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Social Behaviour and Relationships of Przewalski Horses in Dutch Semi-Reserves

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ABSTRACT

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A short-term study was made of 2 groups of Przewalski horses, a bachelor group of 4 juvenile stallions in Ooij Polder and a harem group of 1 stallion and 4 mares. All social interactions were recorded and the nearest and farthest neighbour was noted. Correspondence analysis was used to determine what parameters determined the relationships among the horses.

There was a linear hierarchy among the bachelor stallions. The dominant stallion of the group was also the oldest. The hierarchy was not linear in the harem group, and the 3-year-old stallion was subordinate to the 5-year-old mares. He was also most likely to be farthest from other horses. The mares of the same age, who had also arrived in the park at the same time, tended to be one another's nearest neighbours.

The frequency of aggression is higher among Przewalski horses than among domestic horses of similar ages. Correspondence analysis revealed that head-threats and other forms of aggression accounted for more of the variance in the data than any other behaviour, but submission, play and social interactions also contributed.

INTRODUCTION

Of 7 equid species surviving until the present time, 6 are near extinction. The last 600 individuals of the only true wild horse left in the world, the Przewalski horse, are scattered over 80 zoos or private collections on 3 continents (Volf, 1986). Most of them live in small paddocks with or without grass, and are stabled during the night. All of them get supplementary food.

Only anecdotal information is available on the behaviour of Przewalski horses in the wild (Mohr, 1971). Several studies have been published on Przewalskis in captivity: Dobroruka (1961) in Prague Zoo; Lewtas (1973) and Hutson (1975) in Marwell; Mackler and Dolan (1980) in San Diego; Lichtenstein (1980) and Martens (1981) in Oberwil; Skiff (1982) in Minnesota.

Most of these studies were of short duration and therefore do not give quantitative data on long-term relationships. Nevertheless, what is known about

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their social behaviour resembles closely the findings on feral horses, which have been extensively studied under a variety of ecological conditions (Welsh, 1975; Feist and McCullough, 1976; Wells, 1978; Miller, 1980). Projects have recently evolved to gradually release some of the horses into a more natural environment.

To reduce losses of horses during the transition from zoos to the wild, a thorough knowledge of their behaviour is required in order to choose the best strategy for their re-introduction.

The social relationships of the Przewalski horses, and specifically their aggressiveness, must be well understood before releasing them into a reserve where several breeding-units, which means several adult stallions, have to co-exist.

A recent study (Skiff, 1982) has shown that frequency of agonistic behaviour may well be influenced by enclosure size; aggression is greater in the smaller enclosures. Another study (Martens, 1981) indicates that aggressiveness in young (<4 years old) Przewalski horses is lower than in adults living under the same conditions (Lichtenstein, 1980).

Most of the zoos have to take young males (1–2 years) away from their family groups to avoid injuries caused by the adult stallion. Young females are often rejected as well. One function of this dispersal in young horses is to reduce inbreeding, a fact which is well known for Camargue horses (Duncan et al., 1984).

Incompatibility can also occur between the adult members of a group, often when introducing a "foreign" female. Only one adult stallion can be kept in an enclosure where mares are present.

This short-term study (5 weeks fieldwork) was undertaken as a feasibility study in order to test methods developed for observations on a natural herd of horses in the Camargue (South of France). It has helped to design research plans for future long-term observations in the two semi-reserves in Holland. The spatial structure and interactions exchanged are used to describe relationships and individual bonds. Dominance hierarchy and aggressiveness are investigated, and compared to results obtained from Camargue horses.

METHODS

Both semi-reserves are located on polders (drained land below sea-level), the Ooij near Nijmegen and another near Lelystad. The Ooij pasture measures 16 ha, the Lelystad pasture ca 4; both are fenced.

The polder soil is soft and produces a protein-rich vegetation. Because of the softness of the soil, the horses need hoof trimming once a year. Bark-eating is common to compensate for a lack of roughage in the grass. It occurs more often in Lelystad than in the Ooij, where the horses forage on a dune-like surface of ca. 5 ha with poorer vegetation. A watering place, created for the horses, is available in each pasture.

The horses are out day and night in all seasons. Only exceptionally is additional food (pellets, hay) given to them. Except for wardens and keepers, nobody enters the pastures, but visitors are quite frequent, especially in Lelystad, and they occasionally feed the horses through the fence.

Field methods

Tape recorder, stopwatch and field glasses were used in the field. Computer facilities were available at the Station Biologique de la Tour du Valat, Camargue, for the interaction analysis.

Two groups of horses were observed. The first consisted of 4 young stallions between 2 and 3 years old (Table 1). Sampsa, Tello and Reep have been together since 1982, Askan was introduced in autumn 1982. The second group consisted of a 3-year-old stallion and 4 mares, 2 of them 2 years old, the other 2, 5 years old (Table 1). Apoll and the 2 young mares have been together since spring 1982, the 5-year-old mares were introduced in autumn 1982.

Observations were made in the Ooij between 7 and 14 March 1983 and in Lelystad between 16 and 28 March; 8 days at each place, 4 h every day. Observation hours were equally distributed between dawn and dusk (08.00–19.00 h). Observations were carried out in the pasture by following the horses at a distance of ca. 15 m. Systematic recording started after the time it took the horses to get accustomed to the presence of the observer.

TABLE 1

Horses observed

	Sex	Year of birth	Studbook number	Origin	Semi-reserve
Stallion group					
Tello	M	80	881	Bern	Ooij-Polder
Sampsa	M	80	885	Helsinki	
Reep	M	81	957	Leipzig	
Askan	M	81	1007	Cologne	
Harem group					
Apoll	M	80	915	Cologne	Nature-park
Nora[1]	F	81	1001	Bern	Lelystad
Mira	F	81	996	Leipzig	
Lola[2]	F	78	770	Marwell	
Laura[3]	F	78	769	Marwell	

[1]Nora was pregnant during the study period.
[2]Lola was the only mare who had had a foal before arriving in Holland.
[3]Laura showed typical signs of being in estrus.
Genetic relationships between the study animals: Reep and Mira, paternal half-siblings; Tello and Nora, full siblings; Apoll and Askan, full siblings; Lola and Laura, paternal half-siblings.

All data were dictated into a tape recorder and transcribed later. All horses in a group were observed simultaneously. Identification was easy, based on different coat colours, general shapes and appearance of mane and tail.

The closest and the farthest horse to each horse was recorded every 10 min. This interval was chosen after a study made by Wells and Feh (internal report Tour du Valat, 1976), which shows that in grazing horses the probability of having the same nearest neighbour drops drastically after 8 min. Therefore the interval of 10 min guarantees a certain independence of the samples.

All interactions were recorded and timed to the nearest second for all animals in a group. This was possible because of the small number of animals present in each group. The definition of interaction was: "a movement of part or of the whole body of a horse visibly directed against another horse". The definitions were taken from two as yet unpublished ethograms on the domestic (Hughes, 1983) and the Przewalski (R. Lichtenstein, unpublished results, 1984) horse. Several interactions, such as attacks, chases, suckling or stallion rituals, never occurred during the observation hours.

Analysis

The frequency of "being closest" and "being farthest" was calculated for each horse. The matrix produced this way for each group was summed to one side (e.g. the number of times Tello was closest to Askan has been summed to the number of times Askan was closest to Tello). In addition, the total amount of "being closest" and "being farthest" to any horse of his group was calculated for each horse.

Agonistic interactions were considered to be those in which interactions between animals resulted in an increase in distance between them. These agonistic behaviours were of 2 types: defensive-agonistic and aggressive-agonistic. Defensive-agonistic (kick and kick-threat) behaviours, in all age and sex classes, are usually directed up the dominance-hierarchy (Wells, 1978). They occur in other contexts (e.g. play, reaction of a mare against the mounting attempt by a stallion, fighting for rank position) than aggressive-agonistic behaviours. Aggressive-agonistic behaviours are head threats and bites. Aggressiveness is considered to be measured by the frequency of different agonistic interactions.

Only the situations where the horses were not disturbed (visitors) or fed (pellets, hay) were analysed for frequency analysis, which made a total of 22 h per horse. The interactions were grouped into functional categories (Table 2).

The observation protocol, methods of analysis and number of hours observed were the same for Przewalski and Camargue stallions (Feh, 1987). The seasons correspond. Their social status, living in a stallion group, was identical also. The composition of the groups where the stallions lived was different for

TABLE 2

Interaction categories

Name	Function	Interactions
(1) Approach	Reduce distance	Approach
(2) Follow	Maintain distance	Follow
(3) Social investigation	Social investigation	Smell Nose-nose contact Nose-tail contact Nose-body contact
(4) Social comfort	Social comfort	Mutual grooming Rubbing Head-body contact Head-back contact
(5) Head-threat	Agonistic	Supplant Head-threat
(6) Bite	Agonistic	Bite
(7) Kick-threat	Defensive agonistic	Kick-threat
(8) Kick	Defensive agonistic	Kick
(9) Submission	Submission	Snapping (tooth clapping)
(10) Play	Play	Play bite, rear
(11) Reproductive behavior	Reproduction	Nose-genital contact Approach with vocalisation Copulation

the Camargue horses, as was the time-span over which they were observed (2 months for the Camargue stallions, 8 days for the Przewalskis).

As the frequency distributions of interactions is far from normal, medians instead of means have been calculated to compare between groups. The Mann–Whitney *U*-test and the Median-test (Siegel, 1956) were used to test differences.

Correspondence analysis

To take account of the frequency of all interactions in describing the relationships between two individuals, the data were analysed by correspondence analyses. Correspondence analysis considers the "relationships" as coordinates on the axes (e.g. Tello–Askan or Askan–Tello) in the function of the frequency of the different interactions which occurred between this pair of horses.

This multivariate method (Benzécri, 1973) is widely used in analysis of the

species composition of plots of vegetation in relation to variables such as soil chemistry. The method has two great advantages: firstly being multivariate, it allows relationships between pairs of horses to be described by the sum of *all* the interactions which occur between the animals; secondly, it identifies the social interactions which characterize particular types of relationships. Full descriptions of the method can be found in Hill (1974).

As applied here, the data were broken down into contingency tables where the columns are the frequency of interactions, and the lines are pairs of horses: actors/receivers. The X^2 distance between lines (pairs) is calculated and the axes of the ordination are calculated so that the largest possible part of the variance in the X^2 values is accounted for by the projection of the lines on the first axis. Thus, pairs with the same type of interactions are close together on the axis. The same process is repeated with the interactions (columns) so that interactions are projected on to the axis close to pairs of horses which show relatively high frequencies of these interactions.

The quality of the representation is given by: the percentage of the total variance in the contingency table accounted for by each axis: the "contribution" of each line and column of the table.

RESULTS AND DISCUSSION

Spatial structure

Stallion group

Sampsa had the highest frequency of being nearest to all other horses, and Tello the lowest (Table 3). This means that Tello was often isolated, whereas Sampsa very rarely was. The strongest association (Table 4) existed between Sampsa and Reep; second strongest between Sampsa and Tello. These results are confirmed by the numbers found for "being farthest", as these pairs had the lowest frequency of being farthest apart.

Sampsa seems to be the central horse of the group, surrounded by Reep and Tello. Sampsa, Tello and Reep were the first to live on the Ooij-pasture, and

TABLE 3

Frequency of "being nearest to" and "being farthest from" all other horses in the stallion group[1]

	Being nearest	Being farthest
Tello	122	170
Askan	133	164
Reep	129	148
Sampsa	184	86

[1]Number of samples for each horse, 142.

TABLE 4

Frequency of "being nearest" and "being farthest" (boxed numbers) between horses in the stallion group[1]

	Tello	Askan	Reep	Sampsa
Tello	—	91	64	109
		[116]	[118]	[78]
Askan		—	87	97
			106	[84]
Reep			—	120
				[66]
Sampsa				

[1]Number of samples for each horse, 142.

were joined several months later by Askan. Askan had no outstanding spatial affinity with any other member of the group.

Harem group

Apoll, the stallion, and Laura, a mare in heat, were the horses found most often on their own. They had the lowest frequency of "being nearest" and the highest frequency of "being farthest" to all other horses (Table 5). The mare Nora was very rarely observed on her own. The strongest association occurred between Nora and Mira (Table 6) followed by the association between Laura and Lola, and finally Nora and Apoll. Apoll and Laura, as well as Apoll and Lola, were rarely observed together (Table 6). Nora and Mira had been on the pasture together with Apoll for several months before the arrival of Laura and Lola, who had known each other since birth. This, together with the age-factor (2 years for both Nora and Mira, 5 years for Laura and Lola), probably explains the strong affinities.

TABLE 5

Frequency of "being nearest to" and "being farthest from" all other horses in the harem group

	Being nearest	Being farthest
Apoll	125	191
Laura	123	163
Lola	128	133
Nora	167	63
Mira	137	130

[1]Number of samples for each horse, 136.

TABLE 6

Frequency of "being nearest" and "being farthest" (boxed numbers) between horses in the harem group[1]

	Apoll	Laura	Lola	Nora	Mira
Apoll	—	61	57	88	55
		[104]	[94]	[50]	[79]
Laura		—	100	47	51
			[58]	[55]	[82]
Lola				54	53
				[53]	[64]
Nora				—	114
					[41]
Mira					—

[1]Number of samples for each horse, 136.

Dominance hierarchy

Kick-threats differ from head-threats in certain contexts (see next paragraph), so head-threats and bites have been used to determine the dominance hierarchy. Schein and Fohrman's (1955) method has been used, arranging individuals in an order so that each one receives interactions from the smallest numbers of individuals below it.

Stallion group

As numbers of threats observed were small, the situation where hay or pellets were fed have been taken into account for this analysis. Limited food resources do not qualitatively affect hierarchies in horses (Sereni, 1977). The following linear hierarchy was observed (Table 7), showing only one "reverse" interaction (Reep–Askan).

Tello
↓
Sampsa
↓
Askan
↓
Reep

As other authors have mentioned (Tyler, 1972; Wells, 1978), the hierarchy is based on age, the 2 older stallions, Tello and Sampsa, being dominant over the younger ones, Reep and Askan. The most aggressive stallion, Sampsa, is not the dominant one.

TABLE 7

Dominance hierarchy based on head-threats and bites: stallion group[1]

Initiator	Recipient				
	Tello	Sampsa	Askan	Reep	Total
Tello	—	6	11	12	29
Sampsa		—	12	23	35
Askan			—	4	4
Reep			1	—	1
Total		6	24	39	69

[1]Total observation time: 22 h per horse + 2 h when hay was given to the horses.

TABLE 8

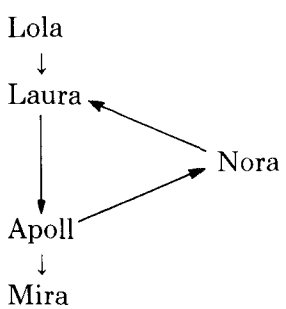
Dominance hierarchy based on head-threats and bites: harem group[1]

Initiator	Recipient					
	Lola	Laura	Apoll	Nora	Mira	Total
Lola	—	5	2	6	8	21
Laura		—	2	5	6	13
Apoll	1		—	7	9	17
Nora	1	7		—	4	12
Mira					—	0
Total	2	12	4	18	27	63

[1]Total observation time: 22 h per horse. No hay feeding.

Harem group

No clear linear hierarchy existed in the harem group (Table 8). Laura, Nora and Apoll show a triangular relationship:



Again, the hierarchy is based on age. The stallion Apoll is not the dominant animal, which is probably due to his youth (3 years).

Camargue stallions form a harem only between the ages of 5 and 6 years, and even at that age, they quite often are not dominant over their mares in the first period after harem formation.

Wells (1978) has shown that kick-threats and kicks were proportionally more frequently given up the hierarchy than head-threats and bites. In the stallion group (Table 7), 22% (6/27) of the kick-threats against 1.4% (1/69) head-threats were given as back-threats. In fact, it would not be possible to establish a clear linear hierarchy in this group if kicks and kick-threats were included in the analysis. In the harem group, 14% (9/63) of the bites and head-threats (Table 8) against 9% (3/33) of kicks and kick-threats were given up the hierarchy, which reverses the situation. As we have seen, however, a clear linear hierarchy has not yet been established in this group. The highest number of kicks and kick-threats were given by Laura, the mare in heat, to Apoll. These kicks occurred mainly in response to the mating attempts of the stallion.

Aggressiveness

The median frequency of head-threats is higher in the harem group (13) than in the stallion group (8.5). So is the median frequency of total agonistic interactions (harem group, 20; stallion group, 12.5; Table 9), but these differences are not statistically significant (Median test). Frequency of agonistic interactions is in general higher in breeding groups than in all-male groups, as is known for Camargue-horses (Feh, unpublished report).

The median proportion of agonistic to non-agonistic interactions was higher

TABLE 9

Aggressiveness[1]

	Head-threat	Bite	Kick-threat	Kick	Proportions	
					Agon./non-agon.	Aggr./defen. agon.
Tello	15	1	1	1	0.31 (18/59)	8.00 (16/2)
Askan	2	0	2	3	0.32 (7/22)	0.40 (2/5)
Reep	0	0	1	0	0.01 (1/123)	0 (0/1)
Sampsa	29	2	6	4	1.14 (41/36)	3.10 (31/10)
Apoll	16	1	2	1	0.22 (20/92)	5.67 (17/3)
Laura	13	0	3	13	2.23 (29/13)	0.81 (13/16)
Lola	20	1	5	6	4.57 (32/7)	1.91 (21/11)
Nora	11	1	2	0	0.78 (14/18)	6.00 (12/2)
Mira	0	0	0	1	0.04 (1/29)	0 (0/1)

[1]22 h of observation per horse. Non-agonistic: all interactions except head-threat, bite, kick-threat, kick.

in the breeding group (0.78) than in the all-male group (0.31, Table 9). This difference is statistically significant (Mann–Whitney U-test, $P<0.05$).

The median proportion of aggressive–agonistic to defensive–agonistic interactions in the 2 groups are similar (1.909 and 1.8).

When comparing the aggressiveness of young Przewalski stallions to the aggressiveness of young Camargue stallions (Apoll, Tello and Sampsa compared to 8 Camargue stallions of the same age), one can see that the frequency of head-threats and bites given is significantly higher in Przewalskis than in Camargue horses (Mann–Whitney U-test, $P<0.01$).

Threats and bites given at 3 years

Przewalski stallions:	16	17	31					
Camargue stallions:	8	2	5	6	9	4	2	10

(Significant at $P<0.001$)

The frequency of kick-threats and kicks given is higher in the five 2- or 3-year-old Przewalski stallions compared to the 8 Camargue stallions of the same age. The median for the 5 Przewalski horses is 3, whereas only 1 Camargue stallion out of 8 addressed one kick-threat to another horse in 22 h of observation.

Social relationships

The correspondence analysis used to characterize the different relationships indicates the percentage of variance accounted for per axis, the coordinates of each relationship and each interaction, and a value for the contribution to the construction of each axis by the relationships and the interactions. It takes into account the frequencies of all different interaction categories to describe a relationship.

Stallion group

Percentage of variance accounted for:

Axis 1: 39.50
Axis 2: 23.86
Axis 3: 15.66
Axis 4: 9.00
87.96%

This means that nearly 90% of all variance in the data was accounted for.

By far the most important interaction for the first axis is head-threat. For Axis 2, submissive behaviour and play contributed most to its construction. The third axis is best explained by the interaction approach, the fourth by social comfort, kick-threat, kick and social investigation. The most important relationship in the construction of Axis 1 is Sampsa–Reep (the name of the

first horse in a relationship is the name of the initiator of the interaction). Reep–Askan and Reep–Sampsa contributed most to Axis 2. For Axis 3 it was Sampsa–Tello, and for Axis 4, Tello–Askan.

The different interactions and relationships do not necessarily have to be on the same side of the center of the axis (Fig. 1). For example, if the interaction head-threat contributes most to the first axis and the relationship Sampsa–Reep does the same, it should be checked whether both points have their coordinates on the same side of the center of gravity (intersection of the axes) before it is possible to say that the relationship of Sampsa to Reep is characterized by the high frequency of threats given from Sampsa to Reep. (To minimize confusion only the first two axes have been represented in Figs. 1 and 2.)

The different relationships can now be explained by superimposing the results obtained (Table 10). If a relationship did not make a very important contribution to an axis, it has been put in the column of the axis where the contribution was largest (Table 10). The different types of relationship can be characterized as follows (see Table 10 and Fig. 1):

1. Friendly	Social comfort and investigation	Approach
	Tello ⟷	Askan
	Tello ⟷	Sampsa
2. Play	Approach	Play
	Askan ⟷	Reep
3. Aggression and submission	Head-threat and bite	Submission
	Tello ⟷	Reep
	Sampsa ⟷	Reep
4. Aggressive- and defensive-agonistic	Head-threat	Kick and kick-threat
	Sampsa ⟷	Askan

The same analysis was performed for Camargue stallions of the same age who were also in a stallion-group (Feh, 1987). Their behaviour seemed to be more homogeneous and their social "role" better defined. The relationships between them were mainly based on approaches, social comfort, social investigation and play. None of them had a relationship with another stallion based mainly on aggressive interactions.

Harem group

The same procedure was used to describe the relationships in the harem group. Percentage of variance accounted for:

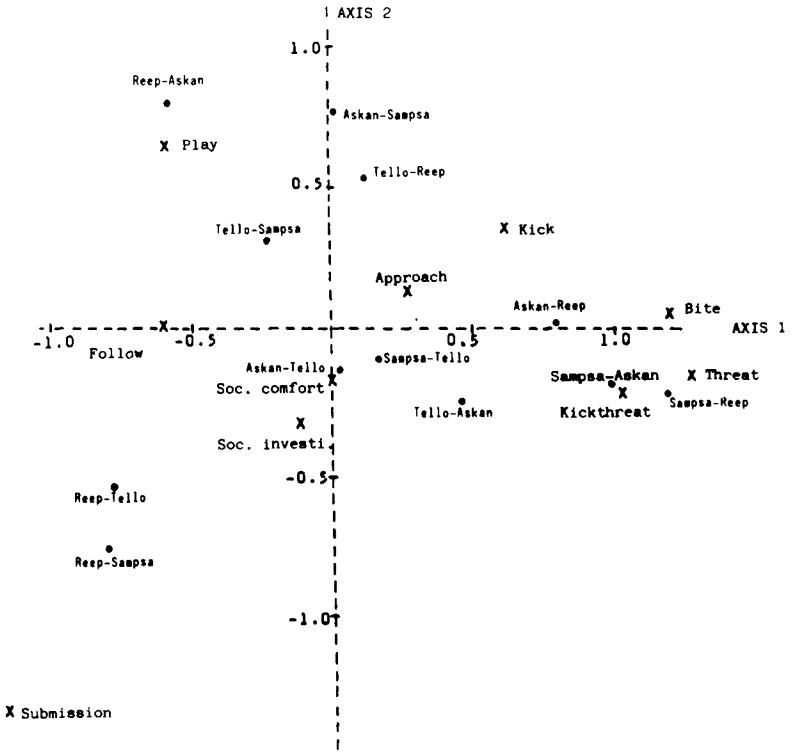


Fig. 1. Correspondence analysis representation of the first 2 axes. Group Tello.

TABLE 10

Important contributions from relationships superimposed on important contributions from interactions[1]

Relationships	Axis 1 1 Headthreat	Axis 2 1 Play 2 Submission	Axis 3 1 Approach 2 Bite	Axis 4 1 Soc. comfort 2 Soc. invest. 3 Kick-threat 4 Kick
Tello-Askan				⊗ 1 2
Askan-Tello			× 1	
Tello-Reep			× 2	
Reep-Tello		× 2		
Tello-Sampsa				× 1 2
Sampsa-Tello			⊗ 1	
Askan-Reep			× 1	
Reep-Askan		⊗ 1		
Askan-Sampsa				× 3 4
Sampsa-Askan	× 1			
Reep-Sampsa		⊗ 2		
Sampsa-Reep	⊗ 1			

[1]Circled crosses, most important contributions.

Axis 1:	30.99
Axis 2:	18.27
Axis 3:	15.43
Axis 4:	13.51
Total	78.20%

Almost 80% of the variance is accounted for by the first 4 axes. By superimposing the results obtained from the most important contributions to the axes, the different types of relationship can be characterized as follows (see Table 11 and Fig. 2).

Mare–mare

1. Friendly	Social comfort		Social comfort
	Mira	⟷	Nora
2. Aggression			
Hierarchy established	Head-threats		
	Lola	⟷	Mira
	Lola	⟷	Laura
	Laura	⟷	Mira
Hierarchy non-established	Head-threats		Head-threats
	Lola	⟷	Nora
	Laura	⟷	Nora

Stallion–mare

1. Reproductive–defensive	Reproductive		Kicks
	Apoll	⟷	Laura
2. Play–defensive	Play		Kicks
	Apoll	⟷	Lola
	Apoll	⟷	Mira
3. Friendly–defensive	Social comfort		Kicks
	Apoll	⟷	Nora

The typical interactions between mares are head-threats to establish or maintain the dominance hierarchy. The only exception is the relationship between the 2 young, not yet adult, mares, which is based on social comfort. The relationships of all mares with the stallion are characterized by their defensive–agonistic attitudes if he initiates reproductive-, play- or social-comfort-

TABLE 11

Important contributions from relationships superimposed on important contributions from interactions[1]

Relationships	Axis 1 1 Head-threat 2 Reproduct.	Axis 2 1 Kick 2 Play	Axis 3 1 Reproduct. 2 Play	Axis 4 1 Soc. comf. 2 Play
Apoll-Laura	⊗ 2		⊗ 1	
Laura-Apoll		⊗ 1		
Apoll-Lola			⊗ 2	⊗ 2
Lola-Apoll		× 1		
Apoll-Nora				× 1
Nora-Apoll		× 1		
Apoll-Mira		× 2		
Mira-Apoll		× 1		
Lola-Laura	× 1			
Laura-Nora	× 1			
Nora-Laura	× 1			
Laura-Mira	× 1			
Lola-Nora	× 1			
Nora-Lola	× 1			
Lola-Mira	× 1			
Nora-Mira				× 1
Mira-Nora				⊗ 1

[1]Circled crosses, most important contributions.

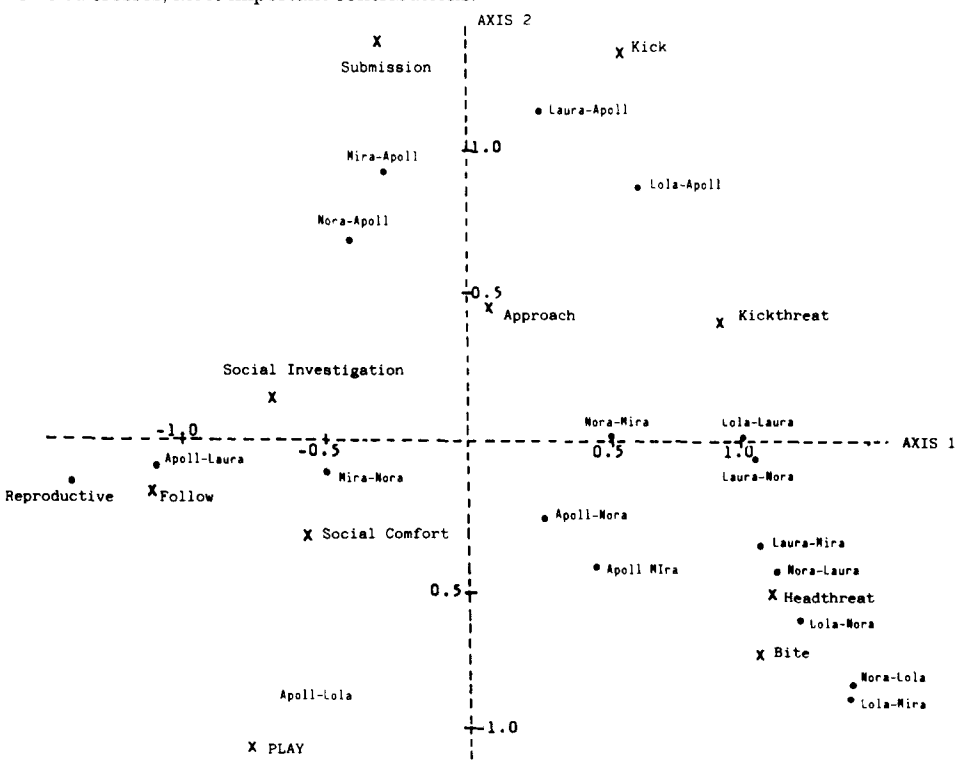


Fig. 2. Correspondence analysis representation of the first 2 axes. Group Apoll.

interactions. Apparently, at the age of 3 years he is not yet accepted in the role of a harem-stallion.

CONCLUSIONS

Methods developed for Camargue horses, for both field work and analysis, were adequate for this feasibility study on Przewalski horses in a relatively large enclosure. Correspondence analysis proved to be useful in displaying the parameters on which relationships are based.

To compare the aggressiveness of Przewalski horses with that of domestic horses, one would ideally observe a mixed group of the same age. Nevertheless, this study brings indication that Przewalski horses are more aggressive than a domestic breed, even at a "non-aggressive" age (before adulthood) and in a non-competitive situation, where no mares are present and food is abundant and evenly dispersed. This is confirmed by the fact that individual relationships of Przewalski stallions in this study were mainly based on agonistic interactions, whereas in Camargue stallions, the main characteristics of these relationships are "comfort" behaviour such as "mutual grooming" and distance-reducing interactions like "approach" and "follow" (Feh, 1987). It is possible, however, that the higher frequency of agonistic interactions in Przewalski horses is due to the fact that they have not been together for a very long time compared to the Camargue stallion, who had lived in the same herd since birth.

Individual preferences exist, as in all other horses. The social position of the harem stallion could indicate that, as in feral horses, sexual and social maturity do not evolve simultaneously; at the age of 3 years, the stallion bred mares but was not dominant over all of them.

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REFERENCES

Benzécri, J.-P., 1973. L'Analyse des dormecs. Z. L'Analyse des correspondance. Dunod, Paris, 620 pp.

Dobroruka, L.J., 1961. Eine Verhaltensstudie des Przewalski-Urwildpferdes (*Equus przewalskii* Poliakov 1881) in dem Zoologischen Garten Prag. In: Equus 1. Hrsg. von Z. Veselovsky. S. 89-104 Prag.

Duncan, P., Feh, C., Gleize, J.C. and Malkas, P., 1984. Reduction of inbreeding in a herd of horses. Anim. Behav., 32: 520-527.

Feh, C., 1987. Etude du développement des relations sociales chez les étalons de race Camargue et de leur contribution à l'organisation sociale du groupe. Thesis, University of Aix-Marseille.

Feist, J.D. and McCullough, D.R., 1976. Behavior patterns and communication in feral horses. Z. Tierpsychol., 41: 337-371.

Hill, M.O., 1974. Correspondence analysis; a neglected multivariate method. Appl. Sat., 23: 340-354.

Hughes, B., 1983. Ethogram of the domestic horse. Unpublished.

Hutson, A.D., 1975. Aspects of the social behaviour of Przewalski horses. Department of Biological Sciences, Portsmouth Polytechnic, unpublished.

Lewtas, P.N., 1973. Aspects of the social behaviour of Mongolian wild (Przewalski) horses. Department of Biological Sciences, Portsmouth Polytechnic, unpublished.

Lichtenstein, R., 1980. Vergleichende Untersuchungen zur Gruppenstruktur von Wildequiden. Lizentiatarbeit, Zoologisch Institut Universität Bern, unpublished.

Mackler, S.F. and Dolan, J.M., 1980. Social structure and herd behavior of *Equus przewalskii* Poliakov, 1881 at the San Diego Wild Animal Park. In: Equus Band 2, Heft 1. Hrsg. von H. Dathe. S. 55-69. Berlin-O: Tierpark Berlin.

Martens, M., 1981. Vergleichende Untersuchungen zur sozialen organisation einer Przewalski-Jungtiergruppe. Diplomarbeit, Zoologisch Institut Universität Bern, unpublished.

Miller, R., 1980. Band organization and stability in Red Desert feral horses. In: R.H. Denniston (Editor), Proc. Conf. Ecology and Behavior of Feral Equids. University of Wyoming, Laramie, pp. 113-123.

Mohr, E., 1971. Das Urwildpferd. 2. Aufl. die neue Brehm-Bücherei 249. Wittenberg, Ziemsen.

Schein, M.W. and Fohrman, M.H., 1955. Social dominance relationships in a herd of dairy cattle. Br. J. Anim. Behav., 3: 45-55.

Sereni, J.L., 1977. Recherches sur lévolution de la structure sociale et du comportement alimentaire d'un groupe de chevaux camarguais. Thèse de troisième cycle (Sciences du Comportement, option Ethologie). Marseille, 85 pp.

Siegel, S., 1956. Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill.

Skiff, E.M., 1982. The effect of enclosure design on social interactions and daily activity patterns of the captive Asiatic wild horse (*Equus przewalskii*). M. Sc. Thesis, University of Minnesota.

Tyler, S.J., 1972. The behaviour and social organization of the New Forest ponies. Anim. Behav. Monogr., 5 (Pt. 2): 87-195.

Volf, J., 1986. Pedigree Book of the Przewalski Horse. Zoological Garden, Prague.

Wells, S., 1978. The behaviour and social structure of a herd of Camargue horses. M. Sc. Thesis, University of Cambridge, unpublished.

Wells, S.M. and von Goldschmidt-Rothschild, B., 1979. Social behaviour and relationships in a herd of Camargue horses. Z. Tierpsychol., 49: 363-380.

Welsh, D.A., 1975. Population, behavioural and grazing ecology of the horses of Sable Island, Nova Scotia. Ph.D. Thesis, Dalhousie University.