



## Coping in groups of domestic horses – Review from a social and neurobiological perspective

Machteld C. VanDierendonck\*, Berry M. Spruijt

*Behavioural Biology, Utrecht University,  
Padualaan 8, PO Box 80086, 3508 TB Utrecht, The Netherlands*

### ARTICLE INFO

*Article history:*  
Available online 13 March 2012

*Keywords:*  
Horses  
Social dynamics  
Endogenous opioids  
Ethological need

### ABSTRACT

Many sport horses live solitary, with no physical contact to other horses allowed for years, for many different reasons including limiting risk of injuries caused by other horses. Other horses are (semi-) permanently housed in large groups, because their owners perceive this is “natural” and thus good for their horses’ welfare. Indeed, sometimes this leads to increased aggression and individuals who cannot cope with social stress and limited space. However, usually humans determine the social composition of these groups of geldings and mares, possibly leading to other interactions as known from natural equine societies. In this review paper the underlying neurobiological mechanisms of social relationships and social dynamics in modern horses were assessed. Ultimately, it can help to define hypotheses to determine strategies what could be most optimal non-voluntary social compositions of domestic groups and adjust introduction techniques so the individuals can cope optimally, i.e. to show the lowest ethological and physiological stress indicators over both short and long period of time.

Based on neurobiological evidence it is shown that indispensable behaviours like exploration and grooming are displayed because of their rewarding properties. Endogenous opioids play a pivotal role in rewarding the individual and motivate it to perform these behaviours, irrespective of the short-term biological success of such indispensable behaviours. Equine allogrooming and play in domestic groups have been addressed to assess whether they fulfilled the four ethological need criteria: (i) performed by all individuals; (ii) self-rewarding; (iii) have a rebound effect and (iv) in absence of a proper substrate (i.e. social partner) chronic stress is induced. Indeed it was assessed whether equine allogrooming and play are ethological needs. Not only in domestic non-voluntarily composed groups but it is evidenced why it is also an ethological need for individually housed sport horses. Summarising: social relationships and interventions especially in relation to preferred partners, have rewarding properties in the brain and seem therefore important for the main coping mechanisms of domestic horses in large groups and most likely also for feral horses.

© 2012 Elsevier B.V. All rights reserved.

### 1. Introduction

Feral horses are social animals, which have adopted early predator detection and flight as their prime defence

mechanisms. They rely on survival strategies centred on the formation of cohesive social bonds within their family or bachelor bands (Mills and Nankervis, 1999). Many problems in the husbandry of social animals are due to the fact that the limits for social adaptive abilities are exceeded (Mignon-Grasteau et al., 2005; Spruijt et al., 2001). Equines are a domestic species that are often housed individually, so the problem is opposite that of many other production animals that are kept in too large groups. In this literature

\* Corresponding author. Tel.: +31 342476067; fax: +31 342475656.  
E-mail addresses: [machteld@equusresearch.nl](mailto:machteld@equusresearch.nl)  
(M.C. VanDierendonck), [B.M.spruijt@uu.nl](mailto:B.M.spruijt@uu.nl) (B.M. Spruijt).

review it is assessed if domestication has changed the neurobiological and social needs in horses and how they can cope in large groups. Seemingly, adaptation abilities of domestic horses may have been (slightly) changed in one way or another during domestication and the following selective breeding. However, 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 (Jensen and Andersson, 2005; Mignon-Grasteau et al., 2005): studies on reintroduced horses, large herbivores and even pigs – which have a relative higher influence of artificial selection for meat production compared to horses or cattle – have all shown that most of the natural behaviours are still shown by the animals when allowed living feral (Berger, 1986; Boyd and Keiper, 2005; Goodwin, 2002; Jensen, 1986, 1988, 1995; Jensen et al., 1993; Lazo, 1995). Konik horses and Heck cattle in the Dutch Oostvaardersplassen wetland reserve are even considered “de-domesticated” (Koene and Gremmen, 2002; Vulink, 2001), while mink and foxes have been domesticated in few generations by selecting only against fearfulness (Harri et al., 2003). Most changes due to domestication have to do with fear and general activity or reactivity, but less in the social domain (like individual relationships, social communication skills, etc.).

Above it was shown that domesticated horses becoming feral still show a high frequency of social behaviours and a very organised social organisation. Therefore, it is questionable if domesticated animals are still able to cope sufficiently with the modern husbandry practices in which often horses are kept solitary, sometimes only with social-contact-at-a-distance for long periods. However, there has been a strong artificial selection of the last decades, which could have altered the social needs in equines. Owners state many different reasons including limiting risk of injuries caused by other horses. Or, on the other side, many owners hope to improve the welfare of their horses by allowing their horses to spend (all) time in the field with other horses, while it is unknown how the social coping possibilities are affected by domestication. Moreover, the composition of these non-voluntary domestic equine groups normally does not reflect the composition of feral social groups: in the first place the individuals have not chosen to be in that particular composition and usually cannot leave. Moreover, the males are often castrated while usually the mares are intact and have reproductive motivations (Curry et al., 2007) resulting in different interactions and motivations as compared to natural equine societies. There is a call from the owners and welfare bodies to get more insight into the coping possibilities (large) non-voluntary domestic groups and ways to reduce risks at introduction or mixing adult horses (Hartmann et al., 2009; Hartmann, 2010; Jorgensen et al., 2009).

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. However, in domestic horses with their often abnormal sex ratio's and non-voluntary composition it could be different, mainly due to

the difference in sexual drive and competition between the sexes as well as different positions in inter- and intra band competition of the males compared to feral horses.

Besides studies predominantly focussing on dominance (McDonnell and Haviland, 1995; Rho et al., 2004; Vervaeke et al., 2007; Waran, 1997; Weeks et al., 2000; Wernicke and VanDierendonck, 2003) there are not many social field studies in this kind of non-voluntary groupings investigating the (regulation) of social needs and thus, coping of the animals (Lemasson et al., 2009). Often these studies have conflicting results due to the different social backgrounds/experiences of the group members. The social adaptability of mares and geldings in groups raised in the same herd was assessed in a series of several field studies (Sigurjónsdóttir et al., 2003; VanDierendonck et al., 1995, 2004, 2009). In these studied domestic herds there was a very low level of human influence and there were neither feeding constraints nor confounding variables such as differences in ontogeny or (social) environment. During the studies the social needs of all individuals were assessed; it was assessed whether or not the horses actively defended their social position and their specific affiliative and agonistic relations (Sigurjónsdóttir et al., 2003; VanDierendonck et al., 1995, 2004, 2009). These studies will form the backbone in this review coinciding which a neurobiological and social perspective and it will be tested – theoretically – whether the adaptive ability and coping of these animals has indeed changed compared to wild equids. Therefore, it needs to be explored what the underlying mechanisms of agonistic and affiliative social behaviour are in this kind of settings. Can physical affiliative behaviours (allo-grooming or play) be defined as an “ethological need” in domesticated horses in non-voluntary composed groups/herds. If so, subsequently, consequences for husbandry systems will be presented.

### *1.1. Affiliative behaviour, agonistic behaviour and interventions*

The social structure, social strategies and social interactions have been investigated in mare – gelding herds (Sigurjónsdóttir et al., 2003; VanDierendonck et al., 1995, 2004, 2009). 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 (VanDierendonck et al., 2009).

#### *1.1.1. Agonistic behaviour: offensive behaviour and submission important*

Despite the low aggression rates in the groups studied (VanDierendonck et al., 1995), 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 (VanDierendonck et al., 1995). It was shown, that equine rank orders can be optimally constructed by using a cluster of five behaviours: four offensive threats with the head (attack, bite, threat to bite, approach with ears flattened), and one submissive behaviour: avoidance (VanDierendonck et al., 1995). The results clearly show that

the distinction between offensive and defensive aggression is a prerequisite to establish a reliable rank order, since aggression with the hind legs was used both offensively and defensively and, thus, context dependent. These hind leg threats appeared, therefore, to be unreliable as a parameter for dominance relationships (Sigurjónsdóttir et al., 2003; VanDierenonck et al., 1995, 2004, 2009). These results are important since they contrast strongly with indiscriminately mixing defensive and offensive behaviours as described earlier (Haupt and Wolski, 1979; Roberts and Browning, 1998). Secondly, it was shown that the use of submissive behaviours as a rank order criterion is essential.

### 1.1.2. *Affiliative social relations: familiarity more important than kinship*

In horses the two major affiliative behaviours performed are allogrooming (performed by all sexes and ages) and play (mainly performed by younger animals and geldings) (McDonnell and Poulin, 2002; Tyler, 1972; Waring, 2003).

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 (Cameron et al., 2009; Khalil and Kaseda, 1997; Linklater et al., 1999; Monard et al., 1996; Rutberg and Keiper, 1993). However, since kinship is difficult to assess in feral herds, it was shown by above mentioned authors that familiarity (animals who have physically been together in the same band) could be the underlying mechanisms, as in most feral herds familiarity usually will also coincide with kinship and avoids the difficulty to explain recognition of a genetic relationship. 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). However, it is unknown whether kinship and familiarity are recognised in domestic horses, therefore it was tested with pedigrees known for 3–4 generations in Sigurjónsdóttir et al. (2003) and VanDierenonck et al. (2004). Surprisingly, a correlation between the overall strength of affiliative relationships and kinship was shown, among all sex-age groups. In several other studies (Cameron et al., 2009; Curry et al., 2007; Kimura, 1998), adult mares formed strong preferred partners usually among each other. The studies by Sigurjónsdóttir et al. (2003) and VanDierenonck et al. (2004) provided possibilities to test whether these preferred relationships between the adult mares were only based on kinship or rather on familiarity. Indeed, 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 have been obtained for the other sex-age groups (unpublished results). Thus, also in domesticated horses in non-voluntary groups, familiarity was more important than kinship. It could, therefore, be concluded that horses select affiliative partners on the basis of familiarity rather than kinship. Proops et al. (2009) confirmed in a neat experiment, that domestic horses indeed individually recognise each other based on sight and sound,

as shown by matching cross-modal representations. Also Krueger and Flauger (2008) and Krueger and Heinze (2008) showed that domestic horses still show social cognition, in the sense that the relative social status of a “demonstrator” horse influenced the behaviour of an “observer” horse in an arena or in a social feeding test. These observations can influence on the prediction of the expected ease in which domesticated horses could be introduced, by using their social cognition skills for instance by placing a new to be introduced horse together with a member of the group where it has to be introduced in (Hartmann et al., 2009).

### 1.1.3. *Interventions: a useful tool for a horse to maintain social position and specific relations*

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; Feh, 1999; Kaseda and Khalil, 1996; Linklater, 2000; Linklater and Cameron, 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 reported on triadic social interactions in other non-primate species with intact males), e.g. interventions in zebra (Schilder, 1990), within-group alliances among dolphins (Connor et al., 1992), and after-conflict affiliation in spotted hyena's (Hofer and East in Schino, 2000).

VanDierenonck et al. (2009) assessed many interventions, the majority in affiliative interactions, in their study group. In contrast to zebra's (Schilder, 1990), almost no interventions took place in agonistic interactions. Both in the zebra study and in the study on horses (VanDierenonck et al., 2009) almost all animals intervened apparently to safeguard their social position and specific relations. In both species, especially the interaction of preferred partners was altered by performing an intervention. The active “protection” of preferred affiliative relationships, by means of interventions, showed the high motivation of domestic horses in a non-voluntary grouping to safeguard their social position and specific relations (VanDierenonck et al., 2009).

In zebra and primates, kinship plays an important role in interventions (Schilder, 1990), while in VanDierenonck et al. (2009) 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 combined with the observations that allogrooming has a calming effect (Feh and de Mazieres, 1993), (re)-conciliation is expected to occur after a conflict. Unfortunately, the frequency of (re)conciliation was too low in these study groups to analyse this possible explanation. Cozzi et al. (2010) have shown reconciliation – as measured by Post-Conflict/Matched Control method – in a group of 7 horses 2 geldings and 5 mares, (studied for 108 h). However, it is disputable whether all “conflicts” identified in this study, should have been categorised as a real conflict since also behaviours that can be used both defensively and offensively (like threat to kick, kick, buck)

had been included. And very doubtfully potentially sexual behaviours (like “genital sniff”) and “neutral” behaviours (like “approach” and “follow”) had been included as affiliative behaviours.

## 2. Social needs of domesticated horses – neurobiological evidence

### 2.1. *Is affiliative behaviour essential for domestic horses?*

In the above-discussed studies a complex social structure was shown in non-voluntary groupings of domestic horses, in which the animals defended their social position and specific relations, many other studies confirm complex social structures (Waring, 2003). In most studies, affiliative relations, as shown by the frequencies of allogrooming and play, occurred relatively frequent – as compared to feral horses. Play is regarded as an important ontogenetic activity, allowing an animal to develop motor, social and cognitive skills and facilitate the development of social functioning and anti-predatory behaviour. Play may also enhance the animal’s adaptive capacities also in captivity (Goodwin and Hughes, 2005; Vinke et al., 2005).

Below we attempt to estimate the social adaptive capacity of the domestic horses. 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”, as selected above in the reward involvement.
- Discussion on the consequences of the results combined with the result of the “ethological need” evaluation for the housing of horses.

### 2.2. *Importance of allogrooming and play interactions in the domestic setting*

#### 2.2.1. *Neurobiological explanation of the need of social behaviour*

The indispensable need for social behaviours as described in the above studies from an ethological perspective can be understood if one considers the underlying mechanisms. According to Spruijt et al. (2001) successful adaptation to an (domestic or natural) environment can be defined as “the maintenance of the balance between positive (reward, satisfaction) and negative (stress) experiences and is reflected in the sensitivity of mesolimbic dopaminergic reward systems”. These reward systems have the biological function of regulating the satisfaction of their needs. Animals have to meet environmental (safety, shadow, protection towards the elements, etc.) and internal demands (for instance hunger). But these needs have to be met in a most efficient way, thus at lowest price in terms of energy and risk.

The integration of ethology, economy and neuroscience has been called neuro-economics and involves efficient decision-making (for a review Platt et al., 2010). Ethological and ecological concepts are provided with underlying

mechanisms what has extensively been addressed in neuroscience, but then often in studies on cognition and addiction (Platt et al., 2010)

Reward systems are feedback signals of the outcome of the investment; let us say finding food (profit) after looking for it. Reward systems provide positive feedback to the animal that the preceding behaviour was successful and the animal satisfies its hunger and experiences pleasure. Thus, reward systems provide the energy to invest (dopamine mediates wanting) and measure the profit (opioids mediate liking).

They are playing a key role in the economy of behaviour. Cabanac (1992) already used the phrase “pleasure is the money of the brain” (Cabanac, 1992). Efficiency requires setting priorities between different needs. The rewarding properties of many needs are mediated by the mesolimbic dopamine.

Short-term needs like the need to eat have immediate physiological consequences (eating results in increased blood glucose concentrations and gastro-intestinal neuropeptides communicating with the brain, for instance). Such consequences (such as enhanced blood glucose levels or signals of the intestines communicating with brain) occur when a behavioural response leads to a direct fulfilment of this need, i.e. these consequences are monitored in the brain and provide direct (physiological) feedback (Mench and Sheamoore, 1995; Spruijt et al., 2001). The activation of those motivational systems with rapid measurable physiological consequences can be monitored and, thus, regulated on a short-term. However, behaviours with long-term consequences such as reproduction, exploration and grooming, lack direct physiological feedback regulatory mechanisms (Spruijt et al., 2001). For instance, the success of mating in terms of offspring, the long-term consequence of affiliative are so far in the future that the animal cannot assess the direct efficacy of its action. Also it is often the number of repeatedly displayed behaviours, which have functional effects; for instance one grooming bout has no or little effect, but repeated grooming has effect on the condition of the fur. The same argument is valid for social behaviour; its indirect effects on the long-term social cohesion, higher level of safety, more feeding time due to shared vigilance, “cultural transmission” of known locations of saltlicks, etc. cannot be measured and compared to the investment it requires. Surprisingly, those behaviours, which in ethology have been described as indispensable, are mediated by reward systems. It led Spruijt et al. (2001) to postulate that for a guaranteed regular display of those behaviours with “long-term benefits” reward systems play a pivotal role as extensively shown in pigs, birds, rats, primates and humans (Spruijt et al., 2001). Several authors have also shown that endogenous opioids and dopamine are involved in reproductive behaviour, play, grooming, exploration, social behaviour etc. so the animals do experience short-term satisfaction of released endorphins when performing these behaviours (Mench and Sheamoore, 1995; Van Ree et al., 2000). Therefore, it is not the consequence of the behaviour itself but its mere occurrence, which is rewarding and stimulates the animal to display it. Thus, irrespective of its biological success, the animal is motivated to execute those behaviours.

It is not surprising it that those behaviours are susceptible to develop into stereotypes as they are self-rewarding and under deviating circumstances such as chronic stress when reward systems are sensitised and with time is abundantly available animals may display such behaviours as a compensation for another unsatisfied need. This has been extensively described in [Mason and Rushen \(2006\)](#).

It is beyond the scope on a review on horses to describe the neurobiology of various behaviours as each of them has been extensively documented in literature for play see [Vanderschuren et al. \(1997\)](#) and for grooming [Spruijt et al. \(1992\)](#). But is relevant to mention criteria, which have to be met for claiming reward involvement:

First, for self-grooming in rats and allo-grooming in primates the effects of opioids have been studied by injecting endorphins and naloxone an opioid antagonist in animals ([Fabre-Nys et al., 1982](#); [Schino and Troisi, 1992](#); [Keverne et al., 1997](#)). In rats peptides of the POMC family: melanocortines and endorphins, induce grooming, which can be counteracted by naloxone and haloperidol, a dopamine antagonist ([Alvaro et al., 2003](#)). Morphine induces play, which can be counteracted by naloxone ([Trezza et al., 2011](#)).

Second, another criterion is the property of opioids systems to develop tolerance after repeated activation ([Aloyo et al., 1983](#); [Jolles et al., 1978](#)). Tolerance means that a higher dose of the same drug is required for achieving the same effect. This is also seen in grooming behaviour ([Aloyo et al., 1983](#); [Jolles et al., 1978](#)). The blockade of tolerance by naloxone is an argument that the display of the behaviour involves activation of opioid systems, which account for tolerance when not blocked by an antagonist ([Aloyo et al., 1983](#); [Jolles et al., 1978](#)). It cannot be elicited within a certain interval to the same extent (see review on grooming by [Spruijt et al. \(1992\)](#)). Of course the tolerance of opioid systems is part of a regulatory mechanism to prevent overexpression of certain behaviours. All these effects of underlying mechanism of grooming are reviewed in [Spruijt et al. \(1992\)](#).

The third criterion is the rebound effect seen after a period of deprivation ([Baldwin and Baldwin, 1976](#)). This increased sensitivity of reward systems is known as sensitization another property of reward (dopamine) systems; this property is also part a regulatory mechanism, as is tolerance. Grooming and play both show this phenomenon. This is also shown in horses (see Section 2.2.2.3).

Fourth, rewarding behaviours may function as a reinforcer. This has been shown in T-maze discrimination tasks in juvenile rats ([Humphreys and Einon, 1981](#); [Normansell and Panksepp, 1990](#)) and place conditioning paradigms in rats ([Calcagnetti and Schechter, 1992](#); [Carlsen and Heimer, 1986](#)). In these studies and also the study of [Vanderschuren et al. \(1997\)](#) it is shown that opioid receptors activation mediate the rewarding properties of social play. These behaviours induce a state, which in humans coincides with “pleasure” and in animals as well.

In case of play behaviour, the long-term effect is self-evident, and has been documented in reviews on play ([Groos, 1898](#); [Small, 1899](#)). The involvement of opioid

receptor activation in social behaviour is in line with a large body of evidence of its involvement early in life in mother-related stimuli, thus, attachment behaviour in chicks, mice, rats and primates ([Barr et al., 2008](#); [Carden et al., 1991](#); [Kalin et al., 1988, 1998](#); [Moles et al., 2004](#); [Panksepp et al., 1994](#)), as well as in the regulation of social behaviour.

In short, such behaviours have a strong rewarding consequence and the animals display such behaviours because of their rewarding consequence. If such behaviours are highly rewarding and if welfare is defined as the balance of stress and reward, then the absence/deprivation of such behaviours have 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 in line with this reasoning ([Nelson and Panksepp, 1998](#)).

The role of neuro-hormones such as oxytocin and vasopressin has been left out. They do play an important role in attachment and bonding (for reviews see [Insel et al. \(1998\)](#)) and [Oreland et al. \(2010\)](#). They also exert their activity via the Nucleus accumbens where also mu opioid receptors are involved in social behaviours are present ([Trezza et al., 2011](#)). If opioids mediate the rewarding properties of social behaviour, then oxytocin facilitates the motivation of these behaviours. But as reward systems play a more general role then in social behaviour alone we focus here more on the rewarding aspects as mediated by opioids and dopamine.

Thus allogrooming and play in horses probably also have “long-term benefits”, and their display is maintained by self-rewarding properties. Although there are no neurophysiological data available for allogrooming and play in horses, the pivotal role of opioids in other vertebrates like primates, rodents, cats, is so convincing that there is no reason to suggest otherwise in the case of horses ([Meyerson, 1981](#); [Fabre-Nys et al., 1982](#); [Keverne et al., 1989](#); [Schino and Troisi, 1992](#); [Heyne, 1996](#); [Depue and Morrone-Strupinsky, 2005](#)).

### 2.2.2. Are allogrooming and play in equines “ethological needs”?

At the level of behaviour 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](#), p. 167, lines 8–10). 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 behavioural criteria as well ([Vinke, 2004](#)), some of which will be discussed for horses below.

#### 2.2.2.1. Allogrooming and play are regularly performed by all animals.

All individuals of the species should regularly perform affiliative social behaviour under various environmental conditions. Foals start allogrooming and playing within the first or second week of age with their dam or siblings ([Waring, 2003](#); unpublished results MvD). Moreover, in several studies, including [VanDierendonck et al. \(1995, 2004\)](#) and [Sigurjónsdóttir et al. \(2003\)](#) it is shown that most individuals of an equine non-natural composition 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. These preferred partnerships are very consistent over the years, not only for adult mares but also for other sex-age groups. 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 (VanDierendonck et al., 2004). 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). Already Tyler (1972) described these stable long-term affiliative relationships among adult mares.

**2.2.2.2. Allogrooming and play are self-rewarding.** Allogrooming and play in domestic horses induce “pleasure” as the immediate feedback mechanism as discussed in Section 2.2.1. 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 (Feh and de Mazieres, 1993; McBride et al., 2004). An expression of sensual pleasure “. . . exhibits behavioural evidence that intense pleasure is occurring. . .” (Waring, 2003, p. 278, lines 2–3). 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 are seen from a young age onwards (Goodwin and Hughes, 2005). This suggests self-rewarding properties not only for allogrooming but also for play.

Experiments by VanDierendonck et al. (2007) indicate that horses housed in a social-contact-at-a-distance system vividly anticipated to an opportunity for physical head and neck contact with a novel horse for 5 min (twice per week). Physiological and ethological stress reactions occurred after cessation of the 5-min period of possible social contact, suggesting frustration. In a study with farmed foxes, Møe et al. (2006) concluded that anticipatory behaviour of an expected reward (i.e. physical social contact in the above mentioned case) might be useful for the development of indicators of positive emotional states.

**2.2.2.3. Rebound effect of allogrooming and play observed after periods of deprivation.** There is only one study (Christensen et al., 2002) 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 months. 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 cannot be excluded that this was also part of the primary bonding rituals for the single housed horses.

**2.2.2.4. 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 cannot 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 (McGreevy, 2004; Zeitler-Feight, 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 very often. 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: Bachmann and Stauffacher, 2002; Bachmann et al., 2003; Cooper and Albentosa, 2005; Cooper and McGreevy, 2002; Kiley-Worthington, 1983; McBride and Long, 2001; McGreevy et al., 1995; Waran and Henderson, 1998). 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.

**2.2.2.5. Conclusion ethological need assessment in equine affiliative behaviours.** “Ethological need” criteria (Vinke, 2004) have been assessed for allogrooming and play. The conclusion of this review is that allogrooming must be regarded as an “ethological need” for all horses older than one year, since all of the criteria are met (see Sections 2.2.2.1–2.2.2.4). 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 (Bekoff and Beyers, 1998; Cameron et al., 2008; Vanderschuren et al., 1997). In VanDierendonck et al. (2009) it is shown that a high “take over” of play frequency by interveners, 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 MvD). In view of this result, and in view of the functions of play that have been demonstrated during the ontogeny in several species (like dogs, mink, primates, rats to name a few) (Bekoff and Beyers, 1998; Cameron et al., 2008; Vanderschuren et al., 1997), social play must be regarded as an “ethological need” for horses especially geldings and foals. In play minor dominance problems may be solved without serious aggression (Goodwin and Hughes, 2005). This conclusion leads to the suggestion that horses who cannot perform social allogrooming or play are at a serious risk of developing negative welfare issues.

### 2.3. 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. The question arises whether the intervener has a specific intention when intervening or whether a simple explanation is possible, as 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, in VanDierenonck et al. (2009) the intervener might have terminated the on-going dyadic interaction, but in 70% did 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: when a threat of ones relationship with another animal is perceived as aversive the relationship is worth to defend. This emotion 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. Indeed, the number of interventions in this kind of subgroups was significantly higher than could be expected with familiar animals VanDierenonck et al. (2009).

#### 2.4. Likelihood of general application of the above results in domestic husbandry systems.

It is unlikely that there are relevant breed differences, since the relative recent domestication in relation to the evolution. The above described mechanism and involvement of the neurological reward systems in the brain, explain why housed domestic horses always will show the need to socially interact. Moreover, reward systems involved in “ethological needs” and stereotyped behaviours have been widely shown in vertebrates. In several horse studies, execution of stereotypes is associated with an increase in endogenous opioids (Henderson, 2007; Lebelt, 1998; Pell and McGreevy, 1999). However, it is inconclusive in others (McGreevy and Nicol, 1998). While on the other hand, studies show that stable designs that satisfy an individual’s affiliation needs either prevent or help to “treat” behavioural disorders related to social isolation (Henderson, 2007; Mills, 2003; Mills et al., 2002; Ninomiya et al., 2007; Visser et al., 2008).

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. Therefore, it remains, to be determined what minimal social experience horses must have had during their ontogeny to be able to adequately behave socially when socially housed.

### 3. Main conclusions

Affiliative relationships are crucial for social cohesion of equine individuals in non-voluntary composed herds. Affiliative behaviour might be mechanistically explained by the fact that the execution of allogrooming or play is self-rewarding, by the production of endogenous opioids. Moreover, allogrooming and, to a lesser extent, play could be classified as an “ethological need”. This leads to the most plausible conclusion that performing affiliative social behaviour is indispensable to domestic horses. Domestic horses living in a complex social system safeguard their social position, and specific relations by means of interventions especially in affiliative interactions.

This social relationships and interventions, induced by endogenous opioids, seem equines main coping mechanisms in large (domesticated) herds.

### Conflict of interest

We declare to have no conflict of interest.

### Acknowledgments

We would like to thank all those that have contributed to the content of this paper, Prof. B. Colenbrander and G. Desmet for checking the English and all students helping with the studies.

### References

- Aloyo, V.J., Spruijt, B.M., Zwieters, H., Gispen, W.H., 1983. Peptide-induced excessive grooming in the rat: the role of opiate receptors. *Peptides* 4, 833–836.
- Alvaro, J.D., Taylor, J.R., Duman, R.S., 2003. Molecular and behavioral interactions between central melanocortins and cocaine. *J. Pharmacol. Exp. Ther.* 304 (1), 391–399.
- Bachmann, I., Stauffacher, M., 2002. Prevalence of behavioural disorders in the Swiss horse population. *Schweiz. Arch. Tierh.* 144 (7), 356–365.
- Bachmann, I., Audige, L., Stauffacher, M., 2003. Risk factors associated with behavioural disorders of crib-biting, weaving and box-walking in Swiss horses. *Equine Vet. J.* 35 (2), 158–163.
- Baldwin, J.D., Baldwin, J.I., 1976. Effects of food ecology on social play: a laboratory simulation. *Z. Tierpsychol.* 40 (1), 1–14.
- Barr, C.S., Schwandt, M.L., Lindell, S.G., Higley, J.D., Maestripieri, D., Goldman, D., Suomi, S.J., Heilig, M., 2008. Variation at the mu-opioid receptor gene (OPRM1) influences attachment behavior in infant primates. *Proc. Natl. Acad. Sci. U. S. A.* 105 (13), 5277–5281.
- Bekoff, M., Beyers, J.A., 1998. *Animal Play. Evolutionary, Comparative and Ecological Perspectives*. Cambridge University Press, Cambridge, UK.
- Berger, J., 1986. *Wild Horses of the Great Basin*. University of Chicago Press, Chicago.
- Boyd, L., Keiper, R., 2005. Behavioural ecology of feral horses. In: Mills, D.S., McDonnell, S.M. (Eds.), *The Domestic Horse: The Origins, Development and Management of its Behaviour*. Cambridge University Press, Cambridge, pp. 55–82.

- Cabanac, M., 1992. Pleasure: the common currency. *J. Theor. Biol.* 155, 173–200.
- Calcagnetti, D.J., Schechter, M.D., 1992. Place conditioning reveals the rewarding aspect of social interaction in juvenile rats. *Physiol. Behav.* 51, 667–672.
- Cameron, E.Z., Setsaas, T.H., Linklater, W.L., 2009. Social bonds between unrelated females increase reproductive success in feral horses. *Proc. Natl. Acad. Sci. U. S. A.* 106 (33), 13850–13853.
- Cameron, E.Z., Linklater, W.L., Stafford, K.J., Minot, E.O., 2008. Maternal investment results in better foal condition through increased play behaviour in horses. *Anim. Behav.* 76, 1511–1518.
- Carden, S.E., Barr, G.A., Hofer, M.A., 1991. Differential effects of specific opioid receptor agonist on rat pup isolation calls. *Brain Res. Dev. Brain Res.* 62, 17–22.
- Carlsen, J., Heimer, L., 1986. The projection from the paraetaenia thalamic nucleus, as demonstrated by the phaseolus vulgaris-leucoagglutinin (PHA-L) method, identifies a subterritorial organization of the ventral striatum. *Brain Res.* 374, 375–379.
- Christensen, J.W., Ladewig, J., Sondergaard, E., Malmkvist, J., 2002. Effects of individual versus group on social behaviour in domestic stallions. *Appl. Anim. Behav. Sci.* 75 (3), 233–248.
- Connor, R.C., Smolker, R.A., Richards, A.F., 1992. Dolphin alliances and coalitions. In: Harcourt, A.H., de Waal, F.B.M. (Eds.), *Coalitions and Alliances in Humans and Other Animals*. Oxford University Press, Oxford, pp. 413–443.
- Cooper, J.J., Albentosa, M.J., 2005. Behavioural adaptation in the domestic horse: potential role of apparently abnormal responses including stereotypic behaviour. *Livest. Prod. Sci.* 92 (2), 177–182.
- Cooper, J.J., McGreevy, P., 2002. Stereotypic behaviour in the stabled horse: causes effects and prevention without compromising horse welfare. In: Waran, N. (Ed.), *The Welfare of Horses*. Kluwer Academic Publishers, Dordrecht, pp. 99–124.
- Cozzi, A., Sighieri, C., Gazzano, A., Nicol, C.J., Baragli, P., 2010. Post-conflict friendly reunion in a permanent group of horses (*Equus caballus*). *Behav. Process.* 85 (2), 185–190.
- Curry, M.R., Eady, P.E., Mills, D.S., 2007. Reflections on mare behavior: social and sexual perspectives. *J. Vet. Behav.* 2 (5), 149–157.
- Depue, R.A., Morrone-Strupinsky, J.V., 2005. A neurobehavioral model of affiliative bonding: implications for conceptualizing a human trait of affiliation. *Behav. Brain Sci.* 28 (3), 313–350.
- Fabre-Nys, C., Meller, R.E., Keverne, E.B., 1982. Opiate antagonists stimulate affiliative behaviour in monkeys. *Pharmacol. Biochem. Behav.* 16 (4), 653–659.
- Feh, C., 1999. Alliances and reproductive success in Camargue stallions. *Anim. Behav.* 57, 705–713.
- Feh, C., de Mazieres, J., 1993. Grooming at a preferred site reduces heart rate in horses. *Anim. Behav.* 46 (6), 1191–1194.
- Goodwin, D., Hughes, C.F., 2005. Equine play behavior. In: Mills, D.S., McDonnell, S.M. (Eds.), *The Domestic Horse: The Origins, Development and Management of its Behaviour*. Cambridge University Press, Cambridge, pp. 150–157.
- Goodwin, D., 2002. Horse behaviour: evolution, domestication and feralisation. In: Waran, N. (Ed.), *The Welfare of Horses*. Kluwer Academic Publishers, Dordrecht, pp. 1–18.
- Groos, K., 1898. *The Play of Animals*. D. Appleton, New York.
- Harcourt, A.H., de Waal, F.B.M., 1992. *Coalitions and Alliances in Humans and Other Animals*. Oxford University Press, Oxford.
- Harri, M., Mononen, J., Ahola, L., 2003. Behavioural and physiological differences between silver foxes selected and not selected for domestic behaviour. *Anim. Welfare* 12 (3), 305–314.
- Hartmann, E., 2010. Managing horses in groups to improve horse welfare and human safety. PhD Thesis. Swedish University of Agricultural Sciences, Uppsala.
- Hartmann, E., Christensen, J.W., Keeling, L.J., 2009. Social interactions of unfamiliar horses during paired encounters: effect of pre-exposure on aggression level and so risk of injury. *Appl. Anim. Behav. Sci.* 121, 214–221.
- Henderson, A.J.Z., 2007. Don't fence me in: managing psychological well being for elite performance horses. *J. Appl. Anim. Welfare Sci.* 10 (4), 309–329.
- Heyne, A., 1996. The development of opiate addiction in the rat. *Pharmacol. Biochem. Behav.* 53 (1), 11–25.
- Hofer, H., East, M.L., 2000. Conflict management in female dominated Spotted Hyenas. In: Aureli, F., de Waal, F.B.M. (Eds.), *Natural Conflict Resolution*. University of California Press, Berkeley, pp. 232–234.
- Haupt, K.A., Wolski, T.R., 1979. Equine maternal behaviour and its aberrations. *Equine Pract.* 1 (1), 7–20.
- Humphreys, A.P., Eimon, D.F., 1981. Play as a reinforcer for maze-learning in juvenile rats. *Anim. Behav.* 29, 259–270.
- Insel, T.R., Winslow, J.T., Wang, Z., Young, L.J., 1998. Oxytocin, vasopressin, and the neuroendocrine basis of pair bond formation. *Adv. Exp. Med. Biol.* 449, 215–224.
- Jensen, P., 1986. Observations on the maternal behaviour of free-ranging domestic pigs. *Appl. Anim. Behav. Sci.* 16 (2), 131–142.
- Jensen, P., 1988. Maternal behaviour and mother young interactions during lactation in free-ranging domestic pigs. *Appl. Anim. Behav. Sci.* 20 (3–4), 297–308.
- Jensen, P., 1995. The weaning process of free-ranging domestic pigs – within litter and between litter variations. *Ethology* 100 (1), 14–25.
- Jensen, P., Andersson, L., 2005. Genomics meets ethology: a new route to understanding domestication, behavior, and sustainability in animal breeding. *Ambio* 34 (4–5), 320–324.
- Jensen, P., Vestergaard, K., Algers, B., 1993. Nestbuilding in free-ranging domestic sows. *Appl. Anim. Behav. Sci.* 38 (3–4), 245–255.
- Jensen, P., Toates, F.M., 1993. Who needs behavioral needs – motivational aspects of the needs of animals. *Appl. Anim. Behav. Sci.* 37 (2), 161–181.
- Jolles, J., Wiegant, V.M., Gispens, W.H., 1978. Inhibition of behavioural effect of ACTH(1–24) and opioids by repeated administration. *Neurosci. Lett.* 9, 261–266.
- Jorgensen, G.H.M., Borsheim, L., Mejdell, C.M., Sondergaard, E., Bøe, K.E., 2009. Grouping horses according to gender-effects on aggression, spacing and injuries. *Appl. Anim. Behav. Sci.* 120 (1–2), 94–99.
- Kalin, N.H., Shelton, S.E., Barksdale, C.M., 1988. Opiate modulation of separation-induced distress in non-human primates. *Brain Res.* 440, 285–292.
- Kalin, N.H., Shelton, S.E., Rickman, M., Davidson, R.J., 1998. Individual differences in freezing and cortisol in infant and mother rhesus monkeys. *Behav. Neurosci.* 112 (1), 251–254.
- Kaseda, Y., Khalil, A.M., 1996. Harem size and reproductive success of stallions in Misaki feral horses. *Appl. Anim. Behav. Sci.* 47 (3–4), 163–173.
- Keverne, E.B., Martensz, N.D., Tuite, B., 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* 14 (1–2), 155–161.
- Keverne, E.B., Nevison, C.M., Martel, F.L., 1997. Early learning and the social bond. *Ann. N. Y. Acad. Sci.* 15 (807), 329–339.
- Khalil, A.M., Kaseda, Y., 1997. Behavioral patterns and proximate reason of young male separation in Misaki feral horses. *Appl. Anim. Behav. Sci.* 54 (4), 281–289.
- Kiley-Worthington, M., 1983. Stereotypes in horses. *Equine Pract.* 5 (1), 34–40.
- Kimura, R., 1998. Mutual grooming and preferred associate relationships in a band of free-ranging horses. *Appl. Anim. Behav. Sci.* 59 (4), 265–276.
- Koene, P., Gremmen, B., 2002. Wildheid gewogen. Samenspel van ethologie en ethiek bij de-domesticatie van grote grazers. NOW project 210-11-302. ISBN 90-6754-682 (in Dutch).
- Krueger, K., Flauger, B., 2008. Social feeding decisions in horses (*Equus caballus*). *Behav. Philos.* 78 (1), 76–83.
- Krueger, K., Heinze, J., 2008. Horse sense: social status of horses (*Equus caballus*) affects their likelihood of copying other horses' behavior. *Anim. Cogn.* 11 (3), 431–439.
- Lazo, A., 1995. Ranging behavior of feral Cattle (*Bos taurus*) in Donana-National-Park, SW Spain. *J. Zool.* 236, 359–369.
- Lebelt, D., 1998. Stereotypic behaviour in the horse: general aspects and therapeutic approaches. *Prakt. Tierarzt.* 79, 28–32.
- Lemasson, A., Boutin, A., Boivin, S., Blois-Heulin, C., Hausberger, M., 2009. Horse (*Equus Caballus*) Whinnies: a source of social information. *Anim. Cogn.* 12 (5), 693–704.
- Linklater, W.L., 2000. Adaptive explanation in socio-ecology: lessons from the equidae. *Biol. Rev.* 75 (1), 1–20.
- Linklater, W.L., Cameron, E.Z., 2000. Tests for cooperative behaviour between stallions. *Anim. Behav.* 60, 731–743.
- Linklater, W.L., Cameron, E.Z., Minot, E.O., Stafford, K.J., 1999. Stallion harassment and the mating system of horses. *Anim. Behav.* 58, 295–306.
- Mason, G., Rushen, J., 2006. *Stereotypic Animal Behaviour. Fundamentals and Applications to Welfare*, second edition. CABI, Oxford.
- Mcbride, S.D., Hemmings, A., Robinson, K., 2004. A preliminary study on the effect of massage to reduce stress in the horse. *J. Equine Vet. Sci.* 24 (2), 76–81.
- Mcbride, S.D., Long, L., 2001. Management of horses showing stereotypic behaviour, owner perception and the implications for welfare. *Vet. Rec.* 148 (26), 799–802.
- McDonnell, S.M., Poulin, A., 2002. Equid play ethogram. *Appl. Anim. Behav. Sci.* 78 (2–4), 263–290.
- McDonnell, S.M., Haviland, J.C.S., 1995. Agonistic ethogram of the equid bachelor band. *Appl. Anim. Behav. Sci.* 43 (3), 147–188.

- McGreevy, P., 2004. Equine Behavior. A Guide for Veterinarians and Equine Scientists. Saunders, Edinburgh.
- McGreevy, P., Cripps, P.J., French, N.P., Green, L.E., Nicol, C.J., 1995. Management factors associated with stereotypic and redirected behavior in the thoroughbred horse. *Equine Vet. J.* 27 (2), 86–91.
- McGreevy, P., Nicol, C., 1998. Physiological and behavioral consequences associated with short-term prevention of crib-biting in horses. *Physiol. Behav.* 65 (1), 15–23.
- Mench, J.A., Sheamoore, M.M., 1995. Moods, minds and molecules – the neurochemistry of social-behavior. *Appl. Anim. Behav. Sci.* 44 (2–4), 99–118.
- Meyserson, B.J., 1981. Comparison of the effects of beta-endorphin and morphine on exploratory and socio-sexual behaviour in the male rat. *Eur. J. Pharmacol.* 69 (4), 453–463.
- Mignon-Grasteau, S., Boissy, A., Bouix, J., Faure, J.M., Fisher, A.D., Hinch, G.N., Jensen, P., Le Neindre, P., Mormede, P., Prunet, P., Vandeputte, M., Beaumont, C., 2005. Genetics of adaptation and domestication in livestock. *Livest. Prod. Sci.* 93 (1), 3–14.
- Mills, D.S., 2003. Medical paradigms for the study of problem behaviour: a critical review. *Appl. Anim. Behav. Sci.* 81 (3), 265–277.
- Mills, D.S., Nankervis, K.J., 1999. *Equine Behaviour: Principles and Practice*. Blackwell Science Ltd., Oxford.
- Mills, D.S., Alston, R.D., Rogers, V., Longford, N.T., 2002. Factors associated with the prevalence of stereotypic behaviour amongst thoroughbred horses passing through auctioneer sales. *Appl. Anim. Behav. Sci.* 78 (2–4), 115–124.
- Møe, R.O., Bakken, M., Kittilsen, S., Kingsley-Smith, H., Spruijt, B.M., 2006. A note on reward-related behaviour and emotional expressions in farmed silver foxes (*Vulpes vulpes*). Basis for a novel tool to study animal welfare. *Appl. Anim. Behav. Sci.* 101 (3–4), 362–368.
- Moles, A., Kieffer, B.L., D'Amato, F.R., 2004. Deficit in attachment behavior in mice lacking the mu-opioid receptor gene. *Science* 304, 1983–1986.
- Monard, A.M., Duncan, P., 1996. Consequences of natal dispersal in female horses. *Anim. Behav.* 52, 565–579.
- Monard, A.M., Duncan, P., Boy, V., 1996. The proximate mechanisms of natal dispersal in female horses. *Behavior* 133, 1095–1124.
- Nelson, E.E., Panksepp, J., 1998. Brain substrates of infant–mother attachment: contributions of opioids, oxytocin, and norepinephrine. *Neurosci. Biobehav. Rev.* 22 (3), 437–452.
- Ninomiya, S., Sato, S., Sugawara, K., 2007. Weaving in stabled horses and its relationship to other behavioural traits. *Appl. Anim. Behav. Sci.* 106 (1–3), 134–143.
- Normansell, L., Panksepp, J., 1990. Effects of morphine and naloxone on play-rewarded spatial discrimination in juvenile rats. *Dev. Psychobiol.* 23, 75–83.
- Oreland, S., Gustafsson-Ericson, L., Nylander, I., 2010. Short- and long-term consequences of different early environmental conditions on central immunoreactive oxytocin and arginine vasopressin levels in male rats. *Neuropeptides* 44, 391–398.
- Panksepp, J., Nelson, E., Siviy, S., 1994. Brain opioids and mother–infant social motivation. *Acta Paediatr. Suppl.* 397, 40–46.
- Pell, S.M., McGreevy, P.D., 1999. A study of cortisol and beta-endorphin levels in stereotypic and normal thoroughbreds. *Appl. Anim. Behav. Sci.* 64 (2), 81–90.
- Platt, M., Watson, K.K., Hayden, B.Y., Shepherd, S.V., Klein, J.T., 2010. Implications for understanding the neurobiology of addiction. In: Kuhn, C.M., Koob, G.F. (Eds.), *Advances in the Neuroscience of Addiction*, second edition. CRC Press, Boca Raton.
- Proops, L., McComb, K., Reby, D., 2009. Cross-modal individual recognition in domestic horses (*Equus caballus*). *Proc. Natl. Acad. Sci. U. S. A.* 106 (3), 947–951.
- Range, F., Noe, R., 2005. Can simple rules account for the pattern of triadic interactions in juvenile and adult female sooty mangabeys? *Anim. Behav.* 69, 445–452.
- Rho, J.R., Srygley, R.B., Choe, J.C., 2004. Behavioral ecology of the jeju pony (*Equus Caballus*): effects of maternal age, maternal dominance hierarchy and foal age on mare aggression. *Ecol. Res.* 19 (1), 55–63.
- Roberts, J.M., Browning, B.A., 1998. Proximity and threats in highland ponies. *Soc. Networks* 20 (3), 227–238.
- Rutberg, A.T., Keiper, R.R., 1993. Proximate causes of natal dispersal in feral ponies – some sex-differences. *Anim. Behav.* 46 (5), 969–975.
- Schilder, M.B.H., 1990. Interventions in a herd of semi-captive plains zebras. *Behaviour* 112, 53–83.
- Schino, G., Troisi, A., 1992. Opiate receptor blockade in juvenile macaques: effect on affiliative interactions with their mothers and group companions. *Brain Res.* 576 (1), 125–130.
- Sigurjónsdóttir, H., VanDierendonck, M.C., Snorrason, S., Þorhallsdóttir, A.G., 2003. Social relationships in a group of horses without a mature stallion. *Behaviour* 140 (6), 783–804.
- Small, W.S., 1899. Notes on the psychic development of the young white rat. *Am. J. Psychol.* 11, 80–100.
- Spruijt, B.M., van Hooff, J.A.R.A.M., Gispen, W.H., 1992. Ethology and neurobiology of grooming behavior. *Physiol. Rev.* 72 (3), 825–852.
- Spruijt, B.M., van den Bos, R., Pijlman, F.T.A., 2001. A concept of welfare based on reward evaluating mechanisms in the brain: anticipatory behaviour as an indicator for the state of reward systems. *Appl. Anim. Behav. Sci.* 72 (2), 145–171.
- Trezza, V., Damsteegt, R., Achterberg, E.J., Vanderschuren, L.J.M.J., 2011. Nucleus accumbens  $\mu$ -opioid receptors mediate social reward. *J. Neurosci.* 31 (17), 6362–6370.
- Tyler, S.J., 1972. The behaviour and social organisation of the New Forest Ponies. *Anim. Behav. Monogr.* 5, 85–196.
- Van Ree, J.M., Niesink, R.J.M., Van Wolfswinkel, L., Ramsey, N.F., Kornet, M.L.M.W., Van Furth, W.R., Vanderschuren, L.J.M.J., Gerrits, M.A.F.M., Van Den Berg, C.L., 2000. Endogenous opioids and reward. *Eur. J. Pharmacol.* 405 (1–3), 89–101.
- Vanderschuren, L.J.M.J., Niesink, R.J.M., Van Ree, J.M., 1997. The neurobiology of social play behavior in rats. *Neurosci. Biobehav. Rev.* 21 (3), 309–326.
- VanDierendonck, M.C., de Graaf-Roelfsema, E., van Breda, E., Wijnberg, I.D., Keizer, H.A., van der Kolk, J.H., Barneveld, A., 2007. Intensified training induces ethological effects. In: de Graaf-Roelfsema, E. (Ed.), PhD Thesis. Standardbreds. Endocrinological and Behavioural Adaptations to Experimentally Induced Physical Stress in Horses. PhD Thesis Faculty of Veterinary Medicine, Utrecht University, pp 168–188.
- VanDierendonck, M.C., De Vries, H., Schilder, M.B.H., 1995. An analysis of dominance, its behavioural parameters and possible determinants in a herd of Icelandic horses in captivity. *Neth. J. Zool.* 45 (3–4), 362–385.
- VanDierendonck, M.C., Sigurjónsdóttir, H., Colenbrander, B., Thorhallsdóttir, A.G., 2004. Differences in social behaviour between late pregnant, post-partum and barren mares in a herd of Icelandic horses. *Appl. Anim. Behav. Sci.* 89 (3–4), 283–297.
- VanDierendonck, M.C., de Vries, J., Schilder, M.B.H., Colenbrander, B., Þorhallsdóttir, A.G., Sigurjónsdóttir, H., 2009. Interventions in social behaviour in a herd of mares and geldings. *Appl. Anim. Behav. Sci.* 116 (1), 67–73.
- Vervaeke, H., Stevens, J.M., Vandemoortele, H., Sigurjónsdóttir, H., de Vries, H., 2007. Aggression and dominance in matched groups of subadult Icelandic horses (*Equus caballus*). *J. Ethol.* 25, 239–248.
- Vinke, C.M., 2004. Cage enrichments and welfare of farmed mink. PhD Thesis. Faculty of Veterinary Medicine, Utrecht University.
- Vinke, C.M., van Leeuwen, J., Spruijt, B.M., 2005. Juvenile farmed mink (*Mustela vison*) with additional access to swimming water play more frequently than animals housed with a cylinder and platform, but without swimming water. *Anim. Welfare* 14 (1), 53–60.
- Visser, E.K., Ellis, A.D., Van Reenen, C.G., 2008. The effect of two different housing conditions on the welfare of young horses stabled for the first time. *Appl. Anim. Behav. Sci.* 114 (3–4), 521–533.
- Vulink, J.T., 2001. Hungry herds: management of temperate lowland wetlands by grazing. PhD Thesis. University of Groningen.
- Waran, N.K., 1997. Can studies of feral horse behaviour be used for assessing domestic horse welfare? *Equine Vet. J.* 29 (4), 249–251.
- Waran, N.K., Henderson, J., 1998. Stable vices: what are they, and can we prevent them? *Equine Pract.* 20 (5), 6–8.
- Waring, G.H., 2003. *Horse Behavior*, second edition. William Andrew Publishing, Norwich, NY.
- Weeks, J.W., Crowell-Davis, S.L., Caudle, A.B., Heusner, G.L., 2000. Aggression and social spacing in light horse (*Equus caballus*) mares and foals. *Appl. Anim. Behav. Sci.* 68 (4), 319–337.
- Wernicke, R., VanDierendonck, M.C., 2003. Soziale organisation und Ernährungszustand der Konik-Pferdeherde des Naturreservates Oostvaardersplassen (NL) im Winter. Eine Lehrstunde durch wild lebende Pferde. *KTBL-Schrift.* 418, 78–85 (in German).
- Zeitler-Feight, M.H., 2004. *Horse Behaviour Explained*. Mason Publishing Ltd., London.