected compared to random interactions (Chapter 4 and 5). These preferred partnerships are very consistent over the years, not only for adult mares (chapter 5) but also for other sex-age groups (unpublished results). Within the adult mares group it was shown also that the relative allogrooming frequencies were similar per individual over the years, provided the adult mare was in the same reproductive state. The strongest allogroom bonds were between adult mares, which is not surprising since the adult mares can form stable bonds which keep harems together for years (Linklater et al. 1999). These preferences are defended by means of interventions (chapter 6).

Allogrooming and play are self rewarding and may provoke anticipation

Allogrooming and play in domestic horses, which have long term consequences, should induce 'pleasure' as the immediate feedback mechanism. It is rather easy to elicit either a reciprocal-grooming reaction or an expression of 'sensual pleasure' (Waring 2003) by making scratching movements comparable to allogrooming around the withers of any horse (McBride et al. 2004). An expression of sensual pleasure "…*exhibits behavioural evidence that intense pleasure is occurring*…" (Waring 2003, pg 278 line 2-3) (Figure 2). This is especially easy with (young) foals. Horses that auto-groom (= self rewarding) indeed show the same response (unpublished observations). Both solitary locomotory and object play in horses is seen from a young age onwards (chapter 3) (Goodwin and Hughes 2005). This suggests self rewarding properties not only for allogrooming but also for play.

Preliminary experiments indicate that horses housed in a social-contact-at-a-distance system vividly anticipate to an opportunity for physical contact with a novel horse for five minutes (twice per week). Physiological and ethological stress reactions occurred after cessation of the five minute period of possible social contact, suggesting frustration (VanDierendonck et al. in prep).

Figure 2 Sensual pleasure in a foal. See also nose of skewbald horse before chapter 4.

Rebound effect of allogrooming and play observed after periods of deprivation

There is only one study investigating possible rebound effects of allogrooming and/or play after social isolation. This study in young stallions showed a rebound effect in allogrooming and play, after being housed singly (with rails between neighbouring stable) or in pairs for 9 month. They were subsequently released in a large enclosure (Christensen et al. 2002). After release, the singly housed horses showed increased levels of allogrooming and (social) play compared to the pair housed horses. However, it can not be excluded that this was also part of the primary bonding rituals for the single housed horses.

Does absence of allogrooming and play induce chronic stress?

There are no data available of horses that could interact freely and where at the same time allogrooming is prevented. Hence, it can not irrefutably be proved that absence of affiliative behaviour in horses induces chronic stress. However, there is 'circumstantial evidence' that absence of allogrooming, play and other social contacts could lead to chronic stress (chapter 1 and 2) (Zeitler-Feicht 2004, McGreevy 2004). In horses chronic stress can lead to abnormal behaviours, often classified in stereotypes, hyper-reactivity or hypo-reactivity. Stereotypic behaviour in horses has been subject of peer reviewed studies hundreds of times. Most epidemiological, etiological and/or treatment oriented equine stereotypy studies have in common that among the highest risk factors are solitary housing, irregular (physical) contact with conspecifics, box designs which minimise contact between neighbours, no time at pasture etc. (just to mention a few: (Kiley Worthington 1983, McGreevy et al. 1995, McGreevy et al. 1995, Waran and Henderson 1998, McBride and Long 2001, Bachmann and Stauffacher 2002, Cooper and McGreevy 2002, Bachmann et al. 2003, Cooper and Albentosa 2005). Already in 1839, (Holmes 1839) qualifies crib biting as a 'disease of domestication' due to the "prison" in which some horses of the rich live (chapter 1). In cases of locomotory stereotypes like box walking and weaving, it can help to provide the horse with a mirror (Cooper et al. 2000, Mills and Davenport 2002). However, the mirror does not seem to help in the treatment of other types of stereotypes.

Unfortunately, none of these authors explain what they consider 'social contact' nor do they refer specifically to affiliative contact, but it is clear that social contact in general is important in relation to stereotypes.

Are allogrooming and play indispensable for horses?

'Ethological need' criteria (Vinke 2004) have been assessed for allogrooming and play. The conclusion is that allogrooming must be regarded as an 'ethological need' for all animals older than one year, since all of the criteria are met. For play too few data are available to assess whether they meet these criteria. Moreover, play is functionally a more complex behaviour than allogrooming: in play locomotory and social factors are often combined, and the intentions often toggle between affiliative and dominance, and play can be performed with more than two participants (Mench and Sheamoore 1995). On the other hand, both solitary and social play is very functional and rewarding as shown in many species (Vanderschuren et al. 1997, Bekoff and Beyers 1998). As the data in this thesis (chapter 4 and 6) show a high 'take over' of play frequency by interveners, despite less tight preferred relationships our preliminary conclusion is that being able to play is also an 'ethological need', at least for sub-adults and adult geldings, but not for mares. Foals, especially the colts, play even at a higher frequency than the other sex-age classes (unpublished results). In view of this result and in view of the functions of play that have been demonstrated during the ontogeny in several species (Vanderschuren et al. 1997, Bekoff and Beyers 1998) social play must be regarded as an 'ethological need' for foals.

Are interventions elicited by emotions?

Interventions in affiliative behaviour have a corrective or preventive function as suggested earlier by Schilder (1990): when an individual notices a preferred partner allogrooming or playing with another animal, this interaction may influence the relation between the observing individual and the preferred partner. The observing individual may then correct the interaction by interfering and thus preventing a potential weakening of its bond with that preferred partner (chapter 6). The question arises whether the intervener has a specific intention when intervening or whether a simple explanation is possible, as recently shown by primates (Range and Noe 2005), with the same effects but beyond the scope of the intervener. As it is known that allogrooming is rewarding, the approach of the intervener to allogrooming individuals could simply be explained by reward seeking behaviour. If a preferred partner is involved the intervener has experienced the 'pleasure' of being groomed by that animal before. However, the intervener may terminate the ongoing dyadic interaction, but in 70% does not start allogrooming with one of the initial pair of animals itself. Thus, stopping a grooming interaction cannot be explained by this mechanism of reward seeking, certainly not when a preferred partner is involved.

An alternative explanation could be that noticing a preferred partner induces a specific emotional state in the intervener. This state may show resemblance with human jealousy and has also been suggested to occur in plains zebras (Schilder, 1990).

Such a state may even be induced with a larger probability in horses that were member of the small groups that were newly introduced, since these horses probably had a greater need to maintain good associations with the small pool of familiar members, when exploring unfamiliar horses, terrain and resources (chapter 6). The number of interventions in these subgroups was significantly higher than could be expected with familiar animals (chapter 6).

Are humans adequate social partners for solitary horses?

One important aspect is only marginally addressed in publications on the equine husbandry: whether in horses with only humans as social companions, the 'ethological need' to allogroom may sufficiently be fulfilled when their keepers groom them. In theory (Spruijt et al. 2001), for some horses this type of grooming could be adequate to experience 'pleasure'. However, this will only function when grooming is performed at the preferred areas and at a sufficient frequency and duration per day (McBride et al. 2004). Unfortunately, many horses are punished when they react to manual grooming with reciprocal grooming. Often the keeper misinterprets this as biting and reacts aversively. It is not difficult to teach a horse to reciprocally groom gently and suitable for humans though (pers. observation). Human companionship in itself has a calming affect on horses, which is shown by higher heart rates and lower heart rate variability of horses which were alone in a box compared to being with a handler who hand-stroked the horse as a form of social support (Visser 2002). However, chapter 6 shows that for a horse there is more to social relationships than just allogrooming. It will be obvious that play between an adult horse and a human handler can only take place under strict conditions.

Are the result generally applicable?

The validity of the conclusions with respect to horses which have a totally different social ontogeny than the horses in our study groups must be addressed. First, it is unlikely that there are relevant breed differences, since most types of abnormal behaviour are reported for many breeds (McBride and Long 2001, Bachmann et al. 2003, Zeitler-Feicht and Buschmann 2004). Moreover, reward systems involved in 'ethological needs' and stereotyped behaviours have been widely shown in vertebrates. In several horse studies, execution of stereotypes are associated with an increase in endogenous opioids (Lebelt 1998, Pell and McGreevy 1999). However, it is inconclusive in others (McGreevy and Nicol 1998).

Unfortunately, when horses lack appropriate social (learning) experiences during ontogeny, problems can be expected when these horses are socially housed later on. Although these horses have an indispensable need for social contact, they often lack the appropriate social skills to react adequately to e.g. submission or other social signals. Often these horses also lack the use of the appropriate aggressive behaviours in certain situations. This may lead to dominance problems and stress. It remains therefore to be determined what minimal social experience horses must have had during their ontogeny to be able to adequately behave socially when socially housed.

Group housing systems

Aggression and avoidance

One of the major concerns in group housing are dominance related issues. Dominance problems may lead to injury from aggression due to for instance wrong group composition or too frequent changes therein. Other causes could be overcrowding, inadequate design of the area, competition for limited resources or reduced resting times for subordinate individuals (Zeitler-Feicht and Prantner 2000, Mills and Clarke 2002, Vervuert and Coenen 2002). Low ranking horses run higher risks and may even get exhausted or undernourished (Fader and Sambraus 2004). The problems involving low ranking animals are often being underestimated, since often overt aggression may be absent. The keepers can assess dominance relationships, with the help of the elements extracted in chapter 3, to get understanding who are the 'real' lower ranking animals. Most reliable assessments will be obtained when avoidance is combined with threats with the head. Early detection can help to prevent possible problems.

Dominance and residency / familiarity

Dominance combined with residency are important factors to consider when introducing new horses (chapters 3 and 6). Indeed, introduction of new groups of horses in a residence herd induces stress and subordination in the introduced horses (Alexander and Irvine 1998, McGreevy 2004). Since also interventions specifically take place between familiar and unfamiliar animals (chapter 6) and may lead to stress, it is therefore recommended first to familiarise the new horses to each other, or a single new horse to some resident horses, before introducing the new horse / new horses into a resident group.

Dominance and play

As shown, play is often a mixture of affiliative and quasi aggressive behaviours, performed by foals, sub-adults and adult geldings (chapter 3, 4, 6). In play minor dominance problems may be solved without serious aggression (Goodwin and Hughes 2005). In domestic settings, play is often discouraged or even made impossible, due to the owners' perception of risks of injuries. However, risks of 'play' injuries could be more serious in instable or overcrowded groups, than in stable groups. Such injuries are more likely to be caused by dominance disputes than by play interactions per se.

Figure 3
Individual social housing.

Housing horses with insufficient social skills

Welfare of horses with insufficient social skills still should be improved in individual stables, while facilitating allogrooming with a suitable partner. Several individual stable designs with possibilities to allow partial physical contact between horses are available for this purpose (Figure 3).

Grouping of horses

When a new group of horses has to be formed, the fewest dominance problems are expected in mixed sex mixed age groups. However, when a group of horses needs to be split, it is suggested to separate adult mares from adult geldings and sub-adults (chapters 3, 4, 6). In this way one keeps the possibility for social learning of adult behaviour by sub-adults. Interestingly, the adult geldings were very active in allogrooming, kept playing until old age and frequently intervened (chapters 3, 4, 6). Adult geldings had preferred partners in the sub-adult group both in allogrooming and play. These data suggest that the behaviour and the spatial and rank position of the adult geldings can be best compared to feral bachelors. Bachelor bands, usually have low aggression levels due to lower levels of testosterone compared to harem stallions (McDonnell and Murray 1995, Schwarzenberger et al. 2004, Khalil et al. 1998).

Directions of solutions for some other group housing problems

Based on the above results some additional problems can be predicted in group housing systems and associated solutions can be formulated:

- Adult geldings show a linear hierarchy among their sex-class based on castration age. The more sexual experiences geldings had before castration, the more problems one may expect specially when other geldings with a similar social/sexual background are already present (chapter 3). When problems are to be expected based on the history of the new gelding(s), gradual introduction is preferred.
- Socially housed horses will form allogrooming relationships with preferred partners, and will benefit from these social interactions and from free locomotion. However, occasionally this may pose a practical problem since a few horses can become hyperattached to each other. Subsequently, when these horses are used individually this temporary separation may lead to separation anxiety (Zeitler-Feicht 2004). It therefore important to recognise the development of strong relationships at an early stage. Preventive conditioning of these individuals to temporary separation would prevent hyperattachment.
- Promising technological approaches to group housing with computer controlled feeding are emerging. However, in the studied herds, social facilitation of feeding behaviour takes place (chapter 2, 4, 5). This could hamper the sequential feeding most often required for automatic feeding systems (Vervuert and Coenen 2002, Zeitler-Feicht 2004, MvD pers.obs.). This can probably be minimized in a well designed area with enough space and places to forage (ad lib low value roughage feeders besides normal feeding places) or individually announced feeding.

Future directions

This research has solved some problems, but still many more need to be addressed:

- The practical applications of equine social needs and their underlying mechanisms.
- Does human presence / allogrooming compensate for the lack of social interaction / allogrooming by conspecifics?
- The application of new emerging ‘stress reducing’ compounds (Pheromones).
- Welfare implications of different social husbandry systems.
- Improvement of (early) social management for individually housed horses.
- Optimising social ontogenetic experiences.

MAIN CONCLUSIONS

The affiliative relationships were crucial for social cohesion of the herds. The main affiliative behaviours performed were allogrooming, play and close proximity. The strength of these relationships was positively correlated and consistent over the years. Kinship was of minor importance, in contrast to observations in feral horses. In the herds that were studied, familiarity was more important than kinship. For affiliative relationships the general underlying determinants were sex-age class, familiarity and reproductive state.

Five relevant behaviours emerged which reliably described dominance relationships. In all herds, clear linear rank orders could be constructed, determined by factors reflecting social experience (age, residency, age at castration, but not reproductive state) rather than physical strength.

These domestic horses lived in a complex social system in which they safeguarded their social network by means of interventions. Interventions in allogrooming or play were performed when at least one member of the initial interaction was a preferred partner of the intervener. Interveners from the unfamiliar, introduced groups intervened when one of their group members allogroomed with an unfamiliar animal.

Affiliative behaviour might be mechanistically explained by the fact that the execution of allogrooming or play is self-rewarding. Moreover, allogrooming and, to a lesser extent, play could be classified as an 'ethological need'. This leads to the hypothesis that performing affiliative social behaviour is indispensable ("a natural addiction") to domestic horses. The consequences of these results were discussed in relation to husbandry systems: individuals must be able to perform these interactions regularly, otherwise welfare cannot be guaranteed. Individually housed horses should have possibilities to allogroom with suitable neighbours (figure 3). Group housing with computerised feeding is possibly a good solution to combine affiliative needs with locomotion and controlled feeding.

* * *

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THE IMPORTANCE OF SOCIAL RELATIONSHIPS IN HORSES

CHAPTER 8

Summary

SUMMARY

Feral horses are social animals, which have adopted early predator detection and flight as their prime defence mechanisms. They rely on survival strategies centered on the formation of cohesive social bonds within their family or bachelor bands. Many problems in the husbandry of social animals in general, and of horses more in particular, are due to the fact that the limits of their (social) adaptive abilities are exceeded. Although it is likely that coping capacities of domestic horses have changed during domestication - as a result of selective breeding - in some aspects, evidence also suggests that the fundamental social characteristics of horses have remained relatively unchanged. Field studies in (semi)natural environments are an excellent way to study the social life of horses. They may provide the scientific knowledge necessary to elucidate the social needs of domestic horses kept under human supervision.

In this thesis, social structure, social strategies and social interactions are investigated in groups of Icelandic horses kept in captivity (the Netherlands) and in (semi)natural environments (Iceland). Thereby, it is investigated whether individual horses use interventions as an instrument to influence their social network. In the last field study two additional small groups of animals were introduced in a resident group, to investigate familiarity as a social variable. Finally, the importance of positive social interactions as an ethological need in domestic horses are evaluated. The results of this thesis provide science based arguments to predict the horse's possibility to cope with the social factors in modern husbandry systems (isolation or overcrowding) in order to improve optimal welfare of horses in captivity.

After a general introduction (**chapter 1**), a literature review is presented on sociality among feral horses and the role of social bonds in different feral equine social organisations (**chapter 2**) and the impact of sociality in captivity. During the last decades, the main use of horses changed from predominantly labour, to sports, leisure and pleasure. It is argued that types of interactions between humans and horses as well as husbandry practices reflect differences in the human approach towards horses: a) the co-operative approach and b) the human-dominance & equine–submission approach. Most management practices are driven by (dominant) human requirements and costs limitations, but often ignore basic equine needs. In modern horse husbandry systems there is a tendency towards either too little (confinement with physical social isolation) or too much social contact (overcrowding) which both can lead to chronic stress. In general, chronic stress can induce various forms of abnormal behaviour. It has been shown for instance, that up to 30% of horses in the western world suffer from abnormal behaviour related to various less optimal husbandry practices, or to human–horse (mis)communication. In this chapter, it is argued that increased social contact between horses may be essential in order to prevent the development of abnormal behaviours. Although dissatisfaction with the possibilities of social interaction, free locomotion and foraging behaviour has stimulated the design of group housing systems, competition for scarce resources (food, salt, water, resting places) may lead to unwanted side effects like increased aggression and displacement. It is concluded therefore, that knowledge on the social dynamics within these systems is needed and should be integrated

with knowledge on species-specific characteristics of social behaviour of horses in more natural environments.

In **chapter 3**, a study was designed to find a simple set of behaviours which reliably reflect dominance. Dominance relationships between individuals of a herd were analysed and special attention was paid to the position of a gelding within such a herd. Five relevant behaviours were distinguished which adequately describe dominance relationships. They include four offensive behaviours using the head and one submissive behaviour: avoidance. Avoidance behaviour appeared to be the most reliable single predictor of dominance-submission relationships. Aggression with the hind legs however, was used both offensively and defensively and appeared therefore, not suitable as a predictive parameter for dominance relations. On the basis of these five behaviours, a (nearly) linear dominance hierarchy could be described within the herd. The mares and geldings were interspersed in the rank order of the total group, with five mares ahead of the first gelding. The rank order position of the animals was significantly correlated with age and residency, but not with height. This means that the rank position of a horse was more likely the result of its social experience, than of strength or mass. For geldings the rank order was completely linear and correlated with the age at which they were castrated confirming the social experience theory.

In **chapter 4**, social relationships within a mare-gelding group of Icelandic horses were studied in Iceland, and possible relationships between preferred bonding and kinship relations were investigated. Because of the advantage of 24 hrs light in Iceland, we were in the unique position to study these relationships continuously. In addition to dominance relations (see chapter 3), special attention was paid to affiliative behaviours (allogrooming and play) and proximity relations in order to be able to describe preferred bonds. The results show that social structure in the domestic herd was dominated by affiliative behaviours. The horses preferred to bond within the same sex-age class and were also in close proximity of those ‘friends’. Two subgroups, based on close affiliative and proximity relationships, could be distinguished: adult mares in one group, adult geldings, sub adult mares and geldings and yearlings in the other group (foals were not included in the analysis). Adult mares did not play at all, while sub-adult mares played significantly less than all male groups. The closer the adult mares were in rank, the more they also allogroomed each other. Kinship was related to all affiliative behaviours as well as proximity. It is speculated that the relative high allogrooming rates between adult mares (compared to feral horses), low aggression rates and the increased social interaction frequencies of sub adults are related to the absence of adult stallions.

It appears both from chapter 3 and chapter 4 that the role of adult mares in the domestic herd differs from that of adult geldings and sub-adult animals and foals (mares are more often high ranking and less opportunistic in their mutual relationships than geldings). In **chapter 5** different social roles of adult mares were analysed and related to differences in their reproductive state. Most adult mares foaled during the study, but each year also barren control mares were present. There were significant changes in the social behaviour and interactions of mares after foaling, both compared to their own behaviour pre-partum and to that of barren control mares. Irrespective of the seasonal effect, allogrooming frequencies dropped significantly more in post partum mares compared to control mares. Individual differences in allogrooming frequencies were remarkably consistent across the non-consecutive study years, provided the mares were in the same reproductive state. Post partum mares and their foals, separated off in a distinct spatial subgroup. Familiarity appeared to be a more important factor than kinship in the selection of a preferred partner. Since in the study presented in chapter 4 no unfamiliar animals were present, the data in this study could not be partially calculated with a correction for either kinship or familiarity.

Finally the social dynamics of mare–gelding herds were assessed through the analysis of interventions (**chapter 6**). In this study, an intervention is defined as the behavioural action of one animal (the intervener) who actively interferes in an ongoing interaction between a dyad with the apparent aim of altering that interaction (verified by post-hoc analyses of disturbed and undisturbed interactions). Many interventions took place during dyadic affiliative interactions between two other horses. Interventions in allogrooming or play were performed significantly more often when at least one member of the initial interaction was a preferred partner of the intervener. The stronger the preferred association in allogrooming was between the intervener and members of the initial dyad, the higher the chance the intervener would displace one initial member and continue allogrooming with the other. Interveners from the smaller introduced groups (relative unfamiliar from the resident herd) intervened significantly more often when one of their group members allogroomed with an unfamiliar animal, possibly because it might be of high importance to safeguard reliable social relationships within the small introduced groups.

In **chapter 7** the main findings of **chapter 2-6** are evaluated, placed in a wider context and assessed in terms of the social needs of the horse. In addition, the implication of these results for equine welfare under husbandry conditions, is discussed. It is concluded that social life of domestic horses is dominated by preferred bonds which are established and maintained by allogrooming, play, proximity and dominance interactions. Individuals regulate their social network by means of interventions in interactions between other members of the herd, which in itself is complex.

To assess the implications of these findings for horse husbandry, several steps are taken. Firstly, it is argued that the execution of affiliative behaviours may be rewarding in itself. Secondly, it is investigated whether the execution of affiliative behaviour is not only self-rewarding but also whether it can be classified as an ‘ethological need’. ‘Ethological needs’ are behaviours which are so important for the animal that husbandry systems that lack the possibilities to execute such behaviours will cause chronic stress. Taken together, it is concluded that allogrooming as well as play satisfy the criteria for an ‘ethological need’

Finally, the implications are discussed of the results obtained in chapter 2-6 combined with the outcome of the ‘ethological need discussion’ on modern western horse husbandry. It is concluded that all horses need physical social contact, but that horses, which lack appropriate social learning experiences during ontogeny, may be hampered in their social functioning later in life. Solutions for problems, including dominance problems, in individual social housing (chapter 7 figure 3) and group housing are presented.

In conclusion, domestic horses live in complex social organisations. Dominance relationships are related to social experience. Horses have consistent affiliative relationships in allogrooming, play and proximity and safeguard their own social network by means of interventions. Allogrooming and play can be considered as an 'ethological need' which can cause chronic stress when horses are deprived from the possibility to execute these behaviours. Thus, the performance of social interactions is a necessity for domestic horses which notion should be reflected in modern husbandry and management systems.

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CHAPTER 9

Samenvatting
Affiliations of co-authors
Acknowledgements
Curriculum Vitae
List of publications

NEDERLANDSE SAMENVATTING

Wilde paarden zijn sociale dieren, die vroege detectie van roofdieren en de direct daarop volgende vlucht als hun primaire verdedigingsmechanisme hebben ontwikkeld. Hun overlevings-strategieën zijn gecentreerd rond de vorming van goede en betrouwbare relaties binnen hun familie- of vrijgezellengroep. In het algemeen zijn veel problemen bij sociale dieren die door de mens worden gehouden, en bij paarden in het bijzonder, het gevolg van het feit dat de mogelijkheden van de (sociale) adaptatie (aanpassing) aan het leven in gevangenschap ontoereikend zijn. Het lijkt waarschijnlijk dat de sociale vaardigheden van gedomesticeerde paarden tijdens domesticatie zijn aangepast ten gevolge van gericht fokbeleid. Toch zijn er aanwijzingen dat bij de huidige gedomesticeerde paarden de fundamentele sociale behoeften onveranderd zijn gebleven. Veldstudies onder (semi)natuurlijke omstandigheden zijn een uitstekende manier om de sociale interacties en de noodzaak daarvan bij gedomesticeerde paarden te onderzoeken. De hier gepresenteerde studies kunnen kennis opleveren die noodzakelijk is om de sociale behoeften van door de mens gehouden paarden te evalueren.

In dit proefschrift worden de sociale structuur, sociale strategieën en sociale interacties binnen kuddes van IJslandse paarden bestudeerd. De kuddes werden bedrijfsmatig gehouden in Nederland en in IJsland (aldaar onder semi-natuurlijke omstandigheden). In deze kuddes is onderzocht in hoeverre de individuen sociale interventies gebruiken als instrument om het sociale netwerk te beïnvloeden. Tijdens één van de veldstudies zijn twee kleine hechte groepjes paarden in een grote residentiele groep geïntroduceerd om 'onbekendheid' als een sociale variabele te introduceren. In het laatste hoofdstuk wordt geëvalueerd of het kunnen uitvoeren van positieve sociale interacties een 'ethologische behoefte', een noodzaak, is voor gedomesticeerde paarden. De resultaten van dit proefschrift leveren wetenschappelijke argumenten die voorspellen hoe men de huisvesting en management van paarden zou kunnen aanpassen, vooral in systemen waar paarden in mogelijk ontoereikende sociale omstandigheden leven, zoals regelmatig gevonden in de hedendaagse paardenhouderij (isolatie of overbevolking). Het doel daarbij is het optimaliseren van het welzijn van gehouden paarden.

Na de algemene introductie (**hoofdstuk 1**), wordt een literatuuroverzicht gepresenteerd waarin wordt gefocust op sociaal gedrag bij (ver)wilde(rde) paarden en de rol die sociale bindingen spelen in verschillende organisatievormen bij niet gedomesticeerde paarden en paardachtigen en bij gedomesticeerde paarden (**hoofdstuk 2**). Gedurende de laatste decennia is het gebruik van paarden veranderd van voornamelijk werkpaard naar een paard gebruikt voor sport, ontspanning en plezier. Er zijn twee typen interacties tussen mens en paard: de samenwerkingsbenadering en de mens-dominant & paard-submissief (ondergeschikt) benadering. Dit verschil komt ook tot uiting bij de verschillende typen huisvestings- en managementsystemen. De meeste van deze worden beinvloed door menselijke drang naar kostenbesparingen, maar daarbij is vaak geen aandacht voor de basale behoeften van het paard. In veel van de moderne systemen is er een tendens naar hetzij te weinig (opsluiting met fysieke sociale isolatie) hetzij naar te veel sociaal contact ('overbevolking').

Beide kunnen tot chronische stress leiden, zo is bijvoorbeeld aangetoond dat tot 30% van de paarden in de westerse wereld abnormaal gedrag vertonen. Dit is vooral gerelateerd aan verschillende, minder optimale huisvestings- en managementsystemen, of is te wijten aan miscommunicatie tussen mens en paard. In dit hoofdstuk wordt beargumenteerd dat een toename van sociaal contact tussen paarden essentieel zou kunnen zijn om abnormaal gedrag te voorkomen. Het gebrek aan mogelijkheden voor paarden om sociaal gedrag, vrije beweging en foerageergedrag te vertonen heeft geleid tot het toepassen van groephuisvestingssystemen. Echter in deze systemen zou te grote competitie voor beperkte middelen (voedsel, water, zout, rustplekken) kunnen leiden tot ongewenste neveneffecten zoals toename in agressie en het voortdurend verjagen. Derhalve is meer kennis over de sociale dynamiek van dergelijke huisvestingssystemen noodzakelijk en deze kennis zou moeten worden geïntegreerd met de soort-specifieke karakteristieken van het sociale gedrag van paarden onder meer natuurlijke omstandigheden.

In **hoofdstuk 3** wordt een studie beschreven die bepaalt welke gedragingen betrouwbaar dominantie weerspiegelen. Dominantierelaties werden bestudeerd en geanalyseerd tussen alle dieren in een kudde, met de speciale aandacht voor de positie van de ruinen. De dominantierelaties tussen de dieren konden adequaat geevalueerd worden door slechts vijf gedragingen te gebruiken. Deze gedragingen omvatten vier offensieve gedragingen met het hoofd en het submissieve gedrag ‘wijken’. Uit de analyses bleek dat het ’wijken’ de meest betrouwbare voorspeller van dominantie-submissie relaties was. Agressie met de achterbenen (of het dreigen daarmee) werd zowel offensief als defensief gebruikt en daarom was dit gedrag geen geschikte voorspellende parameter voor dominantierelaties. Op basis van de vijf gedragingen konden lineaire dominantierangordes beschreven worden binnen de kudde. Zowel merries als ruinen kwamen over de hele rangorde voor, hoewel de eerste vijf posities door merries werden ingenomen De rangpositie was significant gecorreleerd met leeftijd en residentie-tijd, maar niet met de schofthoogte van het paard. Dit houdt in dat de rangpositie van een paard waarschijnlijk meer afhankelijk was van sociale ervaring dan van kracht of gewicht. Tussen de ruinen onderling was de rangorde geheel lineair en alleen gecorreleerd met de leeftijd waarop ze waren gecastreerd. Dit bevestigt de theorie dat sociale ervaring medebepalend is voor een rangpositie.

In **hoofdstuk 4** worden de sociale relaties tussen IJslandse merries en ruinen beschreven, zoals bestudeert in een kudde op IJsland. Dit bood de unieke mogelijkheid om deze relaties permanent te observeren daar er in het grootste deel van de observatie periode 24 uur licht per dag was. De mogelijke relatie tussen voorkeurs partners en genetische verwantschap was mede onderwerp van analyse. Naast de dominantie relaties (zie hoofdstuk 3), werd speciale aandacht gegeven aan zogenaamde affiliatieve gedragingen (affiliatief = aardig, sociaal positief, zoals wederzijds knabbelen [figuur 2 in hoofdstuk 1] en spel) en vlak-naast-elkaar-staan, om zo goed mogelijk de voorkeursrelaties te kunnen analyseren. De resultaten laten zien dat de sociale structuur van de kudde werd gedomineerd door affiliatieve interacties. De paarden hadden een voorkeur een band te onderhouden met dieren uit dezelfde sex-leeftijd klasse en stonden vaak naast deze ‘vrienden’. Er konden twee subgroepen onderscheiden worden, gebaseerd op sterke affiliatieve relaties en vlak-naast-elkaar-staan: volwassen merries vormden de ene groep, de volwassen ruinen, samen met de nog niet volwassen merries, ruinen en jaarling hengsten, vormden de andere groep (de gegevens van de veulens werden niet meegenomen in de analyse). De volwassen merries speelden vrijwel nooit, terwijl de nog niet volwassen merries significant minder speelden dan de verschillende groepen mannelijke dieren. Naarmate volwassen merries meer een gelijkwaardige rangpositie hadden, knabbelden zij elkaar vaker. Genetische verwantschappen waren zowel gecorreleerd met alle affiliatieve gedragingen als met vlak-naast-elkaar-staan. In dit artikel werd gespeculeerd of de relatief hoge frequenties van wederzijds knabbelen tussen de volwassen merries (in vergelijking met wilde paarden), de lage agressie frequenties en de verhoogde sociale interactiefrequentie van de nog niet volwassen dieren mede werden beïnvloed door de afwezigheid van volwassen hengsten.

De resultaten van hoofdstukken 3 en 4 wijzen er op dat de rol van de volwassen merries in een gedomesticeerde kudde anders is dan die van volwassen ruinen, de nog niet volwassen dieren en de veulens (de merries hebben relatief vaak een hoge rang en zijn minder opportunistisch in hun wederzijdse relaties dan ruinen). In **hoofdstuk 5** zijn de verschillende rollen van de volwassen merries geanalyseerd en gerelateerd aan verschillen in hun reproductieve status (drachtig, veulen aan de voet etc.). De meeste volwassen merries kregen een veulen gedurende de studies, maar er waren ieder jaar ook volwassen, niet drachtige (controle) merries aanwezig. Er waren significante veranderingen in de sociale interacties tussen de fokmerries en andere dieren na het veulenen, zowel ten opzichte van hun eigen gedrag voor het veulenen als in relatie tot het gedrag van de controle merries. Onafhankelijk van het seizoenseffect daalde de frequentie van wederzijds knabbelen significant meer bij de merries na het krijgen van hun veulen dan bij de controle merries. Individuele verschillen in de frequentie van wederzijds knabbelen waren opmerkelijk consistent tussen de (niet aaneensluitende) studiejaren mits de merries in dezelfde reproductieve staat waren. Na de geboorte scheidden de merries zich samen met hun veulens ruimtelijk af van de hoofdgroep, in een duidelijke subgroep. ‘Bekendheid’ bleek een belangrijkere factor dan genetische verwantschap in de selectie van een voorkeurspartner. Omdat in de studie zoals gepresenteerd in hoofdstuk 4 geen ‘onbekende’ dieren aanwezig waren, konden daar de data niet berekend worden met een correctie ‘onbekendheid’ of juist voor genetische verwantschap, en is de invloed van ‘onbekendheid’ dus niet bepaald.

Tot slot werd de sociale dynamiek binnen de merrie-ruinen kuddes bestudeerd door middel van de analyse van interventies (**hoofdstuk 6**). In deze studie is een sociale interventie gedefinieerd als een bepaalde actie van één dier (de interveniant) die actief ingrijpt in een reeds gaande interactie tussen twee andere dieren met de schijnbare intentie deze interactie te beïnvloeden (geverifieerd door een post-hoc analyse van verstoorde en niet verstoorde interacties). Veel van de interventies vonden plaats in affiliatieve interacties tussen twee andere dieren. Interventies in wederzijds knabbelen en spel werden significant vaker uitgevoerd als minstens een van de twee dieren in de oorspronkelijke interactie een voorkeurspartner was van de interveniant. Hoe sterker de relatie was tussen de interveniant en één of beide oorspronkelijke knabbelaars, hoe groter de kans dat de interveniant één van de twee dieren wegduwde en met het andere dier ging knabbelen. Intervenianten van de kleine geïntroduceerde groepjes (die relatief onbekend waren voor de dieren van de grote residentiele kudde) intervenieerden significant vaker als een lid van hun groep knabbelde met een relatief 'onbekend' dier. Dit zou kunnen omdat het heel belangrijk is om te kunnen terugvallen op betrouwbare sociale relaties binnen de kleinere geïntroduceerde groepen tijdens de introductie periode.

In **hoofdstuk 7** zijn de belangrijkste resultaten van **hoofdstukken 2-6** geëvalueerd, in een bredere context geplaatst en beoordeeld in termen van wat (sociaal gezien) essentieel is voor een paard. Daarenboven worden de implicaties van deze resultaten voor het welzijn van paarden onder verschillende huisvestings- en managementcondities bediscussieerd. Er wordt geconcludeerd dat het sociale leven van gedomesticeerde paarden gedomineerd wordt door voorkeursrelaties. Deze worden tot stand gebracht en onderhouden door wederzijds knabbelen, spel, vlak-bij-elkaar-staan en dominantie interacties. De individuen reguleren hun sociale netwerk door interventies in de interacties tussen andere leden van de kuddes.

Om de implicaties van deze resultaten voor paardenhuisvesting te kunnen beoordelen, zijn verschillende stappen genomen. In de eerste plaats is beargumenteerd waarom het uitvoeren van affiliatief gedrag (neurobiologisch) op zichzelf belonend is. Op de tweede plaats is onderzocht of het uitvoeren van affiliatief gedrag niet alleen zelfbelonend is, maar ook of dit gedrag kan worden geclassificeerd als een zogeheten 'ethologische noodzaak'. Ethologische noodzakelijke gedragingen zijn zo belangrijk voor het dier, dat als de mogelijkheden ontbreken deze gedragingen uit te voeren dit chronische stress kan veroorzaken. Samengevat kan worden geconcludeerd dat zowel wederzijds groomen als spel voldoen aan de criteria om als 'ethologische noodzaak' te worden gekwalificeerd.

Tot slot zijn de implicaties van de resultaten van het onderzoek voor de moderne westerse paardenhouderij beschreven. De conclusie is dat alle paarden fysiek sociaal contact nodig hebben. Paarden die niet de juiste mogelijkheden hebben om sociaal te leren en sociale ervaring op te doen tijdens hun opgroeiperiode, hebben het later moeilijker om normaal sociaal te functioneren. Oplossingen voor deze problemen, inclusief dominantieproblemen in individuele sociale huisvesting (zie hoofdstuk 7 figuur 3) en groepshuisvesting worden aangegeven.

Samenvattend blijken gedomesticeerde paarden te leven in complexe sociale organisaties. Dominantierelaties zijn daarbij gerelateerd aan sociale ervaring. Paarden hebben langdurige en consistente affiliatieve relaties, weerspiegeld door met name wederzijds beknabbelen, spel en vlak-bij-elkaar-staan. Ze beschermen hun sociale netwerk door middel van interventies. Wederzijds knabbelen en spel kunnen beschouwd worden als een 'ethologische noodzaak', waarbij chronische stress kan ontstaan als paarden verhinderd worden om deze interacties aan te gaan. Dus, de uitvoering van sociale interacties is een noodzaak voor gedomesticeerde paarden. Het is dan ook belangrijk dat in moderne huisvestings- en managementsystemen mogelijkheden geboden worden om dit gedrag te kunnen uitvoeren.

◆

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CHAPTER 2

Social contact in horses: implications for human-horse interactions

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CHAPTER 3

An analysis of dominance, its behavioural parameters and possible determinants in a herd of Icelandic horses in captivity

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CHAPTER 4

Social relationships in a group of horses without a mature stallion

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CHAPTER 5

Differences in social behaviour between late pregnant, post-partum and barren mares in a herd of Icelandic horses

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CHAPTER 6

Interventions in social behaviour in a herd of mares and geldings

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Dit proefschrift heeft uiteindelijk een zeer lange geschiedenis, met vele etappen. Eigenlijk wilde ik diergeneeskunde studeren, maar het 'lot' was mij telkenmale niet gunstig gezind. Ondertussen heb ik biologie gestudeerd. Aan het einde van mij studie biologie wilde ik dan toch graag een onderzoek doen aan mijn grote liefde die ik al als veertienjarige ontdekt had in Dartmoor: gedragsonderzoek aan paarden. Bovendien, gedragsonderzoek aan paarden is een interessant overgangsgebied tussen de biologie en de diergeneeskunde. Het lag voor de hand dat te doen op de Breidablik. Daar was ik toch al kind aan huis en er leefde een, voor Nederlandse begrippen, unieke kudde paarden. Mijn diepste dank gaat dan ook in de eerste plaats uit naar Pa en Ma van Nunen, dat zij mij de mogelijkheid hebben gegeven onderzoek te doen aan de kudde en in hun huis te wonen. Helaas overleed Pa afgelopen najaar en kan hij dit niet meer meemaken, maar als haar gezondheid het toestaat zal Ma er wel bij zijn. Het zal mij een eer zijn. Vele maanden en daarna weekeinden en vakanties bracht ik op De Boerderij door. Mijn dank gaat dan ook uit naar Anja, Fons, Rian, Maarten, Carla en Niek die mij accepteren in hun familie en inmiddels allen goede vrienden geworden zijn. Zo vaak was ik er dat zelfs herdershond Freya mij uitkoos als een van haar baasjes. Dit terwijl de meeste andere bezoekers slechts 'gedoogd' werden. Vele uren, vakanties en min of meer spannende ritten hebben we samen mee gemaakt. Is was dan ook natuurlijk voor mij Anja te vragen een van mijn paranimfen te zijn

Aan deze kant zat het dus wel goed maar een begeleider vinden was een ander probleem. Er zijn niet veel mensen in Nederland die objectief en gestructureerd ethologisch onderzoek deden (en doen) aan paarden. Matthijs Schilder was de aangewezen persoon en werkte aan zebra's maar had het altijd erg druk, het is me toch gelukt hem te overtuigen. Ik kwam bij een zeer interessante vakgroep, geleid door de charismatische Jan van Hooff. Onderzoek aan primaten voerde er de boventoon, maar dat was geen probleem: ik heb zeer genoten van de hoogstaande wetenschappelijke presentaties en de discussies die er waren tussen de toenmalige promovendi. Met de onmisbare hulp van Han de Vries ben ik door de berg van data gekomen en dit onderzoek leidde uiteindelijk zelfs tot het eerste artikel van dit proefschrift. Op deze plaats wil ik nogmaals mijn zeer grote dank uiten aan Han de Vries. In al die jaren dat ik in mijn eentje in het buitenland werkte was Han altijd bereid statistisch advies te geven als ik dat nodig had voor mijn artikelen en rapporten. Ook Matthijs was al die jaren bereikbaar op de achtergrond. Inmiddels zijn we directe collegae en heb ik het meeste wat met paardengedrag te maken heeft van hem overgenomen en is hij co-promotor van dit proefschrift. Wie had dat toen gedacht.

Helaas was onderzoek aan paarden niet mogelijk direct na het afstuderen dus werd het modellen bouwen op het Hugo de Vrieslab. Kan je later met paarden ook wat mee, was de redenering. Een goede tijd heb ik er gehad waar ik veel geleerd heb, vooral over de randvoorwaarden van goed wetenschappelijk onderzoek doen. Peter, Raymond, Lex, Jan-Jacob, Bas P., Alejandro en de vele anderen heb ik daar leren kennen, dank hiervoor.

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Intussen waren we naar Nederland verhuisd. Ook hier schrijven, projecten doen, op en neer naar IJsland, gedragsgestoorde paarden (of eigenaren) behandelen, opleidingen opzetten. Een van de projecten was in de Oostvaardersplassen, waar ik Ruth en Jetteke en later Erik J. begeleidde in onderzoek. Een spannende tijd hebben we gehad, met de onmisbare hulp van Jan en Leo en alle andere boswachters. Helaas kwam er een abrupt einde aan het veldwerk door de MKZ. Maar het is nog steeds heerlijk langs te komen en in het beheersgebouw bij te praten en het gedrag van de Koniks in de relatieve vrijheid te bestuderen.

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CURRICULUM VITAE

Machteld van Dierendonck werd geboren op 10 maart 1961 te Amsterdam. In 1980 haalde ze het diploma Atheneum β aan het Amsterdams Montessori Lyceum. Daarna heeft ze het propedeusejaar afgerond aan de Vrije Hogeschool te Driebergen. Zij werd meerdere keren uitgeloot voor de studie diergeneeskunde. Intussen studeerde ze Biologie aan de Universiteit van Amsterdam, met hoofdvak sociale ethologie aan de Universiteit Utrecht. De studie Biologie werd in 1987 met succes afgerond, met als afstudeer onderwerp gedragsonderzoek aan paarden. Omdat de economische situatie het onmogelijk maakte in paardengedragsonderzoek verder te gaan werkte ze op het Hugo de Vrieslaboratorium van de Universiteit van Amsterdam aan een wiskundig model dat hoogveengroei beschrijft. In 1990 en 1991 heeft ze, naast haar reguliere werk, samen met Russische en Mongoolse wetenschappers, het research- en monitoring-plan ontwikkeld voor de reïntroductie van de Takhi (het Przewalski-paard) in het Hustain Nuruu Steppe Reservaat in Mongolië. Dit werk werd uitgevoerd voor de Stichting Reservaten Przewalskipaard (FRPH). Toen de Russische wetenschappers ter elfder ure toch niet dit werk konden uitvoeren is ze in 1992 meegevlogen met 16 Takhi naar Mongolië. Aansluitend is ze daar een paar maanden gebleven om de Mongoolse reservaat-medewerkers te helpen het monitoringplan te implementeren en tevens de eerste fase van de opzet van een steppereservaat te begeleiden. In 1993 keerde ze terug naar Hustain Nuruu als project-assistent, dankzij financiering van het Nederlandse Ministerie van Ontwikkelingssamenwerking. Haar taak was toen het opzetten van het wildonderzoek en onderzoek naar de adaptatie (aanpassing) van de Takhi, naast de opleiding van Mongoolse biologen en advies bij de inrichting en het beheer van het reservaat.

Ondertussen verhuisde ze in 1992 naar Stockholm (Zweden), waar ze een begin heeft gemaakt met de uitwerking van de Mongoolse data en opleidingen paardengedrag gaf. In het najaar van 1994 is ze getrouwd en verhuisde ze met haar partner naar Rome (Italië). In Italië heeft ze, naast het publiceren van Mongoolse resultaten, een aantal projecten m.b.t. gedragsonderzoek en welzijn bij paarden gedaan. Tevens zijn de eerste klinisch-ethologische (paarden) patiënten behandeld, waarbij soms overleg was met voornamelijk Britse collegae. Één opdrachten leidde tot voorstellen voor gedragsonderzoek in IJsland. Deze voorstellen zijn 3 jaar op rij gehonoreerd, het laatste jaar met de hoogste wetenschappelijke rating. In 1998 zijn zij en haar partner naar Nederland verhuisd. In 1997 is ze gevraagd lid te worden van de Equid Specialist Group (ESG), een Species Survival Committee (SSC) van de International Union for Conservation of Nature and Natural Resources (IUCN). Een SSC adviseert de IUCN ten aanzien van status, beheer en beleid van populaties van, in dit geval, wilde paardachtigen (zebra's, wilde ezels en Takhi). De ESG combineert de expertise van wetenschappers die zich bezighouden met paardachtigen op vele gebieden. Terug in Nederland werkte ze de IJslandse resultaten uit, was ze als consultant/onderzoeker betrokken bij diverse projecten op het gebied van stress, welzijn en/of gedrag van paarden en werd gevraagd voor haar klinisch-ethologische expertise. Sinds 2002 werkt ze in deeltijd bij de vakgroep Ethologie en Welzijn, Faculteit Diergeneeskunde, Universiteit Utrecht. Ze ontwerpt en begeleidt gedragsonderzoek, vaak binnen multidisciplinaire onderzoeken op de 'Hoofdafdeling Paard' of voor externe opdrachtgevers. Ook begeleidt ze studenten die onderzoek uitvoeren. Ze staat aan de basis van het adaptatie-onderwijs voor aankomende paardendierenartsen. Incidenteel worden, in samenwerking met de veterinairen, klinisch-ethologische patiënten behandeld. De doelstelling is deze activiteit in de toekomst verder uit te bouwen, naast onderzoek en onderwijs. Hiernaast geeft ze les aan een aantal HBO-opleidingen, bijscholingen aan dierenartsen, en voert advies/consultancy opdrachten uit.

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SOME PERSONAL CONCLUSIVE REMARKS

Many details of horse behaviour will never be known, since the horse is too expensive to keep under strictly controlled circumstances. Therefore the so called homology postulate should be used in practical situations where no scientifically based solutions are available. The homology postulate declares: “an educated estimate in which an animal gets the benefit of the doubt to declare the results of studies from other animals, combined with knowledge of the biology of the species, applicable to the animal”. Futhermore, despite this thesis concentrates on the social aspects of the life of a domestic horse, however, the horse is not only a social creature, but a complete animal with an individual personality (Visser 1920). To increase welfare of horses, one has to have a holistic approach: the total is greater than the sum of the parts (only when an animal has a healthy body and a sound brain, can it function optimally).

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