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Ecology and social structure of the Gobi khulan *Equus hemionus* subsp. in the Gobi B National Park, Mongolia

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Abstract

The status of the Gobi khulan *Equus hemionus* subsp. is recorded as "insufficiently known" in the Species Survival Commission's Equid Action Plan. Recent counts confirm that Mongolia holds the most important population of the whole species. Since 1953, the animals have benefited from a protected status, but this is now challenged. A 5-year study in the B part of the Gobi National Park on one subpopulation showed that it has remained stable over the past 15 years with an adequate mean reproductive rate of 15% and a 50% survival rate over the first year. Age/sex related mortality and prey analysis indicate that wolf predation probably has some impact on the population, in particular for 4–6-year-olds of both sexes at the start of reproduction. Desert and mountain steppes are the khulan's year-round preferred habitat, but 'oases', play an important role at the beginning of lactation. Anthropogenic factors affect both home range and habitat use through direct intervention or permanent occupation of the scarce water sources. Khulans of this subpopulation, unlike other Asian and African wild asses, form year-round stable, non-territorial families. These families and all-male groups join together into "bands" in winter, and herds of several hundred animals, where reproductive rate is highest, form throughout the year. The existence of such herds may thus be critical for the breeding success of the population. Our study provides the first detailed quantitative data for this subspecies, which will help to monitor changes in the future.

Keywords: *Equus hemionus*; Ecology and social structure; Gobi National Park; Mongolia

1. Introduction

During the late Pleistocene, 40,000 years ago, Asian wild asses are known to have roamed as far as West Germany (Kurten, 1968). Like many other large bodied mammals, equids vanished from numerous biogeographic regions during a mass extinction about 12,000 years ago, even though the number of species seems to have remained more or less constant (MacFadden, 1992). The range of Asian wild asses has continued to shrink ever since. In the 13th century, Marco Polo (1958) refers to the presence of numerous herds in Persia, the Middle East, Arabia, Turkestan and the Gobi. During the same period, mention of khulans is made in the "Secret History of Mongolia" (Pelliot, 1949). Since then, "Khulan", is still used as a name for children in Mongolia. Today, the most abundant population of the species, representing > 50% of the total number, occurs in the southern part of Mongolia. All other populations have shrunk to a few hundred individuals (Fig. 1).

The taxonomy of wild asses for the whole of Asia is still not entirely clarified. It is now widely accepted from morphological as well as chromosomal and mitochondrial DNA analysis that the Tibetan wild ass or kiang (*Equus kiang*), is a species of its own (Ryder and Chemnick, 1990). The holotype of *Equus hemionus* described by Pallas in 1775 was based on a specimen collected close to the north-eastern boundary of Mongolia (Fig. 2). Six geographically isolated subspecies of *E. hemionus* are presently recognized (Equid Specialist Group, 1992) of which one, the Syrian wild ass (*Equus hemionus hemippus*), became extinct in 1927. The others are the onager (*Equus hemionus onager*) from Iran, the

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Turkmene and Kazakh khulan (*Equus hemionus kulan*), the latter sometimes being referred to as (*Equus hemionus finschii*) and the Indian khur (*Equus hemionus khur*). Groves and Mazak (1967) differentiate between the Gobi khulan *Equus hemionus luteus* in southern Mongolia/northern China and the North Mongolian dziggetai *Equus hemionus hemionus* on the basis of colour differences. Our own observations revealed that colour contrast varies extensively between individuals and seasons, especially for breeding stallions which become reddish in summer. The Mongolian Red Book (Shirevdamba et al. 1997) refers only to *E. h. hemionus* and the list of Mongolian vertebrates to *E. hemionus* (Reading et al., 1994). A molecular study conducted jointly by the Equid Specialist Group, IUCN and the Mongolian Academy of Sciences is presently under way in order to clarify whether the distinction between two Mongolian subspecies is justified or not.

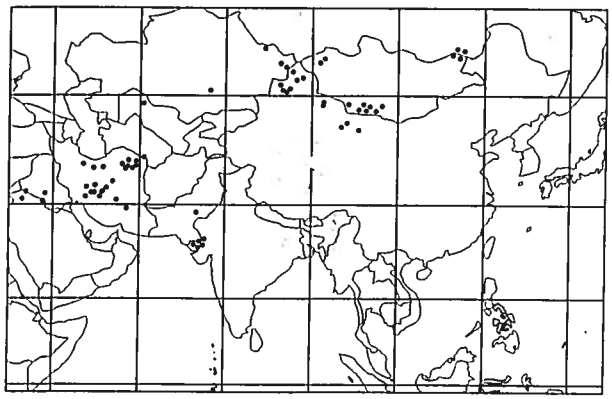

Fig. 1. Reported sightings of *Equus hemionus* between the end of the eighteenth century and the beginning of the twentieth century (Harper, 1945; Groves and Mazak, 1967; Schlawe, 1986).

The former range of the Mongolian khulan between the seventeenth and the middle of the nineteeth century encompassed the greater part of Outer Mongolia, small areas of Siberia and Manchuria, the western part of Inner Mongolia and the northern part of Xinjiang (Harper, 1945). Following the contraction of their range to the extreme south of Mongolia, observations from the last 20 years show a tendency for khulans to move further eastwards again (Reading et al., 2000). Estimates of the total population of khulans in Mongolia were 15,000 individuals in the 1970s and 1980s (Shirevdamba et al., 1997). A recent count calculated that there may be from 33,000–63,000 khulans in Mongolia (Reading et al., 2000). The animals are not evenly distributed over their range (Fig. 2). From west to east, three main concentrations occur, one in the B part of the Gobi National Park, the second in the A part and the highest concentration in the South-Gobi (Reading et al., 2000). The presence of khulans in the Jungarian Gobi (Gobi B National Park) has been reported since the eighteenth century (Harper, 1945).

Khulans have been protected in Mongolia since 1953. They were included in the CITES list, Appendix I, in 1973 and are registered as an endangered species in the Mongolian Red Book (Shirevdamba et al., 1997). The recent increase of domestic herds even in remote regions of the Gobi intensifies competition, and the protected status of the khulan is now challenged. The restriction of their range to the most arid parts of the country may not represent their optimal habitat and may make them more vulnerable. No quantitative study on their ecology was available. The aim of our study, therefore was to

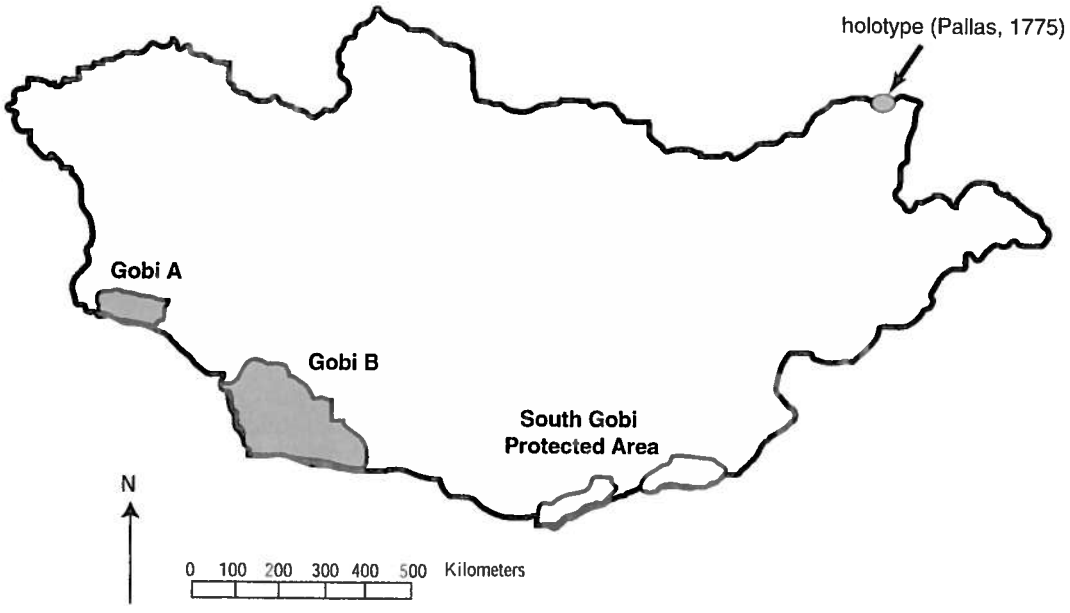

Fig. 2. The three strictly protected areas in Mongolia, where the most important concentrations of khulans occur.

contribute basic information on fluctuations in numbers, adult sex-ratio, reproductive rate, yearling survival and age/sex analysis of mortality, home range and habitat preferences as well as observations on the social system of one subpopulation in the B part of the Gobi National Park. The detailed quantitative data we collected will help to monitor these parameters in the future.

2. Methods

2.1. Study area

The 9000 km^2 of the B part of the Gobi National Park is located in southwest Mongolia (Gobi-Altai and Khovd district) as a part of the Jungarian basin (Fig. 2). Altitude ranges from 1100 to 2500 m. Climate is strongly continental with monthly air temperatures varying between −28° and 36°C. Precipitation averages 100 mm per year, with 70 days snow cover (Zhirnov and Ilinski, 1986).

Descriptive phyto-sociological studies made by Hilbig (1990) distinguish the following four major vegetation types: mountain steppe (*Agropyron cristatum*, *Stipa krylovii*), desert steppe (*Stipa* spp., *Artemisia* spp.), shrub desert (*Haloxylon ammondendron*, *Stipa* spp., halophytes) and oasis (*Phragmites australis*, *Juncus* spp., *Achnatherum splendens*). Nomenclature follows Hilbig (1990).

Nomads are allowed to cross the Park and camp during their spring and autumn migrations. The southern part of the Park towards the Chinese frontier is occupied by border guards, their families and their domestic herds of sheep, goats and camels permanently occupy all the water holes.

2.2. Observations and analysis

Observations were made for roughly 6 weeks in 5 consecutive years (1992–1996). The exact time-table was 6–20 June and 10–30 October in 1992, 20 July–28 August in 1993, 22 June–9 August in 1994, 5 October–8 November in 1995 and 15 September–4 November in 1996. Observations were made with a telescope from a car, a horse or on foot, totalling 1500 h. It was only possible to age and sex khulans under good light conditions in the mornings and evenings. We used morphological as well as behavioural criteria (Feh et al., 1996). Identification of individual khulans was based on scars and missing parts of tails and ears. Three such distinctive marks had to be present on one animal before we registered it as identified.

Counts were made on 2 or 3 consecutive days from dawn to dusk. We stopped on the track at the same places and climbed nearby hills with the telescope. Visibility reaches 30 km and it was therefore possible to count the khulans and recognize foals up to a distance of 10 km, as no other animals of the same colour and size class occur in the region. In consequence, we are confident of missing only a few animals over the whole of Gobi B. Simultaneously to the counts, the different groups were mapped for the home range analysis. On other days, we covered only a part of the Park in order to establish the khulan's grazing and resting patterns. All vegetation types were equally covered by these observations, which were again evenly distributed between dawn and dusk. We studied the home range and habitat use of one herd, the "180 herd" with its identified individuals, by following it on several consecutive days.

A group was defined as such when its diameter was less than the distance between two groups and members showed coordinated movements during an observation period, usually for more than 4 h. Analysis of composition was confined to groups for which all individuals could be assigned to a given age/sex class: foals, yearlings and stallions and mares > 20-years-old. We calculated medians rather than means because the frequency distribution of group size was far from normal.

Skeletons were found on random itineraries over the whole of Gobi B. Each was numbered with a permanent marker so as not to count them more than once over the different years. We used the hoof form, tufts of hair, particularly the ones from mane and tail, as well as the molar dentine pattern (MacFadden, 1992) to positively distinguish the species from skeletons of domestic horses. For ageing (and sexing in adults of > 4 years), we used the key based on teeth eruption and wear developed for domestic horses (Hayes, 1987), as the two species seem to have a similar longevity (Schlawe, 1986).

We collected wolf (*Canis lupus*) droppings from 35 different sites on random itineraries throughout Gobi B. As foxes (*Vulpes vulpes* and *Vulpes corsac*) are common in Gobi B, we analyzed only droppings whose diameter exceeded 25 mm (Thompson, 1952). Identification of prey items was made with the help of a specialist, Yves Kaiser, and based on bone splinters or hair which were compared to previously identified samples from whole carcasses.

A plant cover analysis for the different vegetation types was made using a minimum of eight point-quadrats for each type, as proposed by Daget and Poissonnet (1971).

3. Results

3.1. Population size and fluctuations

On our track itineraries in 1994, 1995 and 1996, we counted, respectively, 1445, 1595 and 1506 khulans, so there were annual fluctuations of about 10% without a

Table 1
Frequency of group size (G) and percentage of khulans (Kh) recorded in three group sizes in summer and winter over 5 years (1992–1996)

Group size	Summer 1992		Summer 1993		Summer 1994		Mean summer		Winter 1992		Winter 1995		Winter 1996		Mean winter		Mean total	
	% G	% Kh	% G	% Kh	% G	% Kh	% G	% Kh	% G	% Kh	% G	% Kh	% G	% Kh	% G	% Kh	% G	% Kh
1–10	81.5	11.6	80.0	7.8	91.9	13.7	84.5	11.0	48.7	11	55.3	8.5	62.8	9.3	55.6	9.6	70.0	10.3
11–50	7.9	6.7	3.3	1.4	4.0	6.0	5.1	4.7	44.7	46.1	36.2	34.3	27.9	16.5	36.3	32.3	20.7	18.5
51–850	10.4	81.9	16.1	90.7	3.9	76.7	10.3	83.1	7.8	42.9	8.4	57.2	9.2	74.2	8.5	58.1	9.4	70.6
Groups, n =	38		30		74		142		39		47		43		129		271	
Khulans, n =	1073		1171		1397		3641		935		1486		1506		3927		7568	
Median group-size	4.0		4.5		3		4.0		10		8		8		8		6.25	

tendency towards increase or decrease. A survey carried out by Sokolov and Orlov (1980) in 1975/1976 amounted to 1250 animals. Extrapolations from aerial and road counts conducted in 1980/1981 (total number of animals seen: 252) gave an estimation of 1500 individuals (Zhirnov and Ilinski, 1986). Over the past 15 years, the population inside the B part of the Gobi National Park and its immediate surroundings has apparently remained stable.

3.2. Social groups, structure and size

Group size varied between 1 and 850. The overall median group size was 6.25 individuals (Table 1), with 70% of the groups (range 49–92%) spanning between one and 10 animals. But 71% of the khulans (range 34–85%) lived in groups of 51–850 animals. Group size varied in relation to seasons, the median doubling between summer and winter (median test, $P < 0.05$). We observed more small groups (1–10 individuals) in summer and more medium-sized groups (from 11 to 50 individuals) in winter. The number of large groups (50–850 individuals) did not vary between seasons.

Small sized groups usually consisted of stallions only or of families of stallions, mares and young animals. Medium-sized "bands" and large herds invariably split up into distinctive family or all-male groups when we watched them over several hours. The typical family (median over 5 years, $n=99$) was composed of one stallion (range 1–18), 2.35 mares (range 1–24) and 0.5 foals (range 0–16); the typical all-male group ($n=87$) consisted of 2.5 stallions (range 1–17; Table 2). Over the 5 years, we met all-female groups only four times. Again, the family groups and all-male groups were significantly larger in winter (median test, $P<0.05$). We never saw solitary males in winter. The proportion of females to males in family groups varied between 1.4 and 2.8 (mean 2.0), without a difference between seasons.

Over the years, we regularly encountered three large groups of similar size (450, range 425–475; 180, range 150–210; 80, range 75–85). It was not possible to ascertain whether these had a stable core of individuals or not. However, in the "180 herd", 14 individuals (eight adult stallions and six adult mares) could be identified and were seen in the same herd from 1993 to 1996.

3.3. Seasonal home range and habitat use in relation to vegetation types and pasture use by herders

The total home range of the population encompasses the whole of Gobi B with the exception of the southern part occupied by the border guards, where no khulans were seen. In addition, they roamed over an area of ca. 630 km^2 outside the Park in a northeastern direction. We never observed them more than 30 km from a permanent spring or an oasis. Their range was more

restricted in summer than in winter. In the beginning of the summer during the birth season, they concentrated around the Khonin Us oasis, where water (12 permanent waterholes) and food were abundant and no herders were present. We saw them less frequently in the western part of the Park around the oasis Takhin Us which is more often occupied by the herders. These findings are consistent with the observations by Zhirnov and Ilinski (1986) on the same population, except that the khulans used the southern region of the Park more extensively in the 1980s.

We were able to locate the "180 herd" with its 14 identified individuals during each observation period from 1993 to 1996. Its home range covered an area of ca. 400 km^2 including three permanent watering places and other herds were observed to overlap it on several occasions.

Despite the extensive areas of shrub desert found in Gobi B, making up close to 45% of the whole area (Table 3), we observed khulans only rarely (6%) on these, either in summer or in winter (Table 4). Over the whole year, khulans grazed or rested most often on desert steppe vegetation (40.6%), followed by oases (30.8%) and mountain steppes (22.6%; Table 4). There were marked differences between the seasons in selection of oases and desert steppes. The former were used in the beginning of spring, when most foals are born, and the herds moved to the desert steppes in autumn and early winter. Although we made no systematic night observations, we usually found the "180 herd" in a range of 10 km from the place where we had seen them last on the previous night. There was no indication of a migration pattern or specific day/night habitat switch. From the 36 nights spent in a hide close to waterholes, it became clear that khulans never came to drink before dawn or after dusk, so these places seemed to be the only ones being subject to distinct day/night activities. These seasonal differences in habitat use are easily interpreted when looking at the plant composition and density of the different vegetation types (Table 3). Khulans, like all equids, are grazers specialized on moncotyledons such as the perennial grasses *Stipa* spp., *Agropyron* spp., *Achnatherum splendens* and reeds (*Phragmites*) and rushes (*Juncus* spp.), the highest

Table 2
Group composition, medians and range (in parentheses) of khulans

	Summer				Winter				Total
	1992	1993	1994	Total	1992	1995	1996	Total	
Families									
Stallions >2 years	1(–)	1(–)	1(1–5)	1(1–5)	2(1–6)	2(1–18)	2(1–3)	2(1–8)	1(1–18)
Mares >2 years	2(1–5)	1(1–3)	2(1–12)	2(1–12)	4(1–12)	3(2–24)	2.5(1–6)	3(1–24)	2.25(1–24)
Foals	0(0–1)	0.5(0–2)	1(0–3)	0.5(0–3)	0.5(0–7)	2(0–16)	0(0–1)	0.5(0–16)	0.5(0–16)
Groups, n =	23	12	17	52	18	21	8	47	99
All-male groups									
Stallions	2(1–9)	2(1–4)	2(1–17)	2(1–17)	4(1–16)	3(2–8)	3(2–4)	3(1–8)	2.5(1–17)
Groups, n =	8	6	48	62	9	13	3	25	87

Table 3
The different vegetation types of the Gobi B National Park (based on data from eight point-quadrats for each vegetation type)[a]

Vegetation type	Plant cover %	Estimated area Km^2	Dominant species in decreasing order of abundance
Oasis 1 (1–10 m from waterholes)	85.2		*Juncus* spp. *Triglochin* spp.
Oasis 2 (10–30 m from waterholes	35.2	20	*Leymus* spp. *Phragmites australis*
Oasis 3 (>30 m from waterholes	20.8		*Achnatherum splendens* *Leymus* spp.
Desert steppe	8.8	4000	*Stipa glareosa* *Stipa gobica* *Anabasis brevifolia*
Mountain steppe	9.5	900	*Agropyron cristatum* *Stipa krylovii*
Shrub desert	18	4000	*Haloxylon ammondendrum* *Allium* spp.

[a] The total area of the Gobi B National Park covers 8920 km^2

densities of which occur in the oases, followed by mountain and desert steppes. The typical shrub desert vegetation is mainly composed of "saxaul" *Haloxylon ammondendrum* and annual *Allium* species that are of minor or very seasonal value.

3.4. Demographic parameters and reproductive rate

The mean adult sex-ratio (animals of > 2-years-old) calculated over the 5 years was 1.0 (Table 5).

Excluding the June 1992 observations taken before the end of the parturition period, one out of 3.1 mares of more than 2 years had a foal (Table 5, range 1.83–6.25). The reported age at first breeding in mares is 3–4 years (Raschek, 1973; Schlawe, 1986), so we estimate that only one out of two reproductive mares has a foal every year. Survival over the first months is included in these percentages.

The peak parturition period for Gobi khulans takes place between mid-June and mid-July. Excluding the June 1992 data, because they was collected before most of the foals were born (Table 6), the mean percentage of foals after peak parturition in the Gobi B population over the 5 years was 14.5% (range 8.6–19.1). The difference between years may be explained by the high spring rainfall from 1993 to 1995 and a drought in spring 1996. Over the last 3 years, the percentage of foals was consistently higher in the big herds (16.9, 16.6 and 9.6% respectively) when compared to bands or isolated family groups outside herds (11.8, 4.3 and 3.9% respectively).

The mean percentage of yearlings in the population was 5.7% (range 2.5–8.8%, Table 6). Comparing the percentage of yearlings to the percentage of foals the previous year, less then half (mean 37%, range 15–56%) of the khulans born seem to survive their first year.

A khulan's life span in captivity can reach 26 years (Schlawe, 1986). In the Gobi, the oldest animal we found dead was between 12- and 14-years-old (Table 7). Besides the high mortality observed in the very young age classes, which is usual for many mammals, most khulans (46.4%) died in their prime age between 4 and 8 years, particularly between 4 and 6 (29.3%). This corresponds to the age where both sexes are at the beginning of their reproductive lifespan. Apparently, there was no difference in mortality between stallions and mares (Table 7). We met sick animals only twice, two mares showing discomfort behaviour and rolling on the ground, visibly suffering from colic probably due to endo-parasites or another disease. Two foals of about two weeks were found with a broken leg. We never saw emaciated or even thin khulans during our observations, but then we lack data from the end of winter.

3.5. Wolf predation

Our sample size of wolf dropping sites is small ($n = 35$) but collected randomly over the whole of Gobi B

Table 4
Percentage of grazing and/or resting khulans observed on the different vegetation type

Year	Summer				Winter				Total number of kulans tallied
	June–August				Oct–Nov				
	Oasis	Mountain steppe	Desert steppe	Shrub desert	Oasis	Mountain steppe	Desert steppe	Shrub desert	
1992	98.1	0	0.9	1.0					1010
1992					2.0	34.7	58.5	4.8	1190
1993	71.3	13.5	0.4	14.8					2374
1994	1.5	57.0	40.1	0.8					2181
1995					0.2	30.0	63.4	6.4	4146
1996					11.4	0	80.2	8.4	1461
Mean	57.0	23.5	13.8	5.5	4.5	21.6	67.4	6.5	

Table 5
Adult khulan sex-ratio and mare/foal ratio in summer (SU) and winter (WI) 1992–1996

	SU 92	WI 92	SU 93	SU94	WI95	WI 96	Mean
Female/male ratio (> 2-years-old)	1.3	1.4	0.7	0.7	0.85	1.1	1.0
Mare/foal ratio (> 2-years-old)	21.66	3.21	2.0	2.33	1.88	6.25	3.13 (without June 1992)
n =	125	190	55	201	336	51	

Table 6
Percentage of khulan foals and yearlings in the population

Year		June		July		August		October		Number of animals tailled
		n	%	*n*	%	*n*	%	*n*	%	
1992	Foals	5	2.1					106	19.1	235/554
	Yearlings	7	5.9					8	5.6	119/143
1993	Foals					31	12.4			250
	Yearlings					5	5.6			90
1994	Foals			229	15.8					1445
	Yearlings			12	6.0					201
1995	Foals							158	16.6	951
	Yearlings							42	8.8	480
1996	Foals							123	8.6	1427
	Yearlings							5	2.5	203

Table 7
Age-sex related mortality of khulans based on skeletons

Sex	Age in months (m) or years (y)								Total
	< 1 m	< 9 m < 2 y	< 2 < 4 y	< 4 < 6 y	< 6 < 8 y	< 8 < 10 y	< 10 < 12 y	< 12 < 14 y	
Indeterminate	2	9	5						16
Females	2			6	2	1	1	1	13
Males				6	5		1		12
n =	4	9	5	12	7	1	2	1	41
Percentage	9.8	22	12.2	29.3	17.1	2.4	4.8	2.4	100

Table 8
Prey species from 35 wolf dropping sites

Species	*n*	Relative percentage	Absolute percentage
Wild mammals			
Khulan *Equus hemionus*	8	14.0	22.9
Goitered gazelle *Gazella subgutturosa*	6	10.5	17.1
Tolai hare *Lepus tolai*	18	31.6	51.4
Gerbils *Meriones* spp.	11	19.3	31.4
Unidentified small rodents	3	5.3	8.6
Domestic mammals			
Camel	1	1.8	2.9
Horse	1	1.8	2.9
Sheep	1	1.8	2.9
Birds			
Unidentified passerine	1	1.8	2.9
Reptiles			
Unidentified lizard	1	1.8	2.9
Insects			
Unidentified beetles	5	8.8	14.3
Plant matter	1	1.8	2.9
Total prey	57	100	
Total samples	35	163	

National Park. In 82.8% of all samples, we found hares, gerbils or other small rodents (Table 8). Domestic animals were present in only 8.7% of the samples and birds, reptiles, insects and plants in 23%. Parts of hair or teeth of khulans and black-tailed gazelles (*Gazella subgutturosa*), the two large herbivores of Gobi B, occurred in 14 samples (40%).

Direct observations on wolves' predatory behaviour on khulans were made on previous occasions (Feh et al., 1994). Furthermore, both during the observations in the winters of 1995 and 1996, wolf packs of four–five individuals pursued the regularly watched "180 herd" on several days, but without a successful kill. All authors having watched Mongolian khulans mention wolves as predators (Andrews, 1932; Bannikov, 1958; Zhirnov and Ilinski, 1986; Dulamtseren et al. 1989). Other predators were never observed or heard of attacking khulans.

4. Discussion

4.1. Population stability and habitat use

Maximum rates of population increase in free-living equids without predators observed in The 'Granite range' feral horses in Nevada reached 31% per year (Berger, 1986). Wolfe (1979) gave a range of 20–25% for other populations of mustangs. The reproductive rate over 5 years (mean: 15%, close to 40% survival over the first year) is similar to other populations of *E. hemionus*: 11.8 and 14.8% in Mongolian khulans (Bannikov, 1975), 15.6% and a 50% survival over the first year in Turkmenian khulans from Badchys (Solomatin, 1973), 19.7% in Turkmenian khulan from Barsa Kelmes (Raschek, 1973). This is evidently adequate to sustain the number of khulans in the Gobi B National Park over the past 15 years (Zhirnov and Ilinski, 1986). Several factors may explain this apparent stability. First, the carrying capacity of the pasture may have been reached and, as a result, part of the population has emigrated. The best but limited possibility (Fig. 2) would be towards the west, as the Altai mountain range prevents northward movements. The lack of unoccupied water places in the east and the border guards permanently monopolizing the southern springs probably hinder major movements in these directions. Emigration over the border towards China seems a possibility, but only a few hundred khulans are reported for the whole of the country (Xiaoming and Schaller, 1996), so survival seems to be compromised, very probably due to poaching.

Secondly, competition with herders affects the habitat use and home range of the study population. Our results are similar to those obtained by many other authors. Between 1943 and 1945, Bannikov (1958) recorded 95% of khulans throughout Mongolia on desert steppes dominated by feathergrass (*Stipa* spp.). Andrews (1932) in spring 1922 saw the biggest concentrations of khulans around a lake and on the adjoining desert and mountain steppes.

Apart from the vegetation type, blood-sucking insects such as tabanids and mosquitoes as well as snow had short-term influences on habitat use. Close to the Khonin Us oasis in July 1994, we counted up to 54 tabanids on a domestic horse during the daytime and ca. 150 mosquitoes at dawn and dusk. During this time, no khulans were observed staying in the oasis which was only used for drinking. The uninterrupted snow cover present in 1995 and 1996 made individuals disperse more widely in search of food. At the same time, the daily range of groups had shrunk. When the snow cover was highest (20–50 cm), the animals grazed on the lower mountain slopes in order to avoid snow drifts. When it partly melted on the warmer desert steppe, they grazed in the plains, actively searching for the snow patches to eat from. Zhirnov and Ilinski (1986) reported similar observations for the same population.

4.2. Predation and social behaviour

Few observations were made at the end of winter, but the absence of thin animals seen throughout our study suggests that other factors than limited resources affect population growth and that predation may play a considerable role in khulan deaths. The high mortality observed in adults of both sexes at the start of their reproductive lifespan may indicate that both stallions and mares are more exposed to attacks from wolves during this time period, females when giving birth and males during fights or subsequent to wounds resulting from fights. The analyses of wolf prey species seems to show the predators' interest in khulans. Apart from small mammals such as hares and gerbils present in 80% of the samples, khulans are eaten more often than the more abundant but lighter black-tailed gazelles (*Gazella subgutturosa*), the only other relatively large herbivore of the region.

Khulans have developed an elaborate anti-predator defence strategy through group formation. Khulan stallions of the Gobi B population stay with the mares and foals year round and actively take part in the defence of offspring (Feh et al., 1994, this study). When several family groups join up, as is usually the case in winter, khulan stallions from different families chase wolves cooperatively.

Like us, both Dulamtseren (1989) and Bannikov (1958) observed family and all-male groups in Mongolian khulans, and a comparable group structure and composition was observed in Turkmenian wild asses by Solomatin (1973) and Raschek (1973). All authors having studied Mongolian khulans report the existence of

big herds, such as Dulamtseren (1989), Bannikov (1958) or Andrews (1932) for the first half of this century. More recently, Owen and Munkhtuya (personal communication) saw two herds of ca. 900 individuals in the Galpin Gobi (South-Gobi district). In 1994, Schaller, (1994; personal communication) met two herds of 234 and ca. 500 khulans. Finally, Mix et al. (1995) identified four herds consisting of 500–650 khulans each during an aerial count, and on our own expedition in September 1996 we saw one herd of 1241 individuals.

The observed three-level society in this khulan population reveals a complexity of social organisation unheard of before in any ungulate, and very probably affects the demography of the population. Two types of social systems have been described in equids: feral horses (Berger, 1986), plains and mountain zebras (Klingel, 1972) either form small and permanent family groups or all-male groups. These species live in mesic environments with large and cooperatively hunting predators. In the two species found in desert habitats without large predators, Grévy zebras (Ginsberg, 1987) and feral domestic donkeys (Mochlman, 1974), only females and their recent offspring form permanent bonds and dominant males establish mating territories. *Equus hemionus* as a species represents an interesting exception to this fixity of group types. Both onagers in Israel (Saltz and Rubinstein, 1995) and the Indian khur (Shah, 1993) display all-female groups and territorial males, whereas the Turkmenian wild ass and this population of Gobi khulan live in family or all-male groups. Onagers and khur live in places devoid of large and cooperatively hunting predators, whereas both the Turkmenian asses and the khulans from our study site suffer from wolf predation. Moreover, data collected on the South-Gobi population, where wolves are much scarcer than in the Gobi B National Park, show that the proportion of all-female groups is much higher in this location (Enkhbold, 1998; Schaller, 1998). In equids, predator pressure from large and cooperatively hunting species rather than resource distribution apparently is the key to social groupings (Feh et al., 1994). Male help in predator defence of offspring and the existence of large herds therefore seem to be important for general breeding success, as the percentage of foals is significantly higher in herds than in isolated groups.

5. Conservation

Out of seven species of equids existing at the present time, four are threatened with extinction (Equid Action Plan, 1992). Only the plains zebra (*Equus burchelli)*, the kiang (*Equus kiang)* and the wild asses (*E. hemionus)* live in populations of several thousand individuals. The total range of the latter has greatly shrunk over the past centuries and they have now fragmented into six geographically isolated populations with five recognized subspecies of some hundred individuals each, except in Mongolia where the largest population is found.

In Mongolia, most individuals of the three subpopulations now live in strictly protected areas (Fig. 2, the Gobi National Park A part (ca. 40 000 km^2), B part (ca. 9 000 km^2) and the Baga Gobi Strictly Protected area. According to complaints from local herders, both the Gobi B and the South-Gobi populations are expanding. However, any northward extension of the Gobi B population is limited by the Altai mountain chain, and eastward movement of the South-Gobi population will meet the major obstacle of the fenced railway from Irkutsk to Bejing. Owing to the increase of livestock since the privatization of herds in 1991, all permanent waterholes of the region have been occupied (Samyia, personal communication). During our own observations in 1996, we saw khulans drinking only from the holes they dug down to 60 cm in the otherwise dry riverbeds. Therefore, this population may push north-eastwards in search of better watering and grazing opportunities, giving up their former range.

Our 5-year observations on the Gobi B khulans, which live on better quality habitat than the two other subpopulations, show that their range has shifted from south to north when compared to Zhirnov and Ilinski's (1986) data collected in the beginning of the 1980s. During our systematic counts, we recorded the number of khulans seen inside and outside the Park limits. We observed 40% of khulans on the foothill regions north of the Park. In winter 1996, when large herds of khulans transgressed the Park boundaries northwards to graze on the mountain steppes, riders interfered and drove them back inside the Park. When tents were put close to the oases, khulans avoided them. Poaching may occur (the usual flight distance of the animals from cars was ca. 2 km), but we were unable to assess its importance. For all the above mentioned reasons, it is doubtful that an important number of animals can sustain themselves outside the Park borders.

Recently, intensive killing of wolves has been organized in Gobi B, partly in an attempt to protect the livestock, and partly in order to protect the released Przewalski horses (*Equus przewalskii*). This might not only cause an increase in khulans and gazelles, and therefore, enhance competition for grazing with domestic herds, but it might also affect the small grazing mammal populations such as hares and gerbils and exacerbate competition even further.

The Gobi B subpopulation of khulans is not critically endangered. The calculated effective population size of 940, assuming all adults participate in reproduction, is close to the 1000 individuals needed to avoid long term "genetic deleterious mutation degradation" (Lynch, 1996). For the survival of the khulan population in the whole of Mongolia, there is hope in the form of the

recent government pledge to declare 30% of the country as protected areas.

Demographic factors are important for the conservation of endangered species. It is increasingly recognized in conservation biology that social behaviour affects mortality or natality rates as well as the genetic diversity of a population (Durant, 2000). Our study provides a basis for the follow-up of these parameters. The existence of large herds seems to be important for reproductive rate of the population. This asks for specific habitat requirements, namely extensive patches of dense grasses, reeds or rushes not more than 30 km from an abundant and undisturbed watering place .

The taxonomy question has to be resolved urgently in order to know at which level conservation actions should be taken.

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