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ARTICLE

Dominance relationships and patterns of aggression in a bachelor group of Sorraia horses (*Equus caballus*)

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Abstract The influence of individual factors on dominance rank and the relationship between rank distance and patterns of aggression predicted by models of evolutionarily stable strategies (ESS) of animal conflict were investigated in a managed bachelor group of Sorraia horses, *Equus caballus*. The group was composed of four to six stallions 3- to 12-years-old during the study period. The dominance hierarchy was significantly linear and rank was not related to age, weight, height or aggressiveness. Frequency and intensity of agonistic interactions were low, but higher-ranking stallions did not receive lower aggressiveness than lower-ranking stallions. There was some evidence that dominance relationships were more contested among close-ranking stallions, as predicted. Agonistic-related interactions among close-ranking stallions served similar functions to those among distant-ranking stallions, but the latter interacted more frequently than expected for access to resting sites and/or resting partners. Therefore, we found some evidence that agonistic-related interactions among distant-ranking stallions play a larger role in providing access to valuable and defendable resources than those among close-ranking stallions. Nevertheless, the fact that space to escape from aggression was limited and breeding access was independent from dominance rank may have reduced the benefits relative to costs of aggression and therefore limited the occurrence of contests over dominance and resources.

Keywords Horse · *Equus* · Dominance relationship · Rank · Agonistic interaction

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Introduction

Dominance relationships and hierarchies reduce aggression between group-living animals by resolving conflicts of interest over access to resources in a ritualized way (Richards 1974; Kaufmann 1983; Van Doorn et al. 2003a). Once dominance relationships are established, these are maintained largely by submissive behaviours of subordinates (Kaufmann 1983). However, clearness and stability of dominance relationships may differ between pairs of individuals within the same social group (Matsumura and Kobayashi 1998). According to models of evolutionarily stable strategies (ESS) for animal conflict, intensity of aggression and stability of dominance relationships depend on the benefits of obtaining the contested resource relative to the costs of aggression, asymmetries in fighting ability (i.e. resource holding potential) and arbitrary asymmetries (Maynard Smith and Parker 1976; Matsumura and Kobayashi 1998; Van Doorn et al. 2003a, b). These models predict that dominance relationships should be more unstable and aggressiveness should be higher when the benefits of obtaining a resource are high relative to the costs of aggression, and the probability of winning a contest (i.e. difference in fighting ability) is high (Maynard Smith and Parker 1976; Matsumura and Kobayashi 1998). In contrast, when costs of aggression outweigh potential benefits, dominance relationships should be stable and contests should be rare and settled without intense aggression, on the basis of any asymmetry between individuals (Maynard Smith and Parker 1976; Matsumura and Kobayashi 1998).

Feral and domestic horses develop linear or near-linear dominance hierarchies based primarily on age in bands (e.g. Tyler 1972; Wells and von Goldschmidt-Rothschild 1979; Van Dierendonck et al. 1995) and bachelor groups (Feist and McCullough 1976; Feh 1988). The band is the breeding unit, which consists of a stable association of mares, their offspring and one or more unrelated stallions that defend and maintain the mare group and their mating opportunities from other males, as is typical of female defence polygyny, year round (Klingel 1975; Feist and McCullough 1976; Salter and Hudson 1982; Berger 1986; Linklater et al. 1999). Young males and females disperse from natal bands around 2- to 3-years old, upon reaching sexual maturity (Klingel 1975; Salter and Hudson 1982; Berger 1986; Khalil and Kaseda 1997; Kaseda et al. 1997). Females usually join other bands directly, but males integrate bachelor groups for a few years where they have the opportunity to develop social skills and practice the role-specific behavioural patterns that are necessary to form, maintain and successfully defend a band (Hoffmann 1985; Boyd and Houpt 1994; McDonnell and Haviland 1995; Khalil and Kaseda 1998). Bachelor groups are more unstable than bands and may include 2–15 or more young males that separated from the natal band, and/or older males that have lost their band (Feist and McCullough 1976; McDonnell and Haviland 1995; Khalil and Kaseda 1998).

Not all bachelor males become band stallions (Salter and Hudson 1982), which is the reproductive strategy that provides greatest male reproductive success (Asa 1999). Higher-ranking bachelors are usually the first to acquire mares (Feist and McCullough 1976) and transition of a bachelor stallion to a band involves little aggression among bachelors (McDonnell and Murray 1995). Moreover, higher-ranking stallions could potentially benefit from lower aggressiveness received, such as reported for higher-ranking mares (Rutberg and Greenberg 1990; Heitor et al. 2006).

Benefits afforded by high rank could outweigh the costs of aggression and cause subordinates to contest dominance relationships and try to reverse them. Agonistic-related interactions may serve two concurrent functions: to obtain access to resources and to assert or contest dominance relationships (Johnson 1989). Assuming that agonistic-related interactions impose some cost on both participants, contests over dominance should be aimed preferentially at group members with whom dominance relationships are more likely to be reversed. Close-ranking animals are expected to have potentially less stable relationships due to their more evenly matched benefits relative to costs of aggression, fighting ability or other rank-related factors (Johnson 1989). Subordinates may then be predicted to contest relationships most often with close-ranking dominants and dominants are expected to reassert their dominance status most frequently with close-ranking subordinates. As a result, close-ranking animals are predicted to have less clear dominance relationships and display higher aggressiveness towards each other than distant-ranking animals. The higher aggressiveness that has been reported among close-ranking horses is consistent with these predictions (e.g. Arnold and Grassia 1982; Houpt and Keiper 1982; Boyd 1991).

Subordinates will likely lose contests with distant-ranking dominants due to the large disparity in fighting ability relative to the dominant. Contests over resources among distant-ranking animals are then predicted to occur when the benefits of obtaining the resource are high relative to the costs of aggression. Therefore, agonistic-related interactions among close-ranking animals are predicted to be more frequent and intense, serving mainly to assert dominance, whereas agonistic-related interactions among distant-ranking animals are predicted to be less frequent and intense, involving mostly valuable and defendable resources (Kitchen et al. 2005).

The present study examines the influence of individual factors on dominance rank, and tests the predictions of ESS models regarding dominance relationships and patterns of aggression in the sole existing bachelor group of Sorraia horses. The Sorraia horse is a Portuguese autochthonous breed that is believed to be a direct descendant of the primitive South Iberian horse (Luís 2006). This horse breed presents high inbreeding levels (Luís 2006) and is considered to be at critical-maintained risk status by FAO due to its effective number of less than 200 individuals with less than 100 brood mares (Scherf 2000). The studied Sorraia bachelor group is managed and therefore differs from feral bachelor groups in several ways. The group includes only adult stallions and no juveniles, horses do not choose group members and are kept within an enclosed pasture, which limits space available to escape from other males if necessary. Moreover, a few males are removed each breeding season to be used in pasture breeding of Sorraia mare groups and then return to their bachelor condition at the end of the breeding season. Therefore, unlike feral bachelors, Sorraia stallions have breeding access to mares without having to fight for them and such access is independent from male social skills and dominance rank.

In this study, we investigate whether dominance rank among Sorraia stallions is related to factors that are relevant to fighting ability: age, weight, height and aggressiveness. Moreover, we test the following predictions, which can be drawn from ESS models of animal conflict and dominance: (1) higher-ranking stallions receive lower aggressiveness than lower-ranking stallions; (2) dominance relationships are more contested among close-ranking stallions; (3) agonistic-related interactions among close-ranking stallions play a larger role in asserting dominance relationships and a smaller role in providing access to valuable resources than agonistic-related interactions among distant-ranking stallions.

Materials and methods

Subjects and study site

The subjects were four to six stallions that compose the only existing Sorraia horse bachelor group (i.e. all-male group), which is privately owned at Fontalva Estate (Elvas, Portugal). The group consisted of a 3-year-old, three 4-year-olds, a 5-year-old and a 12-year-old male (Table 1). The oldest stallion (Ag) was the sire of all the other males. The 5-year-old (Sd) and one of the 4-year-old males (Tl) were full brothers. The horses were kept on a 15-ha pasture enclosed by wire fences, where they fed mainly on grass. Water was available from a watering-pond and from a trough during summer. Two domestic donkeys were pastured with the horses and a herd of wild calves was also kept on the pasture for short periods of time. Stallions had occasional visual and auditory access to a group of Sorraia mares, their offspring and a breeding stallion located in a non-adjacent pasture.

Two months before the beginning of this study, five stallions had been removed from the group to be sold. The oldest stallion (Ag) and one of the 4-year-old males (Tb) had also been removed to be used in pasture breeding, and returned to the group during the study period. The youngest stallion (Ut) had some breeding experience in the year before this study because he escaped one night and bred the mares that were kept in a nearby pasture. The other males had no breeding experience.

Data collection

A 1-month period of observation was performed prior to the beginning of systematic data collection to habituate the horses to the presence of an observer and to construct the ethogram. After this period, observations were conducted on foot between 0730 and 1730 hours solar time, from 11 March to 30 June 2004 and from 16 September to 29 October 2004. The observer kept a minimum 3-m distance to the horses and data were recorded on prepared sheets or dictated into a tape recorder. Data were collected for a total 141 h, of which 117.5 h consisted of focal sampling. Individual sampling times are presented in Table 1. Three observation periods can be distinguished according to the number of stallions present in the group. Horses were sampled on average 20.0 h per horse in the first observation period (four males), 6.1 h per horse in the second period (five males) and 5.0 h per horse in the third period (six males). Horses could be individually recognised by differences in body size, morphology and coat colour. Sample periods lasted 25 min and were performed in a sequence, by sampling each stallion at a time in random order until all males had been sampled, at least once per day. In addition, one sample period per sequence was conducted on all horses simultaneously, during the time when the group was composed of four males.

Data on social interactions were collected by focal sampling (Altmann 1974). We recorded agonistic-related interactions, which consisted of non-aggressive displacements, and aggressive interactions: mild threats, bite threats, bites, kick threats, kicks, chases (see Heitor et al. 2006 for a complete description), strike threats and arched neck threats (according to definitions by McDonnell and Haviland 1995). We also recorded other types of interactions, including approaches and leaves across one body-length, following, mutual grooming, friendly contacts (body contacts made with ears forward or laterally positioned), play fight and mounting. We noted the behaviour category, identities and activities of both the initiator and receiver(s), reaction of the receiver(s) and context of all social interactions. Reactions were grouped in categories: avoid/withdraw (receiver turns head or moves away from

Table 1 Data on individual characteristics of subjects

Name	Label	Birth date	Weight (Kg)	Height rank	Sampling time (h)
Afogado	Ag	18 March 1992	450	5	6.2
Sedutor	Sd	30 December 1998	380	1	31.5
Taralhoco	Ta	27 December 1999	447.5	6	29.5
Trombo	Tb	31 December 1999	450	3.5	11.6
Toleirão	Tl	12 January 2000	385	3.5	32.2
Untuoso	Ut	15 February 2001	400	2	30.3

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:

- Redirect: interaction is sent to an individual immediately after receiving an interaction from another individual.
- Response: the receiver had just sent an interaction to the initiator (affiliative or agonistic-related), moved closer (proximity) or moved away (separation). Only movements of the receiver within two body-lengths of the initiator are considered.
- Interference: the receiver was involved in an interaction with another individual.
- Space: the receiver had not reduced its distance to the initiator and was not involved in other interactions. Subcategories were defined according to the spatial position of the initiator:
  - Maintain space: initiator sends an interaction while maintaining position.
  - Obtain space: initiator sends interaction after changing position.
  - Replace: initiator sends an interaction and then occupies the previous position of the receiver.
  - Surpass: initiator sends an interaction and then occupies a different position from that of the receiver and from its own initial position.

In addition, instantaneous samples (Altmann 1974) were performed at 5-min intervals to note the identities of all individuals within five body-lengths of the focal animal and the activity of every horse in the group. Activities were recorded according to definitions by Boyd and Houpt (1994) as feeding, drinking, standing, standing resting, recumbent resting, locomotion, self grooming, investigation (includes elimination marking and non-interactive investigations), alert, interaction, or other (all behaviours not included in the previous categories).

Horses were weighed on a weighing-scale at the end of the period of field observations. Stallions were ranked according to relative height at the withers on the basis of photographs and visual assessment when two animals were separated by less than 0.5 m, throughout the period of field observations.

Data analysis

We determined dominance relationships among stallions over the whole study and within each of three periods when group composition changed due to the return of the two stallions that had been used for breeding. Dominance relationships were assessed by the distribution of agonistic-related interactions, excluding kicks and kick threats due to their defensive function. The stallion that initiated the majority of agonistic-related interactions that caused avoidance or withdrawal reaction within each dyad was considered to be the dominant. The directional consistency (DC) index of agonistic-related interactions that caused avoidance or withdrawal was computed as a descriptive measure. This index was expressed as the proportion of interactions that were given in their more frequent direction relative to the total number of interactions that occurred.

Linearity of dominance relationships was tested by means of Laudau's index of linearity h and Kendall's coefficient of consistence K, based on the number of circular triads d (Appleby 1983a; De Vries 1995). Linearity was significant (see Results) and therefore stallions were ordered in a dominance hierarchy. The 'I and SI' method (De Vries 1998) was used to rank individuals, by finding the ordering that minimises the number of inconsistencies (i.e. an individual A dominant to B is ranked below B in the hierarchy), and the strength of the inconsistencies (i.e. absolute difference between the ranks of two individuals involved in an inconsistency). Finally, stallions were assigned an ordinal rank that increases from the bottom to the top of the hierarchy.

Spearman's rank correlation coefficient tested the relationship between dominance rank, age, weight, height rank and aggressiveness. We computed aggressiveness as the mean frequency of agonistic interactions given or received from each individual (total aggressiveness), mean frequency of agonistic interactions given to each subordinate (aggressiveness towards subordinates) and intensity of agonistic interactions (proportion of bites, kicks and chases).

To test whether dominance relationships were more contested among close-ranking males, we analysed the correlations between rank distance, aggressiveness and clearness of dominance relationships by using the K_r matrix correlation test (Hemelrijk 1990). Rank distance was computed as the absolute difference of dominance rank between two individuals. Aggressiveness was measured as the absolute frequency (i.e. number of interactions per hour), relative frequency (i.e. absolute frequency divided by the proportion of time spent within five body-lengths) and intensity of agonistic interactions that each dyad was involved in. Relative frequency was computed to correct for the opportunity to interact, which is higher between horses that spend more time in proximity to each other. Dominance relationships were considered to be clearer in dyads with lower proportion of agonistic interactions ignored or replied, higher asymmetry of agonistic interactions or higher proportion of displacements within agonistic-related interactions. Asymmetry within each dyad A–B was computed as (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. Displacements were used to measure clearness of dominance relationships because moving away from an approaching animal is a passive acknowledgement of its dominance (Van Dierendonck et al. 1995; De Vries 1998).

Time budgets were computed as the mean percentage of time spent in each activity by the horses. We performed a Chi-square test of independence based on a simulation procedure (Estabrook et al. 2002) to compare the activities of initiators and contexts of agonistic-related interactions directed towards adjacent-ranking stallions (absolute rank distance = 1) with those directed to distant-ranking stallions (absolute rank distance >1). Chi-square goodness-of-fit was used to compare frequencies of agonistic-related interactions directed to adjacent-ranking and distant-ranking males during each activity with their expected values. Expected frequencies were computed separately for each stallion, based on individual time budget and number of interactions directed to adjacent-ranking or distant-ranking males, and then summed across all stallions.

Standard statistical tests were performed on Statistica 5.1 (StatSoft, http://www.statsoft.com/) and were two-tailed unless otherwise stated. Matrix correlation tests were run on MatrixTester v2.2.3b by C.K. Hemelrijk and were one-tailed (we report right tail probabilities, P_r, or left tail probabilities, P_l, based on 2,000 permutations). Chi-square tests of independence using a simulation procedure were performed on ACTUS2 by C.B. Estabrook and G.F. Estabrook (probabilities based on 10,000 simulations). The cut-off for significance was set at 0.05 but some trends were considered at an alpha level of 0.1.

Results

Dominance relationships

Agonistic interactions were given at low frequencies (mean ± SD): 0.80 ± 0.38 h^{-1} per individual (0.16 ± 0.08 h^{-1} per partner). Out of 263 agonistic-related interactions, we recorded 77 displacements (29.3%), 56 mild threats (21.3%), 76 bite threats (28.9%), 27 bites (10.3%), nine strike threats (3.4%), three arched neck threats (1.1%), 11 kick threats (4.2%), two kicks (0.8%) and two chases (0.8%). Out of 180 agonistic interactions to which the reaction of the receiver could be determined, 116 (64.4%) caused avoidance or withdrawal, 42 (23.3%) were ignored, 14 (7.8%) were replied with an agonistic interaction, five (2.8%) were replied with an agonistic interaction while withdrawing, two (1.1%) were replied with an affiliative interaction and one (0.6%) was replied with both affiliative and agonistic interactions.

During the first period when four males were present, dominance relationships could be determined between all pairs of stallions. In the second period, after the 4-year-old stallion (Tb) returned to the group, dominance relationships between the previously lowest-ranking male (Ta) and the two males above him changed: one of the relationships was reversed (Ta–Ut) and the other relationship (Ta–Tl) was tied (one recorded interaction in each direction). Moreover, the dominance relationship between Ta and the newly returned stallion (Tb) was unknown because no agonistic-related interactions were recorded between them during the second period, and the relationship between Ut and Tb was almost tied (3 vs 2 interactions in each direction). In the third period, after the return of the oldest stallion (Ag), there were three unknown relationships (two of them were those that changed between periods 1 and 2, Ta–Ut and Ta–Tl) and two tied relationships (between Ag and two other males). By incorporating ad libitum data, we were able to resolve the two tied relationships, but not the three unknown relationships.

Due to the high proportion of tied and unknown relationships in periods 2 and 3, and to the impossibility of finding a statistically significant level of linearity in groups with less than six individuals (Appleby 1983a), we did not construct separate dominance hierarchies for each period. The dominance hierarchy and rank of each stallion was therefore based on the total number of agonistic-related interactions that caused withdrawal or avoidance reactions from the receiver throughout the whole study (Table 2). The dominance hierarchy was significantly linear (Laudau's index of linearity: $h = 1.00$; Kendall's coefficient of consistence: $K = 1.00$, $d = 0$, $N = 6$, $P = 0.022$, probability obtained from Appleby 1983a, Table I, p 603) and the directional consistency index was 0.84. The 12-year-old stallion and the 4-year-old stallion that returned to the group occupied the highest and the lowest position in the dominance hierarchy, respectively (Table 2).

Table 2 Total number of agonistic-related interactions that caused withdrawal or avoidance reactions (excluding kicks and kick threats)

Initiator	Receiver						
	Ag	Sd	Tl	Ut	Ta	Tb	Total
Ag	–	1	1	1	2	1	6
Sd	1	–	34	21	25	3	84
Tl	0	5	–	16	17	5	43
Ut	1	0	3	–	20	7	31
Ta	0	0	3	13	–	1	17
Tb	0	0	2	2	0	–	4
Total	2	6	43	53	64	17	185

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

Factors related to dominance rank

Dominance rank was not significantly correlated with age, weight, height (age: $r_s = 0.54$, weight: $r_s = -0.29$, height: $r_s = -0.17$, $N = 6$, $P > 0.05$), total aggressiveness ($r_s = 0.77$, $N = 6$, $P > 0.05$), aggressiveness towards subordinates ($r_s = 0.60$, $N = 5$, $P > 0.05$) or intensity of given agonistic interactions ($r_s = 0.06$, $N = 6$, $P > 0.05$). Furthermore, frequency and intensity of agonistic interactions received were not related to dominance rank (frequency: $r_s = -0.66$, $N = 6$, $P > 0.05$; intensity: $r_s = 0.40$, $N = 5$, $P > 0.05$). Frequency and intensity of agonistic interactions received by the two highest-ranking stallions and by the lowest-ranking stallion (range: frequency: 0–0.08 h^{-1}; intensity: 0–0.1) was lower than the frequency and intensity received by the three middle-ranking males (range: frequency 0.26–0.30 h^{-1}; intensity: 0.16–0.22).

Rank distance and contests over dominance

Over the whole study, 48 (25.8%) of 186 agonistic interactions were directed to dominants and asymmetry was 0.694 ± 0.357 (where 1 means complete asymmetry). Asymmetry of agonistic interactions was significantly lower among close-ranking stallions ($K_r = 19$, $N = 6$, $P_r = 0.03$). The proportion of threats ignored or replied ($K_r = -4$, $N = 6$, $P_l = 0.31$) and the proportion of displacements within agonistic-related interactions ($K_r = 0$, $N = 6$, $P_r = 0.49$) were not significantly correlated with rank distance. High-intensity agonistic interactions occurred only among the four males that were present throughout the whole study and their frequencies were too low to analyse the correlation between the proportion of interactions ignored or replied and rank distance. Absolute frequency of agonistic interactions tended to be higher among close-ranking stallions, but relative frequency and intensity of agonistic interactions were not correlated with rank distance (Table 3).

Absolute frequency and intensity of agonistic interactions were not higher in dyads with less clear dominance relationships (Table 3). Relative frequency of agonistic interactions was significantly higher among dyads with lower proportion of displacements (Table 3).

Activities and contexts of agonistic-related interactions

Time spent in each activity by the horses and contexts of agonistic-related interactions are presented in Tables 4 and 5. Out of the recorded 246 agonistic-related interactions where both the context and activity of the initiator could be determined, the greatest percentage of interactions occurred during feeding, to surpass another horse (22%), maintain space (8.5%) or replace another horse at his feeding site (7.3%). Maintain space when standing resting (6.9%) and surpass another individual while in locomotion (5.7%) were the next most common situations.

Contexts of agonistic interactions-related interactions directed to adjacent-ranking stallions were not significantly different from those directed to distant-ranking males ($\chi^2 = 11.5$, $P = 0.23$; contexts “space” with undetermined subcategory and “redirect after affiliative interaction” were excluded from analysis). The following activity categories were merged for statistical analysis: “standing resting” with “recumbent resting”, “alert” with “investigation”, “drinking” with “other”. There was a significant difference between the activities of initiators of agonistic-related interactions directed to adjacent-ranking males and those directed to more distant-ranking males ($\chi^2 = 13.8$, $P = 0.04$): interactions initiated when standing resting were directed to adjacent-ranking stallions less frequently than expected, and more frequently to distant-ranking stallions. Agonistic-related interactions directed during each activity differed significantly from expected (Chi-square goodness of fit: adjacent rank: $\chi^2 = 104.3$, $df = 7$, $P < 0.01$; distant rank: $\chi^2 = 49.6$, $df = 7$, $P < 0.01$): interactions directed both to adjacent-ranking males and distant-ranking males were more frequent than

Table 3 Correlations between frequency and intensity of agonistic interactions, rank distance and measures of clearness of dominance relationships, as assessed by the K_r matrix correlation test

Behavioural measure	Absolute frequency of agonistic interactions		Relative frequency of agonistic interactions		Intensity of agonistic interactions	
	K_r	P	K_r	P	K_r	P
Rank distance	−20	0.07	−10	0.23	−12	0.15
Asymmetry	−11	0.24	5	0.37	−5	0.36
Displacements	−12	0.15	−28	0.01	−2	0.45
Threats ignored/replied	8	0.31	8	0.28	3	0.42

Table 4 Time-budget of stallions (mean ± SD)

Activity	Percentage of time
Feeding	40.7 ± 5.8
Drinking	0.3 ± 0.2
Standing	4.9 ± 2.4
Standing resting	45.1 ± 7.9
Recumbent resting	1.5 ± 1.3
Locomotion	4.1 ± 0.8
Self grooming	1.4 ± 1.0
Investigation	0.5 ± 0.1
Alert	0.7 ± 0.3
Interaction	0.6 ± 0.3
Other	0.1 ± 0.1

Table 5 Contexts of agonistic-related interactions (mean ± SD)

Context	Percentage
Space[a]	6.5 ± 7.2
Maintain space	24.5 ± 15.1
Obtain space	4.2 ± 6.3
Replace	7.1 ± 10.1
Surpass	23.5 ± 20.6
Response to affiliative interaction	12.9 ± 13.3
Response to agonistic-related interaction	3.6 ± 3.7
Response to separation	1.0 ± 1.5
Response to proximity	9.3 ± 9.5
Redirect after affiliative interaction	0.5 ± 1.3
Redirect after agonistic-related interaction	4.2 ± 4.0
Interference in affiliative interaction	2.7 ± 4.4

[a] Includes interactions initiated in context space, with undetermined subcategory

expected when the initiator was standing and less frequent when he was resting.

Discussion

Dominance relationships established among stallions in this bachelor group were less clear than relationships among mares in a Sorraia breeding group (Heitor et al. 2006), as evinced by the lower percentage of withdrawal/avoidance reactions (64.4% vs 84.8%), higher percentage of agonistic interactions directed to dominants (25.8% vs 1.9%) and lower asymmetry of agonistic interactions (0.694 vs 0.952) in the bachelor group. These findings are consistent with the sex differences observed in 1-year-old Icelandic horses by Vervaecke et al. (2007), and suggest that males contest dominance relationships more frequently than females. Males may contest dominance relationships more often than females because benefits of high rank are higher for polygynous males than for females (Trivers 1972; Vervaecke et al. 2007).

Dominance relationships among males were also less stable, as changes occurred after the two breeding stallions returned to the group. Group composition was more stable in the Sorraia breeding group than in the bachelor group and this difference may account for the reported differences in dominance relationships. Although bachelor stallions have been reported to re-establish previous dominance relationships after months of separation (McDonnell and Murray 1995), rank changes caused by changes in group composition are common (Keiper and Sambraus 1986; Boyd and Houpt 1994). However, the changes in dominance relationships may only be apparent, due to sampling bias generated by the low number of agonistic-related interactions recorded in this study.

Despite having less clear dominance relationships, the mean frequency of agonistic interactions given by males ($0.80\ h^{-1}$ per individual) was similar to that given by mares ($0.81\ h^{-1}$) and lower than the frequency given by all adult horses ($1.19\ h^{-1}$) in the Sorraia breeding group (Heitor et al. 2006). Frequency of agonistic interactions was also higher in a breeding group than in a bachelor group of Przewalski horses, although this difference was not significant (Feh 1988). Vervaecke et al. (2007) found no significant difference in aggressiveness between a male group and a female group of 1-year-old Icelandic horses. However, the mean frequency of agonistic interactions given per individual per partner among Sorraia males ($0.16\ h^{-1}$) was slightly higher than in the breeding group (mares: $0.09\ h^{-1}$; adults: $0.11\ h^{-1}$). The frequency of agonistic interactions given per individual in this study is within the range reported for bachelor groups of Przewalski horses (Feh 1988: $0.76\ h^{-1}$; Christensen et al. 2002: $1.46\ h^{-1}$) and domestic horses (Christensen et al. 2002: $0.63\ h^{-1}$). Consistent with the findings of other studies on horse bachelor groups (Feh 1988; Christensen et al. 2002; Vervaecke et al. 2007), breeding groups (e.g. Houpt and Keiper 1982; Keiper and Sambraus 1986; Keiper and Receveur 1992; Heitor et al. 2006) and feral stallions in multi-male bands (Miller 1981), intensity of agonistic interactions was low, consisting mostly of threats.

The dominance hierarchy was significantly linear, such as reported for other bachelor groups (Feist and McCullough 1976; Feh 1988; Tilson et al. 1988; Vervaecke et al. 2007) and breeding groups (e.g. Tyler 1972; Wells and von Goldschmidt-Rothschild 1979; Keiper and Receveur 1992; Van Dierendonck et al. 1995; Heitor et al. 2006). The two oldest stallions attained the highest rank positions but, contrary to the findings from these studies, age was not significantly correlated with dominance rank in this bachelor group. Age difference between the stallions may not have been large enough to produce meaningful asymmetries in benefits/costs of aggression and fighting ability, or to be reliably assessed by the horses and used as an arbitrary asymmetry. Moreover, age usually has greater influence on rank in groups with stable membership (Boyd 1991). The influence of age is sometimes associated with length of residency, and this association may have been weakened by the frequent removals and reintroductions of horses in this group. The influence of length of residency may therefore account for the low rank position attained by the youngest among the two reintroduced stallions, although he was not the youngest bachelor stallion. Low rank positions are commonly attained by newcomers in a group (Wells and von Goldschmidt-Rothschild 1979; Keiper and Sambraus 1986; Monard and Duncan 1996).

Male rank was unrelated to weight and height. Weight was also unrelated to female rank in the Sorraia breeding group (Heitor et al. 2006). The influence of weight and height on horse dominance rank is not consistent in the literature. In mixed-sex groups of domestic horses, rank was positively correlated with weight in one study (Houpt et al. 1978) but not in another (Houpt and Keiper 1982). Mare rank was positively correlated with height in some studies (Clutton-Brock et al. 1976; Rutberg and Greenberg 1990) but not in others (Van Dierendonck et al. 1995). The small influence of physical characteristics on both male and female rank may be due to the fact that sexual dimorphism is minimal in horses and fighting ability seems to depend more on social experience and motor skills than on height or weight (Keiper and Sambraus 1986; Van Dierendonck et al. 1995; Weeks et al. 2000).

Alternatively, stallion rank may have been determined by arbitrary asymmetries (e.g. historical or social asymmetries) generated by the outcomes of previous agonistic interactions. For example, winner and loser effects can have a strong influence on dominance relationships and hierarchies, independent from asymmetries in fighting ability (Chase et al. 1994; Van Doorn et al. 2003a, b). Winners of previous agonistic interactions may display higher aggressiveness in subsequent interactions and be more likely to win them again, whereas losers may have become more likely to show submission. The loser effect would seem more important among Sorraia stallions because total aggressiveness and aggressiveness towards subordinates were not significantly correlated with rank. Horses that displayed higher total aggressiveness achieved higher rank in some studies (Arnold and Grassia 1982; Tilson et al. 1988; Boyd 1991; Boyd and Houpt 1994; Weeks et al. 2000; Vervaecke et al. 2007), but not in others (Wells and von Goldschmidt-Rothschild 1979; Van Dierendonck et al. 1995; Heitor et al. 2006). The lack of significant influence of aggressiveness towards subordinates is consistent with the findings of other authors (Clutton-Brock et al. 1976; Weeks et al. 2000; Heitor et al. 2006).

In contrast to mares (Weeks et al. 2000; Heitor et al. 2006), higher-ranking stallions did not receive lower frequency or intensity of agonistic interactions than lower-ranking stallions. Therefore, higher-ranking stallions do not benefit from lower costs incurred from received aggression. Frequency and intensity of agonistic interactions received were highest among the three middle-ranking stallions whose dominance relationships seemed to change after reintroduction of the breeding stallions. In addition, asymmetry of agonistic interactions was significantly lower and absolute frequency of agonistic interactions tended to be higher among close-ranking stallions than distant-ranking stallions. These findings provide some evidence to support the hypothesis that dominance relationships are more contested among close-ranking stallions. Close-ranking zebra stallions also had more unstable dominance relationships and lower asymmetry in their relationships, but frequency of agonistic interactions was not related to rank distance (Schilder 1988). By contrast, dominance relationships were not more contested among close-ranking mares in the Sorraia breeding group (Heitor et al. 2006). The frequency of agonistic interactions was highest towards close-ranking subordinate horses in some studies (Tyler 1972; Arnold and Grassia 1982; Boyd 1991; Boyd and Houpt 1994) but not in others (Clutton-Brock et al. 1976). Some authors reported that high intensity agonistic interactions occur more often among horses of similar rank (Houpt and Keiper 1982; Keiper and Receveur 1992), but we found no significant correlation between intensity of agonistic interactions and rank distance in the Sorraia bachelor group. In a group of red deer males, relative frequency of agonistic interactions outside the breeding season was not related to rank distance and their intensity was lower among close-ranking animals (Appleby 1983b).

Aggressiveness was not generally higher among males with less clear dominance relationships, but relative frequency of agonistic interactions was significantly higher among stallions that were involved in a lower proportion of displacements within agonistic-related interactions, as also reported for mares (Heitor et al. 2006). A lower proportion of displacements may indicate that dominance relationships are less clear and the higher relative frequency of agonistic interactions may be used to assert them.

Contexts of agonistic-related interactions among close-ranking males were not significantly different from those among distant-ranking stallions. However, agonistic-related interactions directed to distant-ranking males when standing resting were more frequent than expected, suggesting that these interactions are more closely linked to access over defendable resources than interactions directed to close-ranking males. Resting sites under the trees are valuable and defendable resources during summer, as horses congregate in the shade to avoid the high temperatures and stand in antiparallel position to mutually fend off flies (Tyler 1972; Wells and von Goldschmidt-Rothschild 1979). By contrast, food patches are less valuable and defendable resources for grazers at pasture, due to their large and relatively homogenous distribution (Rutberg and Greenberg 1990). Consistent with this view, agonistic-related interactions were not initiated more frequently than expected by chance during feeding, and those that were initiated during feeding were mostly to surpass another horse, not to take its place at a food patch.

Overall, we found some evidence that stallions contested dominance relationships more frequently with close-ranking stallions. However, frequency and intensity of agonistic interactions were low, suggesting that males avoided the costs of aggression. The fact that space available to escape from aggression of other males was limited, mares were only occasionally visible and breeding access was independent from dominance rank may have reduced the benefits relative to costs of aggression and therefore limited the occurrence of contests over dominance.

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