



Social organization and dispersion of introduced kulans (*Equus hemionus kulan*) and Przewalski horses (*Equus przewalski*) in the Bukhara Reserve, Uzbekistan

Karim Bahloul*, Olga B. Pereladova†, Natalia Soldatova‡, Galina Fisenko‡, Ekaterina Sidorenko‡ & Antoine J. Sempéré*

*Centre d'Etudes Biologiques de Chizé (CEBC), 79360 Villiers en Bois, France

†Nature Conservation, Sadki-Znamenskoye, Vilar, Moscow 113628, Russia

‡Ecocenter 'Goitred gazelle', Bukhara Cagan 705014, Uzbekistan

(Received 22 February 2000, accepted 6 September 2000)

Asiatic wild asses and Przewalski horses initially inhabited steppe, semi-desert and desert areas, but Przewalski horses became extinct in the wild, and kulans disappeared at the beginning of the 20th century, except for a small population in Turkmenistan. The Bukhara Breeding Centre (Uzbekistan) was created in 1976 for reintroduction and conservation of wild ungulate species. In 1977–1978, five kulans (two males and three females), from Barsa-Kelmes island on the Aral sea, were introduced into the reserve. The group increased to 25–30 animals in 1989–1990, when eight Przewalski horses from Moscow and St Petersburg zoos were introduced. We analysed the home ranges, preferred habitats and social interactions of these closely related species during 1995–1998 by seasonal and group composition. Horses and asses formed a reproductive group and a secondary non-reproductive group. The home range of the secondary group was larger than the reproductive group and seemed to be less dependent from the watering places. Przewalski horses were less adapted to semi-desert conditions (both water and vegetation needs) than kulan.

© 2001 Academic Press

Keywords: Przewalski horses; kulans; Central Asia; home range; behaviour

Introduction

Asiatic wild asses ('kulans'—*Equus hemionus* spp.) and Przewalski horses (*Equus przewalski*) inhabited steppe, semi-desert and deserts of temperate Eurasia. Unlike kulans, horses preferred more mosaic ecosystems, demonstrated less local migratory activity and smaller home ranges, being fixed to a greater extent to watering places

Address for correspondence: Dr Antoine J. Sempéré, 79360 Villiers en Bois, France.

K. Bahloul, present address: UMR 5578 CNRS, Bat 404, 4e étage, Université Claude Bernard - Lyon 1, 43 Bld du 11 novembre 1918, 69622 Villeurbanne Cedex, France.

(Grum-Grizimailo, 1892, 1896; Geptner, *et al.*, 1961). Both species were limited mainly to deserts, since humans disturbed their semi-arid habitats during the 18–19th centuries (Zhironov & Lushekina, 1991; Sokolov & Orlov, 1980; Dobchin, 1970).

Plans to reintroduce the Przewalski horses depended on zoo animals, and Mongolia, China, and the former Soviet Union were recommended as areas of reintroduction (Flint *et al.*, 1990).

Asiatic wild asses had disappeared from the European part of the USSR and by the beginning of the 20th century, only 40 animals survived in southern Turkmenistan. Since then special conservation and restoration measures have resulted in a population of 5000–6000 *E. hemionus* Pallas in an area of 100,000 km², and about 3000 kulans (in 1998), mainly in Badhis Nature Reserve (Turkmenistan) (Atumuradov, Kuztnetsov, pers. comm.).

Przewalski horses and Asian wild asses exhibit two basic social systems (Baskin, 1976): type I consists of small non-territorial harem-like groups and bachelor groups and type II consists of territorial males associated with varying group of females (Klingel, 1967, 1968, 1969, 1975; Rubenstein, 1986; Berger, 1988). Equid social structures can be species-dependent, e.g., *E. grevyi* and *E. zebra* in which all populations retain the same structure (Berger, 1988; Ganslosser & Dellert, 1997). Social structures can also be population-, density- and ecologically-dependent, as has been shown for other ungulates (Esmark 1964; Lent 1965, 1974; Henshaw, 1970; Bubenik, 1985; Pereladova, 1988). This was difficult to prove for Przewalski horses, as until now we did not have free populations in natural conditions with a developed social structure, where such observations could be carried out. But the level of aggressiveness of dominant Przewalski stallions in Askania Nova aggregations (Klimov, 1988) suggests the likelihood of territoriality. Unique data from Mongolian experiments (Bouman, 1998) demonstrates a differentiation of home ranges between the three harem groups, which can be accompanied by true territoriality. For the kulans we can find all variants of area usage in populations with different densities, from strict territoriality to large nomadic aggregations of animals of different sex and age (Geptner *et al.*, 1961; Rashek, 1966; Bannikov, 1963, Solomatin, 1973). Anyway, different factors, namely semi-captivity, high predator-pressure and food availability, can induce more permanent associations (type I) among Asian wild asses, with one or two males increasing the social diversity and flexibility for this species (Rubenstein, 1986; Ginsberg, 1988, 1989; Feh *et al.*, 1994).

Some kulans from a population of the Barsa-Kelmes island on Aral sea were introduced in 1977 (three animals) and 1978 (two animals) to the Bukhara Breeding Centre, but the fenced territory is too small for a free development of the group and artificial management has been carried out since 1991–1992, since when an important population growth has occurred. Przewalski horses were brought to the Centre from the Moscow and St Petersburg zoos in 1989 and 1990. For the first period animals were kept in small pens, and the group was composed of one adult male and four adult females and was set free on the main fenced area in summer 1991 (Pereladova *et al.*, 1999).

In the territory of the Bukhara Breeding Centre, asses and horses are dependent on a southern watering place, especially during summer, and on grazing places concentrated in the middle and south of the Bukhara Breeding Centre. We hypothesised that such conditions would induce a permanent or temporary (summer) type I organisation in the population of kulans.

Since they are less adapted to desert conditions than kulans, Przewalski horses from zoos are supposed to be much more dependent on watering places, which could reduce their home-range in the southern reserve and limit their expansion to the other areas. Moreover, because of the existence of a bachelor group and a possible second stallion group, conflicts with the initial stallion group will increase for access to the watering place.

As these two species are close relatives, and their possible areas of conservation and restoration overlap to a great extent, it is important to analyse their overlapping and interactions within the same limited areas.

In a previous article, we analysed the adaptation of Przewalski horses to the new conditions in the Bukhara Breeding Centre (Pereladova *et al.*, 1999) but interactions and comparative space utilization between kulan and Przewalski horses of the reserve have never been published. Moreover, to our knowledge, no information is available on interactions and areas of these two species in the wild.

The purpose of our work was to study the space utilization and the behavioural and ecological interaction of the groups of kulans and Przewalski horses in the Bukhara Breeding Centre, and to offer a plan for expanded introduction for the species in similar habitats.

Materials and methods

Study area and climate

The Bukhara Breeding Centre was created in 1976 for reintroduction and conservation purposes. It is situated in the South of the Kyzyl-kum Desert, Uzbekistan, 40°N; 65°E. The reserve has a fenced area of 5126 ha. The reserve stretches over 15 km from south-east to north-west and is 3 km wide (Fig. 1).

The main zones of vegetation in the Bukhara Breeding Centre are composed of Graminae (*Phragmites communis*, *Aeluropus litoralis*, *Poa bulbosa*, etc.), Chaenopodiaceae (*Salsola* spp, *Astragalus* spp, *Halloxylon aphyllum*, etc.) and, mainly in the south, tamarisk (*Tamarix* sp) which makes a large part of the autumn, winter and spring diet of horses (for further details see Pereladova *et al.*, 1998, 1999).

The climate is typically hyper-continental. Rains occur from November to May, with a maximum in March (30 mm) and an annual average rainfall of 143 ± 49 mm. Temperatures vary from $+2.4 \pm 1.5^\circ\text{C}$ in winter (December–February) to $+28 \pm 0.7^\circ\text{C}$ in summer (June–August). The annual average temperature is $+15.1 \pm 10^\circ\text{C}$ and the minimum usually occur in January (-15°C) and the maximum occur in July ($+44^\circ\text{C}$). Spring (March–May) is warm, $+25.1 \pm 3^\circ\text{C}$, and autumn is cold, $+6.5 \pm 1.2^\circ\text{C}$ (Pereladova *et al.*, 1998).

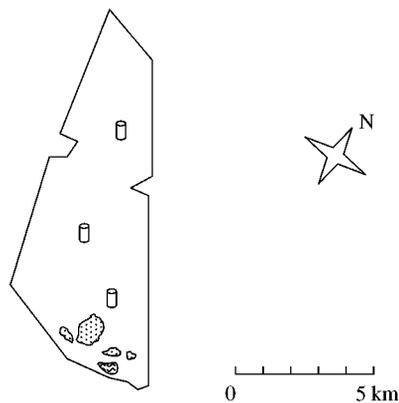


Figure 1. Map of the Bukhara breeding centre: □ Observation towers, ▨ temporary watering place, ▩ permanent watering place.

Study animals and methods

The size of the populations of all ungulate species was known from annual censuses beginning in 1978 (Pereladova *et al.*, 1998). Special observations the development of horse groups had been carried out in 1995–98.

The population of kulans grew slowly from 1978 to 1982 (seven animals) then rapidly until 1991 (37 animals) (Fig. 2). The peak kulan population was observed in 1993 (39 animals) then the population was artificially regulated and has been stable at 16–18 animals since 1995. The kulan population comprised a main group of females without newborns, together with sub-adult and adult males; a bachelor group of four males; a group of females with newborns and young from the previous year.

The number of Przewalski horses increased regularly from 1991 onwards, reaching a population of 12 animals in 1996 (Fig. 2). All the adaptation phases and the variations in size and composition of the groups were analysed and described in a previous study; all the horses are identified (ear tags, skin marks or individual characteristics of the coats) with sex and ages (Pereladova *et al.*, 1999). Until 1995, all the animals were in one group. Since 1996 there have been two groups: the group of the dominant stallion, with mares and newborns; and a group of 2–3 bachelor males. In 1997, the dominant male of the main group died and was replaced by a bachelor male.

Observations

Different observers carried out observations of the movements, home range uses and interactions between kulans and horses at different times between 1987 and 1993 (Pereladova *et al.*, 1999). Between May and July 1994 and May and July 1995, horses and kulans were recorded twice daily (morning and evening). Observations (using binoculars) were made from the three 20-m-high towers located in the south, middle and north of the territory. Other additional observations were made from vehicles, using the roads of the Reserve, and on foot when brushes obscured areas. Between November 1995 and March 1998, the positions of horses and asses were noted down at least once a week. Our records of the locations and structures of the groups were combined with those of other studies of the behaviour and social structure of the two

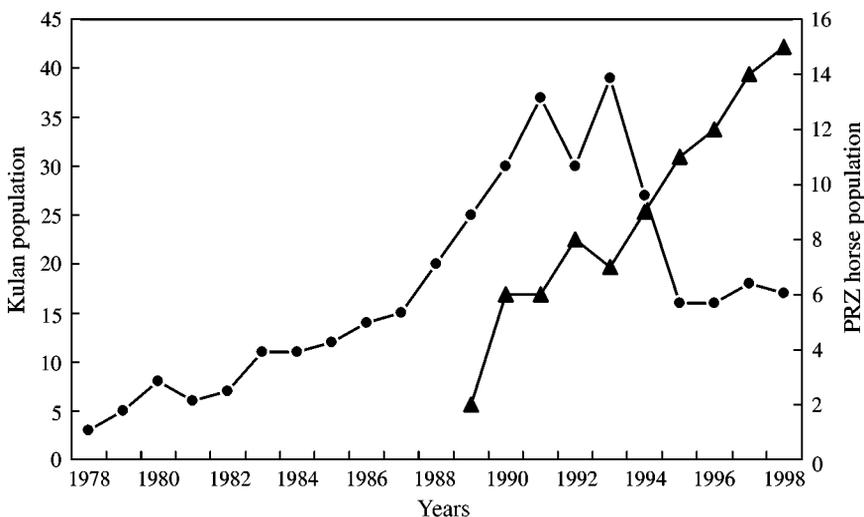


Figure 2. Development of the populations of kulans (*Equus hemionus kulan*) (—●—) and Przewalski horses (*Equus przewalski*) (—▲—) in the Bukhara breeding centre.

equids, especially of the Przewalski horses, made by Fisenko and Sidorenko by following the groups at a distance (from some two dozen metres) (the presence of an observer was even accepted within the group by the Przewalski horses).

The positions of horses and kulans in the Bukhara Breeding Centre were determined using 500-m side-quadrats.

A total of 374 positions for kulans (277 for the main group and 107 for the bachelor group) and 335 positions for Przewalski horses (219 for the stallion group and 86 for the bachelor group) were recorded during the study. Home ranges were established according to these positions, and for home-range analysis, we divided observations into different periods as follows:

- (1) 1 January –1 March 1996, period winter 1;
- (2) 1 March –4 June 1996, period spring 1;
- (3) 4 June –7 September 1996, period summer 1;
- (4) 7 September 1996–10 March 1997, period winter 2;
- (5) 10 March –4 June 1997, period spring 2;
- (6) 4 June –7 September 1997, period summer 2;
- (7) 7 September 1997–10 March 1998, period winter 3.

Statistical analysis

We used the MC Paal (Micro Computer Programs for Analysis of Animal Locations) version 1.22, (Stüew & Blohowiak, 1985) to analyse animal locations. Home-range areas were calculated by Minimum Convex Polygon method (Jourich & Turner, 1969). Harmonic mean transformations were used for area occupation by including 100, 95, 90, 85 and 80% of locations in the analysis.

We used Statview 4.5 software (1992–1996 Abacus concepts) for all statistical tests.

We tested independence among number of locations and home-range size with the Spearman's coefficient of correlation (Rho).

We used paired Wilcoxon rank test for the comparison of home-ranges between groups for each period, and Kruskal–Wallis ANOVA for the home range variations of a group between periods. Home-range overlaps between two groups were calculated with the minimum Convex Polygon maps (Jourich & Turner, 1969) as [(area shared/area of group 1) + (area shared/area of group 2)]/2.

Results

Przewalski horses home range

The home ranges of the stallion group were smaller than the bachelor group for six consecutive periods tested between 1996 and 1998 ($U = -1.753$, $n = 6$, $p = 0.04$). The exception was summer 1997 when the previous dominant male died and was replaced (Fig. 3). It resulted in a larger home range and a non-stable period for the new stallion and his group. The average home range was 7.77 km^2 for the stallion group and 15.37 km^2 for the bachelor group. The figures also fluctuated more for the stallion group ($SE = \pm 6.51$) than for the bachelor group ($SE = \pm 2.36$) although fluctuations were not significantly different ($F = 5.587$, $df. = 5$, $p = 0.0822$) because the home ranges of the stallion group varied from 3 km^2 (summer 1996) and 2.5 km^2 (winter 1998) to 16.9 km^2 (summer 1998). That is why there was no significant correlation between the home-range sizes of the two groups ($r = +0.4514$, $n = 6$, $p = 0.37$).

The home range in winter (6.5 km^2) was not significantly lower than the spring (11.7 km^2 , $U = 1$, $n = 2$, $p = 0.43$) and summer ones (10 km^2 , $U = 0$, $n = 2$, $p = 0.12$),

Table 1. *Overlapping between stallion and bachelor groups of Przewalski horses throughout the study period*

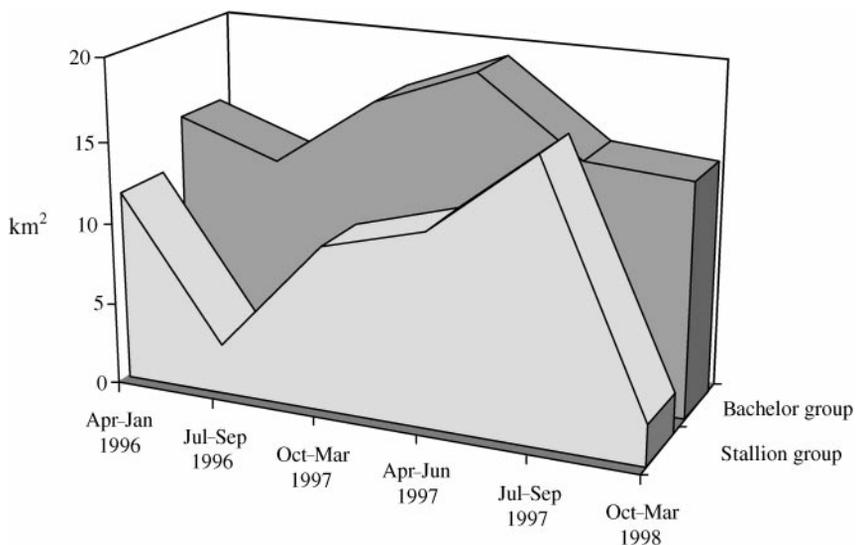
Period	Overlapping between stallion and bachelor group (%)
Spring 1996	20.02%
Summer 1996	6.78%
Winter 1996–97	0%
Spring 1997	19.5%
Summer 1997	42.14%
Winter 1997–98	4.17%

probably because of the high variation between 1996 and 1997 for the same season. Consequently, the seasonal variations in home-range size for the stallion group were not significant ($H = 2$, $df. = 2$, $p = 0.3679$).

The seasonal variations of home-range size for the bachelor group were not significant either ($H = 1.238$, $df. = 2$, $p = 0.539$) (mean = 15.371 ± 2.36 , $n = 6$) and fluctuations between 1996 and 1997 were much more reduced than those of the stallion group (maximum: 19.25 km^2 and minimum: 12.5 km^2).

The overlapping of stallion and bachelor home ranges (Table 1) did not vary between seasons ($h = 3.429$; $df. = 2$; $p = 0.18$), although it was lower in winter than during the other periods. It was maximum in summer 1997 (42.14%), intermediate in spring 1996 (20.02%) and 1997 (19.5%) and minimum in winter 1996–97 (0%), winter 1997–98 (4.17%) and summer 1996 (6.78%).

Before being set free, and for the first year after, during winter (Fig. 4), the stallion group showed only one activity centre, near tower 1 and a big salt lake or near the enclosures, where they were used to receiving food. The bachelor group had a bi- or multi-modal distribution, with two main centres of activity, one slightly to the north of the stallion group and the second one varying from tower 2 to the north-west of the small hill (Fig. 5).

**Figure 3.** Home ranges of the stallion group vs. Bachelor group of Przewalski horses, for each period.

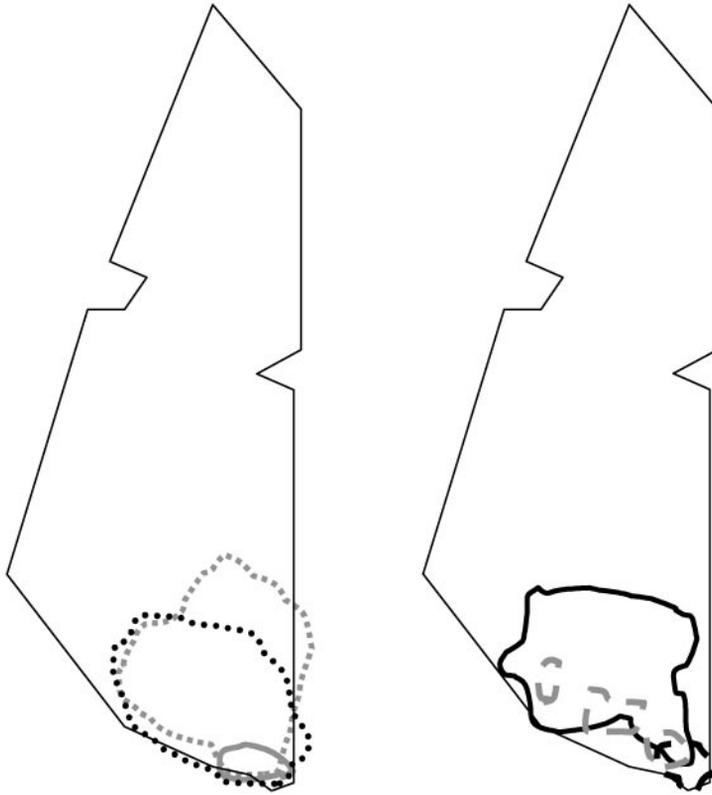


Figure 4. Activity center (harmonic means) of the stallion group of Przewalski horses: (—), April–June 1996; (---), July–September 1996; (- · - · -), October 1996–March 1997; (.....), April–June 1997; (●●●●), July–September 1997; (○—○), October 1997–March 1998.

Kulan home ranges

The home ranges of the secondary group of kulans were large but not different from those of the main group during the four periods tested except in spring 1996 (Main group: 18 km^2 vs. 9.75 km^2 for secondary group), but the difference was not significant ($U = -0.7303$, $n = 4$, $p = 0.233$) (Fig. 6).

The seasonal home-range sizes for the main group were similar from spring 1996 to summer 1997 ($14.6 \pm 2.2 \text{ km}^2$, $n = 6$), ($H = 1.179$, $\text{df.} = 2$, $p = 0.555$) although a small decrease was observed during the last winter (3.5 km^2).

For the secondary group, the home-range size was the same during the three seasons ($20.8 \pm 3.8 \text{ km}^2$, $n = 4$) ($H = 1.8$, $\text{df.} = 2$, $p = 0.4$) although it was smaller during the first spring in 1996 (9.8 km^2).

The overlapping of the main and the secondary groups (Table 2) was calculated for spring 1996 (65.7%) and 1997 (68.75%), summer 1996 (76.55%) and winter 1996–1997 (68.37%). It was highly invariable ($69.843\% \pm 2.337$) between seasons ($F = 66.542$, $\text{ddl} = 2.1$, $p = 0.2665$).

Finally, there was no significant correlation between the seasonal home-range sizes of the two groups ($r = +0.3024$, $n = 4$, $p = 0.698$).

The activity centre of the main group of kulans was very large, which means a higher diversity of home range uses than the Przewalski horses. Nevertheless, activity was concentrated in the south of the reserve (Fig. 7).



Figure 5. Activity center (harmonic means) of bachelor group of Przewalski horses: (—), April–June 1996; (---), July–September 1996; (· · · · ·), October 1996–March 1997; (· · · · ·), April–June 1997; (· · · · ·), July–September 1997; (---), October 1997–March 1998.

For the secondary group, as for the bachelor group of Przewalski horses, there were frequently two or more activity centres, one in the south and the other one in the north of the small hill (Fig. 8).

Coupled analysis (Kulans vs. Przewalski horses)

The home range of the main group of kulans was higher than that of the Przewalski stallion group during all the six periods tested during the study ($U = -1.8869$, $n = 6$, $p = 0.0296$) (Fig. 9).

Table 2. Home range overlapping between the main and the secondary groups of kulans

Period	Overlapping of the main and secondary group of kulans (%)
Spring 1996	65.7%
Summer 1996	76.55%
Winter 1996–97	68.37%
Spring 1997	68.75%

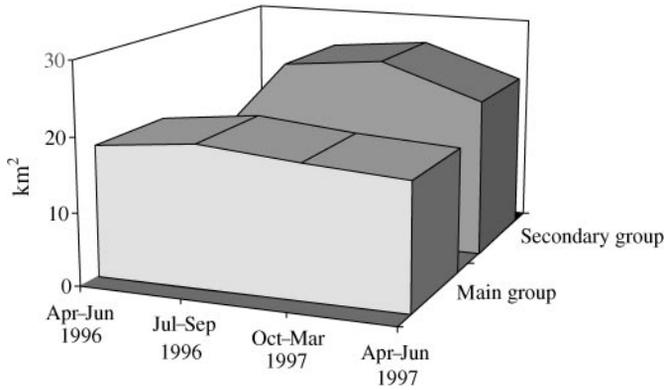


Figure 6. Home ranges of the main group vs. secondary group of kulans for each period.

The overlapping of the two groups (Table 3) varied seasonally ($F = 18.507$, $df. = 2, 3$, $p = 0.0205$), with a minimum in winter ($6.78\% \pm 5.48$), intermediate in summer ($19.73\% \pm 8.82$) and maximum in spring ($60.28\% \pm 4.29$).

There is no significant correlation between the seasonal home-range size of the two groups ($r = 0.4363$, $n = 6$, $p = 0.387$).

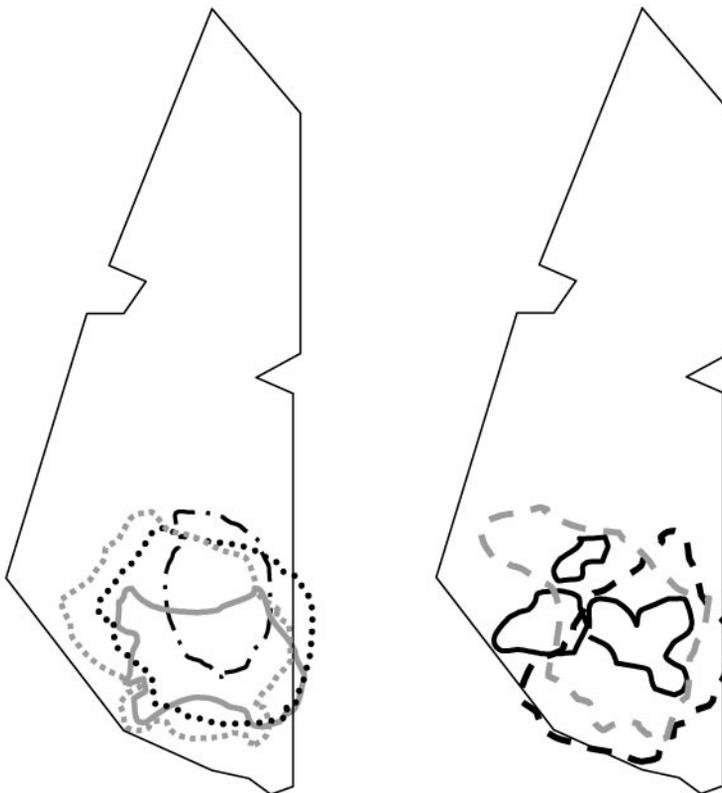


Figure 7. Activity center (harmonic means) of main group of kulans: (—), April–June 1996; (■ ■ ■), July–September 1996; (■ ■ ■ ■), October 1996–March 1997; (■■■■), April–June 1997; (●●●●), July–September 1997; (—), October 1997–March 1998.

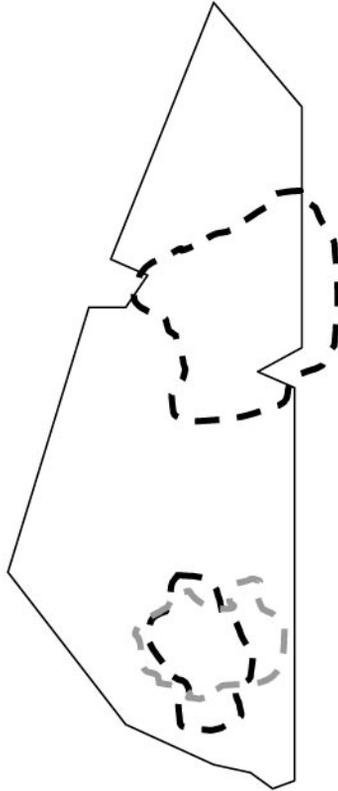


Figure 8. Activity center (harmonic means) of secondary group of kulans: (— — —), April–June 1996; (— — —), July–September 1996; (.....), October 1996–March 1997; (.....), April–June 1997.

Discussion

One of the important signs of the horses' adaptation is regular foaling, at least every two years (Duncan, 1992) and the seasonal fenology of reproduction, normal for wild animals, but lost by Przewalski horses in zoos (Boyd & Houpt, 1994). A few years after reintroduction in 1992 in the Bukhara breeding centre (Uzbekistan), Przewalski horses

Table 3. Home range overlapping between Przewalski stallion group and kulan main group

Period	Overlapping between Przewalski stallion group and kulans main group (%)
Spring 1996	64.6%
Summer 1996	10.91%
Winter 1996–97	1.29%
Spring 1997	55.99%
Summer 1997	28.55%
Winter 1997–98	12.26%

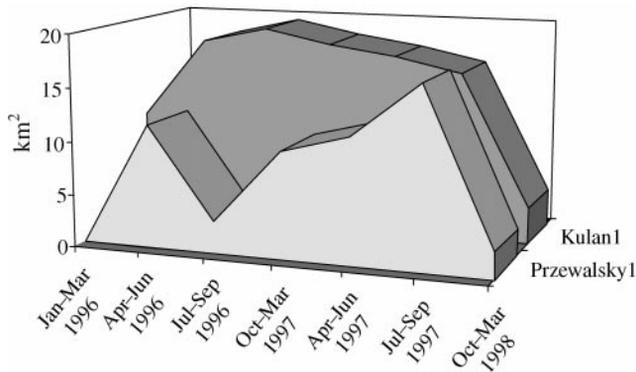


Figure 9. Stallion group of Przewalski horses *vs.* main group of kulans.

have adapted to their new arid environment (Pereladova *et al.*, 1999). By 1997 there was a third seasonal foaling in 4 years for the mares, which testified to the adequate adaptation and good individual condition of animals. The development of Przewalski horse groups followed a similar pattern that kulans and when the newborn males survived 1 year, they formed a new bachelor group (Pereladova *et al.*, 1999).

For both Przewalski horses and kulans, males were excluded from the main groups at 1 or 2 years of age, either by the dominant males during the reproductive period or by their mothers during or just after the next foaling. Consequently, they were pushed outside the home range of the main groups of their species, further to the north-west.

For both species, the secondary groups were still using the south part of the reserve mainly for water and partly for green food resources, when coming for watering. Consequently, the animals of the secondary groups were forced to increase their home range in order to avoid the main groups while retaining access to watering places. This was confirmed by the poly-modal centres of activity for the secondary groups of both species, one in the south and the other in the north-west.

In any case, according to previous fragmentary data, (Grum-Grzimalo, 1892, 1896) the typical structure of home ranges for wild Przewalski horses consisted of some preferable pastures, connected with watering places, where horses could be seen mainly at dawn, traditional routes, and areas where they spent most of daytime, combining pasturing, comfortable behaviour and rest. The latter preferred daytime parts of home ranges were typically situated 5–7 km from the main watering places, in open steppe, semi-desert or even desert areas, while watering places with preferable vegetation—were typically situated in some hilly areas, on the lower slopes of mountains, etc. In our study, this very type of home-range structure was registered for the bachelor group of Przewalski horses, composed of animals born in the Center, which had never had any contact with people, or had never been given any additional food. By contrast, during the dry 1996 autumn–winter period, the main group of initial zoo animals still came to the south and arrived near the buildings of the Center where spots of lucerne still grew in some fields or just chose areas with preferable vegetation, which were situated mainly around the lakes. Therefore, their registered home-range size was small over this period. Even for the main group, we could see some tendency towards a bi-centred composition of the home range (spring–summer 1997): animals were registered mainly not far from the lake in morning and evening times, while in the daytime they were 3–4 km away from the lakes and out of bushes in an open area. This was the period when the former zoo animals had already got adapted to semi-wild life in desert conditions (Pereladova *et al.*, 1999). Besides, spring–summer 1997 was the period when territorial demonstrations of the dominant male became regular in contacts with the 3-year-old bachelors. The overlapping of the stallion and bachelor home ranges was small, because the stallion group of zoo animals had a small home range, with all its parts frequently used and so

easier to prevent from intrusions by bachelors. Anyway, it was smaller in winter because the home range of the stallion group was reduced to the extreme south, where they could find additional food, and also because the bachelor group can do longer without water (period of autumn vegetation of grasses and brushes) and consequently they stayed more in the middle and north of the reserve. The sizes of home ranges were larger in spring and summer, as well as overlapping, because of the regular need for water, changes in dynamics of activity and condition of summer vegetation, but also because spring corresponding to the breeding period, the attractive effect of females on bachelors (pheromones) was not completely excluded.

Kulans are typically more migratory-active and better adapted to desert conditions (Geptner, 1961); that is why they can regularly do without water, or use water with very high salinity (Rashek, 1966). Moreover, the animals that were brought to the Centre were initially wild. So, it was no surprise to see that the home ranges of kulans were always larger, than those of Przewalski horses, and that kulans approached only occasionally areas in the south where people are present, having their main centres of activity in the middle part of the whole area. The secondary group of kulans had simply moved its home range slightly to the north-west without necessity to increase significantly its size compared to the main group. As the home ranges of both the main and secondary groups of kulans were large throughout the year, there were no important seasonal variations, which confirms the fact that they were not as dependent on water and fresh grass as Przewalski horses.

The level of overlapping of the groups' home ranges was different for each species and between main and secondary groups of either species. There was territoriality between groups of kulans in nature, but not strict in different seasons (Bannikov, 1963; Baskin, 1976; Rashek, 1966). In any case the home ranges of the main reproductive groups were more constant and stable. Subdominant animals composed the bachelor groups (and other types of secondary groups). They were pushed out of the main groups for different reasons. They have to stay in less favourable biotopes and are more mobile. All groups needed to have an access to watering places, and this necessity was more vital for the main group, which includes newborns and lactating mares in summer. Such dependence on water and feeding places was at the origin of conflicts with farmers in Turkmenistan when the kulans from the Badhis reserve left the reserve in spring and summer and spread to the surrounding agricultural lands. Consequently, numerous kulans were killed, and by 2000, their number had dramatically decreased (Sempéré, personal data).

During the breeding season (late spring) the dominant male was more aggressive towards bachelors because the females were in oestrus—the home range of the secondary group of kulans was therefore the largest, with a high level of overlapping but with free possibilities to avoid each other in time, using the same areas.

As it was already discussed, the home ranges of both Przewalski horse groups were strongly overlapping in the area around the watering places, especially in summer. But a strict time differentiation was registered in the usage of watering places, so that bachelors were rather rarely registered at a distance of visual contact with the main group until October 1997. The home range of the main group increased from the period of setting the group free on the main area (summer 1991) till April–June 1996. In summer 1996, three mares were with new-borns, being more fixed to watering places and better food resources—so the home range decreased; later on it increased again until September 1997.

Horses reach their statute of dominant males when they are 5 years old and can replace older dominant males in horses groups (Baskin, 1976; Boyd & Houpt, 1994; Duncan, 1992). The new dominant male which was 4 years old (present results) had to confirm his new position as a stallion. The home range became very limited (including only the main preferable biotopes) in order to be more easily controlled. Simultaneously territorial demonstrations of the new dominant male were registered.

There was a question about the overlapping of kulan and Przewalski horse home ranges. When the horses were set free on the main area, they had a very small home range, which stretched to the very limits of the southern part of the home range of the main group of kulans, but the animals divided the area in time and were never registered at less than 2500 m from each other (Pereladova *et al.*, 1999). Further, the home range of horses increased and kulans practically stopped using the south-eastern part of the Centre. They continued to use overlapping parts of their home ranges in turn (time-differentiation of area usage) and it was probable that horses disturbed kulans. Therefore, for kulans, the southern part of their home range corresponded mainly to the necessity for them to have access to drinking water.

In spring, Kulans and horses shared 60% of their home range, which means that they were probably competing for fresh grass during this period, while the overlapping decreases in summer and is even smaller in winter (6.8%) because of the retreat of horses to the extreme south-eastern part of the reserve and the decrease in need for water resources for kulans during this period. Moreover, the females of kulans are pregnant in spring and the needs for food are higher because it corresponds to higher energetic needs.

Consequently, the two species do not compete in natural conditions, but for the reintroduction project, a wide area of fresh grass in spring and free access to water resources for horses are necessary. From October 1997 to March 1998 the home ranges of the main groups of both species were the smallest within all the analysed period because of a comparatively dry winter and the necessity to have access to water resources, but overlapping was very small (4%), as not only time differentiation of area usage was registered, but also true territorial behaviour of the new Przewalski horses dominant stallion.

In conclusion, it has been shown that kulans and Przewalski horses demonstrated differences in area usage strategy even while the groups were similarly developing within the limits of the same fenced area. They can inhabit one area without serious conflicts, avoiding competition by the way of using time differentiation of the usage of key points, such as limited water resources. One of the reintroduction methods could well consist in releasing a mixture horses and asses in suitable habitats, within their historical area and without agricultural lands and domestic horses in the surrounding. Still, in reintroduction programmes of the Przewalski horses in semi desert environments, it is important to take into consideration that Przewalski horses must be well adapted to these environments as was the case in our study area (Bukhara Breeding Centre). Kulans are more adapted to desert conditions than horses and could seriously compete with them should water and food resources be limited, if the kulan population is well developed in size and social structure, and if groups of not-initially-adapted horses are set free within the same area.

We are very grateful to the Ministry of Ecology of Uzbekistan, 'Gosbiocontrole' - Mr A-K. Atadjanov, and the Directors of the Bukhara breeding centre, for enabling our work to take place, and the director of the Moscow Zoo VV Spitsin and his staff for the initial animals for our common experiment.

The observation of the group, which had been interrupted in 1990 because of political and economical problems, has been renewed since May 1993 thanks to collaboration with CNRS, France, on PICS 266; in March 1995–August 1996 the work was supported by the Mac Arthur foundation—personal grant. Special thanks to my son, Jean Philippe Sempère, for correction and help in improving the manuscript.

References

- Bannikov, A.G. (1963). Wild ungulates of Barsa-Kelmes island. *Journal of Wildlife and Wildlife Management* ('Ochota i ochotничie kchozaistvo'), **3**: 22–23.
- Baskin, L.M. (1976). *Behavior of ungulates*, M, Nauka. 295 pp. (in Russian).

- Berger, J. (1988). Social systems, resources and phylogenetic inertia: an experimental test and its limitations. In: Slobodchikoff, C.N. (Ed.), *The ecology of social behaviour*. pp. 157–188. London: Academic Press. 429 pp.
- Bouman, I. (1998). The reintroduction of Przewalskii horses in the Hustain Nuruu Mountain forest steppe reserve in Mongolia. An integrated conservation development project. Nederlandsche Commissie voor internationale natuurbescherming, *Mededelingen*, **32**: 50.
- Boyd, L. & Houpt, K.A. (Eds) (1994). Przewalski horse – the history and the biology of the endangered species, State Univ. New-York Press, Albany, 313 pp.
- Bubenik, A.B. (1985). Reproductive strategies in Cervides; In: Fennessy, P.F. & Drew K.P. (Eds.) *Biology of deer Production. Royal Society of New Zealand, Bulletin*, **22**: 367–374.
- Dobchin, N. (1970). New data on Przewalski horses. Tr. IX Mezhd. Kongressa biologov-ohotovedov. M.: 858–860. (in Russian).
- Duncan, P. (1992). Horses and Grasses: the nutritional Ecology of Equids and their Impact on the Camargue, *Ecological studies*, Vol. 87, Springer-Verlag. 288 pp.
- Esmark, Y. (1964). Rutting behaviour in reindeer (*Rangifer tarandus* L.). *Animal Behaviour*, **12**: 159–163.
- Feh, C., Boldsookh, T. & Toureno, C. (1994). Are family groups in equid's a response to cooperative hunting by predators? The case of Mongolia kulans. *Terre et al vie - Revue D Ecologie Applique*, **49**: 11–20.
- Flint, V.E., Pereladova, O.B., Mirutenko, M.V. & Jirnov, L.V. (1990). Experimental programme on free Przewalski horses populations creation in Kazakhstan - Middle-Asian region. In: *Rare and endangered species of mammals of the USSR*. (Eds. V.E. Sokolov) pp. 98–113. Moscow, Science, (in Russian).
- Ganslosser, U. & Dellert, B. (1997). Experimental alterations of food distribution in two species of captive equids (Burchelli, E. & Hemionus Kulan, E). *Ethology, Ecology & Evolution*, **9**: 1–17.
- Geptner, V.G., Nasimovitch, A.A. & Bannikov, A.G. (1961). *Mammals of the Soviet Union*. Vol. 1, Ungulates. Moscow, High school. 776 pp.
- Ginsberg, J.R. (1988). Social organisation and mating strategies of an arid adapted equid: the Grevy's zebra. Ph.D. thesis, Princeton University, Princeton.
- Ginsberg, J.R. (1989). The ecology of female behavior and male mating success in the Grevy's zebra. *Symposia of the Zoological Society of London*, **61**: 89–110.
- Grum-Grzimalo, G.E. (1892). Wild horse (*E. przewalski*). Niva, 17.
- Grum-Grzimalo, G.E. (1896). Description of the expedition To the West China. V.1, St.Peterbourgh, Russian Geographical Society.
- Henshaw, J. (1970). Consequences of travel in the rutting of reindeer and caribou (*Rangifer tarandus*). *Animal Behaviour*, **18**: 256–258.
- Jourich, R.I. & Turner, F.B. (1969). Measurements of noncircular home range. *Journal of Theoretical Biology*, **22**: 227–237.
- Klimov, V.V. (1988). Space-ethological organisation of Przewalski horses (*Equus Przewalski*) herds in Askania Nova. In: *The Przewalski horse and its restoration in nature in Mongolia*, Moscow, FAO/UNEP, 1986; pp. 160–179, (in Russian).
- Klingel, H. (1967). Soziale organisation und Verhalten freilebender Steppenzebras. *Zeitschrift für Tierpsychologie*, **24**: 580–624.
- Klingel, H. (1968). Soziale Organisation und Verhaltensweisen von Haltmann und Bergzebras. *Zeitschrift für Tierpsychologie*, **25**: 76–88.
- Klingel, H. (1969). Dauerhafte Sozialverbände beim Bergzebra. *Zeitschrift für Tierpsychologie*, **26**: 956–966.
- Klingel, H. (1975). Die soziale organization der Equiden. Verhandlungen der Deutschen Zoologischen Gesellschaft: 71–80.
- Lent, P.C. (1965). Rutting behaviour in berren-ground caribou population. *Animal Behaviour*, **13**: 259–264.
- Lent, P.C. (1974). A review of rutting behaviour in moose. *Natur. can.*, **101**: 307–323.
- Pereladova, O.B. (1988). On the stability of the subspecies characteristics of bukhara deer rutting behaviour in different ecological conditions. Bulletin of Moscow Society of Nature Dealers, *ser. biol.*, **93**: 25–34 (in Russian.)
- Pereladova, O.B., Bahloul, K., Sempéré, A.J., Soldatova, N.V., Schadilov, U.M. & Prisiadznuk, V.E. (1998). Influence of environmental factors on a population of goitred gazelles (*Gazella subgutturosa subgutturosa*, Guldenstaedt, 1780) in semi-wild conditions in an arid environment: a preliminary study. *Journal of Arid Environments*, **39**: 577–591.

- Pereladova, O.B., Sempéré, A.J., Soldatova, N.V., Dutov, V., Fisenko, G. & Flint, V.E. (1999). Przewalski's horse—adaptation to semi-wild life in desert conditions. *Oryx*, **1**: 12.
- Rashek, V.A. (1966). Ecology of kulan and its acclimatisation on Barsa-Kelmes island. Ph.D.Thesis, M., MSU. 24 pp.
- Rubenstein, D.I. (1986). Ecology and sociality in horses and zebras, p. 282–302. In: Rubenstein, D.I. & Wrangham, R.W. (Eds), *Ecological aspects of social evolution*. Princeton: Princeton University Press.
- Sokolov, V.E. & Orlov, V.N. (1980). Works of Mongolian Commission of the Academy of Sciences of the USSR. 349 p. (in Russian).
- Solomatin, A.O. (1973). *Kulan*. Moscow, Science ('Nauka'). 144 pp.
- Statview 4.5 software. 1992–1996. Abacus concepts, Inc., 1918 Bonita avenue, Berkeley, CA, U.S.A.
- Stüew, M. & Blohowiak, C.E. (1985). Micro-Computer Programs for the Analysis of Animal Locations (Mc PAAL). Conserv. Res. Cent., Natl. Zool. Park. Smithsonian Inst., Front Royal, Virginia.
- Zhirnov, L.V. & Luschekina, A.A. (1991). The Ungulates of the Eurasia arid zone (problems of conservation and rational use). In 'Ongulés/Ungulates 91', Spitz, F., Janeau, G., Gonzales, G. & Aulanier, S. (Eds), SFEPM-IRGM, Paris-Toulouse, p. 339–342.