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

M.C. van Dierendonck[a,b,*], H. Sigurjónsdóttir[c],
B. Colenbrander[b], A.G. Thorhallsdóttir[d]

[a]*Department of Animal Science and Society, Faculty of Veterinary Medicine,*
Utrecht University, Postbox 80168, 3508 TD Utrecht, The Netherlands
[b]*Department of Equine Sciences, Faculty of Veterinary Medicine,*
Utrecht University, Postbox 80151, 3508 TD Utrecht, The Netherlands
[c]*Iceland University of Education, Reykjavik, Iceland*
[d]*The Agricultural University, Hvanneyri, Iceland*

Abstract

Group dynamics and the social behaviour of mares were investigated in the periods before and after foaling during two 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 h a day for 5–6 weeks; i.e. a total of 1483 h. 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

* Corresponding author. Tel.: +31 30 2532516; fax: +31 30 2539227.
E-mail address: m.c.vandierendonck@vet.uu.nl (M.C. van Dierendonck).

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.

1. 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; Zeitlerfeicht, 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 Crowell-Davis, 1994; Weeks et al., 2000; Christensen et al., 2002a,b), little data is available on complex groups with both (sub)adult geldings and breeding and non-breeding mares (see however 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). 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') (Van-Dierendonck et al., 1995; Sigurjónsdóttir et al., 2003). 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 Crowell-Davis, 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; Sigurjónsdóttir et al., 2003). In the closest feral counterpart of this type of herd, the multiple stallion harems, 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 probably also worse than in herds with a single harem stallion (Linklater, 2000; Sigurjónsdóttir et al., 2003). 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, 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-olds) 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 (see also Sigurjónsdóttir et al., 2003). 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.

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

	1997 (n)	1999 (n)	1997 (mean ± S.D.), age (years)	1999 (mean ± S.D.), age (years)
Pregnant mares[a] (>6 years)	12	14	14.8 ± 3.3	16.4 ± 3.7
Post partum mares[a]	7	13[b]	13.9 ± 3.6	16.5 ± 3.8
Barren control mares (>6 years)	5	4(5)[b]	15.0 ± 3.8	16.0 ± 7.0
Adult geldings (≥4 years)	5	4	6.2 ± 3.0	13.5 ± 3.1
Sub adult males (1–3 years)	6	4	1.3 ± 0.5	3.0 ± 1.4
Sub adult females (1–4 years)	6	4	2.2 ± 0.8	3.3 ± 1.0
Foals	7	13		

[a] During the observation periods of 1997 and 1999, 7 and 14 mares foaled, respectively.
[b] 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.

2. 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.

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 Southwest 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, eight animals (including four 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 eight 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 five generations, as described by Hartl and Clark (1997).

2.1. 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-min 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-h daylight in Iceland, the data were collected continuously, 24 h a day. To prevent any structural bias in recordings, the observers worked in 8-h shifts with one overlapping hour at each shift change, so that shift changes were not at the same time of the 24 h 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 h in 1997 and 828 h in 1999, and 666 spatial samples were recorded.

2.2. 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 h 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 the 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 two horse-lengths of each other.

Dominance relationships and rank orders were determined on the basis of five behavioural elements, namely submission and four 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 h.

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:

(1) (partial) row-wise tau matrix permutation test (2000 permutations) for matrix comparisons (DeVries, 1993);
(2) Wilcoxon signed ranks test for related samples;
(3) Mann–Whitney U-test for unrelated samples;
(4) Spearman's rank correlation (Rho) and Pearson's correlation coefficients for rank correlations;

(5) Landau's '*h*' (DeVries, 1995) for linearity;
(6) preferred partners were identified using standardised residuals (SR; 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 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.

3. Results

3.1. Dynamics of allogrooming

3.1.1. 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 $\pm$ 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 and 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: $P < 0.05$).

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
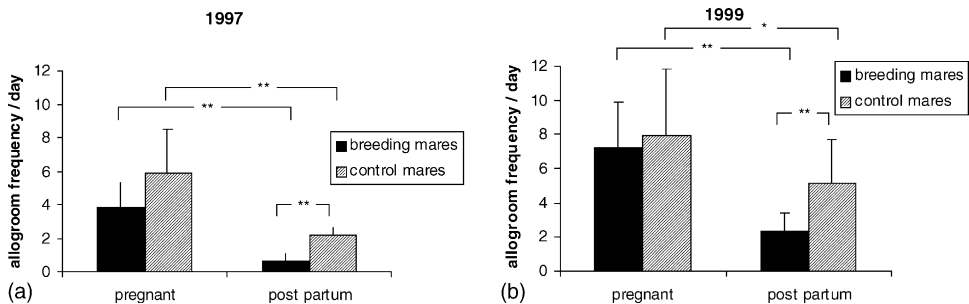

Fig. 1. (a and b) Daily allogrooming frequencies for individual, adult breeding and control (barren) mares (mean $\pm$ S.D.) in 1997 (a) and 1999 (b). (*, **) indicates where frequencies differ significantly ($^*P < 0.05$; $^{**}P < 0.01$) (dependent subgroups via Wilcoxon's signed rank test; independent subgroups via the Mann–Whitney U-test).

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

	Tests[a]	1997			1999		
			P	n_1, n_2		P	n_1, n_2
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.

[a] *Tests*: WSR: Wilcoxon signed ranks test; MWU: Mann–Whitney U-test.

(pregnant, post-partum or barren: Kendall row-wise correlations for 1997: $\tau_{rw} = 0.16$, $n = 29$, $P < 0.001$; 1999: $\tau_{rw} = 0.13$, $n = 36$, $P < 0.001$).

3.1.2. 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 S.D.]. 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.

3.2. Dynamics in proximity

3.2.1. 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- versus 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 versus post-partum, Wilcoxon signed rank = 2.37, $P < 0.02$: for post partum versus control, Mann–Whitney $U = −2.84$, $P < 0.003$).

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

3.2.2. 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
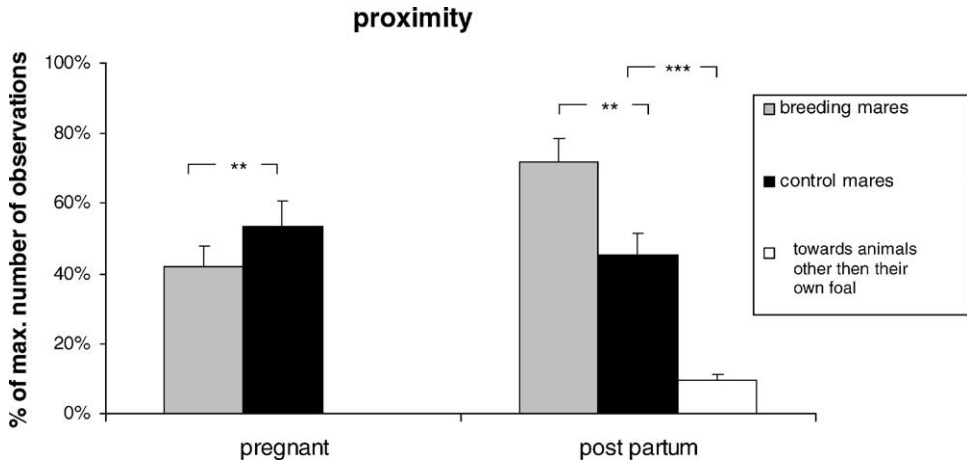
Fig. 2. Mean (±S.D.) frequencies with which adult breeding and control (barren) mares were within two horse lengths of each other (proximity scores). For foaling mares, the additional column represents the frequencies that a mare was proximate to an animal other than her own foal. (**, ***) indicates 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).

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.

3.2.3. Overlap between allogrooming and proximity results

Dyadic proximity frequencies and allogrooming frequencies overlapped significantly ($\tau_{rw} = 0.32$, $n = 29$, $P < 0.001$). 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).

3.2.4. Kinship and familiarity

Allogrooming and proximity were significantly related to kinship (allogrooming 1997, $\tau_{rw} = 0.17$, $n = 29$, $P < 0.001$; 1999, $\tau_{rw} = 0.28$, $n = 36$, $P < 0.001$: proximity 1997, $\tau_{rw} = 0.19$, $n = 29$, $P < 0.001$). 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 $\tau_{rw;XY.Z} = 0.38$, $n = 36$, $P < 0.001$).
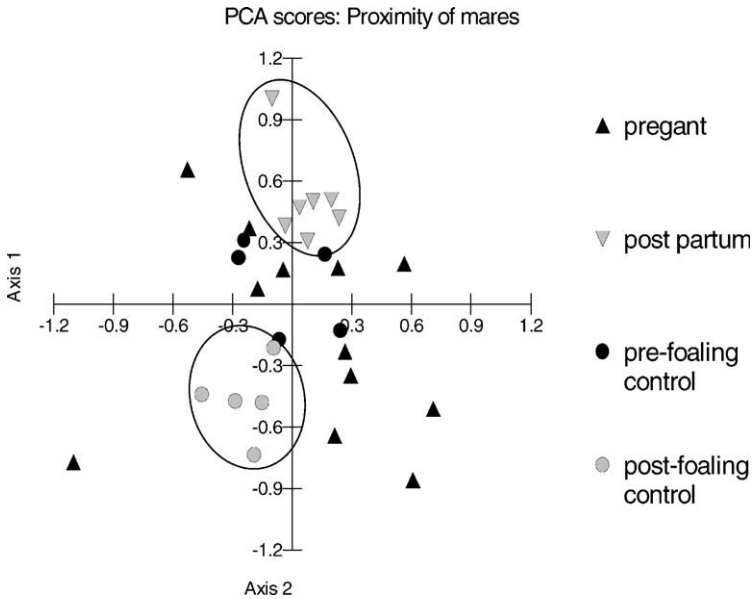
PCA scores: Proximity of mares

Fig. 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.
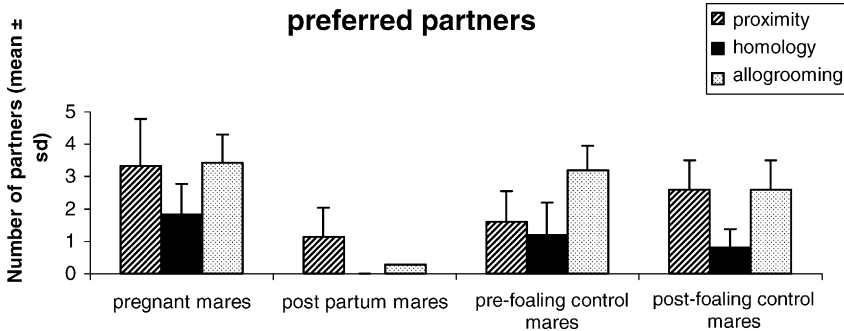

Fig. 4. The relative number (mean ± S.D.) of preferred partners for allogrooming or proximity. Homology was when the same adult mare was the preferred partner for both allogrooming and proximity.

3.3. Dominance

3.3.1. Rank order

For all mares, the position in the dominance hierarchy was remarkably consistent across the two 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
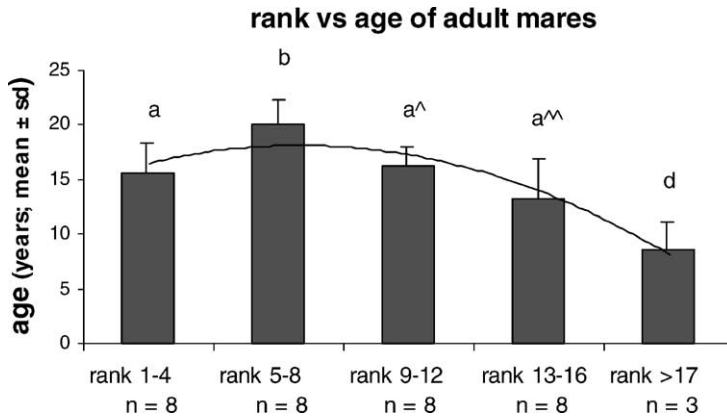
Fig. 5. Age of adult mares (mean ± S.D.) in the various dominace rank categories. (a–d) Different letters indicate columns with mean ages that differed significantly ($P < 0.05$: Mann–Whitney U-test). $a^\wedge$ and $a^{\wedge\wedge}$ indicate groups that tended to differ (a vs. $a^{\wedge\wedge}$, $P < 0.09$; $a^\wedge/a^{\wedge\wedge}$, $P < 0.06$). The line of best fit was expressed by the quadratic regression $y = -1.3x^2 + 5.8x + 11.9$ ($R^2 = 0.54$, d.f. = 32) and indicated a dominance hierarchy with the form: older mares > oldest mares > younger mares.

position during pregnancy; $n = 20$). Possibly because the mares tended to become more aggressive at this time (Wilcoxons signed ranks test $Z = -1.9$, $n = 20$, $P = 0.052$).

The calculated linear rank order (DeVries, 1998) that fitted best the dominance relationships observed had only nine 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, d.f. = 22, $P < 0.02$: combined over the two 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, d.f. = 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 $\tau_{rw} = 0.219$, $n = 24$, $P < 0.001$ and 1999: $\tau_{rw} = 0.300$, $n = 32$, $P < 0.001$, no control for seasonality). However, closeness in dominance rank was not related to allogrooming frequency, spatial proximity or reproductive state.

4. 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 (see Sigurjónsdóttir et al., 2003 for discussion).

4.1. 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.

4.2. 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 sub-adults 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 five times more often than towards other adult mares. 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.

4.3. 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).

4.4. 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 (VanDierendonck 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.

4.5. 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).

5. 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) and Christensen et al. (2002a) emphasise the significance of stable social contact.

References

Asa, C.S., 1999. Male reproductive success in free-ranging feral horses. Behav. Ecol. Sociobiol. 47 (1–2), 89–93.

Bachmann, I., Stauffacher, M., 2002. Housing and exploitation of horses in Switzerland: a representative analysis of the status quo. Schweizer Archiv Fur Tierheilkunde 144 (7), 331–347.

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.

Barber, J.A., Crowell-Davis, S.L., 1994. Maternal-behavior of Belgian (*Equus caballus*) mares. Appl. Anim. Behav. Sci. 41 (3–4), 161–189.

Brambell, F.W.R., 1965. Command paper 2836: Report of the technical committee to enquire into the welfare of animals kept under intensive husbandry systems. HMSO, London.

Christensen, J.W., Ladewig, J., Sondergaard, E., Malmkvist, J., 2002a. Effects of individual versus group stabling on social behaviour in domestic stallions. Appl. Anim. Behav. Sci. 75 (3), 233–248.

Christensen, J.W., Zharkikh, T., Ladewig, J., Yasinetskaya, N., 2002b. Social behaviour in stallion groups (*Equus przewalskii* and *Equus caballus*) kept under natural and domestic conditions. Appl. Anim. Behav. Sci. 76 (1), 11–20.

Clutton-Brock, T.H., Greenwood, P.J., Powell, R.P., 1976. Ranks and relationships in highland ponies and highland cows. Z. Tierpsychol. 41, 202–216.

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, The Netherlands, pp. 99–124.

DeVries, H., 1993. The rowwise correlation between two proximity matrices and the partial rowwise correlation. Psychometrika 58 (1), 53–69.

DeVries, H., 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Anim. Behav. 50, 1375–1389.

DeVries, H., 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. Anim. Behav. 55, 827–843.

DeVries, H., Netto, W.J.P., Hanegraaf, L.H., 1993. MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. Behaviour 125 (3–4), 157–175.

Estep, D.Q., Crowelldavis, S.L., Earlcostello, S.A., Beatey, S.A., 1993. Changes in the social-behavior of drafthorse (*Equus caballus*) mares coincident with foaling. Appl. Anim. Behav. Sci. 35 (3), 199–213.

Feh, C., 1999. Alliances and reproductive success in Camargue stallions. Anim. Behav. 57, 705–713.

Feh, C., Mazieres, J. de., 1993. Grooming at a preferred site reduces heart rate in horses. Anim. Behav. 46 (6), 1191–1194.

Feist, J.D., McCullough, D.R., 1976. Behavior patterns and communication in feral horses. Z. Tierpsychol. 41 (4), 337–371.

Hartl, D.L., Clark, A.G., 1997. Principles of Population Genetics, third ed. Sinauer Ass, New York, USA.

Jezierski, T., Gebler, E., 1984. Beobachten zum Sozialverhalten von Polnischen Primitiv Pferden. Z. Tierz. Züchtungsbio. 101 (2), 143–152.

Kaseda, Y., Khalil, A.M., Ogawa, H., 1995. Harem stability and reproductive success of Misaki feral mares. Equine Vet. J. 27 (5), 368–372.

Kimura, R., 1998. Mutual grooming and preferred associate relationships in a band of free-ranging horses. Appl. Anim. Behav. Sci. 59 (4), 265–276.

Klingel, H., 1975. Social organisation and reproduction in equids. J. Reprod. Fertil. Suppl. 23, 7–11.

Kolter, L., 1984. Social relationships between horses and its influence on feeding activity in loose housing. In: Proceedings of the International Congress on Applied Ethology in Farm Animals, Kiel, pp. 151–155.

Lebelt, D., 1998. Stereotypic behaviour in the horse: general aspects and therapeutic approaches. Prak. Tierarzt 79, 28–32.

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., Minot, E.O., Stafford, K.J., 1999. Stallion harassment and the mating system of horses. Anim. Behav. 58, 295–306.

Linklater, W.L., Cameron, E.Z., Stafford, K.J., Veltman, C.J., 2000. Social and spatial structure and range use by Kaimanawa wild horses (*Equus caballus*: equidae). N. Z. J. Ecol. 24 (2), 139–152.

Manly, B.F.J., 1994. Multivariate Statistical Methods. A primer, second ed. Chapman & Hall, London, UK.

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., Haviland, J.C.S., 1995. Agonistic ethogram of the equid bachelor band. Appl. Anim. Behav. Sci. 43 (3), 147–188.

McGreevy, P.D., 1997. Do stabled horses cope. J. Biol. Educ. 31 (3), 207–211.

Mills, D.S., Nankervis, K.J., 1999. Equine Behaviour: Principles and Practice, Blackwell Science, London, UK.

Mills, D.S., Clarke, A., 2002. Housing, management and welfare. In: Waran, N. (Ed.), Welfare of Horses. Animal Welfare Series, Kluwer Academic Pubishers, Dordrecht, pp. 77–97.

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. Behaviour 133, 1095–1124.

Roberts, J.M., Browning, B.A., 1998. Proximity and threats in Highland Ponies. Soc. Networks 20 (3), 227–238.

Rutberg, A.T., Greenberg, S.A., 1990. Dominance, aggression frequencies and modes of aggressive competition in feral pony mares. Anim. Behav. 40, 322–331.

Schilder, M.B.H., 1990. Interventions in a herd of semi-captive plains zebras. Behaviour 112, 53–83.

Sigurjónsdóttir, H., Vandierendonck, M.C., Snorrason, S., Thorhallsdottir, A.G., 2003. Social relationships in a group of horses without a mature stallion. Behaviour 140 (6), 783–804.

Siegel, S., Castellan Jr., N.J., 1988. Non parametric statistics for the behavioural sciences, McGraw-Hill, Singapore.

Spruijt, B.M., van Hooff, J.A., Gispen, W.H., 1992. Ethology and neurobiology of grooming behaviour. Physiol. Rev. 72, 825–852.

Tyler, S.J., 1972. The behaviour and social organisation of the New Forest ponies. Anim. Behav. Monogr. 5, 85–196.

VanDierendonck, M.C., DeVries, 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.

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.

Wood-Gush, D.G.M., Galbraith, F., 1987. Social relationships in a herd of 11 geldings and two female ponies. Equine Vet. J. 19 (2), 129–132.

Zeitlerfeicht, M.H., 1996. Minimum requirements for the welfare of group, loose housed horses. Tierarztliche Umschau 51 (10), 611–614.

Zeitler-Feicht, M.H., Prantner, V., 2000. Recumbence resting behaviour of horses in loose housing systems with open yards. Archiv Fur Tierzucht 43 (4), 327–335.