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Ecology and social behavior of the midday gerbil Meriones meridianus: Insights from long-term research in the wild and seminatural environments

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ABSTRACT

The present review provides a compilation of the published data on the ecology and social behavior of midday gerbils. Both field studies and observations under semi-natural conditions provide evidence that the midday gerbil is a nocturnal, primarily granivorous rodent that lives in highly seasonal habitats. A typical feature of the midday gerbils' spatial organization is formation of multi-male–multi-female associations (breeding colonies) in which male home ranges overlap each other and with female ranges to a great extent, while females tend to occupy exclusive home ranges. The mating system of this species can be defined as polygynandry or promiscuity; males appear to compete for access to receptive females. The social structure in the midday gerbil is primarily based on aggressive interactions between conspecifics resulting in a dominance hierarchy among males and site-dependent dominance among females, especially during the breeding season. After the cessation of reproduction, a tendency towards more pronounced gregariousness appears, and midday gerbils form wintering groups; gerbils, however, lead solitary lives within these groups. Overall, the data presented expand our understanding of socio-ecology of gerbils.

Keywords: Midday gerbil; Ecology; Reproduction; Spatial organization; Scent marking.

1. Introduction

Gerbils (subfamily Gerbillinae, Rodentia) are a diverse group of rodents distributed across steppe, semi-desert and desert habitats of Europe, Asia, and Africa [1,2]. The diversity of gerbils and the ease with which some species (e.g., the Mongolian

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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 [3–6]. Unfortunately, the relevant information is widely scattered, not always complete, and sometimes conflicting. Moreover, not all aspects of the socio-ecology of gerbils have been studied equally, even in relatively well-studied species. The subfamily Gerbillinae includes about 110 species [7], 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* [8] and *Psammomys obesus* [9, 10]; others are gregarious, with the formation of relatively stable multi-male—multi-female associations (called breeding colonies; [11]), like in *Gerbillus dasyurus* [12,13], *Meriones meridianus* [4, 14], *Meriones hurrianae* [15–18], *Tatera indica* [19,20], *Taterillus pygargus* [21]; for a small number of species, a family-group lifestyle is characteristic, like in *Meriones unguiculatus* [4,5,22], *M. libycus* [4,23–26] or *Rhombomys opimus* [27–29]. Diurnal species, like *Meriones unguiculatus, M. libycus, Psammomys obesus* and *Rhombomys opimus* are relatively well studied. In most of other species, spatial organization has been studied only via a mark-recapture or radio tracking; direct observations of their social behaviors have been carried out in only a few species [4]. Therefore, much more research remains to be done to fill this knowledge gap.

Gerbils are 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 are natural carriers of these diseases and other important epidemics in different regions around the world [30–34]. Several natural foci of plague and tularemia exist in the Caspian Sea region and the persistence of these zoonotic foci increases the risk of re-emergence as people living in these areas may be in contact with rodents and fleas occasionally [35–38]. 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 midday gerbil *Meriones meridianus* (Pallas 1773) is a medium-sized (body mass averages 52.0 ± 0.6 g in adult males and 46.0 ± 0.5 g in adult females; [39]), nocturnal rodent inhabiting semi-desert and desert habitats of the Caspian Sea region and Central Asia [1,7]. Within the area of this species, the climate is arid or semi-arid and continental with relatively hot summers and cold dry winters [35].

Midday 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 [4,35–38,40,41]. Social behavior (specifically, aggressive encounters) has repeatedly been implicated as increasing the probability of pathogen transmission between individuals [42,43]. This is why many studies focus on the role of social behavior and demography of rodents in the maintenance and transmission of rodent-born diseases [44]. As for the midday gerbil, little is known about how social behavior and population dynamics of this species influences 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 midday gerbils, published mainly in Russian, to provide a detailed overview for one of nocturnal gerbil species. I would like to emphasize that studies conducted in other countries (e.g., Mongolia and China) provide very little information, based on direct observations in the wild, about the social organization and social behavior of midday gerbils.

I carried out ecological and behavioral studies of the midday gerbil in the wild (in the northwestern Caspian Sea region, the Black Lands area) and semi-natural environments (in large outdoor enclosures in Moscow region) in 1989–1995 [3,4,45–47]. To collect

data on the local population density of the gerbils and demographic structure, 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. 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. For direct observations of the gerbils [46], squares of 2.5 × 2.5 m were laid out in the enclosures, 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. Each animal was given an individual mark for long-distance identification. This was achieved by applying unique markers to the pelage of each individual with a permanent black wool dye. The gerbils partially fed on some herbs and grasses growing in the enclosures, but mainly were provided with a mixture of oats and sunflower seeds as well as fresh vegetables (carrot, cabbage, beetroots) *ad lib*. The animals were observed at night time using not bright artificial illumination. There were no signs of the influence of this illumination on the behavior of gerbils. Continuous observations of the gerbils lasted up to four months (from June to September). 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) [4,5].

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 midday gerbil, since these aspects of the socio-ecology of this species are unknown to many zoologists.

2. A brief outline of ecology

Most data on the habitat, food, activity, and reproduction of midday gerbils are obtained due to the field studies carried out in the Caspian Sea region [4,14, 40,48–53]. In this region, the gerbils prefer ridge-hilly sandy plains with sparse discontinuous vegetation of shrubs, grasses and herbs including *Tamarix ramosissima, Atriplex tatarica* (quinoa), *Achillea micrantha* (yarrow), *Agropyron fragile* (Siberian wheatgrass), *Artemisia lercheana* and *A. arenaria* (sagebrush), *Calamagrostis epigeios* (wood small-reed), *Cynanchum acutum* (stranglewort), *Centaurea arenaria* (sand cornflower), *Corispermum orientale* (family Amaranthaceae), *Eragrostis minor* (family Poaceae), *Koeleria glauca* (bluehair grass), *Gypsophila paniculat*a (common gypsophila), *Bassia prostrata* (forage kochia), *Senecio erucifolium* (family Asteraceae), *Silene multiflora* (family Caryophyllaceae), *Stipa capillata* (bunchgrass), *Tragus racemosus* (European bur grass), and some others [36,54,55].

The midday gerbil is primarily a granivorous species, but also uses leaves and stems of some herbs, as well as some insects (e.g., ants, darkling beetles, grasshoppers), for food [49,56,57]. Food, as a rule, is patchily distributed and unstable over time in the habitat of midday gerbils. All year round, the gerbils feed on seeds and some green and underground parts of grasses and herbs like *Agropyron fragile, Avena strigosa* (sand oats), *Alhagi camelorum* (camel's-thorn), *Artemisia arenaria, Salsola kali* (common saltwort, or tumbleweed), *Agriophyllum squarrosum* (Russian thistle), *Calligonum junceum* (family Polygonaceae), *Cuscuta europaea* (European dodder), *Achillea micrantha, Astragalus spp.* (goat's-thorn), *Cirsium arvense* (field thistle), *Sonchus arvensis* (field milk thistle); in winter, midday gerbils primarily use seeds of various plants for food, and in spring they

switch to green plants [50,56]. Midday gerbils do not hibernate; in autumn (mainly in October) these rodents hoard high-calorie food, e.g. seeds of sand oats, camel's-thorn, sagebrush and other plants [50,58]. Food caches (usually weighing 300–500 g) were found in many burrows of midday gerbils [50].

Midday gerbils are pronounced psammophils [35,40,51,56,57]. Most burrows are found to be located in shrub microhabitats. The underground tunnel structure is usually simple and basically with one opening. The length of tunnels reaches 4 m, and blind branches depart from them up to 20–25 cm; the depth of tunnels is 40–200 cm. As a rule, a burrow has one or two nest chambers as well as several chambers with food caches [35]. In summer, midday gerbils often seal the entrances to their burrows. Several nest burrows are found to be located within each individual home range [14].

Fields studies showed that midday gerbils are nocturnal, making them difficult to observe in the field [4,35,57]. However, due to direct observations under semi-natural conditions, two peaks of their activity at night time were revealed [4,46,47]. In winter, midday gerbils exhibited both nocturnal and diurnal activity [35].

Population density is found to show large fluctuations between years and across different parts of the species' range; in preferred habitats it can reach 60–70 animals/ha [4,14]. The breeding season lasts from February–March to October peaking in spring and fall [40,48,49,51,59]. During the breeding season, overwintered females produce two to four litters; young females born early in the breeding season can mature and breed in that season, producing one or two litters. The average number of pups per litter varied from 4.1 to 5.5 in different populations [40,49,51,57,60]. After weaning and emergence from their natal burrows, young individuals remain within their mother's home range for several days and then disperse; after dispersal, young gerbils usually occupy individual home ranges [14,52,59]. The operational sex ratio was relatively stable in different seasons of the year and was approximately 1:1 [48]. In the population of midday gerbils in the Minqin Desert in Gansu, China [61], the female-to-male ratio ranged from 0.67:1 to 0.91:1 in different years. This sex ratio may be an inherent feature of midday gerbils in the area itself, or male gerbils may be easier to capture. The activity of male midday gerbils is generally higher than that of females; therefore, males have a higher probability of being captured, resulting in more males than females in the sample [61].

The midday gerbil exhibits a mating system in which males actively seek receptive females during the breeding season. Moreover, the mating system of this species involves male-male competition for receptive females and obviously has some features of polygynandry as well as promiscuity [14,52]. In the enclosures, we regularly observed several males following a receptive female in a chain and taking turns mating [4,46]. Field studies and direct observations provide evidence that males and females do not form pair bonds and meet only for mating; the young disperse soon after weaning [4,14,46,52,59]. Some authors [61] suggest that the habitat conditions of midday gerbils are conducive to formation of social monogamy. However, species considered socially monogamous should exhibit pair bonding and biparental care in the wild, defend the territory occupied by a breeding pair, invest in their territories by the construction of common burrows or other shelters, have young with an extended period of maturation [62]. These features of social monogamy are not found in natural populations of the midday gerbil. Nevertheless, the microsatellite site analyses of genetic structure [61] revealed three types of mating systems in midday gerbils obtained from a population of the Minqin desert area: monogamous (19 groups), polyandry (4 groups), and polygyny (5 groups). These findings are reported to be consistent with the prediction that midday gerbil mating systems are dominated by monogamy. This is also consistent with a previous study where midday gerbils showed characteristics of monogamy, such as a high level of paternal behavior and a high level of ultrasound vocalizations in suckling pups, in the laboratory [63,64]. This conclusion on a predominant monogamous mating system in the midday gerbil based solely on experimental studies is not well-founded because it contradicts to the field data on population ecology and social behavior of

midday gerbils [3,4,14,46,52,53,65]. Moreover, the authors of the study [61] did not provide any data on the spatial organization of midday gerbils collected in the area, but the spacing pattern can be the most likely precursor of predominant mating system [4]. The data obtained in the genetic study [61] can be explained by the fact that despite the promiscuous mating system typical of the midday gerbil, females as well as males in some populations of this species have a limited number of sexual partners to mate with (e.g., because of a lower population density), and this results in occasionally monogamous or polygynous matings, but not in social monogamy.

Some theoretical models [66,67] predict the relationships between the spatial distribution of food resources, spacing patterns, population density, and mating systems. As for midday gerbils, during the breeding season they form relatively stable multi-male–multi-female associations in their natural populations (see below) irrespective of the distribution of food resources [4], and thus multiple mates are available for both males and females, and promiscuity results, like in some *Clethrionomys* (= *Myodes*) or *Microtus* species [11,66]. Unlike some other rodent species [67], the spacing patterns of midday gerbils are not dependent on population densities (see below). Therefore, taking into account recent data [61], the predominant mating system in the midday gerbil can be considered polygynandrous or promiscuous, as well as facultatively polygynous or monogamous.

3. Use of space, social behavior and social organization

The studies of midday gerbils in their natural habitat in the Black Lands area [14,52,53] provide evidence that adults of both sexes occupy individual home ranges, meaning that these gerbils do not live in pairs. During the breeding season, male midday gerbils are not territorial and can range over relatively large areas. Besides, stable aggregations of males in the vicinity of ranges of receptive females were found (**Figure 1**, A), so that male ranges overlapped each other and with female ranges to a great extent. As a result, multi-male–multi-female breeding colonies were formed, like, for example, in *Myodes* (= *Clethrionomys*) *glareolus* [11] or *Gerbillus dasyurus* [12]. Within the study plot of 1 ha (**Figure 1**), two breeding colonies can be distinguished: one consisting of six males and seven females, and the other consisting of seven males and four females. Female home ranges averaged 330 ± 49 m2 and were mutually exclusive (**Figure 1**, B); male home ranges averaged 1,053 ± 220 m^2 [14,52]. Within another study plot of seven hectares, five breeding colonies of the midday gerbil were found, each including four to seven adult males and two to nine breeding females [14].

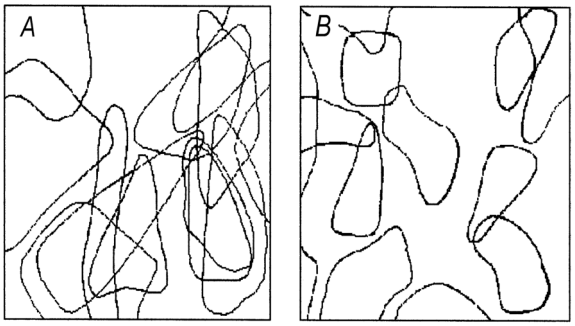

Figure 1. Map of the distribution of smoothed minimum convex polygon home ranges (contours obtained from recapture data) of adult males (**A**) and females (**B**) of the midday gerbils within the study plot of 1 ha during the breeding season (April 1984) in the Black Lands area (after Tchabovsky, 1993, with permission).

In general, home range sizes for both males and females were found to be variable and dependent on population density and availability of food resources. Specifically, female home ranges varied from 330 to 5,100 m^2 in different populations [14,52,59,68]. In the Kara-Kum desert, male home ranges averaged 2,363 ± 1,150 m^2 [14]. Long-term studies in the wild provide evidence that female home ranges are relatively stable in time and space, forming the basis of the spatial organization of this species during the breeding season [14]. Territoriality, i.e. protection of the home range (at least, the core area), seems to be typical of female midday gerbils [46,59]. This spatial structure appears to be independent of the population density of this species.

After the cessation of reproduction, a tendency towards more pronounced gregariousness appears: gerbils form wintering groups consisting of five or more individuals, gathering in a wintering burrow [35,40,51,52,59]. Every

wintering group occupied a common home range of 300–400 m^2 with a single nest burrow. Despite their tendency to form aggregations, midday gerbils, however, lead solitary lives within the wintering groups, and their interactions are rarely observed, as compared to the rate of interactions and nature of contact between individuals during the breeding season. In particular, during the entire observation period, only 11 interactions (nasal sniffs and tactile contact) were recorded [14].

A very specific *M. meridianus*' colony in the Black Lands area was found [14], where midday gerbils have inhabited some abandoned cattle-breeding farms and sheep corrals with large earthworks (300–600 m^2) and abundant weeds growing there in fairly loose soil; these earthworks were surrounded by habitats with much harder soil. Within the colony, three multi-male–multi-female associations were identified, in which breeding females occupied home ranges that overlapped each other to a large extent. Moreover, aggressive encounters typical of breeding females (see below) were rarely observed there, because the periods of above-ground activity of females with overlapping ranges were mutually exclusive in time. Such a situation can be explained by the above tendency to form aggregations, which is very characteristic of this gerbil species. This finding suggests that this tendency may not only occur during the winter season, but during the breeding season as well, if preferred habitats with better burrowing conditions are very limited. It should be noted, however, that no other similar colonies of midday gerbils were found. Therefore, occurrence of such a colony during the breeding season is rather an exception than a rule in populations of the midday gerbil [4].

Very little is known about social behavior of midday gerbils. Popov et al. [14] observed the gerbils in the wild (the Black Lands area) and recorded 217 interactions between adult individuals of both sexes during the breeding season. The majority of them (52.5%) were aggressive encounters (chases and fights) in both homo- and heterosexual dyads. Numerous displays of sexual behaviors such as sexual pursuit and copulation (a total 14.3% of the interactions) were recorded as well. These data, however, are not sufficient to characterize the social organization of the midday gerbil during the breeding season. To fill this gap, social interactions between adult midday gerbils monitored in the large outdoor enclosures were studied in detail [4,46,47]. Three groups of the gerbils each consisting of three adult females and three to six adult males were under direct observations. A total of 3,648 social interactions of the gerbils were recorded (**Table 1**).

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

Interactions	Males (n = 12) Interactions, addressed to				Females (n = 9) Interactions, addressed to			
	Males		Females		Males		Females	
	N	%	N	%	N	%	N	%
Peaceful	293	24.6	692	63.8	192	19.9	14	6.0
Ritualized agonistic	54	4.5	155	14.3	99	10.3	41	17.5
Overt aggressive	559	47.0	172	15.9	393	40.7	146	62.4
Avoidance	283	23.8	65	6.0	281	29.1	33	14.1
Total	1189	100	1084	100	965	100	234	100

The data presented in **Table 1** show that the majority of interactions between adults of the same sex (70.8 % in males and 77.5 % in females) were aggressive encounters and avoidance. Despite the high frequency of aggressive interactions in the enclosure groups, the aggressiveness did not lead to the death of the gerbils. The majority of peaceful and ritualized agonistic interactions were recorded in heterosexual dyads. These data provide evidence that relationships between adults in populations of the midday gerbil are primarily based on overt

aggressive interactions and/or mutual avoidance. During the breeding season, these interactions result in a dominance hierarchy among males and a site-dependent dominance among females [14,46]. Displays of sexual behaviors such as sexual pursuit and copulation (n = 176) were also recorded but not included in **Table 1**.

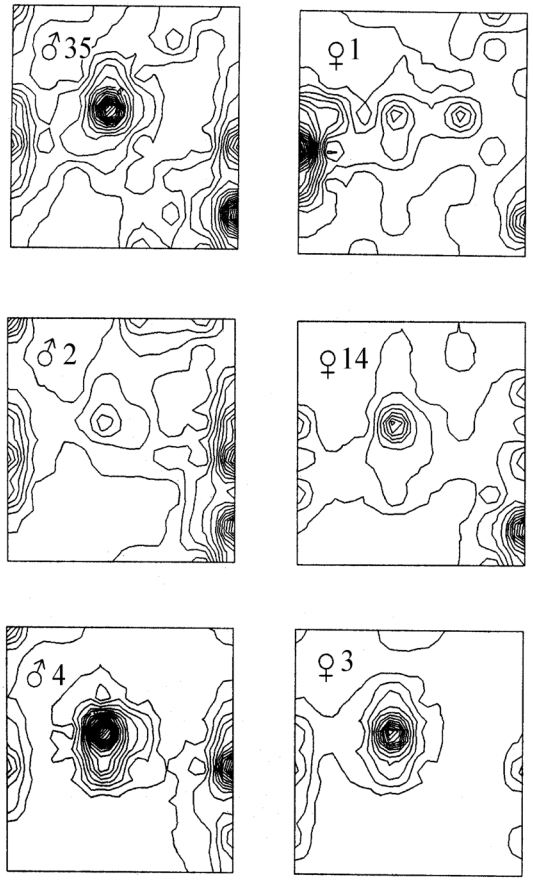

Figure 2. Contour mapping of the frequency of visual registration of midday gerbils in the enclosure of 20 × 20 m. Contour lines connect points of equal frequency of registrations per area unit (square 2.5 × 2.5 m). Higher density of the lines corresponds to the activity centers of the gerbils related to their nest burrows (after Gromov, 2000).

Below, more informative data characterizing the use of space and social behavior of gerbils in one of the enclosure groups (**Figure 2**) are presented. This group consisted of three males (# 2, #4 and #35) and three females (#1, #3 and #14). Males moved freely throughout the enclosure, and their activity centers overlapped each other and the females' activity centers; it looked like the males did not have defined home ranges, but roamed over the enclosure area. On the contrary, activity centers of the females associated with their nest burrows were mutually exclusive (**Figure 2**).

Thus, males did not exhibit territorial behavior, but rather established a dominance hierarchy, and male #35 dominated over males #2 and #4, while male #2 occupied a sub-dominant position, and male #4 was a subordinate. Male #35 (dominant) visited the nest burrows of females #3 and #14 most often, while male #2 (sub-dominant) more often interacted with female #14 near her nest burrow and less often with two other females; male #4 (subordinate) was predominantly in contact with female #3; all the males rarely appeared near the nest burrow of female #1. As for the females, their relationships can be defined as territoriality based on a site-dependent dominance, but they defended the core area in the vicinity of their nest burrows only. Judging from the field data and the results of direct observations in the semi-natural enclosures, it can be concluded that male and female midday gerbils occupy overlapping individual home ranges rather than live in pairs during the breeding season.

Figure 3 provides an additional illustration of the relationships between the gerbils. Peaceful interactions were much more common in heterosexual dyads (**Figure 3**, A). Males #35 and #2 were active in contact with the females, while male #4 was passive. The frequency of interactions with the males initiated by females was quite low, with the exception of interactions between female #1 and male #2. Overall, female #1 had more contact with the males than female #3, while female #14 was passive in this regard. Therefore, there were individual preferences for peaceful interactions between the males and females.

Aggressive interactions initiated by the males were addressed mainly to individuals of the same sex (**Figure 3**, B). The interactions between males were found to be asymmetric that reflects the establishment of a dominance hierarchy. Aggressive encounters of the females were found to be not asymmetric, and their relationships could be defined as territoriality based on site-dependent dominance.

This refers to a relationship in which an individual dominates other conspecifics within its home range. Apparently, aggressive interactions play a leading role in the social organization of the midday gerbil during the breeding season.

Figure 3, C shows the frequency and direction of ritualized agonistic displays (mainly side-way postures). These behaviors were observed mainly in interactions between the opposite-sex individuals: receptive females exhibited side-way postures when males approach them, and males, in turn, demonstrated a similar behavior in response to aggressive attacks initiated by the females. In the interactions between same-sex individuals, displays of side-way postures were rarely observed. Apparently, ritualized agonistic displays contribute to the suppression of aggressiveness in relationships between opposite-sex individuals during the breeding season.

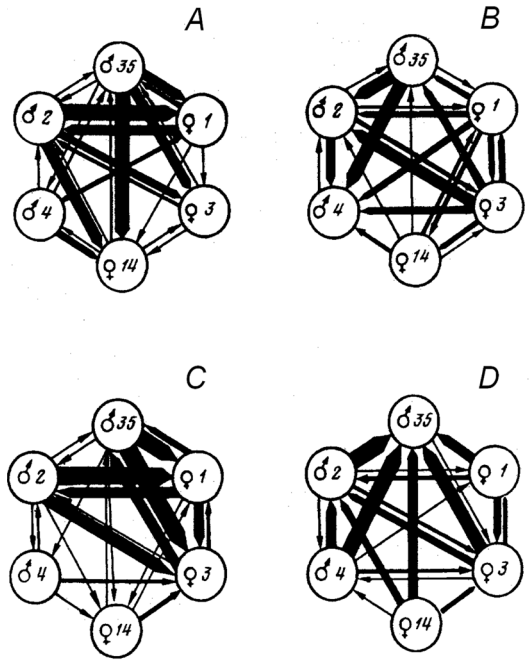

Figure 3. Occurrence and direction of interactions between the gerbils in the enclosure: **A** – peaceful interactions (n = 513), **B** – aggressive encounters (n = 530), **C** – ritualized agonistic interactions (mainly side-way postures, n = 166), **D** – avoidance (n = 186). Thickness of the arrows is proportional to the number of initiated acts in each dyad (after Gromov, 2000).

Both frequency and direction of avoidance (**Figure 3**, D) indicate that this behavior also plays an important role in the social organization of the midday gerbil during the breeding season. In the enclosure group, all females, as well as both males of lower rank, avoided contact with the dominant male #35. The relationships between the females developed in such a way that they mutually avoided contact with each other.

The relationships between males in other enclosure groups were generally similar to those between males #2, #4 and #35, reflecting the establishment of a dominance hierarchy. All females occupied nearly exclusive ranges in the enclosures. Thus, one can conclude that relationships between same-sex individuals during the breeding season are based on mutual antagonism, while interactions between opposite-sex individuals can be called moderately tolerant. The dominance hierarchy ensured the greater reproductive success for high-ranking males: observations in the enclosures have shown that dominant and sub-dominant males mate with females in 75% of cases [14,46].

The results of observations of the gerbils in the semi-natural enclosures are consistent with data obtained in the wild [4,14,35,52]. During the breeding season, midday gerbils form aggregations (multi-male–multi-female breeding colonies) where male home ranges overlap each other and with female ranges to a great extent, while adult females occupy nearly exclusive home ranges. Within these breeding colonies, males competing for access to receptive females establish a dominance hierarchy. After the cessation of reproduction in late autumn, breeding colonies disintegrate, and midday gerbils form wintering aggregations, where individuals lead solitary lives and rarely interact, compared to the rate of their interactions during the breeding season.

The seasonal changes in the spatial and social organization of *M. meridianus* related to the annual cycle of reproduction might be critical both in maintaining pathogen populations and the rates of pathogen transmission. Besides, transmission of pathogens during the breeding season may result from frequent agonistic encounters (primarily between males). This is a situation that should

promote epizootics.

4. Scent marking

Midday gerbils have a ventral sebaceous gland and use its secretion for scent marking [4,69]. This ventral gland looks like a fusiform pad, and its size averages 103 ± 4 mm^2 in males (n = 22) and 49 ± 6 mm^2 in females (n = 10; [47]). 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. Observations in the wild as well as in the semi-natural enclosures [4,47,69] have shown that the objects of ventral rubbing include burrow entrances, soil hammocks, small stones, and lumps of ground, both inside the home ranges of the gerbils. Scent marks with the ventral gland secretion may have a role in individual recognition. Specifically, Halpin [70] provided evidence that Mongolian gerbils (*Meriones unguiculatus*) can differentiate between the ventral gland secretions from different individuals. It can be assumed that midday gerbils are also able to distinguish relevant scent marks from different conspecifics. Along with ventral rubbing, midday gerbils, like Mongolian gerbils [5], 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 by its anterior legs, the animal builds up a conic hillock ("signal heap") covering the drop of urine and fecal pellets.

Direct observations in the enclosures showed that scent marks with the ventral gland secretion were more common than "signal heaps", and of the 2,352 scent-marking events recorded, 56.5% was ventral rubbing, and 42.9% was building "signal heaps". Such a bias might be explained by the nocturnal activity of midday gerbils, whose "signal heaps" are hardly visible at night and do not serve as visual marks, like in diurnal Mongolian gerbils [5]. In addition to these kinds of scent-marking behaviors, female midday gerbils mark their home ranges by genital rubbing, but the proportion of these scent-marking events is very small (0.6%). Thus, the most common scent-marking patterns in midday gerbils are ventral rubbing and building "signal heaps".

Table 2. Frequency of scent-marking events (Mean ± SE per 1 hour of the above-ground activity) in adult and young gerbils in the semi-natural enclosures (after Gromov, 2000).

Age and sex	Number of individuals	Ventral rubbing	Building "signal heaps"
Adult males	12	10.2 ± 2.6	6.1 ± 1.2
Adult females	9	3.0 ± 1.5	3.0 ± 0.6
Young individuals	7	0.9 ± 0.9	0.5 ± 0.3

Scent-marking behaviors of midday 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 9 weeks by building "signal heaps"; first events of ventral rubbing were observed at the age of 10–11 weeks [4].

Table 3. Frequency of scent-marking events (Mean ± SE per 1 hour of the above-ground activity) in female midday 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	2.4 ± 1.0	3.3 ± 0.9
II	5.0 ± 1.4	5.3 ± 1.0

In female midday 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 midday gerbils exhibited a higher rate of scent-marking activity within the ranges of the breeding females [4].

Long-term observations of midday 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 [4,69]. Seasonal dynamics of ventral rubbing was obviously related to seasonal changes of the integrity of the ventral gland and its functioning [4]. At the non-breeding period (in autumn), the rate of ventral rubbing was decreased by 10–20 times as compared to 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.

Behavioural observations revealed a close association between the scent-marking activity and social hierarchy in male midday gerbils: individuals of a higher social rank displayed scent marking more frequently than subordinate individuals (**Figure 4**). 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 [71,72].

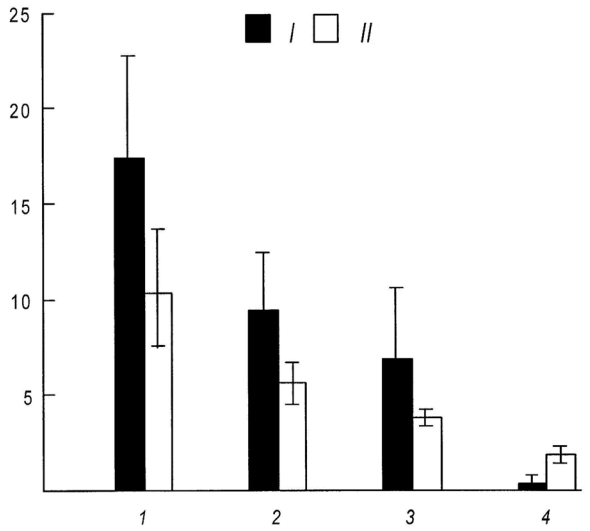

Figure 4. Relationship between social status and scent-marking activity in male midday gerbils. I–ventral rubbing, II–building "signal heaps". 1–4–relative social rank. Vertical axis–number of scent-marking events per 1 h of above-ground activity. Means are given ± SE (after Gromov, 2000).

To summarize, one can conclude that ventral rubbing and building "signal heaps" are the most common scent-marking patterns in the midday gerbil. The ventral gland secretion is known to be implicated in individual recognition [70,73] as well as mate recognition [74,75]. "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 [72]. Possession of a home range/ territory is very important for any adult individual, especially for breeding females, so scent marking could be considered also as a means of home range familiarization [76,77]. Thus, scent marking in midday gerbils is a complex and multi-functional phenomenon.

5. Conclusion

The midday gerbil is a nocturnal, primarily granivorous rodent that lives in highly seasonal habitats and displays seasonal fluctuations in reproduction. During the breeding season, a typical feature of the midday gerbil' spatial organization is formation of multi-male–multi-female associations (breeding colonies) in which male home ranges overlap each other and with female ranges to a great extent, while females tend to occupy exclusive home ranges. Female home ranges are relatively stable in time and space, forming the basis of the spatial organization of this species during the breeding season. Territoriality, i.e. protection of the home range, seems to be typical of female midday gerbils. The predominant mating system of this species can be defined as polygynandry or promiscuity; males appear to compete for access to receptive females. Under some environmental conditions, however, monogamous and polygynous matings may occur. To clarify these aspects of the reproductive biology of the midday gerbil, further studies should be carried out.

The social organization in the midday gerbil is primarily based on aggressive interactions between conspecifics resulting in a dominance hierarchy established in males and site-dependent dominance among females. After the cessation of reproduction, a tendency towards more pronounced gregariousness appears, and midday gerbils form wintering groups consisting of several individuals of both sexes. Every

wintering group occupies a common home range with a single nest burrow. Despite their tendency to form aggregations, midday gerbils, however, lead solitary lives within the wintering groups, and their interactions are rarely observed.

Scent marking behavior in the midday gerbil is a multi-functional phenomenon. Ventral rubbing and building "signal heaps" are the most common scent-marking patterns. The ventral gland secretion may be implicated in individual recognition, and "signal heaps" containing urine may convey more complex information indicating not only species and individual identity, but sex, age, social status and reproductive condition. Possession of a home range/ territory is very important for any adult individual, especially during the breeding season, so scent marking could be considered as a means of territory familiarization or even monopolization. In addition, scent marking might be used by female gerbils as a reproductive tactic to attract mates.

Statements and Declarations

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