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Movement initiation in groups of feral horses

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ABSTRACT

Herds of ungulates, flocks of birds, swarms of insects and schools of fish move in coordinated groups. Computer models show that only one or very few animals are needed to initiate and direct movement. To investigate initiation mechanisms further, we studied two ways in which movement can be initiated in feral horses: herding, and departure from the group. We examined traits affecting the likelihood of a horse initiating movement i.e. social rank, affiliative relationships, spatial position, and social network. We also investigated whether group members join a movement in dominance rank order. Our results show that whereas herding is exclusive to alpha males, any group member may initiate movement by departure. Social bonds, the number of animals interacted with, and the spatial position were not significantly associated with movement initiation. We did not find movement initiation by departure to be exclusive to any type of individual. Instead we find evidence for a limited form of distributed leadership, with higher ranking animals being followed more often.

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1. Introduction

Ungulates, such as horses, move around in coordinated groups. The members of herds of ungulates, flocks of birds, swarms of insects and schools of fish have been described coordinating their movements. Models show that coordinating with nearby neighbours is sufficient to result in movement of the group, and when a small percentage of individuals start moving, or move in a certain direction, the whole group may follow (Gueron et al., 1996; Parrish et al., 2002; Seeley, 2002; Camazine et al., 2003; Rands et al., 2003; Couzin et al., 2005; Parrish and Viscido, 2005; Sumpter, 2006; Hemelrijk and Hildenbrandt, 2008, 2011, 2012; Mirabet et al., 2008; Conradt et al., 2009; Hildenbrandt et al., 2010; Pillot et al., 2011).

Whether animals initiate their movements in reality as suggested by theoretical studies remains an issue (Petit and Bon, 2010). However, a number of empirical studies of different species have shown that, as predicted by the computer models mentioned above, only a few individuals need to move to initiate the movement of the group in a certain direction, such as in groups of African

Buffalos (Prins, 1995), schools of fish (Reebs, 2000) and dolphins (Ward et al., 2008; Lusseau and Conradt, 2009), and even in human crowds (Dyer et al., 2009; Faria et al., 2010).

In certain taxa, movements may be initiated by individuals of one sex, for example by males in mountain gorillas (Schaller, 1964), and by females in some lemur species (Erhart and Overdorff, 1999). The frequency with which an individual initiates movement has been shown to correlate with the frequency of its agonistic interactions with other group members, i.e. with its dominance rank based on wins and losses in agonistic encounters (African Buffalo: Prins, 1995; cattle: Šárová et al., 2007, 2010; pigeons: Nagy et al., 2010; hyenas: Holekamp et al., 2000; feral dogs: Bonanni et al., 2010; horses: Tyler, 1972; Heitor et al., 2006). It may correlate with the frequency of its affiliative interactions with other group members, i.e. with its social bonding, which are usually analyzed from affiliative behaviour (primates: Byrne et al., 1990; King et al., 2008; feral dogs: Bonanni et al., 2010). In the wording of network science, movement initiation may correlate with the animals' connectedness in the group, i.e. with the number of connections through affiliative and agonistic behaviours with other members of the group (dolphins: Lusseau, 2007; Lusseau and Conradt, 2009). Furthermore, the influence individuals have on movement may depend on their spatial position within the group (Camazine et al., 2003). Animals in the spatial centre of the group are often of high social rank, as in cattle (Kabuga, 1993) and primates (Hemelrijk, 2002; Puga-Gonzalez et al., 2009). Similarly to primates (Hemelrijk, 2002; Puga-Gonzalez et al., 2009), horses at the centre of the

group participate in mutual grooming more often than those at the periphery (Schneider and Krueger, 2012). They therefore have the opportunity to build up more social bonds, which may, in turn, increase their influence on movement of other group members.

There are several reasons why horses are an interesting taxon for the study of the impact of single individuals on the initiation and direction of movements. Horses live in relatively stable social units, called bands, family groups or harems (Klingel, 1972; Moehlman, 2005, see for review: Linklater, 2000). These usually consist of between two and 25 individuals, including one to five stallions and several mares with their offspring (Tyler, 1972; Berger, 1977; Moehlman, 2002). Stallions without a harem gather in bachelor bands (Berger, 1977). Groups have been shown to synchronize daily and seasonal patterns of movements with each other in response to water, food, or climate (Feist and McCullough, 1976; Berger, 1986; Linklater et al., 1999) and show inter-group hierarchies at resource patches (Miller and Denniston, 1979; Franke Stevens, 1988, see for review: Linklater, 2000).

The most common types of movement initiation in horses are departure of an individual from the group, and herding. It is debated whether departures from the group can only initiate group movement if they are carried out by older, high ranking females, so called "lead mares" (Feist and McCullough, 1976), or whether all members of the group can initiate movement by departure, as claimed for Przewalski horses (Bourjade et al., 2009). Herding is thought to be unique to alpha males (Berger, 1977; Feh, 2005).

For both herding and departures, it may be expected that the movement initiation rate would be higher for individuals who interact with a larger number of their group members, regardless of whether the interactions are agonistic or affiliative (Croft et al., 2008; Lusseau and Conradt, 2009), and for individuals in central spatial positions (Kabuga, 1993; Couzin et al., 2002; Hemelrijk, 2002). Generally, individuals with many and strong social bonds (i.e. affiliative relationships) may be expected to initiate more movements than less bonded individuals, partly because bonded females have been shown to protect each other's offspring (Cameron et al., 2009) and may therefore also move together to remain in close proximity. Furthermore, because horses usually have a linear dominance hierarchy (Houpt et al., 1978), social rank may also affect the degree to which horses are followed when they depart from the group (Tyler, 1972; Heitor et al., 2006).

To study these factors, we observed movement initiations and social behaviours in three groups of feral horses. We derived the horses' social ranks by applying an average dominance index (ADI), which we chose for its robustness and computational simplicity (Hemelrijk et al., 2005). The horses' affiliative relationships and group structures were established from behavioural data of the groups of horses by applying common network analysis. This measures the quantity and quality of relationships between pairs of individuals and among group members (see for review: Croft et al., 2008). Additionally, we measured the spatial position of the horses when the groups were grazing or resting. Animals either stayed at the centre, in an inner zone, or at the periphery of their group.

We analyzed whether (a) particular "lead mares" initiate movements by herding and by departures from the group. Furthermore, we evaluated whether the likelihood of initiating movements is affected by the animals (b) rank, (c) social bonding, and (d) connectedness. We also examined whether (e) in small groups all animals interact with each other, whereas in large groups they do not, and whether (f) high ranking animals stay in the centre of the group and initiate movements from the centre. The spatial position of the animals would therefore indicate the likelihood of initiating movements. Finally, we assessed (g) the effect of social rank on the number of individuals that followed a departing animal, and whether they follow the others in the order of their rank.

2. Materials and methods

2.1. Animals

We investigated the behaviour of 55 feral horses (*Equus ferus caballus*). They are members of 3 social groups (groups 1–3) of a population of about 300 feral horses 'Cavalli di Esperia', which roam freely in the mountains near Frosinone, Italy. The horses' ages ranged between 1 and 23 years at the time of the study, but precise ages were only known for half of them. Foals up to the age of 1 were not considered in this study, because of their special status in the social organization of the groups (Rutberg and Keiper, 1993). Each group consisted of several females and their offspring, and 1–3 males. Group 1 consisted of 11 animals, including 1 male; group 2 had 19 animals, including 1 male; group 3 had 25 animals including 3 males. All horses were individually identified by their brands and colouration (Table 1). The horses are provided with water in the summer and hay in the winter. Other than that, the horses feed on the natural vegetation in the area. Once a year they are rounded up for the branding of females and removal of most male offspring.

2.2. Data sampling

The horses' behaviours and movements were sampled ad libitum (continuous recording) for 14 h per group in May 2009, and their spatial organization by scan sampling (instantaneous sampling, hourly) during 15 h per group in May 2010 (Martin and Bateson, 2007). Behavioural data for social rank calculation were also collected in October 2009 and May 2010 for a previously published study. The groups' hierarchies were shown to be stable throughout the observation periods. For detailed data on hierarchy calculations and the horses' individual affiliative and agonistic behaviour see Schneider and Krueger (2012). All observations were made during daylight hours, for no longer than six and a half hours at a stretch. For each group, they were spread on average over 4 separate days and over a period of no more than 15 days. Movements and social behaviours were observed when the groups were grazing, or roaming freely through a mountain range, and when all group members were visible. In a few cases, observations were made when at least three-quarters of the group members were visible and the position of the remaining group members had been recorded. The spatial organization was noted when all horses were visible, and when they stopped moving and were grazing or resting. At these times each horse was between 1 and 20 m from the next and the group was within an area with a radius of 100 ± 20 m.

Before recording the data the horses were habituated to the presence of the observers. The observers stayed in view of the horses, about 100–200 m away. When the horses were calm and continued grazing, which took between 1 and 2 h on 1–3 consecutive days depending on the group, the distance was slowly reduced to about 50 m while the observers identified the horses. When the groups changed locations the observers followed on foot. If necessary, binoculars were used for observation.

Three observers participated in each observation, so that two could continue observing while one person was writing. They noted movement initiations by herding or departures from the group, the social behaviour, the spatial organization of the horses and the order during movement. These parameters were defined as follows:

(1) Initiation of movement

(1a) Herding: can move individual animals or whole groups. A typical herding posture indicates an animal's intention to chase some or all of its group members in a certain direction (McDonnell and Haviland, 1995; McDonnell, 2003; Fig. 1b). Herding was

Table 1
Data of individual horses, movement initiations by departures and herding.

Group	Horse ID[a], description	Rank	Sex	Departures			Herdings	
				No. departures	% departures being followed	Mean (No. following horses/followed departures)	No. cases whole group follows	Whole[b] group moves
1	1, stallion	1	Male	32	44	4	3	3
	2, dark brown	2	Female	32	44	2.2	1	0
	4, haflinger, bald-faced	3	Female	10	50	1.4	0	0
	5, haflinger	4	Female	34	41	2.4	1	0
	6, black, brand 692	5	Female	22	36	3.1	1	0
	9, white	6	Female	36	11	5.5	2	0
	10, black, brand 785	7	Female	29	31	1.4	0	0
	11, black	8	Female	21	19	3.5	1	0
	12, chestnut	9	Female	24	12.5	4	1	0
	13, black, brand 362	10	Female	44	20	2.7	1	0
	14, black	11	Female	14	14	2	0	0
Group 1: mean ± SD				27.1 ± 10	29.32 ± 14.5	2.93 ± 1.25	1 ± 0.89	0.27 ± 0.9
2	1, black, brand 142	1	Female	14	57	3	0	0
	2, stallion	2	Male	14	71	4	1	2
	3, brownish	3	Female	7	57	1	0	0
	4, black, brand 148	4	Female	17	41	1.14	0	0
	5, black, brand 355	5	Female	10	30	8	1	0
	6, black, diagon.stripe	6	Female	10	60	1.3	0	0
	7, black, brand 87	7	Female	14	21	1	0	0
	9, black, brand 668	8	Female	14	29	2	0	0
	10, black curly mane	9	Female	6	83	1.8	0	0
	11, black, brand 665	10	Female	20	5	1	0	0
	12, dark brown	11	Female	24	17	1.25	0	0
	15, white	12	Female	32	28	2.5	1	0
	16, black, brand 003	13	Female	16	25	7.25	1	0
	17, bay	14	Female	20	15	1.7	0	0
	18, black, brand 425	15	Female	18	33	5	1	0
	19, black, brand 09	16	Female	15	27	1.75	0	0
	20, black, brand 192	17	Female	20	40	1.6	0	0
	21, black, brand 843	18	Female	19	5	1	1	0
	22, black, brand 911	19	Female	27	15	7	1	0
Group 2: mean ± SD				16.68 ± 6.51	34.68 ± 21.92	2.8 ± 2.32	0.37 ± 0.49	0.1 ± 0.46
3	1, dark brown	1	Female	5	40	2	0	0
	2, black, brand 676	2	Female	14	57	1.25	0	0
	3, black, brand 951	3	Female	5	40	2	0	0
	4, black, brand 698	4	Female	4	25	1	0	0
	5, stallion	5	Male	14	43	1.33	0	5
	6, black, brand 226	6	Female	3	33	3	0	0
	7, black, brand 475	7	Female	8	37.5	1.7	0	0
	8, bay	8	Female	8	12.5	1	0	0
	10, black, brand 190	9	Female	2	0	0	0	0
	11, huge black	10	Female	9	78	1.14	0	0
	12, light bay	11	Female	14	14	2	0	0
	13, brownish	12	Female	6	33	1.5	0	0
	14, black, brand 433	13	Female	4	75	3	0	0
	16, black, brand 431	14	Female	10	0	0	0	0
	17, black, brand 430	15	Female	11	45	1.8	0	0
	18, black, brand 867	16	Female	8	25	1	0	0
	19, black, brand 344	17	Female	7	0	0	0	0
	20, black, brand 912	18	Female	6	83	1.2	0	0
	21, black, brand 962	19	Female	9	33	1.33	0	0
	22, haflinger stallion	20	Male	2	0	0	0	0
	23, white	21	Female	26	23	1.5	0	0
	25, haflinger yearling	22	Male	0	0	0	0	0
	26, black, brand 78	23	Female	8	0	0	0	0
	27, yearling, black	24	Female	0	0	0	0	0
	28, black, brand 350	25	Female	7	0	0	0	0
Group 3: mean ± SD				7.6 ± 5.5	27.88 ± 26.1	1.1 ± 0.93	0	0.2 ± 1

[a] Brands were noted when visible.
[b] Herding made the whole group move on each occasion.

counted as movement initiation (Fig. 1b), if any or all of the animals moved in the direction indicated by the individual doing the herding. The number of animals responding was recorded for each instance of herding.

(1b) Departure from the group: A departure was recorded when a particular animal moved ≥3 m away from the closest group member towards unoccupied space. Unoccupied space could be inside or outside the group's perimeter, and if the animal started to move
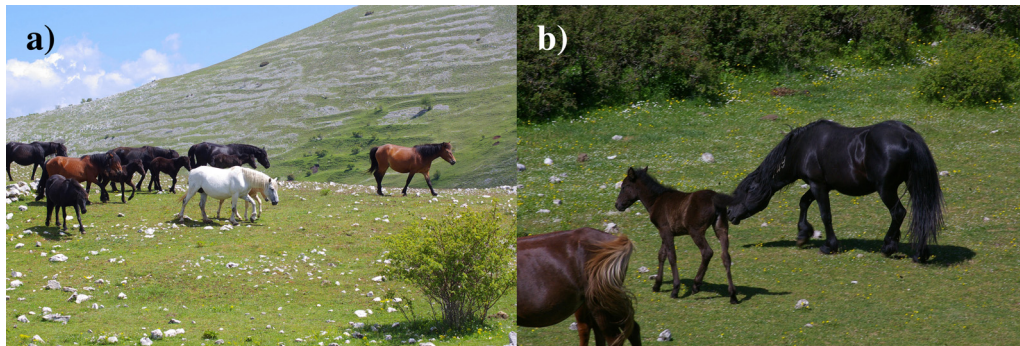
Fig. 1. Movement initiations. (a) depicts a movement initiation by a mare (far right) departing from the group. (b) depicts a stallion (far right) herding a foal and other group members.

from the centre of the group it may or may not have passed other group members on the way. A movement was considered a departure if the animal moved towards unoccupied space in a single continuous bout that was observed for up to 10s, or if it moved in multiple bouts, with in-between stops of ≤2s, that were observed for up to 30s (Fig. 1a).

Departures were considered to have initiated movement when several conditions were met:

i) When at least 1 animal spontaneously followed the departer either immediately (after ≤4s) or after a delay (after <60s).
ii) When the animal(s) followed the departer for approximately 50% of the distance or more covered by the departer.
iii) When the animal(s) followed at an angle of approximately 15° or less to the departer's direction (Fig. 1a).

Movements of mares towards each other that led to the exchange of social behaviours were not counted as movement initiations, because the approached animal did not follow the movement direction of the first horse to move. The number of animals responding was recorded for each departure from the group.

(2) Social behaviour

We counted agonistic actions of group members, such as threats to bite or to kick, bites, kicks, chases, retreats, and approaches as well as affiliative behaviours, such as mutual grooming, and approaches in order to groom (one animal approaching another preceding mutual grooming), mutual approaches (both animals approach each other), or neutral approaches (one animal approaching another without the approached animal making any perceptible response) (Feist and McCullough, 1976; McDonnell and Haviland, 1995; McDonnell, 2003; Fedurek and Dunbar, 2009).

The classification of behaviours as either affiliative or agonistic was determined by the response of the receiver. For example, if a receiver responded to an approach by moving towards the initiator, giving no perceptible response or engaging in reciprocal grooming, this may indicate a desire for friendly interaction and proximity (Silk et al., 2003; Cameron et al., 2009) and was considered affiliative. In contrast, approaches that elicited a retreat by the approached animal, or a threat to kick or to bite, or actual kick or bite etc. were considered agonistic.

(3) Spatial organization

When the members of each group were grazing or resting in areas with a radius of 100 ± 20 m, and were between 1 and 20 m from each other, we drew spatial distribution graphs once an hour (± 15 min) during the 15 h of observation in 2010 ($N = 15$). On the

graphs we defined three spatial positions: the centre, the inner zone, and the periphery of the group.

a) Centre: we analyzed the geometric centre of the spatial distribution graphs and described the horse closest to the middle as central. In cases in which several horses were equally distant from the centre they were all said to be central.
b) Inner zone: all horses that were not at the centre of the group and not on the peripheral line were said to be in the inner zone.
c) Periphery: we connected all horses on the external border of the group with a line and described these horses as peripheral.

(4) Order of following

For movements initiated by departure, we analyzed the order in which the animals followed. We recorded the initiator and the followers in the order in which they followed, distinguishing front and rear position in pairs. The initiating horse was referred to as the front horse, and the next the rear horse, then the rear horse became a front horse when it was followed by another animal, and so forth. For example, if 4 horses were involved in a movement, we evaluated 3 pairs of horses: first and second, second and third, third and fourth. From this, we can infer who walks behind whom and the relationship these 2 animals may have, but we cannot conclude precisely which horse the followers intended to follow. For example, a horse may walk behind the third horse in the line, but intend to follow the first horse. For this reason, we analyzed movements in pairs of animals, as previously done with pigeons (Nagy et al., 2010).

2.3. Data processing and analysis

All cases in which horses departed from the group were recorded as departures. If a departing horse was followed, it was counted as a movement initiation. For each horse we calculated the percentage of departures leading to movement initiation.

To compare the level of response to herding with the level of response to departing from the group, we analyzed the percentages of group members moving in response to each.

2.4. Behavioural recording and measurement

Behaviours were recorded as follows:

a) For agonistic interactions the aggressor received one point for the aggression and one point if the challenged animal retreated.
b) For affiliative interactions involving mutual approaches and mutual grooming, one point was allocated to each of the two participating animals. For neutral approaches (with no perceptible

response by the approached animal) and grooming approaches (followed by mutual grooming thereafter) one point was allocated to the initiating animal only.

2.5. Average dominance index (ADI)

We determined the dominance rank of individuals by observing agonistic encounters, such as approaches, retreats, threats to bite or to kick, bites, kicks, and chases (Feist and McCullough, 1976; McDonnell, 2003). The horses displayed 769 agonistic interactions in group 1, 706 agonistic interactions in group 2, and 756 agonistic interactions in group 3. We used a modified average dominance index (ADI) for the analysis of the dominance ranks. It is calculated as follows: The dominance index per pair of individuals, w_{ij} is the number of times an individual i won against a certain opponent j (x_{ij}) divided by the total number of agonistic encounters between the pair ($x_{ij} + x_{ji}$). It thus becomes, $w_{ij} = x_{ij}/(x_{ij} + x_{ji})$. Individuals were counted as winners when their interaction partner retreated one step or more. If two individuals were not involved in an encounter with each other, this pair 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 $1/N\sum w_{ij}$. A higher value indicates a higher dominance rank in the group. The method has been shown to be more robust than several others (Hemelrijk et al., 2005). For comparisons of ranks between groups we calculated the relative social ranks in each group by dividing the absolute rank by the number of group members.

2.6. Connectedness, social bonding, and group structure

To evaluate group structure and each horse's social bonding and connectedness within their group, we applied common network analysis (see for review: Wasserman and Faust, 1994; Croft et al., 2008); regarding network measures, we analyzed the number of agonistic and affiliative interactions for each horse (i.e. a weighted but undirected degree, Croft et al., 2008; Fig. 2a). Each group represented one social network, as illustrated in Fig. 2. The nodes represent the individuals and the edges represent their interactions.

To analyze social bonding, we considered the frequency of affiliative behaviours among group members (Fig. 2b). We merged the instances of mutual grooming and of mutual and neutral approaches together, as all three actions are highly inter-related in horses (Cameron et al., 2009). The horses displayed 119 affiliative interactions in group 1, 302 affiliative interactions in group 2, and 178 affiliative interactions in group 3. We assumed that, in horses, dyads which frequently display such affiliative interaction have strong social bonds (Cameron et al., 2009) as has been shown for primates (Silk et al., 2003; Fedurek and Dunbar, 2009).

We measured the connectedness of each group member by adding the total number of agonistic interactions to the total number of affiliative interactions (including neutral approaches) for each horse.

To analyze the group structure, we investigated whether horses are organized in small-world networks in which all group members interact directly and regularly with each other. Small-world networks can be measured by analysing a group's clustering coefficient and the average path length from the agonistic and affiliative interactions among group members. The clustering coefficient shows the proportion of group members that interact with each other, and ranges from 1 for interactions with all animals to 0 for no interactions. The average path length gives a value showing whether animals pass on their information directly to each other, with 1 for direct information transfer and greater than 1 for information passed via other animals. In small world networks

the clustering coefficient and the average path length of a group approach the value 1 (Watts and Strogatz, 1998; Fig. 2a).

2.7. Spatial organization

For each horse we calculated the percentage of instances in which it was recorded (a) at the centre, (b) in the inner zone, or (c) at the periphery from 15 spatial distribution graphs per group.

2.8. Statistics

For statistical analysis and figures we used the SPSS 20 software package and the R-Project statistical environment (R Development Core Team, 2013), and to analyze network metrics we used the software package Ucinet (Borgatti et al., 2002). Data sets were analyzed separately for each social group. For parametric large datasets we used t-tests. To compare datasets of small sample sizes we used non-parametric tests. Correlations were calculated with the Kendall-tau-b test. Mann–Whitney U-exact tests were applied to compare independent datasets, Wilcoxon-exact tests to compare dependent datasets, Binomial tests for likelihood equations in binomial datasets and Chi-square tests for likelihood equations in metric datasets. Finally, statistical results from different groups were combined using Fisher's combination test (Fisher, 1925). All tests were two-tailed and the significance level was set at 0.05.

3. Results

3.1. Herding

Herding behaviour was shown exclusively by the 3 alpha males (i.e. by the stallion of the group, or the highest ranking stallion if there was more than one stallion in the group; Fig. 1b). It was shown neither by lower ranking males nor females (Fisher's combination test: $N = 3$, $\chi^2 = 46.76$, $P < 0.001$, Table 1).

Alpha males were higher ranking than most members of their group (Fisher's combination test: $N = 3$, $\chi^2 = 50.66$, $P < 0.001$, Table 2) but not always in the top position. In the smallest group (group 1: $N = 11$) the alpha male was top ranking, in the middle sized group (group 2: $N = 19$) he was rank 2 and a mare was top ranking, and in the largest group (group 3: $N = 25$) the alpha stallion was in rank position 5 and mares had the highest four ranks. Alpha males were similar to other individuals in their group in their connectedness, their degree of social bonding (all $P > 0.05$, Table 2; Fig. 2b), and their spatial position within their group (all $P > 0.05$ for peripheral, inner and central positions, Table 2).

In all three groups, herding always caused the whole group to move (Fisher's combination test: $N = 3$, $\chi^2 = 46.76$, $P < 0.001$), and initiated group movement more consistently than departure (Fisher's combination test: $N = 3$, $\chi^2 = 17.48$, $P = 0.007$; group results: Table 2; Fig. 4).

3.2. Departures from the group

All horses, except two yearlings in group 3, departed from the group (numbers of individual departures: Table 1; mean departures per group: Table 3). No member of any group departed significantly more often than any other member of their own group, irrespective of age or sex (t-test: group 1: $N = 11$, $T = 0$, $P = 1$; group 2: $N = 19$, $T = 0.003$, $P = 0.99$; group 3: $N = 25$, $T = 0$, $P = 1$; Table 1).

The higher the social rank of the horse, the more often it was followed by others (Fig. 1a; Fisher's combination test: $N = 3$, $\chi^2 = 28.7$, $P = 0.004$, results for separate groups: Table 3, individual data: Fig. 3, Table 1).

The percentages of initiations of movements did not correlate with the animal's connectedness in the group (Fig. 2a, all $P > 0.05$,
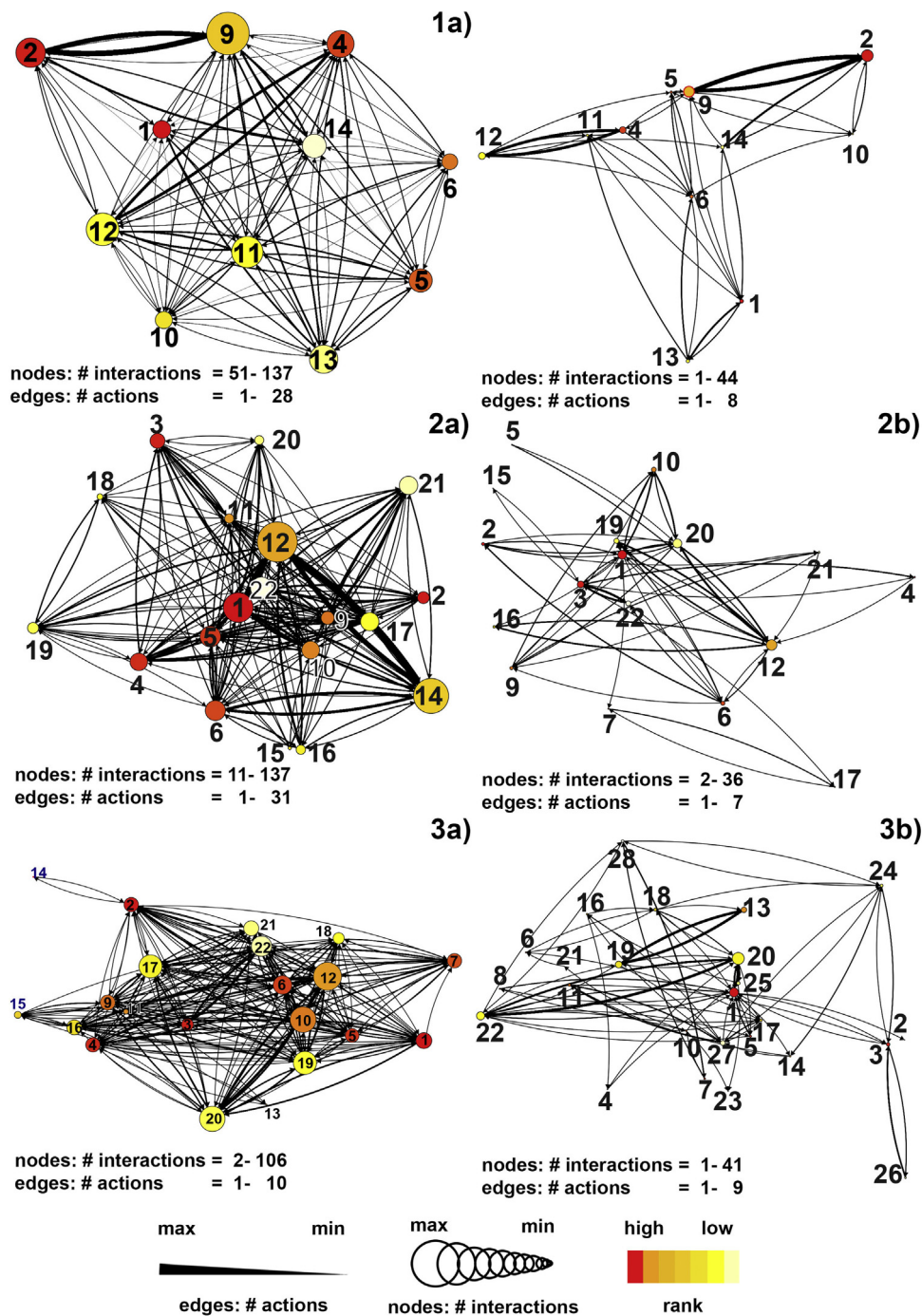
Fig. 2. (a) Connectedness and (b) social bonding. The graph depicts networks of the horse groups 1, 2 and 3. The animals (i.e. nodes) are represented by the dots and numbered with their ID (Table 1), with no. 1 being the highest rank. The size of the dots depicts the total number of interactions of one animal with all its group members. The arrows (i.e. edges) between the nodes represent the behaviours displayed between individual horses, and are "directed", i.e. they point in the direction of the particular behaviours displayed, and "weighted", i.e. their thickness represents the number of behaviours displayed (for more information see Croft et al., 2008). (a) depicts the horses' agonistic and affiliative behaviours used for calculating their connectedness and (b) the affiliative behaviours used for analysing their social bonds. We have chosen a spring embedded design that places the animals that are connected to most other animals in the middle. Note that the network for each social group resembles a typical small world network, in which animals interact directly with most group members with approximately the same frequency (Watts and Strogatz, 1998).

Table 3), nor with its social bonding (Fig. 2b, all $P > 0.05$, Table 3), nor with its spatial position in the group (mostly $P > 0.05$ for peripheral, inner and central positions), apart from the largest group (group 3: $N = 25$) where central animals initiated fewer movements than other group members (Kendall-Tau-b test: $N = 21$, tau = -0.461, $P = 0.04$). However, the other spatial positions did not correlate with movement initiations for group 3 (inner zone and periphery), and none correlated for groups 1 and 3 (all $P > 0.05$). Notably, in this

largest group (group 3: $N = 25$), departure by a single individual never led to movement of the whole group.

3.3. Group structure

Each horse interacted with nearly all other members of its group directly. This is clear from the clustering coefficient of each group being close to 1 (group 1: $N = 11$, clust. coeff. = 0.96; group 2: $N = 19$,

Table 2
Herding behaviour, its effectiveness and relationship to social variables and spatial position.

Group	N	Effectiveness herding[a]		Male rank[b]		Male connectedness[b]		Male social bonding[b]		Male spatial position[b]
		Z	P	Z	P	Z	P	Z	P	All P
Group 1	11	−1.61	0.08	−2.93	**0.001**	−0.95	0.55	−1.58	0.18	>0.05
Group 2	19	−1.93	**0.05**	−3.72	**<0.001**	−0.55	0.74	−1.57	0.21	>0.05
Group 3	25	−2.42	**0.04**	−4.286	**<0.001**	−1.53	0.16	−1.53	0.16	>0.05

[a] Effectiveness of initiating movements by herding compared with departure, Mann–Whitney U-exact test.
[b] Social rank, connectedness, social bonding, and spatial position of herding alpha males compared with departing animals, Mann–Whitney U-exact test. Significant results are depicted in bold.

Table 3
Departures from the group, their numbers and correlation with social variables and spatial position.

Group	N	Indiv. departures		MI and rank[a]		MI and connectedness[a]		MI and social bonding[a]		MI and spatial position[a]
		Ave.	SD	tau	P	tau	P	tau	P	P
Group 1	11	27	10	−0.62	**0.008**	0.15	0.53	0.28	0.24	Most > 0.05
Group 2	19	16.7	6.5	−0.44	**0.009**	0.31	0.07	0.24	0.17	All > 0.05
Group 3	25	7.6	5.5	−0.39	**0.008**	0.26	0.08	0.09	0.57	All > 0.05

[a] Correlations between percentages of movement initiations (MI), and rank, connectedness, social bonding, and spatial position, Kendall-Tau-b test. Significant correlations are depicted in bold.

clust. coeff. = 0.73; group 3: N = 25, clust. coeff. = 0.55) and the average path length for information transfer being close to 1 also (group 1: N = 11, path length = 1.05, group 2: N = 19, path length = 1.4; group 3: N = 25, path length = 1.45; Fig. 2a). This implies that information was mostly transferred directly and not via other group members. Therefore, horses may be considered to be organized in small-world networks. Note that with increasing group size the clustering coefficient decreases and the path length increases. The larger the group the fewer the horses which interacted with each group member directly.

When grazing or resting almost all horses were equally likely to be located at the centre, in the inner zone or at the periphery of their group (all P > 0.05), and the rank of the horses did not correlate with their spatial position (all P > 0.05 for being central, in the inner zone or at the periphery of their group). However, in group 1,

Fig. 4. Success of departing versus herding. Herding is more successful than departing in initiating movement (Table 2). The y-axis depicts the % of group members that were moved through herding and departures. Whiskers depict the standard deviation, * stands for $P \leq 0.05$.

two females were more likely to be central (Chi-square test: N = 9, χ^2 = 8.33, df = 3, P = 0.04).

3.4. Movement order

In groups 1 and 3, but not in group 2, the horses usually followed each other in rank order, i.e. the leading horse was followed by a lower ranking horse significantly more often, and this horse was followed by an even lower ranking horse and so on (group 1 and 3: Binomial test both P < 0.05; group 2: Binomial test: P > 0.05, see Table 4). For all groups combined, following in rank order
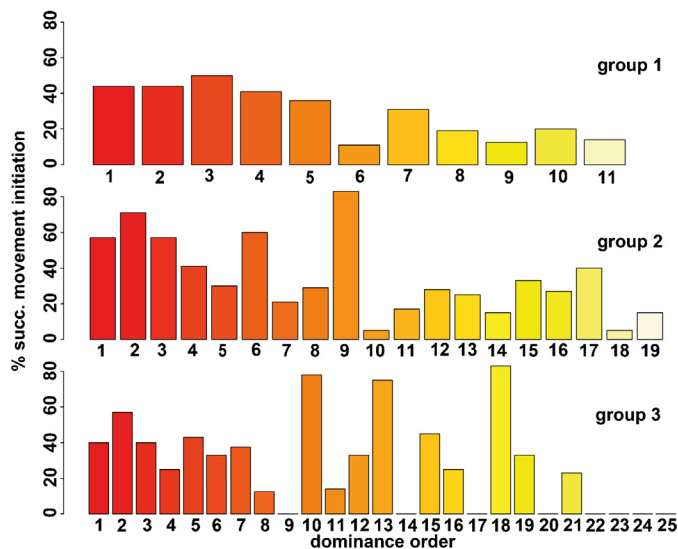

Fig. 3. Distribution of movement initiations by departing among group members. The graph depicts the horses of group 1, 2 and 3. The x-axes list individual horses according to their social rank, with the rank decreasing along the axes and with the intensity of the grey shade (i.e. with the change from red over yellow to white in the coloured online version). The y-axes show the individual percentages of movement initiations by departing no matter how many animals followed at each occasion. Please note that the percentages were calculated for individual performances, and do not add up to 100 for one group.
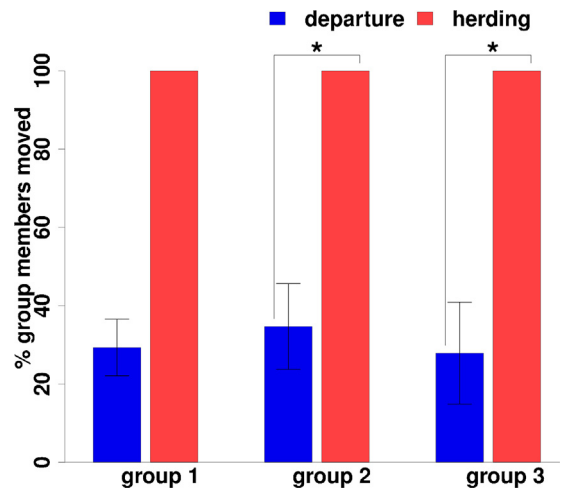
Table 4
Leader dominance in pairs of horses during movements, Binomial test. Significant values are depicted in bold.

Group	N = horses	N = pairs	% leader is dominant	P (leader is dominant)
Group 1	11	129	63	**0.003**
Group 2	19	89	53	0.67
Group 3	25	88	59	**0.018**

was not significant (Fisher's combination test for all groups: $N = 3$, $\chi^2 = 20.45$, $P = 0.06$).

4. Discussion

Consistent with previous theoretical and empirical studies, we found the actions of a single individual may cause some or all members of a group to move. When this happened by herding we classified it as despotic, because a single leader imposed global movement of all group members (Henzi et al., 1998; Walther, 1991; King et al., 2008). In the present study, herding was exclusively shown by alpha males and, irrespective of the group's size, it caused the whole group to move on each occasion. However, in an earlier study of feral horse groups of various sizes, herding was sometimes directed at selected, individual group members (Feist and McCullough, 1976). The reported cases included stallions gathering stray mares into their harem, or herding a mare within their harem in the attempt to mate with her. No cases like these were observed in this study, maybe because of low mating competition as surplus males were largely removed.

Furthermore, movements of a few animals and of the whole group could be initiated by the departure of any individual group member. Stallions, mares, and offspring older than one year all initiated movement by departing. This is comparable to what has been called "distributed leadership" in fish (Levin and Grillet, 1988) or "variable leadership" in geese and other species (Lamprecht, 1992; Mirabet et al., 2008).

4.1. Sex and rank is decisive in movement initiation by herding

Initiation of group movement by herding was only displayed by alpha males, and neither by lower ranking males nor females. Thus herding appears to depend on both sex and rank, and as it was only done by males, it may serve to control females and their offspring.

4.2. Movement initiation by departure from the group depends on social rank

When departing from the group, high ranking animals were followed more often than subordinates. It has been argued that dominants may initiate more movements because they make more departures (Petit and Bon, 2010), but in the present study there was no correlation between rank and number of departures. The departure of dominants resulting in the movement of others more often than the departure of subordinates is consistent with findings in other species (African Buffalo: Prins, 1995; white faced capuchins: Leca et al., 2003; Tonkean Macaques: Sueur and Petit, 2008; brown lemurs: Jacobs et al., 2008; cattle: Šárová et al., 2007, 2010; pigeons: Nagy et al., 2010; hyenas: Holekamp et al., 2000; feral dogs: Bonanni et al., 2010).

Similar to findings in Canada geese (Raveling, 1969) and bar-headed geese (Black, 1988) the departure of immature horses (between 1 and 3 years of age) very rarely initiated movement by others. This may be because of their youth, and consequently low rank, as age and rank are correlated in most horse groups (Houpt et al., 1978; Keiper and Sambraus, 1986; Linklater et al., 1999). It may be that young subordinates follow the movements of older, more dominant horses to benefit from their greater experience, as has been shown in elephants, primates and dolphins (King et al., 2008; Lusseau and Conradt, 2009; McComb et al., 2011). In other words, the preference to stay with the majority of group members and not to follow a single, departing individual, as in sheep (Pillot et al., 2011), may be even stronger when a subordinate rather than a dominant animal leaves the group.

As in pigeons (Nagy et al., 2010), there was a significant trend for horses to follow each other in rank order in groups 1 and 3:

i.e. the leading horse was followed by a lower ranking one, and this horse was followed by an even lower ranking one, and so on, but not in group 2. It should, however, be noted that while this trend is significant in groups 1 and 3, it still only applies in 63% and 59% of cases respectively, and 53% in group 2. Group 2 showed the same trend, but not significantly so. We can therefore conclude that dominant horses initiate more movements and that the order during movement usually, but not always, reflects the dominance hierarchy of the group.

Our results support previous studies on movement decisions in equids, which suggest that dominant equids lead more often than subordinates (Klingel, 1964, 1967; Feist and McCullough, 1976; Heitor et al., 2006). However, contrary to some studies in horses (e.g. Feist and McCullough, 1976) and to widespread popular belief, our findings do not support the theory that particular females initiate all movements and therefore take permanent leadership roles.

The consistent influence of social rank on movement initiations, and almost significant effect on movement order in feral horses, is in line with our previous study in which we showed that horses copy the following behaviour of higher ranking animals (Krueger and Heinze, 2008). Horses may pay more attention to higher ranking animals because they are usually older and the information provided by them may be more reliable than that provided by lower ranking or juvenile animals (Menzel, 1973; Reebs, 2000; List, 2004). A similar pattern is found in baboons where all group members react instantaneously to alarm calls given by high ranking adults, but not to those given by juveniles (Seyfarth and Cheney, 2003).

4.3. Group structure, social bonds, and spatial position

The number of interactions with other group members was similar for all individuals. Therefore the horses in the present study can be considered to be organized in small-world networks (Watts and Strogatz, 1998; Croft et al., 2008), in which most members interact with each other directly and with similar frequency. This group structure provides the basis for equal information transfer and thus for rapid transfer of movement information among all group members. Nevertheless, the number of group members with which animals interacted did not correlate with the number of movements initiated.

We also find no evidence that horses preferentially follow those group members with which they maintain strong bonds, either for departure or herding. This contrasts with findings in feral dogs (Bonanni et al., 2010) and primates (Menzel, 1973; Byrne et al., 1990; King et al., 2008), where social bonds were a significant factor in the initiation of movements. Furthermore, spatial position did not appear to affect movement initiation. Firstly, the horses did not show socially sorted spatial structures (Hemelrijk, 2000) when grazing or resting, and secondly, contrary to our initial expectations, when individuals were at the centre, they did not initiate movement more often than horses in other positions. In the largest group, central individuals actually initiated fewer movements than others.

Our findings differ from studies in primates and cattle, where dominant animals stay at the centre of the group (Kabuga, 1993; Hemelrijk, 2002; Puga-Gonzalez et al., 2009) and generally initiate the majority of movements (also referred to as the hierarchical or centralized control model, see for review Petit and Bon, 2010). Although dominant horses are more likely to initiate movements, they may start from any spatial position. Our findings are in line with a recent theoretical study (Sueur et al., 2012) which proposes that animals display distributed leadership when living in decentralized social organizations, such as the horses' small world networks.

4.4. Comparisons between groups

Comparisons between the groups should be treated with caution because of the small number of groups in this study ($N = 3$). Still we found some interesting trends concerning the social ranks, group structure, spatial position and movement initiations in the different groups.

The stallions were lower in rank in the larger groups, which is consistent with theoretical findings where it has been argued that larger groups are more unstable (Mesterton-Gibbons and Dugatkin, 1995; Pusey and Packer, 2003). Furthermore, the finding that in the larger groups (2 and 3) not all the group members interacted directly with each other is consistent with the theory of groups splitting into subgroups as they become increasingly larger (see for review: Croft et al., 2008).

Both the increasing costs of maintaining a large, unstable group and the increasing risks of losing contact within such groups (Pusey and Packer, 2003) may be the reasons why fewer animals departed from larger groups, those that did were followed by fewer group members, and fewer movements of the whole group were initiated. This needs to be tested in a follow-up study with a large number of groups of different sizes.

4.5. Self-organized movement or democratic decisions?

Coordinated movement has been said to be a result of self-organization and has been shown in a variety of animal species (e.g.: Prins, 1995; Šárová et al., 2007; Nagy et al., 2010) and humans (Dyer et al., 2009). However, it remains unclear whether, and if so, how, movement can be initiated through democratic decisions (Conradt and Roper, 2005). Some theoretical studies claim global decision making is necessary to come to a democratic decision on where to go, and may include some kind of voting process among the group members on whether or not to follow (List, 2004; King and Cowlishaw, 2009).

For example, recruitment behaviour has been considered to be evidence of voting processes. Tonkean macaques are described as displaying recruitment behaviour, such as switching between moving a couple of steps away from the group, then stopping and glancing back at their group members, until the group follows (Sueur and Petit, 2010). Other studies discuss particular behaviours of the whole group as evidence of voting on movements. African buffalos were thought to vote on the potential movement direction by lying oriented to their preferred direction (Prins, 1995). However, more recent findings suggest that cows may coincidentally align with each other because they all adjust their body orientation to the magnetic field (Begall et al., 2008). Furthermore, groups of geese orientated in the same direction and showed a heightened arousal state and increased vocalisations before departure, but whether this can be considered evidence of voting is unclear (Ramseyer et al., 2009).

Theoretical modelling proposes that animals can increase their influence on group movement initiations, without any communication or knowledge of other group members' needs, simply by heading towards their own target rather than aligning with their neighbours. However, they would do so at a risk of group fragmentation, and therefore of losing the safety and information of the group (Conradt et al., 2009). This may explain why animals with high needs for resources, such as food, water, shelter or mating partners, lead group movement more often, such as lactating plains zebra females which lead the group to water (Fischhoff et al., 2009). In horses, animals in need may have a higher incentive to make the group move but, as in many other taxa, may be more likely to be followed the higher their social rank (African Buffalo: Prins, 1995; cattle: Šárová et al., 2007, 2010; pigeons: Nagy et al., 2010;

hyenas: Holekamp et al., 2000; feral dogs: Bonanni et al., 2010; horses: Tyler, 1972; Heitor et al., 2006).

In a nutshell, it remains difficult to clearly demonstrate democratic decisions over movement initiations in animals. Consistent with recent findings in Przewalski horses (Bourjade et al., 2009), in our present study there were no indications that feral horses use vocalisations or body postures to initiate movement behaviour when departing from the group, and thus there is no clear evidence for voting or democratic decisions to move. We therefore suggest that horses coordinate their movement by self-organization, as animals of many taxa have been shown to do (Conradt, 2012).

5. Conclusion

In conclusion, horses start moving as a result of herding by alpha males and as a result of departures from the group by single individuals. Departing individuals can be any group member and not particular females, as has often been suggested. Our study subjects displayed a limited kind of distributed leadership in movement decisions, because even though all group members may depart from the group, high ranking animals are followed more often than low ranking animals.

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