

ARE FAMILY GROUPS IN EQUIDS A RESPONSE
TO COOPERATIVE HUNTING BY PREDATORS?
THE CASE OF MONGOLIAN KULANS
(*EQUUS HEMIONUS LUTEUS* MATSCHIE)

Claudia FEH*, Tsagaany BOLDSUKH** and Christophe TOURENQ*

Direct adaptive responses to the environment as well as phylogenetic constraints have been put forward to explain the evolution of social or breeding systems in mammals without leading to definite conclusions. In ungulates (Jarman, 1974), a correlation between resource distribution and body-size seems to predict the social organisation of a species. However, non-ruminants like equids were neglected in this analysis.

For the seven species of equids presently alive, two types of breeding systems are known :

Type I — Feral horses (Berger, 1986), plains zebras (Klingel, 1967) and mountain zebras (Penzhorn, 1984) all form small and permanent family groups usually consisting of one male, one to two females and their offspring. They maintain longterm, sometimes life-long relationships between adult individuals of both sexes. All-stallion groups occur in all three species. Both sexes disperse at puberty.

This is necessary if direct inbreeding like mother-son or father-daughter matings are to be avoided, as stallions tenure length of females exceeds the time for young animals to reach puberty (Clutton-Brock, 1989). The behavioural mechanism underlying dispersal originates in familiarity (Duncan *et al.*, 1984). Young females leave the group they have grown up in, even if the family stallion is not their father. After a short period of wandering, they join another reproductive unit and rarely change thereafter. Young stallions live in stallion groups for one or two years before forming their own family. Low-ranking stallions often form alliances in order to defend females against rivals (Berger, 1986 ; Feh, 1990).

Type II — Far less is known on the social organisation of the four remaining species of equids. Detailed studies were carried out on Grévy's zebras (Ginsberg, 1987), feral domestic donkeys of African origin (Moehlman, 1974) and the Indian subspecies of the Asiatic wild ass, the Khur (Shah, pers. comm.). They all show that permanent bonds only exist between females and their recent offspring and that dominant males normally establish mating territories.

* Station biologique de la Tour du Valat, Le Sambuc, F-13200 Arles, France.

** Academy of Sciences, Sukhbaatar square 3, Ulaan Baatar 11, Mongolia.

Why and how these two different types of social systems originated in species so morphologically similar has already been discussed. According to Rubenstein (1986), scattered food distribution and low food abundance should favour small groups composed of mothers and their recent offspring; indeed, asses and Grévy's zebras do live in xeric and therefore less predictable environments. On the other hand, Berger (1988) emphasized the importance of phylogenetic inertia when looking at equid breeding systems. He experimentally showed that mountain and Grévy's zebras could adopt different social systems when confronted with identical patterns of food-distribution. However, MacCourt (1979) has shown that some feral donkeys living in a very rich environment may form year-round harems. Nevertheless, his study was short term (one year) and most of the reproductive males were vasectomized.

According to this classification of equid social systems, Asian wild asses should behave like their African counterparts, both of them living in similar semi-desert or desert environments. This is the case for one sub-species, the Indian Khur (*Equus hemionus khur*). Unfortunately, nothing is known about the Tibetan Kiang (*Equus hemionus kiang*), considered by some authors to belong to another species. As for the Kulan, our knowledge is limited to the studies of Solomatin (1973) and Bannikov (1958), who observed the Asian wild ass over several years in Kazakhstan. Some observations were also made in Mongolia by Bannikov (1958). Their findings may be summarised as follows :

During the breeding season (May-September), Kulans aggregate in family groups consisting of one male, 3.8 females and 2.3 young animals. Solitary males are observed, but there is no indication of territoriality. Male-tenure length of females lasts for several years, « until very old males are expelled after serious fights ». Mate-guarding by stallions is commonly seen. Stallions are first to defend their offspring against predators. Family-groups join together after the breeding season (October) in herds of hundreds, to migrate to their winter-pastures.

Although purely descriptive, these studies indicate that Kulans do not display the typical wild ass breeding system in their xeric environment, as the resource distribution theory would predict. Why is this not the case ? Resource distribution might not be the only cause of equid social organisation and breeding systems. Bonds between males and females in horses, plain zebras and Kulans might also have been influenced by predator pressure. Their main predators (wolves, lions, hyenas), are large and hunt in packs, whereas the predators of the other species or subspecies are smaller and/or solitary hunters : the Indian wolf for Khur, and jackals for African wild asses.

Could bonds between male and female equids thus have evolved under the pressure of cooperatively hunting predators in order to defend their offspring more successfully ?

Mongolian Kulans provide a unique opportunity to investigate this hypothesis, as they live in a typically xeric environment, and as they are the only wild asses on both continents suspected to have both a cooperative breeding system between males and females, and group hunting predators (wolves). However, Bannikov's studies lacked quantitative data based on individual follow-ups. The goal of the present short term study was therefore, first to establish whether individual follow-ups were feasible, and second to undertake preliminary quantitative surveys on group composition during two breeding seasons, and in early winter.

THE STUDY SITE AND THE KULANS

STUDY SITE

The B part of the Gobi National Park is located in the Dzungarian Gobi in SW Mongolia (Gobi-Altai district). It encompasses 9 000 km² at altitudes ranging from 1 100 to 2 500 m. The climate is continental with air temperatures ranging annually from - 28 °C to + 36 °C. Precipitation averages 100 mm per year, with 70 days snow cover (Zhirnov & Ilynski, 1986).

Vegetation

Descriptive phyto-sociological studies made by Hilbig (1990) distinguish the following four major vegetation types : Mountain steppe, desert steppe, shrub desert and oases. Our study site during the two reproductive seasons, was located at one of these oases, Khonin Us, (latitude 45° 20' N, longitude 94° 10' E), a ca. 8 km² area including a dozen small (ca. 2-3 m²) permanent water holes. The soil is salty. Here, three major plant communities were identified. In the immediate surroundings of water holes (1 to 10 m), vegetation covers 85.2 % of the ground and is mainly composed of *Juncus* spp. (38.4 %) and *Triglochin* spp. (26 %). From 10 to 30 m away from water holes, plant cover (35.2 %) is made of two species only, *Elymus* spp. (28 %) and *Phragmites communis* (7.2 %). Further away (more than 30 m from water holes), plant cover is reduced to 20.8 % and mainly composed of *Achnatherum splendens* (15.2 %) and *Elymus* spp. (4.4 %). All three vegetation types were heavily grazed.

Our winter observations were made at ca. 80 km from the same oasis. Here, the vegetation type was desert steppe, composed of *Stipa glareosa* and *Anabasis brevifolia* (Plant cover 8.8 %).

THE STUDY ANIMALS

In the spring of 1992, a maximum of 450 Kulans were present at or around the oasis throughout the observation period. Their numbers decreased regularly between 10.00 h and 16.00 h, when most of the animals left for the surrounding shrub-desert area. Numbers also decreased for several hours after cars were driven through the oasis. The Kulans usually came to drink at the water holes between 20.00 h and 21.00 h. No foals were seen the first day of our visit, but 4 were born during the following week. Our observations therefore coincided with the onset of the breeding season.

During the summer of 1993, Kulans were more dispersed, probably owing to the high rainfall of the previous spring. In July, only a few (< 20) were observed daily at the oasis. From the eight of August till the end of the month, 150 to 350 Kulans were seen each day, as the neighbouring water holes were beginning to dry up.

In the winter of 1992, the animals were found in the surrounding desert steppe. As there was a thin snow layer (ca. 5 cm) during most of our study-period, we surmise that the kulans had left the vicinity of the water-holes and scattered more widely.

OBSERVATION PERIODS

In 1992, the total number of our observation hours was 64 in spring. Systematic observations were made on 5 consecutive days (9-13 June 1992), mostly from a cliff close to a waterhole, or by following the animals on foot. Kulans could be approached at a distance of ca. 50 m. Because of poor light conditions and distance which sometimes made sexing and ageing of the animals impossible, only 27.5 h of observation provided data which could be used to determine group composition.

In 1993, four weeks were spent in summer at the oasis (July 30th to August 25th), including 13 days in a hide to identify individual animals and record interactions.

In winter, observations were made from October 14th to October 24th 1992. We followed the animals by car or on foot. Our total number of observation hours was 46.

The following criteria were used to define groups : (1) The diameter of a group is smaller than the distance to the next group, and (2) members of a given group stay together throughout the observation period.

To age Kulan skulls, we used the method developed for domestic horses, based on teeth eruption and wear (Hayes, 1987). The longevity of both species is apparently the same in captivity (Schlawe, 1986).

RESULTS

GROUP COMPOSITION

In spring, 56 groups were identified totaling 208 animals. In winter, data were gathered on 33 groups, including 173 adults and 43 foals (Fig. 1).

All-male groups and family groups were observed in both seasons.

All-male groups : The mean number of individuals in all-male groups ($n = 18$) in spring was 2.78 (range 1-9), the median being 2. In winter, the mean size of all-male groups was 3.5 ($n = 10$, range 1-6), the median being 4. This difference between spring and winter is significant (Median-test based on Fisher, $p = 0.05$).

Family groups : 38 family groups were observed in spring including 142 animals (38 males, 95 adult or subadult females, 5 yearlings and 20 newborn foals). Only one adult male was present in each of these groups. The mean number of females was 2.50 (range 1-5), the median being two. So the « typical » family group was made up of one adult male and two females. In winter, the mean number of males per group ($n = 23$) increased to 2.43 (range 1-5), the median being 2. In addition, the number of females was significantly higher than in spring (mean 5.09, range 1-12, median 4. Median test $\chi^2 = 8.397$, $p < 0.01$). The « typical » group in winter was therefore composed of two males and four females.

There was no indication of territorial males and no group consisted of only females and offspring.

Group composition at water holes : Solitary stallions and all-male groups were the first to come to drink in the morning and evening. Family groups never came

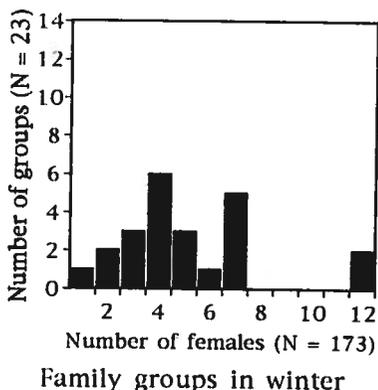
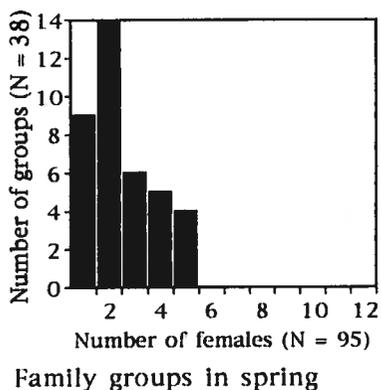
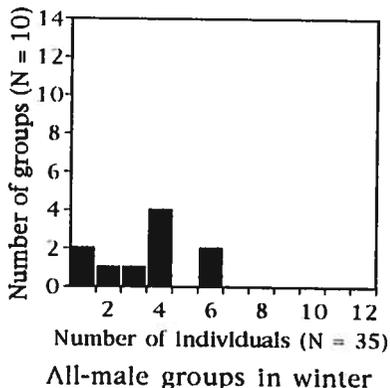
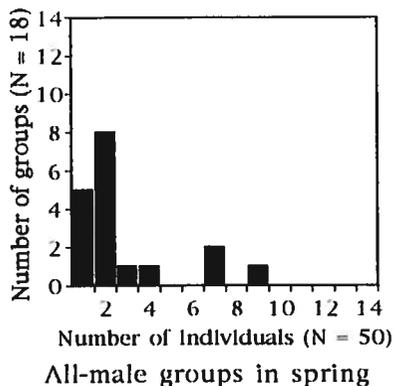


Figure 1. — Composition of all-male groups (top) and family groups (bottom) in spring (left) and winter (right).

to drink on their own ; they first herded together in the desert steppe around the oasis, before approaching water holes. Family groups with foals of the year were the last to come to drink.

AGE STRUCTURE OF SKULLS

Ten Kulan skulls were found in our study area during the 1993 summer, and aged. Four animals had died in their first year, and one each in its second, third, fourth, fifth, sixth and ninth year. Mortality is therefore highest in very young animals. Half of the skulls were found close to water holes inside the oasis, the other half in the surrounding shrub-desert. All skulls of adult Kulans (> 4 years, n = 4) were found close to water holes.

INTERACTIONS

All typical interactions of family-forming equids (Feist, 1976) were observed in Mongolian Kulans. Such was the case for :

- mutual grooming. Most groomings (24 out of 31) occurred at the same place where horses preferentially groom each other (Feh & de Mazières, *in press*).
- submissive behaviour of young animals towards adults (« snapping »)
- threats to bite and kick with ears laid back
- play-fights including rearing, biting and kicking.

Special attention was given to encounters between family stallions. All (n = 54) followed the same pattern observed in feral horses. The stallion left his females in the typical prancing posture (Fig. 3) to join another stallion. When they met, nose-nose contact was established, followed by a foreleg kick and sniffing of the flanks. These were sometimes followed by hindleg kicks and defecation. Both stallions then separated and in all cases went back herding their females. The herding posture was the same as the one adopted by feral stallions, neck and head in one extension line towards the ground. Kulan stallions, in contrast to horses, always keep their mouth open during herding.

Other differences observed in comparison with horses were the postures adopted during « prancing », and shortly before an open-mouth attack on another stallion. In contrast to horses, Kulan stallions held their head high and not tucked in, and did not arch their neck or raise their tails as horses do. During prancing, the head was held horizontally, whereas shortly before attacks, the head was held above the horizontal line (Fig. 2).

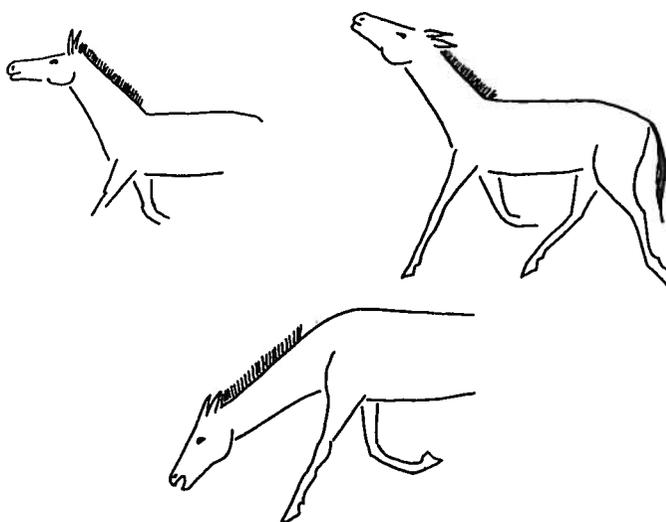


Figure 2. — Postures of Kulan stallions. Top left, prancing before stallion encounters ; top right, threat to attack ; below, herding mares.

MORTALITY AND ANTI-PREDATOR BEHAVIOUR

On a previous visit to the Gobi B National Park after the breeding season (October 1990), a total of 150 Kulans were observed close enough and on a fixed transect to be able to identify 10 foals of the year. If we suppose that female Kulans have their first foal at 4 (after a gestation length of 11 months), and if the sex ratio of the population is equal, only one out of every 5.5 reproductive females had been able to produce one surviving offspring that year. The reproductive potential and the survival rate of foals in the Gobi population of Kulans seems therefore to be much lower than expected. As all animals observed were apparently in good body condition, predation by wolves provide the most likely explanation for the scarcity of young animals of the year.

Wolf tracks along Kulan trails were seen daily. Furthermore, one direct observation of Wolf predation was made on August 6th 1993, from our hide. The following field notes vividly describe the incident.

0715. Dawn. A stallion and a mare Kulan fight three wolves attacking a small foal. Dozens of repeated attacks. Stallion mainly using open-mouth bite-attempts and foreleg kicks, mare mainly hindleg kicks, staying close to the foal. One Wolf brings the foal down and kills it, the others being occupied with Kulans. The Wolf pack is made of one lactating female and two other wolves, full size but more slender (subadults?)

0740. Wolves feeding. New attacks from both Kulans. A third Kulan, a stallion, joins up and participates in the attacks. The first stallion drives him away after 10 minutes, as he shows interest in the mare.

0750. Sunrise. Wolves feeding. Occasional attacks from mare. Stallion at 100 m.

0815. Mare 30 m from dead foal. Stallion and mare join in three new attacks. Wolves avoid them and return to the foal carcass seconds later.

0845. Stallion and mare grazing 50 m from Wolves. Wolves feeding.

0910. One Wolf (subadult) leaves towards North.

0915. Second Wolf leaves towards North. Mare and stallion pursue it over several hundred meters. Threatening attitude. Wolf runs.

0930. Both Kulans back. Approach and threaten the lactating female who leaves towards South, running, pursued by Kulans. Stallion and mare then come back, grazing 200 m from foal remnants.

1700. Eleven Black Vultures (*Aegypius monachus*) feed on carcass for two hours. Kulans still present.

2230. (Same ?) lactating female Wolf comes from South with two pups. Feeding for 30 min.

The female foal was 4 to 6 weeks old.

Neither Kulans nor Wolves were seen the next day.

DISCUSSION

Our preliminary observations on group composition and scarcity of foals, as well as the information gathered on anti-predator behaviour of Kulans, support the hypothesis that male-female bonds in this species might result, at least in part, from the pressure exerted by cooperatively hunting wolves. The group composition of the observed population of Kulans resembles plains zebra and horses more closely than equids traditionally living in desert environments such as African wild asses and Grévy's zebras. Even group size seems to correspond; feral horses, plains and mountain zebras, like kulans, have a median group size of two to three females per family group (Berger, 1986; Klingel, 1967; Penzhorn, 1984). Interestingly, the number of adult males and females in kulans doubles between spring and winter, for family and all-male groups alike, despite the fact that food is much more dispersed. These results raise two questions: 1) Why do kulans resemble plains zebra and horses rather than the desert living species, and why are they in contrast with another subspecies of wild asses, the K_hur? 2) Why does group size increase in winter? The most plausible explanation is found in predator pressure

by wolves. The only other ungulate prey available for wolves in the same region is a small number of black-tailed gazelles, *Gazella subgutturosa*. This view is shared by Dulamtseren (1970) who states that kulans are the main prey for wolves in winter, that wolves hunt in packs only in winter in the Gobi and that Kulan stallions are first to defend their group against predators. Wolves are also the main predators of Turkmenian wild asses, *Equus hemionus kulan* (Heptner & Naumov, 1974), which form family groups similar to the ones observed in Mongolian kulans (Solomatin, 1973).

Bonds between males and females in horses, plain zebras, mountain zebras and kulans therefore may have been influenced by predation. Plain zebra populations in the Serengeti suffer from a heavy predation-pressure by lions, *Panthera leo*, and hyenas, *Crocuta crocuta* (Sinclair & Norton-Griffiths, 1982) due to the fact that they are more constantly available than wildebeest, *Connochaetes taurinus* (Schaller, 1972, p. 211, fig. 38). This seems not to be the case for the Grévy's zebras studied by Ginsberg (1987). Kruuk (1972) was also able to show that hyenas, when intent on hunting zebras, form packs of up to 27 individuals (average 10.8), whereas these packs do not exceed 6 individuals (average 1.4) when they hunt wildebeest where only the mother defends her calf. Plain zebra stallions were also observed defending group members against lions (Klingel, 1972), hyenas and wild dogs (Schaller, 1972). Bonds between males and females in equids may thus have evolved under the pressure of cooperatively hunting predators in order to better defend their offspring.

SUMMARY

Attempts to account for the diversity of breeding systems in ungulates have concentrated on ruminants (Jarman, 1974), and non-ruminant species, like equids, were largely neglected. Equids are basically known to have two types of breeding systems correlated with two different types of resource distribution: Species living in mesic environments like mountain zebras, *Equus zebra*, (Penzhorn, 1984) and plain zebras, *Equus burchelli*, (Klingel, 1967) or feral horses (Berger, 1986) all form small and permanent family groups, usually consisting of one male, one to two females and their offspring. Sometimes, two breeding stallions form coalitions (Berger, 1986), and small all-male groups occur in all three species. On the contrary, in species living in xeric and therefore unpredictable environments like African wild asses, *Equus asinus*, (Moehlman, 1974) and Grévy's zebra, *Equus grevyi*, (Ginsberg, 1987), dominant males are territorial and bonds exist only between females and recent offspring, probably to minimize group-size while foraging. According to this classification based on resource distribution, Asian wild asses, *Equus hemionus*, ssp. should adopt the second type of social system. However, not all of them do so. Why is this not the case?

Resource distribution might not be the only determinant of breeding systems in equids. Apart from phylogenetic inertia mentioned for mountain and Grévy's zebras (Berger, 1988), predators might also play an important role. The Indian wild asses, *Equus hemionus khur*, (Shah, pers. comm.) living in xeric environments (with small and solitary hunting predators present, *Canis lupus pallipes*), typically adopt type 2 breeding system. Bannikov's (1958) descriptive study already suggested that Mongolian kulans, *Equus hemionus luteus*, living in a similar desert-environment (together with large and cooperatively hunting predators, *Canis lupus chanco*), might adopt type 1 breeding system. Our own

observations on group-composition of kulans carried out in the Gobi National Park, during the breeding season and in winter, support this view. Not only were kulans found to be non-territorial and to live in family- or all-male groups like horses, plain and mountain zebras, but they doubled their group size in winter, at a time when food was more dispersed but predator pressure high. This contrast suggests that understanding differences in grouping patterns between subspecies of wild asses may help to shed light on equid social systems in general.

RÉSUMÉ

Les tentatives d'explication de la diversité des stratégies de reproduction des Ongulés se sont bornées jusqu'ici aux ruminants (Jarman, 1974) ; les non-ruminants, et en particulier les Equidae, ont été pour la plupart négligés. Or, on connaît chez eux l'existence de deux modalités reproductrices corrélées aux deux types différents de répartition des ressources alimentaires. Les espèces de milieux moyennement riches, comme les zèbres de montagne *Equus zebra* (Penzhorn, 1984) et les zèbres de plaine *E. burchelli* (Klingel, 1967), ainsi que les chevaux retournés à l'état sauvage (Berger, 1986) forment tous de petits groupes familiaux permanents, consistant en un mâle et une ou deux femelles accompagnées de leur descendance. Parfois, deux étalons reproducteurs peuvent former des « coalitions » (Berger, 1986). Enfin, de petits groupes de « mâles célibataires » existent dans les trois espèces. A l'opposé, les Equidae de milieux très arides, à ressources rares et imprévisibles, comme les *Equus asinus* sauvages d'Afrique (Moehlman, 1974) et les zèbres de Grévy *E. grevyi* (Ginsberg, 1987) possèdent des mâles dominants territoriaux, et des liens sociaux durables ne s'observent chez eux qu'entre les mères et leurs jeunes descendants — probablement pour minimiser la taille des groupes lors de leur recherche de nourriture. Il devrait en être de même chez les ânes sauvages asiatiques *Equus hemionus*. Cependant ce n'est pas le cas de toutes les sous-espèces connues, et l'on peut se demander pourquoi.

Peut-être la distribution des ressources dans l'habitat n'est-elle pas la raison profonde (la « cause ultime ») des différences de modalités de reproduction des Equidae. Outre l'« inertie phylogénétique » invoquée pour *E. zebra* et *E. grevyi* par Berger (1988) ; il se pourrait que les prédateurs aient également joué un rôle important. L'Ane sauvage indien *E. hemionus khur* (Shah, com. pers.) qui vit dans un milieu aride où n'existent que de petits prédateurs chassant en solitaires (les *Canis lupus pallipes*) a adopté la seconde stratégie, alors que le Kulan de Mongolie *E. hemionus luteus* tout aussi désertique mais attaqué par de grands prédateurs chassant en groupes (les *Canis lupus chanco*) suit la première stratégie (Bannikov, 1958).

Nos propres observations, faites au Parc National du Gobi en début de période de mise-bas et en hiver, confirment ce fait. Non seulement les mâles kulans ne sont pas territoriaux, mais ils vivent en groupes familiaux ou en groupes de mâles, tout comme les chevaux retournés à l'état sauvage et les zèbres de Burchell ou de montagne. La taille de leurs groupes sociaux double même en hiver, malgré la raréfaction et la dispersion de leur nourriture et la forte pression de prédation.

Les différences entre sous-espèces d'ânes sauvages peuvent peut-être nous éclairer sur l'origine des différences existant entre systèmes sociaux chez les Equidae en général.

ACKNOWLEDGMENTS

We would like to thank Mr. A. Avirmed, director of the Gobi National Park, Dr. Gombyn Zorig, Dr. T. Adyasuren and Dr. T. Shirevdamba from the Ministry for Nature and Environment for all their help in making this study possible. The « Basler Stiftung für Biologische Forschung », the Mammal Conservation Trust, the « Association pour le cheval de Przewalski » and WWF France provided financial support. Many thanks to them.

REFERENCES

- BANNIKOV, A. (1958). — Zur Biologie des Kulans. *Z. f. Saugetierk.*, 23 : 157-168.
- BERGER, J. (1986). — *Wild Horses of the Great Basin*. Chicago : Chicago University Press.
- BERGER, J. (1988). — Social systems, resources and phylogenetic inertia : An experimental test and its limitations. In : *The Ecology of Social Behaviour*, C.N. Slobodchikoff (ed.), pp. 157-186. London : Academic Press.
- CLUTTON-BROCK, T.H. (1989). — Mammalian mating systems. *Proc. R. Soc. London. B*, 236 : 339-372.
- DULAMTSEREN, B. (1970). — *Mammals of Mongolia*. Ulaan Baatar : Academy of Sciences (in russian).
- DUNCAN, P., FEH, C., GLEIZE, J.C., MALKAS, P. & SIMPSON, M. (1984). — Reduction of inbreeding in a natural herd of horses. *Anim. Behav.*, 32 : 520-527.
- FEH, C. (1990). — Long-term paternity data in relation to different aspects of rank for Camargue stallions. *Anim. Behav.*, 40 : 995-996.
- FEH, C. & DE MAZIÈRES, J. (in press). — Grooming at a preferred site reduces heart-rate in horses. *Anim. Behav.*
- FEIST, J.D. & MCCULLOUGH, D.R. (1976). — Behaviour patterns and communication in feral horses. *Z. f. Tierpsychol.*, 41 : 337-371.
- GINSBERG, J. (1987). — *Social Organisation and Mating Strategies of an Arid adapted Equid : the Grevy's zebra*. PhD. thesis, Princeton University.
- HAYES, M.H. (1987). — *Veterinary Notes for Horse Owners*. Stanley Paul, London.
- HEPTNER, V.G. & NAUMOV, N.P. (1974). — *Die Saugetiere der Sowjetunion*, Band 1. Jena : Gustav Fischer Verlag.
- HILBIG, W. (1990). — *Die Pflanzengesellschaften der Mongolei. Biologische Ressourcen der Mongolischen Volksrepublik*. Halle : Martin-Luther-Universität.
- JARMAN, P. (1974). — The social organisation of antelope in relation to their ecology. *Behav.*, 48 : 215-267.
- KLINGEL, H. (1967). — Soziale Organisation und Verhalten freilebender Steppenzebras. *Z. f. Tierpsychol.*, 24 : 580-624.
- KLINGEL, H. (1972). — Das Verhalten der Pferde. In : *Handbuch der Zoologie*, J.G. Helmcke, D. Starck & H. Wermuth (eds.), pp. 1-68. Berlin : Walter de Gruyter Verlag.
- KRUUK, H. (1972). — *The Spotted Hyena*. Chicago : University of Chicago Press.
- MACCOURT, W. (1979). — The feral asses of Ossabaw island. *Symposium on the Ecology and Behaviour of Wild and Feral Equids*, University of Wyoming, pp. 71-84.
- MOEHLMAN, P. (1974). — *Behaviour and Ecology of Asses*. PhD thesis, University of Wisconsin.
- PENZHORN, B. (1984). — A long-term study on social organisation and behaviour of Cape Mountain zebras. *Z. f. Tierpsychol.*, 64 : 97-146.
- RUBENSTEIN, D. (1986). — Ecology and sociality in horses and zebras. In : *Ecological Aspects of Social Evolution*, D. Rubenstein & R. Wrangham (eds.), Princeton University Press.
- SCHALLER, G. (1972). — *The Serengeti Lion*. Chicago : University of Chicago Press.
- SCHLAWÉ, L. (1986). — Seltene Pfleglinge aus Dschungarei und Mongolei : Kulane, *Equus hemionus hemionus*, Pallas 1775. *Zool. Garten, N.F.*, 56 : 299-323.
- SINCLAIR, A.R.E. & NORTON-GRIFFITHS, M. (1982). — Does competition or facilitation regulate migrant ungulate populations in the Serengeti ? A test of hypotheses. *Oecologia*, 53 : 364-369.
- SOLOMATIN, A.O. (1973). — *The Wild Ass*. Moscow : Academyia Nauk. (in russian).
- ZHIRNOV, L.V. & ILYNSKI, V.O. (1986). — *The Great Gobi National Park - A refuge for rare animals of the Central Asian deserts*. UNEP, Moscow.