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# Social relationships in a herd of Sorraia horses
# Part II. Factors affecting affiliative relationships and sexual behaviours

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**Abstract**

The influence of age, dominance rank, kinship and aggressiveness over affiliative relationships and sexual behaviours were analysed in a herd of Sorraia horses, *Equus caballus*, kept under extensive management. Subjects were 10 adult mares 5–18 years old that had known each other since birth, and a stallion introduced into the group for breeding for the first time. Kinship coefficient and dominance rank were the most important factors affecting affiliative relationships. Bonds were reciprocal and stronger among mares with higher kinship. Mares spent more time in proximity to close-ranking and lower-ranking females. Mares with stronger affiliative relationships or higher relatedness were not less aggressive towards each other. Affiliative relationships between the stallion and the mares were not reciprocal: lower-ranking mares formed stronger bonds with the stallion but he preferred the less genetically related mares for proximity. However, the stallion was involved in sexual behaviours more frequently with the mares that were more genetically related to him. These results suggest that kinship beyond close relatives may affect affiliative relationships both among familiar and among unfamiliar horses. However, the influence of kinship does not imply that horses possess a kin recognition system and alternative explanations are discussed.

*Keywords:* Horse; *Equus*; Affiliative relationship; Rank; Kinship; Aggressiveness

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## 1. Introduction

Horses are non-territorial social equids (Klingel, 1975). The social and breeding unit is the band, a stable association of mares, their offspring and one or more stallions that defend the mare group and their mating opportunities from other males year round (Linklater, 2000). Individuals of both sexes disperse from their natal bands upon reaching sexual maturity (2–3 years old) and form new bands or join existing ones (Klingel, 1975; Salter and Hudson, 1982; Berger, 1986; Feh, 1999). The function of natal dispersal in female horses is to prevent close inbreeding (Duncan et al., 1984; Monard and Duncan, 1996; Monard et al., 1996).

Stable relationships between the stallion and the mares of his band enhance reproductive success by reducing stallion harassment and inter-mare aggression associated with band change and male takeovers (Berger, 1983; Kaseda et al., 1995; Linklater et al., 1999). Moreover, oestrus detection is improved by such long-term bonds (Salter and Hudson, 1982) and large inputs of time are not required to maintain them when females are in oestrus (Duncan, 1980).

Sexual attraction of the stallion to mares is affected by their coat colour, size, days from ovulation, age and dominance rank (Waring, 1983; McDonnell, 2000a). Although the sex that provides the greatest parental investment (in horses: the female) is expected to be most selective in the choice of mating partners (Trivers, 2002), the stallion could benefit from mating preferentially with the mare that is most likely to successfully raise a foal when several mares are receptive simultaneously. In fact, stallions have been reported to select the dominant oestrous mare for copulation when more than one oestrous female is present (Asa et al., 1979). Higher-ranking mares may benefit from higher quality diets, produce faster growing offspring (Duncan, 1992), and their foals may be more protected against aggression (Rutberg and Greenberg, 1990; Boyd and Houpt, 1994; Weeks et al., 2000). Female success in raising offspring also improves with age, because older mares target their investment better due to experience (Cameron et al., 2000). Therefore, the stallion could be expected to mate preferentially with older and higher-ranking mares when he has a choice. Moreover, mares

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play the major role in informing the stallion of their reproductive status, stimulation of the stallion and timing of copulation (Bristol, 1982; McDonnell, 2000b). Hence, mares that solicit the stallion during oestrus more often or more overtly may get involved in higher frequencies of sexual sequences. As residual reproductive value declines with age (Cameron et al., 2000), older oestrous mares are predicted to initiate sexual interactions with the stallion more often than younger oestrous females to increase the probability of conception.

Social bonds among mature mares contribute to band stability and are reflected in proximity during daily activities and participation in affiliative interactions such as mutual grooming (Wells and von Goldschmidt-Rothschild, 1979; Arnold and Grassia, 1982; Waring, 1983; Kimura, 1998). Cooperation among mares is uncommon and they seldom aid each other in contests against group members (Berger, 1986; Monard and Duncan, 1996). Therefore, bonding with kin or with unrelated dominants is not expected to afford protection against aggression from other individuals, as it does in some primate species (de Waal, 1991; Chapais et al., 1994). Nevertheless, it could be expected that horses are less aggressive towards preferred partners and bonding would confer protection against aggression from the social partner.

Preferred social partners of females in natal bands are usually matrilineal relatives: mother and siblings (Tyler, 1972; Wells and von Goldschmidt-Rothschild, 1979; Monard et al., 1996). Dispersal decreases the probability that mares find close relatives in the new band (Linklater, 2000), so usually these bonds are broken and new bonds are formed (Waring, 1983). Nevertheless, close relatives may form strong and long-term affiliative relationships as adults when they integrate the same new band or when they rejoin the natal group (Tyler, 1972; Waring, 1983; Monard and Duncan, 1996). Moreover, affiliative relationships have been found to be stronger among mares with higher kinship outside the family unit (Sigurjónsdóttir et al., 2003) and among mares with similar age and close dominance rank (Clutton-Brock et al., 1976; Wells and von Goldschmidt-Rothschild, 1979; Monard and Duncan, 1996; Kimura, 1998; Sigurjónsdóttir et al., 2003).

The aim of this study is to assess the influence of age, dominance rank, kinship and aggressiveness over affiliative relationships and sexual behaviours in a managed herd of Sorraia horses. Unlike in feral bands, managed horses are artificially forced to be together and do not choose group members, but they can choose whom to bond with. The study herd was composed of mares that had known each other since birth and the stallion was a new member of the group. Moreover, the horses were highly genetically related and some of them were close relatives via the mother. By investigating the factors that affect affiliative relationships in such conditions, we expect to gain further insight into the way horses integrate information about age, dominance rank and kinship into individual social strategies.

We tested the following hypotheses—(1) factors that affect affiliative relationships among mares: (i) reciprocity and symmetry: mares form stronger affiliative relationships with those that form stronger bonds with them; (ii) similarity: affiliative relationships are stronger among mares with similar age, similar rank or higher kinship, but absolute dominance rank does not influence a mare's attractiveness as a social partner; (iii) aggressiveness dependence: affiliative relationships are stronger among horses that are less aggressive towards each other; (iv) aggressiveness is lower among more genetically related mares. (2) Factors that affect affiliative relationships and sexual behaviours between the stallion and the mares: (i) the stallion forms stronger affiliative relationships with mares that are older, higher-ranking or less genetically related to him; (ii) mares that form stronger bonds with the stallion are involved in higher frequencies of sexual behaviours when in oestrus; (iii) mares that are older, higher-ranking or less genetically related to the stallion are involved in higher frequencies of sexual behaviours when in oestrus and when more than one oestrous female is present.

## 2. Materials and methods

### 2.1. Subjects and study site

The study was conducted on a Sorraia horse herd at Alter studfarm (39°11′N, 7°39′W), Portugal. The Sorraia horse was recovered in 1937 from 12 founders (5 males and 7 females) and is considered to be at critical extinction risk status by the Food and Agriculture Organization (Galal and Hammond, 1996) due to its small effective number and high inbreeding levels (Oom and Cothran, 1994). In this herd, the mean inbreeding coefficient, $F$, is $0.436 \pm 0.065$ (mean ± S.D.).

The horses were alternately kept on two 5.5- and 17.2-ha enclosed pastures surrounded by 1.5 m high wire fences and walls. Water was available from temporary water lines maintained during the rainy season and water canals connected to reservoirs and watering-ponds. Vegetation consisted primarily of grasses that composed most of the horses' diet.

The herd was rounded up and taken to a paddock a few times per year for pregnancy detection, foal removal, branding, tail and mane shearing and collection of blood samples for paternity analyses. Veterinary care was provided when necessary and supplementary feed was given during summer. Pasture breeding was implemented since 1998, by releasing and keeping a stallion in the mare group from February to June every year. A record was kept of identity, birth date and parents' identity of every horse born into the herd. Weaning and foal removal from the group is performed when foals are approximately 6 months of age but some females rejoin the herd at 3 years of age to be bred.

Subjects were 10 adult mares that had known each other since birth, and a stallion that was placed with them for reproduction for the first time and had prior experience in pasture breeding (Table 1). A foal was born during the study period, fathered by a different stallion released with the mares in the previous year.

### 2.2. Data collection

Observations were made on foot between 5 December 2000 and 7 June 2001 for 386 h. Horses could be observed from a 3 to 10 m distance without disturbance and data were recorded on prepared sheets or dictated into a tape recorder. Animals were

Table 1
Data on individual characteristics of subjects

| Name | Label | Sex | Age (years) | Dominance rank | Close relatives via the mother |
|---|---|---|---|---|---|
| Afogado | Ag | M | 9 | 2 | |
| Barroca | Ba | F | 18 | 6 | |
| Derreta | De | F | 16 | 11 | Hora[a], Mubia[b] |
| Hera | He | F | 12 | 9 | |
| Hora | Ho | F | 12 | 10 | Derreta[a], Mubia[c] |
| Ibaga | Ib | F | 11 | 5 | Pimba[b] |
| Ibeta | It | F | 11 | 8 | Jabeta[a] |
| Jabeta | Jb | F | 10 | 7 | Ibeta[a] |
| Lomba | Lb | F | 9 | 4 | |
| Mubia | Mb | F | 8 | 3 | Derreta[d], Hora[e] |
| Pimba | Pb | F | 5 | 1 | Ibaga[d] |

Sex: M, male; F, female; age: reporting to June 2001; dominance rank: highest score means highest rank.

[a] Full-sister.

[b] Daughter.

[c] Niece.

[d] Mother.

[e] Aunt.

individually recognized by coloured markings and identification numbers on collars, differences in body size, morphology and coat colour. Sample periods lasting 25 or 30 min were randomly assigned to each horse without repetition on a given day and evenly distributed between 07:30 and 16:30 h solar time. Total sampling time was on average 80.4 h per mare (range 74.9–88.1) and 54.5 h for the stallion.

For every social interaction, the behaviour category, identities of the initiator and receiver(s), reaction of receiver(s) and context were noted using focal sampling (Altmann, 1974). Whenever one or two individuals were close enough to the focal animal at the beginning of its sample period so that all their interactions could be seen, they were also observed as focal animals as long as they remained visible. If during sampling they moved apart, the previously assigned focal animal was followed. We recorded affiliative interactions, sexual behaviours and agonistic-related interactions: displacements, mild threats, bite threats, bites, kick threats, kicks, chases, attacks and herding (see Heitor et al., 2006, for a complete description). We considered the following non-sexual affiliative interactions performed while the initiator kept its ears pointing forward or laterally:

(1) *Approach*. Moving to within two body-lengths of another horse that does not immediately move away and staying there for at least 10 s without initiating physical contact with it.
(2) *Follow*. Moving immediately behind another horse that had just initiated locomotion and was within three body-lengths, for at least 10 s without initiating physical contact with it.
(3) *Mutual grooming*. Two horses stand head to tail and nibble, lick or rub the muzzle at each other's body.
(4) *Friendly contact*. Body contacts not reciprocated by the receiver.

Sexual interactions consisted of courting behaviours (approach, follow and body contacts), presenting to the stallion, mounting and copulation. Behavioural sequences composed of at least one of these behaviours will be termed 'sexual sequences', excluding mare presentations that were not followed by other sexual behaviours. A mare was considered to be in oestrus on a given day if at least one of the following situations was observed—(1) mare displayed sexual behaviours at least once that day; (2) when receiving sexual behaviours from the stallion, mare remained calm, with raised tail and one of the following components: (i) straddled hindlegs, (ii) clitorial winking, (iii) voiding small amounts of urine; (3) copulation. A mare was considered as not being in oestrus if she was pregnant or if no copulation was observed and when sexually stimulated by the stallion displayed kicks or kick threats and squealed or moved away (Asa et al., 1979; Waring, 1983). Intervals of 1–3 days between oestrous days (decided on the basis of the previous criteria) with missing data of a mare's reproductive state, were also recorded as oestrous days.

Simultaneously, instantaneous samples (Altmann, 1974) were taken at 5-min intervals to record the identity and distance of the focal animal's nearest neighbour (relative to the closest body part). Nearest neighbour was recorded as being 'mutual' (when the nearest neighbour has the focal animal as its nearest neighbour) or 'not mutual'. Furthermore, identities of all individuals within one body-length and between one and five body-lengths (one body-length and five body-lengths associates, respectively) of the focal animal were noted. One body-length (ca. 1.5 m) corresponds approximately to the horse's individual distance, which is commonly 1 or 2 m (Waring, 1983).

### 2.3. *Data analysis*

#### 2.3.1. *Analysis of dominance*

Dominance rank was available from Heitor et al. (2006). The types of agonistic-related interactions that occurred most frequently and with significant asymmetric distribution across dyads (displacements, mild threats, bite threats and bites) were used to assess dominance. Only interactions that caused withdrawal or avoidance reactions from the receiver were included in the analysis. A binary matrix of dominance relationships was constructed, considering an individual to be dominant to the other if it had initiated the majority of these agonistic-related interactions (row individuals dominant to column individuals are indicated by 1 and otherwise by 0). Linearity was significant, as tested by means of Kendall's coefficient of consistence *K* (Appleby, 1983a; de Vries, 1995). The dominance order was determined by the 'I and SI' method (de Vries, 1998), which minimizes the number of inconsistencies (i.e. instances of an individual dominating another higher in rank) and the strength of the inconsistencies (i.e. absolute difference between the ranks of the two individuals involved in an inconsistency). Horses were then assigned an ordinal dominance rank where highest values indicate highest rank.

### 2.3.2. *Relationships among mares*

We constructed matrices of given interactions (initiators in rows and receivers in columns), received interactions (transposed form of the emission matrix) and involvement in interactions (given plus received). Aggressiveness was calculated as the absolute frequency (total number), relative frequency (number of interactions per time spent within five body-lengths) and intensity (proportion of bites, kicks, chases and attacks) of involvement in agonistic interactions. An association index was computed for each dyad A–B as the average of the proportion of time that A had B as its associate and the proportion of time B had A as its associate.

Matrices of relative frequency and intensity of agonistic interactions and matrices of proximity (time spent as nearest neighbour and association indices) were computed by converting the proportions into whole numbers (multiplied by 1000 or 10,000). We also constructed test matrices of absolute rank and age differences (symmetric), matrices of age and dominance rank of column individuals (rows all equal), a matrix of close relatives via the mother (binary matrix where close relatives are indicated by 1 and others by 0) and a matrix of kinship coefficient between all dyads. Kinship coefficient between each pair of horses was computed from pedigree data up to the founder animals (1937).

Correlations between matrices of social interactions and proximity and between these matrices and those of age, rank and kinship (test matrices) were analysed by means of the $K_r$ matrix correlation test and its partial form (Hemelrijk, 1990a,b). We assessed the similarity of the distribution of the four categories of affiliative interactions and proximity measures to choose those that would be used as measures of affiliative relationships. The $K_r$ matrix correlation test was also used to test for 'relative reciprocity', a distribution pattern in which each animal gives a type of interaction more often to those from whom it receives more frequently in return (Hemelrijk, 1990b). When relative reciprocity was significant, Mantel *Z* and *R* matrix correlation tests were run to test for symmetry or 'absolute reciprocity' (Hemelrijk, 1990b). Significance was based on a randomization distribution of 2000 permutations. Whenever reciprocity was significant, involvement in affiliative interactions was used in statistical tests instead of given and received interactions.

### 2.3.3. *Relationships between the stallion and the mares*

Spearman's rank correlation coefficient was used to test for reciprocity and to assess the correlations between mare factors (age, rank and kinship coefficient relative to the stallion) and affiliative interactions, proximity and frequency of sexual sequences. Statistical tests used frequency of involvement in interactions instead of given and received interactions whenever reciprocity was significant. The frequencies of sexual sequences involving the oldest, the highest-ranking and the less related mare among those in simultaneous oestrus were compared with the respective mean frequencies involving other oestrous mares by means of Wilcoxon paired-sample tests.

All statistical tests were one-tailed, unless otherwise stated (right tail probabilities, $P_r$, or left tail probabilities, $P_l$, are reported in matrix correlation tests). The cut-off for significance was 0.05, but some trends were considered at an alpha level of 0.1. Standard statistical tests were performed on Statistica 5.1© StatSoft, Inc. Matrix correlation tests were executed on Matsquar and MatrixTester v2.2.3b© by Hemelrijk.

## 3. Results

Adult horses maintained proximity with group members, but frequencies of affiliative interactions given per individual per partner were low, especially those involving physical contact: $0.291 \pm 0.090$ approaches $h^{-1}$, $0.006 \pm 0.004$ followings $h^{-1}$, $0.058 \pm 0.052$ friendly contacts $h^{-1}$ and $0.004 \pm 0.005$ mutual grooming bouts exchanged $h^{-1}$ (mean ± S.D.). Pairs of horses spent on average $4 \pm 3\%$ of their time within one body-length and $18 \pm 5\%$ of their time between one and five body-lengths of each other (mean ± S.D.). Horses had as the nearest neighbour an individual who also had them as the nearest neighbour for $64.4 \pm 7.7\%$ of the time.

### 3.1. *Relationships among mares*

Affiliative interactions were distributed in similar ways and tended to be directed to whom mares spent more time in proximity with, as revealed by the significant positive correlations between given affiliative interactions and proximity measures (Table 2). The five body-lengths association index was not significantly correlated with most other measures, suggesting that it may not be a good indicator of affiliative relationships. Therefore, mares that were involved in higher frequencies of affiliative interactions and spent more time within one body-length of each other or as nearest neighbours will be assumed to have formed stronger affiliative relationships.

### 3.1.1. *Reciprocity and symmetry hypothesis*

The correlation between given and received interactions was significantly positive for approaches ($K_r = 192$; $Z = 166{,}018$; $R = 227{,}872$; $n = 10$, $P_r < 0.001$) and friendly contacts ($K_r = 169$; $Z = 7410$; $R = 225{,}206.5$; $n = 10$, $P_r < 0.001$), weakly positive for mutual grooming ($K_r = 11$, $n = 8$, $P_r < 0.1$) and not significant for following ($K_r = 16$, $n = 10$, $P_r > 0.05$). Therefore, only approaches and friendly contacts were distributed with relative reciprocity and symmetry (Hemelrijk, 1990b).

Table 2
Pairwise correlations between matrices of given affiliative interactions and proximity measures, as assessed by the $K_r$ test

| | Ap | Fl | FC | MG | NN | AI 1 | AI 1–5 |
|---|---|---|---|---|---|---|---|
| Ap | – | 0.0005 | 0.0015 | 0.0130 | 0.0010 | 0.0010 | 0.0110 |
| Fl | 86 | – | 0.0020 | 0.0055 | 0.0525 | 0.0035 | 0.4380 |
| FC | 118 | 69 | – | 0.0030 | 0.0105 | 0.0005 | 0.1849 |
| MG | 39 | 38 | 50 | – | 0.1604 | 0.0440 | 0.2339 |
| NN | 105 | 45 | 67 | 17 | – | 0.0005 | 0.0050 |
| AI 1 | 128 | 74 | 168 | 32 | 149 | – | 0.4740 |
| AI 1–5 | 93 | 4 | −33 | −13 | 118 | −3 | – |

Values of $K_r$ are presented below the diagonal and the respective one-tailed probabilities are shown above the diagonal, with Ap: approach, Fl: follow, FC: friendly contacts, MG: mutual grooming, NN: nearest neighbour, AI l: one body-length association index and AI 1–5: Five body-lengths association index.

#### 3.1.2. Similarity hypothesis

Close-ranking mares spent significantly more time as nearest neighbours ($K_r = -80$, $n = 10$, $P_l < 0.05$). However, they neither spent more time as one body-length associates nor were involved in higher frequencies of affiliative interactions (Table 3).

Age difference was not significantly correlated with any of the proximity measures (Table 3). Contrary to our predictions, mares with greater age difference tended to be involved in more approaches and friendly contacts and they followed significantly more often those more different in age ($K_r = 53$, $n = 10$, $P_r < 0.05$).

Kinship coefficient was positively correlated with all types of affiliative interactions and proximity measures (Table 3). Close relatives via the mother did not form stronger affiliative relationships but they were involved in mutual grooming significantly more often ($K_r = 24$, $n = 10$, $P_r < 0.05$). Nevertheless, out of 32 mutual grooming bouts, 13 (40.6%) occurred between two unrelated mares, the oldest and the youngest, and one mother–daughter pair was never observed mutual grooming.

Mares were involved in approaches significantly more often with lower-ranking mares and tended to be followed by them more frequently (Table 3). Therefore, lower-ranking mares spent significantly more time as nearest neighbours to other females ($K_r = -50$, $n = 10$, $P < 0.05$; two-tailed). These correlations remained significant when controlling for aggressiveness, except for the correlation with time as nearest neighbour when absolute frequency of agonistic interactions was partialled out ($\tau_{K_r xyz} = -0.080$, $n = 10$, $P > 0.05$; two-tailed). Twenty-five out of the 32 observed mutual grooming bouts (78.1%) involved the youngest and lowest-ranking mare.

#### 3.1.3. Aggressiveness dependence hypothesis

Aggressiveness was significantly higher among mares that approached each other more frequently (Table 4). Absolute frequency of agonistic interactions was also higher among mares that spent more time as nearest neighbours ($K_r = 65$, $n = 10$, $P_r < 0.05$) and their intensity was higher in dyads that were more frequently involved in friendly contacts ($K_r = 30$, $n = 10$, $P_r < 0.05$). Nevertheless, when rank was controlled for, approaches no longer correlated significantly with relative frequency and intensity of agonistic interactions (relative frequency: $\tau_{K_r xyz} = 0.180$, $n = 10$, $P < 0.1$; intensity: $\tau_{K_r xyz} = 0.106$, $n = 10$, $P > 0.05$). Therefore, mares with stronger affiliative relationships were not less aggressive towards each other.

#### 3.1.4. Aggressiveness and kinship

The absolute and relative frequencies of agonistic interactions were not correlated with close relationships via the mother (absolute: $K_r = -10$, $n = 10$, $P_l > 0.05$; relative: $K_r = -12$, $n = 10$, $P_l > 0.05$) but intensity of aggression was lower among close relatives ($K_r = -34$, $n = 10$, $P_l < 0.05$). Moreover, aggressiveness was not lower among mares with higher kinship coefficient (absolute: $K_r = 25$, $n = 10$, $P_r > 0.05$; relative: $K_r = -1$, $n = 10$, $P_l > 0.05$; intensity: $K_r = 9$, $n = 10$, $P_r > 0.05$).

### 3.2. Relationships between the stallion and the mares

Friendly contacts between the stallion and the mares were reciprocal ($r_s = 0.587$, $n = 10$, $P < 0.05$) but approaches were not ($r_s = 0.439$, $n = 10$, $P > 0.05$). Only the youngest mare was observed mutual grooming with the stallion and he never followed the mares.

Table 3
Correlations between measures of affiliative relationships among mares (interactions and proximity) and the factors age, rank and kinship, as assessed by the $K_r$ test

| Measure | Rank difference | | Age difference | | Close relatives | | Kinship coefficient | | Rank | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $K_r$ | $P(1)$ | $K_r$ | $P(1)$ | $K_r$ | $P(1)$ | $K_r$ | $P(1)$ | $K_r$ | $P(2)$ |
| Approach g + r | −21 | 0.296 | 58 | 0.095 | 23 | 0.135 | 135 | 0.0005 | −169 | 0.001 |
| Follow g | 3 | 0.471 | 53 | 0.011 | 20 | 0.099 | 59 | 0.0160 | −39 | 0.133 |
| Follow r | −21 | 0.227 | 24 | 0.199 | 17 | 0.148 | 43 | 0.0554 | −46 | 0.075 |
| Friendly contacts g + r | −3 | 0.455 | 60 | 0.064 | 11 | 0.288 | 66 | 0.0495 | −70 | 0.183 |
| Mutual grooming g + r | −16 | 0.284 | 22 | 0.251 | 24 | 0.028 | 58 | 0.0200 | −59 | 0.127 |
| Nearest neighbour | −80 | 0.013 | −33 | 0.162 | 10 | 0.314 | 82 | 0.0105 | −50 | 0.039 |
| Association 1 bl | −43 | 0.146 | −22 | 0.306 | 12 | 0.291 | 69 | 0.0465 | −75 | 0.196 |

Association 1 bl: one body-length association index; g: given; r: received; $P(1)$: one-tailed probability; $P(2)$: two-tailed probability.

Table 4
Correlations between measures of affiliative relationships among mares (interactions and proximity) and measures of aggressiveness, as assessed by the $K_r$ test

| Measure | Absolute frequency | | Relative frequency | | Intensity | |
|---|---|---|---|---|---|---|
| | $K_r$ | $P(1)$ | $K_r$ | $P(1)$ | $K_r$ | $P(1)$ |
| Approach g + r | 144 | 0.001 | 94 | 0.023 | 67 | 0.043 |
| Follow g | 7 | 0.365 | −10 | 0.378 | 10 | 0.341 |
| Follow r | 6 | 0.405 | −16 | 0.283 | 24 | 0.169 |
| Friendly contacts g + r | 34 | 0.197 | −6 | 0.451 | 81 | 0.014 |
| Mutual grooming g + r | 14 | 0.322 | −9 | 0.396 | 20 | 0.236 |
| Nearest neighbour | 65 | 0.016 | 5 | 0.452 | 25 | 0.208 |
| Association 1 bl | 32 | 0.239 | −24 | 0.310 | 44 | 0.128 |

Association 1 bl: one body-length association index; g: given; r: received; $P(1)$: one-tailed probability.

Table 5
Correlations between measures of affiliative relationships between the stallion and the mares (interactions and proximity) and the factors age, rank and kinship, as assessed by the Spearman's rank correlation coefficient

| Measure | Rank | | Age | | Kinship coefficient | |
|---|---|---|---|---|---|---|
| | $r_s$ | $P(1)$ | $r_s$ | $P(1)$ | $r_s$ | $P(1)$ |
| Approach g | −0.354 | >0.05 | −0.120 | >0.05 | −0.594 | <0.05 |
| Approach r | −0.842 | <0.0025 | −0.537 | <0.1 | −0.190 | >0.05 |
| Follow r | −0.668 | <0.025 | −0.437 | >0.05 | 0.262 | >0.05 |
| Friendly contact g + r | −0.482 | <0.1 | −0.348 | >0.05 | −0.374 | >0.05 |
| Nearest neighbour | −0.705 | <0.025 | −0.434 | >0.05 | −0.433 | >0.05 |
| Association 1 bl | −0.553 | <0.1 | −0.346 | >0.05 | −0.681 | <0.025 |

Association 1 bl: one body-length association index; g: given; r: received; $P(1)$: one-tailed probability.

The stallion was approached and followed significantly more often by the lower-ranking mares but he did not approach them more frequently (Table 5). Therefore, he spent significantly more time with lower-ranking mares as nearest neighbours and tended to have them as one body-length associates mainly due to their effort in maintaining proximity. The stallion also tended to be involved in friendly contacts more often with the lower-ranking mares. No significant correlation was found between mare age and affiliative interactions or proximity but the stallion tended to be approached more frequently by the younger mares (Table 5). The stallion approached significantly more often and spent more time within one body-length of the less genetically related mares (Table 5).

Mares that formed stronger relationships with the stallion did not get involved in higher frequencies of sexual sequences during oestrus (Table 6). Contrary to our expectations, mares that he approached more often ($r_s = -0.654$, $n = 10$, $P < 0.05$) and spent more time as one body-length associates ($r_s = -0.659$, $n = 10$, $P < 0.05$) had significantly lower frequencies of involvement in sexual sequences when in oestrus.

The stallion was observed copulating with all but the oldest mare, but only five copulations were recorded during focal samples. All mares, except one that was pregnant, came into oestrus simultaneously with at least one other mare during the nine observation days following the stallion's introduction in the group (two to six mares simultaneously). During this time, 9 out of the 13 oestrus periods recorded in this study occurred and 50 sexual sequences were observed, of which 38 (76%) were initiated by the stallion. Higher-ranking or older mares were not more frequently involved in sexual sequences during the whole study (Table 6) or during simultaneous oestrus periods (rank: $T = 14$, $n = 9$, $P > 0.05$; age: $T = 10$, $n = 8$, $P > 0.05$). Contrary to our predictions, the stallion was involved in sexual behaviours significantly more often with oestrous mares that were more related to him both over the whole study ($r_s = 0.831$, $n = 10$, $P < 0.0025$) and when more than one oestrous mare was present (Wilcoxon paired-sample test: $T = 3$, $n = 9$, $P = 0.01$).

Table 6
Correlations between the frequency of sexual sequences and mare age, rank, kinship and measures of affiliative relationships between the stallion and the mares, as assessed by the Spearman's rank correlation coefficient

| Measure or factor | $r_s$ | $P(1)$ |
|---|---|---|
| Age | −0.300 | >0.05 |
| Rank | −0.085 | >0.05 |
| Kinship coefficient | 0.831 | <0.0025 |
| Approach given | −0.654 | <0.025 |
| Approach received | −0.043 | >0.05 |
| Follow received | 0.374 | >0.05 |
| Friendly contacts given + received | −0.486 | <0.1 |
| Nearest neighbour | −0.311 | >0.05 |
| One body-length association | −0.659 | <0.025 |

$P(1)$: one-tailed probability.

## 4. Discussion

### 4.1. Relationships among mares

Affiliative relationships among mares were reciprocal and based mainly on kinship. Mares with higher kinship coefficient formed stronger bonds and thus relatedness had an influence on the strength of affiliative relationships beyond close relatives, as Sigurjónsdóttir et al. (2003) have also observed. However, close relatives via the mother *per se* did not form stronger bonds, a finding which contrasts to the reports of others (e.g. Tyler, 1972; Monard and Duncan, 1996).

These results do not imply that horses possess a kin recognition system, defined as a system whose use and function is to assess kinship of conspecifics (Grafen, 1990). Horses that are more genetically related may have similar environmental and social needs or have similar temperament (Wolff et al., 1997) and hence associate more and exchange more affiliative interactions. Kinship-based bonds could then be a case of ancillary kin bias, which consists of differential behaviours towards kin and non-kin as a result of factors that are only incidentally correlated with kinship (Tang-Martinez, 2001). Alternatively, kinship-based bonds could stem from an ability to discriminate by genetic similarity as a by-product of individual, group or species recognition systems (Grafen, 1990; Tang-Martinez, 2001), together with a tendency to bond with the more genetically similar individuals. If discrimination of genetic similarity does occur, it seems to be of a proportional kind (Tang-Martinez, 2001) because individuals behaved as if they could make fine discriminations of the degree of relatedness. Horses recognize each other by visual, auditory and olfactory cues (Tyler, 1972; Feist and McCullough, 1976). They could perhaps match self-produced cues with those of other individuals and then adjust behaviour towards them according to the goodness of fit between their own cues and those of others.

Nevertheless, kinship did not affect aggressiveness. Przewalski horses (*Equus przewalskii*) are usually less aggressive towards close kin than to more distantly related individuals (Boyd and Houpt, 1994), but in this herd aggressiveness was not lower among more related individuals and only intensity of aggression was lower among close relatives via the mother.

Dominance rank also affected affiliative relationships and was related to the effort in maintaining proximity. Close-ranking individuals spent more time close to each other, similar to what has been observed in other horses (Clutton-Brock et al., 1976; Wells and von Goldschmidt-Rothschild, 1979; van Dierendonck et al., 1995; Kimura, 1998), red deer stags (Appleby, 1983b) and rhesus monkeys (de Waal, 1991). This may have been because intensity of aggression tended to be higher among distant-ranking mares (Heitor et al., 2006), which could cause a subordinate to move further away from a dominant after being aggressed. Lower-ranking mares were more preferred partners for proximity than higher-ranking mares. This may be related to the fact that two of the higher-ranking mares and one middle-ranking mare exhibited laminitis, a foot disease in which there is a rotation and/or distal displacement of the third phalanx, causing acute pain while walking (Stokes, 2003). That sometimes caused them to remain behind in group movements, spending large amounts of time apart from the rest of the herd. Moreover, higher-ranking mares may be approached less often because approaching dominants increases the probability of receiving agonistic interactions from them. Indeed, aggressiveness was higher among mares that frequently approached each other and spent more time as nearest neighbours. Proximity may cause an increased need to obtain and defend space to perform daily activities, which seemed to be the main function of aggression in this herd (Heitor et al., 2006). Therefore, as referred to by Clutton-Brock et al. (1976) and Weeks et al. (2000), aggressiveness was not lower among preferred partners.

Frequency of mutual grooming was very low in this herd and some mares were never observed participating in it. Mutual grooming enables horses to obtain care of the coat in areas of the body difficult for them to reach and is associated with important social functions such as strengthening of social bonds (Feist and McCullough, 1976; Arnold and Grassia, 1982; Boyd and Houpt, 1994), appeasement (Feist and McCullough, 1976) and reduction of social tension (Feh and de Mazières, 1993). In this herd, more related mares groomed more often, in accordance with the observations of Keiper (1988) and Sigurjónsdóttir et al. (2003). Clutton-Brock et al. (1976) and van Dierendonck et al. (1995) found no relation between mutual grooming frequencies and kinship. Some authors reported that mares groomed more often those of similar rank (Clutton-Brock et al., 1976; Sigurjónsdóttir et al., 2003) but that was neither apparent in this study nor that of van Dierendonck et al. (1995).

### 4.2. Relationships between the stallion and the mares

The stallion did not form stronger affiliative relationships with older or higher-ranking mares. Lower-ranking mares formed stronger affiliative relationships with the stallion, but he preferred the less genetically related mares for proximity. The stallion was the second lowest-ranking horse (Heitor et al., 2006) and lower-ranking individuals may spend more time close to each other because they receive similar frequencies of aggression from higher-ranking mares. The fact that affiliative relationships between the stallion and the mares were not reciprocal also suggests that selective pressure for male–female bonding may act differently between the sexes.

Mares that had stronger affiliative relationships with the stallion were not involved more frequently in sexual behaviours. This can be partly due to the fact that most oestrus periods, and particularly simultaneous oestrus periods, occurred soon after the stallion's introduction in the group, while affiliative relationships with the unfamiliar mares were still being established.

Contrary to our predictions, mares that were more related to the stallion were involved more often in sexual behaviours during the whole study and during simultaneous oestrus periods. Feral horses do not seem to avoid mating with close kin *per se* but with familiar individuals of their natal band, which are usually close relatives (Duncan et al., 1984; Monard and Duncan, 1996; Monard et al., 1996). In this herd, although all mares were unfamiliar to the stallion, kinship played a role in sexual behaviours but in the opposite direction of that predicted.

The stallion was not involved more often in sexual sequences with older or higher-ranking mares. This finding is similar to that of Bristol (1982) who, contrary to Asa et al. (1979), reported that the stallion did not mate more frequently with the dominant mare among those in oestrus.

Care should be taken when interpreting our results because higher frequencies of involvement in sexual sequences may be related to lower success of mating attempts (i.e. success: copulation with ejaculation). We could not analyse the relation between frequencies of sexual sequences and success of mating attempts due to the low number of copulations recorded during focal samples. In this herd, some oestrous mares showed consistently aggressive or ambivalent reactions to sexual behaviours or minimal behavioural signs of oestrus, as in other studies (Asa et al., 1979; Bristol, 1982; Waring, 1983; McDonnell, 2000b). Therefore, the stallion could have to make a greater number of mating attempts with these mares to achieve a successful copulation. Lack of correspondence between the perceived chemical and behavioural signs of oestrus could also lead the stallion to tease the mares more often to assess their reproductive state. Moreover, mating attempts were sometimes unsuccessful due to interference from other mares (Heitor et al., 2006). Sexual interference behaviours were performed over 21.6% of 153 sexual sequences and their function is currently being investigated (Heitor et al., in preparation). If mares that are more genetically related to the stallion tend to refuse his sexual advances more often or receive more sexual interferences, this could explain the higher frequencies of sexual sequences involving the more related mares. More data should be collected to allow a detailed analysis of mare sexual behaviours, sexual interferences and success of mating attempts, before we can draw clear conclusions based on the frequency of sexual behaviours.

### *4.3. Final remarks*

It is remarkable that kinship was the major factor affecting affiliative relationships in this Sorraia horse herd, despite its high inbreeding levels and concurrent low genetic variation (Oom and Cothran, 1994). To our knowledge, a relation with kinship, beyond close relatives via the mother, has only been reported by Sigurjónsdóttir et al. (2003).

Kinship affected affiliative relationships among mares differently from relationships between the stallion and the mares. Mares preferred the more related females for bonding, but the stallion tended to prefer the less related mares for affiliative relationships. The finding that kinship beyond close relatives affected relationships between mares and an unfamiliar stallion suggests that kinship may affect bonds among unfamiliar individuals. The proximate and ultimate causes of the influence of kinship over affiliative relationships in both stallions and mares deserve further study.

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