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Social relationships in a herd of Sorraia horses Part I. Correlates of social dominance and contexts of aggression

Filipa Heitor, Maria do Mar Oom, Luís Vicente *

Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, Edifício C2, 1749-016 Lisboa, Portugal

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Abstract

Factors related to dominance rank and the functions of aggression were studied in a herd of Sorraia horses, *Equus caballus*, under extensive management. Subjects were 10 adult mares 5–18 years old and a stallion introduced into the group for breeding. Dominance relationships among mares were clear, irrespective of rank difference, and remained stable after introduction of the stallion. The dominance hierarchy was significantly linear and rank was positively correlated with age and total aggressiveness. Higher-ranking mares received lower frequency and intensity of agonistic interactions. Nevertheless, higher-ranking dominants were not more likely to elicit submission from their subordinates than lower-ranking dominants. Neither close-ranking mares nor mares with less clear dominance relationships were more aggressive towards each other. Agonistic interactions seemed to be used more importantly in regulation of space than to obtain access to food or to reassert dominance relationships. Contexts of aggression were related to mare rank. The results suggest that dominance relationships based on age as a conventional criterion were established to reduce aggressiveness in a herd where the costs of aggression are likely to outweigh the benefits.

Keywords: Horse; *Equus*; Dominance; Rank; Agonistic interaction; Aggressiveness

1. Introduction

Dominance can be defined at a dyadic level as an 'attribute of the pattern of repeated agonistic interactions between two individuals, characterised by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation' (Drews, 1993). The status of the former is dominant and that of the latter is subordinate.

At a group level, it has been proposed that dominance relationships function to reduce aggression and bring stability to the social group (Richards, 1974; Kaufmann, 1983). Aggression involves energetic costs, risks of injury and is known to decrease reproductive success in horses, by reducing rates of conception and increasing rates of fetal and foal mortality (e.g. Duncan, 1982; Berger, 1986; Linklater et al., 1999). New members in a group get involved in increased aggression while dominance relationships are asserted among them (Richards, 1974; Addison and Baker, 1982; Arnold and Grassia, 1982; Linklater et al., 1999). Nevertheless, once these relationships are established, a dominant animal usually needs only to approach or threaten a subordinate to gain access to a resource (Houpt, 1979). Therefore, the reduction of aggression and the stability of dominance relationships depend largely on submissive and avoidance behaviours of subordinates (Kaufmann, 1983).

Nevertheless, in certain conditions, benefits of aggression may outweigh the costs. Models of evolutionary stable strategies (ESS) predict that, when competing for a resource, animals should take into account the value of the disputed resource, injury costs and the probability of winning (Matsumura and Kobayashi, 1998). Intensity of aggression should be greater and dominance relationships should be more unstable when the resource is of great value relative to the cost of aggression and probability of winning a fight is high (Matsumura and Kobayashi, 1998). When fighting costs outweigh potential benefits, ESS theory predicts that contests are settled without intense aggression, on the basis of any detectable difference between

* Corresponding author. Tel.: +351 217524311; fax: +351 217500028.
E-mail address: lmvicente@fc.ul.pt (L. Vicente).

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individuals, even if the difference is uncorrelated with the benefits/costs of aggression or fighting ability (Maynard Smith and Parker, 1976; Matsumura and Kobayashi, 1998). In such conditions, contests over dominance status are rare and dominance relationships remain stable.

In feral and domestic horse groups, dominance relationships are usually transitive, forming linear or near-linear hierarchies which are relatively stable over time (e.g. Tyler, 1972; Wells and von Goldschmidt-Rothschild, 1979; Rutberg and Greenberg, 1990; van Dierendonck et al., 1995; Sigurjónsdóttir et al., 2003). Dominance rank may depend on a horse's age (e.g. Clutton-Brock et al., 1976; Wells and von Goldschmidt-Rothschild, 1979; Rutberg and Greenberg, 1990; van Dierendonck et al., 1995; Sigurjónsdóttir et al., 2003), height, weight (e.g. Houpt et al., 1978; Rutberg and Greenberg, 1990), aggressiveness (e.g. Houpt et al., 1978; Arnold and Grassia, 1982; Weeks et al., 2000), physical condition, social experience (Waring, 1983), maternal rank (van Dierendonck et al., 1995; Weeks et al., 2000) and length of residency in the herd (Boyd and Houpt, 1994; van Dierendonck et al., 1995).

If dominance rank would remain stable, advantages associated with high rank could increase a female's reproductive success (Côté, 2000). High-ranking mares may be preferred mating partners (Asa et al., 1979) and benefit from low aggression directed to them and their offspring (Rutberg and Greenberg, 1990; Boyd and Houpt, 1994; Weeks et al., 2000). High-ranking mares may also benefit from higher quality diets and produce faster growing offspring which breed earlier in some circumstances (Duncan, 1992).

Benefits associated with high rank could pay subordinates to contest particular dominance relationships where chances of reversal are highest. Close-ranking individuals are expected to be more similar regarding the value of resources relative to costs or other rank-related characters (Johnson, 1989). Hence, one would expect that subordinates contest relationships most often with close-ranking dominants and dominants reassert their status most frequently with close-ranking subordinates. This would cause higher aggressiveness, lower submissiveness and lower asymmetry of agonistic interactions among close-ranking animals. Higher frequencies of agonistic-related interactions among close-ranking individuals have been reported in goats (Côté, 2000) and primates (e.g. Johnson, 1989; de Waal, 1991). Nevertheless, a relation between aggressiveness and rank difference does not imply perception of rank, which is unlikely in non-primates (Appleby, 1993).

In this study, we investigate the correlates of dominance rank and the functions of aggression in a Sorraia horse group kept under extensive management. We asked the following specific questions: (1) Are age, weight and aggressiveness related to mare dominance rank? (2) Does introduction of a stallion increase aggressiveness and affect dominance relationships among mares? (3) Are higher-ranking mares more capable of eliciting submission from their subordinates than lower-ranking mares? (4) Is aggressiveness higher among close-ranking mares or among mares with less clear dominance relationships? (5) Is mare rank related to time-budgets and contexts of aggression?

2. Materials and methods

2.1. Subjects and study site

The Sorraia horse is a Portuguese native breed considered to be in critical risk status of extinction by the Food and Agriculture Organization (Galal and Hammond, 1996). The study herd was kept at Alter studfarm (39°11′N, 7°39′W), Portugal, on two 5.5- and 17.2-ha enclosed pastures surrounded by 1.5-m high wire fences and walls. Horses fed on grasses throughout the year and supplementary feed was given only in summer. Water was available from temporary water lines, watering-ponds and water canals connected to reservoirs.

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. A stallion is released and kept in the mare group for pasture breeding from February to June every year. Foals are weaned and removed from the group at approximately 6 months of age and 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 placed with them for breeding for the first time (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 for 386 h between 07:30 and 16:30 h solar time, from 5 December 2000 to 7 June 2001. 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 could be individually recognized by identification numbers on collars, differences in body size, morphology and coat colour. Series of 30- or 25-min sample periods were randomly assigned to each individual without rep-

Table 1
Data on individual characteristics of subjects

Name	Label	Sex	Age (years)	Weight rank	Close relatives via the mother
Afogado	Ag	M	9	6	
Barroca	Ba	F	18	8	
Derreta	De	F	16	5	Hora[a], Mubia[b]
Hera	He	F	12	4	
Hora	Ho	F	12	3	Derreta[a], Mubia[c]
Ibaga	Ib	F	11	11	Pimba[b]
Ibeta	It	F	11	9	Jabeta[a]
Jabeta	Jb	F	10	10	Ibeta[a]
Lomba	Lb	F	9	7	
Mubia	Mb	F	8	1.5	Derreta[d], Hora[e]
Pimba	Pb	F	5	1.5	Ibaga[d]

Sex: M, male; F, female; Age: reporting to June 2001; weight rank: highest score means highest weight.
[a] Full-sister.
[b] Daughter.
[c] Niece.
[d] Mother.
[e] Aunt.

Table 2
Description of agonistic-related interactions

Agonistic-related interaction	Description
Non-aggressive	
Displacement	Ears pointing forward or laterally and moving to within two body-lengths of another animal that immediately moves away
Aggressive or agonistic	
Mild threat	Ears laid back and looking or walking towards another horse
Bite threat	Ears laid back and at least one of the following: (1) extension of head and neck towards another horse, (2) fast movement towards another horse for no more than three body-lengths
Bite	Ears laid back, head raised, open mouth and extension of head and neck towards another horse, attempting to close teeth on its body
Kick threat	Ears laid back and at least one of the following: (1) backward movement, (2) hindquarters turn, (3) hindlimb raising, (4) hindlimb projection backwards while moving away
Kick	Ears laid back and projection of one or both hindlimbs towards another horse, attempting to strike it
Chase	Ears laid back, head raised, closed mouth and pursuing another animal for more than a three body-lengths distance
Attack	Ears laid back, head raised, open mouth and pursuing another animal for more than a three body-lengths distance, attempting to close teeth on its body
Herding	Ears laid back, head lowered and fast movement towards another animal, sometimes swinging head sideways and closing teeth on its body

etition on a given day. Total sampling time was on average 80.4 h per mare (range 74.9–88.1) and 54.5 h for the stallion.

Focal sampling (Altmann, 1974) was used to note data on social interactions: behaviour category, identities and activities of both the initiator and receiver(s), reaction of the receiver(s) and context. Whenever one or two individuals were close enough to the assigned focal animal at the beginning of its sample period so that all their interactions could be seen (usually within five body-lengths), they were also observed as focal animals. If during sampling they moved apart, the previously assigned focal animal was followed.

We recorded agonistic-related interactions (Table 2), sexual behaviours and four categories of non-sexual affiliative interactions: approach (across a two body-lengths distance), following, mutual grooming and friendly contacts (body contacts made with ears forward or laterally positioned). Reactions to social interactions were grouped in categories: avoid/withdraw (receiver turns head or moves away from the initiator), reply (receiver interacts with the initiator) or ignore (receiver does not turn head, move away or interact with the initiator). Contexts were grouped in the following categories:

(1) *Proximity*. The receiver had just reduced the distance to the initiator of the interaction or its foal. Includes subcategories 'non-sexual proximity' (distance reduction to the initiator, excluding courting behaviours), 'sexual proximity' (courting behaviours) and 'foal proximity' (distance reduction only to the initiator's foal).
(2) *Response*. The receiver had just sent an interaction other than an approach or following to the initiator. Includes subcategories 'response to affiliative interaction', 'response to agonistic interaction' and 'response to sexual interaction'.
(3) *Interference*. The receiver was involved in an interaction with a third individual at the time of the interaction. Includes subcategories 'affiliative interference', 'agonistic interference' and 'sexual interference' according to the nature of the interaction that receives interference.
(4) *Space*. The receiver had not reduced its distance to the initiator and was not involved in other interactions. Includes subcategories 'space after agonistic interaction' (initiator had just received an agonistic-related interaction from an individual other than the receiver) and 'space acquisition' (all other situations).

Simultaneous with focal samples, we took instantaneous samples (Altmann, 1974) at 5-min intervals to note the activity of the focal animal and the identities of all individuals within five body-lengths of it. Activities were recorded as feeding (ingesting plant material), inactive (standing or lying), locomotion (walking with head raised, trotting or galloping) or other (every behaviour not included in the previous categories).

2.3. Data analysis

2.3.1. Analysis of dominance

Firstly, among the types of agonistic-related interactions observed, we selected those that had a significant asymmetric distribution across dyads and therefore seemed adequate to assess dominance relationships. The K_r matrix correlation test was used to measure asymmetry, which was defined as a significant negative association between emission and receipt matrices (Hemelrijk, 1990). Herding, chases, attacks and kicks were excluded because their frequencies were too low to test for asymmetry. Displacements and the remaining aggressive behaviours, except kick threats, showed significant asymmetry (displacements: $K_r = -116$, $n = 10$, $P_l < 0.05$; mild threats: $K_r = -99$, $n = 10$, $P_l < 0.05$; bite threats: $K_r = -125$, $n = 10$, $P_l < 0.05$; bites: $K_r = -37$, $n = 10$, $P_l < 0.05$, left tail probability).

Secondly, we constructed a matrix for each of these four behaviour categories including only those interactions that elicited a submissive response ('withdraw/avoid' reaction). Paired matrix correlation K_r tests revealed that their distribution patterns were significantly similar and thus the four matrices were merged into one (Table 3). This matrix was converted into

Table 3
Total number of displacements, mild threats, bite threats and bites that caused withdrawal or avoidance reactions

Initiator	Receiver										
	De	Ho	He	It	Jb	Ba	Ib	Lb	Mb	Ag	Pb	Total
De	–	19	21	23	24	15	27	27	32	51	42	281
Ho	0	–	12	14	24	22	28	40	25	12	35	212
He	0	0	–	26	19	8	29	23	31	5	22	163
It	0	0	0	–	3	13	10	11	14	1	10	62
Jb	0	1	0	0	–	54	3	59	66	22	78	283
Ba	0	0	0	0	0	–	64	53	49	12	41	219
Ib	0	0	0	0	29	0	–	56	34	14	43	176
Lb	0	1	0	0	1	1	0	–	42	23	49	117
Mb	0	0	0	0	0	0	0	0	–	99	78	177
Ag	0	0	0	2	4	3	2	6	2	–	7	26
Pb	0	0	0	0	0	0	1	0	1	6	–	8
Total	0	21	33	65	104	116	164	275	296	245	405	1724

Individuals are disposed in descending order of dominance rank from left to right in column labels and top to bottom in row labels.

a binary matrix of dominance relationships in which row individuals dominant over column individuals are assigned 1 and otherwise 0. In each dyad, an individual was considered to be dominant over the other if it had initiated the majority of interactions.

Linearity of dominance relationships was significant, as assessed by the Kendall's coefficient of consistence K, based on the number of circular triads d (Appleby, 1983a; de Vries, 1995). Hence, the horses were ordered in a linear hierarchy by the 'I and SI' method (de Vries, 1998), which finds a ranking of individuals by first minimizing the number of inconsistencies (an individual A dominant to B is ranked below B in the hierarchy) and then the strength of the inconsistencies (absolute difference between the ranks of two individuals involved in an inconsistency). Three rankings with equal number and strength of inconsistencies were obtained and the one with the smallest number of interactions given up the hierarchy was chosen. Individuals were then assigned an ordinal rank increasing from the bottom to the top of the hierarchy.

2.3.2. Factors related to dominance rank

Associations between dominance rank and age, weight rank, aggressiveness and ability to elicit submission from subordinates were assessed by the Spearman's rank correlation coefficient. Weight rank was assigned on the basis of photographs together with weight estimates from thoracic perimeter measures (Oom and Costa-Ferreira, 1987): W (weight) = TP (thoracic perimeter)$^3 \times 80$. Aggressiveness was measured as the mean number of agonistic interactions given or received from each individual per hour (total aggressiveness), mean number of agonistic interactions given to each subordinate per hour (aggressiveness towards subordinates) and intensity of agonistic interactions (proportion of bites, kicks, chases and attacks). The ability to elicit submission was assessed by the proportion of displacements within agonistic-related interactions and the proportion of agonistic interactions ignored or replied by subordinates.

The Wilcoxon paired-sample test was used to test for an increase in frequencies of agonistic interactions directed to mare subordinates after introduction of the stallion and to test for higher frequencies of agonistic interactions towards the stallion than towards mare subordinates.

2.3.3. Rank distance, clearness of dominance relationships and aggressiveness

We considered that dominance relationships were less clear in dyads with greater proportion of agonistic interactions ignored or replied, lower asymmetry or lower proportion of displacements relative to agonistic-related interactions. The proportion of displacements was used to measure both the probability of submitting to dominants (see section above) and how clear dominance relationships were, because moving away from an approaching animal is a passive acknowledgement of its dominance (van Dierendonck et al., 1995; de Vries, 1998). The following measure of asymmetry was used for each dyad A–B (van Dierendonck et al., 1995): $|f_{AB} - f_{BA}|/(f_{AB} + f_{BA})$ where f_{AB} is the number of interactions given from A to B and f_{BA} is the reverse. Aggressiveness was measured as the absolute frequency, relative frequency (relative to time spent within five body-lengths) and intensity of agonistic interactions that each dyad was involved in. We constructed matrices of absolute rank difference, aggressiveness and clearness of dominance relationships (proportions were converted into whole numbers) and used the K_r matrix correlation test (Hemelrijk, 1990) to assess correlations between them.

2.3.4. Activities and contexts of agonistic interactions

Spearman's rank correlation coefficient was used to test for a relationship between mare rank and proportion of time spent in each activity. The proportions of agonistic-related interactions that occurred in 'space' and 'non-sexual proximity' contexts during each activity were compared to the proportion of time spent in that activity by means of the Wilcoxon paired-sample test. A chi-square test of independence using a simulation procedure (Estabrook et al., 2002) was performed to test for differences in the context of agonistic interactions initiated by low-ranking (ranks 1–3), middle-ranking (ranks 4–7) and high-ranking (ranks 8–10) mares.

Standard statistical tests were performed on Statistica 5.1 ©StatSoft, Inc. and were two-tailed unless otherwise stated. Matrix correlation tests were run on Matsquar and MatrixTester v2.2.3b ©by Hemelrijk and were one-tailed (right tail probabilities, P_r, or left tail probabilities, P_l, are reported). Chi-square tests of independence using simulations were performed on ACTUS2 ©by Estabrook and Estabrook. The cut-off for significance was set at 0.05 but some trends were considered at an alpha level of 0.1.

3. Results

3.1. Analysis of dominance

Agonistic interactions were given at low frequencies: $1.189 \pm 0.657\,h^{-1}$ per individual (0.112 ± 0.067 per partner) among adults and $0.810 \pm 0.519\,h^{-1}$ per individual (0.09 ± 0.058 per partner) among mares (mean ± S.D.). The greatest percentage of the 2000 agonistic-related interactions among adult horses (herding excluded) consisted of low-intensity behaviours: displacements (32.7%), mild threats (34.2%) and bite threats (26.4%) were the most frequent, followed by bites (2.9%), kick threats (2.8%), kicks (0.6%), chases (0.35%) and attacks (0.15%). Most agonistic interactions caused a submissive response from the receiver: 84.8% elicited an avoid/withdraw reaction, 14.9% were ignored, 0.08% were replied with an agonistic interaction and 0.23% were replied with an affiliative interaction.

Among mares, only 18 out of 975 (1.9%) observed agonistic interactions were given to dominants and asymmetry was high (0.952 ± 0.125, where 1 means complete asymmetry). Linearity was significant in both the mare hierarchy (Kendall's coefficient of consistence: $K = 0.975$, $d = 1$, $n = 10$, $P < 0.05$, probability obtained from Appleby, 1983a, Table 1, p. 603) and the complete adult hierarchy (Kendall's coefficient of consistence: $K = 0.891$, $d = 6$, $\chi^2 = 61.06$, d.f. = 20, $n = 11$, $P < 0.05$).

3.2. Factors related to dominance rank

There was a significant positive correlation between mare dominance rank and age ($r_s = 0.774$, $n = 10$, $P < 0.05$) but not between dominance rank and weight rank ($r_s = 0.170$, $n = 10$, $P > 0.05$). Higher-ranking mares tended to give higher total aggressiveness than lower-ranking ones ($r_s = 0.636$, $n = 10$, $P < 0.1$). Aggressiveness towards subordinates ($r_s = -0.583$, $n = 9$, $P > 0.05$) and intensity of given agonistic interactions ($r_s = -0.367$, $n = 9$, $P > 0.05$) were not related to dominance rank. Higher-ranking mares received lower frequency and intensity of agonistic interactions (frequency: $r_s = -0.952$, $n = 10$, $P < 0.001$; intensity: $r_s = -0.890$, $n = 10$, $P < 0.005$).

The stallion was the second lowest ranking individual. Mares' dominance rank did not change and aggressiveness towards subordinates did not increase significantly after he entered the group (Wilcoxon paired-sample test: $T = 20$, $n = 9$, $P > 0.05$; one-tailed). Aggressiveness directed to the stallion tended to be greater than aggressiveness towards female subordinates during the first month after his arrival and over the whole study (Wilcoxon paired-sample test: $T = 9$, $n = 9$, $P < 0.1$; one-tailed).

The proportion of displacements within agonistic-related interactions directed by higher-ranking mares to subordinates was not greater than that directed by lower-ranking ones ($r_s = -0.033$, $n = 9$, $P > 0.05$; one-tailed). Contrary to our expectations, low-intensity agonistic interactions directed by higher-ranking mares were more often ignored or replied by their subordinates than agonistic interactions directed by lower-ranking mares ($r_s = 0.717$, $n = 9$, $P < 0.05$; one-tailed). High-intensity agonistic interactions were seldom ignored (5.6%) and never replied by subordinates, whether initiated by higher-ranking or lower-ranking dominants.

3.3. Rank distance, clearness of dominance relationships and aggressiveness

Both the proportion of interactions ignored or replied ($K_r = 33$, $n = 10$, $P_r > 0.05$) and asymmetry ($K_r = 12$, $n = 10$, $P_r > 0.05$) were not significantly correlated with rank difference. Contrary to our predictions, the proportion of displacements within agonistic-related interactions tended to be higher among close-ranking mares ($K_r = -63$, $n = 10$, $P_l < 0.1$). Therefore, dominance relationships were not less clear among close-ranking mares.

Absolute frequency of agonistic interactions was not correlated with rank difference ($K_r = 31$, $n = 10$, $P_r > 0.05$). Contrary to our expectations, relative frequency and intensity of agonistic interactions tended to be higher among distant-ranking mares (relative frequency: $K_r = 59$, $n = 10$, $P_r < 0.1$; intensity: $K_r = 58$, $n = 10$, $P_r < 0.1$). Frequencies of agonistic interactions, but not their intensity, were higher among mares that were involved in lower proportions of displacements (absolute frequency: $K_r = -63$, $n = 10$, $P_l < 0.1$; relative frequency: $K_r = -82$, $n = 10$, $P_l < 0.05$; intensity: $K_r = 17$, $n = 10$, $P_r > 0.05$). However, neither the asymmetry of agonistic interactions (absolute frequency: $K_r = -32$, $n = 10$, $P_l > 0.05$; relative frequency: $K_r = -18$, $n = 10$, $P_l > 0.05$; intensity: $K_r = -3$, $n = 10$, $P_l > 0.05$) nor the proportion of interactions ignored or replied (absolute frequency: $K_r = -10$, $n = 10$, $P_l > 0.05$; relative frequency: $K_r = -1$, $n = 10$, $P_l > 0.05$; intensity: $K_r = 38$, $n = 10$, $P_r > 0.05$) were correlated with aggressiveness.

3.4. Activities and contexts of agonistic interactions

Adult horses spent on average $60.4 \pm 10.3\%$ of the time feeding, $35.3 \pm 8.7\%$ inactive, $1.9 \pm 1.4\%$ in locomotion and $2.1 \pm 1.2\%$ performing other activities, mostly grooming on objects or tree trunks (mean ± S.D.). The proportion of time spent in each activity was not correlated with mare rank (feeding: $r_s = -0.127$; inactivity: $r_s = 0.127$; locomotion: $r_s = -0.018$; other: $r_s = 0.127$; $n = 10$, $P > 0.05$). Horses were not involved in agonistic interactions more often than expected during feeding or inactivity but agonistic interactions occurred during locomotion more often than chance (Table 4). Displacements were also given during locomotion and other activities more often than expected (Table 4).

Table 4
Differences between the proportions of displacements ($n = 10$) and agonistic interactions ($n = 11$) given and received during each activity and their expected proportions, as assessed by the Wilcoxon paired-sample test

Activity	Displacements given		Agonistic interactions given		Displacements received		Agonistic interactions received	
	T	P	T	P	T	P	T	P
Feeding	27	>0.05	31	>0.05	24	>0.05	15	>0.05
Inactivity	15	>0.05	18	>0.05	27	>0.05	19	>0.05
Locomotion	5	0.02	3	0.005	18	>0.05	2	<0.005
Other	3	0.01	21	>0.05	13	>0.05	27	>0.05

Table 5
Percentage of agonistic interactions initiated in each context subcategory

Context	Percentage of agonistic interactions (mean ± S.D.)
Space acquisition	65.91 ± 8.61
Space after agonistic interaction	4.26 ± 3.32
Affiliative interference	1.73 ± 2.92
Agonistic interference	0.26 ± 0.46
Sexual interference	2.00 ± 2.47
Non-sexual and foal proximity	16.31 ± 5.89
Sexual proximity	2.39 ± 2.65
Response to affiliative interaction	3.49 ± 5.20
Response to agonistic interaction	0.73 ± 1.42
Response to sexual interaction	2.92 ± 2.93

The greatest percentage of agonistic interactions occurred in space (70%) or proximity contexts (19%) (Table 5). Only six agonistic interactions were directed as a response to agonistic interactions received. Interferences in affiliative or agonistic interactions involving other horses were rare. Mares were observed aggressing the stallion and/or another mare when they were involved in sexual behaviours (‘sexual interference’), causing their interruption.

Contexts of agonistic interactions directed by mares were associated with their rank ($\chi^2 = 85.42$, $P < 0.05$, based on 10 000 simulations). High-ranking mares initiated aggression more frequently than expected for ‘proximity’ contexts and less frequently for ‘affiliative interference’, ‘sexual interference’ and ‘space after agonistic interaction’. Middle-ranking mares interacted less frequently than expected for ‘proximity’ contexts. Low-ranking mares initiated aggression more frequently than expected for ‘affiliative interference’ and ‘space after agonistic interaction’ and less frequently than chance for ‘space acquisition’.

4. Discussion

In this herd, the dominance hierarchy was significantly linear. Rank was positively correlated with age, but the oldest mare did not occupy a high position in the hierarchy. These findings are in accordance with the reports of several authors (e.g. Wells and von Goldschmidt-Rothschild, 1979; Rutberg and Greenberg, 1990; van Dierendonck et al., 1995; Sigurjónsdóttir et al., 2003). Older mares may have greater fighting ability due to increased experience or have more to gain in contests over resources than younger females. As mares get older, the value of resources relative to costs of aggression is expected to increase, because fertility increases until 12–14 years of age (Matos, 1996) and costs in terms of future reproductive success decrease (Rutberg, 1986). Alternatively, age could be a conventional criterion that is used to settle disputes: animals would learn to submit to older group members early in life, when differences in body size and social experience are greatest, and thereafter dominance relationships would be maintained by individual recognition (Rutberg, 1986). Length of residency in the group was related to mare age and may explain the influence of age on rank as well.

Length of residency has been reported to affect rank by other authors (Boyd and Houpt, 1994; van Dierendonck et al., 1995) and may also account for the stallion’s low position in the hierarchy. In some horse groups, an adult stallion was the highest ranking individual (e.g. Feist and McCullough, 1976; Waring, 1983), but not in others (Houpt et al., 1978; Wells and von Goldschmidt-Rothschild, 1979; Houpt and Keiper, 1982; Keiper and Sambraus, 1986). In this study, aggressiveness towards the stallion, the new member in the group, tended to be higher than towards mares. Increased aggressiveness towards new members has also been observed by other authors (e.g. Addison and Baker, 1982; Arnold and Grassia, 1982; Linklater et al., 1999).

Dominance relationships were very clear and seldom contested, even among close-ranking mares. This was apparent from the low proportion of agonistic interactions directed to dominants, asymmetry of agonistic interactions, predominance of withdrawal or avoidance reactions and high proportion of displacements, which are in accordance with the findings from other studies (e.g. Clutton-Brock et al., 1976; Houpt and Keiper, 1982; Keiper and Sambraus, 1986). Aggressiveness was low but the frequencies of agonistic interactions per horse (1.189 among adults and 0.81 among mares) were higher than those reported in feral horses (Houpt and Keiper, 1982: 0.15–0.24; Sigurjónsdóttir et al., 2003: 0.135). Neither close-ranking mares nor mares with less clear dominance relationships showed higher aggressiveness towards each other. Contrary to our expectations, relative frequency and intensity of agonistic interactions tended to be higher among distant-ranking than close-ranking mares. Tyler (1972) and Arnold and Grassia (1982) reported that the frequency of aggressive acts was higher towards close-ranking subordinates. Clutton-Brock et al. (1976) and Waring (1983) found no correlation between aggressiveness and rank distance. In a group of red deer stags, frequency of agonistic interactions was not related to rank distance and their intensity was lower among close-ranking animals (Appleby, 1983b). Moreover, neither aggressiveness nor dominance relationships among mares changed after the stallion's arrival. The fact that such stable and clear dominance relationships existed even among close-ranking mares, with likely similar benefits and costs of aggression, lends further support to the possibility that age is a conventional criterion. If all individuals were to recognize the conventional rule of submitting to older animals, it would not pay subordinates to contest dominance relationships, whether with close- or distant-ranking dominants (Matsumura and Kobayashi, 1998).

Contrary to our predictions, agonistic interactions from higher-ranking dominants were more often ignored by their subordinates than those from lower-ranking dominants. High-ranking mares often threatened immediately after being approached by subordinates (context 'proximity'), when the latter had just gained access to a resource. Mares may find more valuable a resource they had just begun to use (e.g. a food patch) and be less willing to move away and leave it. Weeks et al. (2000) found no correlation between mare rank and aggression ignored.

In accordance with earlier findings from other authors (e.g. Clutton-Brock et al., 1976; Houpt et al., 1978; Weeks et al., 2000), higher-ranking mares tended to exhibit higher total aggressiveness and received lower frequency and intensity of aggression in this study. These findings suggest that higher-ranking mares incur lower costs related to received aggression (e.g. injury), but suffer higher costs of giving agonistic interactions than lower-ranking mares. However, mare rank was not related to aggressiveness towards subordinates, as other studies referred as well (Clutton-Brock et al., 1976; Weeks et al., 2000).

One cost of high rank associated with giving aggression may be higher levels of stress hormones that inhibit reproduction (Creel et al., 1996). The analysis of activities and contexts of agonistic-related interactions provided further insight into the functions of aggression and its possible benefits and costs in horses. Agonistic-related interactions were used primarily in regulation of space and maintenance of individual distances during daily activities, especially locomotion. During movements to other parts of the pasture, horses travelled in single files in close proximity and invaded each other's space. Invasion of a horse's personal space (1–2 m) is a common cause of aggression (Tyler, 1972; Houpt and Keiper, 1982; Waring, 1983; Keiper and Sambraus, 1986). In this group, sometimes horses threatened subordinates after being aggressed by dominants to try to obtain space to move away from the latter, as Tyler (1972) has also observed.

Because 'space' is a broad context, its meaning is best interpreted together with the data on horses' activities. Time-budgets in this herd were similar to those reported for other horses (Duncan, 1980; Rutberg and Greenberg, 1990; Boyd and Houpt, 1994). The frequency of agonistic-related interactions over food was proportional to the time spent feeding and the latter was not related to mare rank. Displacements occurred more often than chance for access to more defendable resources, such as tree trunks or branches for grooming. These results seem to support the view that food-related aggression is not generally important in grazers that feed on widely dispersed and undefendable resources (Rutberg and Greenberg, 1990). Aggression over access to food is probably more important to horses receiving supplemental feed (Clutton-Brock et al., 1976; Houpt, 1979; Weeks et al., 2000). Rutberg and Greenberg (1990) reported increased aggression at water holes but little food-related aggression in feral ponies, and even in poor foraging conditions horses may not increase frequencies of agonistic interactions for access to food (Berger, 1986). Food access was not related to rank in other ungulate species as well (bighorn sheep: Eccles and Shackleton, 1986; mountain goats: Fournier and Festa-Bianchet, 1995). Despite this, agonistic-related interactions received during feeding may decrease feeding efficiency of lower-ranking animals (Appleby, 1980; Barrette and Vandal, 1986; Rutberg, 1986).

The finding that horses interfered with interactions of others suggests that relationships between third parties had some interest to them, particularly sexual interactions. Interference in sexual behaviours was the most frequent form of interference and has also been observed in feral horses (e.g. Tyler, 1972; Waring, 1983; Berger, 1986) and Przewalski horses (Kolter and Zimmermann, 1988). Interferences in affiliative interactions have been described by Kolter and Zimmermann (1988) and Sigurjónsdóttir et al. (2003) and were mostly performed by low-ranking mares in this study. Interventions in aggression of group members occurred seldom in this herd and are also uncommon in feral horses (Berger, 1986).

Overall, our findings suggest that the costs of aggression outweigh the benefits in this herd of horses, and therefore clear dominance relationships were established to reduce aggression to a minimum. However, this study was conducted during a time when food availability was sufficient to meet the horses' needs and seasonal variations should be considered. During summer, supplemental feed, water, shade and proximity to partners for mutually fending off flies become more valuable and defendable resources, which may cause increased aggressiveness.

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