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Third party interventions on affiliative interactions protect social bonds

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Abstract

Third-party interventions are defined as the interruption of dyadic interactions by third animals through direct physical contact, interposing or threats. Previous studies focused on analysing interventions against agonistic encounters. However, evaluations of interventions against affiliative behaviours in relation to the intervening animal’s social relationships and its social and spatial position are missing. Therefore, horses are an interesting model species, as interventions occur against affiliative interactions most frequently. We analysed 67 interventions in affiliative interactions, displayed between 64 feral horses (*Equus ferus caballus*) in three groups. Particular, high ranking females intervened in the affiliative interactions of group mates in the stable horse harems. Intervening animals took an active part in affiliative and agonistic encounters within the group, but did not occupy particularly social roles or spatial positions in the group. They generally supported preferred group mates when intervening and thus protect their own social bonds. Some species may prevent competition for preferred partners from escalating into more costly agonistic encounters by protecting their social bonds through affiliative interventions.

Keywords: third-party intervention, horse, social bond, social network, rank

Intervention behaviour primarily has been evaluated in monkeys and apes (deWaal 1992, Silk 1992, Prud’homme & Chapais 1996, Flack et al. 2006), in goats (Keil & Sambraus 1998), fallow deer (Jennings et al. 2009), in goats (Keil & Sambraus 1998), fallow deer (Jennings et al. 2009), hyenas (Zabel et al. 1992), dogs (de Villiers et al. 2003, Ward et al. 2009), dolphins (Connor et al. 1992), and cichlid fish (Walter & Trillmich 1994). Previous evaluations have dealt with third-party interventions on agonistic interactions. It has been assumed that intervener animals occupy certain social positions as only a few particular individuals in a group display intervention behaviour in many species, with others rarely or never intervening (spotted hyaena: Zabel et al. 1992, wild dogs: Villiers et al. 2003, pigtailed macaques: Flack et al. 2006, zebras: Schilder 1990, horses: Sigurjónsdóttir et al. 2003, van Dierendonck et al. 2009). For agonistic encounters in primates Flack et al. (2006) found interveners to be strongly connected in three of four affiliative social networks, but not occupying any unique position. When they removed the intervening animals, aggression levels rose within the group. They concluded that interveners may engage in policing to prevent the escalation of aggressions within the group. However, deWaal (1992), and Petit & Thierry (1994) argued that interveners support preferred animals by protecting them in agonistic encounters.

Several studies have evaluated the position of interveners in dominance hierarchies. Interveners in agonistic encounters were often high-ranking (Engh et al. 2000, Flack et al. 2006, Jennings et al. 2009), and usually they ranked higher than the supported and challenged animals (e.g. bovines: Sambraus 1969, goats: Keil & Sambraus 1998, fallow deer: Jennings et al. 2009). However, rank relationships were not found to influence interventions on affiliative interactions in zebras (Schilder 1990), and in horses interveners were claimed to be lower in rank than both the supported and the targeted animal (Heitor et al. 2006, van Dierendonck et al. 2009).

In addition to social bonds and social ranks, the spatial position of animals in their groups could be an important factor in the decision to intervene. In prior

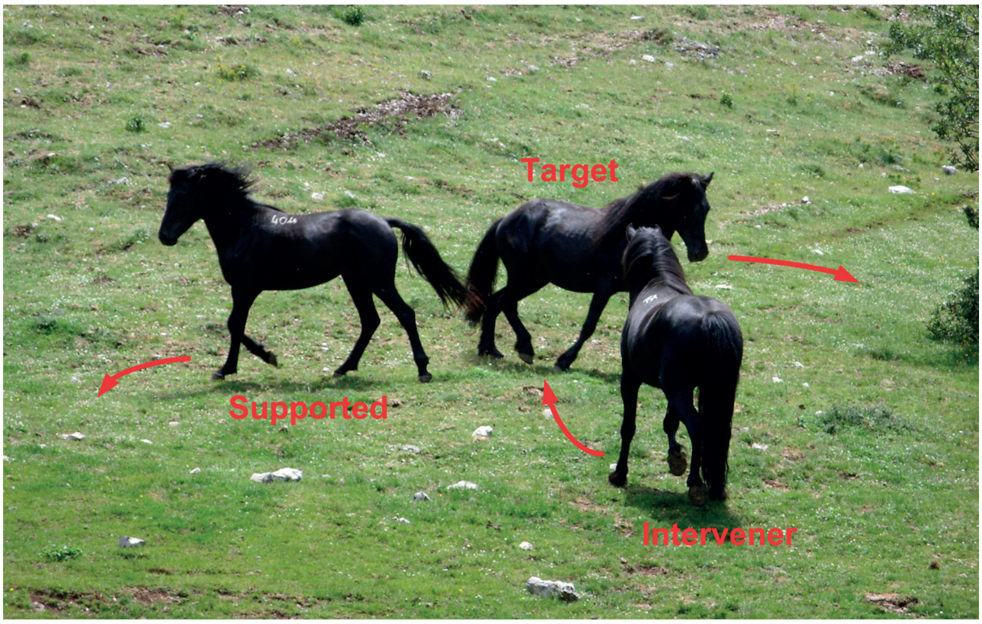

Figure 1.
3rd party intervention. A third, previously uninvolved animal intervenes in an interaction of two others. Only the target is challenged.

studies a central spatial position coincided with the likelihood of obtaining a higher social rank, building up more social bonds, and having a greater influence on decision processes (Hemelrijk 2002). A high frequency of intervention behaviour may be shown by animals in a central position in the group, simply because they are nearer to dyadic interactions more often than animals at the perimeter.

The present study examined the social rank of interveners against affiliative interactions, challenged horses (i.e. the target) and not challenged horses (i.e. supported horses, Fig. 1) by calculating an Average Dominance Index (ADI), chosen for its reliability and computational simplicity (Hemelrijk et al. 2005). We evaluated whether interveners selectively challenged preferred or non-preferred animal, or whether they selected the target at random. Additionally, we investigated the social position of interveners, supported horses, and challenged horses in their social networks by applying network metrics. Finally, we observed the spatial positions of interveners within their group.

We hypothesise that, comparable to interventions on agonistic encounters, interveners are (i) of high social rank (Flack et al. 2006, Jennings et al. 2009, Engh et al. 2000), (ii) have stronger social bonds with the horses they support than with targets and other group mates (deWaal 1992), and (iii) occupy a particular social position in the social networks of their group (Flack et al. 2006). Similar to other decision making processes, we (iv) expect interveners to stay in a distinct spatial position within their group (Hemelrijk 2002).

METHODS

Animals

In the present study we observed 4 feral horse harems with 84 animals out of 300 free ranging Esperia-ponies in the Italian Abruzzi Mountains. The social groups' age and sex composition and their social behaviours were comparable to other feral horse populations (Schilder 1990, VanDierendonck et al. 2009, Berger 1977). Each of the harem groups consisted of several females and their offspring, and 1 to 3 males (group 1: N=14, 1 male, group 2: N=20, 1 male, group 3: N=30, 1 alpha males and 2 immature males (1 to 3 years old), group 4: N=20, 1 male). The horses' ages ranged between 1 and 28 years, but precise ages were only known for half of them. Foals were not considered in this study, because of their special status in the social organisation of the groups (Rutberg & Keiper 1993). Group members in feral horses are usually unrelated (Rutberg & Keiper 1993). Within the study period the composition of the groups changed only slightly (emigration: median: 1, min.: 0, max.: 3, immigration: median: 2, min.: 0, max.: 6). All horses were individually identified by their brands and colouration. Once a year they were rounded up for branding of the females and the removal of most males older than 5 months.

Data collection

In Mai and Oktober 2009 and in Mai 2010 the groups were observed for 15 hours each , but less when they could not be located again (minus a mean of 98min, SD = 57min for 1 observation period in each group, minus 10h for the 1st observation period in group 4).

Behaviour category	Behaviour type	Group 1			Group 2				Group 3			
		May 2009	May 2010	Sum	May 2009	October 2009	May 2010	Sum	May 2009	October 2009	May 2010	Sum
Agonistic	Threat to bite	66	75	141	75	43	114	232	65	49	115	229
(used for analysis of dominance hierarchy)	Threat to kick	11	7	18	5	6	16	27	18	7	20	45
	Bite	7	4	11	8	5	8	21	6	2	12	20
	Kick	10	0	10	14	2	4	20	5	4	9	18
	Chase	20	12	32	26	14	7	47	38	8	72	118
	Approach followed by a retreat	69	56	125	82	61	63	206	82	44	51	177
	Retreat	171	146	317	198	122	199	519	198	82	268	548
Affiliative	Mutual grooming	9	37	46	32	64	63	159	37	65	55	157
(used for analysis of social bonds)	Grooming approach	5	23	28	27	47	32	106	14	44	27	85
	Mutual approach	25	39	64	1	30	42	73	8	43	20	71
	Neutral approach	36	34	70	23	39	16	78	30	27	7	64
Intervention	Agonistic context	2	1	3	0	0	0	0	1	3	1	5
	Affiliative context	6	11	17	4	5	7	16	11	7	16	34

Table 1. The interveners' social bonds with supported and targeted horses.

	ID	Foal at foot			Average ADI	Dominance hierarchy agonistic								Social bonds affiliative				Interventions	
		May 2009	Oct. 2009	May 2010		Threat to bite	Threat to kick	Bite	Kick	Chase	Approach followed by retreat	Retreat of focal animal	Retreat from focal animal	Mutual groom.	Grooming approach	Mutual approach	Neutral approach	Agonistic context	Affiliative context
Group 1	1*				0.79	16	1	5	1	8	15	3	46	3	0	11	6	1	0
	2	**NA**		**X**	**0.75**	**17**	**5**	**1**	**0**	**3**	**17**	**10**	**43**	**8**	**4**	**22**	**4**	**1**	**7**
	3	**NA**			**0.34**	**4**	**1**	**0**	**0**	**1**	**4**	**20**	**8**	**4**	**0**	**6**	**6**	**0**	**6**
	4	NA			0.58	24	1	1	0	4	10	21	41	17	5	13	0	1	0
	5	NA			0.33	5	1	0	1	0	4	26	9	2	0	4	1	0	0
	6	NA		X	0.80	16	7	0	2	8	28	9	60	11	4	25	19	0	2
	7	NA			0.65	22	0	1	1	2	11	17	35	3	0	3	3	0	0
	8	NA			0.25	5	0	1	1	0	5	36	6	2	0	0	2	0	0
	9	NA	X		0.45	12	1	0	0	3	9	32	22	6	5	10	3	0	0
	10	NA	X	X	0.56	9	1	0	3	1	11	28	24	0	0	1	10	0	0
	11	NA			0.24	3	0	0	1	0	3	47	4	18	5	13	10	0	0
	12	NA	X	X	0.13	1	0	0	0	0	0	32	2	4	0	4	2	0	0
	13	NA			0.58	7	0	0	0	2	8	13	17	10	4	11	2	0	2
	14	NA			0.07	0	0	0	0	0	0	23	0	4	1	5	2	0	0
Group 2	1*				0.67	12	0	1	0	9	14	5	33	41	13	29	8	0	0
	2		X	NA	0.53	19	5	0	2	5	9	22	37	9	2	6	0	0	0
	3			NA	0.39	6	1	0	0	0	3	20	10	22	12	5	3	0	0
	4	X		NA	0.22	7	2	0	0	2	4	40	12	6	1	6	2	0	0
	5	X		NA	0.41	6	1	1	0	0	11	42	17	6	3	10	4	0	0
	6	X		NA	0.49	8	1	1	0	4	17	26	32	30	9	14	9	0	0
	7	X		NA	0.65	3	0	0	0	2	7	9	12	1	1	0	0	0	0
	8			NA	0.56	7	2	2	0	0	20	27	31	5	3	9	4	0	2
	9		X	NA	0.30	8	0	6	1	4	2	62	19	23	11	10	5	0	1
	10			NA	0.14	4	0	0	1	0	1	27	5	1	0	1	1	0	0
	11	X	X	NA	0.74	20	1	4	4	3	25	2	55	60	25	7	7	0	3
	12	**X**		**NA**	**0.74**	**12**	**0**	**1**	**0**	**0**	**12**	**14**	**23**	**42**	**5**	**9**	**4**	**0**	**6**
	13			NA	0.49	5	0	1	0	0	4	10	9	1	1	4	2	0	0
	14			NA	0.79	19	10	0	1	7	9	7	45	11	3	5	3	0	3
	15	X	X	NA	0.57	34	1	2	3	0	15	29	51	8	2	8	11	0	0
	16	X		NA	0.47	11	1	1	0	3	4	23	18	0	0	2	0	0	0
	17			NA	0.77	30	0	0	4	3	17	17	52	17	6	8	7	0	1
	18		X	NA	0.68	12	2	0	3	3	20	19	39	15	6	0	2	0	0
	19			NA	0.31	6	0	1	0	2	8	51	15	11	2	5	3	0	0
	20		X	NA	0.16	3	0	0	1	0	4	67	5	9	1	8	3	0	0
Group 3	1*				0.64	5	7	0	3	50	13	6	74	43	4	8	2	0	0
	2				0.42	13	2	1	0	2	7	33	23	9	3	4	0	0	1
	3			X	0.55	9	2	2	0	4	12	19	29	11	4	2	2	0	2
	4	X	X	X	0.58	14	0	2	0	5	4	15	24	0	0	2	2	0	0
	5	X		X	0.81	19	4	2	1	3	13	12	40	5	3	5	6	0	2
	6		X		0.57	10	0	0	1	4	9	23	25	8	0	9	8	1	0
	7			X	0.33	7	2	0	0	3	3	22	15	3	0	6	2	2	2
	8	X		X	0.84	20	2	2	0	3	15	2	41	18	6	2	1	0	3
	9				0.36	7	0	1	0	2	4	38	14	11	3	5	3	0	0
	10	X		X	0.67	8	1	1	1	2	7	5	19	11	3	2	3	0	0
	11	X		X	0.39	7	0	0	0	3	7	25	17	4	1	12	6	0	0
	12				0.35	3	0	1	1	0	2	23	6	3	1	3	4	0	0
	13	X		X	0.28	4	2	0	0	1	6	42	11	2	2	4	0	0	0
	14	X		X	0.68	23	4	1	1	3	13	20	45	12	4	0	2	0	2
	15				0.47	4	1	1	2	2	8	31	15	17	5	10	4	0	1
	16			**X**	**0.43**	**6**	**0**	**0**	**0**	**0**	**1**	**21**	**7**	**9**	**3**	**18**	**6**	**0**	**9**
	17	**X**			**0.76**	**33**	**7**	**2**	**1**	**8**	**16**	**15**	**65**	**34**	**16**	**8**	**2**	**0**	**9**
	18	X			0.68	9	5	0	1	4	7	9	26	3	1	9	1	0	0
	19				0.48	11	4	2	0	3	4	17	19	38	9	3	2	0	2
	20			X	0.48	8	0	0	1	4	4	20	17	5	2	1	2	0	0
	21	X		X	0.26	1	0	0	1	0	1	14	2	2	1	1	1	0	0
	22				0.41	0	0	0	0	0	3	10	3	3	0	0	2	0	0
	23	X		X	0.16	0	1	0	4	0	1	30	5	10	1	6	2	0	0
	24				0.36	1	1	0	0	0	1	3	2	5	2	1	0	0	0
	25				0.18	0	0	0	0	0	0	12	0	10	4	5	1	0	0
	26				0.00	0	0	0	0	0	0	1	0	0	0	0	0	0	0
	27				0.40	7	0	1	0	3	2	14	11	13	4	5	0	0	0
	28			X	0.26	0	0	1	0	9	3	37	7	15	2	7	0	2	0
	29				0.11	0	0	0	0	0	0	17	0	5	0	2	0	0	0
	30				0.19	0	0	0	0	0	0	12	0	5	1	2	0	0	1

Animals that intervened above average are depicted in bold.

* Alpha male of particular group.

Table 2
Behaviours of individual animals in all observation periods

Group 1 could not be observed in October 2009. All observations were distributed over daylight hours, were not longer than six and a half hours at a stretch and spread over 4 separate days on average within no more than 15 days. When groups split up we observed the subgroup with at least 2/3 of the animals, or observed both subgroups equally.

Two observers participated in each observation, so that one could continue observing while the other one was writing. When locating a group for the first time, the observers remained about 100 to 200 meters away for about 30 minutes to habituate the horses to their presence. When the horses were calm and continued grazing the distance was slowly reduced to about 10 to 50 meters while the observers identified the horses. If necessary a binocular was used for observation.

Behaviours

The behaviours were observed ad libitum for recording the rare third-party interventions (Altmann 1974). We observed agonistic behaviours, such as threats to bite, threats to kick, bites, kicks, chases and retreats (Feist & McCullough 1976, McDonnell & Haviland 1995), and affiliative behaviours such as mutual grooming [26], as well as grooming approaches (one animal approaching another preceding mutual grooming), mutual approaches (both animal approach each other), or neutral approaches (one animal approaching another without the approached animal making any perceptible response). Mutual, neutral, and grooming approaches may reveal the desire for friendly interaction and proximity to preferred animals (Silk et al. 2003, Cameron et al. 2009), whereas approaches which elicited a retreat by the approached animal may be perceived as an agonistic threat.

All agonistic interactions were treated as unidirectional. The aggressor received one point for the aggression and one point when the challenged animal retreated. Affiliative behaviours were treated bidirectional. Both participants in affiliative interactions received one point. Only neutral approaches and grooming approaches were counted as one point for the initiator of affiliative interactions.

An intervention was counted when an affilative interaction between two horses was terminated by the aggression (threat, bite, kick or chase) or approach of a third horse (Jennings et al. 2009, Ward et al. 2009, Fig. 1). Only one of the two interacting horses was challenged and, thereafter, retreated from the intervener. The number of interventions was corrected for the observed opportunities to intervene, i.e. the total number of affiliative interactions, in which either the supported horses or the targeted horses were involved.

Dominance hierarchies

For each group in each observation period we calculated the ADI from their agonistic encounters as follows: The dominance index per pair of individuals, w_{ij} is the number of times an individual won against or attacked a certain opponent divided by the total number of agonistic interactions in which the pair was involved with each other, thus $w_{ij} = x_{ij} / (x_{ij} + x_{ji})$. If a pair of individuals was not involved in agonistic interactions with each other, it was excluded from the analysis. The average dominance index of an individual is the average of all its dominance indices with all its interaction partners, thus $1/N \Sigma_j w_{ij}$. A higher value indicates a higher dominance in the group (Hemelrijk et al. 2005).

Social bonds

For the analysis of the horses' social bonds, we considered the frequency of exchanged affiliative behaviours between group member dyads. Behaviour scores were corrected for observation time and the number of possible interaction partners (n - 1). It was assumed that dyads which showed affiliative interactions more frequently have stronger social bonds (apes: Fedurek & Dunbar 2009, Silk et al. 2003, horses: Cameron et al. 2009).

Network analysis

The social networks were assembled separately for each group, for the respective observation periods, and for the affiliative and agonistic behaviours. Graphical visualizations of these networks were created, in which nodes (i.e. dots) represent the individuals, and edges (i.e. lines between the nodes) represent the behaviours displayed between the individuals (Croft et al. 2008, Fig.2). We analysed the individuals' weighted degree of interacting in their networks, i.e. the total number of behaviours for all edges that are connected to a node. Interactions can be treated as directed (from an actor to a receiver) or undirected (interactions are similarly counted for both interacting animals) (Croft et al. 2008). We used a weighted and undirected degree for analysing the number of interactions which involve focus animals, a weighted and directed indegree for the number of edges that reach a node when the focus animals are the receivers, and a weighted and directed outdegree for the number of edges that leave a node when the focus animals are the actors (Croft et al. 2008). All measurements were corrected for the number of potential interaction partners (n 1), and the average of all observation periods was calculated for each measurement.

Spatial group structure

When the feral horse groups were grazing or resting we recorded the group members' spatial distribution once per hour (N = 15) in May 2010. We distinguished between three spatial zones: horses could be central, in the inner zone, or at the periphery of the group.

Group no.	Observation period	N	Grooming with mutual approach		Grooming with neutral approach		Mutual approach with neutral approach	
			r_S	P	r_S	P	r_S	P
1	2009	13	0.675	0.01	0.119	0.7	0.225	0.5
1	2010	15	0.954	<0.001	0.539	0.04	0.6	0.02
2	2009	20	0.242	0.3	0.454	0.03	0.242	0.3
2	2009b	20	0.655	0.001	0.553	0.008	0.68	0.001
2	2010	20	0.689	0.001	0.606	0.003	0.575	0.005
3	2009	29	0.432	0.02	0.191	0.3	0.441	0.02
3	2009b	30	0.633	<0.001	0.309	0.08	0.353	0.04
3	2010	30	0.584	<0.001	0.056	0.7	−0.1	0.5

Table 3
Correlations between data sets used for social bond analyses (Spearman correlation tests)

Data analysis

For statistical analysis and the depiction of the data we used the SPSS 17 software package and the R-Project statistical environment (2011), and for analysing network metrics we used Ucinet (Borgatti et al. 2002). The Tau Kr matrix correlation test (Tau Kr test) was computed with the MatrixTester (v2.2.4, 2010, Hemelrijk 1990). We tested the data for normal distribution (K-S Test). Thereafter, Mann-Whitney U Exact-tests were used for comparing nonparametric independent data sets, and chi-square Exact-tests for likelihood equations in metric datasets. The Pearson correlation test was used for analysing parametric data and Spearman correlation tests for nonparametric data. We used the Tau Kr test to compare social interaction matrices. Individuals that were never involved in interventions or that were not present in all observation periods were excluded from the analysis. 2000 permutations were performed for the matrices with less than ten horses, and 4000 permutations for those that had between ten and fifteen horses. For the matrix correlations the one-tailed probability in the right half of the distribution was calculated (Hemelrijk 1990). The results of the Tau Kr test and the Mann-Whitney U Exact-tests were analysed for the combined three observation periods but separately for the groups. Test results from the groups were combined by using Fisher's combination test. All tests were two-tailed (unless otherwise stated) and the significance level was set at 0.05.

The interventions in group 4 were not considered because the groups dominance hierarchy was not stable between the observation periods (Pearson correlation test, May 2009 to October 2009: r = 0.44, N = 14, p = 0.12, May 2009 to May 2010: r = 0.49, N = 13, p = 0.09) and group instability may affect intervention behaviour. For the analysis of intervention behaviours in the remaining three groups we combined groups and observation periods, because the affiliative and agonistic behaviour structures were significantly similar between groups and observation periods (Milo et al. 2002, Supplementary data). Separate group results are provided if needed. When calculating the interveners' rank and social network parameters males were excluded from the analysis because males never intervened in affiliative interactions at all.

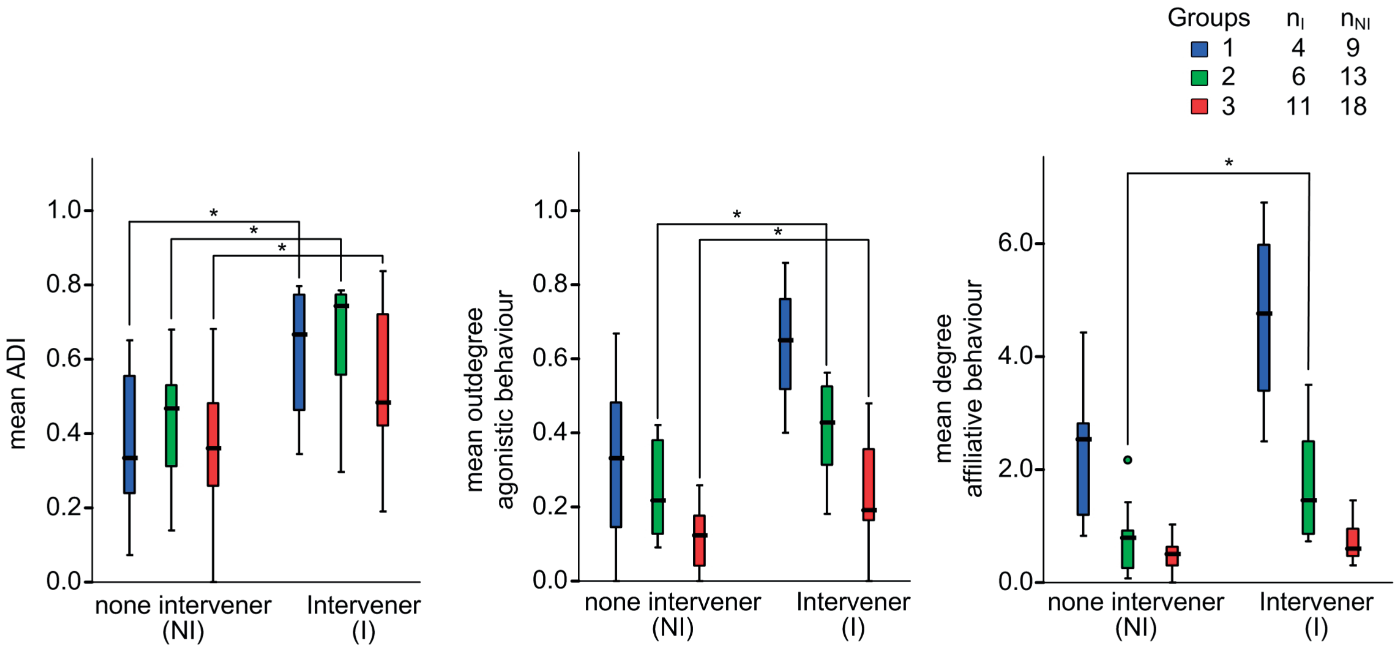

Figure 2. The interveners' and the group mates' (a) social rank (ADI), (b) display of agonistic behaviours (outdegree), and (c) participation in affiliative behaviours (degree). The data depicted here include stallions. Note that some differences between interveners and noninterveners are not significant, but were significant when stallions were excluded (see Results, Intervener). The box plots are subdivided by the median, interquartile ranges are depicted by whiskers, and outliers by dots. *P < 0.001.

Intervention matrices* Social bond matrices	Supported matrix					Target matrix				
	N†	Actor matrix		Receiver matrix		N†	Actor matrix		Receiver matrix	
		τK_r	P	τK_r	P		τK_r	P	τK_r	P
Group 1	6	0.74	**0.002**	0.57	**0.03**	8	−0.047	0.59	−0.12	0.72
Group 2	8	0.45	**0.002**	0.52	**0.001**	13	0.042	0.36	0.07	0.3
Group 3	13	0.45	**0.001**	0.48	**<0.001**	14	−0.004	0.51	−0.008	0.52

gnificant *P* values are depicted in bold.

[*] Tau K_r test.

[†] $N =$ number of individuals per group that were involved in at least one intervention and present in all three observation periods.

Table 4
The interveners' social bonds with supported and targeted horses

RESULTS

The 67 interventions against affiliative behaviour in the remaining 3 groups were performed by 21 of the 59 female horses and addressed 20 different supported and 31 different targeted horses. 5 females performed 55% of all interventions. The alpha males and the lower ranking males were not observed to intervene against affiliative behaviour (Chi-square test, X 2 2 = 1, N = 5, P < 0.001), but were the supported horse in 30 interventions and 5 times the targeted horses. The support for alpha males was more frequent in spring (79 %) than in autumn (21%). Interveners intervened in a median of 4% of the affiliative interactions of their supported horses. Generally, a horse was not targeted and supported by the same intervener (chi-square: X 2 2 = 5.33, N = 12, df = 1, P = 0.04), although 2 of the 21 interveners did target and support the same horse. In these cases the third horse differed when the particular horse was either supported or targeted.

Intervener

In all three groups interveners ranked significantly higher than non-interveners (Fisher's combination test, X 2 2 = 21.08, P = 0.002, separate groups: Fig. 3). Interveners had stronger social bonds with supported horses than with targeted horses or other group mates (Fig. 2, table 1). They directed more affiliative interactions towards the horses they supported and received more affiliative interactions from the supported horses than from other group mates (all P < 0.05, table 1).

In their social networks interveners tended to be involved in significantly more affiliative interactions than their group mates (Fisher's combination test, X 2 2 = 16.04, N = 3, P = 0.02, group 2: Mann-Whitney U Exact-test, U =15, N1 = 6, N2 = 13, P = 0.04, Fig. 2 and 3). They displayed more affiliative interactions (Fisher's combination test, X 2 2 = 15.55, N = 3, P = 0.02, group 1: Mann Whitney U = 2, N1 = 4, N2 = 9, P = 0,01, Fig. 3) and more agonistic interactions (Fisher's combination test, X 2 2 = 21.32, N = 3, P = 0.002, group 2: Mann Whitney U Exact-test, U = 13, N1 = 6, N2 = 13, P = 0,02, group 3: Mann Whitney U Exact-test: U = 45, N1 = 11, N2 = 18, P = 0,01) towards all the group mates. But interveners did not receive significantly more affiliative or agonistic behaviours from their group mates (Mann-Whitney U Exact-test, mostly P > 0.05).

Supported horses

The rank of supported horses did not differ significantly from their group mates (Fisher's combination test: X 2 2 = 2.41, N = 3, P = 0.88). Supported horses had significantly stronger social bonds to the particular interveners than to other horses, as each directed more of their affiliative behaviour towards, and received more affiliative behaviour from, their particular intervener horse (Fisher's combination test: directed behaviour: X 2 2 = 30.39, N = 3, P < 0.001, received behaviour: X 2 2 = 21.47, N = 3, P = 0.002).

In their social networks supported horses were involved in significantly more affiliative interactions than other group mates (Fisher's combination test, X 2 2 = 18.57, N = 3, P = 0.005), but did not differ in their aggressive behaviour from their group mates (Mann-Whitney U Exact-test, mostly P > 0.05). They initiated affiliative interactions more often than their group mates in group 2 and 3, but not in group 1 (Fisher's combination test, X 2 2 = 13.24, N = 3, P = 0.04), but did not receive more affiliative behaviours than others (Mann-Whitney U Exact-test, mostly P > 0.05).

Targets

Targeted horses did not differ from their group mates in their social rank (Fisher's combination test: X 2 2 = 4.54, n = 3, P = 0.6), their social bonding (all P > 0.05, table 1), or their involvement, display or achievement of agonistic and affiliative behaviours (Mann-Whitney U Exact-test, mostly P > 0.05).

Spatial group structure

Horses in general (Chi-square test, all P > 0.05) and the particular interveners, targeted and supported horses (Fisher's combination test, all P > 0.05) had no preferences for staying in the central, inner or peripheral zone of their group.

DISCUSSION

In the present study intervening horses were significantly higher ranking than their group mates, which is in line with the high social rank of interveners in agonistic encounters in other species (Flack et al. 2006, Jennings et al. 2009, de Villiers et al. 2003). High ranking animals may have a higher incentive to perform third-party interventions simply because of their low costs when challenging subordinates (Silk et al. 1992, Jennings et al. 2009, Dugatkin 1998).

Intervener horses took an active part in the majority of their affiliative and agonistic encounters, similarly to horses that reconcile, appease or console their group mates (Cozzi et al. 2010), but did not occupy any particular identifiable positions, as in macaques that intervene in agonistic encounters (Flack et al. 2006). It appears that social activity and the display of regulating social behaviours, such as intervention, reconciliation and 3rd party affiliation, are bound to high social rank in some species (Flack et al. 2006).

The present study is the first to show that interveners in affiliative encounters support preferred animals. Moreover, the intervening horses had no particular social relationships to the targeted horses. It is necessary to establish whether interveners support preferred or non-preferred animals to arrive at any conclusion about the underlying mechanism. If interveners challenge non-preferred animals they may try to keep them from interacting with their preferred partners. If they challenge the preferred animal itself they may punish it for interacting with other partners (deWaal 1992, Flack et al 2006, Clutton-Brock & Parker 1995). However, if interveners choose their targets at random they may demonstrate high rank by establishing winner-effects(Dugatkin 1998)or practice offensive behaviour which could influence their rank relationships later on, such as in young dog interventions in affiliative play fights (Ward et al. 2009). In the present study, the few cases in which interveners challenged preferred animals and supported non-preferred animals may have served for establishing social ranks, or the recruitment of new social partners (Schilder 1990). Both hypotheses need to be evaluated in a long term study.

Furthermore, intervention participants did not occupy particular spatial positions. Interveners rather appear to decide with whom they will interact regardless of their spatial position. Still interventions are likely to occur, when the intervened interaction takes place in close proximity to the intervener, which coincides with the fact that horses usually stay close to preferred partners (Jennings et al. 2009, Sigurjónsdóttir et al. 2003).

We suggest that high ranking female horses intervene in affiliative interactions to protect their social bonds with preferred group mates. Females may gain direct benefits from protecting social bonds in terms of increasing their reproductive success. As foals may be attacked and killed by predators or by stallions (Duncan 1982), higher infant survival can be assured where two socially bonded females mutually protect their offspring (Silk et al. 2003, Cameron et al. 2009). Furthermore, social bonds reduce male (Connor et al. 1992, Cameron et al. 2009) and female harassment (Nguyen et al. 2009), and so increase direct individual welfare and reproductive success (Linklater et al. 1999). Moreover females may have increased their reproductive success by supporting and bonding with the alpha males (Linklater et al. 1999). This hypothesis is supported by the observation that most of the mares' support for alpha males occurred in the breeding season in spring.

Furthermore, horses may build up stronger bonds with kin (Sigurjónsdóttir et al. 2003) and may have a higher incentive to intervene when kin are involved (Widdig et al. 2006). In the present study the exact relatedness for most of the free-ranging Esperia-ponies was not known. But, kin protection is not likely to be the major reason for the protection of social bonds by 3rd party interventions in free roaming feral horse groups, because these horses are usually unrelated as the majority of offspring disperses before maturity (Rutberg & Keiper 1993).

The high rank of horses that intervene in affiliative encounters contrasts with the results of prior studies where an inversed rank influence was found (VanDierendonck et al. 2009, Heitor et al. 2006). This discrepancy may be caused by variations in group compositions. It has been argued that the social hierarchy is less well developed in domestic horse groups without the permanent presence of uncastrated males than it is in stable harem groups (Sigurjónsdóttir et al. 2003). Thus the comparison to previous studies on domestic horse groups with the stable and long lived harems of this study is limited, as animals in groups with unstable hierarchies may intervene to influence the dominance hierarchy, as observed in agonistic interactions in other species (Prud'homme & Chapais 1996, Engh et al. 2000, Jenks 1988).

In conclusion, it is striking that, in contrast to primates (Flack et al. 2006), female horses protect their social bonds primarily by intervening in affiliative and not in agonistic encounters. We suggest that some species may be more efficient in protecting their social bonds by intervening in affiliative interactions and prevent competition for preferred partners to escalate so that more costly interventions in agonistic encounters are not needed. It is yet to be proven whether this is a widespread phenomenon in social animals.

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We declare that all research presented in the manuscript was conducted in accordance with all applicable laws and rules set forth by their governments and institutions, and all necessary permits were in hand when the research was conducted.

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Supplementary data, 3rd party intervention in horses

METHODS APPENDIX

The structure of agonistic and affiliative behaviours in horses

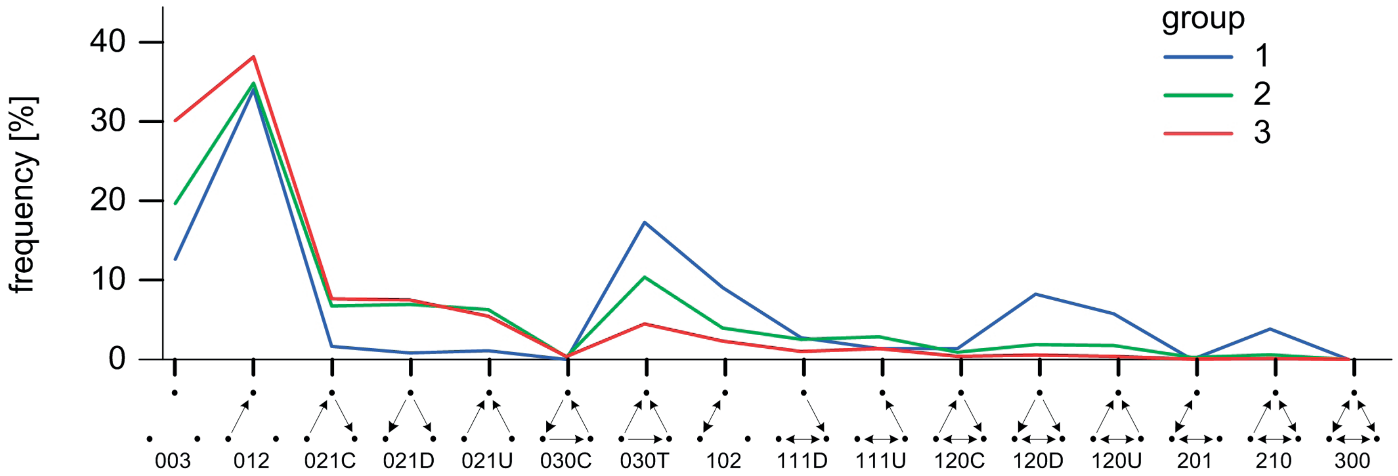
In examining similarities in local network structures Milo et al. (2002) emphasised the evaluation of small sub-networks, so called motifs (see for review Croft et al. 2008, pp. 155-158). By counting the frequency of 16 different triadic motifs (i.e. combinations of edges between three nodes, so called triads, Croft et al. 2008; Fig. 4), similarities in the direction and frequency of exchanged information or interactions can be evaluated within and between networks, for example between behaviour categories, animal groups, animal species or communication networks such as the World Wide Web (Milo et al. 2004).

In the recent study we found that the structures of affiliative and agonistic behaviours in horses were significantly similar between groups and observation periods (Fisher's combination test, all P < 0.001; see group data in table 2). As networks that are similar in structure appear to have the same function (Milo et al. 2002) it is justified to merge the groups and observation periods when analysing the frequency of behaviour motifs and of affiliative and agonistic behaviours in the social behaviour networks. Separate group results will be provided if needed.

Additionally, we found that the horses' agonistic and affiliative networks differed fundamentally in the frequency of unidirectional behaviours. The agonistic networks had more unidirectional behaviours within triads than the affiliative networks (Wilcoxon Signed rank test, ,Z = -3.72, N = 18, P < 0.001; Fig. 4). The frequency of mutual, bidirectional behaviours within triads was similar in agonistic and affiliative networks (Wilcoxon Signed rank test, Z = -0.65, N = 27, P = 0.53) and no interaction triads were frequent for both behaviour categories (Wilcoxon Signed rank test, Z = -1.6, N = 3, P = 0.25). This general difference in behaviour structure calls for analysing 3rd party interventions on agonistic and affiliative behaviours separately as they may have arisen from different backgrounds. As the number of interventions in agonistic encounters was insufficient for statistical tests, we decided to analyse only the interventions in affilative interactions.

The first item of the triad name encodes the number of bidirectional, mutual relationships, the second item encodes the number of unidirectional relationships and the third item encodes the number of not interacting dyads within a particular horse triad. D stands for down, U for up, C for cyclic, and T for transitive. The lines for each group simply help to depiction the parallelism between groups without implying continuity (Milo et al. 2004).

a) agonistic network



b) affiliative network

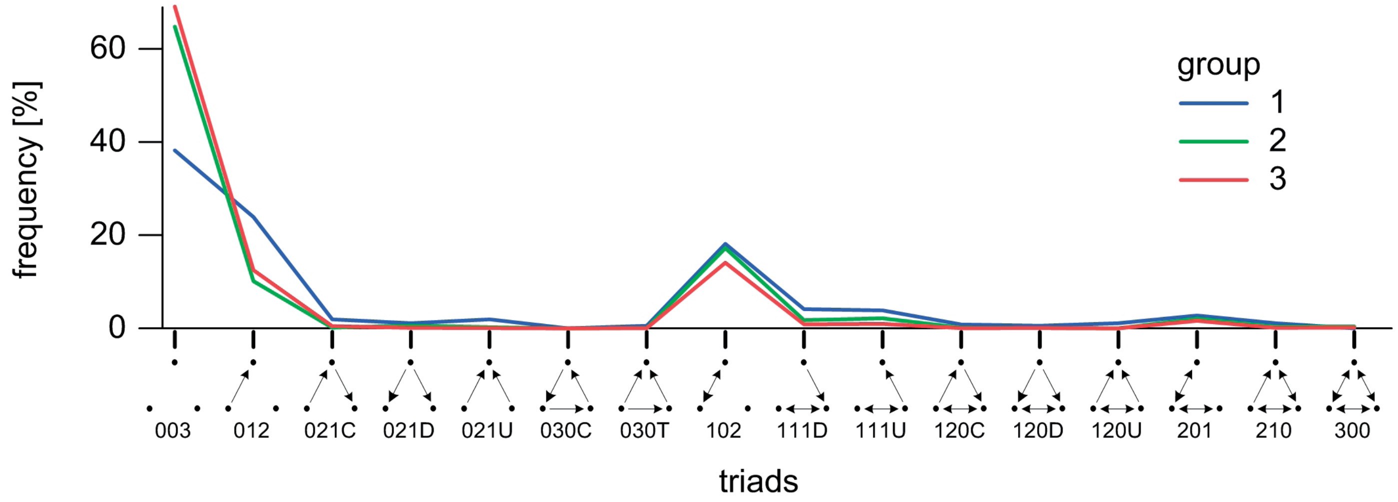


Figure 1 supplementary data: Frequency of motifs in A) the agonistic and B) the affiliative behaviour networks for each group in May 2009.

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