

Behaviour of Bachelor Males of the Przewalski Horse (*Equus ferus przewalskii*) at the Reserve Askania Nova

Verhalten einer Hengstgruppe von Przewalskipferden (*Equus ferus przewalskii*) im Reservat Askania Nowa

Tatjana L. Zharkikh^{a,*}, Lesley Andersen^b

^aBiosphere Reserve 'Askania Nova', Frunze 13, Askania Nova, Kherson Region, 75230 Ukraine

^bHartpury College, Hartpury, Gloucestershire, GL 19 3BE, UK

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Abstract

The aim of this study was to investigate social relationships between Przewalski horses at a high density in a bachelor group housed in a 3.5-ha enclosure. The group consisted of 16 males aged 5 to 16. Behavioural data were collected during 18 days, total 216 h. Fifteen minute focal animal sampling was used; each horse was observed three times a day for a total of 45 min. The occurrence of 25 behaviours was recorded, and group spacing behaviour was studied using nearest neighbour recordings. The group divided into four subgroups; this supports earlier findings of bachelor groups ($n \geq 10$) dividing into two or more subgroups if they included several males aged > 5 years. The total frequency of social interactions was $14.6 \pm 1.1 \text{ h}^{-1}$. Although the density of the group in this study was higher than in other zoos, the males interacted agonistically only 3.6 h^{-1} . The most frequently observed social behaviour categories were friendly interactions. This study shows possibilities to use some investigative behaviours (marking, flehmen, olfactory investigation, etc.) as indicators of social status of animals in a group.

Keywords: Equid; Przewalski horse (*Equus ferus przewalskii*); Bachelor group; Social behaviour

*Corresponding author. Biosphere Reserve 'Askania Nova' Frunze 13 75230 Askania Nova, Kherson Region Ukraine. Tel./Fax: +380 5538 61232.

E-Mail: tatjanazharkikh@rambler.ru (T.L. Zharkikh).

Introduction

The Przewalski horse (*Equus ferus przewalskii*) became extinct in the wild in the mid-1960s. However, the species has been successfully maintained in captivity for more than 100 years. Despite the fact the horses had never been studied in their natural habitat, it is known that Przewalski horses use the harem system of social organization (Keiper, 1986). The horses live in small, permanent harem groups composed of females, their offspring, and a harem stallion. Adult males that do not belong to harem bands either live in bachelor groups or temporarily live alone.

At the present time, a multitude of studies concerning behaviour in harem groups of Przewalski horses in zoos have been published (Boyd, 1988; Hogan et al., 1988; Keiper, 1988; Kolter & Zimmermann, 1988; Mackler & Dolan, 1980). There is much less information about bachelor groups (Tilson et al., 1988; Wakefield, 1996). Kolter & Zimmermann (2001) gave a detailed analysis of management of bachelor groups of Przewalski horses and their behaviour in zoos and semi-reserves except the Reserve “Askania Nova”. Since regional programmes for the Przewalski horse (EEP, SSP, SMP) were established in the mid 1980s, almost all zoos discarded the practice of keeping adult Przewalski stallions in isolation. In this connection a question about their behaviour in mix-aged groups is rather topical as often increasing aggression becomes a problem for wild Equids in captivity. Some comparative behavioural studies have revealed that of Przewalski horses and domestic horses, the former are more aggressive (Feh, 1988; Christensen et al., 2002). Kolter & Zimmermann (2001) reported that about 10% of the Przewalski bachelor population in captivity died between 1986 and 2000 as a result of injuries caused by fights. In Askania Nova, about 8% of bachelors died by the same reason between 1992 and 2003.

As no zoo but Askania Nova Reserve has an experience of keeping large groups of bachelors ($n > 10$) in rather small enclosures, the aim of the present investigation is studying relationships between Przewalski horse males at a high density in a bachelor group.

Materials and Methods

Animals

Przewalski horses have been kept at Askania Nova Reserve since 1899. For more than 25 years, one or several bachelor groups have been kept at the Reserve; each group consists of 2 to 43 males of different ages. Colts under the age of 2 years live in their natal groups on pasture. At the age of 2 they are removed to a group of young bachelors in a 90-ha separate steppe enclosure where they remain until 4–5 years of age. Males above the age of 5 are removed to another mixed-age bachelor group, up to 43 specimens in number, housed in a 3.5-ha enclosure without edible vegetation. The enclosure is fenced about with wire net 2 m in height. There are a shed and a water trough in the enclosure (Fig. 1).

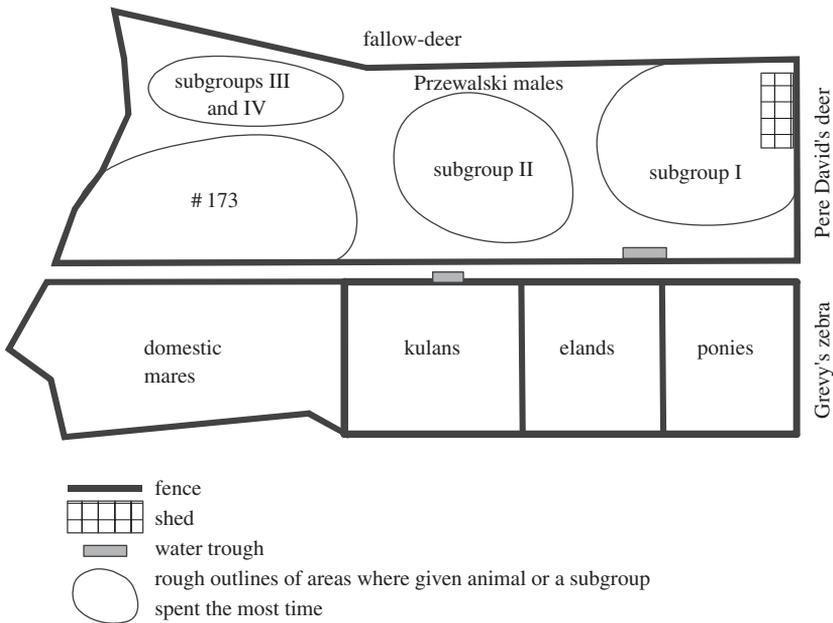


Fig. 1. Shape and structures of the enclosure for the Przewalski stallions.

Once a day some hay (10 kg per horse) is brought to the enclosure. The males get some oats (0.5 kg per horse) twice a week and vegetables (cabbage and marrow) several times in summer. There are not feeding-troughs; the feed is scattered all over the enclosure.

Three adult males of the Turkmenian kulan are housed together with the Przewalski males. Enclosures with other species of Equids, viz. a group of domestic mares (5 to 8 specimens), breeding groups of kulans and Shetland ponies (a male, two females and offspring in each), and a male of the Grevy's zebra are situated opposite the Przewalski males' enclosure. A corridor of 8-m in width parts the enclosures (Fig. 1). The group of domestic mares is let go to the corridor for watering twice a day, sometimes they are let graze there at night. During the period of the present study, the domestic mares were released from their enclosure to the corridor three times; they walked along the fence of the Przewalski males' enclosure from 16° to 8° in the next morning. In 2003 the group of adult Przewalski males consisted of 16 specimens aged 5 to 16 years (Table 1).

Data collection

The study was conducted between July 30 and August 16, 2003 (18 days). All observations for the study were made by the authors. Before the study a preliminary observation was made for 5 days in order to get the horses accustomed to the

Table 1. Identity of Przewalski males in a bachelor group at Askania Nova Reserve

Studbook No.	Brand	Age, years	Studbook No.	Brand	Age, years
1608	43	16	2686	25	9
1712	59	15	2862	30	8
2131	113	12	2874	44	8
2142	119	12	2881	49	8
2146	127	12	3138	98	5
2286	164	11	3146	87	5
2310	157	11	3161	85	5
2368	173	11	3183	80	5

The male with brand 43 was a harem stallion for 3 years; the male with brand 30 was a harem stallion for 1 year.

presence of the observers. Although no formal interobserver accuracy tests were conducted, the observers had trained with one another during the preliminary observation.

During the actual observation period the mean daily temperature was 22.2°C (max. 32°C), relative air humidity was 66%, maximum wind speed came to 4–10 m/sec. Observers sat quietly on the ground inside the enclosure watching the horses by turns from 6° to 18°. Observers could change their position sometimes. All horses were recognized by their freeze brands, ear notches, and individual marks such as body size, coat colour, shoulder spots, etc. A 10 × 45 monocular was used when necessary. Observers alternated in carrying out the day observation; total observation time was equally divided between the observers.

Group spacing behaviour was studied to get information about social attachments between the males. There were two sample sessions of 12 hours each. The 1st session was carried out on the 11th day after starting the observations; the 2nd one was carried out on the 18th day, after the observations had been completed. Nearest neighbour sampling was used (Feh, 1988; Christensen et al., 2002), in which the nearest horse (1st neighbour) and 2nd nearest horse (2nd neighbour) of each horse were recorded every 10 min. The 1st neighbour of a particular horse was defined as the horse with any part of its body closer than any other animal to the head of the focal animal. The 2nd neighbour was likewise the 2nd nearest horse. The distance between neighbours was estimated as within one horselength (<2 m); more than one horselength but less than 5 m; or more than 5 m. In total, 72 recordings per horse were collected within 12 hours (144 recordings per horse for 2 days, 24 hours).

Twenty five behaviours grouped into functional categories were observed and listed in Table 2.

The focal animal sampling was used to obtain the data (Altmann, 1974). According to the method, all occurrences of the specified behaviours of an individual were recorded during each sampling period. The length of each sample period was 15 minutes. Besides a focal animal's actions, behaviours directed to him by others were recorded, that is all acts in which the focal animal was the actor or receiver were recorded. Sometimes during a sample session on a focal horse, aggressive interactions between other horses were recorded, if it did not prevent the

Table 2. Ethogram of recorded behaviour

Behaviour	Description
Aggression/defence	
1. Avoidance	Movement that maintains or increases an individual's distance from an approaching horse. While making way for the dominant horse, the subordinate horse usually lays its ears back.
2. Displacement	Approach of one horse with ears back causes another to move away so that distance is maintained or increased, without noticeable aggression.
3. Threat to bite	A bite intention movement with the ears laid back and neck extended with no contact.
4. Bite	A bite with lips retracted and contact is made with the target horse.
5. Strike	A rapid motion of one or both forelegs in the anterior direction.
6. Threat to kick	A horse with ears back looks back at another and moves a little back with apparent intention to kick if the opponent doesn't step back. The both hindlegs do not lift off the ground, but one of the hindleg can bend being kept in readiness to kick.
7. Kick	One or both hindlegs lift off the ground and rapidly extend backwards toward another horse, with apparent intent to make contact.
8. Chase	A horse chases another one at the gallop with intention to bite the opponent.
9. Fight	High-level prolonged mutual aggression involves bites, strikes, kicks, chase etc. Usually the opponents squeal.
10. Push	Pressing of the head, neck, shoulder, body or croup against another in an apparent attempt to displace the target animal.
Friendly behaviour	
11. Play	Play includes playful nips, pounces, etc. A playful character of the interaction is indicated by the ears oriented forward or laterally, lips protruded, and teeth covered. Vocalization (squeal or scream) is not produced.
12. Mutual grooming	Two horses standing beside one another groom each other's body with their teeth.
13. Rubbing with the head	Rubbing up and down with the forehead or cheek against a companion.
14. Rubbing with the chin	A horse rubs with the chin against the back or croup of a companion.
15. Friendly touching	A horse touches his companion lightly with the nose or lips. The ears usually in lateral position.
16. Head-on-body	A position where a horse puts its chin on the back or rear of a companion.
17. Pass head under another's neck	A horse passes under the chin of a companion as if rubbing its back against the companion.
18. Pass the mane	A horse standing opposite a companion passes its mane under the companion's chin and neck. Another horse may or may not reciprocate.
19. Rubbing with the whole body	A horse passing by a companion, rubs itself slightly against the companion.
Investigative behaviour	
20. Nose-nose interaction	Two males approach each other with arched necks, touch noses standing either opposite each other or side by side. Squeal always follows, a stomp almost always occurs.
21. Olfactory investigation	Sniffing various parts of another horse's body, including the head, neck, flank, genitals, and tail or perineal region. Another horse may or may not reciprocate. No squeal or other vocalization.
22. Marking (faecal pile display)	After defecation a horse turns round and sniffs its own faeces. However the behaviour is mostly in association with defecation (urination) and existing faecal piles. It includes approach a faecal pile, sniff and paw it, defecation or urination on the top of the pile and sniff it again.
23. Flehmen	The upper lip is curled dorsally and the head and neck are outstretched and elevated.
Sexual behaviour	
24. Mounting	A horse raises its chest and forelegs onto another horse's back as during copulation.

Table 2. (continued)

Behaviour	Description
25. Herding (snaking)	Combination of head threat with the ears back and forward locomotion. The head of the horse extended and the neck lowered below horizontal and oscillated from side to side. The behaviour directs the movement of another horse.

The above-mentioned behaviours are mainly based on descriptions in Houpt & Boyd (1994), McDonnell and Haviland (1995), and Waring (2003); besides the list includes some behaviours not described by other researchers (see §§ 13–19).

observations on the focal horse. The data were used to construct the dominance matrix.

Each horse in the group was drawn randomly from the list of group members until all group members had been observed once; the process was then repeated. The order of focal animals to be observed changed every day in that each horse was observed at different time. Observations lasted from 6° to 18° (12 hours), each horse was observed three times a day for a total of 45 min. Such observations were carried out during 16 days, hence the whole observation time totalled 192 h, that is each horse was observed for a total of 12 h.

Data analysis

Data on group spacing behaviour were analyzed by the calculation of the frequency of recordings at a specified distance (<2 m, or 2–5 m, or >5 m) from other horses (frequency of neighbours) for each horse in the following way: the number of recordings at a specified distance from other horses was summed and then divided by doubled number of all recordings (288) in order to get the final result within the range from 0 to 1. The zero value means that the horse was never observed within a specified distance category; one means he always kept a specified distance between himself and others.

The index of association was calculated to determine individual social preferences the degree of social attachments between horses (Young, 2003). For each pair of horses the number of times they were at a distance of less than 5 m., i.e. within distances A or B, was summed and then the number received was divided by 288 (the total number of recordings for both the horses). The index of association ranges between 0 (the horses were never recorded close together) and 1 (they were always nearby). As only two nearest neighbours were recorded for each horse, the index of association was understated in subgroups where there were more than 3 horses attached to each other. The next criterion was devised to estimate the extend of the attachments. If the index of association between any two horses is higher than the average value of indexes across all pairs, then an assignable (clear) association between the horses exists.

Frequencies of behaviours were calculated per horse-hour (h^{-1}).

To analyze the dominance hierarchy in the group, aggressions and avoidance were used. For the purpose, the number of effective aggressions, i.e. aggressions that forced a recipient to recede, was counted. The animal which won the most encounters with another one, that is showed more effective aggressions, was positioned in the hierarchy order above the latter.

Nonparametric Wilcoxon test (W) was used to compare various average indexes. Spearman rank correlation coefficient (r_s) was used to calculate correlations between age and such the factors as aggressiveness, the number of friendly interactions, flehmen, frequency of marking, also between aggressiveness and marking (Ivanov, 1990). Differences with $P < 0.05$ were considered statistically significant.

No significant difference between the two sample sessions on group spacing behaviour was found (W , $P > 0.05$), therefore the data were combined.

Results

Most of the Przewalski males ($n = 15$) spent their time in the close vicinity of other males, and the frequency of any neighbour within one horselength ($< 2 \text{ m}$) averaged 0.69 ± 0.02 (mean \pm Se). Correspondingly, they spent much less time keeping the distance more than 5 m from others (0.22 ± 0.02), or within 2–5 m (0.09 ± 0.01). The male with freeze brand #173 was an exception, because he kept apart from other males all the time, and the frequency of neighbours at the distance more than 5 m averaged 0.98. However, #173 spent his time close to the enclosure of domestic mares (Fig. 1).

The index of association varied between 0 and 0.87 (mean \pm Se 0.10 ± 0.02). Only male #173 did not associate with any other male. Other males combined into four subgroups, each was 3 to 5 in number (Table 3). The index of association between any two members of a subgroup was better than the average value of indexes across all pairs, i.e. > 0.10 . Bonds between members in subgroups III and IV were more complicated than bonds in subgroups I and II. The index of association between males #113 and #119 was under 0.1, yet they both were included in the subgroup III as they had rather strong bonds with other members of the subgroup. Besides the clear membership in subgroup III, male #119 had close relations with males #49 and #44. Therefore the three males were considered as separate subgroup IV. A low association existed between male #164 of subgroup III and male #49 of subgroup IV; yet, their index of association was just a little better than 0.10. Further #164 did not associate with #44, therefore #164 was not included in subgroup IV. Frequencies with which #164 was seen in the company of #49 were more a function of #164's tolerance for #49's presence in the company with #119 rather than of #164's attempts to associate with this subgroup. Although there were no significant differences between indexes of association in the first and second sessions, some tendencies to strengthening of association between subgroups III and IV were noticed.

Table 3. Indexes of association in the group of Przewalski males

Brands	subgroup I				subgroup II				subgroup III				subgroup IV			
	173	127	43	80	157	85	30	87	98	113	25	59	164	119	49	44
173																
127					0.01					0.01	0.01			+		
43		0.68	0.87											0.01		
80			0.67													
157																
85																
30																
87																
98																
113																
25																
59																
164																
119																
49																
44																

+ Index of association < 0.005 . Empty cells mean 0.0.

There were two types of subgroups. Behaviour of members of the subgroup III did not have qualitative differences, i.e. they all used almost the same set of behaviours (the subgroup of type 1). In subgroups of type 2 such as I, II, and IV dominant males (#127, #157, and #119 correspondingly) showed herding to other members of their subgroups. The dominant males did not allow the members of their subgroups to approach males of other subgroups. They used herding to keep subgroup members from wandering away and attacked non-members when the latter came too close. Also dominant males could break in on scuffles between their subordinates – they either kicked the scuffling individuals or simply wedged themselves in between the combatants.

The close presence of domestic mares influenced behaviour of #173. This male displayed 42.4% of his aggressive acts during those 3 days when domestic mares grazed in the corridor between their enclosure and the Przewalski males' one. He showed herding towards the mares and faecal pile display, violently attacked and drove away other males if the latter came to 'his' mares at a distance of 50–60 m. All other males including #127 lost encounters if they were close to the mares.

Despite the fact that a special recording of spatial distribution of the horses in their enclosure was not made, the areas where certain horses or subgroups spent the most time were roughly fixed (Fig. 1). Spatial distribution of the males depended on what subgroup they belonged to. Almost all the time male #173 stayed opposite the domestic mares' enclosure or convoyed them along the fence if the mares were

grazing in the dividing corridor. The opposite end of the Przewalski’s enclosure was occupied by subgroup I. Male #127 often threatened those males of other subgroups who went to the water trough. The latter had to wait until members of subgroup I went away at the distance of about 30–40 m. If #173 went just to water he yielded to #127 too. However, if domestic mares grazed in the corridor, #173 controlled all the space nearby and forced even subgroup I out of its preferable area. Subgroup III usually stayed in the centre of the enclosure, just between #173’s and #127’s areas. The rest of the males had to keep to the periphery of the enclosure in order to avoid aggressions from the dominant males.

A linear dominance hierarchy was present in each subgroup; however, the dominance relationships between all the males in the entire group were more polygonal (Table 4).

As #173 successfully kept subgroup I off the domestic mares’ enclosure it should be admitted that #173 dominated over #127.

Behaviours such as mounting (an attempt of mounting) and rubbing with the whole body against a companion were recorded once during the study. Frequencies of other behaviours are showed in Figure 2.

The total frequency of social interactions was $14.6 \pm 1.1 \text{ h}^{-1}$. The Przewalski males showed more friendly behaviours than aggressive/defensive behaviours (7.71 ± 1.01

Table 4. Dominance hierarchy of the Przewalski males’ group

Brands	Recipient														Total		
	173	127	43	80	157	85	30	87	98	113	119	164	25	59		44	49
173		12	9	7	53	54	50	48	51	10	10	10	99	10	52	54	903
127	5		38	26	11	11	11	12	11	69	71	81	69	76	82	50	1152
43				16							1	1		1	2	1	22
80					1	1	1					1				1	5
157	2		4			13	17	8	3	11	12	11	11	10	72	72	759
85							2	55	23	3	0	4	4	7			110
30						1		3	1	1		1	1	1		1	10
87						1			3	5	6	8	5	6	6	9	49
98									1	2	7	3	4	4	4	4	29
113			3								29	25	23	14	13	9	116
119							5	3		4		65	16	25	35	32	185
164						1	6	4					35	4	19	24	93
25							6	2	8	3		4		21	10	19	73
59							2	3	1			2			8	5	21
44																15	15
49																	0
Total	7	12	54	49	164	190	203	253	206	304	345	410	372	367	306	300	3542

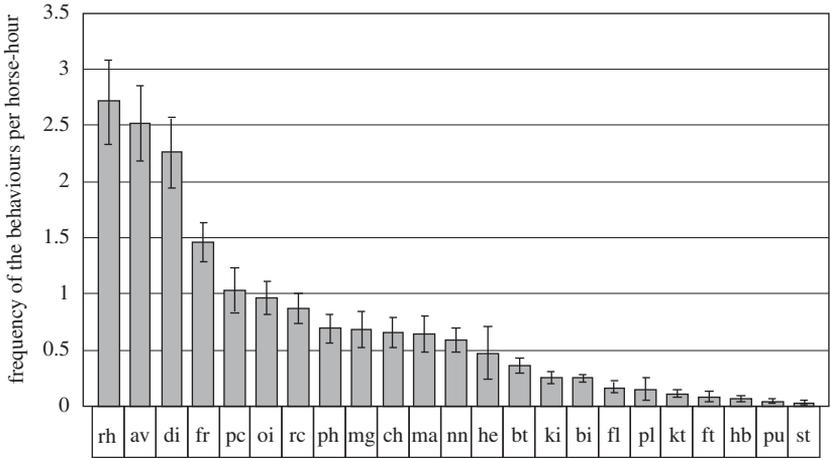


Fig. 2. Frequency of different behaviours (both exhibited and received) of Przewalski stallions. rh-rubbing with the head, av-avoidance, di-displacement, fr-friendly touching, pc-pass under one’s chin, oi-olfactory investigation, rc-rubbing with the chin, ph-pass the head under another’s neck, mg-mutual grooming, ch-chase, ma-marking, nn-nose-nose interaction, he-herding, bt-bite threat, ki-kick, bi-bite, fl-flehen, pl-play, kt-kick threat, ft-fight, hb-head-on-body, pu-push, st-strike. Bars represent standard errors.

versus $4.89 \pm 0.53 \text{ h}^{-1}$, $W, P < 0.05$). None of the males but four dominant males (#173, #127, #157, 119#) performed herding.

As expected, the number of aggressive interactions was higher on the days where the horses got additional feeding – oats and vegetables ($4.78 \pm 0.47 \text{ h}^{-1}$), whereas on other days (the horses got only hay) they showed 3.09 ± 0.26 aggressions per horse-hour; yet, this difference is not significant ($W, P > 0.05$). No significant correlation between age and aggressiveness was found ($r_s = 0.39, P > 0.05$), likewise age was not significantly correlated with the number of friendly acts ($r_s = -0.17, P > 0.05$).

Four dominant males (##173, 127, 157, and 119) showed the highest number of aggressions (Table 4). Moreover, such an aggression as chase was performed by ##173, 127, and 157 only. On meeting on the line between their preferable areas, two dominant males usually showed faecal pile display and/or nose-nose interaction. Sometimes fights of low intensity occurred, after that the dominant males herded away their subordinates. The interesting fact was that dominant males were rather tolerant towards young, 5-year-old males of other subgroups, and they did not show aggressions if the young males approached without their own dominants. Several times the most aggressive dominant male #127 allowed young males of subgroup II to eat hay in his immediate proximity (literally, head to head), when #157 was far off.

During the study, 35.5% of all aggressions occurred within subgroups. The highest level of aggression within subgroups was recorded in subgroup I, as its members directed on average $66.4 \pm 24.8\%$ of their aggressions at each other. Members of subgroup IV treated each other in a very friendly manner, as only $15.8 \pm 0.6\%$ of aggressions occurred within the subgroup. Average aggressiveness within subgroups

II and III were $33.6 \pm 9.5\%$ and $30.7 \pm 1.6\%$ correspondingly. The dominant males of subgroups I and II directed the least numbers of their aggressions at members of their own subgroups, 16.8% and 5.6% correspondingly, whereas each subordinate member of subgroup I showed more than 91% to each other; subordinate members of subgroup II showed 20.0% to 56.7% aggressions within their subgroup. There was found no much difference between the numbers of aggressions directed by dominants toward members of their subgroups and non-members within other subgroups.

Non-agonistic interactions accounted for 63% of all social contacts, out of them 53% were friendly interactions. During the study, 98% of all friendly acts occurred within subgroups. Investigative behaviours accounted for about 15% of all behaviours. In general, the males exhibited olfactory investigation to members of their own subgroups as frequently as to non-members (48% of all olfactory investigations were recorded between members of the same subgroup). As for nose-nose interactions, males preferred to interact with non-members, since about 74% of all nose-nose interactions were recorded between members of different subgroups. The males who were far in rank from each other tended to sniff each other without squealing or stomping, whereas the males who were close in rank usually showed a complete nose-nose interaction.

Two different marking behaviours were recorded, there were marking with faeces and marking with urine. Only dominant males of subgroups I and II marked with their own urine the fresh faeces and urine of their subordinates, the frequencies were 0.08 h^{-1} and 0.25 h^{-1} respectively. Once the dominant male #127 performed urine marking on faeces of his subordinate male #43 after the latter had showed faecal pile display.

A significant positive correlation between age and frequency of marking behaviour was found ($r_s = 0.80$, $P < 0.01$): all males above 9 years showed faecal marking, all 5-year-old males and one of three 8-year-old males did not perform marking. Also, the number of marking correlated positively with the number of aggressive acts produced ($r_s = 0.76$, $P < 0.01$).

The average frequency of marking behaviour in the four dominant males (#173, 127, 157, and 119) was $1.42 \pm 0.08 \text{ h}^{-1}$; whereas in others who exhibited the marking, $0.68 \pm 0.15 \text{ h}^{-1}$. The difference is significant ($P < 0.05$).

The complete marking sequence was not always performed. The second sniffing of elimination was not performed after marking for about 30% of all marking events. A significant correlation between age and the percentage of complete marking sequences was not found ($r_s = -0.48$, $P > 0.05$); nor did the percentage of complete marking sequences correlate with the rank in the hierarchy ($r_s = -0.19$, $P > 0.05$).

Out of 130 recorded marking events, 17 events were successions of faecal marking of the same stud-pile by two or three males one after another. Subordinate males marked elimination of a higher ranking male three times; in other events, a higher ranking male was the last to mark the stud-pile.

A significant correlation between age and frequency of flehmen was not found ($r_s = 0.36$, $P > 0.05$). The males sometimes showed flehmen after they had sniffed elimination of others, also oats could induce flehmen.

Mounting was recorded once: when the dominant male #113 of subgroup III made an attempt to mount #119, the latter violently resisted.

The relationships between Przewalski males and kulan males remained neutral. Sometimes the kulans and the most aggressive Przewalski males #173 or #127 ate hay just 'head to head' in spite of the fact that #173 drove away any conspecific, and #127 drove away any conspecific except for the members of his subgroup. During the observation period it was noted that the close presence of zebras, Shetland ponies and a breeding group of kulans in the nearby enclosures did not influence Przewalski males' behaviour.

Discussion

The present study supports that bachelor herds can be kept in close quarters without problematic aggression (which may be contrary to what was previously believed). Even if the density of the group is high the aggressive potential of the animals may be expressed within acceptable levels so that no serious injuries occur.

Some factors determined the reduction of aggressions within the group.

First the Przewalski males divided into several subgroups. Members of the same subgroup not only tended to spend the most time in the close vicinity of each other, but also directed friendly acts almost exclusively towards each other, which indicated obvious social bonds between them. Members of the same subgroup kept within a certain area in their enclosure; thus, they did not have to interact too often. The fact that a herd of Przewalski males may divide into subgroups was known from an earlier study in Askania Nova (Zharkikh, 1998). There were two herds (one herd $n = 38$ aged between 2 and 15 years; another one $n = 40$ aged between 2 and 12 years) kept in different pasture enclosures of 80 ha. In both cases, the complete herd was divided into subgroups of types 1 and 2. Dominant males above 6 years of age were initiators of forming of subgroups of type 2; they insistently pursued and herded their subordinates. Then, just the dominants kept their subgroups apart. They chased away non-members even if the latter showed no aggressions. If most of males in a bachelor herd are immature the subgroups may not be formed. In another study on the social behaviour of Przewalski males ($n = 11$, age 2 to 4 years; $n = 2$, age 9 and 13 years), the horses did not spread out on their 75-ha pasture, but grouped up tightly (Christensen et al., 2002). However, two elder stallions sometimes left the group and rambled alone. Therefore, there is probably a strong coherence between spatial distribution and the age structure of a bachelor group. Numerous observations on the behaviour of Przewalski males on pasture in the next years (unpublished data), revealed the fact that if a bachelor group ($n \geq 10$) included several males aged 5 years and above, the group divided into two or more subgroups of both types.

What is a cause of forming of subgroups of type 2 in bachelor herds? Some authors (Tilson et al., 1988; Walther et al., 1983) suppose the young males in bachelor groups receive some degree of protection by associating with the dominant male in a separated subgroup (described in this study as subgroups of type 2). This

assertion was not completely supported in the present study as a level of aggressiveness within a subgroup was higher in two subgroups of type 2 (I and II) out of three than in the subgroup of type 1 (III). Besides that, adult males were members of subgroups of type 2 as subordinates.

It may be speculated that if males are kept in restricted areas (enclosures) without contacts with mares, some adult males may treat their mates like mares and show some behaviours typical for harem stallions. Among the major social roles of harem stallions is herding, which has a function to maintain band stability and group cohesion in general (Waring, 2003; Boyd & Keiper, 2005; Feh, 2005). Keiper & Sambras (1986) defined herding by stallions as a sexual rather than an aggressive interaction. In the literature on free-ranging horses, no one described that males performed herding (snaking) towards other males in bachelor herds. In bachelor herds under domestic environment, herding was observed in domestic horses (McDonnell & Haviland, 1995) and in Przewalski horses in zoos and semi-reserves (Tilson et al., 1988; Woger, 1997). In the present study, only dominant males of subgroups of type 2 (#127, #157, and #119) showed herding to group members of their subgroups tightly. The high level of aggressions in the dominants related to their efforts to defend their subgroups against intruders. That should be considered as harem stallion behaviour.

The hypothesis is supported by the fact that qualitative and quantitative characteristics of behaviours of male #173 who was concerned with domestic mares, was similar to the dominants of subgroups of type 2. Besides, frequencies of marking behaviour in the four dominant males were significantly higher than in others. Two of the males did urine marking on faeces and urine of the members of their subgroups. It is very likely that a dominant claims his right to members of its own group by marking their eliminations. Marking also could mask their scent. It is known that dominant harem stallions tend to mark more eliminations from other horses than bachelors do (Turner et al., 1981; reviewed by Waring, 2003). McDonnell (1986) considered marking as well as herding to be parts of reproductive behaviour of harem stallions. In recent studies, marking with urine was observed only in dominant harem stallions or in those bachelors who had often contacts with females (Hoffman, 1985; Boyd & Kasman, 1986; Boyd & Keiper, 2005). Dominant harem stallions chose rather to defecate on faeces of other males and to urinate on faeces of females (Haupt & Boyd, 1994). Therefore, peculiarities of marking behaviour may be indicators that the dominant males behaved like harem stallions.

Forming and then keeping up stability of subgroups of type 2 depends only on the will and physical abilities of their dominant males. Thus, the composition of subgroups of type 1 might be more unstable. It is worth mentioning that age and previous breeding experience of a certain male did not influence his ability to form subgroups of type 2. The present study as well as earlier investigations (Zharkikh, 1998; Christensen et al., 2002) revealed that former breeding stallions did not form such subgroups of type 2 in bachelor herds. Moreover, stallions with breeding experience could submit to younger males.

Second, the level of aggression was also reduced by establishing hierarchies within the complete group as well as within subgroups. The literature on feral horses reveals

that linear hierarchies are common in bachelor groups (Feist, 1971; Tyler, 1972; Tilson et al., 1988). However, Houpt and co-workers (1978) found that in small groups (up to 9 horses) strong linear hierarchies were recorded; whereas in larger groups (when group size exceeds 10), triangular relationships were also formed. The present study supports the above-mentioned findings, as a clear linear dominance hierarchy was present in each subgroup, while relationships in the complete group were considerably more complicated. Besides that, an obvious inter-subgroup dominance was recorded (Table 4). In the present study, age and prior breeding experience did not have influence on the rank in the hierarchy. A number of authors reported that age was an important rank determine factor (reviewed by Dierendonck et al., 1995; and Waring, 2003). As most other studies included juveniles under 3 years, the results of the studies might influence the conclusion that hierarchies are largely based on age. Other authors supposed that individual temperament rather than age and prior experience appeared to be the primarily factor in determining position in the hierarchy, at least in adult males (Tilson et al., 1988). Although mounting (an attempt) was recorded once during the present observations, this supported a statement by Schilder & Boer (1987) that the behaviour could indicate a dominant position of its performer to the receiver.

There was no special investigation to what extent close presence of a dominant male affected on the result of an encounter between a member of his subgroup and a non-member. Yet, the members of subgroup III could make an effective threat to subordinate males of subgroups I and II, if the latter moved far from their dominants #127 and #157 respectively. In their turn subordinate males of subgroups I or II could make members of subgroup III recede if dominants #127 or #157 were close. In harem bands of Przewalski horses, the social situation including rank order may change depending on the nearness of other members of the band (Kolter & Zimmermann, 1988).

High frequencies of interactions may influence welfare of animals at a high density. Social activity of Przewalski males in the present study was several times as large in comparison with bachelors of free-ranging feral horses in the USA, mainly because the Przewalski group was space restricted. Hoffman (1985) reported that the bachelors interacted with each other 2 to 3 times per hour whereas frequency of social contacts in the present study varied from 6 to 21 times per hour.

In this study, the most frequently observed social behaviour categories were friendly interactions, despite the fact that food-related aggression emerged from the domestic style supplemental feeding. On the contrary, in bachelors of feral horses in the USA, agonistic behaviour followed by defecation-marking and driving comprised roughly $\frac{2}{3}$ of the total events (Hoffman, 1985). In zoos and semi-reserves, the social life in Przewalski bachelor groups mostly consists of friendly interactions (Kolter & Zimmermann, 2001). Sixty to 95% of all behaviours are comprised of high intensity behaviours such as play and mutual grooming (Weber, 1995; Woger, 1997). Males under 5 years play the most frequently; yet, elder males are observed playing 1 to 3 times per hour (Kolter & Zimmermann, 2001). In the present study, friendly interactions of low intensity (various friendly body-body contacts) were prevalent, whereas high intensity interactions made up only 11% of

all friendly interactions or less than 6% of the total social activity. In this study, bachelors played less than Przewalski males in other zoos. Thirty out of 32 play bouts were play between 5-year-old males and elder males, young males initiated 72% of the play bouts. All the plays were of short duration; most of them were merely 2–3 slight nips, short bouts of playful fighting occurred rarely.

Frequencies of agonistic behaviour in bachelor groups vary. Adult Przewalski bachelors at Hunnesrück semi-reserve showed agonistic interactions 6 h^{-1} (Weber, 1995), bachelors at Minnesota Zoo showed such interactions on average 1.35 h^{-1} (Tilson et al., 1988). Although the group size in the present study was large whereas the size of the enclosure was relatively smaller than in other zoos, bachelors interacted agonistically only 3.6 h^{-1} , and most of aggressions were shown near haycocks and the water trough. Aggressiveness of dominant males was caused by their ambition to protect their subgroups. Aggressions of high intensity such as fights were rarely observed (Fig. 2); more than half of fights occurred between dominant males from different subgroups. Kolter & Zimmermann (2001) mentioned that violent fights occurred only if an animal wanted to change its rank in the hierarchy.

That relatively low level of aggressions in the study group was probably attributed to the fact that the Przewalski males frequently used the behaviours grouped into the category of 'Investigative behaviour'. Such sets of behaviours very likely help to explore the status and strength of a rival without using aggressions.

Olfactory inspections are a characteristic feature of social behaviour of stallions. It is still unknown how much information they get from olfactory investigation; yet, Kolter & Zimmermann (2001) considered that short sniffing possibly served for an exchange of olfactory information about statuses of group members. Some authors (Hoffman, 1985; Houpt & Boyd, 1994) designated simple sniffing of various parts of another horse's body as communicative behaviour or as a greeting ritual, whereas a nose-nose interaction was designated as agonistic behaviour. Stomps were often observed during nose-nose interactions; yet, it did not indicate the agonistic nature of the behaviour sequence. As rivals did not intend to hit against each other, in this study a complete nose-nose interaction (as well as one without stomping) was believed to be a ritualized demonstration rather than an aggression per se. In the present study, nose-nose interactions were more often recorded between males from different subgroups, and thus the behaviour possibly has a function of the maintenance of the social hierarchy. Further investigation in this area would be desirable.

Marking behaviour most likely serves the same function of an information exchange. To all appearance, marking behaviour should be characterized as two diverse categories viz. a display of own faeces and marking per se. The first category does not associate with existing stud-piles. Usually two harem stallions display their own faeces while meeting each other. One of them produces some faeces with following sniffing. Another one could approach the faeces and do the ritual in turn, but it did not always occur. In Askania Nova, harem Przewalski stallions always show such display of their own faeces at presence of horses not belonging to their harems. So, display of own faeces is designated as demonstrative/provoking behaviour. Marking behaviour per se consists of two subcategories viz. marking

of existing stud-piles and marking eliminations of subordinate members of a group/subgroup.

Marking of existing stud-piles is evidently a category of investigative behaviour, as by sniffing a pile a male can get information about other males who have defecated onto the pile before. In addition, the marking can serve to sort out the status of the performing male, that is a category of demonstrative/communicative behaviour. A number of authors found out that the succession of the marking stallions depended on their rank (Feist & McCullough, 1976; Tschanz, 1985; McDonnell & Haviland, 1995). However, in the present study, some low-ranking males could add their faeces to the stud-pile just after high-ranking males. Weber (1995) also did not find a strict relation between a rank in the hierarchy and the succession of the marking in Przewalski bachelors.

Marking depends on age. Domestic stallions show marking per se no earlier than at the age of 3 years (Hoffman, 1985), whereas Przewalski stallions show the behaviour somewhat later. In the present study, all 5-year-old males and one of three 8-year-olds did not mark, whereas others showed marking.

Conclusion

When keeping a bachelor group of Przewalski horses at a high density, a few factors may conduce to the reduction of aggression. Among the factors, there is a division of the complete group into several subgroups, which spend the most time within a certain area in their enclosure.

Bachelor males may unite into subgroups of two different types. Although a dominance hierarchy was established in subgroups of both types, the dominant members in subgroups of type 2 showed some behaviours, which were typical for harem stallions, i.e. herding (snaking) of subordinates, defence them against non-members, and marking with urine.

Such dominants may constitute a threat for other males that were not included into their subgroups. In zoo practice, however, such a dominant male may be the best candidate for picking him out as a harem stallion.

This study also shows possibilities to use various types of investigative behaviour as indicators of social status of animals in a group, which should be in focus in continuing investigation of the species.

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Zusammenfassung

Das Ziel dieser Studie war, das Verhalten von Przewalskipferden bei hoher Besatzdichte in einer Junggesellengruppe auf einer Fläche von 3,5 ha zu untersuchen. Die Gruppe bestand aus 16 männlichen Tieren im Alter von 5 bis 16 Jahren. Verhaltensdaten wurden über 18 Tage gesammelt, insgesamt 216 h. Fünfzehnminütige fokussierte Tierbeobachtung wurde angewendet; jedes Pferd wurde drei Mal am Tag beobachtet, insgesamt 45 Minuten. Das Auftreten von 25 Verhaltensweisen wurde aufgezeichnet und das Raumverhalten wurde untersucht indem "nächste Nachbar" aufgezeichnet wurde. Die Gruppe teilte sich in vier Untergruppen; was frühere Ergebnisse von der Teilung von Junggesellengruppen ($n \geq 10$) in zwei oder mehr Untergruppen unterstreicht; vorausgesetzt die Gruppen enthielten männliche Tiere über 5 Jahre. Die gesamte Frequenz der sozialen Interaktionen war $14,6 \pm 1,1$ Pferd/ Std. Obwohl die Besatzdichte der Gruppe in dieser Studie höher war als in anderen Zoos, verhielten sich die Tiere nur 3,6 Pferd/ Std agonistisch. Am häufigsten wurde freundliches Sozialverhalten beobachtet. Diese Studie zeigt Möglichkeiten einige investigative Verhaltensweisen (markieren, fehmen, olfaktorische Erkundung, etc.) als Indikator für die soziale Stellung des Tieres in einer Gruppe zu verwenden.

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