BRILL

Behaviour 159 (2022) 403–441

Behaviour
brill.com/beh

Review

Ecology and social behaviour of the Mongolian gerbil: a generalised review

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Received 25 November 2020; initial decision 22 March 2021; revised 25 August 2021; accepted 2 September 2021; published online 20 September 2021

Abstract

The present review provides a compilation of the published data on the ecology and social behaviour of Mongolian gerbils. Behavioural observations in the wild show that the Mongolian gerbil is a diurnal social rodent living in extended family groups. Seasonal breeding is typical of Mongolian gerbils in their natural habitat. Social monogamy seems to be characteristic of the Mongolian gerbil reproductive strategy, which however does not exclude facultative polygyny and promiscuity. A typical feature of the space use system in this species is territoriality. Social relationships in family groups may be defined as a subordination hierarchy. The hierarchy order is primarily determined by the age of the animals and maintained chiefly by the subordinates' behaviour patterns. The complex social organisation in the Mongolian gerbil is characterised by cooperation in different activities. Cooperation appears to enhance the survival of family groups of this species under the extreme climatic conditions of Central Asia.

Keywords

Mongolian gerbil, ecology, social behaviour, family-group lifestyle, reproduction, mating system, hierarchy, cooperation.

1. Introduction

The Mongolian gerbil (*Meriones unguiculatus* Milne-Edwards, 1867) is a burrowing rodent inhabiting semi-desert grasslands and steppe regions of Mongolia, north-eastern China and southern Siberia, Russia (Tanimoto,

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1943; Khamaganov, 1954; Leont'ev, 1954, 1957; Ågren et al., 1989a; Gromov, 2000a, Liu et al., 2007). There is also evidence that Mongolian gerbils can penetrate into typical desert regions (e.g., in southern Mongolia), although with a low population density (Rogovin & Shenbrot, 1995).Within the area of this species, the climate is arid or semi-arid and continental with relatively hot summers and cold, dry winters (Bannikov, 1954; Khamaganov, 1954; Leont'ev, 1954; Liu et al., 2007, 2009a).

The Mongolian gerbil has become a popular laboratory subject in biomedical and behavioural studies, since a stock was established in the United States in 1954 (Randall & Thiessen, 1980). Despite *M. unguiculatus'* long history, current popularity, and versatility as an animal model, a review of the literature indicates the lack of a single comprehensive and detailed source of information about its ecology and social behaviour, especially in English. The not numerous published works (Ågren et al., 1989a, b; Gromov, 2009, 2011a; Liu et al., 2007, 2009a, b, 2017; Hurtado-Parrado et al., 2015; Wang et al., 2011, 2017; Deng et al., 2017a, b; Wang, 2017) do not fill this gap.

The author has carried out ecological and behavioural studies of the Mongolian gerbil in the wild (in Tuva region, southern Siberia, Russia), under semi-natural conditions (in large outdoor enclosures in Moscow region) and in a laboratory from 1976 to 2008, and has published a series of articles as well as two monographs (mainly in Russian) (Krylova & Gromov, 1977; Gromov & Popov, 1979; Sokolov & Gromov, 1998; Gromov, 1981, 1992, 1994, 1997, 2000a, b, 2009, 2011a, b, 2015). In Tuva region, the study areas were semiarid grasslands intermixed with croplands and fallow fields. To collect data on the local population density and demographic structure of the gerbils, as well as on their social behaviour, a capture-mark-release technique was used. Gerbils were trapped in original wire-mesh traps baited with bread aromatized by sunflower oil. On the first trapping occasion, the animals were sexed and weighted. Each individual was given a number by toe-clipping for permanent identification and an individual mark for long-distance observations. This was achieved by applying unique markers to the pelage of each individual with a permanent black wool dye. The animals were observed through binoculars on 0.3–0.5 ha study plots. Within each study plot, a grid of squares 10 × 10 m or 5 × 5 m was laid out, and the corners of the squares were marked by small flags with numerical symbols. With reference to these flags, the positions of the observed animals were identified. The same technique was used for behavioural observations of the gerbils under semi-natural conditions in two outdoor enclosures of 20 × 20 m, where squares of 2.5 × 2.5 m marked by small flags were also laid out to identify the positions of the observed animals. The observations lasted up to three months (from early June to early September) in the wild and up to five months (from May to October) in the outdoor enclosures. Due to these long-term field studies and observations of the gerbils under semi-natural conditions over the years, sufficient data on group composition, use of space, scent marking, and social behaviour of the species have been gathered.

A detailed analysis of the published literature on the ecology and social behaviour of the Mongolian gerbil revealed the lack of consensus on the mating system, reproductive strategies and social organisation of the species (see, for example, Ågren et al., 1989a; Gromov, 2000a; Scheibler et al., 2004; Randall, 2007; Liu et al., 2009a, 2017; Deng et al., 2017; Wang, 2017). Specifically, some authors reported a monogamous mating system in Mongolian gerbils, while others suggested that the gerbils reproduced communally with plural female breeders or exhibited a promiscuous mating pattern. Besides, some authors reported that male Mongolian gerbils exhibit dominance hierarchy and combat competition over mates, though there is strong evidence for a family-group lifestyle in this species (Gromov & Popov, 1979; Ågren et al., 1989a; Gromov, 1992). The present review provides compilation of available data and their analysis to draw well-founded conclusions concerning different aspects of the ecology and social behaviour of the Mongolian gerbil.

2. Habitats, food, and activity

Mongolian gerbils are found in a variety of habitats, but prefer a typical steppe habitat with sandy and loamy soils and sparse discontinuous vegetation of grass, herbs and shrubs (Bannikov, 1954; Khamaganov, 1954; Leont'ev, 1954; Xia et al., 1982; Ågren et al., 1989a; Gromov, 2000a, 2011a). In Tuva region, however, these rodents were revealed to be not characteristic of the virgin steppe habitat. Small colonies of Mongolian gerbils were found along intermountain valleys and edges of earthen roads, in dry river beds, as well as on cattle-breeding farms and sheep corrals with plentiful weedy vegetation. Larger colonies of the species were found on cereal-growing and fallow fields (Gromov & Popov, 1979; Gromov, 1981, 2000a, 2011a).

As a rule, food is patchily distributed and unstable over time in the habitat of Mongolian gerbils, excluding cereal-growing fields (Ågren et al., 1989a;

Gromov, 2000a). During spring and summer, the gerbils usually feed on leaves and stems of various plants, including *Chenopodium* spp., *Atriplex* spp., *Artemisia* spp., *Salsola colina*, *Setaria viridis*, *Leymus chinensis* (Bannikov, 1954; Khamaganov, 1954; Leont'ev, 1954; Ågren et al., 1989a; Gromov, 2000a). In Tuva region, the sites of sheep corrals are usually covered by plantations of *Chenopodium album*; this herb is found to be a preferred food of the gerbils in summer (Gromov, 2000a). Among other preferred food plants, there are camel's-thorn, *Alhagi camelorum* (Khamaganov, 1954) and *Artemisia sieversiana* (Ågren et al., 1989a). During autumn and winter, the gerbils usually feed on stems and seeds of some herbs and grasses (for example, *Chenopodium* spp., *Atriplex* spp., *Cannabis sativa*, *Setaria viridis*), as well as on grains of some cereals (for instance, wheat, millet and oats) that they cooperatively gather during summer and autumn and store in special chambers in their burrow systems for survival during winter when food is scarce (Bannikov, 1954; Leont'ev, 1954; Ågren et al., 1989b).

Laboratory studies provided conflicting information concerning the temporal patterns of the gerbil activity. For example, Thiessen et al. (1968) and Roper (1976) reported a unimodal peak of nocturnal activity in running-wheel experiments. But other observations of the gerbils in their home cages indicated activity throughout the 24-h period (Lerwill, 1974). Ågren (1976) as well as Roper & Polioudakis (1977) observed mainly diurnal activity of the gerbils in semi-natural enclosures. Randall & Thiessen (1980) also observed the gerbils in outdoor enclosures in an area of natural habitat in Texas (USA) and revealed that the animals were primarily diurnal during the mild daytime temperatures of spring and autumn (May and October), but completely switched their activity to the night in July and restricted daytime activity to the early morning and late evening in August, thus avoiding daytime temperature extremes. The discrepancies in the cited reports of the gerbil activity from the laboratory studies and the observations under semi-natural conditions probably result from a combination of varying test and housing conditions.

Behavioural observations of the gerbils in their natural habitat in Tuva region (Gromov & Popov, 1979; Gromov, 1981, 1992, 2000a) provide evidence for primarily diurnal behaviour of these rodents with relatively short periods of underground activity and avoidance of daytime temperature extremes in the hot summer months only. This evidence contradicts the conclusion of Randall & Thiessen (1980), but their study was conducted in

Texas where the mean daytime temperature in May and July was about 40 °C, whereas it rarely exceeds 30°C during the same months in Tuva region.

In the Trans-Baikal area (southern Siberia, Russia), Mongolian gerbils were reported to be diurnal all year (Leont'ev, 1954, 1957). In the winter (December–February), the gerbils were active outside their burrows for not more than 6 hours during the daytime, and in the summer (June–August) up to 18 hours. In July, both diurnal and nocturnal activity of the gerbils was recorded. Similar behavioural patterns were observed in the animals kept in the large outdoor enclosures in Moscow region (Gromov, 1992, 2000a). Thus, the Mongolian gerbil is a species with variable, temperature-dependent but primarily diurnal activity.

3. Population density, sex-age structure and reproduction

Population density is known to show large fluctuations between years and habitats of the Mongolian gerbil (Xia et al., 1982; Orlenev, 1987; Ågren et al., 1989a; Gromov, 1992, 2000a). In the Tuva region, two main types of the Mongolian gerbil colonies have been identified, in dependence on their size and population density (Orlenev & Pereladov, 1981; Orlenev, 1987; Gromov, 1992, 2000a). The colonies of the first type were associated with cereal-growing and fallow fields of large size (tens and hundreds of hectares). In such a habitat, the population density of the gerbils was high and relatively stable, reaching 100–150 and sometimes even 220 animals/ha. The number of burrow entrances in this habitat could be as great as 1300–1500 per ha. The colonies of the second type were spatially isolated and established within relatively small areas (under 1–3 ha) near villages, on cattle-breeding farms, functioning and abandoned sheep corrals, as well as along edges of earthen roads, where soil was sufficiently loose. As a rule, such colonies were not abundant and often included only one breeding pair with their offspring, but some of them were relatively large, and the population density there reached 60–70 animals/ha. In the virgin steppe habitat, the local densities of the gerbils were lowest and averaged 5.6 animals/ha (range 2–30 animals/ha). Besides, the distribution of small colonies was found to be very uneven and dispersed in dependence on the soil and vegetation conditions. Many of these small colonies existed for only 1–3 years.

Of the 408 gerbils, captured or collected dead on the surface of fallow fields in July–August 1976 after a heavy and cold rainfall, 68% were adults (6–36 months old), 20% were subadults (2–5 months old) and 12% were juveniles (Krylova & Gromov, 1977; Krylova, 1978). The sex ratio (males:females) among adults was 2.3:1 in July and 1.5:1 in August.

According to Ågren et al. (1989a), at Xilinhot (Inner Mongolia, P.R. China), the mean density of the gerbils within the study areas with bush plantations, fallow and potato fields was 64.3 animals/ha (range 42.0–90.6). Of the 126 gerbils captured in June 1984, 27% were adults (mean body mass was 60.3 g for males and 58.9 g for females), 54% were subadults (mean body mass was 42.3 g for males and 41.9 g for females) and 19% were juveniles. The sex ratio was 2.2:1 among adults and 1.4:1 among subadults.

Thus, the reproductive proportion in the Mongolian gerbil populations was primarily male biased. However, Liu et al. (2009a) have found female-biased populations of the gerbils in north-central Inner Mongolia (China): according to these authors, sex ratios (the proportions of females) fluctuated over time, ranging from 0.52 to 0.77 and averaging 0.60.

Mongolian gerbils are known to be characterised by relatively high reproductive rates under laboratory conditions: according to Cheal (1983), the number of pups per litter ranged from 1 to 9 (average 5.1), and mean number of litters per dam per year was 9.5. So, the mean number of pups per dam per year was as much as 48.5. Contrary to the laboratory populations, reproductive intensity and output were found to be relatively low in the natural populations (Liu et al., 2009a). For example, the proportion of reproducing females was low (24%), and 80.5% of reproducing females bred only once, and 19.5% of females only bred more than once during the breeding season.

In the field studies performed in the Trans-Baikal area, Khamaganov (1954) and Leont'ev (1954) showed that the breeding season in the populations of Mongolian gerbils starts in February-March and lasts up to June. Benimetsky (1974) measured the weight of gonads of Mongolian gerbils and found significant seasonal variation consistent with the data published by Khamaganov (1954) and Leont'ev (1954). For example, the relative weight of testes in Mongolian gerbil males averaged 177 $\pm$ 39 mg/100 in October, 1082 $\pm$ 23 mg/100 in January, 1521 $\pm$ 59 mg/100 in May and 1404 $\pm$ 73 mg/100 in July. The weight of ovaries in Mongolian gerbil females was also found to be variable in accordance with seasonality in reproduction of this species.

By means of population studies of *M. unguiculatus* performed in Inner Mongolia, P.R. China (Liu et al., 2007, 2009a, 2013), seasonal changes in the reproductive parameters such as the cohort-specific age of maturity, the proportion of sexually mature animals, the proportion of reproducing animals, and the ratio of recruits to breeding females were revealed. Specifically, monthly proportions of reproductively active males were found to be higher during March–August and then declined towards autumn. Female reproductive performance showed a similar seasonal pattern as did that of males: the reproductively active females were observed every month from March to August, but almost no reproductively active females were captured during September–October. Peak recruitment was recorded in April, March and June. Thus, the reproduction in *M. unguiculatus* is terminated in autumn; winter is a season of preparation to the reproduction, and spring-summer is the breeding period.

During the breeding season, adult females produce up to three litters. According to Thiessen (1968), litter size varies tremendously, from 1 to 12, with an average of 4.8. In the wild, the number of embryos per pregnant female averaged 6.4–7.5 in different populations (Khamaganov, 1954; Leont'ev, 1954). Young females born in the spring mature quickly and may start breeding in the same year (in June-August), producing usually one litter. The observed minimum body mass at maturity was 33.0 g for males and 34.0 g for females; the minimum age of maturity for each sex was about two months (Liu et al., 2017).

Thus, seasonal breeding is typical of Mongolian gerbils in the wild, where their reproduction and recruitment occur primarily from March to August, with a breeding lull in autumn; however, a minority of gerbils was reported to breed from December to February (Liu et al., 2017). In their long-term study, Liu et al. (2017) collected data on the reproductive parameters of Mongolian gerbils and did not find any sex-specific differences in their observed longevity, age at maturity, and observed reproductive lifespan.

4. Group size and composition

According to Leont'ev (1954, 1962), the number of gerbils trapped in a burrow unit varied from 2 to 28 individuals. As a rule, all the animals caught in a burrow unit belonged to a family group consisting of adults and their offspring. The composition of five family groups trapped in July-August 1948 was accurately identified (Leont'ev, 1954): two groups were composed of a pair of adults with several subadults (up to four individuals) and juveniles (up to four individuals); two other groups had lost adult males and included two and three adult females and several subadult and young individuals; one group included a subadult male and two subadult females only. It was concluded that Mongolian gerbils live in extended family groups during the breeding season.

When studying the gerbils in Tuva region (Gromov & Popov, 1979; Gromov, 1981, 1992, 2000a), animals observed using the same burrow system were considered as a social group. Further analysis of their behavioural interactions has supported the conclusion that Mongolian gerbils live in extended family groups. As a rule, such groups included one adult male, one or two, less frequently, three adult females, and their male and female offspring (subadults and juveniles, Table 1). The number of young individuals in a group depends on the number of reproducing females who in spring and summer bring in as many as three litters, each including four to seven young animals. The number of animals in large family groups can amount to 28. Large reproductive individuals (adults) were considered founders of the family group. Along with complete family groups (adult parents with their offspring), there were several incomplete family groups lacking one or both members of a potential founding pair.

Ågren et al. (1989a) published data on the composition of nine groups of the gerbils. The number of animals in these groups ranged from two to about 17 including juveniles. Four of the nine groups were composed of one large reproductive individual of each sex, plus offspring from up to three litters. In

Table 1.
Composition of 27 family groups of Mongolian gerbils in their natural habitat in Tuva region (after Gromov, 1992).

Number of groups	Number of adult males	Number of adult females	Number of litters	Number of young individuals
11	1	1	2-3	up to 10
7	1	2	2-3	up to 11
2	1	3	3-4	up to 28
2	–	1	1-2	5–6
2	1	–	2	6–7
1	2	–	2	11
1	–	2	2	10
1	–	–	2	6

one case, a male-female pair with no offspring was found. There were also four incomplete family groups lacking one or both adults.

Liu et al. (2009a) captured Mongolian gerbils in north-central Inner Mongolia (China) from late April to late October 2006 within a trapping plot situated on a 9-ha grassland. In total, 164 social groups and 46 solitary individuals at 30 burrow systems were identified on the plot. Social groups consisted of 2–18 individuals and were divided into two categories: so-called communal groups and male-female pairs. A communal group consisted of either a same-sex pair or more than two adult animals. The authors have distinguished 142 communal groups (68%) and 22 male-female pairs (10%). The communal groups consisted of 0–4 breeding males, 0–3 breeding females and 0–11 juveniles, and averaged 6.7 individuals per burrow system. Among solitary individuals, there were 27 females and 19 males. Thus, the category of communal groups included both complete and incomplete family groups. Unfortunately, there was no indication how to distinguish between them to calculate their numbers and proportions. It should be noted that the average number of individuals in so-called communal groups was relatively low, while the number of solitary individuals was relatively high in the gerbils' colony. Such a situation seems to be associated with a relatively low population density within the study site. Population sizes were found to increase initially from the spring to the summer and then declined toward the autumn and the winter. Conservative estimates (population size divided by the area of the trapping plot) of the gerbil densities ranged from 3.5–18.8 animals/ha, respectively (Liu et al., 2009a).

Investigations in Tuva region (Gromov & Popov, 1979; Gromov, 1981, 1992, 2000a, 2011a) showed that monogamous family groups (i.e., adult pairs with their offspring) and polygynous family groups (i.e., an adult male with two or three adult females and their offspring) occurred both in the large gerbil colonies on fallow fields and in the small gerbil colonies on the sites of sheep corrals, as well as in the virgin steppe habitat. Specifically, of the 14 family groups observed in the large gerbil colonies, nine groups were monogamous, and five groups were polygynous; of the nine family groups observed in the small gerbil colonies, six groups were monogamous, and three groups were polygynous. Thus, the monogamous family groups were found to occur twice as often as the polygynous family groups in the Mongolian gerbil populations, irrespective of their density. This conclusion, of course, is based on comparison of small data samples, so further investigations are needed to obtain more valid results.

Summarising these studies, one can conclude that the most common social units in populations of the Mongolian gerbil are extended family groups with one adult male and one or two adult females and their offspring. Occurrence of incomplete family groups may be associated with the death of some adults, but there are other reasons for the absence of the adults in the family groups as well (see below).

5. Variation in group composition and offspring dispersal

The composition of social units in populations of the Mongolian gerbil is variable: survival, reproduction, emigration, and immigration — all these processes affect the structure of social units. Inter-specific variation in family group composition was found to occur due not only to different numbers of adults and young individuals, but also due to other factors resulting in dispersal of some adult individuals from their family groups (Gromov, 1992).

Specifically, in the incomplete family group with two adult males, the latter shared a common territory for a long period of time and interacted peacefully, though one of the males had a higher social rank. These males seemed to be close relatives (father and his son or two brothers). In six weeks of observations, some changes in the behaviour of the subordinate male were noticed. This male had chosen a small area located not so far from the territory of his native group, cleaned up an old, abandoned burrow system, and then started to protect this new home range from all conspecifics except for the members of his native group. The latter, however, did not visit the range often, and, when entering, displayed the behaviour typical of visiting a strange territory. Soon, a subadult female appeared in the subordinate male's home range, and the animals formed a new breeding pair. It should be noted that the male did not forget his former group and occasionally visited the old territory. The encounters between the male and the members of the former family group remained quite peaceful up to the end of observations in late August.

In addition to this case, it was revealed that some other adult individuals being the group founders also left their family groups to join other groups. For instance, in a family group with two adult females and one adult male, the latter once moved to a neighbouring incomplete family group where an adult male had been lacking. The ‘transit operation’ was rather ‘painless’ for both family groups, though agonistic encounters of the male with the young animals from the second group were observed during several days after the transition.

Competition for reproductive opportunities among female group-mates was also found to take place, and some adult females left their natal ranges for reproductive opportunities. The same reason seems to result in dispersal of some adult males. Several cases of such changes in the composition of family groups were revealed in the gerbil colonies on partially ploughed fallow fields with a considerable reserve of vacant space (Orlenev, 1987; Gromov, 1992, 2000a).

In late summer, the composition of many family groups may be also changed as a result of dispersal of subadults born in the spring. In the Trans-Baikal area, dispersal of most young gerbils born in March–April occurred in June–August (Leont’ev, 1954). Young gerbils born in late summer or early autumn did not disperse and remained prepubertal until the following spring; during the winter, they stayed in the parental burrow and dispersed next spring. Liu et al. (2017) reported that there was evidence of male-bias dispersal for the cohort of overwintering gerbils, while the gerbils dispersed in the year of their birth were not sexually biased in this respect. The majority of dispersal occurred in spring and summer. Thus, the Mongolian gerbil could be regarded as a species with restricted offspring dispersal.

Similar data were obtained in the studies of the gerbils in Tuva region where dispersal of the young born in the spring started in the late summer (Gromov, 1992, 2000a). Specifically, observations in August 1977 showed that there were some family groups where subadult individuals exhibited a new pattern of behaviour. They were found to be regularly leaving the territory of their family groups, exploring the adjacent areas, inspecting the abandoned burrows and cleaning them, digging new ones aside from the territory of their own family group.

In one of the large family groups with three breeding females and not less than four litters, there was an elder litter consisting of only females born in the spring. This large family group occupied the area of an abandoned sheep corral located in a small intermountain valley. In late August, the elder litter of females had left the territory of the family group and settled in one of abandoned burrow systems of Daurian pikas, *Ochotona daurica* (these animals were found to compete with the gerbils for the vacant space in the virgin steppe habitat). This burrow system was located some 80 m off the gerbils' territory. For several days, the subadult females lived as a separate group. Then, after the young Daurian pikas started expanding their colony, and frequent aggressive encounters of the gerbils with pikas were observed, the 'migrants' had to return to their native territory where they remained till the end of the study in early September. It should be noted that this family group occupied the isolated site of the sheep corral, and the nearest gerbil colony was at a distance of 2 km. The virgin steppe habitat surrounding the sheep corral was characterised by difficult-to-excavate hard soils, and the only place with sufficiently loose soil was located within the sheep corral. In other words, there were no territory vacancies for the dispersing gerbils except for the abandoned burrow systems of Daurian pikas. Therefore, the group of subadult females had no chance to settle into a new territory occupied by young Daurian pikas and had to come back to the sheep corral.

In another case, a subadult male moved in early August to a vacant burrow system twenty meters off his group's territory and began to mark and defend the range he had just occupied. In a few days, a subadult female from the neighbouring family group joined the male, and these two animals formed a new breeding pair.

In large colonies of the gerbils on the fallow fields, several litters of subadult individuals were also found to have left their family groups in the late summer and successfully occupied new vacant territories. Their further destiny has remained unknown because the study was terminated in early September (Gromov, 1992).

It should be emphasised that dispersal of subadult individuals was not caused by aggression of the adults, and in all cases the interactions between members of the family groups remained peaceful. Thus, dispersal of entire groups of subadult individuals from their native family groups as well as transition of some adults from their family groups to other ones may also result in formation of incomplete family groups at the end of the breeding season.

In a study performed in north-central Inner Mongolia, China (Wang et al., 2017), 24 dispersing male gerbils out of 159 captured males and 18 dispersing female gerbils out of 168 captured females were identified during the entire study period (from 28 April to 21 October in 2006). Of the 24 male dispersers, there were three juveniles, nine subadults, and 12 adults. The captured female dispersers included four juveniles, five subadults, and nine adults. One juvenile, two subadult, and four adult females reproduced at their dispersal destinations. The four dispersing adult females also bred before their dispersal. Average dispersal distances of male and female gerbils were 82 ± 34 m and 67 ± 30 m, respectively. The authors supposed that it is the territoriality of the gerbils that might restrict their dispersal to short distances.

In general, live trapping data as well as visual observations indicate equal dispersal propensities of male and female gerbils. It should be noted that the offspring dispersal in populations of the Mongolian gerbil involves not only single individuals, but entire groups of littermates as well. Such groups do not break up for a while, perhaps successfully survive the winter, and further dispersal occurs next spring.

6. Use of space

Direct observations of Mongolian gerbils in their natural habitat in Tuva region (Gromov & Popov, 1979; Gromov, 1981, 1992, 2000a, 2011a; Orlenev, 1987) provide evidence that a typical feature of their space use system is territoriality. Each family group occupies a home range of a more or less fixed size that is exclusive of the ranges of adjacent family groups. All adult and subadult members of each family group take part in scent marking and defending their territory against any conspecific intruders.

In Tuva region, the size of the family-group territories ranged from about 100 to 1600 m^2 (on average about 750 m^2) during the breeding season, and the minimum protected area occupied by a pair of adult individuals was about 100 m^2. The protected territories of adult females in the family groups ranged from about 100 to 1000 m^2 (on average about 520 m^2). In the Xilinhot area (Ågren et al., 1989a), the size of the gerbils territories ranged from about 325 to 1550 m^2. According to Wang et al. (2011), the average monthly home range sizes of social groups of Mongolian gerbils were about 310 m^2 during the breeding season (from April to August) and 265 m^2 during the non-breeding period (from September to October). It is suggested that the size of family-group territories in Mongolian gerbils is not limited by food in a typical steppe habitat where green plants are abundant and renewable during the growing season (Wang et al., 2011).

Ågren et al. (1989a) have found an essential correlation between total territory size and family group size. According to Wang et al. (2011), a positive correlation was also revealed between home range size and the number of males in the family group during the breeding season, whereas during the non-breeding period, home range size was correlated with the number of resident females. According to Ågren et al. (1989a), territory size was significantly correlated with the body mass of the largest male of each family group. However, Wang et al. (2011) did not find any correlation between home range size and the body mass of the largest males or females in social groups.

Studies performed in Tuva region (Gromov, 1992, 2000a) showed that in most family groups with a pair of founders, male and female nested together during both the breeding and non-breeding seasons and maintained a pair bond permanently unless one mate died or disappeared from the study site. In most family groups with two or three reproducing females, each of them was revealed to occupy an exclusive range within the family-group territory and defended it against other breeding female(s) of the group. There was the only incomplete family group with two adult females (without an adult male) as well as a few complete family groups with two adult females where the females used a common territory, but in this case only one of the females was in reproductive conditions (Orlenev, 1987; Gromov, 1992). The females using a common territory seem to be close relatives (mother and her daughter or two sisters).

In family groups with two or three mutually exclusive females, the male home range entirely overlapped the ranges of the females, and its size was, as a rule, larger than the sum of the females' ranges. Such polygynous males were found to spend a significantly greater portion of time within the ranges of receptive, pregnant or lactating females of their family groups (Gromov, 1992).

At high densities (e.g., on some agricultural and fallow fields), little overlap between both neighbouring family-group territories and exclusive ranges of breeding females was found, with no empty space left between them. At low densities (e.g., on partially ploughed fallow fields with considerable reserves of vacant space), many neighbouring family-group territories were found to be non-overlapping, sometimes with a large empty space left between them, and tended to be arranged randomly on the study plots (Gromov, 1992, 2000a). According to Wang et al. (2011), home range overlap averaged 5.7% and ranged from 0.04 to 17.2%. Mongolian gerbils often visited neighbouring burrow systems during the breeding season. However, during the non-breeding period, home ranges of several social groups were spatially separated from each other.

Aggressive interactions between members of the neighbouring family groups enabled the determination of exact location of the boundaries between the neighbouring territories. Usually, there was a narrow overlap zone not exceeding 2–3 m in width where an observer could see the most frequent boundary encounters and agonistic conflicts, mainly two-way chases, between the owners of adjacent territories. The locations of two-way chases also indicated exact points of a reversed locus-dependent dominance. The boundary encounters were observed in Mongolian gerbils during the breeding season (late spring–mid summer) as well as in late summer and early autumn (Gromov & Popov, 1979; Gromov, 1981; 2000a). Thus, territoriality based on a locus-dependent dominance is typical of Mongolian gerbils during both the breeding and non-breeding seasons. Ågren et al. (1989a, b) came to the same conclusion and supposed that the territory could be defended to protect food resources during the reproductive season as well as food stores during autumn, winter and early spring.

Wang et al. (2011) reported that the home ranges of social groups of Mongolian gerbils overlapped more during the breeding season than during the non-breeding period. This conclusion however is rather doubtful, because it is based on capture-recapture method only, and the size of a composite home range was calculated by combining the capture locations of all individuals of a social group (Wang et al., 2011). But during the breeding season, both adult male and female Mongolian gerbils may visit adjacent territories very often, and many of their capture locations actually indicate an increased social activity outside of their own territories rather than the increased overlap of neighbouring home ranges (Gromov, 1992, 2000a).

Observations of the gerbils under semi-natural conditions (in two outdoor enclosures of 400 m^2) showed that the area of the enclosures allowed two exclusive family groups occupying defended territories of nearly equal size (about 200 m^2) to coexist during the entire observation period (May–September). Comparison of the Mongolian gerbils in their natural habitat and under semi-natural conditions revealed no essential difference in the space use system (Table 2). The family groups of the gerbils observed in the large outdoor enclosures exhibited little overlap of their territories (judging from the TOC values), a high level of a relative exclusiveness of use of space

Table 2.
Mean values (± SE) of the territory overlap coefficient (TOC) and the relative Exclusiveness of use of space (E, Alho, 1979) in adult males and females of the Mongolian gerbil in their natural habitat (I) and in the outdoor enclosures (II).

Index	Males			Females		
	I	II	p^*	I	II	p^*
TOC	0.43 ± 0.12	0.30 ± 0.05	0.277	0.12 ± 0.04	0.26 ± 0.07	0.088
E	0.87 ± 0.05	0.92 ± 0.02	0.277	0.98 ± 0.01	0.95 ± 0.01	0.070

Both the TOC and *E* values are calculated in dyadic comparisons (after Gromov, 1996).
p^*, Mann-Witney *U*-test.

(judging from the *E* values; Alho, 1979), and a locus-dependent dominance displayed by adult and young individuals (Gromov, 1992, 2000a).

Visual observations in the wild revealed a sex-related pattern of territory use (Ågren et al., 1989a; Gromov, 1992, 2000a). Within each family-group territory, the adult male visited the largest proportion. When both adult parents were present in the family group, the females visited significantly less (about half) of the area than males. In the incomplete family groups (without adult male), however, the adult females visited the largest proportion of the family-group territory.

In addition to the territorial family groups, there were some non-sedentary adult and subadult individuals who widely migrated within one or several gerbil colonies. The presence of such wanderers seems to be associated with specific demographic processes in the gerbil populations related to the disintegration of some family groups and the above mentioned dispersal of the animals (Gromov & Popov, 1979; Orlenev, 1987; Gromov, 1992, 2000a). The wanderers were usually engaged in looking for their sexual partners. When successful, they formed new breeding pairs, occupying some vacant territories. Such breeding pairs were observed in early summer on the sites of the sheep corrals where the gerbil colonies changed their composition from year to year. In 5 of 11 cases recorded by the author (Gromov, 1992, 2000a), the future family-group territory was established by adult females, in three cases — by adult males, and in the three others — by male-female pairs.

For example, in early June 1977, observations on the site of a sheep corral of about 0.3 ha have shown that there was the only resident pair — male M3 and female F4 (family I). On 16 June, three more adult gerbils appeared in the study site: two males (M5 and M6) and one female (F15). M6 and F15 soon formed a breeding pair (family II) and occupied a part of the vacant space. On June 21, a third adult female (F19) appeared in the study site and occupied an abandoned burrow near the territory of family I. M3 displayed active interest towards F19 who joined family I very soon. Both females (F4 and F19) occupied nearly exclusive ranges in the territory of family I up to the end of the observation period (in late August).

By the end of June, when two more females (F21 and F22) appeared in the site of the sheep corral, the colony composition was as follows: family I (M3 with two exclusive females, F4 and F19); family II (M6 and F15); M5 as well as F21 and F22 had no territory of their own, and other gerbils attacked and chased them when they entered the territories of family I and family II. M5 regularly visited the territory of family I and, when M3 was absent, tried to interact with F4. At first, the reaction of F4 toward M5 was aggressive, but later both animals were seen to interact quite peacefully. Peaceful interactions between M3 and F22 were also observed. By the end of June, F21 had disappeared from the study site. By mid-July, F22 settled in a vacant burrow system and established its own defended range. M5 joined F22, and thus family III was formed in the site of the sheep corral.

This example presents a specific situation in nature, namely the simultaneous colonisation of a new area by the dispersal of single or several individuals who settled in the area before the arrival of others. Ågren (1984) observed similar situation in Mongolian gerbils under semi-natural conditions and concluded that breeding pairs of this species form due to mate choice by females, and the possession of a territory is an important criterion of male quality. Therefore, this resource should be provided by a male gerbil before the females make their choice. Observations in the wild, however, showed that the final male-female attachment can be initiated by solitary individuals of each sex. Moreover, some females can be joined to existing breeding pairs, thus forming polygynous family groups (an adult male with two or even three breeding females).

Although a sheep corral represents an area with relatively limited resources (in terms of preferred food vegetation and soft soil for burrowing), some late-comers have no great difficulties in becoming established in this restricted area, on condition, of course, of the availability of sufficient vacant space. Our studies in Tuva region (Gromov & Popov, 1979; Gromov, 1992, 2000a; Orlenev, 1987) showed that the sites of sheep corrals (not exceeding 0.3 ha) had sufficient space to be occupied by not more than three family groups of Mongolian gerbils.

7. Mating system and pair bonds

Mating systems are generally defined by whether multiple mating (mating with more than one individual of opposite sex) occurs in males, females or both. Descriptions of monogamy and polygyny, for instance, assume that females mate with a single male.

Although the literature reports a monogamous mating system in Mongolian gerbils (Marston & Chang, 1965; French, 1994; Clark & Galef, 2001; Scheibler et al., 2004), it seems to be not strictly true. Under laboratory conditions, male gerbils were reported to live peacefully with two or three females, mating with each (Cheal, 1983). Such a situation, however, very rarely occurs in the wild, judging from data based on the total trapping of the gerbils in their burrows (Leont'ev, 1954, 1962) and behavioural observations of the animals in their natural habitat (Gromov & Popov, 1979; Gromov, 1981, 1992, 2000a; Ågren et al., 1989a). In family groups with one adult male and two adult females sharing a common home range, only one of the females was found to be in reproductive conditions, and the male mated with this female only. The same reproductive skew occurred in family groups with a breeding pair and their subadult male-female offspring. This reproductive skew seems to be a result of social suppression of reproduction. However, if two or three females occupied exclusive ranges within the family-group territory, all of the females were in reproductive conditions, and the male copulated with each of them.

Accordingly, although most family groups in natural populations of Mongolian gerbils consist of a breeding pair and their offspring, the mating system of the species can not be defined as obligatory monogamous, because an essential portion of the family groups (up to 1/3) are polygynous. Moreover, mating is not entirely monogamous even in male-female pairs, because oestrus females were seen to visit adjacent territories to mate with neighbouring males or strangers (Ågren et al., 1989a; Gromov, 1992, 2000a). The same behaviour was recorded in male Mongolian gerbils entering the territories of neighbouring family groups to mate with receptive females (Gromov, 1992, 2000a). Similar situations, when a female copulated with different males in two different territories, in her own and in a neighbouring one, were also observed under semi-natural conditions (Ågren, 1976; Gromov, 1992). Bearing in mind such features of reproductive behaviour as well as male-biased sexual size dimorphism, Wang (2017) considered the Mongolian gerbil a social rodent of promiscuous mating. Thus, there are different points of view on the mating system of this species.

Nevertheless, Mongolian gerbils do display distinct characteristics of monogamy such as shared home ranges and nests even beyond the breeding season, selective aggression against strangers but not toward the partner, long-term pair bonds, shared parental care, and delayed sexual maturation. However, these features of reproductive biology of *M. unguiculatus* are combined with the formation of numerous polygynous social units coexisting with monogamous pairs in the same colonies, as well as with extra-pair mating displayed by both sexes. Thus, the Mongolian gerbil has a variable mating system that could be defined as social (behavioural) monogamy combined with facultative polygyny and promiscuity.

Social monogamy means that animals form persistent pair bonds, which are manifested by a preference for social contact with the mating partner even when other conspecifics are available; the partners maintain a close association after fertilization, and care for the young, but mating may not be exclusive (Barlow, 1988; Reichard, 2003). Long-term field studies revealed that males and females of the Mongolian gerbil establish, as a rule, persistent pair bonds maintained for months (Gromov & Popov, 1979; Gromov, 1992, 2000a). Besides, both sexes display parental behaviour (Elwood, 1975, 1979, 1983; French, 1994; Weinandy & Gatterman, 1999; Clark & Galef, 2000; Gromov, 2009). Specifically, laboratory studies have shown that in pairs rearing young, females and males spent similar amounts of time in the nest, and males displayed such care-giving activities as retrieving, huddling and grooming (Gromov, 2009, 2011b). In the wild, males were seen to bring nesting material to the burrows occupied by pregnant and lactating females. The breeding females in the polygynous family groups had a male's part-time help (Gromov, 2000a). Therefore, social monogamy seems to be characteristic of the Mongolian gerbil reproductive strategy, which however does not exclude facultative polygyny and promiscuity. In established pairs, a female may preferentially associate with the male to whom she is pair-bonded, but engage in extra-pair copulations with another male. It should be emphasised that mating ranging from monogamy to polygyny and promiscuity is observed in individuals within the same colony of the gerbils. It means that a variable mating system of the Mongolian gerbil is not a result of variation in population density or spatial distribution of females. Moreover, the large proportion of polygynous family groups is found in the large male-biased gerbil colonies with a very high population density (Krylova & Gromov, 1977; Orlenev, 1987; Gromov, 1992, 2000a).

8. Social behaviour and social organisation

During the observations in the wild and under semi-natural conditions, the following behavioural patterns were recorded.

8.1. Peaceful interactions

Nasal sniff: Two animals face each other and briefly touch and sniff noses.

Ano-genital sniff: An animal approaches another, usually from behind, and actively sniffs its ano-genital region.

Olfactory investigation: An animal sniffs any area of another animal's body, except nose and the ano-genital region.

Following: An animal moves behind the other animal maintaining close proximity with the partner.

Climbing: An animal puts its forepaw on the back of a second animal and attempts to climb up, or may actually do so.

Allogrooming: Episodes of licking, scratching, and/or rubbing (grooming) between conspecifics.

Soliciting of mutual grooming: An animal solicits mutual grooming from a conspecific; two situations have been recorded: (1) an animal (groomee) presents its head under that of the other animal (groomer); (2) an animal (groomee) rolls on to its side and presents the underside of the head and neck to the other animal.

Sitting together: Episodes when two or several animals were observed sitting together or huddling in a close tactile contact.

8.2. Agonistic interactions

Side-way posture: One animal turns sideways to a conspecific; two animals stand parallel to each other in a 'tense posture'.

Boxing: Two animals face each other standing in an upright posture on their hind legs with their forepaws in contact and push each other by means of rapid movements of the forepaws.

Wrestling: One animal (dominant) lies over another conspecific (subordinate) in a supine position without biting; in this way, a dominant animal sometimes commits forced grooming of the subordinate animal.

8.3. *Overt aggressive interactions*

Attack: A rapid and sudden approach movement towards other animal usually resulting in fleeing of the opponent.

Chase: One animal rushes after another by more than one body length; in the context of boundary encounters, the attacked animal flees by running while the aggressor follows closely behind; chasing could be one-way (from location A to location B), two-way, and/or roles may change, that is animal 1 chases animal 2 from A to B, whereupon roles shift and 2 chases 1 back to A again.

Fight: A comprehensive pattern in which two animals grip each other's flanks in ventro-ventro contact, along with biting, kicking, rolling over, and/or leaping into the air.

8.4. *Avoidance*

Avoid: An animal turns and moves or runs away from a conspecific before physical contact is made.

8.5. *Social organization*

Comparison of the social behaviour of Mongolian gerbils in the wild (16 family groups, 128 individuals in total) and under semi-natural conditions (7 family groups, 73 individuals in total) revealed no significant difference in terms of the relative frequency (proportion) of inter- and intra-group interactions (Tables 3 and 4) as well as the asymmetry of dyadic encounters (Gromov, 1981, 1992, 2000a).

The data presented in Table 3 show that peaceful and agonistic interactions are not typical of Mongolian gerbils when encountering non-family members. Not so numerous peaceful interactions were recorded chiefly in heterosexual dyads. Most encounters (up to 95%) were overt aggressive and concerned with territorial defence (usually chases representing 2/3 of the total aggressive interactions). Such behaviour indicates a locus-dependent dominance characterising the inter-group relationships.

According to Ågren et al. (1989a), the adult males were the most active in chasing associated with territorial defence. However, our observations (Gromov & Popov, 1979; Gromov, 1992, 2000a, b) showed that females, both adult and subadult, did not yield to males in this activity. Moreover, females chased same-sex individuals more often than did males. It should be noted that aggressive interactions between the adult females from neighbouring

Table 3.
Number (N) and proportion (%) of interactions of Mongolian gerbils with non-family members in the wild (Tuva region) and the outdoor enclosures of 400 m^2.

Interactions	Male				Female			
	Interactions, addressed to				Interactions, addressed to			
	Males		Females		Males		Females	
	N	%	N	%	N	%	N	%
In the wild								
Peaceful	9	13.8	20	21.5	12	14.6	1	2.2
Agonistic	0	0	3	3.2	0	0	1	2.2
Overt aggressive	49	75.4	68	73.1	63	76.9	42	93.4
Avoidance	7	10.8	2	2.2	7	8.5	1	2.2
Total	65	100	93	100	82	100	45	100
In the enclosures								
Peaceful	15	2.0	91	19.4	80	21.5	5	1.4
Agonistic	2	0.3	32	6.8	2	0.5	4	1.1
Overt aggressive	686	91.1	333	70.9	255	68.4	350	95.4
Avoidance	50	6.6	14	3.0	36	9.7	8	2.2
Total	753	100	470	100	373	100	367	100

Adult and subadult individuals only are included in the dataset (after Gromov, 2000b).

family groups were not more frequent and intense than between the breeding females occupying exclusive ranges within a family-group territory.

Thus, both adults and subadults in each family group, and even younger individuals, participate in defence of their territory displaying a locus-dependent dominance when encountering neighbours or strangers, except for some interactions between opposite-sex conspecifics during the breeding season. The asymmetry of dyadic interactions between neighbours defending their own territories is found to be low thus indicating the equipotential interrelations typical of a locus-dependent dominance (Gromov, 1992, 2000a). The data presented in Table 3 also demonstrate a lack of significant differences in the behaviour of the gerbils (in terms of the proportions of relevant interactions) in the wild and under the semi-natural conditions of large open enclosures.

The data presented in Table 4 show that, contrary to interactions between groups, social contacts within family groups are characterised by primarily peaceful behavioural patterns while aggressive interactions were rarely observed (except for encounters between breeding females occupy-

Table 4.
Number (N) and proportion (%) of interactions between members of family groups of Mongolian gerbils in the wild (Tuva region) and the outdoor enclosures of 400 m^2.

Interactions	Male				Female			
	Interactions, addressed to				Interactions, addressed to			
	Males		Females		Males		Females	
	N	%	*N*	%	*N*	%	*N*	%
In the wild								
Peaceful	373	81.4	210	78.0	179	78.9	156	80.0
Agonistic	82	17.9	57	21.2	47	20.7	37	19.0
Overt aggressive	0	0	1	0.4	0	0	1	0.5
Avoidance	3	0.7	1	0.4	1	0.4	1	0.5
Total	458	100	269	100	227	100	195	100
In the enclosures								
Peaceful	1066	80.0	1551	76.7	1804	81.4	1730	80.7
Agonistic	254	19.0	441	21.8	383	17.3	358	16.7
Overt aggressive	7	0.5	18	0.9	6	0.3	38	1.8
Avoidance	7	0.5	12	0.6	23	1.0	16	0.8
Total	1334	100	2022	100	2216	100	2142	100

Adult and subadult individuals only are included in the dataset (after Gromov, 2000b).

ing defended ranges within the family territory). Another typical feature of intra-group relationships is a relatively high rate of agonistic behaviour maintaining a dominant-subordinate hierarchy.

Mostly peaceful interactions are especially typical of male-female pairs and their offspring, as well as groups of subadult and young individuals lacking their parents. In such family groups, both complete and incomplete, social conflicts were observed very rarely: the portion of overt aggressive interactions averaged about 1%, and the portion of agonistic interactions averaged about 11.5%. It should be noted that mostly peaceful interactions were observed in the only incomplete family group with two adult males as well.

Long-lasting stable societies of related individuals, like family groups of the Mongolian gerbil, allow for the development of complex social systems characterised by dominant-subordinate hierarchies. Such a hierarchy has been reported in family groups of Mongolian gerbils kept in 1 m^2 enclosures: the analysis of inter-male behaviour revealed that, with few exceptions, the adult male (the father) received more submissive acts, investigative acts and approaches and less aggressive acts; directed more aggressive acts, investigative acts and approaches and less submissive acts than any other male within the group (Payman & Swanson, 1981). These authors described the father as the 'dominant' male. It should be noted however that such a dominance hierarchy usually develops in stressful conditions, especially in captivity. In the wild, hierarchies are usually tenuous or absent.

Behavioural observations in the natural habitat of the Mongolian gerbil (Gromov & Popov, 1979; Gromov, 1981, 1992, 2000a) show that social hierarchy in family groups of this species is not based on overt aggressive interactions and may be defined as a subordination hierarchy. The hierarchy order is primarily determined by the age-related factor: a pair of adults are the individuals of highest rank (but the male in all cases had a higher rank than the female); subadults are the individuals of a higher rank than younger members of the family group; besides, individuals of higher and lower rank may be distinguished among the littermates. Another important feature is that the hierarchy appears to be maintained chiefly by subordinates' behaviour patterns. A picture of family group social organization could be built up by asking the basic question 'who did what to whom how often'. High-ranking individuals (the founder pair) initiate chiefly investigation (usually nasal and ano-genital sniffing) or agonistic interactions (usually side-way postures, wrestling or forced grooming) directed to other members of the family group when they approach the parents. Low-ranking (subordinate) individuals are mostly initiators of following, climbing on the back of the partner, and the soliciting of mutual grooming. These behaviours are typical of juveniles, and thus could be called infantile or affiliative (in terms of social hierarchy).

An example of such relationships among members of the family group is shown in figure 1. This family group consisted of six individuals: adult male M30, subadult male M43, young male M65, and young females F55, F62, and F64. In this group, all affiliative behaviours such as following and climbing on the back of the partner were directed to M30, M43, and F55. The latter directed the affiliative behaviours to M30 and M43 only (Figure 1A). Agonistic encounters were recorded in each dyad (Figure 1B), but most of them were initiated by subadult male M43; young female F55 also initiated many agonistic interactions while young female F64 rarely exhibited agonistic behaviours directed to other members of the family group. Judging from the summarised indexes of asymmetry of the interactions (the SIA, Gromov,

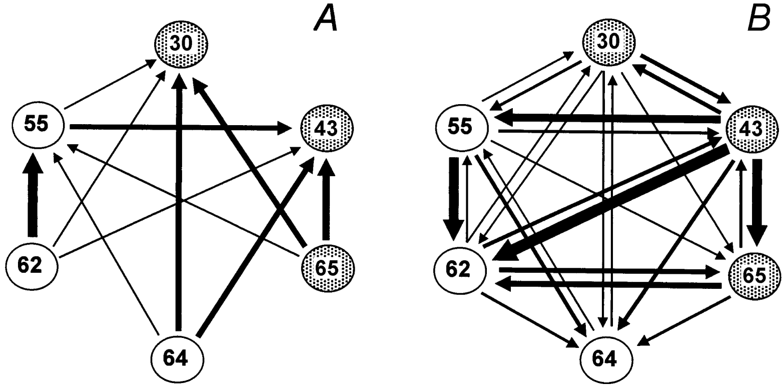

Figure 1. Occurrence and direction of peaceful (A) and agonistic (B) interactions in a family group of Mongolian gerbils. Males: 30, 43, 65; females: 55, 62, 64. Thickness of the arrows is proportional to the number of initiated acts in each dyad.

2000a), adult male M30 was 'dominant' (i.e., the individual with highest social rank), subadult male M43 was 'subdominant', and young female M55 was an individual of the third rank. The SIA values calculated for M65 and F62 were very similar, so these animals divided the fourth and fifth ranks. As for F64, this young female had the lowest rank in the group. Figure 1 demonstrates that no single behaviour pattern could be used as a rank criterion.

Social hierarchy in family groups of the Mongolian gerbil, however, is not associated with a division of labour: all group members participate in different cooperative activities (digging and cleaning underground tunnels, defence and scent marking of the territory, food hoarding, and care of the young). However, the frequency of scent territory marking is found to be correlated with social hierarchy (see below). Besides, the presence of high-ranking individuals (the founder pair) is the main factor resulting in delay of sexual maturation and suppression of breeding among low-ranking members of the family group. Specifically, in complete family groups, only one female was clearly in reproductive condition, although at least one of the subadult females in each group had reached a higher degree of maturation than her littermates. The adult male in extended family groups suppresses the reproduction of subordinates of the same sex. The young that remain in the natal area forgo their own reproduction until dispersal.

As Mongolian gerbils live in highly seasonal habitats and display seasonal fluctuations in some life-history traits associated with reproduction, dispersal, group composition and some other traits, it was suggested that the gerbils modify their social relationships at different life-history stages (Deng et al., 2017a). Some authors distinguish two distinct life-history stages in populations of the Mongolian gerbil: the breeding season (from March to August) and the food-hoarding season (September–October) (see, for example, Deng et al., 2017a, b). Deng et al. (2017a) performed a social network analysis based on the data collected due to a capture-recapture method to examine if there are seasonal changes in social associations of the Mongolian gerbil. The inter-group associations of the gerbils were found to increase during the breeding season and significantly decrease during the food-hoarding season. This finding was reported to correspond with results of the previous study performed by Wang et al. (2011). These authors revealed overlapped home ranges of Mongolian gerbils during the breeding season and enhanced territoriality during the food-hoarding season. Wang et al. (2011) suggested that the home range overlap facilitates reproductive associations between inter-group individuals, whereas enhanced territoriality associated with defence of food stores results in increased within-group associations during the food-hoarding season that may contribute to winter survival of entire family groups. However, as the investigations were based on capture-recapture data, these results provide limited insight into the space use system and social organization of the Mongolian gerbil. In particular, conclusions concerning overlapped home ranges of the gerbils during the breeding season (Wang et al., 2011), as well as the fact that female gerbils, compared to males, have a relatively higher influence over other individuals during the food-hoarding period (Deng et al., 2017a) raise some doubts.

9. Scent marking

Due to numerous laboratory studies, it is well known that Mongolian gerbils have a ventral sebaceous gland and use its secretion for scent marking (Lindzey et al., 1968; Thiessen et al., 1969; Whitsett & Thiessen, 1972; Owen & Thiessen, 1973). In adult males, this gland looks like a fusiform pad approximately 2–3 cm in length, 0.5 cm in width and 0.2 cm in depth. Adult females also possess the sebaceous gland complex, but it is generally about one-half the size of the male's glands. Thus, adult individuals of both sexes are able to mark their home ranges with the ventral gland secretion.

Scent marking by the ventral gland occurs as follows: the animal crawls over some objects, its abdomen closely pressed to the substrate, and leaves the secretion of the ventral gland on that place. In the natural habitat, the objects of ventral rubbing include burrow entrances, soil hammocks, small stones, and lumps of ground, both inside the protected territory and along its border. Scent marks with the ventral gland secretion may have a role in individual recognition. Specifically, Halpin (1974) provided evidence that Mongolian gerbils can differentiate between the ventral gland secretions from different individuals. Therefore, the gerbils can differentiate between the relevant scent marks from members of their family groups and other conspecifics. In the overwhelming majority of cases (89.3%), ventral rubbing was characteristic of adults — the founders of family groups (Gromov, 2000a, 2015).

Along with ventral rubbing, Mongolian gerbils, like great gerbils (*Rhombomys opimus*; Dubiansky, 1962), mark the territory by building so-called 'signal heaps': the animal leaves a drop of urine where the substrate is sufficiently loose; simultaneously, it can also leave one to three faecal pellets at the same place; throwing the substrate beneath its belly by its anterior legs, the animal builds up a conic hillock ('signal heap') covering the drop of urine and faecal pellets. Observations both in the wild and the large enclosures show that building 'signal heaps' is more common than ventral rubbing, and of the 3622 recorded scent marks 58.5% are 'signal heaps' (Gromov, 2000a, 2015). This phenomenon can be explained by diurnal activity of Mongolian gerbils, whose 'signal heaps' may serve as both odorous and visual marks.

In addition to these scent-marking behaviours, Mongolian gerbils mark the territory by genital rubbing and by chinning of some objects, but the proportion of these scent-marking events is very small ($\sim$1%). Thus, the commonest scent-marking patterns in the gerbils are ventral rubbing and building 'signal heaps'.

During the breeding season, the rate of scent marking was rather high and averaged 2.0 marks per one hour of observations per one adult individual (Gromov, 2000a). As a rule, scent marks were unevenly distributed within the gerbil territories, and the loci with numerous scent-marking events were revealed in proximity to burrow entrances, along the commonly used pathways, and near the territory borders.

Scent-marking behaviours of Mongolian gerbils generally appear to be sexually dimorphic: both sexes usually mark, but males do so more frequently. Besides, adults are more active than young individuals, and reproducing animals are more active, in terms of scent marking, than non-breeding ones (Gromov, 2000a, 2015). These sex- and age-related differences seem to be associated with production of gonadal hormones (Lindzey et al., 1968; Owen & Thiessen, 1973).

Observations in the wild as well as in the large enclosures (Gromov, 2000a, 2015) provide evidence that young Mongolian gerbils start to exhibit scent marking at the age of 5 weeks by building 'signal heaps'. First events of ventral rubbing were observed at the age of puberty (10–12 weeks). Although individuals of both sexes at this age do not take part in reproduction in their family groups, this category of animals however exhibited a relatively high rate of ventral rubbing.

In many cases, scent marking is stimulated by exposure to a novel environment, i.e., when a novel, unfamiliar object is introduced into the home range of the individual. Observations in the wild showed that the rate of scent marking significantly increased after alteration or disappearance of habitual landmarks caused, for instance, by rain or wind (Gromov, 2000a, 2015). This fact lends support to the idea that scent marking may serve to make an area familiar to the animal by a system of olfactory labelling. Indeed, the marking activity of gerbils occupying a defended territory was found to be as much as 8–10-times higher the marking activity of individuals that did not possess their own home range or lost it as a result of territorial conflicts. Such a difference has been revealed both in adult and young individuals (Gromov, 2000a, 2015).

Long-term observations of Mongolian gerbils in the large enclosures revealed clearly expressed seasonal variation in their scent-marking activity: the marking frequency was increased during the breeding season (in spring and summer) and declined in autumn and winter (Sokolov & Gromov, 1998; Gromov, 2000a). Seasonal dynamics of ventral rubbing was obviously related to seasonal changes of the integrity of the ventral gland and its functioning (Gromov, 2000a). At the non-breeding period (in autumn and winter), the rate of ventral rubbing was decreased by 10–20 times as compared to the breeding season, but did not fall to zero level. Evidently, there is some basic level of this scent-marking activity not associated with production of gonadal hormones. This low level of spontaneous ventral rubbing sharply increases under influence of gonadal hormones in the breeding season. The rate of 'signal-heap' marking was significantly decreased during the non-breeding season but remained on a higher level than the rate of spontaneous ventral rubbing. In female gerbils, both scent-marking behaviours were found to be related to reproductive condition, peaking in frequency during the periods of receptivity. Therefore, scent marking might be used by female gerbils as a reproductive tactic to attract mates.

Behavioural observations revealed a close association between scent-marking activity and social hierarchy in family groups of Mongolian gerbils: individuals of a higher social rank displayed scent marking more frequently than subordinate individuals (Figure 2). A positive correlation between the social rank and scent-marking activity could support the hypothesis that scent marking is involved in intra-sexual competition among males and associated with status signalling (Gosling & Roberts, 2001; Roberts, 2007). However, individuals possessing ranks 1 and 2 (Figure 2) are the founders of family groups (males and females, respectively), and individuals possessing ranks 3 and 4 are usually subadults of both sexes; other low-ranking members of the family groups are younger individuals of both sexes. Hence, one cannot suggest intra-sexual competition in Mongolian gerbils, because

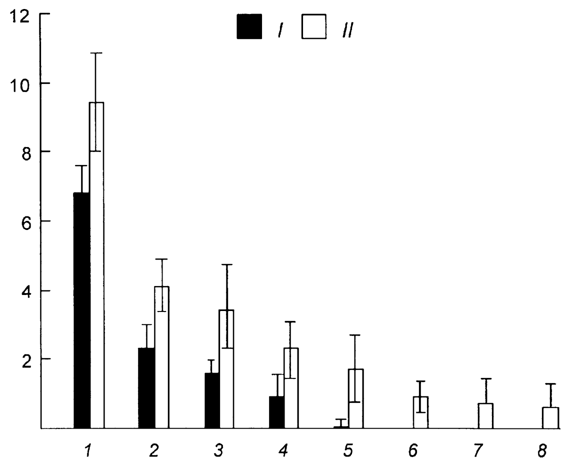

Figure 2. Relationship between social status and scent-marking activity in family groups of Mongolian gerbils. (I) ventral rubbing, (II) building 'signal heaps'. (1) Adult males, (2) adult females, (3–8) relative social ranks of subadults and juveniles. Vertical axis, number of scent-marking events per 1 h of above-ground activity. Means are given ± SE.

they live in family groups. The high correlation between social rank and scent-marking activity revealed in this species can be explained by the influence of other factors, e.g. hormonal and social ones related to delayed sexual maturation and reproductive suppression. In other words, a relationship between social rank and scent-marking activity in Mongolian gerbils seems to be not associated with status signalling only. Specifically, suppressed production of competitive odours related to scent marking in younger, and hence subordinate individuals, could be explained by not only the influence of odours of the high-ranking individuals (i.e., their parents), but a lower level of gonadal hormones as well. Anyway, subadult and young individuals in family groups of the Mongolian gerbil cannot be regarded as competitors for the territory and mates in terms of the status signalling hypothesis.

Correlation analysis did not reveal a significant relationship between locations of the activity centres of the gerbils and their scent-marking behaviour (Gromov, 2000a). In other words, the animals did not mark more frequently the places they used more intensive. Instead, both in the wild and the enclosures, Mongolian gerbils have been observed to deposit the ventral gland secretion and build ‘signal heaps’ in loci where others have left the same scent marks (Gromov, 2000a, 2015). Hence, the animals appeared to be stimulated to mark by the scent of conspecifics, including members of their family groups.

Females were found to mark more frequently the areas located near their burrows, feeding sites and pathways. Besides, the breeding females protecting their home ranges were revealed to mark frequently some loci along the boundaries with the neighbouring females where their scent marks were in close proximity (Figure 3). Males were found to exhibit a higher rate of scent marking within the home ranges of the breeding females. If a family-group territory included the home ranges of two females, the frequency of scent marking in the adult male was much higher within the home range of a receptive, pregnant or lactating female than in other places (Figure 3). Neither males nor females mark frequently the periphery of their protected home ranges except for the narrow overlap zone between neighbouring territories. With a relatively large territory, ‘hinterland’ marking seems to be more economical than marking of the boundaries.

To summarize, one can conclude that ventral rubbing and building ‘signal heaps’ are the most common scent-marking behaviours of the Mongolian

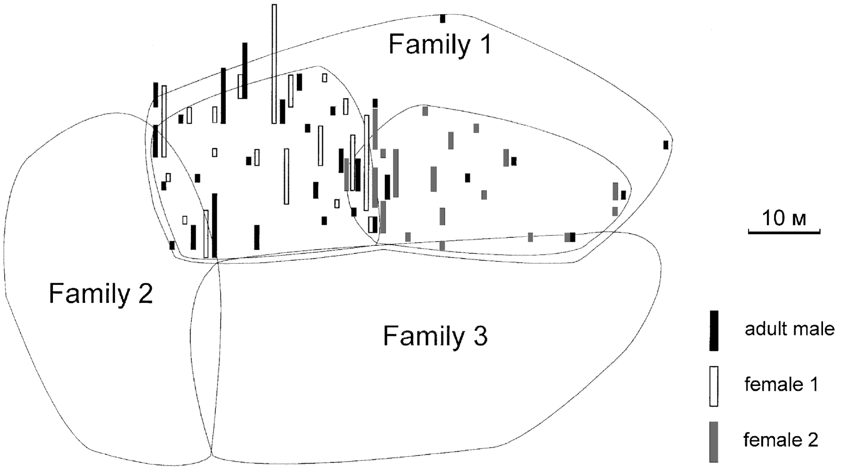

Figure 3. Spatial distribution of ‘signal heaps’ ($N = 277$) recorded during the observation period (July–August) within the family-group territory of Mongolian gerbils. The height of the bars is proportional to the number of scent-marking events (the minimum height of the bars indicates one scent-marking event).

gerbil. The ventral gland secretion is known to be implicated in individual recognition (Halpin, 1974, 1986) as well as in mate recognition (Kumari & Prakash, 1981; Kittrell et al., 1982). ‘Signal heaps’ contain urine and thus may convey more complex information indicating not only species and individual identity, but sex, age, social and reproductive status like in other rodents (Roberts, 2007). An increase in scent-marking activity of adults in response to novelty as well as exhibition of scent marking by young gerbils are consistent with the hypothesis of home range familiarization (Mykytowycz, 1970, 1974): when familiarizing a new territory, animals investigate and mark it; a territory owner tries to saturate the occupied area with its own odour as much as possible. Possession of a home range/territory is very important for any adult individual or family group, so scent marking could be considered also as a means of territory monopolization. In addition to the function of familiarization, the spatial distribution of scent marks supports the idea that scent-marking behaviour of male Mongolian gerbils could be interpreted as functioning in monopolization of reproducing females during the breeding season. Thus, scent marking in Mongolian gerbils is a complex and multi-functional phenomenon.

10. Cooperation as the most important trait of a family-group lifestyle

In species with a family-group lifestyle, both parents usually share the responsibilities for rearing young, and juveniles may also assist in rearing younger siblings. This situation is usually referred to as cooperative breeding (Emlen, 1984), and the caring behaviour towards the young contributed by juveniles is termed alloparental care (Emlen, 1984; Brown, 1987).

No doubt, the Mongolian gerbil is a cooperative breeding species. Cooperation in breeding, first of all, is related to biparental care of the young: the adult male engages in all care-taking activities observed in the female, except for nursing (Elwood, 1975, 1979; Gromov, 2009, 2011b). Moreover, both adults were reported to cooperate via their synchronised presence with the young (temporal coordination or time sharing in the nest) (Weinandy & Gatterman, 1999). Besides, young gerbils that remain in the natal area become non-breeding helpers assisting in the rearing of the infants (Ostermeyer & Elwood, 1984; French, 1994). Specifically, young gerbils interact extensively with their younger siblings from the next litter, exhibiting care-giving activities such as nest attendance, retrieving, huddling over and grooming pups. The presence of the male as well as the helpers is thought to be beneficial to physical and behavioural development of young gerbils, and their major contribution appears to be warmth and additional tactile stimulation of the pups (Gromov, 2009, 2011c).

Field studies as well as observations under semi-natural conditions showed that the Mongolian gerbil is a species with a complex social organisation characterised by cooperation in different activities (Gromov, 1992, 2000a). It was already noted that the gerbils act cooperatively to defend and mark their territories; that is cooperative maintenance of territories is typical of this species. In autumn, animals of both sexes and all age classes actively hoard winter stores (Bannikov, 1954). Behavioural observations show that all members of a family group take part in hoarding of a common food supply (Ågren et al., 1989b; Gromov, 1992, 2000a), so there is clear reason for all animals not to desert their natal burrow. The food-hoarding season (September-October) is reported to be a crucial life-history stage in the Mongolian gerbil for successful over-winter survival (Deng et al., 2017a, 2017b). One can suggest that individuals acting cooperatively to hoard food and defend winter stores benefit more than solitary foragers and thus increase their chances of survival during the severe season. In other words, the inclusive fitness of members of family groups might be higher than the fitness of solitary foragers, and thus natural selection has promoted formation of family groups in populations of the Mongolian gerbil, like in some other rodent species belonging to the Palearctic fauna (Gromov, 2017).

11. Conclusion

The Mongolian gerbil is a diurnal social rodent that lives in highly seasonal habitats and displays seasonal fluctuations in reproduction as well as intraspecific variation in population density and composition of social units. The most common social units are extended family groups composed of one adult male, one or two adult females and their male-female offspring (up to four litters). Along with complete family groups, in *M. unguiculatus* populations there are incomplete families lacking one or both members of a potential founding pair, as well as solitary wanderers of both sexes engaged in looking for their mating partners during the breeding season.

The Mongolian gerbil displays characteristics of monogamy such as shared home ranges and nests even beyond the breeding season, selective aggression against strangers but not toward the social partner, and shared parental care. However, the mating system of this species may not be defined as solely monogamous, because, along with male-female pairs, there are polygynous social units where a male lives with two or even three breeding females. Moreover, both sexes were found to mate not only with their social partners, but also with neighbours and strangers. Thus, the Mongolian gerbil has a variable mating system that could be defined as a combination of behavioural monogamy and polygyny; monogamous pairs and polygynous family groups occur within the same population irrespective of its density.

A typical feature of the Mongolian gerbils' space use system is territoriality. Each family group occupies a home range of a more or less fixed size that is exclusive of the ranges of adjacent family groups. All adult and subadult members of a family group take part in defending their territory against any conspecific intruders. The inter-group relationships may be defined as a locus-dependent dominance.

The social organisation of the Mongolian gerbil family groups is not based on aggressive interactions and may be defined as a subordination hierarchy. The hierarchy order is primarily determined by the age-related factor: a founding pair is the individuals of highest rank, and subadults are the individuals of a higher rank than younger members of the family group; besides, individuals of higher and lower rank may be distinguished among the littermates. The hierarchy is maintained chiefly by subordinates' behaviour patterns, and by the low-ranking rather than the high-ranking animals. The presence of high-ranking individuals is the main factor resulting in delay of sexual maturation and suppression of breeding among low-ranking animals. Young that remain in the natal area forgo their own reproduction until dispersal.

The Mongolian gerbil is a cooperative breeding species. Cooperation in breeding is related to biparental care of young. Moreover, young gerbils that remain in the natal area become non-breeding helpers assisting in the rearing of the infants. Behavioural monogamy and cooperative breeding (in terms of alloparental care displayed by elder offspring) may have evolved as an adaptation to harsh environment.

Mongolian gerbils act cooperatively defending and marking their territories, digging underground tunnels, maintaining nests, hoarding food, and raising young. Thus, the Mongolian gerbil is a species with high cooperative abilities. Cooperation and kinship appear to enhance the survival of family groups of this species under the extreme climatic conditions of Central Asia. To summarise, one can conclude that the Mongolian gerbil is one of the rodent species with the most complex social organisation.

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