

The Roles of Individuals and Social Networking in a Small Group of Domestic Horses at Pasture

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Abstract

100 h (500 horse h) of critically assessed observations were analysed from two pastoral situations on decision making and social networking in a herd of 5 arab and arab x horses of the Druimghigha Stud, behaviourally studied since 1978. Roles such as decision maker (the oldest mare) or follower (the youngest filly) and the popularity of each individual from whom they chose to be near were analysed. Social network analysis indicated the centrality of an individual, cohesive bonds among 3 mares and a sub group of the filly and the gelding. A network closure towards the gelding was also illustrated, while he attempted to build bridges to integrate into the group. Affiliative interactions and responses significantly outnumber aggressive ones ($p < 0.01$) and confirm the importance of social cooperation, rather than a dominance hierarchy which is based on an assumption of competition.

These results are discussed and it is suggested that the most important reason to be social in large herbivores may be to pass on ecological knowledge to increase survival and reproductive success. To do this, individuals must learn to recognize the decision maker with the most knowledge and appropriate personality in order to remain/ become part of the group.

Graphical Abstract



Photo: Eco-Etho Research Centre, La Combe, in the mountains of La Drôme, France.

Keywords: Roles; Decisions; Social networking; Cooperation; Horses

Introduction

Social networking theory was first proposed by Kohler [1] in gestalt psychology. Since then, it has been developed and applied to a number of other species although not so far to horses [2]. The basis of Kohler's theory is that individuals within a social network have structured patterns of thoughts and perceptions which interact and affect the individual pods of the network. Thus how and what an individual perceives, thinks and how he makes decisions, is affected by how others behave and what their knowledge of the environment is. This in turn affects the group's structured thinking and perceiving so that the world, seen through (in this case) the horse's mind, is the result of (i) his physical being, (e.g. his particular body and hunger thirst, warmth, exercise, sleep etc), (ii) the social environment in which he lives (who he is living with, their sexes, ages, and personalities) and (iii) the knowledge he has acquired through his life as a result of learning from others and by trial and error. All of this is affected and effected by emotional states (e.g. anger, happiness, frustration etc,) [3,4]. Roles of individuals and network theory predict that the individual's conception of the world will affect that of the group which in turn

affects the individual resulting in the development of dynamic cultures in mammalian societies.

Social network analysis is used here to understand the relationships within a small group of domestic horses by examining the centrality of pods (decision takers or makers and leadership), cohesive bonds (likes and dislikes), and the connectivity of the individual's socio-centric network.

Movement around their environment is an important behaviour performed by horses. The horse subjects of this study were recorded

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moving between 16 and 20 km per day while grazing on this farm [5]. The distribution of the group and the distances between individuals is indicative of their relationships. If they have mutual likes and dislikes concerning individuals, then they will have intentions and recognize intentions of others (e.g. to approach or avoid). Nearest neighbour and next nearest neighbour data is indicative here.

Decision-making when the group moves may be collective, as suggested by Prins [6] for Cape buffalo (*Syncerus caffer*) and Bourjade [7] for Przewalski horses (*Caballus equus*). Or, movement decisions can predominantly be made by one individual. This individual will have particular characteristics or knowledge as a result of his age, size or social standing, the characteristics that exert an influence on the social network [8]. Greater knowledge about the ecology (sleeping sites, grazing areas, better places for protection against the predators, geology, weather and so on) [3,9] will be necessary in those with centrality. Such an individual may also have an attractive personality [10] to encourage social cohesion. All individuals must be known, recognized and accepted for who they are, in order to develop durable network links. This is not difficult in a small group where family relationships and common past experiences will help [3,11].

Over some 4 decades, the most important parameter concerning social relationships in horses has been a dominance hierarchy [12-16] which prevails in the majority of situations (e.g. foraging for resources: water, food) The idea of a dominance hierarchy (which could cut down competition and risk of injury) was originally outlined by Schjelderup-Ebbe [17] in chicken where a dominance hierarchy gave priority of access to particular individuals in any situation. However, such a dominance hierarchy may not be relevant to large herbivores for two reasons:

Because such a dominance hierarchy assumes that competition for resources within the group will be common. (such as where food has to be found or is in patches rather than widely distributed for many primates, canids and cetaceans). Thus, the social contact in large herbivores may not be controlled by competition within the group as many resources are equally available to all most of the time (food, water, shelter).

It could be recognized that different individuals have different knowledge and skills (e.g. the older individuals may have more ecological knowledge). Consequently, the dominance hierarchy might differ in different situations. If this is the case, then the concept of individual's roles is more appropriate [18,19]. A changing dominance order and a recognition of individual roles, indicates that individuals are recognized by others as having that role. This may be the decision maker concerning movements, a popularity role or avoidance of that individual. Another recognized role might be extrovert, defined here as very socially involved whether performing or receiving aggressive or affiliative behaviours, or one who is introverted, tends to stand outside the social interactions, but could still have priority of access [20].

Testing the thesis that the social network may not confirm to the normally idea of a dominance hierarchy and recognizing that by assuming roles, individuals need to have some idea of the mental abilities, feelings/emotions and knowledge of another in different situations may throw new light on the social organisation, social contact and cognitive abilities of this species and why it evolved.

Humans and non-humans who live in a group have to synchronize some activities to maintain the group, even though sometimes the needs of the individual may be different from that of the group. The need to remain part of the group may be prioritized by individuals so that it

is possible that individuals sacrifice their own desires (e.g. food/water etc.) in order to remain with the group. This type of social cooperation may have become important in the development of social living in large herbivores where normally, competition for resources is rare.

As a result of approximately 6000 years of domestication, humans have some knowledge of horses mental aptitudes (e.g. Brubaker and Udell [21]; Murphy and Arkins [22]; Saslow [23], and a host of books of practical horsemanship from Xenophon 350 BC which cannot be ignored). But, they also have many preconceptions for example that horses are not rational or horses cannot understand words [24,25].

Nevertheless, with practical knowledge of the species, observational and experimental research (both of which must be critically assessed), we know something about equine's perception of the world and mental aptitudes [21-24,26] although many questions remain.

The social organisation of horses has been studied by ethologists since the 1960's but it is now recognized to be more complex than previously considered [3,27-29]. Choice of neighbours, roles that individual play and the type of interactions that individuals have with others, gives us a greater understanding of the social network, their social relationships and what mental aptitudes these animals must have to had such social relationships and its evolutionary significance. We chose a small, well studied, related group of domestic horse to assess it's application.

As a potential prey, the individual and/or group must make fast and effective decisions to survive, and those who have the greatest ecological knowledge are likely to have an advantage. This will favour social learning in order to learn about the environment, for example: where to hide, run, what to eat, where to find it, where to drink, as well as social information: who to follow, who to avoid etc. [3]. Thus, since survival is the aim, in a large herbivores prey species, the social network may have developed primarily to facilitate environmental knowledge networking.

Materials and Methods

The animals and their living conditions

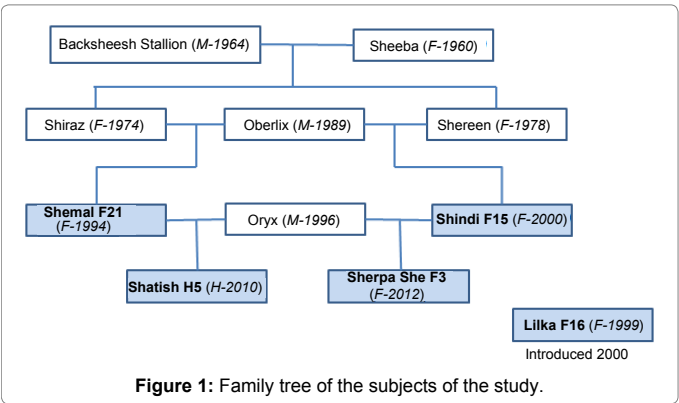
This study was undertaken, on a group of 5 horses raised as a group, 4 mares and 1 gelding (Table 1) at the Eco-Etho Research Centre, La Combe, in the mountains of La Drome, France.

The horses of this study were related, except for Lilka (F16) who was introduced to the group when she was 9 months old, 15 years previously (Figure 1).

The mares Sherpa She (F3), Shindi (F15), Lilka (F16) and Shemal (F21) lived outside all the year with access to a shelter of 100 m². Shatish (H5), the gelding lived in his natal group until 18 months old, thereafter, he lived with his father in a field out of sight although he rejoined his natal group from time to time. He lived with the group for 1 week before the observations began and during the observations, he was with them for 1 h before they began and removed to go with

Name	Sex	Age (year)	Coding
Shindi	F	15	F15
Lilka	F	16	F16
Shemal	F	21	F21
Sherpa She	F	3	F3
Shatish	M	5	H5

Table 1: Name, sex and age of the individuals (F: Female, M: Male).



his father at night. All the animals spent a few hours each week away from the group working on the land, giving lessons, being taught or undergoing training for endurance events, either alone or in various combinations. They were accustomed to this regime from birth.

The horses were observed during the month of March, 5 h per day. The weather ranged from cold and snowy (-2°C) to sunny and warm (25°C).

Methods

The Subjects and training of observers: The recognition of the horses, definitions of the behaviours recorded, and assessment of distances have previously been used by one author [30]. A pilot study to standardize their use and accuracy was run for 20 h before analysed observations were commenced. These horses had been the subject of 1000's h of observations over 6 generations and were unlikely to be affected by the presence of an observer who was at a distance of 150 m and spend 15 min with them before commencing observations. However, any movement related to the observer or her movements were ignored in the analysis. The second author made repeated visits during the observations to ensure agreement, accuracy and no unintended influence of the observers on the animal's movements. Nevertheless, the horses were of course aware of the observers presence.

The horse's behaviour was recorded for 100 h in 2 pastures:

Pasture no 1: Fifty hours in a paddock of approximately 0.5 h on a steep South facing slope where there was little grass but they had access to a circular hay feeder (Figure 2).

Pasture no 2: Fifty hours in a 30 h enclosure with abundant grass, including approximately 1 h cleared bush with surrounding oak and beech forests and two steep valleys with streams (Figure 2).

The movements of the individuals, the aggressive and affiliative behaviours were recorded continuously from the 5 individuals. The proximity data was recorded every 15 min during the observations. The time, weather, place and any odd occurrences (e.g. noises, proximity to cows etc), distance between individuals (Table 2) were recorded. A dictaphone was used to record each individual's behaviour and activity.

Data analysis: Excel software and chi-square tests (χ^2)* using the software R (R386 V 3.3.1) was used:

- To analyse decision making movements.
- To analyse social affinities: (i) Nearest neighbours, and (ii) Next nearest neighbours.
- The distribution of individuals from each other.
- The agonistic and affiliative behavior both performed and received (EXCEL spreadsheet).

*The Chi-square test (χ^2) is to calculate the sum of the differences between real effectif and theorettical effectif. If the differences are very small, there is no relationship between the two variables. Greater is the differences, the greater is the relationship between the two variables.

The social network was constructed using Social Network Analysis [31]. The spatial, aggressive, affliative, cooperative and sexual data for each individual, whether as a performer or a receipient, was transformed into a matrix. Although there were only 5 individuals, the two social analyses used were:

- Ucinet Software for social network analysis [32];
- Netdraw Software for graph visualization [33]. Analytic Technologies Ucinet and Netdraw are complimentary and developed by the authors (Supplementary Figures 1 and 2).

Touch	Less than 1 m	1-5 m	5-15 m	15-30 m	30-50 m	50-100 m	More than 100 m
a	b	c	d	e	f	g	h

Table 2: The distances to the neighbours were codified in the above table.

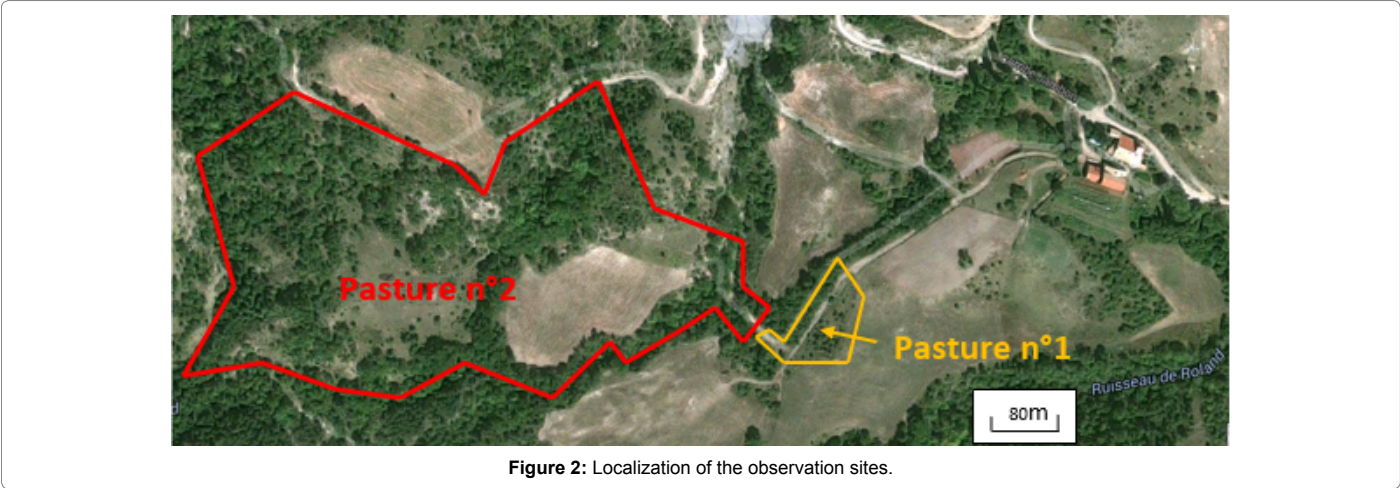


Figure 2: Localization of the observation sites.

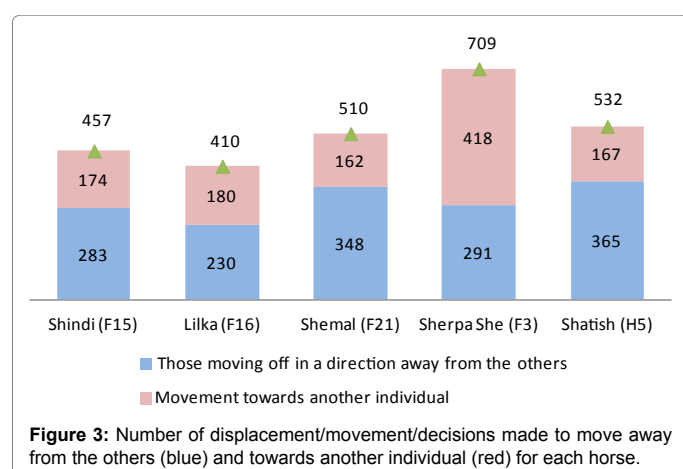
Results

Decision making within the group

Figure 3 gives the total number of recorded movements (2618, 5.24/horse/h). These movements/displacements are divided into (i) blue: those moving off in a direction away from the others, total: 1517 (3.03/horse/h, significantly more frequent than (ii) red: movement towards another individual total: 1101 (2.20/horse/h) (Khi^2 : $p < 0.05$).

Reactions of others to the movements

We calculated the rate of reaction (Moving, Following, Ignoring, Attention) of each individual in relation to the movement of one: A1) The reaction rate of an individual in relation to the movement of other individuals B1. An individual was moving toward another individual.



A2) Measures the rate of reaction of the other individuals when one of them is heading to one of them. B2) The reaction of an individual when an individual of the herd goes towards him/her.

The frequency of the different responses

Attention (purple): For each movement of another, the most common response was to pay attention. Lilka (F16) and Shatish (H5) showed the greatest variation, receiving most attention when they moved (1.92; 1.95), but paying less attention when another individual moved (0.42; 0.37) (Figure 4).

Moving (blue): Movement of the individual or movement by others as a result of that individual's movement was less frequent. Shemal (F21) and Lilka (F16) moving towards others have the highest scores (0.72; 0.37), and Shindi (F15) had the highest scores for moving (0.10) when another individual moves towards her (Figure 4).

Following (red)/being followed: Shemal (F21) had the highest scores (highly significant ($p < 0.01$) for being followed whether she was moving off to different places (0.32) or towards others (0.07). She had the lowest scores for following others (0.01; 0.01), also highly significant (Khi^2 : $p < 0.01$) (Figure 4). This suggests that she was the major decision maker, and her centrality (see below). Sherpa She, the young filly, had the lowest scores for being followed (0.05) and the highest for following (0.09) (Figure 4).

Ignoring (green): The number of times a movement was ignored by the others was scored and is relatively high: around 1/3 of the movements were ignored. It is unlikely that others did not see the movement (see discussion), rather a choice must have been made to ignore it. The least ignored movements were Shemal's (F21) (0.81) (Figure 4), and the individuals ignored most were Shatish (H5) and Sherpa She (F3) (1.42; 1.48) (Figure 4). This again indicates the centrality of Shemal (F21) and the network closure to Shatish (H5).

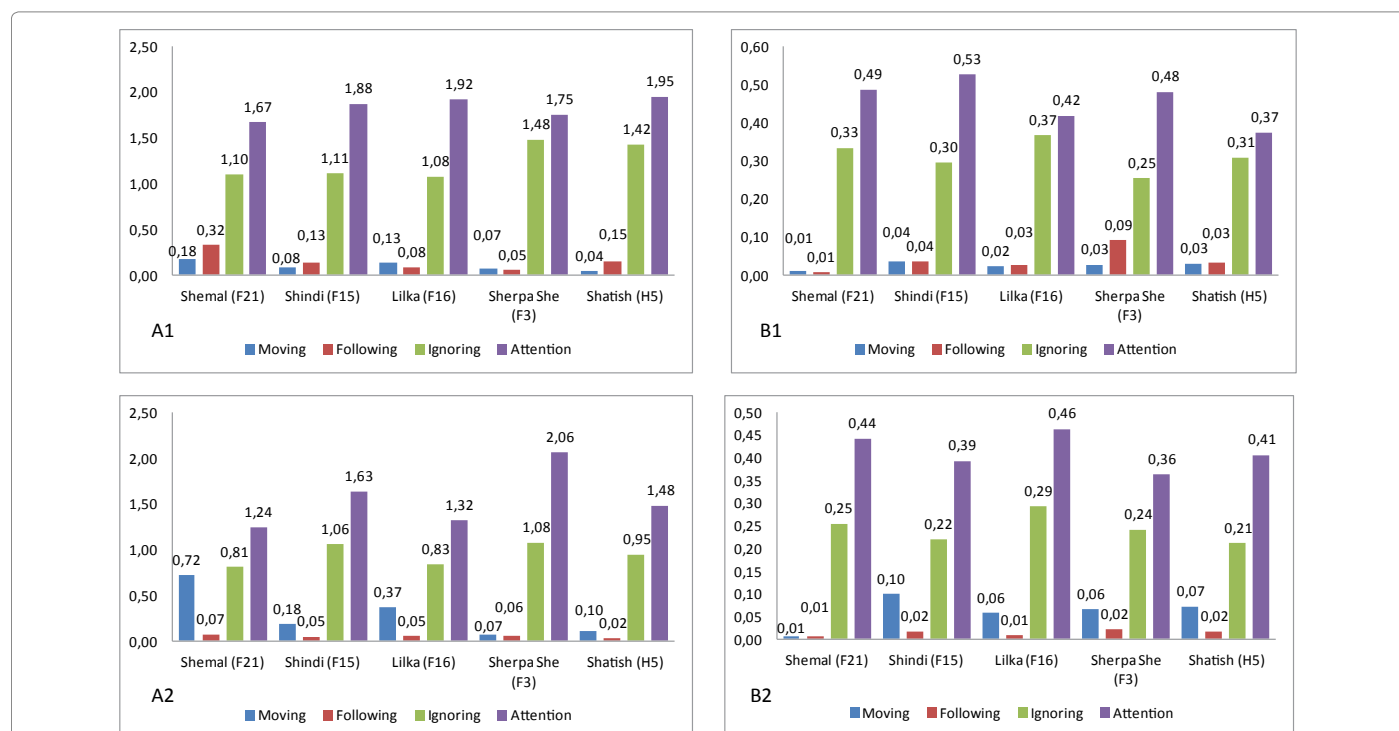


Figure 4: A1: Reactions of the others to the movements of each named individual, B1: Reactions of the individual observing the movement of another individual, A2: Reactions of the others when the named individual moves towards others, B2: Actions of the named individual when another moves towards him/her.

Freeman’s centrality

Linton Freeman, developed basic measures of the centrality of actors based on their degree, and the overall centralization of graphs.

The centrality of degree is the number of connections that an actor (nodes) has. When links are directed, the total number of links sent (out-degree) and the links received (in-degree) are calculated.

- Out-degree usually indicates the influence,
- In degree shows the prestige or popularity.

Shemal (F21) was the most out-degree, thus considered the most influential individual in the group (Table 3 and Figure 5). Sherpa She (F3) was the most in-degree, that is she was closest to others and followed them more than the others making every attempt to become more integrated. The three adult mares behaved similarly, although Shemal (F21) had the most influence on the two youngsters who keep in contact with her. The analysis of the categorical core periphery indicates two sub groups, (1) the 3 mares Shindi (F15) Shemal (F21) and Lilka (F16)), (2) the two youngsters, Sherpa She (F3) and Shatish (H5) (Table 4).

Preferred distances between individuals in the two pastures

Figure 6 gives the total number of observations in the different distance categories for the two pastures. Pasture 1 with little grass but fed hay in a feeder, Pasture 2, where there was only grazing.

In pasture 1, because of the restriction of the food to a hay feeder, it is not surprising that the horses spent significantly more time closer together than in pasture 2 (Figure 6): $p<0.01$ (Khi²): comparing blue histograms in pasture 1 and 2.

The next nearest neighbour distance (red), is also more frequently less than 15 m in pasture 1 than in pasture 2 (Khi²: $p<0.01$).

Thus both the nearest (blue) and the next nearest neighbours (green) are nearer in pasture 1 than 2. In pasture 2, typically the nearest and next nearest neighbours are more frequently more than 15 m away (Khi²: $p<0.01$).

		Outdeg	Indeg
1	Shindi (F 15)	44.000	59.000
2	Lika (F 16)	28.000	43.000
3	Shemal (F 21)	124.000	12.000
4	Sherpa She (F 3)	40.000	126.000
5	Shatish (H5)	57.000	53.000

Table 3: Degree measures (Freeman degree centrality).

Movement	Movement of at least 3 m in 5 s in one direction	
Reaction	Reaction of other individuals to these movements	a) Approach: an individual moved directly towards another by at least 3 m. b) Attention: Assessed from: (i) The turning of the head in the direction of the mover. (ii) A forward or backward pricking of one or both ears in that direction. c) Following: moving off in the same direction as another within 5 s of the first one's movement. d) Ignoring: No movement or change in behaviour as a result of another animal's behaviour directed towards the subject.

Table 4: Decision making movements within the group.

Thus, the preferred proximity to other individuals changes with the situation.

Individual choices in association

Figure 7 shows the number of times each individual was chosen as the nearest neighbour or next nearest neighbour by the others.

The overall popularity of an individual (that is the individual who is chosen most frequently as the nearest neighbour, or next nearest neighbour) was Shindi (F15) with a score of 1170 although she also moved away most from others. She had the role of being popular perhaps because she was part of the cohesive mare group, but not the decision maker. Sherpa She’s (F3) (the filly’s) high score (1010) was affected by the amount of time spent with Shatish (H5). Shatish (H5), the gelding was the least popular, confirming his role in the network as a structural hole or an outsider.

Interestingly, there is a significant difference between who each prefers as their nearest neighbour compared with their next nearest neighbour (Khi²: $p<0.01$). In particular, the central decision maker, Shemal (F21), was not frequently chosen as nearest neighbour, but

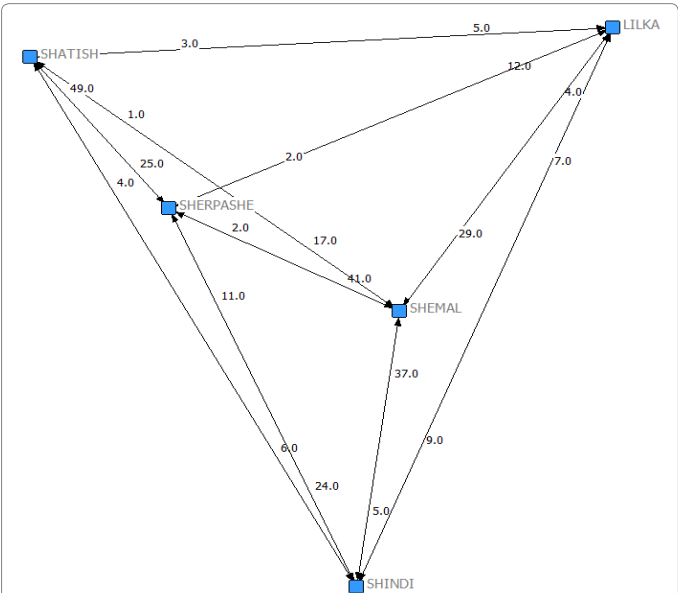


Figure 5: Social network analysis that follows whom. The numbers on the arrows represent the number of interactions between related individuals. When there is interaction the arrow is in both directions and the nearest value of the individual's name represents the number of interaction being imputed to him.

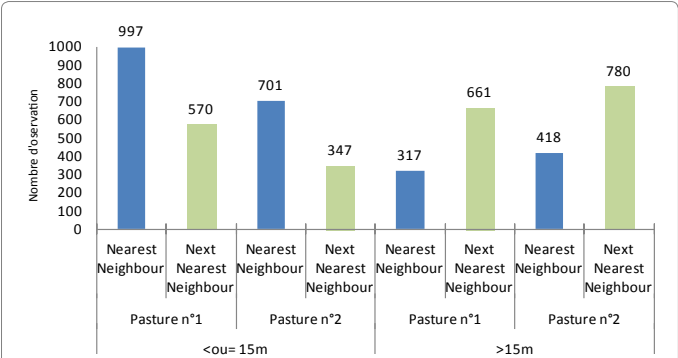


Figure 6: The number of observations below or above 15 m apart for the nearest (blue) and next nearest neighbours (red) in the two different pastures.

more frequently as the next nearest neighbour. Shindi (F15) was almost equally either the nearest or next nearest neighbour. The filly, Sherpa She (F3) was most frequently chosen as the nearest neighbour but only because of her close association with Shatish, but not the next nearest neighbour, and the gelding, Shatish (H5) had the lowest scores on both counts, again confirming his lack of cohesion within the group.

Individual preferences: who they like and who they don't, are in Figure 8. Shemal (F21) shows no particular preference for either of the two adult mares, or the filly, but a definite preference for the females over the gelding, even though he is her son (Khi^2 : $p < 0.01$). Lilka (F16), the unrelated mare, has a particular preference for Shindi (F15) (Khi^2 : $p < 0.01$), and a significant avoidance of Shatish (H5), (Khi^2 : $p < 0.01$). Shindi (F15) has a particular preference for Lilka (F16) (Khi^2 : $p < 0.01$), confirming the strong cohesive bond between these two. Both Shindi (F15) and Lilka (F16) show avoidance of Shatish (H5), (Khi^2 : $p < 0.01$), thus demonstrating the network closure, created for him by the three adult mares.

Sherpa She (F3) and Shatish (H5) spend more time with each other than with the others (Khi^2 : $p < 0.01$). Much of this was social play, nipping, chasing and leaping about.

Aggression and affiliation performed and received within the group

The total number of aggressive and affiliative behaviours performed by the individual (A) and received by that individual (B) are shown in Figure 9.

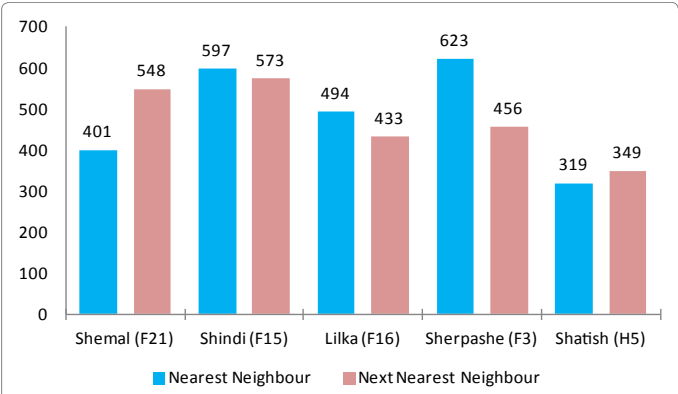


Figure 7: Number of observations that each individual was either the nearest neighbour or the next nearest neighbour to any other horse.

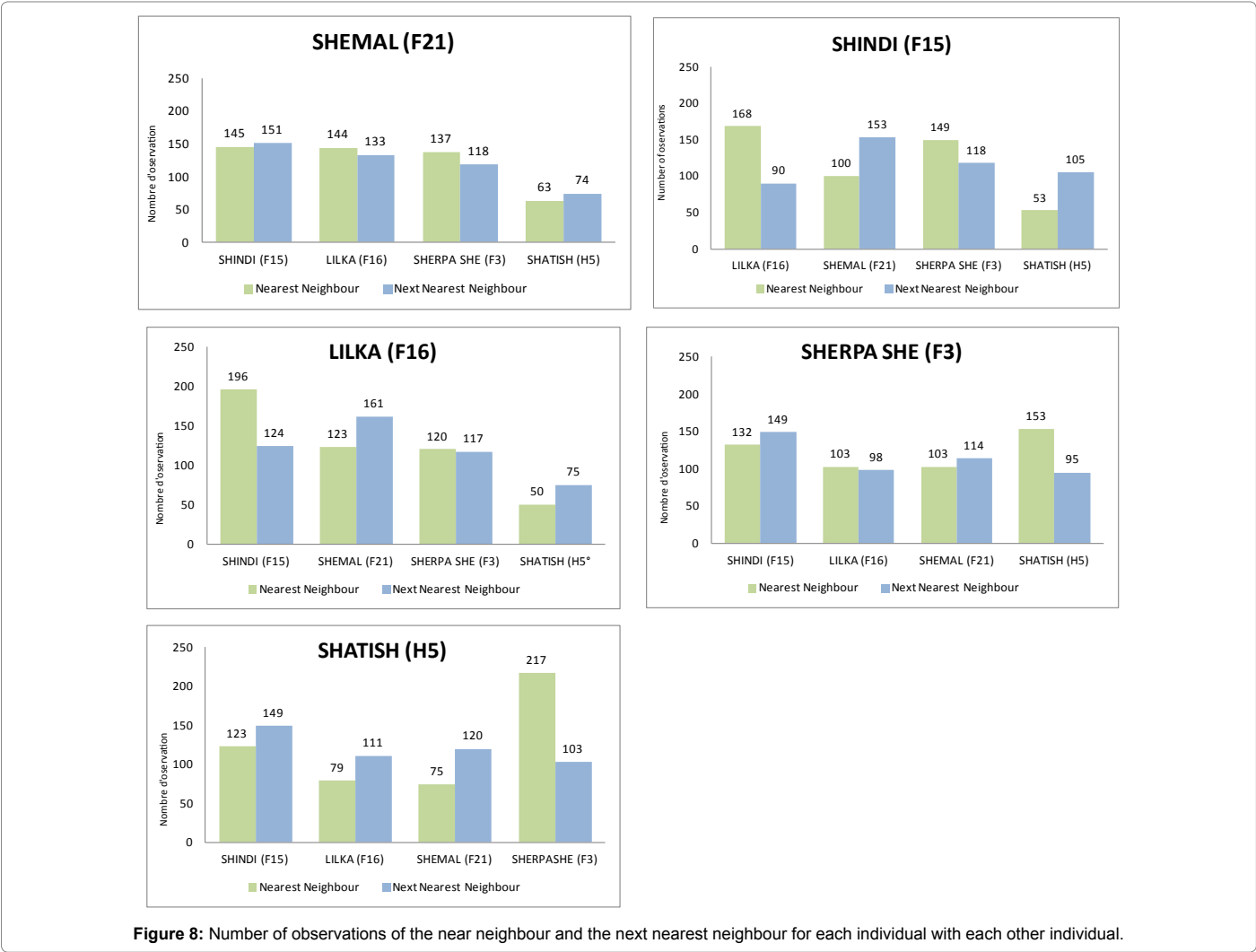


Figure 8: Number of observations of the near neighbour and the next nearest neighbour for each individual with each other individual.

The total affiliation is greater than aggression either performed or received (χ^2 : $p < 0.01$ for both) which indicates that sticking together/cohesion is important in this group, even though in pasture 1, the food resource was restricted and might have lead to more conflicts. Shindi (F15), Lilka (F16) and Shemal (F21), perform more aggressive behaviour than affiliative although the scores are low. All three receive more affiliative than aggressive behaviour. The two youngsters, Sherpa She (F3) and Shatish (H5) however perform much more affiliative behaviour than aggressive, indicating their need to be integrated into the group, but the filly receives more interactions of both types than the others; indicating she is of interest to the others. Shatish (H5) confirms his social position as an outsider, although since he performs a great deal of affiliative behaviour, he is clearly making bridges, that is trying to ameliorate his social integration. The network analysis of the aggressive and affiliative dates is given in Figure 10.

Discussion

The method adopted for measuring decision-making was the individual's movements, either away from the group or towards other members, and the responses elicited from the others. Ignoring the directed movement from/to another was also recorded to help assess this. In a small number of cases ignoring might be explained by the recipient being unaware of the individual's movement. But this is unlikely because horses are visually very acute, have large monocular

visual fields and communicate by subtle visual movement consequently, they are constantly aware of others and the surroundings. As a result, ignoring a movement could be either a conscious decision or simply due to habituation which doesn't have to be conscious.

Analysis indicates the importance of one individual decision maker in the group. Shemal (F21), the oldest mare, moved off most frequently and was followed most frequently. Social network analysis confirms her centrality (Figure 5). Sherpa She (F3), the youngest, was the least likely to be followed or move away but she followed others most.

The social acceptability/popularity of the individual was measured by how often they were chosen as the nearest or next nearest neighbour, who was not the same. Shindi (F15) (one of the older mares) was chosen as the nearest neighbour most often by the others, she could therefore be considered the most popular to be near. But, Shemal (F21), the major decision maker, was frequently chosen as the next nearest neighbour. Shatish (H5), the gelding was the least chosen, either as the nearest or next nearest neighbour.

The third measure was the amount of aggressive or affiliative behavior that was recorded for each individual, either performed or received. All three of the adult mares performed slightly more aggressive behavior than affiliative, but the youngsters performed more affiliative than aggressive, demonstrating their desire to integrate

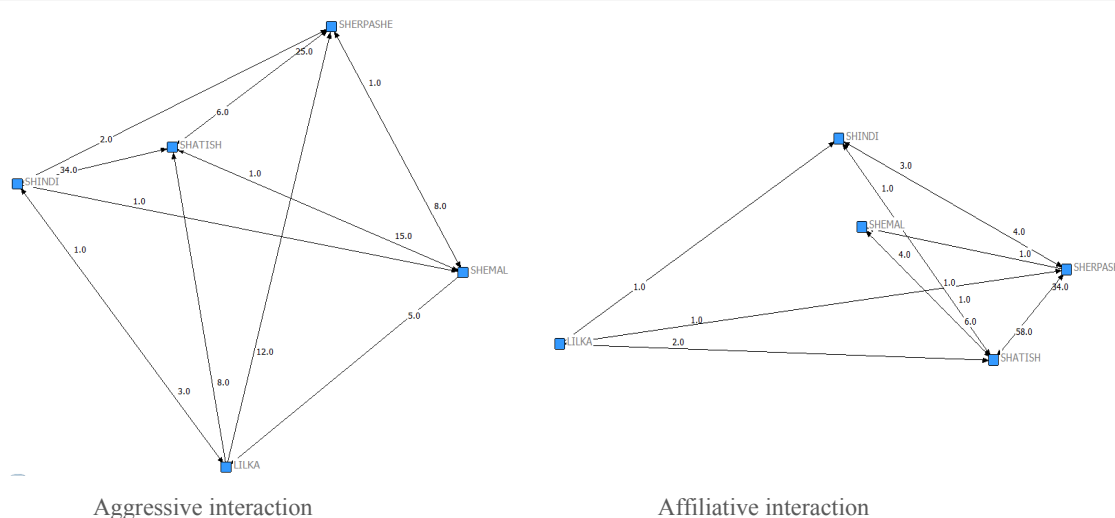


Figure 9: The aggressive and affiliative interaction network. The numbers on the arrows represent the number of interactions between related individuals. When there is interaction the arrow is in both directions and the nearest value of the individual's name represents the number of interaction being imputed to him.

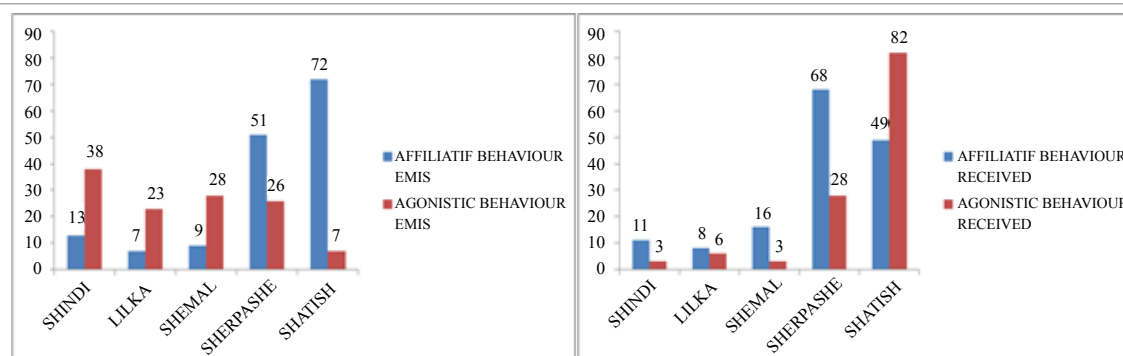


Figure 10: The total number of aggressive and affiliative behaviours performed (A) by the individual and (B) received from all the others.

further with the group. The most aggressive behaviours were directed at Shatish (H5), the gelding; demonstrating that he was not a welcome member of the major group at this stage (Table 5).

The social network analysis shows an obvious centrality of the oldest mare (Shemal (F21)) as stated. The three adult mares: Shemal (F21), Shindi (F15) and Lilka (F16), have cohesive bonds and Sherpa She (F3) and Shatish (H5) are a sub group with reciprocal preferences, probably because of their past lives spent together and similar ages. Both however made efforts to more closely integrate with the adult mare group. Sherpa She (F3) maintained a close bond with her mother even though she is post-pubertal [11,30] but she is not yet accepted as an integral part of the major group. As the youngest, she would be unlikely to have sufficient knowledge to be an important decision maker for the group.

Shatish (H5) occupies a position of mutual closure in the group indicating his lack of integration, partly because of his sex [34], but also probably because he had not always lived with the family group. He receives the most aggression although performing the most affiliation and is the least chosen as a neighbour or next nearest neighbour (Table 6).

The reasons for individual differences in decision making must rest in part on personality [28], past experience and as a result, who likes who.

Family relations explain much of the affiliation [30], nevertheless, this study shows that if a group is raised as a family group where the individuals have passed experiences in common, as would generally be the case in the wild, there is little aggression. Rather, it is a cooperative stable group where individuals and their personalities are well known and environmental knowledge can be easily circulated by social and observational learning that is the network efficiency maximized [21].

Agonistic behaviours	<ul style="list-style-type: none"> Moving rapidly towards another with head & nose extended flat in their direction both ears directed back or flattened against the head biting, opening the mouth and grabbing the skin or muscle of the other. Kicking another: lifting a hind leg and either kicking it out backwards towards the other and/or hitting the other's body with the leg. Turning the croup towards another accompanied by swishing the tail.
Affiliative behaviours	<ul style="list-style-type: none"> Mutual grooming where one individual gently grabs the other's skin or mane with his/her mouth/teeth and moves the head to and fro while scratching and chewing, the ears pointed forward or sideways. The recipient usually imitates this movement on the performer turning the head and looking at another without provocation. Touching or smelling noses, touching other parts of another's body, gentle nipping with the teeth galloping towards another accompanied by neighing. Nicker, low call with the mouth shut, or neighing (mouth open, louder) at another.
Attention to other things	<ul style="list-style-type: none"> The call or sight of the stallion who was at a distance, other farm animals, tractors, other wildlife such as wild boar, roe-deer etc.
Possible fearful reactions: A sudden increase in postural tonus, head and tail raised, head moved in the direction and ears pricked to the stimulus.	<ul style="list-style-type: none"> Loud noises, wind movements (there was wind up to 50 k/h on the mountain). Wind crackling of branches etc. startled running (sudden high postural tonus) towards or away from group.

Table 5: Definition of different behaviors.

		5 (HS)	4 (F 3)	1 (F 15)	2 (F 16)	3 (F 21)
1	Shatish (H 5)	-	49	4	3	1
2	Sherpa She (F 3)	25	-	11	2	2
3	Shindi (F 15)	6	24	-	9	5
4	Lilka (F 16)	5	12	7	-	4
5	Shemal (F 21)	17	41	37	29	-

Table 6: The two sub groups represented as Freeman.

Young horses interacted preferentially with other young when playing and interacting affiliatively. Socially experienced adults are social models or tutors for the young horses [35] which explains, that the three horses that had the most past experiences in common actually demonstrated more agonistic behaviours, and that the majority of the affiliated behaviours come from those who don't have this experience in common.

Movement decisions were not taken as a result of a group decision as been reported in Przewalski horses in an enclosed area [35] and Cape Buffalo [6]. In the present study, the decisions were taken by a particular individual recognized by the others by virtue of their age and personality as they are having greater knowledge and experience [36].

The study and development of social network theory and analysis indicates that individual roles as a result of sex, age, and personality are more important in this small group than an over simplistic dominance hierarchy which assumes an overriding need for competition, even when fed at a restricted resource.

The social-centric network was shown to be a complex mixture of central characters, cohesive bonds with structural holes and bridge making, structured from the individuals in the group. This study allows a greater understanding of the mental attributes of the species and consequently how it may interpret the world. It also suggests that an explanation for the evolution for the social network and cohesive social groups in large herbivores may rest primarily with being able to acquire essential ecological knowledge from others.

Compliance with Ethical Standards

Conflict of Interest

Author Ricci-Bonot C declares that she has no conflict of interest. Author Kiley-Worthington M declares that she has no conflict of interest.

Ethical Approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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