

Ecology and social behavior of the tamarisk gerbil *Meriones tamariscinus*: insights from long-term research in the wild and semi-natural environments

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Abstract

The present review provides a compilation of the published data on the ecology and social behavior of tamarisk gerbils. Both field studies and direct observations under semi-natural conditions provide evidence that the tamarisk gerbil is a nocturnal herbivorous rodent that lives in highly seasonal habitats and displays seasonal fluctuations in reproduction and spatial organization. A typical feature of the tamarisk gerbils' spatial organization is higher mobility of males during the breeding season (as compared with the nonbreeding period) and formation of temporary aggregations of males competing for access to receptive females; the composition of these aggregations was variable and depended on the reproductive condition of the females. Females tend to occupy exclusive home ranges irrespective of their reproductive condition. The mating system of the species can be defined as scramble competition polygyny with some features of polygyny and promiscuity. The tamarisk gerbil has distinct features of a solitary species and its social structure is primarily based on aggressive interactions or mutual avoidance of conspecifics resulting in a dominance hierarchy among males and site-dependent dominance among females during the breeding season. By the end of the breeding season, males become less mobile and occupy nearly exclusive home ranges, consistent with solitary living. The main features of the spatial and social organization of this species, which distinguish it from other solitary rodents, are the higher mobility of males and the formation of temporary multimale–multifemale aggregations during the breeding season. Overall, the data presented expand our understanding of socioecology of gerbils.

Key words: ecology, reproduction, social behavior, spatial organization, tamarisk gerbil.

Gerbils (subfamily Gerbillinae, Rodentia) are a diverse group of rodents distributed across steppe, semi-desert, and desert habitats of Europe, Asia, and Africa (Sokolov 1977; Musser and Carleton 1993). The diversity of gerbils and the ease with which some species (e.g., the Mongolian gerbil, *Meriones unguiculatus*) can be maintained in captivity, has led to their choice as model systems for observational and experimental studies in genetics, ecology, demography, physiology, neurobiology, and psychology.

The social organization, social structure, and mating system of gerbils are diverse and intriguing, making certain gerbil species ideal for addressing both ecological and behavioral questions (Gromov 1997a, 2000, 2022; Randall 2007). Unfortunately, the relevant information is widely scattered, not always complete, and sometimes conflicting. Moreover, not all aspects of the socioecology of gerbils have been studied equally, even in relatively well-studied species. The subfamily Gerbillinae includes about 110 species (Wilson and Reeder 2005), but detailed data on population ecology and social behavior have been collected for only a dozen species. Some species are essentially solitary, like *Gerbillus perpallidus* (Gromov and Ilchenko 2007) and *Psammomys obesus* (Daly and Daly 1975a; Gromov 2001); others are gregarious, with the formation of relatively stable multimale–multifemale

associations (called breeding colonies; Bujalska and Saittho 2000), like in *Gerbillus dasyurus* (Gromov et al. 2000, 2001), *Meriones meridianus* (Popov et al. 1989; Gromov 2000), *Meriones hurrianae* (Agrawal 1967; Fitzwater and Prakash 1969; Kumari and Prakash 1981a, 1984), *Tatera indica* (Idris and Prakash 1985, 1987), and *Taterillus pygargus* (Poulet 1972); for a small number of species, a family-group lifestyle is characteristic, like in *M. unguiculatus* (Ågren et al. 1989; Gromov 2000, 2022), *Meriones libycus* (Daly and Daly 1975b; Ågren 1979; Tchabovsky and Lapin 1989; Tchabovsky et al. 1990; Gromov 2000), or *Rhombomys opimus* (Dubrovsky 1978; Popov et al. 1997; Rogovin et al. 2004). Diurnal species, like *M. unguiculatus*, *M. libycus*, *P. obesus*, and *R. opimus* are relatively well studied. In most of other species, spatial organization has been studied only via mark-recapture or radio tracking; direct observations of social behavior has been carried out in only a few species (Gromov 2000). Therefore, much more research remains to be done to fill this knowledge gap.

Gerbils are known to be natural hosts of a broad range of ticks and fleas and play an important role in transmission of highly dangerous diseases, such as plague and tularemia. Both plague and tularemia are vector-borne infectious diseases transmitted by fleas of numerous wild rodents, which

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are natural carriers of these diseases and other important epidemics in different regions around the world (Gage and Kosoy 2005; Stenseth et al. 2008; Meerburg et al. 2009; Bitam et al. 2010; Shu et al. 2020). Several natural foci of plague and tularemia exist in the Caspian Sea region and the persistence of these zoonotic foci increases the risk of reemergence as people living in these areas may be in contact with rodents and fleas occasionally (Rall 1941; Popov et al. 1995; Perflyeva et al. 2020; Pisarenko et al. 2021). The transmission of infections to humans depends on the epizootic situation which in turn depends on seasonal and other factors resulting in fluctuations in rodent population density. Therefore, regular monitoring of gerbil populations as the natural foci of plague and tularemia is important.

The tamarisk gerbil *Meriones tamariscinus* (Pallas 1773) is a burrowing, medium-sized rodent (body mass averages 118.6 g in adult males and 90.8 g in adult females; Rall 1941) inhabiting semi-desert and desert regions in Russia (the Caspian Sea region), Central Asia, and northwestern China (Sokolov 1977; Vorobei 1986; Wilson and Reeder 2005). Within the range of this species, the climate is arid or semi-arid and continental with relatively hot summers and cold dry winters (Rall 1941).

Tamarisk gerbils have attracted the attention of population ecologists for decades due to their role in desert and semi-desert ecosystems as pests and hosts of arthropod vectors of plague and tularemia in the Caspian Sea region and Central Asia (Rall 1941; Volynkin 1950; Kim 1960; Vorobei 1986; Popov et al. 1995; Gromov 2000; Perflyeva et al. 2020; Pisarenko et al. 2021). Pathogens are known to disperse from one individual host to another via direct transmission (e.g., the deposition of pathogens via bites and scratches), blood-feeding arthropod vectors, or sexual contact. For an infection that is transmitted directly between individuals, the spread of the disease is thought to depend mainly on the rate of contact between individuals. This is why many studies focus on the role of social behavior and demography of rodents in the maintenance and transmission of rodent-borne diseases (Ostfeld and Mills 2007). Social behavior (specifically, aggressive encounters) has repeatedly been implicated as increasing the probability of pathogen transmission between individuals (Glass et al. 1988; Douglass et al. 2001). In addition, dispersal, as well as defense of territories, is likely to be important to the dynamics of disease in rodents (Ostfeld and Mills 2007). As for the tamarisk gerbil, little is known about how social behavior and population dynamics of this species influence transmission between individuals. Thus, behavioral studies could be extremely useful to fill this gap. Here I review multiple studies done on the social system of tamarisk gerbils, often published in Russian, to provide a detailed overview of one nocturnal gerbil species.

I carried out ecological and behavioral studies of the tamarisk gerbil in 1993–1998 in the wild (in the northwestern Caspian Sea region, the Black Lands area; Gromov and Tchabovsky 1995; Gromov et al. 1996; Gromov 2000) and semi-natural environments (in the large outdoor enclosures in Moscow region; Gromov and Gromova 1996; Gromov 1997a, 1997b, 2000, 2007, 2008; Sokolov and Gromov 1997). To collect data on local population density of the gerbils and their demographic structure as well as spatial organization in the wild, a capture–mark–recapture technique was used on a 7.4 ha study plot and adjacent area of about 30 ha. On the first trapping occasion, the animals were sexed

and weighed. For permanent identification, each individual was given a number by toe-clipping. The gerbils used in the observations under semi-natural conditions (in two outdoor enclosures of 20 × 20 m) were the first and second generation of animals obtained from a natural population of the species in the Black Lands area and bred under laboratory conditions. The animals were observed at night time using artificial illumination (10 lamps, each with a power of 60 watts, were placed around the perimeter and in the center of the enclosure at a height of 2–3 m). There were no signs of the influence of this illumination on the behavior of gerbils. This has also been confirmed by direct observations in the wild (Popov and Tchabovsky 1998). Continuous observations of the gerbils lasted up to 5 months (from May to October). During the observations, the following behavioral patterns were recorded: 1) peaceful interactions (nasal sniff, ano-genital sniff, olfactory investigation), 2) ritualized agonistic interactions (side-way postures, boxing, wrestling), 3) aggressive interactions (attack, chase, fight), and 4) avoidance (an animal turns and moves or runs away from a conspecific before physical contact is made) (Gromov 2000, 2022).

The present review provides a compilation and analysis of the data obtained that allow well-founded conclusions concerning different aspects of the ecology and social behavior of the species under study. This review aims to synthesize and integrate the current state of knowledge about the ecology, spatial organization, and social behavior of the tamarisk gerbil, because these aspects of the socioecology of the species are unknown to many zoologists. Moreover, this review may help us better understand the behavior and ecology of other murid rodents, especially solitary and nocturnal ones whose socioecology is poorly studied.

A Brief Outline of Ecology

Most data on the habitat, food, and activity of tamarisk gerbils were obtained in field studies carried out in the northwestern Caspian Sea region (Vorobei 1986; Tchabovsky and Alexandrov 1996; Popov and Tchabovsky 1998; Gromov 2000). In this region, the gerbils prefer semi-desert habitats with *Tamarix ramosissima* shrubs accompanied by *Atriplex tatarica* (quinoa) that grow on sand hills. Other preferred habitats are ridge-hilly sandy plains with sparse discontinuous vegetation of grasses and herbs including *Achillea micrantha* (yarrow), *Agropyron fragile* (Siberian wheatgrass), *Artemisia lercheana*, and *Andryala arenaria* (sagebrush), *Calamagrostis epigeios* (wood small-reed), *Cynanchum acutum* (family Apocynaceae), *Centaurea arenaria* (sand cornflower), *Corispermum orientale*, and *Kochia prostrata* (family Amaranthaceae), *Eragrostis minor* and *Koeleria sabuletorum* (family Poaceae), *Senecio erucifolium* (family Asteraceae), *Silene multiflora* (family Caryophyllaceae), and *Tragus racemosus* (European bur grass) (Popov et al. 1995; Neronov et al. 1997; Isaev and Shilova 2000). There is also evidence that tamarisk gerbils can penetrate into agricultural habitats (Rall 1941; Allabergenov 1989; Popov et al. 1995).

Food, as a rule, is patchily distributed and unstable over time in the habitat of tamarisk gerbils. In spring, summer, and autumn, the gerbils feed on green parts of plants with higher moisture content like *Artemisia scoparia* (sagebrush), *A. tatarica*, *C. arenaria*, *C. acutum*, *Elymus giganteus* (family Poaceae), *Euphorbia seguieriana* (spurge), *Lactuca tatarica* (blue lettuce), *Senecio erucifolium*, leaves of *Tamarix*

romasissima, as well as flowers, fruits, and green shoots of some plants (Rall 1941; Allabergenov 1989; Magomedov and Akhtaev 1993; Gromov 2000). Tamarisk gerbils do not hibernate, but their winter diet is poorly studied. It has been noted only that in winter season gerbils feed on the seeds, shoots, and rhizomes of some grasses and herbs (Rall 1941).

Field data on food caching in the tamarisk gerbil are controversial. Being herbivorous, the gerbils are not thought to hoard food, because green plants are not suitable for long-term storage. However, there is evidence that tamarisk gerbils can hoard high-calorie food (e.g., seeds) during the period of the year when their survival may depend on food caches (e.g., in winter). Specifically, food caches weighing 300–500 g were found in some burrows of tamarisk gerbils (Rall 1941).

When constructing burrows, the gerbils prefer soft soils. Therefore, anthropogenic and agricultural landscapes are also used by them. Most burrows were found to be located in the bush microhabitats. The length of underground tunnels reaches 4–5 m, and blind branches depart from them up to 40–60 cm. As a rule, a burrow has two or three entrances. The depth of tunnels is 50–80 cm in summer and 2–2.5 m in winter (Rall 1941).

Field studies show that tamarisk gerbils are nocturnal, making them difficult to observe in the field (Rall 1941; Karulin et al. 1979). However, due to direct observations both in the wild and under semi-natural conditions, two or three peaks of their activity at night time were revealed (Karulin et al. 1979; Gromov and Gromova 1996; Gromov 2000). According to Karulin et al. (1979), foraging above ground was the dominant activity of gerbils comprising 50–82% of their time budget. Gerbils also spent about 11–28% of their time moving and exploring different parts of their home ranges. The animals spent very little time interacting with conspecifics. According to Popov and Tchabovsky (1998), the main activity of the gerbils was moving and exploring, whereas foraging was the third most frequent activity within their time budget.

Population density was found to show large fluctuations between years and in different habitats—usually from 1 to 15 animals/ha, but can reach 25–30 animals/ha in preferred habitats (Rall 1941). According to our data (Gromov and Tchabovsky 1995; Gromov et al. 1996), the local density of gerbils within our study plot was about 4–5 animals/ha in 1993–1994, but in a ridge-hilly sandy plain it reached 70 animals/ha in 1998 (Gromov 2000).

The breeding season starts in February–March and lasts up to September with two peaks of reproduction—in May and August (Rall 1941; Gromov 2000). During the breeding season, most overwintered females produce only a single litter whereas a small proportion of them (about 3%) produce two litters. Young females born early in the breeding season can mature and breed in that season, producing a single litter. The average number of embryos per pregnant female varies from 4.5 to 4.8 in different populations (Rall 1941; Vorobei 1986). The sex ratio among adults in the populations of this species is about 1:1 (Rall 1941).

The tamarisk gerbil exhibits a mating system in which males actively seek females during the breeding season (Popov and Tchabovsky 1998; Gromov 2000), and males that possess traits associated with mobility may have higher mating success. In other words, male mating success is mostly determined by the ability to locate females. Such a mating system can be defined as scramble competition or competitive searching. It needs to be noted, however, that the mating system of the

tamarisk gerbil also involves male–male competition based on overt aggressive interactions (see below), and has some features of polygynandry as well as promiscuity. Specifically, Popov and Tchabovsky (1998) observed five males gathered near a receptive female within her home range; the males were presumably attracted by scent cues emanating from the female. This situation is consistent with the distribution of male home ranges associated with the location of female home ranges during the breeding season (see Figure 11).

Spatial Organization, Social Behavior, and Social Organization

Adults of both sexes occupy individual home ranges of a large size comprising several thousand square meters (Figure 1; Gromov and Tchabovsky 1995; Gromov et al. 1996; Gromov 2000). During the mating season, male tamarisk gerbils are not territorial and can range over large areas. Aggregations of males in the vicinity of ranges of receptive females were regularly found, so that male ranges overlapped each other and with female ranges to a great extent (Figure 11A). Male and female tamarisk gerbils thus appear to occupy overlapping individual home ranges during the breeding season. Territoriality, that is, protection of the home range, was typical of females and some young individuals, but they defended the core area in the vicinity of their burrows rather than the entire home range (Gromov and Gromova 1996). In the wild, female home ranges averaged $2,267 \pm 332$ m² ($n = 12$) and were mutually exclusive (Figure 11B).

Another typical feature of spatial organization in the tamarisk gerbil is higher mobility of males during the breeding season (in spring and the first half of summer) so that it was not possible to estimate the size of their home ranges accurately. Sometimes we recorded males moving up to 700–900 m away from the original place of capture (Gromov and Tchabovsky 1995; Gromov et al. 1996). As an estimate of male home ranges, we used range length (RL) defined as the straight-line distance between the two most distant points where the male was recorded. In spring and early summer, that is, the mating season, male RL averaged 336 ± 59 m ($n = 10$). After termination of reproduction in late summer and autumn, male RLs were reduced (on average, 165 ± 45 m, $n = 8$), and their spatial distribution became similar to that of the females (Figure 11I). Thus, distinct seasonal changes in spatial organization related to the annual cycle of reproduction were typical of *M. tamariscinus* males. During the breeding season, adult males were very mobile and formed temporary aggregations near the home ranges of receptive females. The composition of these aggregations was variable and depended on the reproductive condition of the females. For instance, males that form an aggregation near the ranges of several receptive females can move to the ranges of other breeding females, forming one or two temporary aggregations of different composition; some males regularly moved between aggregations, temporarily joining one of them (Gromov 2000). By the end of the breeding season, males became less mobile and occupied nearly exclusive home ranges (Figure 11I).

Very little is known about the social behavior of tamarisk gerbils. To fill this knowledge gap, their social interactions under semi-natural conditions in the large outdoor enclosures were studied in detail (Gromov and Gromova 1996; Gromov 2000). In total, four groups of the gerbils each consisting of four adult unrelated individuals (two males and two females

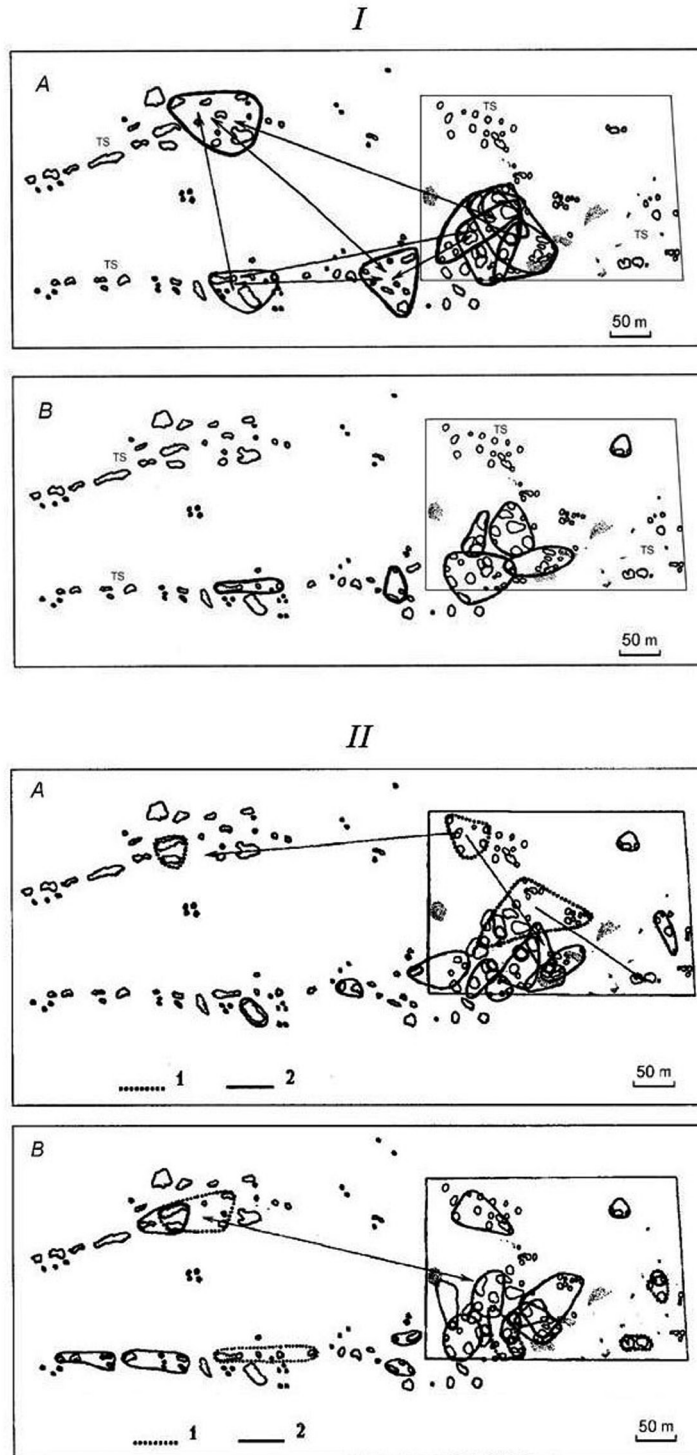


Figure 1. Map of the distribution of smoothed minimum convex polygon home ranges (thick line contours obtained from recapture data) of adult males (A) and females (B) within the study plot of 7.4 ha and on the 30 ha adjacent area during the breeding season (I, May–June 1993) and the nonbreeding season (II, September–October 1994; dotted lines (1) show home ranges of the overwintered gerbils, solid lines (2) home ranges of the gerbils born in spring–early summer). TS—*Tamarix* shrubs. Arrows indicate movements of the males between their different locations and the ranges of the females (after Gromov 2000).

in each group per enclosure) were observed in 1995–1996. A comparative analysis of the social behavior of the gerbils did not reveal significant intergroup differences in spatial organization and social interactions (Gromov 2000).

Most encounters between adults of the same sex (up to 98 %) involved overt aggression and avoidance (Table 1). Most

peaceful and agonistic encounters were recorded in heterosexual dyads, but accounted for only 14% (128 out of 920) of interactions. These data provide evidence that relationships between adults in populations of the tamarisk gerbil are primarily based on overt aggressive interactions or mutual avoidance (Gromov and Gromova 1996; Gromov 2000).

Below, more informative data characterizing the spatial organization and social behavior of the gerbils in one of the enclosure groups observed are presented. The gerbils successfully reproduced, and each female gave birth to two litters, from four to six pups in each. The first litters appeared from their natal burrows in late July–early August, and the second ones emerged aboveground in early September (Gromov and Gromova 1996; Gromov 2000).

Over the course of direct observations in the enclosures, the interactions between adults changed dramatically. Accordingly, the observation period was divided into two parts: period I (the mating period, from the beginning of the observations to the emergence of first litters in July–August) and period II (the nonbreeding period, from the second half of August to the end of observations in late September).

During period I, both adult males moved freely throughout the enclosure, and their home ranges entirely overlapped each other and the female home ranges; males did not appear to have defined home ranges, but roamed over the enclosure area. On the contrary, adult females occupied nearly

exclusive ranges (Figure 2I). Thus, males did not exhibit territorial behavior, but instead established a dominance hierarchy, and male #4 dominated over male #7. As a result, the activity centers of the males competing for access to females were located in different areas of the enclosure. Specifically, the activity centers of male #7 primarily coincided with that of female #8. The gerbils apparently mated in their burrows, but judging from their behavior above ground, both in this and in other enclosure groups, multiple matings of females with both males occurred. As for the females, their relationships may be defined as territoriality based on site-dependent dominance (Gromov and Gromova 1996; Gromov 2000). This refers to a relationship in which an individual dominates other conspecifics within its home range, such as, for example, in Mongolian gerbils (Ågren et al. 1989).

Frequency of agonistic interactions in the enclosure groups was rather high, but the aggressiveness did not lead to the death of the gerbils even when an extraordinary density was achieved—as many as 23 individuals including 8 adults and 15 juveniles per enclosure. Bearing in mind the very large

Table 1. Number (N) and proportion (%) of interactions between adult tamarisk gerbils in the semi-natural enclosures (after Gromov 2000)

Interactions	Males (<i>n</i> = 8)				Females (<i>n</i> = 8)			
	Interactions, addressed to				Interactions, addressed to			
	Males		Females		Males		Females	
	N	%	N	%	N	%	N	%
Peaceful	4	1.0	107	24.1	21	4.4	0	0
Agonistic	5	1.2	58	13.1	42	8.8	2	1.8
Overt aggressive	166	39.8	188	42.3	138	29.0	75	67.0
Avoidance	242	58.1	91	20.5	275	57.8	35	31.3
Total	417	100	444	100	476	100	112	100

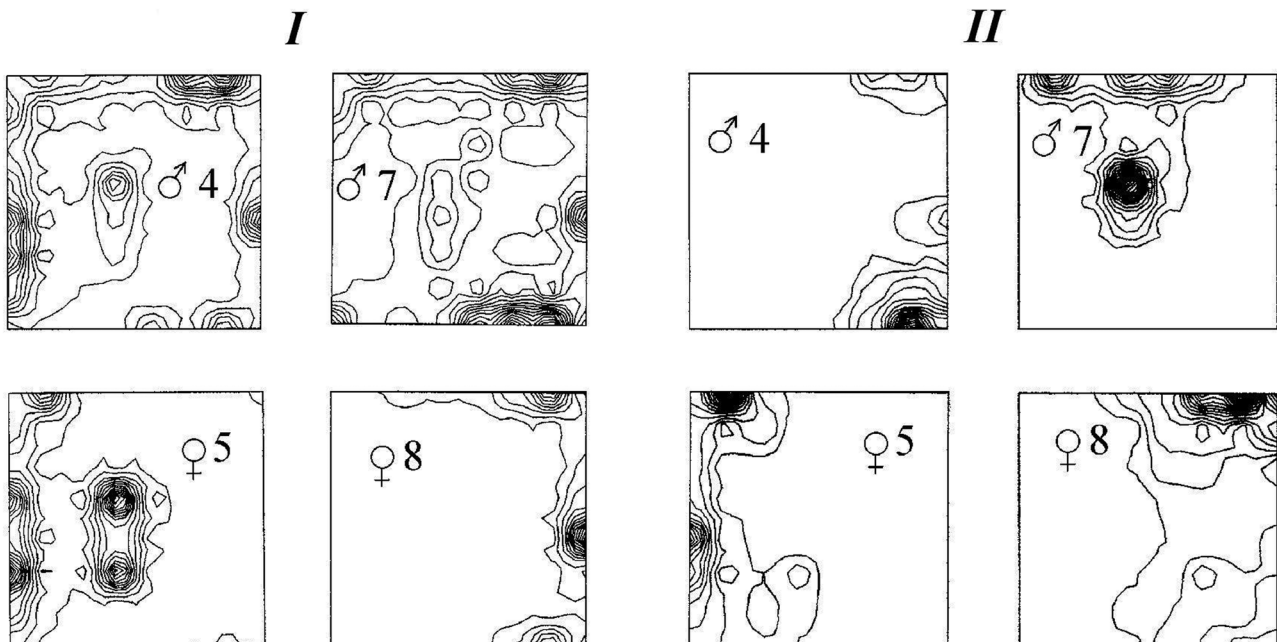


Figure 2. Contour mapping of the frequency of visual registration of tamarisk gerbils during observation periods I (the mating season) and II (after termination of reproduction) in the enclosure of 20 × 20 m. Contour lines connect points of equal frequency of registrations per area unit (square 2.5 × 2.5 m). Higher density of the lines corresponds to the activity centers of the gerbils related to their nest burrows (after Gromov 2000).

M. tamariscinus home ranges in the natural habitat, such a situation in the enclosure populations was unexpected.

Figure 3 provides an additional illustration of the relationships between the gerbils in the enclosure. Peaceful interactions were found to be relatively frequent in encounters of males as well as in heterosexual dyads; in females, only one peaceful encounter was recorded (Figure 3IA). Relationships between adults of the same sex were based on mutual aggression (Figure 3I B). A high frequency of aggressive interactions was also characteristic of the encounters of males with the females. The interactions between the males were found to be asymmetric reflecting the establishment of a dominance hierarchy. In particular, dominant male #4 initiated many more aggressive acts directed at subordinate male #7 (Figure 3IB). The relationships between males in other enclosure groups were generally similar to those between males #4 and #7.

During period II, the relationships changed dramatically. The male home ranges became nearly exclusive and decreased in size; the activity centers of males shifted and lost relation to those of the females (Figure 2II); the frequency of interactions between males and the females decreased (Figure 3II). Judging from the lack of asymmetry in the encounters between males, their relationships became equitable and could be defined as site-dependent dominance, like in the females. Similar changes in the the spatial organization and the relationships between males were observed in other enclosure groups of the gerbils (Gromov and Gromova 1996; Gromov 2000).

Adult females became aggressive toward young gerbils 4–6 days after they were weaned and emerged from the burrows.

Aggressive encounters between young individuals as well as between young and adult gerbils have been noted as well. In 25–30 days, the intensity of the aggressive interactions decreased, because nearly all the young individuals came to occupy small and protected territories not exceeding several square meters. Thus, young individuals successfully competed with adults even within a very limited area of the enclosures (Gromov and Gromova 1996; Gromov 2000).

The results of observations of the gerbils in the semi-natural enclosures are consistent with data obtained in the wild (Gromov 2000). The relationships between adult males competing for females during the breeding season are based on overt aggressive interactions or avoidance resulting in the establishment of a dominance hierarchy. Popov and Tchabovsky (1998) carried out direct observations of individually marked gerbils in their natural habitat in the Black Lands area. In total, these authors recorded 34 interactions between adults, and aggressive encounters comprised a large proportion: 44% in male dyads, 31% in male–female dyads, and 100% in female dyads.

By the end of the breeding season in late summer–early autumn, adult males stop competing for access to females and tend to occupy smaller, exclusive, and perhaps, protected home ranges, like adult females. Adult females occupying exclusive home ranges express territoriality and site-dependent dominance irrespective of their reproductive condition. Young gerbils born in the current breeding season also tend to occupy exclusive home ranges. During the breeding season, the intensity of interactions between tamarisk gerbils in their natural habitat is relatively high. By the end of the breeding season,

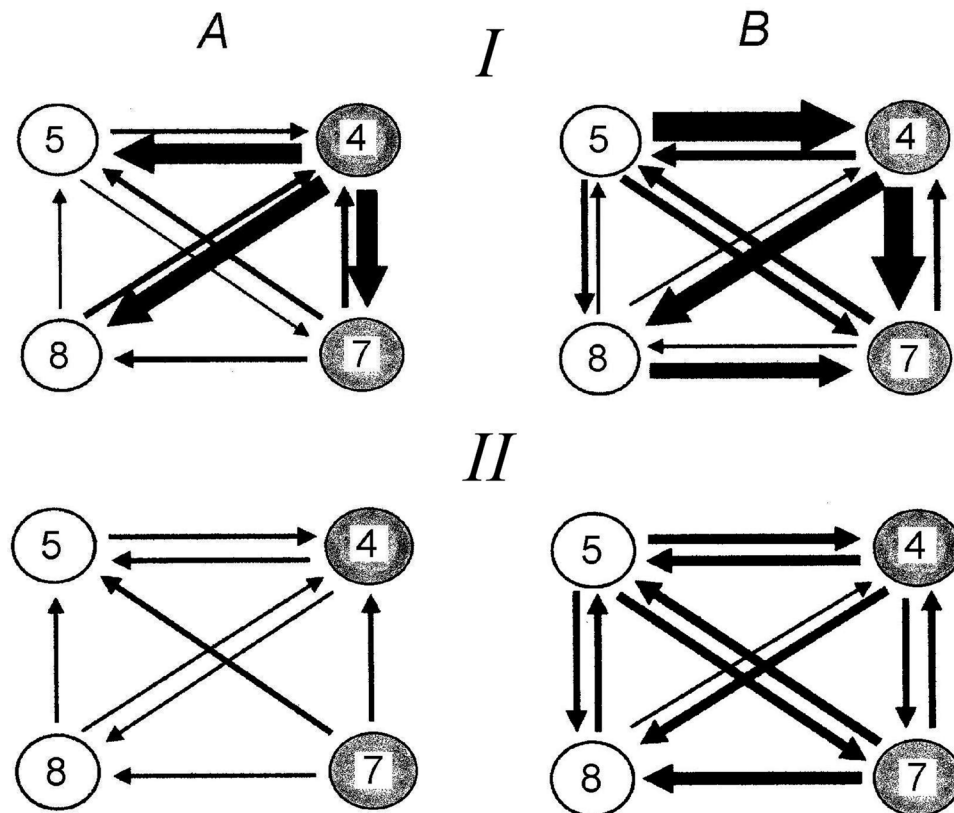


Figure 3. Occurrence and direction of peaceful (A) and aggressive (B) interactions between the gerbils during observation periods I and II in the enclosure. Males are indicated by shaded circles. Thickness of the arrows is proportional to the number of initiated acts in each dyad (after Gromov 2000).

encounters between the gerbils become rare (Gromov and Gromova 1996; Gromov 2000, 2008).

The seasonal changes in spatial organization and social behavior of *M. tamariscinus* males related to the annual cycle of reproduction might be critical both in maintaining pathogen populations and the rates of pathogen transmission. Transmission of pathogens during the breeding season may result from frequent agonistic encounters (primarily between males). Judging from the field data, movements of the males in this population of tamarisk gerbils are much greater during the breeding season. Therefore, the rate of transmission of pathogens in populations of the tamarisk gerbil appears to be highest in the spring and first half of summer. This is a situation that should promote epizootics (Rall 1941; Volynkin 1950).

Scent Marking

Tamarisk gerbils have a ventral sebaceous gland and use its secretion for scent marking (Sokolov and Gromov 1997; Gromov 2000). In adult males, this gland appears as a fusiform pad approximately 4–5 cm in length and 0.6–1.0 cm in width. Many adult females have no visible gland, but in some of them (approximately 40%) the gland is prominent and active; the sebaceous gland complex is approximately half the size of the male glands. Thus, adult individuals of both sexes are able to mark their home ranges with 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. Observations in the wild and in semi-natural enclosures (Gromov and Gromova 1996; Sokolov and Gromov 1997; Gromov 2000) have shown that the objects of ventral rubbing include burrow entrances, soil hammocks, small stones, and lumps of ground. Scent marks with ventral gland secretion may have a role in individual recognition. Specifically, Halpin (1974) provided evidence that Mongolian gerbils can differentiate between ventral gland secretions from different individuals. It can be assumed that tamarisk gerbils are also able to distinguish relevant scent marks from different conspecifics. Along with ventral rubbing, tamarisk gerbils, like Mongolian gerbils (Gromov 2022), mark their home ranges 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 fecal pellets at the same place; throwing the substrate beneath its belly using its forelegs, the animal builds up a conical hillock (“signal heap”) covering the drop of urine and fecal pellets.

Direct observations in the enclosures show that scent marks with the ventral gland secretion are more common than “signal heaps,” and of the 1,190 scent-marking events recorded 66% involved ventral rubbing, whereas “signal heaps” comprise only 30%. This might be explained by the nocturnal activity of tamarisk gerbils, whose “signal heaps” are hardly visible at night time and do not serve as visual marks, like in diurnal Mongolian gerbils (Gromov 2022). In addition to these kinds of scent-marking behaviors, female tamarisk gerbils mark their home ranges by genital rubbing, but the proportion of these scent-marking events is rather small (4%). Thus, the most common scent-marking patterns in tamarisk gerbils are ventral rubbing and building “signal heaps.” Unlike Mongolian gerbils (Gromov 2022), association between scent-marking activity and social hierarchy in male tamarisk gerbils was found to be absent (Gromov 2000).

Scent-marking behaviors of tamarisk gerbils generally appear to be sexually dimorphic: both sexes usually mark, but males do so much more frequently (Table 2). Besides, adults are more active than young individuals, and reproducing animals are more active, in terms of scent marking, than non-breeding ones. Young gerbils start to exhibit scent marking at the age of 7 weeks by building “signal heaps”; first events of ventral rubbing were observed at the age of 10–12 weeks, that is, when the animals became sexually mature (Gromov 2000).

Long-term observations of the gerbils in the semi-natural 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 (Sokolov and Gromov 1997; Gromov 2000). During the non-breeding period, the rate of ventral rubbing was decreased by 10–20 times as compared with the breeding season, but did not fall to zero. Evidently, there is some basic level of this scent-marking activity not associated with production of gonadal hormones. In female gerbils, both scent-marking patterns are related to reproductive condition, peaking in frequency during the periods of receptivity (Table 3). Therefore, scent marking might be used by female gerbils as a reproductive tactic to attract mates. As a result, male tamarisk gerbils exhibited a higher rate of scent-marking activity within the ranges of the breeding females (Gromov 2000).

To summarize, one can conclude that ventral rubbing and building “signal heaps” are the most common scent-marking patterns in the tamarisk gerbil. The ventral gland secretion has been implicated in individual recognition in *M. unguiculatus* (Halpin 1974, 1986) as well as mate recognition in *M. burrianae* (Kumari and Prakash 1981b; Kittrell et al. 1982). Although the evidence is from other gerbil species, this might be true for the tamarisk gerbil as well. “Signal heaps” contain urine and thus may convey more complex information indicating not only species and individual identity, but sex, age, social status, and reproductive condition like in other rodents (Roberts 2007). Possession of a home range/territory is very important for any adult individual, especially for breeding females, so scent marking could also serve as a means of home range familiarization (Mykytowycz 1970, 1974). It is evident that scent marking in tamarisk gerbils is a complex and multifunctional phenomenon.

Socioecology of the Tamarisk Gerbil Compared With Other Gerbil Species and Murid Rodents

It is well-known that animal societies differ in social complexity. Kappeler (2019) offered a conceptual framework for systematic and comprehensive studies of social complexity

Table 2. Frequency of scent-marking events (mean \pm SE per hour of the aboveground activity) in adult and young gerbils in the semi-natural enclosures during observation period I (after Gromov 2000)

Age and sex	Number of individuals	Ventral rubbing	Building “signal heaps”
Adult males	8	8.4 \pm 0.8	3.8 \pm 0.8
Adult females	8	3.5 \pm 1.2	1.0 \pm 0.3
Young individuals	12	0.7 \pm 0.5	0.2 \pm 0.1

Table 3. Frequency of scent-marking events (mean \pm SE per hour of the aboveground activity) in female tamarisk gerbils in the semi-natural enclosures in relation to different phases of their reproductive cycle: I—the second half of pregnancy, II—postpartum estrus and the first 10 days of lactation (after Gromov 2000)

Phases of the reproductive cycle	Ventral rubbing	Building “signal heaps”
I	0.8 \pm 0.3	0.6 \pm 0.2
II	8.8 \pm 2.4	5.7 \pm 3.0

by defining the main components of a social system: social organization, social structure, mating system, and care system. *Social organization* refers to the size and composition of a social unit. In rodents, the species-specific social units are solitary individuals, pairs, aggregations, or family groups. Kappeler (2019) defined three main types of social organization: solitary, pair living, and group living. *Social structure* is defined by the content, quality, and patterning of social relationships emerging from repeated interactions between pairs of individuals belonging to the same social unit. Social relationships can be represented by a dominance hierarchy developed as a result of repeated aggressive interaction, as well as by pair bonding or social bonding (e.g., between members of a family group). *Mating system* is characterized by mating patterns and possible reproductive skew. The resulting emergent patterns at the level of social units allow classification of species as monogamous, polygynous, polyandrous, or polygynandrous (i.e., promiscuous). *Care system* in rodents can be defined as solely maternal, biparental, or alloparental. Many rodent species show intraspecific variation in social organization. In cases where intraspecific variation occurs on a categorical scale, such as in species that switch between pair or group living from year to year, like in *Rhabdomys pumilio* (Schradin et al. 2012; Schradin 2013), classification can be more difficult.

It is well-known that rodents are primarily sedentary animals, especially during the breeding season, with a few exceptions, such as capybaras (Macdonald 1981) or lemmings (Clough 1965; Henttonen 1980). Every adult individual possesses a home range used for various purposes: foraging, construction of shelters and burrows, interactions with conspecifics, reproduction, etc. The spatial organization (i.e., spatial distribution, exclusiveness, and overlap of home ranges) reflects the social organization and social structure of any rodent species (Gromov 2017). In solitary species, same-sex individuals usually occupy mutually exclusive home ranges. Within breeding colonies of gregarious species, females also tend to occupy exclusive home ranges, but ranges of the males may overlap to a large extent. Each breeding pair and family group occupies a common and usually defended home range. Overlapping home ranges of males may contribute to the establishment of a dominance hierarchy.

The interspecific comparative analysis based on quantification of social traits related to the spatial-and-ethological population structure and cooperation (Gromov 2017) made it possible to assess differences between 42 murid rodents, including gerbils. This analysis revealed many high correlations among the variables under comparison. For example, male spacing patterns are highly correlated with male social relationships, and pair bonding is correlated with male parental care. As a result of a principal components analysis, all

the species were divided into three main clusters. The first cluster included several species, which could be regarded as solitary living (e.g., *G. perpallidus*, *P. obesus*, *Microtus montanus*). The second cluster included gregarious species that form relatively stable multimale–multifemale aggregations (e.g., *Clethrionomys glareolus*, *Microtus pennsylvanicus*, commensal mice, and rats). And the third cluster included species with a family-group lifestyle (e.g., *M. unguiculatus*, *R. opimus*, *Microtus ochrogaster*, *Microtus pinetorum*, *Microtus socialis*, *Lasiopodomys brandti*, *Lasiopodomys mandarinus*, *Lagurus lagurus*). There are no fundamental differences between rodent species living in pairs or family groups, because pairs always become family groups when they reproduce. Therefore, the social organization in murid rodents is represented by three main types: solitary individuals, aggregations (breeding colonies), and family groups (Gromov 2017). The comparative analysis also showed that some species occupy intermediate positions between the clusters, because some of them combine features of gregarious species and species living in family groups (like, e.g., *Microtus arvalis*), or solitary and gregarious species (like, e.g., *Peromyscus maniculatus*).

By definition, adults of solitary species lead solitary lives. However, solitary does not mean nonsocial, and solitary rodents typically have nonrandom but individualized social interactions with their neighbors. In mammals, including rodents, solitary living means that both adult males and adult females primarily sleep and forage alone and mainly meet for courtship and mating. According to Makuya and Schradin (2024), however, one can differentiate between species that are obligately solitary living (all individuals are solitary), mainly solitary living (most individuals are solitary living), and facultatively solitary living (most individuals live in pairs or groups and less than 50% solitary).

As for the tamarisk gerbil, a principal components analysis of several parameters characterizing the spatial structure and social interactions in eight murid rodents, including gerbils (Gromov 2007), revealed that this species exhibits many features of solitary living. Consistent with the concept of Kappeler (2019), both males and females of this species lead solitary lives and occupy individual home ranges; the species-specific social units are solitary individuals, especially during the nonbreeding season; pair bonds are lacking even during the breeding season. The mating system of the species can be defined as scramble competition polygyny with some features of polygynandry and promiscuity. As for parental care, only females provide care for young. However, adult males may form temporary aggregations in the vicinity of ranges of receptive females during the breeding season. Based on the results of direct observations in semi-natural enclosures, one can conclude that males may establish a dominance hierarchy within these aggregations, like in breeding colonies of gregarious species, such as *C. glareolus* (Galanina and Serbenyuk 1994; Bujalska and Saitho 2000), *Apodemus sylvaticus* (Bovet 1972; Garson 1975; Montgomery 1979, 1980; Smirin and Shilova 1989), or *M. meridianus* (Popov et al. 1989; Gromov 2000). But unlike breeding colonies of gregarious rodents, which are relatively stable in time and space, temporary aggregations of male tamarisk gerbils are unstable and disintegrate toward the end of the breeding season; during the nonbreeding period (in autumn and winter), adult individuals of both sexes lead solitary lives, occupying nearly exclusive home ranges. On the contrary, in many gregarious rodents, the tendency to aggregate may increase

during the harsh winter season (Madison 1980, 1984; Wolff and Lidicker 1981; Krebs et al. 2007; Gromov 2008).

Conclusion

The tamarisk gerbil is a nocturnal herbivorous rodent that lives in highly seasonal habitats and displays seasonal fluctuations in reproduction and spatial organization. A typical feature of the tamarisk gerbils' spatial organization is higher mobility of males during the breeding season (as compared with the nonbreeding period), as well as formation of temporary aggregations of males competing for access to receptive females. Females tend to occupy exclusive home ranges irrespective of their reproductive condition. By the end of the breeding season, males become sedentary. In general, the tamarisk gerbil has distinct features of a solitary species that forms temporary multimale–multifemale aggregations during the breeding season only; after termination of reproduction, adult individuals of both sexes occupy nearly exclusive home ranges, consistent with solitary living. The mating system of this species can be defined as scramble competition polygyny; it also has some features of polygynandry as well as promiscuity.

The social structure in populations of the tamarisk gerbil is primarily based on aggressive interactions or mutual avoidance of conspecifics. The relationships between adult males competing for access to receptive females during the breeding season are based on overt aggressive interactions that may result in the establishment of a dominance hierarchy in temporary aggregations. As for adult females occupying exclusive home ranges, they express territoriality and site-dependent dominance irrespective of their reproductive condition. After termination of reproduction, adult individuals of both sexes occupy primarily exclusive home ranges, and their interactions become infrequent.

There are different forms of scent marking in the tamarisk gerbil. Ventral rubbing and building “signal heaps” are the most common scent-marking patterns. The ventral gland secretion may be involved in individual recognition, based on evidence from other species of gerbils. “Signal heaps” containing urine may convey more complex information indicating not only species and individual identity, but sex, age, social status, and reproductive condition. Both scent-marking patterns could be considered as a means of familiarization or even monopolization of the home range. In addition, scent marking might be used by females as a reproductive tactic to attract mates.

In the Caspian Sea region, tamarisk gerbils are probably the predominant natural reservoirs for pathogens that cause disease, including plague, in humans. A relatively high population density of this species, fighting, and potential occupation of agricultural habitats are associated with potentially high rates of pathogen transmission. Knowledge of social behavior of the tamarisk gerbil and factors affecting movements and demography of this species are essential to develop models to predict transmission rates of rodent-borne diseases and the potential for outbreaks.

The tamarisk gerbil demonstrates many characteristics of solitary living. The main features of the spatial and social organization of this species, which distinguish it from other solitary rodents, are the higher mobility of males and the formation of temporary multimale–multifemale aggregations during the breeding season. Compared with other gerbils, it can be concluded that the socioecology the tamarisk gerbil combines some features of solitary and gregarious species,

but only during the breeding season. Overall, the data presented expand our understanding of socioecology of gerbils and could be used for broader interspecific comparisons with other murid rodents.

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References

- Agrawal VC, 1967. Field observation on the biology and ecology of the desert gerbil, *Meriones hurrianae* (Rodentia, Muridae) in western India. *J Zool Soc India* 17:125–134.
- Ågren G, 1979. Field observations of social behaviour in a Saharan gerbil: *Meriones libycus*. *Mammalia* 43:135–146.
- Ågren G, Zhou Q, Zhong W, 1989. Ecology and social behaviour of Mongolian gerbils, *Meriones unguiculatus*, at Xilinhot, Inner Mongolia, China. *Anim Behav* 37:11–27.
- Allabergenov K, 1989. [Ecology of the tamarisk gerbil in the Fergana Valley. In: Sokolov VE, editors. *Gerbils as an Important Component of Biota in the Arid Regions of the USSR*.] Tashkent: Fan Press, 75–76. Russian.
- Bitam I, Dittmar K, Parola P, Whiting MF, Raoult D, 2010. Fleas and flea-borne diseases. *Int J Infect Dis* 14:e667–e676.
- Bovet J, 1972. On the social behaviour in a stable group of long-tailed field mice (*Apodemus sylvaticus*). I. An interpretation of defensive postures. *Behaviour* 41:43–54.
- Bujalska G, Saitoh T, 2000. Territoriality and its consequences. *Polish J Ecol* 48(Suppl):37–49.
- Clough GC, 1965. Lemmings and population problems. *Amer Sci* 21:119–131.
- Daly M, Daly S, 1975a. Behaviour of *Psammomys obesus* (Rodentia: Gerbillinae) in the Algerian Sahara. *Z Tierpsychol* 39:298–321.
- Daly M, Daly S, 1975b. Socio-ecology of Saharan gerbils, especially *Meriones libycus*. *Mammalia* 39:298–311.
- Douglass RJ, Wilson T, Semmens WJ, Zanto SN, Bond CW et al., 2001. Longitudinal studies of Sin Nombre virus in deer mouse-dominated ecosystems of Montana. *Am J Trop Med Hyg* 65:33–41.
- Dubrovsky YA, 1978. [*Gerbils and natural foci of leishmaniasis*.] Moscow: Nauka Publications. Russian.
- Fitzwater WD, Prakash I, 1969. Observations of the burrows, behaviour, and home range of the Indian desert gerbil, *Meriones hurrianae* (Jerdon). *Mammalia* 33:598–606.
- Gage KL, Kosoy MY, 2005. Natural history of plague: Perspectives from more than a century of research. *Annu Rev Entomol* 50:505–528.
- Galanina TM, Serbenyuk MA, 1994. [Formation of social relationships in male bank voles *Clethrionomys glareolus* (Microtinae, Rodentia). An ethological analysis.] *Zool Zh* 73:108–119. Russian with English summary.
- Garson PJ, 1975. Social interactions of wood mice (*Apodemus sylvaticus*) studied by direct observation in the wild. *J Zool Lond* 177:496–500.

- Glass GE, Childs JE, Korch GW, LeDuc JW, 1988. Association of intraspecific wounding with hantaviral infection in wild rats (*Rattus norvegicus*). *Epidemiol Infect* 101:459–472.
- Gromov VS, 1997a. [Space use system and social structure in gerbils of genus *Meriones* (Gerbillinae, Rodentia).] *Zh Obshch Biol* 58:35–54. Russian with English summary.
- Gromov VS, 1997b. [Territory scent marking in gerbils: A comparative analysis in four species of genus *Meriones*.] *Zh Obshch Biol* 58:56–80. Russian with English summary.
- Gromov VS, 2000. [Ethological Mechanisms of Population Homeostasis in gerbils (Mammalia, Rodentia).] Moscow: IPEE Press. Russian.
- Gromov VS, 2001. Day-time activity and social interactions in a colony of the fat sand rats, *Psammomys obesus*, at the Negev Highlands, Israel. *Mammalia* 65:13–28.
- Gromov VS, 2007. [The spatial-and-ethological population structure and the evolution of sociality in rodents.]. *Dokl Akad Nauk* 412:561–563. Russian.
- Gromov VS, 2008. [The Spatial-and-ethological Population Structure in Rodents.]. Moscow: KMK. Russian.
- Gromov VS, 2017. The spatial-and-ethological population structure, cooperation, and the evolution of sociality in rodents. *Behaviour* 154:609–649.
- Gromov VS, 2022. Ecology and social behaviour of the Mongolian gerbil: A generalised review. *Behaviour* 159:403–441.
- Gromov VS, Gromova LA, 1996. [Use of space, social relationships, and scent marking of tamarisk gerbils (*Meriones tamariscinus*) under semi-natural conditions.]. *Zool Zh* 75:280–296. Russian with English summary.
- Gromov VS, Ilchenko O, 2007. [Use of space and social organization in *Gerbillus perpallidus* under semi-natural conditions.]. *Zool Zh* 86:1001–1010. Russian with English summary.
- Gromov VS, Krasnov BR, Shenbrot GI, 2000. Space use in Wagner's gerbil, *Gerbillus dasyurus* (Wagner, 1842), in the Negev Highlands, Israel. *Acta Theriol* 45:175–182.
- Gromov VS, Krasnov BR, Shenbrot GI, 2001. Behavioural correlates of spatial distribution in Wagner's gerbil *Gerbillus dasyurus* (Rodentia, Gerbillinae). *Mammalia* 65:111–120.
- Gromov VS, Tchabovsky AV, 1995. [The spatial population structure of the tamarisk gerbil (*Meriones tamariscinus* Pall.) in southern Kalmykia during the non-breeding period.]. *Zool Zh* 74:134–139. Russian with English summary.
- Gromov VS, Tchabovsky AV, Paramonov DV, Pavlov AN, 1996. [Seasonal dynamics of the demographic and spatial structure of a population of the tamarisk gerbil (*Meriones tamariscinus*) in the Kalmykia semi-desert.]. *Zool Zh* 75:413–428. Russian with English summary.
- Halpin ZT, 1974. Individual differences in the biological odours of the Mongolian gerbil. *Behav Biol* 11:253–259.
- Halpin ZT, 1986. Individual odors among mammals: Origins and functions. *Adv Stud Behav* 16:39–70.
- Henttonen H, 1980. Norwegian lemming *Lemmus lemmus*. *Luonnon Tutkija* 84:23–25.
- Idris M, Prakash I, 1985. Social and scent marking behaviour in Indian gerbil, *Tatera indica*. *Biol Behav* 10:31–39.
- Idris M, Prakash I, 1987. Scent marking activity in the Indian gerbil, *Tatera indica* in relation to population density. *Anim Behav* 35:920–921.
- Isaev SI, Shilova SA, 2000. [Biotopic distribution of midday (*Meriones meridianus*) and tamarisk (*M. tamariscinus*) gerbils (Rodentia, Gerbillinae) in southern Kalmykia.]. *Izvestiya RAN Ser Biol* 1:94–99. Russian with English summary.
- Kappeler PM, 2019. A framework for studying social complexity. *Behav Ecol Sociobiol* 73:13. doi: [10.1007/s00265-018-2601-8](https://doi.org/10.1007/s00265-018-2601-8)
- Karulin BE, Nikitina NA, Litvin VY, Khlyap LA, Okhotsky YV et al., 1979. [Nocturnal activity of tamarisk gerbils (*Meriones tamariscinus*) and their home ranges.]. *Zool Zh* 58:1195–1201. Russian with English summary.
- Kim TA, 1960. [On ecology of the tamarisk gerbil (*Meriones tamariscinus* Pall.) in the Kyzyl-Kum desert.]. *Zool Zh* 39:759–765. Russian with English summary.
- Kittrell EMW, Gregg BR, Thiessen DD, 1982. Brood patch function for the ventral scent gland of the female Mongolian gerbil, *Meriones unguiculatus*. *Dev Psychobiol* 15:197–202.
- Krebs CJ, Lambin X, Wolff JO, 2007. Social behaviour and self-regulation in murid rodents. In: Wolff JO, Sherman PW, editors. *Rodent Societies – An Ecological & Evolutionary Perspective*. Chicago: University of Chicago Press, 173–181.
- Kumari S, Prakash I, 1981b. Behavioural responses of *Meriones hurrianae* (Jerdon) to conspecific sebum of ventral sebaceous gland. *Biol Behav* 6:255–263.
- Kumari S, Prakash I, 1981a. Observations on the social behaviour of the Indian desert gerbil, *Meriones hurrianae*. *Proc Indian Acad Sci (Anim Sci)* 90:463–471.
- Kumari S, Prakash I, 1984. Association between scent marking, density and dominance in the Indian desert gerbil *Meriones hurrianae*. *Indian J Exp Biol* 22:421–423.
- Macdonald DW, 1981. Dwindling resources and the social behaviour of capybaras, (*Hydrochoerus hydrochaeris*) (Mammalia). *J Zool* 194:371–391.
- Madison DM, 1980. An integrated view of the social biology of *Microtus pennsylvanicus*. *The Biologist* 62:20–33.
- Madison DM, 1984. Group nesting and its ecological and evolutionary significance in overwintering microtine rodents. *Spec Publ Carnegie Mus Nat Hist* 10:267–274.
- Magomedov M, Akhtaev M, 1993. [Relationship between diet preferences and population conditions of the tamarisk gerbil (*Meriones tamariscinus*) in dependence on the food resource dynamics.]. *Zool Zh* 72:101–110. Russian with English summary.
- Makuya N, Schradin C, 2024. Costs and benefits of solitary living in mammals. *J Zool*. doi: [10.1111/jzo.13145](https://doi.org/10.1111/jzo.13145)
- Meerburg BG, Singleton GR, Kijlstra A, 2009. Rodent-borne diseases and their risks for public health. *Crit Rev Microbiol* 35:221–270.
- Montgomery WI, 1979. Trap-revealed home range in sympatric populations of *Apodemus sylvaticus* and *A. flavicollis*. *J Zool Lond* 189:535–540.
- Montgomery WI, 1980. Spatial organization in sympatric populations of *Apodemus sylvaticus* and *A. flavicollis* (Rodentia: Muridae). *J Zool* 192:379–401.
- Musser GG, Carleton MD, 1993. Family Muridae. In: Wilson DE, Reeder DM, editors. *Mammal Species of the World*. Washington, DC: Smithsonian Institution Press, 501–755.
- Mykytowycz R, 1970. The role of skin glands in mammalian communication. In: Johnston JW, Moulton DG, Turk A, editors. *Advances in Chemoreception. I. Communication by Chemical Senses*. New York: Appleton-Century-Crofts, 327–360.
- Mykytowycz R, 1974. Odour in the spacing behaviour of mammals. In: Birch MC, editors. *Pheromones*. Amsterdam: North-Holland, 327–342.
- Neronov VV, Tchabovsky AV, Alexandrov DY, Kasatkin MV, 1997. [Spatial distribution of rodents under anthropogenic pressure on vegetation in Kalmykia.]. *Ekologia* 5:369–376. Russian with English summary.
- Ostfeld RS, Mills JN, 2007. Social behavior, demography, and rodent-borne pathogens. In: Wolff JO, Sherman PW, editors. *Rodent Societies – An Ecological & Evolutionary Perspective*. Chicago: University of Chicago Press, 478–489.
- Perflyeva YV, Shapiyev ZZ, Ostapchuk YO, Berdygulova ZA, Bissenbay AO et al., 2020. Ticks and tick-borne diseases. *Ticks Tick Borne Dis* 11:101498. doi: [10.1016/j.ttbdis.2020.101498](https://doi.org/10.1016/j.ttbdis.2020.101498)
- Pisarenko SV, Evchenko AY, Kovalev DA, Evchenko YM, Bobrysheva OV et al., 2021. *Yersinia pestis* strains isolated in natural plague foci of Caucasus and Transcaucasia in the context of the global evolution of species. *Genomics* 113:1952–1961.
- Popov CV, Tchabovsky AV, Pavlova EY, 1997. [The great gerbil (*Rhombomys opimus*) in the wild and a laboratory.]. *Zool Zh* 76:224–229. Russian with English summary.
- Popov CV, Tchabovsky AV, Shilova SA, Shchipanov NA, 1989. [Mechanisms of formation of the spatial-and-ethological

- population structure in the midday gerbil under natural conditions and after control measures. In: Sokolov VE, editor. *Fauna and ecology of rodents. Issue 17.* Moscow: Nauka Publications, 5–57. Russian.
- Popov NV, Survillo AV, Knyazeva TV, Varshavsky BS, Podsvirov AV et al., 1995. [Antropogenic transformation of the Black Lands' landscape and its effect on the biota. In: Varshavsky BS, editor. *Biota and the Natural Environments in Kalmykia.*] Moscow-Elista: Korkis Press, 211–221. Russian.
- Popov SV, Tchabovsky AV, 1998. [Behavior of *Meriones tamariscinus* in the wild (judging from direct observations).] *Zool Zh* 77:346–354. Russian with English summary.
- Poulet AR, 1972. Caractéristiques spatiales de *Taterillus pygargus* dans le Sahel Sénégalais. *Mammalia* 36:579–606.
- Rall YM, 1941. [On ecology of the tamarisk gerbil *Meriones tamariscinus*. In: Isaev VM, editor. *Rodents and Their Control. Issue 1.*] Saratov: Microb, 179–207. Russian.
- Randall JA, 2007. Environmental constraints and the evolution of sociality in semi-fossorial desert rodents. In: Wolff JO, Sherman PW, editors. *Rodent Societies – An Ecological & Evolutionary Perspective.* Chicago: University of Chicago Press, 368–379.
- Roberts SC, 2007. Scent marking. In: Wolff JO, Sherman PW, editors. *Rodent Societies – An Ecological & Evolutionary Perspective.* Chicago: University of Chicago Press, 255–266.
- Rogovin KA, Randall JA, Kolosova I, Moshkin M, 2004. Predation on social desert rodent, *Rhombomys opimus*. Effects of group size, composition and location. *J Mammal* 85:723–730.
- Schradin C, 2013. Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philos Trans R Soc London Ser B* 368:20120346. doi: [10.1098/rstb.2012.0346](https://doi.org/10.1098/rstb.2012.0346)
- Schradin C, Lindholm AK, Johannesen J, Schoepf I, Yuen C-H et al., 2012. Social flexibility and social evolution in mammals: A case study of the African striped mouse (*Rhombomys pumilio*). *Mol Ecol* 21:541–553.
- Shu C, Jiang M, Yang M, Xu J, Zhao S et al., 2020. Flea surveillance on wild mammals in northern region of Xinjiang, northwestern China. *Int J Parasitol. Parasites and Wildlife* 11:12–16.
- Smirin YM, Shilova SA, 1989. [Some features of social behavior of *Mus musculus* and *Apodemus sylvaticus*.] *Zool Zh* 68:99–110. Russian with English summary.
- Sokolov VE, 1977. [Systematics of Mammals. Orders Lagomorpha & Rodentia.] Moscow: Vysshaya Shkola. Russian.
- Sokolov VE, Gromov VS, 1997. [Growth and functional activity of the ventral gland and scent marking behavior in midday and tamarisk gerbils (*Meriones meridianus*, *M. tamariscinus*).] *Dokl Akad Nauk* 353:134–137. Russian.
- Stenseth NC, Atshabar BB, Begon M, Belmain SR, Bertherat E et al., 2008. Plague: Past, present, and future. *PLoS Med* 5:e3.
- Tchabovsky AV, Alexandrov DY, 1996. [Space use system of the midday and tamarisk gerbils in Kalmykia.]. *Zool Zh* 75:1842–1850. Russian with English summary.
- Tchabovsky AV, Lapin VA, 1989. [Some features of *Meriones libycus*' social behavior.]. *Zool Zh* 68:95–101. Russian with English summary.
- Tchabovsky AV, Lapin VA, Popov CV, 1990. [Seasonal dynamics of the social organization in *Meriones libycus*.] *Zool Zh* 69:111–125. Russian with English summary.
- Volyntin AA, 1950. [About population growth in midday and tamarisk gerbils after control measures. In: Naumov VP, editor. *Rodents and Their Control. Issue 3.*] Saratov: Saratov University Press, 59–68. Russian.
- Vorobei VA, 1986. [Ecology and geographic distribution of midday and tamarisk gerbils. In: Proc. 1st Conference of young biologist of the Caucasus region, 1986.] Kaphan: Nauka, 76–81. Russian.
- Wilson DE, Reeder DM, editors, 2005. *Mammal Species of the World: A Taxonomic and Geographic Reference.* 3rd edn. Baltimore, MD: Johns Hopkins University Press.
- Wolff JO, Lidicker WZ, 1981. Population ecology of the taiga vole, *Microtus xanthognathus*, in interior Alaska. *Can J Zool* 58:1800–1820.