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AN ANALYSIS OF DOMINANCE, ITS BEHAVIOURAL PARAMETERS AND POSSIBLE DETERMINANTS IN A HERD OF ICELANDIC HORSES IN CAPTIVITY

by

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ABSTRACT

The applicability of the concept of dominance was investigated in a captive herd of 26 Icelandic horses and 5 ponies of different breeds. Eight out of 20 behaviours possibly related to dominance occurred frequently enough to be investigated in detail. For these eight agonistic behaviours the coverage, the unidirectionality in the exchange, and the degree of transitivity (Landau's linerarity index) were calculated. Four offensive behaviours, together with avoidance, were suitable for further analysis with regard to dominance. The patterns of asymmetries with which these behaviours were exchanged were sufficiently similar as to justify the application of the dominance concept and to construct a (nearly) linear dominance hierarchy. The rank order of the castrated stallions was completely linear, the hierarchy of the mares was almost completely linear. The results suggest that offensive and defensive aggressive behaviours should be treated separately and that the concept of dominance is applicable. However, ritualized formal dominance signals between adult horses appear to be (almost) absent. The rank positions of the individuals were correlated with age and residency in the herd but not with height. Middle ranking horses tended to be more frequently in the close vicinity of an other horse than high ranking or low ranking horses. Over and above this correlation at the individual level, it was found that pairs of horses close in rank to each other were more often also spatially close to each other. Being in oestrus did not influence the dominance relationships between mares. For castrated stallions the rank positions were correlated with the age at which they were castrated. This suggests that in male horses experience prior to neutering influences the behaviour afterwards.

KEY WORDS: dominance, rank order, horses, Icelandic horses.

INTRODUCTION

Dominance relationships constitute a major aspect of the social structure of some socially living animals. Often, however, dominance rank orders are constructed without prior investigations as to whether the concept of dominance is valid. This is the case for most of the studies of horse social organization. Following HINDE (1974) our understanding

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of the concept of dominance is that if the main directions of asymmetries in the exchange of a number of behaviours within dyads are identical, the intervening variable 'dominance' can be used to summarise these asymmetries. Subsequently, it is often possible to rank individuals so that a more or less linear rank order results. This constitutes the second aspect of the dominance concept. Thirdly, a formal dominance signal can be assumed to exist when the exchange of this behaviour within each dyad is unidirectional for 100% and if the coverage (the percentage of non-zero dyads) is high enough (*cf.* VAN HOOFF & WENSING, 1987).

Many studies have examined the dominance relationships in both domestic horses (GRZIMEK, 1944; HECHLER, 1971; HOUPT *et al.*, 1978; SERENI & BOISSOU, 1978; HOUPT, 1979; ASA *et al.*, 1979; HOUPT & WOLSKI, 1980; HOUPT & KEIPER, 1982; ARNOLD & GRASSIA, 1982; WOOD-GUSH & GALBRAITH, 1987) and feral horses (EBHART, 1954; TYLER, 1972; CLUTTON-BROCK *et al.*, 1976; FEIST & MCCULLOUGH, 1976; BERGER, 1977; VON GOLDSCHMIDT-ROTHSCHILD & TSCHANZ, 1978; WELLS & VON GOLDSCHMIDT-ROTHSCHILD, 1979; MILLER, 1981; HOUPT & KEIPER, 1982; BERGER, 1986; KEIPER & SAMBRAUS, 1986; RUTBERG & GREENBERG, 1990). KEIPER & RECEVEUR (1992) investigated dominance in Przwalski horses. Almost all authors describe a hierarchy in one way or another; only BERGER (1986) found hardly any stable dominance hierarchy in his feral horse herds, while FEIST & MCCULLOUGH (1976) and VON GOLDSCHMIDT-ROTHSCHILD & TSCHANZ (1978) could only detect a rank order between the males.

Several authors (GRZIMEK, 1944; HOUPT *et al.*, 1978; SERENI & BOISSOU, 1978; ASA *et al.*, 1979; HOUPT & WOLSKI, 1980; HOUPT & KEIPER, 1982) used the rivalry around limited and monopolisable resources to establish the dominance-subordination relationship by using (paired) feeding tests. In such tests a possible influence of other herd members is excluded. HOUPT *et al.* (1978) used paired feeding tests to show that in small herds (up to 9 animals) strictly linear hierarchies were found, while in larger herds (10-11 animals) also triangular relationships were formed. However, dominance relationships found in this way may differ from those found in a free roaming situation and during a longer period of observation.

Unfortunately, authors do not fully agree with regard to the behaviours they use to construct rank orders. For example, HOUPT & WOLSKI (1980) used a mix of offensive and defensive aggressive behaviours. On the other hand, WELLS (1978) and FEH (1988) explicitly state that these two classes of behaviour must be treated separately and SCHILDER (1988) found the same in a detailed analysis of dominance relationships in plains zebra stallions. Many authors (GRZIMEK, 1944; HECHLER, 1971; TYLER, 1972; HOUPT *et al.*, 1978; HOUPT, 1979; WELLS & VON GOLDSCHMIDT-ROTHSCHILD, 1979; HOUPT & WOLSKI, 1980; MILLER, 1981) did not use avoidance behaviour, whereas this was useful in zebras (SCHILDER, 1990). Since aggressive behaviours may well by used by lower ranking individuals against higher ranking ones, the use of aggressive behaviours only in investigating dominance may render an unclear or even invalid picture. This was the reason why in zebra stallions (SCHILDER, 1988) and wolves (VAN HOOFF & WENSING, 1987) aggressive behaviours could not be used to construct a rank order.

To investigate which individual factors might be correlated with the rank position an animal has in the dominance hierarchy it is required that the rank order is (nearly) linear. Landau's linearity index (see MARTIN & BATESON, 1993) can be used to assess the degree of linearity in a set of dominance relationships. If the value of this index exceeds 0.9 the linearity of the hierarchy is sufficiently strong to obtain meaningful correlations between rank positions and individual factors like weight or age. The weaker the linearity of the rank order the less these correlations can be meaningfully interpreted. This problem is encountered in KEIPER & RECEVEUR, 1992.

What different types of individual factors could determine (partially) the rank position in a dominance hierarchy? In the literature the following findings have been reported. Some authors reported that dominance rank correlated with the height of the individuals (HECHLER, 1971, CLUTTON-BROCK *et al.*, 1976, RUTBERG & GREENBERG, 1990). Weight correlated positively with rank in some studies (HECHLER, 1971; CLUTTON-BROCK *et al.*, 1976), but not in others (GRZIMEK, 1945; HOUPT *et al.*, 1978; HOUPT, 1979; HOUPT & WOLSKI, 1980; HOUPT & KEIPER, 1982). Sometimes no correlation with physical characteristics could be shown (ARNOLD & GRASSIA, 1982). Concerning the aspect of age, adult horses are nearly always dominant over immature horses (HECHLER, 1971; CLUTTON-BROCK *et al.*, 1976; HOUPT *et al.*, 1978; HOUPT, 1979; ARNOLD & GRASSIA, 1982; KEIPER & SAMBRAUS, 1986). Also, in many studies (GRZIMEK, 1944; HECHLER, 1971; CLUTTON-BROCK *et al.*, 1976; WELLS & VON GOLDSCHMIDT-ROTHSCHILD, 1979; KEIPER & SAMBRAUS, 1986), the age of adult horses correlated positively with their rank position. In the study of HOUPT *et al.* (1978) age was correlated with rank in 6 out of 9 herds. However, age was not correlated with rank in the studies of FEIST & MCCULOUGH (1976), HOUPT & KEIPER (1982) and ARNOLD & GRASSIA (1982). In the last study a group of horses was introduced into the herd during the study. All these new horses, irrespective of their ages, figured in the bottom part of the rank order. This suggests that residency in the herd could also be a determinant of rank position.

A last factor that might influence rank position is castration. LINE *et al.* (1985) showed that there is a minimal difference in the effect of pre-(<3 yr.) and post-(>3 yr.) pubertal castration in male horses on their sexual and aggressive behaviour. But the total frequency of these behaviours is much lower when castrated. Since pre-castration experience may influence later behaviour, the age at which the stallions were castrated may determine the amount of experience and therefore, may influence the position in the rank order.

In the present study we begin with analysing the patterns of asymmetries in behavioural exchanges with the aim to detect behaviours that represent dominance at the dyadic level and whether dominance can be used as an intervening variable. Subsequently, we investigate for each of these behaviours to what degree it allows the construction of a linear rank order. To this end we calculate for each of the dyadic interaction matrices the Landau linearity index, a directional consistency index, the number of tied dyads and the coverage. Using the behaviours that satisfy these criteria, a highly linear dominance rank order among 21 horses (excluding the juveniles, one deviant mare and the non-Iceland horses) can be constructed. Finally, we investigate if and to what degree the factors age, sex, height, residency in the herd, age at castration, oestrus of a mare and the possession of a young foal are related to the rank position attained or to changes therein. We also investigate whether rank and rank difference correlate with kin, proximity and mutual allogrooming.

MATERIALS AND METHODS

The study group

The herd was established in 1971 and contained all sex-age classes except for an intact stallion. There were 26 Icelandic horses (6 castrated stallions (geldings), 16 mares, 2 juvenile stallions and 2 juvenile mares) and 5 ponies of different breeds (table I). Many of these horses were kin. They lived at the 'Breidablik' farm, Tilburg, The Netherlands. The horses in the herd were living together outside, 24 hours a day the whole year round. The herd could always use a shed (20 × 20 m) and a transition corridor (400 × 8 m). They had (sometimes limited) access to a pasture (140 × 100 m) depending on the food availability. There were five of these pastures in a row, each used in turn for 1-3 weeks. The total area was 6.3 hectare. The herd had always free access to running water provided by automatic drinking bowls. It also had free access to extra mineral supplies. The water bowls and mineral supply could be monopolized.

The observations were made when the herd was allowed to graze in one of the pastures and had done so for at least an hour. The behaviour of the animals was sampled between April 1984 and September 1984 during 433 hours of observation. Some of the adult animals were irregularly used for riding, or were absent for some weeks for breeding purposes. The presence and absence due to riding, out of sight in the shed, breeding, *etc.* of the animals was registered. In all dyads the data have been corrected for temporary absence of individuals.

In order to obtain a homogeneous sample the five non-icelandic ponies were excluded from the analyses. Observations on the juvenile animals were not used for the analyses because we were especially interested in dominance, its behavioural parameters and its possible determinants in adult horses. It has been shown by many horse ethologists that adult horses are (nearly) always dominant over immature horses (HECHLER, 1971; CLUTTON-BROCK *et al.*, 1976; HOUPT *et al.*, 1978; HOUPT, 1979; ARNOLD & GRASSIA, 1982; KEIPER & SAMBRAUS, 1986). This was confirmed in the present study (data not published). We also excluded one adult Icelandic mare (v), because she was very probably suffering from a hormone disorder since she was the only mare not seen in season during the study period. Moreover, she had experienced a false pregnancy during the first three months of this period. Her illness also caused deviant behaviour in different respects, for instance a high frequency of being solitary.

Data sampling and analysis methods
The main body of data was collected using focal animal sampling: 100 * 10 minutes per animal or less according to its presence, and additional data were collected using ad lib sampling (ALTMANN, 1974). The data were collected at randomly distributed times during the daylight period. The order of focal animals to be observed changed every day at random. The ad lib data sets included many aggressive and affiliative encounters. The focal animal and ad lib data sets were compared by calculating the rank correlation coefficient between the individual behavioural frequencies (corrected for presence and absence of each horse) found in each data set. This was done for a number of behaviours relevant to this study. The result was that the two data sets resembled each other so much that they could be lumped and treated as one.

For the analyses concerning linearity of rank orders and the influence of possible influential factors the data set was split as follows:

* Data sampled on days during which a young foal (0-3 weeks) was present (foal-days, N = 28) (Note: Three weeks is the mean time that the young foal moves more than two horse lengths from its dam (TYLER, 1972; CROWELL-DAVIS, 1985); also in 75% of the cases its mother is its nearest neighbour (CROWELL-DAVIS, 1985)).

* Data sampled on days during which at least one mare was in season (oestrus-days, N = 52).

* The days without any of these special features were called normal-days (N = 29).

A mare was considered to be in season when she displayed at least twice that day one or more of the following behaviours: *Presenting:* standing in the neighbourhood of a male with straddled hind legs, lifted tail, ears sideways, sometimes with winkling and loss of small amounts of urine (TYLER, 1972; ASA *et al.*, 1979; VON GOLDSCHMIDT-ROTHSCHILD & TSCHANZ, 1978; VON GOLDSCHMIDT-ROTHSCHILD & GLATTHAAR, 1983); *Winkling:* opening and closing of the labia major exposing the clitoris and the vulva, often with losing urine (WARING, 1983). Further, a mare was considered to be in season if she was sexually mounted by a juvenile stallion or a gelding.

The analysis of dominance — Out of the 127 behavioural elements that were recorded, we selected 20 elements that were possibly related to dominance (see table II). Descriptions of these behavioural elements are given in VON GOLDSCHMIDT-ROTHSCHILD & GLATTHAAR (1983) and WARING (1983). Next, we counted for each behaviour the number of relationships covered by that behaviour (the coverage). If the coverage of a behaviour was less than 15% of all possible dyads this behaviour was excluded from further analyses. This left us with 8 behaviours (all with a coverage of at least 30%) for further analysis (table II). These behaviours were: *attack:* fast movement in the direction of an opponent, with ears flattened: *bite:* bite or bite attempt, followed by chase in some cases; *threat to bite:* movement of the head with flattened ears towards the other animal, usually

TABLE I

Attributes of the horses in the study group

sex	*code*	*breed**	*age (yrs)*	*residence (months)*	*height (cms)*	*1st order relative in herd***	*dam of ad., yl., fl.* ***	*age at castration*
castrated	D	I	20	104	131	no	–	5
stallions	C§	S	±20	150	94	no	–	1
	H	I	18	61	136	no	–	?
	F	I	14	86	128	no	–	3
	B	I	12	143	133	yes	–	7
	S	I	9	108	135	yes	–	5
	O	I	6	72	138	yes	–	1
juvenile	M§	I	1	13	–	yes	–	–
stallions	T§	I	foal	2	–	yes	–	–
mares	s	I	22	138	132	yes	ad. r, yl. M	
	l	I	22	141	127	no	no	–
	b	I	19	152	129	yes	ad. B, ad. m	–
	K	I	19	155	125	yes	ad. k, fl. G	–
	U	I	19	124	130	yes	ad. O	–
	v§	I	19	144	123	no	no	–
	f	I	18	61	135	no	no	–
	P	I	18	155	131	yes	ad. d, yl. g	–
	e§	NF	18	137	130	no	no	–
	p	I	15	114	133	yes	ad. S	–
	a§	C	15	13	146	yes	yl. A	–
	c§	S	13	120	95	no	no	–
	d	I	12	143	133	yes	ad. o	–
	k	I	9	109	128	yes	no	–
	t	I	8	97	136	yes	fl. T	–
	m	I	7	85	134	yes	no	–
	E	I	5	61	132	yes	no	–
	r	I	5	61	136	yes	no	–
	o	I	5	61	136	yes	no	–
juvenile	A§	NF	1	13	–	yes	–	
mares	g§	I	1	12	–	yes	–	–
	G§	I	foal	1	–	yes	–	–

* I = Icelandic horse; S = Shetland pony; NF = New Forest pony; C = Connemara pony.

** This includes son, daughter, mother, brother and/or sister.

*** mother of an other adult (ad.), yearling (yl.) or foal (fl.), e.g. ad. r in the row for mare s means that s is the mother of the adult mare r.

§ Not used for the dominance analyses.

TABLE II

The coverage (% of non-zero dyads) of 20 behaviours possibly related to dominance

Behaviour	*Coverage*	*Used in dominance analyses*
Approach with ears flattened	61	*
Threat to bite	55	*
Bite	54	*
Attack	39	*
Fight	2	
Chase	5	
Drive	6	
Threat to kick	35	*
Kick (kicking back with one hindleg)	32	*
Buck (kicking back with two hindlegs)	32	*
Push	5	
head on back	3	
Walk backwards#	9	
Avoid	87	*
Tooth clapping (snapping)##	10	
Roll over	1	
Urinate over§	<1	
Defecate over§	2	
Non-sexual mount	4	
Rearing	2	

\# Only performed by 8 mares.
\## Only performed by the 5 juveniles.
§ Only performed by the stallions.

head and neck in one line; *approach with ears flattened* and head held high or horizontally; *threat to kick; kick:* kicking back with one hind leg; *buck:* kicking back with both hind legs; *avoidance:* moving away from an other individual after being approached.

For each of these eight behaviours the interaction frequency matrix was investigated with regard to the following properties (see table III);

I The *coverage, i.e.* the number of dyads with non-zero exchange of the behaviour.

II The *number of tied dyads, i.e.* the number of dyads with equal exchange of the behaviour.

III The *directional consistency, i.e.* the total number of instances the behaviour was performed in the main direction within each dyad divided by the total frequency of the behaviour. This Directional Consistency index (DC-index) ranges from 0 (completely equal exchange) to 1 (complete unidirectionality) (see VAN HOOFF & WENSING, 1987). An equivalent index, namely a direction inconsistency index, has been used by NOË *et al.* (1980) and SCHILDER (1988).

IV The *degree of linearity*, measured by Landau's linearity index *h* (see MARTIN & BATESON, 1993).

For the properties I and III we devised the criterion that the value a behaviour has for that property should be higher than the average value of that property averaged across the eight behaviours (*cf.* SCHILDER, 1988). Similarly, for the property II, the criterion

TABLE III

Properties of eight different dyadic interaction frequency matrices

Behaviour	*Total frequency*	*Coverage (non-zero dyads)*	*Number of tied dyads*	*Directional Consistency index*	*Landau's lionearity index h*	
						significance
Bite	351	119	5	0.72	0.30	p<.01
Threat to bite	334	128	0	0.90	0.46	p<.01
Approach with ears flattened	452	146	2	0.90	0.50	p<.01
Attack	239	96	4	0.95	0.30	p<.01
Threat to kick	185	90	11	0.64	0.12	n.s.
Kick	182	75	17	0.49	0.06	n.s.
Buck	158	70	13	0.52	0.07	n.s.
Avoidance	1423	201	6	0.92	0.86	p<<.001

Total number of dyads for each matrix: 210.

was that the value a behaviour has for this property should be lower than the average value. In table III the values reaching this criterion are underlined. For property IV the criterion was that Landau's linearity index should be statisticaly significant (APPLEBY, 1983; DE VRIES *et al.*, 1993). Only if a behaviour satisfied at least two criteria the behaviour was considered to be a possibly suitable indicator of dominance. This was the case for five behaviours: bite, threat to bite, attack, approach with flattened ears, and avoid. If the separate rank orders for these behaviours correlate sufficiently, the relationships between the animals can be summarised in a single hierarchy.

We also investigated the similarities between the patterns of asymmetries in the eight behaviours mentioned in table III by means of two different asymmetry measures for each pair of horses. The first asymmetry measure is defined as: the number of times a behaviour was performed from A to B (f_{AB}) minus the number of times this behaviour was performed from B to A (f_{BA}). By dividing this difference by the sum of f_{AB} and f_{BA} a normalised index of asymmetry is obtained ranging between −1 and +1 (*cf.* SCHILDER, 1988). We can call this the degree of asymmetry between A and B. A second measure, that only takes the direction of the asymmetry into account but not the degree, is obtained by taking the sign of this magnitude of asymmetry, that is: $\text{sign}(f_{AB}\text{-}f_{BA}) = 1$ if $f_{AB}\text{-}f_{BA} > 0$; $\text{sign}(f_{AB}\text{-}f_{BA}) = 0$ if $f_{AB}\text{-}f_{BA} = 0$; $\text{sign}(f_{AB}\text{-}f_{BA}) = -1$ if $f_{AB}\text{-}f_{BA} < 0$. Next, for each of these two asymmetry measures, a principal components analysis (PCA; see *e.g.* TABACHNIK & FIDELL, 1989) has been done with the eight behaviours as variables and the 0.5N(N-1) dyads as cases. Because the asymmetry between A and B is the opposite of the asymmetry between B and A, each dyad is represented only once in the data table (that is: if (A,B) is a case in the data table then (B,A) is not). Table IV presents the results of the PCA based on the signs of the asymmetries. The PCA based on the asymmetry degrees rendered highly similar results and is not shown.

Construction of the final rank order — The following procedure was used to construct the rank order using the five agonistic behaviours that met the above stated criteria.

1) The outcome of the PCA mentioned above shows that the four aggressive behaviours (bite, threat to bite, approach with ears flattened and attack) all have high and quite similar loadings on the first factor. This means that these four behaviours all show a similar pattern of asymmetry across the dyads. Therefore, we decided to add, for

TABLE IV

Factor loadings resulting from a Principal Components Analysis based on the signs of dyadic asymmetrics in 8 behaviours

Behaviour	*Factor 1*	*Factor 2*	*Communality*
Bite	54	-17	.33
Threat to bite	73	4	.54
Approach with ears flattened	77	8	.60
Attack	65	-13	.43
Threat to kick	7	71	.51
Kick	-3	76	.57
Buck	-21	82	.71
Avoidance	-67	2	.45
Variance explained	30%	21%	

each dyad, the frequencies of these four aggressive behaviours. Since we are interested in the dominance relationships as such rather than the strength of these relationships, we converted this frequency matrix into a binary relationship matrix. That is, for each dyad, the animal that showed the highest frequency was given a one and the other animal was given a zero. The matrix that contains the avoidance frequencies was also converted into a binary relationship matrix, but now for each dyad the animal with the lowest frequency was given a one rather than the animal with the highest frequency, in order to make this matrix compatible with the binary aggression matrix. We decided to multiply this binary avoidance matrix by two, because avoiding behaviour is in principle a much better parameter for representing the dominance-subordinate relationship than the aggressive behaviours are. This is so, because by giving way to another approaching animal the avoiding animal acknowledges the other's dominance, whereas aggressive behaviour is not necessarily an expression of one's dominance over an other animal (VAN HOOFF & WENSING, 1987; SCHILDER, 1988). This is in accord with the fact that the avoidance matrix has the highest value of Landau's linearity index and a high directional consistency index (table III).

2) The two relationship matrices thus constructed were added. This combined relationship matrix has the advantage that one can easily see which dyads have a clear or less clear dominance relationship (see fig. 1). The matrix contains the scores 0, 1, 2 and 3. A score of 3 means that in that dyad the dominant individual was dominant on basis of two behavioural parameters: aggression given and avoidance achieved. A score of 2 means that the dominant individual was only dominant on basis of avoidance achieved. In this matrix the horses were ordered according to the number of dominated animals. If, however, in the order thus obtained, the dyadic relationship between two adjacent individuals did not agree with this order then these two individuals were reversed (the 'flipping heuristic', ROBERTS, 1990; DE VRIES *et al.*, 1993). The result of this rearrangement procedure is a matrix in which the sum of scores below the diagonal is approximately minimized (*cf.* SCHEIN & FOHRMAN, 1995). This rendered the final rank order. All different steps in this procedure were done using MatMan, a program for the analysis of sociometric matrices (DE VRIES *et al.*, 1993).

In this way, rank orders were constructed for the complete group as well as for males and females separately (see figures 1, 2 and 3). Finally, a rank order for the complete group was constructed using the method of CLUTTON-BROCK *et al.* (1986), which excludes the influence of age.

The relationship between rank and other factors — Because of the different types of data and the constraints of some statistical tests, a number of different tests had to be used to detect relationships between dominance rank position and several factors that may influence that position. First, all rank orders were tested for linearity by a test proposed by APPLEBY (1983) using the MatMan program (DE VRIES *et al.*, 1993). Correlations between the positions held in these rank orders and the factors (expressed in years), height (in cm at the withers), residency in the herd (in months) and the age the geldings had at castration were calculated. For these comparisons the Spearman rank correlation coefficient (R_s) was used (LEE & LEE, 1982). We wanted to know whether having a newborn foal influenced the rank of the mother and the occurrence of aggressive behaviour. To investigate the latter we calculated a relative aggression score (= Number of aggressive acts/observation time) for the normal-days and for the foal-days and compared these. Another question to be answered was whether the rank positions of the adult offspring were correlated with those of their mothers. For comparisons between rank position and the relative aggressiveness of (adult) offspring (N = 9) and their dams (N = 8) the linear Pearsons correlation coefficient (Rp) was used (LEE & LEE, 1982).

The relationships between rank differences and social or kin bonds were analysed using matrices of allogrooming, proximity and kinship. *Allogrooming* was defined as mutual interactive nibbling between two horses, mainly at each others mane, withers, back and tail base. This behaviour occurred between almost all animals of all sex-age classes. When two animals were within two horse lengthts from each other they were considered to be in each other's *proximity*. Proximity between each pair of horses was recorded every half hour by a scan sample. *Kinship* was defined as a familiar relationship an animal could have knowledge of: mother-offspring, grandmother-grandschild, brother-sister via the mother. Stallion offspring relationships were not included. The correlation between the rank differences between each pair of horses and the social or kin bonds between them is assessed by means of the Mantel test (SCHNELL *et al.*, 1985). To obtain the significance probabilities we employed a permutation procedure which respects the interdependencies of the values within rows and columns of these matrices. The dual normalization procedure described in FREEMAN *et al.* (1992) was used to correct for individual variation in the tendency to allogroom or to be in the proximity of any other horse. We used the program MatMan (DE VRIES *et al.*, 1993), to calculate dually normalized matrices and subsequently perform permutation Mantel tests.

RESULTS

Applicability of the concept of dominance

According to the first criterion stated in the previous section, eight behaviours occurred sufficiently often to be used for assessing dominance. The values the four parameters (coverage, number of ties, directional consistency and linearity) took for the eight selected behaviours as described above are shown in table III. Five behaviours satisfied, at least in two cases, the criterion that a value for a behaviour should be better than the average value for that specific property. None of the behaviours showed a Landau's $h > 0.9$, which is generally taken to denote a strongly linear hierarchy (MARTIN & BATESON, 1993). On the other hand, application of the linearity test (APPLEBY, 1983) showed that for five behaviours there was a significant deviation from non-linearity. *Avoidance* showed the strongest linearity. The results of the Principal Component Analysis (table IV) clearly showed that two groups of behaviours emerge: offensive aggressive behaviours (*bite, threat to bite, approach with ears flattened* and *attack*) and *avoidance* on the one hand, and defensive aggressive behaviours (*kick, buck* and *threat to kick*) on the other hand. The first group of aggressive behaviours are considered to be of an offensive nature, because of the strong approaching tendencies involved. This group is negatively correlated with *avoidance*. The second group of aggressive behaviours is considered to have a more defensive nature, because these behaviours may be shown while retreating. This is in line with observations made by WELLS (1978), WELLS & VON GOLDSCHMIDT-ROTHSCHILD (1979), FEH (1988) and RUTBERG & GREENBERG (1990). Retreating is almost impossible during biting attempts, because these include necessarily a forward movement. Moreover, when using the hind legs the horse already is in a favourable position to withdraw. With regard to the contexts in which aggression occurred, we can say that aggression occurred on the pasture but was more common around the drinking bowls, the mineral supply and in the transition corridor. These last three situations have in common that there is limited availability in the sense that only one animal at a time could use the supply, or, in case of the corridor, could use the space.

The separate rank orders for these five behaviours correlated significantly with each other (table V), so that the use of dominance as an intervening variable (*cf.* HINDE, 1974) is justified and one hierarchy can be constructed, using the combined relationship matrix as described in the Methods section above. Figure 1 presents this relationship matrix based on the dyadic aggression and avoidance relationships. This combined relationship matrix contains only 28.75 circular triads out of the maximum of 385 circular triads possible in a matrix of size 21. This corresponds to a highly significant Laundau's linearity index h of 0.925 ($p \ll 0.01$). There were only 5 blank relationships. Because of the strong linearity present in this set of relationships, we may conclude that a (nearly) linear rank order indeed exists among the 21 Icelandic horses and it is therefore justified to construct this (nearly) linear rank order. In the matrix of fig. 1 the animals have been arranged according to this (nearly) linear rank order following the procedure described above in the Methods section. For the dominance relationships among the mares, the value of Landau's linerarity index turned out to be also very large, namely 0.95 (n = 15; $p \ll 0.01$). The rank-ordered dominance relationships matrix for the mares is presented in fig. 2. For the geldings even a strictly linear hierarchy was found (Landau's h = 1; n =

TABLE V

Spearman rank correlations between five rank orders

Bite	bite				
Threat to bite	0.85	thr. to bite			
Approach flattened ears	0.84	0.92	appr.		
Attack	0.84	0.92	0.87	attack	
Avoidance	0.87	0.93	0.94	0.87	avoid

All correlations are highly significant ($p<0.01$).

	f	P	b	l	K	D	p	s	B	d	U	S	k	F	m	t	O	o	r	E	H
f	*	3	3	2	3	3	3	3		3	3	3	3	3	3	3	3	3	3	3	3
P		*	2	3	2		3	3	3		2	2	3	3	3	3	3	3	2	3	3
b			*	2	3	2	3	2	2	2	3	2	3	2	3	2	3	3	3	3	3
l	1		1	*	3	1	1	1	3	1	3	1	3	3	3	1	3	3	3	3	3
K					*	3	3		3	3	2	2	3	2	3	3	3	3	3	3	3
D			1	2		*	1			3	3	3	3	3	3	3	3	3	3	3	3
p							*	3	3	3	3	3	3	3	3	3	3	3	3	3	2
s					3			*	2		3	2	3	2	3	3	3	3	2	2	3
B	2					3			*	3	1		3	3	3	3	3	3	3	3	3
d			1	2				3		*		3	3	3	3	3	3	3	3	3	3
U										2	*	3	3	3		2	3	2	2	3	2
S												*	2	3	3	3	3	3	3	3	3
k													*	2	3	3	3	3	3	3	3
F													1	*	3		3	3	3	3	3
m															*	3	3	3	3	3	3
t														2		*	3	2		2	3
O																	*	3	3	3	3
o																		*	3	3	3
r																			*	2	1
E																			1	*	3
H																					*

Fig. 1. Dominance relationship matrix for 21 male and female horses based on offensive aggressive behaviour and avoidance behaviour. The individuals are arranged in hierarchical order. The stallions are underlined. 3: the row individual is dominant over the column individual on the basis of aggression given and avoidance achieved. 2: the row individual is dominant over the column individual on the basis of avoidance archieved. 1: the row individual is dominant over the column individual on the basis of aggression given.

	f	P	b	l	K	p	d	s	U	k	m	t	o	r	E
f	*	3	3	2	3	3	3	3	3	3	3	3	3	3	3
P		*	2	3	2	3	2	3	2	3	3	3	3	2	3
b			*	2	3	3	2	2	3	3	3	2	3	3	3
l	1		1	*	3	1	1	1	3	3	3	1	3	3	3
K					*	3	3		2	3	3	3	3	3	3
p						*	3	3	3	3	3	3	3	3	3
d			1	2			*	3		3	3	3	3	3	3
s					3			*	3	3	3	3	3	2	2
U									*	3		2	2	2	3
k										*	3	3	3	3	3
m											*	3	3	3	3
t												*	2		2
o													*	3	3
r														*	2
E														1	*

Fig. 2. Dominance relationship matrix for 15 female horses based on offensive aggressive behaviour and avoidance behaviour. Same legend as fig. 1.

	B	D	S	F	O	H
B	*	3	3	3	3	3
D		*	3	3	3	3
S			*	3	3	3
F				*	3	3
O					*	3
H						*

Fig. 3. Dominance relationship matrix for 6 male horses based on offensive aggressive behaviour and avoidance behaviour. Same legend as fig. 1.

6; p = 0.022). The dominance matrix for the geldings is presented in fig. 3. These three (nearly) linear hierarchies will be used in the subsequent analyses, where we investigate which factors might be related to these rank orders.

Factors related to rank

Rank and sex — The top five places of the rank order of the complete group were taken by older mares; the first gelding (D) takes the 6th place. The rank positions of the males are interspersed with those of the females. It is noteworthy that the relative number of circular triads is highest (*i.e.*, Laundau's h is smallest) when the intra-sexual dominance relationships of the females (fig. 2) and the males (fig. 3) are combined with the inter-sexual relationships into one set (fig. 1). This means that some intersexual dominance relationships are not transitive. Note, for instance, the remarkable subordinate position of the top ranking female f to the top ranking male B (top ranking in the male hierarchy, that is). Note also that the α and ß male B and D in the male hierarchy have reversed rank positions in the complete hierarchy. This is due to the fact there are two mares (p and s) who dominate B but not D, and there is also one mare (l) who is subordinate to D but not to B. It is evident that the dominance relationships between the top ranking males and the high ranking females are not transitive.

Rank and age — Age correlated positively with rank in the linear rank order of the complete group (n = 21) and in the rank order of the females (n = 15; see table VI). However, age was not correlated with rank in males. A female rank order constructed excluding the influence of age (see Clutton-Brock *et al.* (1986) for methods) showed a different picture. This rank order was not significantly correlated with the linear rank order (Rs = 0.15, n = 21, n.s.). Thus, age is an important rank determining factor, at least for the females.

Rank and height — Height correlated negatively with the linear rank order of the complete group (21 horses). So, the smallest horses were highest in rank. On the other hand, height correlated negatively (Rs = −0.60, n = 21, $p<0.01$) with age also. That is, younger animals are larger than the older ones. Height did not correlate significantly with rank in the separate female and male rank orders.

Rank and residency — Rank position was correlated positively with the time of residence in the herd.

Rank and relative aggression and relative submission — The rank position in the hierarchy was, surprisingly, not or very weakly correlated with the relative aggressiveness of the individuals. This means that not the overall amount of aggressive acts performed determines the rank of an

individual, but rather to whom this aggression was directed. Relative submissiveness, on the other hand, correlated significantly with rank.
Rank and age at castration — The male rank order was correlated with the age at which they were neutered ($Rs = 0.97$, $n = 6$, $p<0.05$). That is to say, the older a male was when being neutered the higher his rank position. Below we will show that age at castration in our study herd is strongly related to the amount of sexual experience and to the possibilities to develop male displays towards other (castrated) stallions. Therefore, we can say that not the castration age as such determines the rank order among the castrated males, but rather that the amount of socio-sexual experience of a castrated stallion determines its rank.

Icelandic horses are, in this herd but also on Iceland and at other studs, always living outside in a group. From this herd all sexual experiences of all males are known. The gelding that ranked highest in the male hierarchy (B) was castrated when 7 years old and had for two years his own herd of mares. He sired four of the other herd members. The second ranking gelding (D), who has a higher rank position in the full herd but is dominated by B, had only little sexual experience: as a five year old he had one mare for a few weeks. None of the other geldings have had any sexual experience. All Icelandic horses, except H and F, have lived in 'free roaming' batchelor herds until 5 years old. From H it is only known that he was castrated on Iceland, most likely as yearling. He lived mainly in a small mixed herd. F and C were kept in mixed herds after neutering. So in this herd, age at castration is strongly related to the amount of socio-sexual experience.
Rank and being in oestrus and/or having a foal — Two foals were born during this study. Their dams climbed respectively one and three places in the rank order while their foals were less than three weeks old. This provided us with not more than a weak indication that dams temporarily rank higher when having a new-born foal. The relative aggression scores of both dams increased slightly after giving birth to a foal: for one dam from 1.13 to 1.57 and for the other from 0.72 to 1.00. The mean relative aggressiveness ($n = 21$), on the other hand, decreased from 1.71 to 1.14. No influence of oestrus on the rank position of the mares concerned was evident.
The rank positions of a mare and her adult offspring — The rank positions of mares correlated positively with those of their adult offspring ($Rp = 0.88$). The relative aggressiveness of the dams and those of their adult offspring was also correlated ($Rp = 0.75$, $n = 8$, $p<0.05$). Since there is no correlation between age of dams and age of their offspring nor between age and relative aggressiveness in the group of adult animals, the possibility of the former correlation being due to the latter is unlikely.

TABLE VI

Spearman rank correlations between rank position in the hierarchy and six individual factors

feature	*group*	*Rs*	*n*	*p*
age	complete group	0.74	21	0.002
	mares	0.75	15	0.002
	geldings	0.09	6	ns
height	complete group	-0.54	21	0.002
	mares	-0.45	15	ns
	geldings	-0.54	6	ns
residency	complete group	0.70	21	0.002
	mares	0.65	15	0.02
	geldings	0.94	6	0.01
rel. aggressiveness	complete group	0.36	21	ns
	mares	0.42	15	ns
	geldings	0.83	6	0.05
rel. submissiveness	complete group	-0.89	21	0.002
	mares	-0.80	15	0.002
	geldings	-0.94	6	0.01
castration age	geldings	0.97	6	0.01

n = number of individuals; p = probability

Rank, kinship and social bonds — An interesting question is whether the difference in rank positions between each pair of horses is related to the social bond, measured as the frequency of allogrooming interactions between the two horses or as being in each other's proximity. It is also interesting to investigate the possible relation between rank difference and kinship. To this end we constructed the following dyadic matrices: (1) a kinship matrix: this is a 0-1 matrix, where a 1 means kin (via the mother) and a 0 means not kin; (2) a matrix of rank differences, which indicates how many horses separate any given pair in the hierarchy (see the lower triangular half of the matrix presented in fig. 4), (3) a frequency matrix of mutual allogrooming, and (4) a proximity matrix, which contains for each pair of horses the frequency with which these two horses were within two horse lengths from each other (see the upper triangular half of the matrix presented in fig. 4). All matrices are symmetric. For each pair of these matrices we calculated the Pearson's correlation coefficient and its statistical significance, using a permutation test which respects the interdependencies of the values within rows and columns of these matrices. The MatMan program (De Vries *et al.*, 1993) was used to perform these permutation Mantel tests.

	f	P	b	l	K	D	p	s	B	d	U	S	k	F	m	t	Q	o	r	E	H	Total
f	*	0.5	2.0	1.0	0.0	0.0	2.0	1.5	3.5	0.5	0.0	1.5	1.0	2.0	0.0	1.0	1.5	2.5	0.5	0.0	1.5	22.5
P	0	*	1.0	1.5	2.0	1.5	1.5	3.3	2.0	1.1	1.0	1.8	4.3	1.8	1.7	1.0	2.5	0.8	1.0	0.8	0.5	31.5
b	1	0	*	2.5	1.8	0.8	5.0	5.3	2.5	3.8	2.0	0.8	10.	1.0	4.0	1.8	2.3	2.0	2.0	2.3	1.0	54.2
l	2	1	0	*	1.5	0.5	4.0	3.0	2.0	5.5	1.5	3.5	2.5	4.0	3.5	3.5	3.0	4.0	2.5	2.0	1.0	52.5
K	3	2	1	0	*	3.3	0.5	2.7	1.0	2.3	6.5	1.5	2.3	0.5	2.3	3.3	0.3	1.3	0.5	1.0	0.5	35.1
D	4	3	2	1	0	*	2.3	0.3	4.0	1.3	0.5	5.0	1.0	5.8	1.7	0.8	2.8	0.8	0.8	0.5	1.0	35.7
p	5	4	3	2	1	0	*	4.0	8.0	5.8	3.0	8.3	4.3	3.5	2.3	0.8	3.0	1.0	1.0	1.3	0.5	62.1
s	6	5	4	3	2	1	0	*	2.3	3.0	4.0	0.7	5.3	0.7	0.3	2.3	4.3	1.0	3.0	1.3	0.0	48.3
B	7	6	5	4	3	2	1	0	*	6.3	1.5	9.0	5.3	5.0	2.3	1.5	9.5	1.5	1.3	0.8	1.0	70.3
d	8	7	6	5	4	3	2	1	0	*	4.5	5.0	6.3	1.0	2.7	0.8	4.0	2.5	1.8	2.3	1.5	61.9
U	9	8	7	6	5	4	3	2	1	0	*	1.0	1.0	0.0	0.5	3.0	1.5	3.0	0.0	2.0	0.0	36.5
S	10	9	8	7	6	5	4	3	2	1	0	*	2.7	3.3	4.7	0.3	11.	4.0	1.0	0.5	1.0	66.9
k	11	10	9	8	7	6	5	4	3	2	1	0	*	1.0	7.3	3.0	6.3	1.3	3.0	3.0	1.5	72.7
F	12	11	10	9	8	7	6	5	4	3	2	1	0	*	2.7	1.0	5.3	2.0	1.5	1.5	1.5	45.1
m	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	4.3	6.7	4.0	1.3	2.3	0.5	55.1
t	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	1.3	2.5	2.0	2.5	0.5	37.2
Q	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	4.0	2.5	1.5	2.0	75.6
o	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	5.3	5.5	1.5	50.5
r	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	8.8	1.0	40.8
E	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	0.5	40.4
H	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	*	18.5
Tot	190	171	154	139	126	115	106	99	94	91	90	91	94	99	106	115	126	139	154	171	190	

Fig. 4. This figure shows two triangular halfs of two symmetric matrices. Below the diagonal: matrix of rank differences (*i.e.*, the number of individuals in between each two rank positions). Above the diagonal: matrix of proximity frequences. The column totals give the marginal totals of the full matrix of rank differences. The row totals give the marginal totals of the full matrix of proximity frequences.

The upper panel of table VII shows the results of these tests. It turns out that kinship is not related in any way to difference in rank positions or to one of the social bond measures: proximity and allogrooming. Rank difference, on the other hand, is strongly correlated with proximity (r = -.290, p<.001), that is: the closer two horses are in rank to each other the more frequently they are in each other's proximity. For the correlation between rank difference and allogrooming not more than a weak trend was found (r = -.117, p = .09). Not unexpected, proximity and allogrooming were strongly correlated (r = .491, p<.001).

Horses may differ in their tendencies to get involved in allogrooming interactions with any of the other horses. Similarly, they may differ in their propensities to be in the proximity of any of the other horses. A disadvantage of the Mantel test is that it does not take this individual variation into account. For instance, the correlation between rank difference and proximity obtained above by the Mantel test could be the result of a correlation between an animal's deviation from the mean rank position and its tendency to be in the proximity of any of the other horses. To overcome this problem, FREEMAN *et al.* (1992) suggested the use of an iterative proportional fitting procedure (BISHOP *et al.*, 1975, pp. 97-101) to fit homogeneous margins to observational data matrices like the proximity and allogrooming matrices. By this procedure the matrices are dually normalized; that is, for each pair of horses a value is obtained that represents the number of allogrooming acts (or being in proximity) they would be involved in if all the marginal totals were equal. Subsequent Mantel tests using these normalized matrices are thus corrected for individual variation in behavioural tendencies. To eliminate non-diagonal zero cells a constant of 0.25 was added to these cells before the iterative proportional fitting procedure was applied, as suggested by FREEMAN *et al.* (1992). The dually normalized matrices were calculated by means of a specially written extension of the program MatMan (DE VRIES *et al.*, 1993).

The lower panel of table VII presents the results of the Mantel test using these normalized matrices. The correlations between kinship and the other variables as well as the correlation between proximity and allogrooming did not change much. However, the correlation between rank difference and proximity dropped from a highly significant value of -.290 ($p<.001$) to a just significant value of -.143 ($p = 0.04$). This decrease is apparently due to the strong negative correlation of -.637 that existed between an animal's total sum of rank differences (indicating its deviation from the mean rank position) and its tendency to be in the proximity of any of the other horses (*i.e.*, the correlation between the column totals in fig. 4 and the row rotals in fig. 4). In other words, top ranking and bottom ranking horses stayed less frequently in the close vicinity of another horse than middle ranking horses did. "It's lonely at the top as well as at the bottom." There is one clear exception, namely the mare U, which occupied the middle rank position 11 (marginal total of 90), but at the same time had a very low frequency of being in another horse's neighbourhood (marginal total of 36.5).

The already rather weak correlation between rank difference and allogrooming (r = -.117) decreased to an insignificant value of -.045 when we performed a Mantel test using the dually normalized matrix of allogrooming. The difference between these two correlation values is not quite understandable to us, because the correlation between an animal's deviation from the mean rank position and its general tendency to be involved in allogrooming interactions is only -.031. However, there existed large differences between individuals to get involved in allogrooming, and therefore we felt that the application of the

TABLE VII

Matrix Correlations between kin, rank difference, proximity and social bond

		Correlation r	p-value#	
kinship	rank difference	.063	>.25	ns
kinship	proximity	.061	>.25	ns
kinship	allogrooming	.041	>.40	ns
rank difference	proximity	-.290	<.001	**
rank difference	allogrooming	-.117	.09	tr
proximity	allogrooming	.491	<.001	**
kinship	rank difference	.063	>.25	ns
kinship	proximity	-.003	>.40	ns
kinship	allogrooming	0.82	>.25	ns
rank difference	proximity	-.143	.04	*
rank difference	allogrooming	-.045	>.40	ns
proximity	allogrooming	.468	<.001	**

Upper panel: the dyadic frequency matrices (proximity and allogrooming) are not corrected for individual differences in their propensities for each of these social behaviours.
Lower panel: the proximity and allogrooming matrices are dually normalized by means of fitting homogeneous margins to these matrices (FREEMAN *et al.*, 1992), thereby correcting for individual differences.
# The p-values are two-tailed and based on a permutation test in which the rows and columns of one of the two matrices are simultaneously permuted 10.000 times.
tr = trend $.05 < p < .10$; * = $.01 < p < .05$; ** = $p < .001$.

normalization method by which this individual variation is taken into account was required. Anyway, the conclusion can be drawn that rank difference and allogrooming are not significantly correlated.

DISCUSSION

The applicability of the dominance concept

In this paper we started with analysing what behavioural exchanges reflect dominance relationships in horses. The results demonstrate that only a very limited of behaviours reflected dominance in such a way that they could be used to construct a rank order. An important result is that we were unable to construct a (nearly) linear rank order when defensive aggressive behaviours (threats or kicks with the hind legs) and offensive aggressive behaviours (threats of attacks with the head) were combined. This result is in line with those of WELLS (1978), FEH (1988) and RUTBERG & GREENBERG (1990) on horses and of SCHILDER (1988, 1990) on zebras. It suggests that the habit of combining behaviours of an offensive nature with those of a relatively more defensive nature is unjustified. This conclusion is reinforced by the results of a PCA of the asymmetries in the exchange of eight behaviours, in which the factor loadings of the offensive and defensive behaviours are high on two different factors. The fact that kick and buck show a low degree of transitivity and a relatively low directional consistency suggests that they were used defensively against ranking opponents as well as (offensively?) against lower ranking opponents. On the basis of these results we recommend to keep behaviours involving the head and those involving the rear separated, and to take into consideration avoidance behaviour when investigating dominance in horses.

Just as with zebras (SCHILDER, 1988), the conclusion can be drawn that the concept of dominance is applicable to a certain degree. Also comparable to zebras is that horses do not appear to use formal dominance signals as has been shown for chimpanzees (NOË *et al*, 1980) and wolves (VAN HOOFF & WENSING, 1987). These two species use highly ritualized displays which are (almost) completely unidirectionally exchanged within each dyad and are being shown in a large number of dyads. Such display could therefore be considered as indicators of a formal status rank order. In horses toothclapping and ceremonies involving defecating/urinating over faeces/urine of other individuals could be regarded as dominance related ritualized displays. However, in our study group toothclapping was only performed by the juveniles, which is in agreement with other observations (WARING, 1983). Defecating/urinating ceremonies were alost exclusively performed by adult stallions and were for that matter almost absent in this study (see table II). Therefore, these behaviours could not be used in investigating dominance between adult horses. None of the other behaviours showed sufficient unidirectionality and high enough coverage to be designated as a formal dominance signal. In fact, the behaviour which reflects best the dominance relationship between two horses is avoidance. This is completely in line with the finding that the more two horses are separated in rank the less frequently they are within two horse lengths from each other. This means that if subordinate non-juvenile horses get involved in a conflict with a higher ranking horse, they can only give ground or defend themselves, but are unable to present a display (with the possible exclusion of tooth-clapping) by which they acknowledge the dominance status of the other, thereby possibly reducing its aggression.

Rank and its possible determinants

The hierarchy of the horses does not consist of two disjunct parts, in which all males or all females would occupy the higher positions and the horses of the other sex would occupy the lower rank positions. In the (nearly) linear rank order of the complete group the rank positions of males and females are interspersed (fig. 1). It turned out that the few triangular dominance relationships that existed involved intersexual relationships. The hierarchies of the males and females separately were more linear than the combined hierarchy (figs. 2, 3).

In general, the rank position in the dominance hierarchy correlated strongly with the factors age, residency and castration age and less with the factor height. This can be interpreted by saying that the rank position of an adult horse appears to be determined by the amount of social experience acquired by the horse, rather than by its actual physical strength/height. This interpretation is strengthened by the fact that the rank of the castrated stallions was not correlated with age but with the age at which they were castrated. That is, geldings with a relatively high age at castration have a high rank. This could be a result of differences in the remaining hormone levels due to differences in surgical techniques, but these differences are usually very minor (Voith, 1979). More likely it is an effect of the differential behavioural experiences the animal had before castration. For horses there are no specific reports on this issue available. Line *et al.* (1985) state that there is no difference in sexual and aggressive behaviour in pre- and post-pubertal castrated male horses, but they do not refer to other behavioural experiences. A study by Hart & Hart (1985) showed that about 50% of the dogs that were neutered because of excessive aggression towards other dogs continue to attack dogs after castration. This suggests that experience may play a role here also. For the horses in the present study, hormones as well as the possibilities to mate influenced the socio-sexual experiences of the castrated stallions. This in turn determined strongly the rank order among the castrated males.

We were amazed by the fact that an effect of residency was still detectable, although the mean time of residency was 9.5 years (range: 5-12 years). Residency was, however, in most individuals related to age. The use of the ranking method developed by Clutton-Brock *et al.* (1986) could be a solution to separate these effects. Unfortunately, this method resulted in a lot of ties, which made this rank order unfit for further analysis.

Our results possibly can be best compared with studies involving groups of horses that are together for at least several years (for example Berger, 1986 and Keiper & Sambraus, 1986) rather than with studies in which horses do not know each other for a long time (as for example in the studies of Houpt *et al.*, 1978 and Houpt & Keiper, 1982). The reason for this is that the influence of the factor 'social experience' may be different.

Obviously, hormones also influence the social behaviour of both females and males in times of oestrus. However, in this study, being in oestrus did not have an observable effect on the rank of the female.

The rank positions of dams and their mature offspring were correlated and both correlated with relative aggressiveness. No correlation was found between age of dams and their offspring nor between age and relative aggressiveness. Therefore, the high rank positions of offspring of an aggressive mother are most likely due to aggressivenes of the offspring itself. Some other authors (TYLER, 1972; WELLS & VON GOLDSCHMIDT-ROTHSCHILD, 1979; HOUPT, 1979; HOUPT & WOLSKI, 1980) also showed a relationship between the rank position of dams and their adult offspring. BEAVER & AMOSS (1982) described cases in which aggressive behaviour was correlated with naturally elevated serum testosterone in mares. If there are hereditary factors involved, this would explain why foals tend to be as aggressive as their mothers. But, of course learning factors may be involved too (HOUPT, 1981).

Finally, we found that rank strongly influenced the proximity structure of the horses. At the individual level, it turned out that horses with a rank position close to the mean rank tended to stay more frequently in the proximity of other horses than high ranking or low ranking horses did. Over and above this effect at the individual level, we also found that pairs of horses close in rank to each other tended to stay close in each other's physical proximity. We did not find that rank or rank difference influenced the allogrooming relationships between the horses. Neither did we find any correlation between kinship and rank difference or kinship and the social bond measures (proximity and allogrooming). We conclude that rank and rank difference have a strong direct effect on the interindividual distances between the horses, but probably not on the social bonds between them.

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