SOCIAL STRUCTURE OF PONY (*EQUUS CABALLUS*) MARES IN AN ALL FEMALE HERD ON LUNDY: ANALYSIS OF DOMINANCE RELATIONSHIP AND PREFERRED ASSOCIATE

By

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ABSTRACT

The social structure of a herd of semi-domesticated ponies (*Equus caballus*) was examined during March-April, 2004. The herd consisted of 13 mares that ranged from 4 to 30 years old. Dominance rank was assessed by number of aggressive encounters among the individuals using continuous viewing and recording. Preferred associate was assessed by spatial proximity and positive interaction between individuals. The social structure of ponies was similar to that described in the literature. Dominance rank had a strong linearity and was correlated with age. Ponies also showed subgroup formation with kin-related individuals.
Keywords: *social structure; dominance hierarchy; preferred associate,* Equus caballus*; pony*

INTRODUCTION

Despite their unique characteristics and convenient access, few behavioural studies have been conducted on Lundy ponies. The few that have examined individual behavioural traits on Lundy ponies' diurnal activity patterns have been conducted by Randle and her colleagues (Randle, 1994; Randle & Gill, 2002; Randle *et al.* 2002). No published study to date has examined the social organization of the Lundy ponies.

One of the key issues in behavioural studies of the Equus species is social structure. The social structure of ponies and horses has been mainly studied in two aspects, dominance hierarchy and preferred associate. Establishment of dominance ranking reduces unnecessary agonistic encounters that may ensue between individuals in order to achieve higher mating success or access to scarce food resources; it also reduces the unnecessary energy costs or potential injuries of submissive animals (Lehmann et al., 2003). Much research has found that horses and ponies form a near linear dominance hierarchy, and that dominance rank correlates with age: older animals tend to rank higher in the herd (e.g. Houpt *et al.*, 1978; Keiper & Sambraus, 1986; Rutberg & Greenberg, 1990).

Grooming (which is often mutual among horses and ponies) has important social functions, such as reducing tension between individuals. Feh & Mazieres (1993), for example, found that mutual grooming could produce a positive effect in reducing heart rate of both animals. Wells & von Goldschmidt-Rothschild (1979) and Sigurjónsdóttir *et al.* (2004) found that the formation of subgroups (possibly preferred associates) and mutual grooming partner could be influenced by dominance rank. Kimura (1998) found that nearest neighbour reflected both age and social rank in a family band of free-ranging horses, while mutual grooming occurred irrespective of social rank. Thus choice of preferred associate and grooming partner may be affected by factors over and above dominance rank. Factors such as kinship may influence preferred associate and mutual grooming partner. However, it is usually difficult to identify kinship of animals in the field study and little is known about how kinship influences social structure.

The present study examined the social structure, specifically dominance hierarchy and preferred associate, of the Lundy pony herd. The influence of kinship on preferred associate and social interaction such as mutual grooming was also examined. Social structure and dominance hierarchy of pony mares have been studied in terms of influence on foal's social rank and maternal protectiveness against stallions' infanticide (e.g. Cameron *et al.* 2003; Rho *et al.*, 2004). Keiper & Sambraus (1986) looked at dominance hierarchy in bands of feral horses that included a stallion. They suggested social structure was not influenced by kinship because juvenile status in the band did not correlate with the rank of the dam. However, little is known about what hierarchy mares establish in the absence of stallions and foals, or the effect of kinship. Kinship of animals in natural or semi-naturalistic environments is often difficult to determine, however kinship for the Lundy ponies is well documented. After the removal of a gelding in 2004, the pony herd on Lundy consisted solely of mares ranging in age from 4 to 30 years, living in a semi-natural environment. Thus the influence of kinship on social structure is expected to be more apparent in the Lundy herd due to the absence of either a stallion or gelding.

METHODS

Study area

Lundy is located in the Bristol Channel, about 20 km west of the Devon coast, UK (51o 10'N, 4o 40' W). The island is 4.8 km long from north to south and 800 m wide and is mostly granite with a farmed area at the south and open moorland to the north. The island is run by Landmark Trust and is protected by numerous environmental designations, including Site of Special Scientific Interest. The first ponies arrived on Lundy in 1928 and were originally bred from (or related to) Welsh Mountain ponies. The Lundy ponies have since been bred with Connemara and New Forest stock. Because vegetation on the island is poor, the farmer gives the ponies supplemental food of turnips during the winter. This supplemental feeding was observed three times during our stay on the island. Randle & Gill (2002) designated seven potential zones on the island that the ponies could use.

zones on the island that the ponies could use. However, the ponies spent the entirety of their time in one zone (zone 4 of Randle and Gill's zone classification) during the present study. This area is between the Halfway Wall and Tibbets point, and consists of grassland and heather. Water is available from troughs on the west side.

Study subjects

A total of 13 semi-domesticated pony mares, who ranged from 4 to 30 years in age were observed (Table 1). Many were either directly or indirectly related (Figure 1). Each pony was identified using colouring and markings previously reported by Randle & Gill (2002). Some specific facial and leg markings were not used in their study and therefore more extensive and detailed descriptions are shown in Table 2. The social structure within the herd might have altered in the past years with the death or removal of four ponies. The current oldest mare (Calloo) had been removed from the herd for the winter of 2003/2004 and had been released back into the herd just prior to the present study. The last stallion present in the herd (Lundy Sabine) was removed in 1999, five years before the present study took place. However, some of the ponies and a gelding were removed more recently.

Data collection

Data were collected in daylight during the period of 29 March to 2 April 2004. Observations were made twice daily in 2.5-hour sessions that began 9:00 - 9:30 hours in the morning and 12:45 - 15:45 hours in the afternoon. For observational purposes, the herd was divided into three groups defined by age (younger than 5 years, 6-9 years, and older than 11 years) to be observed by three observers. The allocation of the animals was counterbalanced between observers across the 5-day observation period but it remained the same within a day. In each 2.5-hour observation session, two types of observation (behaviours and spatial proximity) were made simultaneously.

Diurnal behaviour, social behaviour and spatial proximity of a focal pony were recorded during a 15-min observation. Every animal was observed twice daily, once in the morning and once in the afternoon. The diurnal behaviours were observed by scan sampling every minute and they typically fell into the following four categories: 1. Resting - pony lying down or standing dozing (ears back, neck and head lowered); 2. Standing - pony neither resting nor eating, but staying stationary, ears pointed forward and alert; 3. Grazing - pony eating or browsing vegetation; 4. Moving - pony moving at a walk, trot, or canter for more than four consecutive strides.

Social behaviours were recorded by continuous sampling over the 15-minute observation period. Two types of social interactions (positive and agonistic) were recorded for each pony. Positive interaction was nose to nose touching while grazing or standing and mutual grooming. Agonistic interactions included both physical attack (biting or kicking) and displacement behaviour. Although a small number of physical attacks were observed during the feeding of turnips, most aggressive encounters were observed via displacement while grazing. Based on the outcomes of agonistic interactions, a dominance matrix was derived for the herd.

For the purpose of constructing the dominance hierarchy, the animal that displaced another individual or the initiator of agonistic encounter was considered the winner of the interaction, while the recipient or displaced individual was considered the loser.

On completion of each 15-minute observation period, the distances between each of the three observers' focal pony and all the other ponies were simultaneously recorded. Distances, which were classified as either 'less than 1 m apart', 'greater than 2 m but less than 5 m apart', 'greater than 5 m but less than 10 m apart' or 'greater than 10 m apart', were estimated using the body length of the animals. The focal animals for each observer changed every 15 minutes and distances were recorded until all the individuals had been observed during each session.

Inter-observer agreement among the three observers was made prior to the study and was made separately for behaviours and spatial proximity. These adjustments of behavioural and distance assessment among the observers were continued for ten sessions of 15 minutes. For the behaviour, the same pony was observed. The pony behaviours of 'standing' and 'dozing' were recorded by focal sampling every one minute. For the spatial proximity, spatial proximity of the three ponies was observed using the above defined distance categories (i.e. 1-4).

RESULTS

Analysis of diurnal behaviours

Figure 2 shows the proportion of time spent for common diurnal activities. Ponies spent most of their time grazing: exceptions were the afternoon of the first day and the morning of the second day when they spent longer resting. A repeated measures of ANOVA (sessions × behaviour × time of day), using the Greenhouse-Geisser correction where appropriate, confirmed these results by presence of a significant main effect of behaviour, $F_{3,36}$ = 285.535, p<0.05. A significant interaction between sessions and behaviour, $F_{12,144}$ = 8.728, p<0.05 and significant triple interactions between session, behavior and time of day, $F_{12,144}$ = 22.803, p<0.05 revealed that individual grazing and resting behaviours occurred at similar times during the first two days of observations. Therefore, environmental factors such as weather perhaps influenced patterns of behaviours. No other main factors and interactions were significant.

Analysis of dominance hierarchy

A total of 115 agonistic encounters were observed for 13 ponies during the 12.5 hours. Table 3 shows a matrix of the number of agonistic encounters between all the individuals. As commonly seen in this type of data, a large part of the matrix was incomplete (i.e. no agonistic interaction was observed perhaps because aggression between certain pairs was unlikely). Agonistic encounters were more frequently observed with the individuals in the middle age group than those in the oldest or youngest age group. Dominance rank was derived for each pony based on Table 3, using the Batchlder-Bershard-Simpson (BBS) scaling method (Jameson et al. 1999).

The BBS scaling method is based on Thurstone's (1927) paired comparisons and ranks of the individuals are determined by the scale score depending on each individual's proportion of wins and losses and the scale scores of the other individuals met in agonistic encounters. The BBS method is therefore effective even when the entries in the matrix are relatively sparse. The dominance rank computed by the BBS method is shown in Table 1.

Like other statistical methods of dominance ranking (e.g. de Vries, 1998; Brown, 1975; Schein & Fohrman, 1955), the BBS scaling method assumes that the hierarchy is linear or near-linear. Therefore, the linearity of the dominance hierarchy in the herd was examined using Landau's index of linearity (h): $h = 12 / (n^3 - n) \Sigma [v_a - (n - 1) / 2]^2$, where n is total number of individuals in a herd, and v_a is the number of individuals that individual 'a' dominates (Landau, 1951). The index value ranges from 0 (absence of linearity) to 1 (perfect linearity). The linearity index was 0.983, suggesting that the dominance hierarchy was strongly linear.

Using the dominance rank determined by the BBS method, the relation between age and dominance rank was examined. There was a significant Spearman's correlation coefficient (all the ponies: $\rho = 0.577$) suggesting that older animals tend to have more dominant positions in the herd. Since Calloo (the oldest mare) rejoined the herd shortly before the present study took place, the analysis was also done excluding Calloo (all but Calloo: $\rho = 0.748$). The trend was the same, but clearer when Calloo was excluded.

Analysis of preferred associates

Preferred associates were examined using spatial proximity scaling and positive interactions. First, spatial proximity score over 5 days (10 sessions) was averaged (Table 4) and was subjected to multidimensional scaling (MDS) and Cluster analysis, both performed by programs in the SPSS library (SPSS version 12.0, SPSS Inc.). MDS was performed using the ALSCAL program with the Euclidean metric for distance computation. Figure 3 shows the outcomes of the MDS. Kruskal's Formula 1 stress (Kruskal, 1964), a measure of the goodness of fit between the spatial representation and the data, was 0.262, and this spatial representation accounted for 62% of the variance in the data. The herd could be divided into three subgroups. Except for one individual (i.e. Jilly), these subgroups are best explained by kinship (see Figure 1): one group is related to Red Kite (Iona, Charlotte-Louis, and Francis-Anne), one to Stonechat, (Annie, and Hannah), and the other to Belinda (Phoenix and Lerina). The three kin-bound subgroups were also confirmed by Cluster analysis according to Euclidean distance metric (Figure 4). Due to the missing values in the matrix, Jenny and Reed Warbler were excluded from the Cluster analysis.

Table 5 shows the matrix of positive interactions between individuals. This was subjected to MDS and Cluster analysis. MDS was again performed by ALSCAL programs with the Euclidean metric for distance computation. Kruskal's Formula 1 stress was 0.321, and this spatial representation (Figure 5) accounted for 38% of the variance in the data. The small RSQ-value (.38) suggests that a positive interaction between two individuals may not be well represented by the two dimensional spatial representation. Cluster analysis, on the other hand, allowed us to explore the strength of positive interactions between the two individuals. Figure 6 showed the results of the Cluster analysis. The pattern of subgroups with positive interactions was different from that found with spatial proximity. The two ponies (PH and CA) were very different from the rest of the herd in terms of the way they interact. These two individuals, who were the eldest among the herd, distinctively differed in their interactions with the other individuals; they interacted with the other individuals more frequently than the rest of the herd. However, little difference was found amongst the rest of the herd. Neither age nor kinship seems to explain the pattern of subgroups.

DISCUSSION

Diurnal behaviours

The ponies observed typically spent the majority of their diurnal activity grazing. No notable individual differences were found. Randle & Gill (2002) also reported that grazing activities dominated all the other diurnal behaviours, and this pattern of behaviours is common for herbivorous species (Olsman *et al.*, 2003).

Randle & Gill (2002) further reported on the variations of diurnal behaviours: resting behaviour increased during 9:00-10:00, and grazing peaked during the period of 16:00-17:00. However such variation of behaviour was not found found in the present study. Differences between Randle and Gill and the present study could perhaps also be due to seasonal variations in pony behaviours; the former study was conducted during early autumn (mid- September), whereas the latter was conducted in early spring. Berger *et al.* (1999) showed that grazing accounts for the largest amount of total diurnal activity time in Przewalski horses during spring (62% compared to 40% in summer), and is likely due to better vegetation quality and quantity.

A significant increase in resting behaviour, and consequently a significant decrease in grazing behaviour, was observed in the morning of 30 March. The ponies spent a majority of their time sheltering around the Halfway Wall, perhaps due to windy and cold weather on that day. Otherwise, diurnal activity was predominantly grazing.

Dominance rank of Lundy ponies

The herd established almost perfect linearity of dominance relation (h = 0.983). The strong linearity may be because there is very little interference among existing factors that could potentially influence the establishment of dominant relationships in the ponies. The results also indicate that the older ponies were dominant over the younger ponies. The oldest mare, Calloo, had a lower rank than expected. However, this could be a consequence of her isolation from the herd prior to when the present study took place. Despite this, the correlation between dominance rank and age rank was significant even when Calloo was included in analysis. These results were consistent with previous studies with feral *Equus* species (e.g. Houpt & Keiper, 1982; Keiper & Sambraus, 1986; Rho *et al.*, 2004).

Analysis of preferred associate

Preferred associate of ponies was examined with spatial proximity and positive social interactions using MDS and Cluster analysis. Based on spatial proximity, the herd could be divided into three subgroups. Except for one individual, these subgroups are best explained by kinship. These results suggest that ponies that were related by kinship stayed spatially closer to each other than ponies that were not related. To our knowledge, this is the first study that demonstrated influence of kinship (except for mare-foal relationships) on social structure in ponies. Cluster analysis showed that Calloo was separated from the other ponies at relatively high index of association, suggesting that Calloo stayed relatively far away from the other ponies. However, we do not know whether her relative isolation from the other ponies was due to her age or her removal from and subsequent return to the herd.

MDS and Cluster analyses done on positive social interactions showed different patterns for preferred associates than those done on spatial proximity. MDS showed that Calloo and Phoenix differed from the rest of the individuals in their social interactions. With the exception of these two ponies, the herd could be divided into two distinct subgroups. However, the positive interaction matrix has a lower RSQ-value than the spatial proximity matrix and implies that spatial proximity may be a better indicator of preferred associates. Cluster analysis on positive social interaction also showed that Phoenix and Calloo were relatively dissimilar to the rest of ponies. No further clear hierarchical structure was found among the others. These results do not necessarily mean that positive interactions are an ineffective measure of preferred associate. However, in a semi-naturalistic environment, social interactions between ponies are not observed frequently, and therefore the data obtained in a 5-day period may not be sufficiently sensitive to profile accurate preferred associate. Future study could examine structure of preferred associate for a longer observation period using various measures, including those used in the present study.

CONCLUSION

The present study showed that the ponies on Lundy maintained a strong linear dominance relationship, and that dominance rank positively correlated with age. Analyses of patterns in spatial proximity revealed that ponies form subgroups based on kinship, especially with relation to the dam. However, further study would be required to examine whether these subgroups correspond with preferred associate.

Though behavioural studies on semi-domesticated *Equus* have been conducted in past, many interesting questions remain unsolved. For example, how does the dominance relationship change over time? Though established dominance rank among the *Equus* species is known to remain stable over time (Tyler 1972; Houpt & Wolski, 1980), Calloo, the temporarily removed oldest mare, might eventually regain her dominance position. Removal of the eldest individuals or introduction of a stallion may dramatically change the dominance rank, and careful examination of the consequences of such events will reveal how a partnership with a stallion or a matriarch influences mares' dominance ranks. Lundy ponies are unique and ideal subjects for the studies of social structure since kinships of all the individuals are known and behavioural observation could be made from a relatively close distance with little disturbance. These valuable animals should be more appreciated and made use of by the scientific communities such as ethologists and behavioural ecologists.

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Table 1. Subject's name, gender, birth date, dominance rank (BBS method) and kinship.

SUBJECT NAME (CODE)	BIRTH DATE	AGE (YEAR)	DOMIN-ANCE RANK	SIRE	DAM
Lundy Calloo (CA)	14 April 1974	30	9	?	Lundy Sophie
Lundy Stonechat (SC)	25 May 1981	23	5	?	Lundy Swallow
Lundy Phoenix (PH)	29 April 1991	13	1	Mozart	Lundy Belinda
Lundy Cirl Bunting (CB)	15 April 1993	11	2	Braetor Lapwing	?
Lundy Reed Warbler (RW)	1 May 1995	9	4	Braetor Lapwing	Lundy Kittiwake
Lundy Lerina (LE)	21 May 1995	8	3	Braetor Lapwing	Lundy Belinda
Lundy Jilly (JI)	28 May 1997	6	8	Lundy Sabine	Lundy Stonechat
Lundy Jenny (JE)	15 July 1997	6	12	Lundy Sabine	Lundy Shearwater
Lundy Iona (IO)	3 April 1998	6	10	Lundy Sabine	Lundy Red Kite
Lundy Annie (AN)	19 May 1998	5	7	Lundy Sabine	Lundy Stonechat
Lundy Charlotte-, Louise (CL)	19 May 1998	5	11	Lundy Sabine	Lundy Red Kite
Lundy Hannah (HA)	6 May 1999	5	6	Lundy Sabine	Lundy Stonechat
Lundy Francis-Anne (FA)	1 May 2000	4	13	Lundy Sabine	Lundy Red Kite

Table 2. Identification of subjects according to colouration and marking. The description is more extensive and detailed than Randle & Gill (2002).

NAME	COLOUR	DISTINGUISHING CHARACTERISTICS
Calloo	Dark Dun	White star on face
Stonechat	Bay	White coronet- left hind
Phoenix	Cream Dun	White race on face, 3 white socks,left fore black
Cirl Bunting	Cream Dun	Star and snip on face 4 white socks
Reed Warbler	Cream Dun	White race on face, white sock left for, white coronet right hind
Lerina	Dark Dun	White crown left and right hind
Jilly	Dark Bay	White race on face, long white socks left and right hind
Jenny	Dun	Blaze on face and wall eye, 4 white socks
Iona	Bay	Very wide blaze, and white chin, coronet right fore, long socks below hocks right and left hind
Annie	Cream Dun	Stripe on face, black sock right fore
Charlotte-Louise	Bay	Blaze on face, 4 short white socks below fetlocks
Hannah	Cream Dun	Star and black lips, white coronet right fore and right hind, white sock below hock on left hind
Francis-Anne	Bay	Very rectangular blaze on entire face, long socks below hocks on left and right hind

Table 3. Dominance encounter matrix for 13 Lundy ponies. The matrix shows the number of dominance encounter during the entire observation period. Individuals listed in rows are dominant to the individuals listed in columns. Labels of the individuals used in Table are those listed in Table 1.

	CA	SC	PH	CB	RW	LO	JI	JE	IO	AN	CL	HA	FA
CA	0	0	0	0	0	0	0	0	0	0	0	0	0
SC	0	0	0	1	0	0	0	1	2	0	1	1	0
PH	0	0	0	1	1	3	3	0	1	0	0	0	0
CB	0	0	0	0	4	1	5	7	13	2	3	0	3
RW	0	0	0	0	0	3	2	2	0	1	2	1	0
LO	2	3	0	1	0	0	2	4	8	3	1	0	5
JI	0	0	0	0	0	0	0	1	1	0	0	0	2
JE	0	0	0	0	0	0	0	0	0	0	0	0	1
IO	0	0	0	0	0	0	0	0	0	0	5	1	2
AN	0	0	0	0	0	0	0	0	1	0	0	0	2
CL	0	0	0	0	0	0	0	0	1	0	0	0	1
HA	0	0	0	0	0	0	0	0	0	0	1	0	3
FA	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 4. Spatial proximity matrix for 13 Lundy ponies. The matrix shows the mean distance scores during the entire observation period. Labels of the individuals used in Table are those listed in Table 1.

	CA	SC	PH	CB	RW	LO	JI	JE	IO	AN	CL	HA	FA
CA													
SC	3.3												
PH	3.9	3.4											
CB	3.5	3.8	2.3										
RW	2.9	3.6	3.2	3.4									
LO	3.5	3.4	2.9	3.5	3.6								
JI	3.7	3.4	3.1	3.8	2.7	3.5							
JE	3.0	3.9	3.6	3.2		3.6	3.1						
IO	3.5	3.6	3.0	3.7	3.0	3.9	2.7	3.2					
AN	3.7	2.8	3.3	3.5	3.6	3.6	3.4	4.0	4.0				
CL	3.6	3.8	3.2	3.6	3.0	3.9	2.7	3.0	2.5	3.7			
HA	3.4	3.2	4.0	4.0	3.2	3.8	3.4	3.5	3.5	2.9	3.4		
FA	3.5	3.7	3.4	3.8	3.3	3.6	3.5	3.3	2.8	4.0	3.5	3.9	

Table 5. Positive mutual interaction matrix for 13 Lundy ponies. The matrix shows the number of positive mutual interactions during the entire observation period. Labels of the individuals used in Table are those listed in Table 1.

	CA	SC	PH	CB	RW	LO	JI	JE	IO	AN	CL	HA	FA
CA													
SC	3												
PH	7	1											
CB	2	1	2										
RW	1	0	2	0									
LO	0	0	2	0	0								
JI	0	0	4	0	0	2							
JE	4	1	2	1	3	0	0						
IO	1	0	2	1	0	0	0	0					
AN	2	3	0	0	1	0	0	1	0				
CL	1	0	0	1	1	0	1	1	3	0			
HA	0	2	0	1	0	0	1	1	0	3	0		
FA	1	0	0	0	1	0	0	1	1	0	2	0	

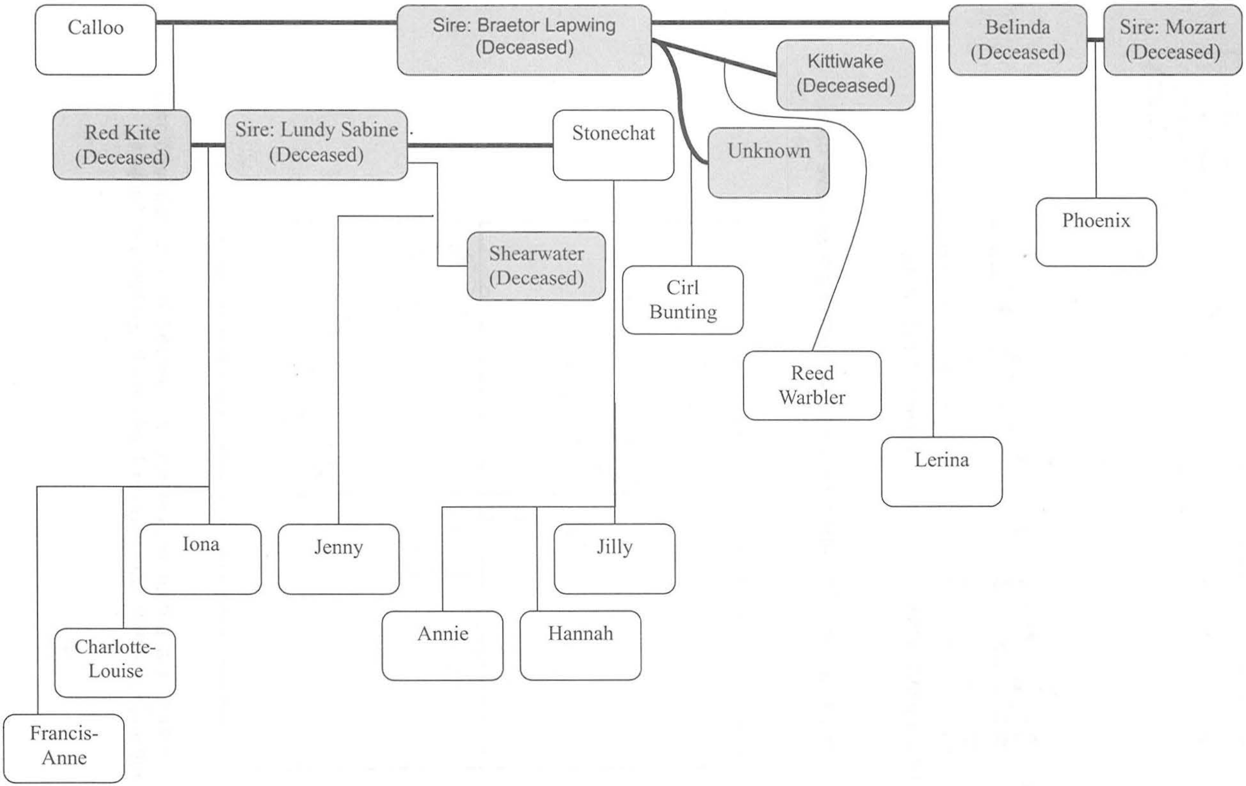

Figure 1: Kin relationship of Lundy ponies. Darkened individuals were either deceased or unknown. Horizontal connections indicate mating partners and vertical relation indicate parents-children relationships.

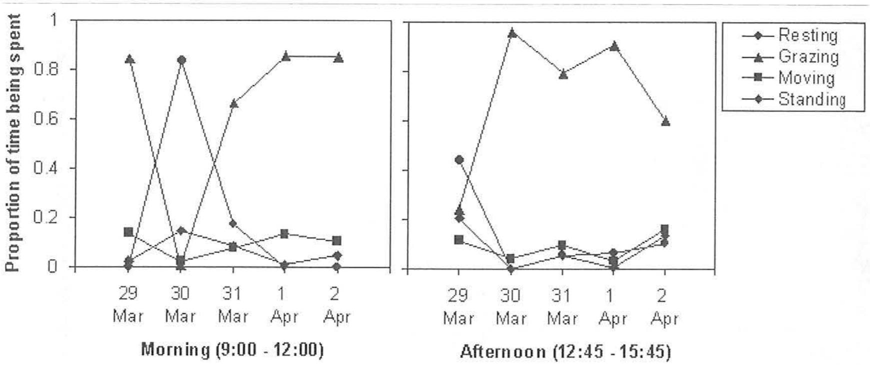

Figure 2. Activity means of the entire herd per day for five consecutive days.

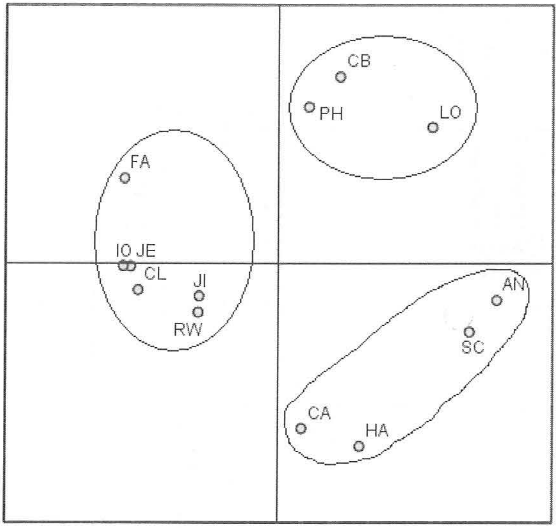

Figure 3. Overall spatial proximity of individuals derived from multidimensional scaling. Labels of the individuals used in Table are those listed in Table 1.

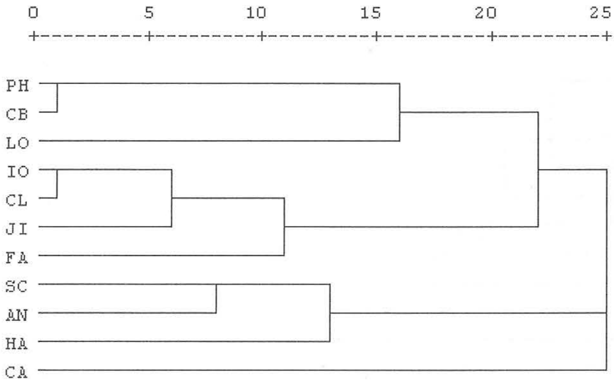

Figure 4. Cluster of spatial proximity. The horizontal axis indicates index of association. Labels of the individuals used in Table are those listed in Table 1.

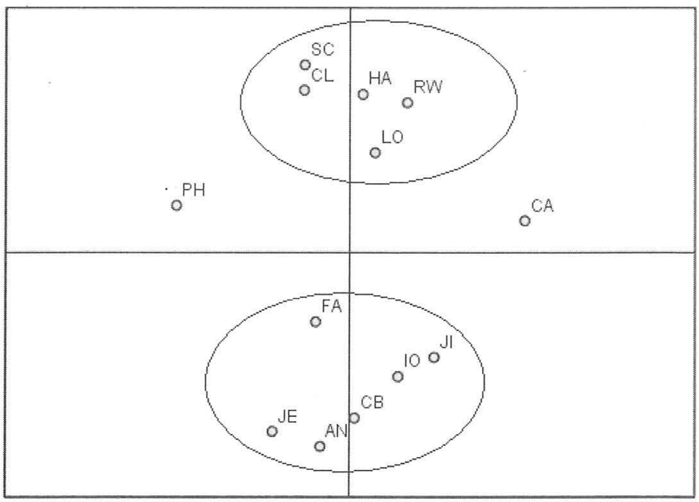

Figure 5. Two-dimensional spatial representation of similarities of positive mutual interactions between two individuals. Labels of the individuals used in Table are those listed in Table 1.

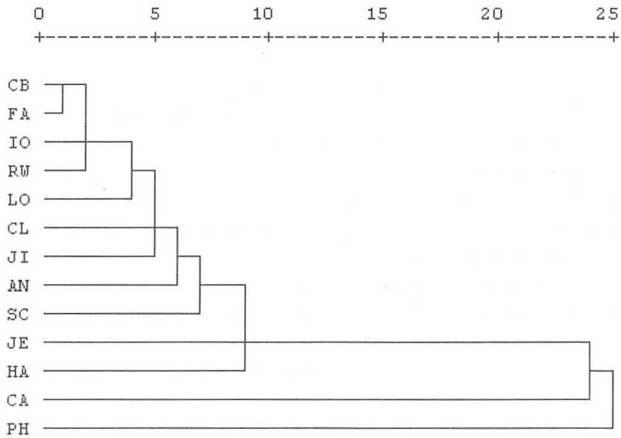

Figure 6. Cluster of positive social interactions. The horizontal axis indicates index of association. Labels of the individuals used in Table are those listed in Table 1.