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The Mongolian gerbil phenomenon: Can the generally accepted conceptual models explain the evolution of sociality, helping and cooperation in this species?

Vladimir S. Gromov

ABSTRACT. The present article provides a compilation of the published data on the life history traits of the Mongolian gerbil (*Meriones unguiculatus*) related to sociality, helping and other cooperative behaviors. The evolution of sociality in rodents means the transition from solitary living to a family-group lifestyle. The Mongolian gerbil is a highly social and cooperative breeding species with the complicated social organization and biparental care. The most common social units of this species are extended family groups. Members of the family groups act cooperatively defending and marking their territories, maintaining nests, hoarding food, and raising young. Thus, the Mongolian gerbil is a species with high cooperative abilities. The generally accepted conceptual models relevant to the evolution of sociality among rodents do not explain the evolution of sociality in the Mongolian gerbil. Predation pressure and spatial distribution of food resources cannot be considered selective forces promoting the formation of family groups. Alloparental care, or helping, is not reproductive altruism in the Mongolian gerbil, and it seems unlikely that this behavior evolved merely due to kin selection under 'Hamilton's rule'. Cooperation is an immanent attribute of a family-group lifestyle. Complex forms of cooperation, in turn, contribute to the evolution of sociality. This evolutionary process can be thought of as some kind of 'stimulation of similar with the similar': pair bonding stimulates cooperation which in turn contributes to the formation of extended family groups typical of this species.

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KEY WORDS: Mongolian gerbil, sociality, evolution, helping behavior, cooperation.

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Феномен монгольской песчанки: Объясняют ли общепринятые теоретические концепции эволюцию социальности, помощничества и кооперации у этого вида?

В.С. Громов

РЕЗЮМЕ. В статье рассматриваются опубликованные данные о биологии и поведении монгольской песчанки (*Meriones unguiculatus*), связанные с эволюцией социальности, помощничества и кооперации. У грызунов под эволюцией социальности подразумевается переход от одиночного к семейно-групповому образу жизни. Монгольская песчанка — социальный вид с кооперативным размножением и сложной социальной организацией, при этом заботу о потомстве проявляют оба родителя. Типичная семейная группа этого вида состоит из пары взрослых особей-родителей и двух-трех выводков молодняка. Все члены семейной группы принимают участие в охране и маркировке участка обитания, обустройстве гнезда, запасании кормов и ухаживании за детенышами, что указывает на широкое развитие кооперации. Общепринятые теоретические концепции не объясняют эволюцию социальности этого вида. В частности, пресс хищников и распределение кормовых ресурсов не могут служить селективными факторами, способствующими формированию семейных групп. Помощничество у монгольской песчанки нельзя рассматривать в качестве репродуктивного альтруизма, возникшего в процессе эволюции в соответствии с "правилом Гамильтона". Кооперация — неотъемлемый атрибут семейно-группового образа жизни, и сложные формы кооперации, в свою очередь, способствуют эволюции социальности. Фактически, этот эволюционный процесс можно рассматривать как результат "стимуляции подобного подобным": парные связи стимулируют кооперацию, которая, в свою очередь, способствует образованию сложных по составу семейных групп, типичных для монгольской песчанки.

КЛЮЧЕВЫЕ СЛОВА: монгольская песчанка, социальность, эволюция, помощничество, кооперация.

Introduction

Rodents are thought to be excellent models to develop paradigms and test hypotheses in socioecology, particularly concerning the evolution of sociality, as well as the evolution of altruistic and cooperative behaviors. In an ultimate sense, sociality means group-living, that in turn may be viewed as a life-history tactic increasing the fitness of group members. The evolution of sociality requires both that individuals get together in groups and that they cooperate within them.

The social units in rodent populations may be classified as follows: solitary dwellers, aggregations (multi-male–multi-female associations, or breeding colonies), and family groups (Gromov, 2008, 2017, 2018). Solitary dwellers, especially of the same sex, use, as a rule, nearly exclusive home ranges and display nonsocial behaviors, such as activity and foraging. Within breeding colonies of many rodent species, adult females tend to occupy nearly exclusive home ranges during the breeding season, whereas adult males maintain much larger and unprotected home ranges located corresponding to the location of the females' ranges. As for species with a family-group lifestyle, interactions within family units essentially differ from those between groups with the former being to include affiliative, cooperative, and nepotistic behaviors. Spatially, members of a family group exhibit essential overlap, including sharing one or more nest burrows. Neighboring family groups occupy nearly exclusive and protected home ranges, and their members exhibit primarily aggressive interactions with other conspecifics. In rodents, the evolution of group living proceeded (and, perhaps, proceeds at present) in two main directions: (1) towards formation of multi-male–multi-female breeding colonies and (2) towards formation of family groups, but it is the latter that is characterized by the most complex social organization. Therefore, the evolution of sociality in rodents means the transition from solitary living to a family-group lifestyle (Gromov, 2008, 2017, 2018).

A primary goal of socioecology is to understand the selective forces driving variation in social systems. Socioecological conceptual models aim to predict the effect of environmental variables on species' ecology and social behavior. A wide variety of suggestions has been proposed about the advantages of living in groups. These suggestions fall into three obvious categories: advantages related to defense or avoidance of predators; advantages related to optimal foraging strategies; and advantages concerned with reproduction (Crook, 1970a; Eisenberg *et al*., 1972; Kleiman & Eisenberg, 1973; Alexander, 1974; Clutton-Brock, 1974; Geist, 1974; Jarman, 1974; van Schaik & van Hooff, 1983; Carr & Macdonald, 1986; Terborgh & Janson, 1986; Jarvis *et al*., 1994; Ebensperger, 1998; McGuire *et al*., 2002; Lacey & Sherman, 2007). Group living is usually thought to enhance access to food resources and/or reduces vulnerability to predation.

According to the generally accepted socioecological models (Crook, 1970a,b; Alexander, 1974; Clutton-Brock ,1974; Clutton-Brock & Harvey, 1976; Crook *et al*., 1976; Grove, 2012), group size is a core trait defining social systems and social complexity, so understanding group-size evolution is suggested to be critical to understanding the evolution of sociality (Hass & Valenzuela, 2002; Downes & Hoefer, 2004; Pollard & Blumstein, 2008). Such a view is traditional and based primarily on comparative studies of social organizations in birds, bats, primates and ungulates whose individuals may aggregate in large flocks, packs, troops and herds which are referred to as most social (Crook, 1970a,b; Bradbury & Vehrencamp, 1977; Jarman, 1974; Lott, 1984; Terborgh & Janson, 1986).

The evolution of intra-specific altruism and cooperation is generally studied within the framework of kin selection theory (Hamilton, 1964; Grafen, 1984; West *et al*., 2007). According to Hamilton (1964), groups of closely related individuals are a necessary condition for the evolution of altruism and cooperative behaviors via kin selection.

A well-known phenomenon of intra-specific altruism is alloparental care, or helping, exhibited by cooperatively breeding mammals, including some rodent species (Jennions & Macdonald, 1994; McGuire & Bemis, 2007; Solomon & Keane, 2007; Vásquez, 2016). Cooperative breeding is defined as a situation where more than a pair of individuals exhibit parent-like (helping) behavior towards young of a single brood (Koenig & Pitelka, 1981). In rodents, activities defined as helping include feeding, retrieving, and huddling over pups, as well as pup grooming (Emlen, 1991; Solomon & French, 1997; Gromov, 2023). In behavioral ecology, alloparental care is viewed as reproductive altruism that is costly to the actor and beneficial to the recipient (Davies *et al*., 2012). If the actor suffers cost C and the recipient gains a benefit B as a result of the altruistic act, then the gene causing the actor to behave altruistically will increase in frequency if $r \times B - C > 0$, where r is the coefficient of relatedness of the actor to the recipient. This result is known as 'Hamilton's rule' (Charnov, 1977). Put into words, altruistic behavior can be favored if the benefits to the recipient (B), weighted by the genetic relatedness of the recipient to the actor (r), outweigh the costs to the actor (C). If an individual has a choice between rearing its own offspring and helping its mother to produce offspring, the expression above becomes $B/C > 1$, assuming that the individual's own offspring and its mother's offspring, both have $r = 0.5$. Therefore, helping will be favored by kin selection if by the individual's help its mother produces more extra offspring than the individual has 'sacrificed' through providing help.

As for cooperation, the following definition is accepted in behavioral ecology: a behavior is cooperative if it provides a benefit to another individual (recipient) and has been selected for (at least partially) because of its beneficial effect on the recipient. The latter clause is added to exclude behaviors, which merely provide a one-way by-product for others. This definition thus includes all altruistic and some mutually beneficial behaviors (West *et al*., 2007; Davies *et al*., 2012).

A number of theoretical models have been proposed to explain the origin and persistence of intra-specific cooperation, but there is much confusion about the relationship between these models. In particular, Lehmann & Keller (2006) developed a conceptual framework that delineates the conditions necessary for the evolution of altruism and cooperation. They showed that at least one of the following conditions needs to be fulfilled: (1) direct benefits to the focal individual performing a cooperative act; (2) preferential interactions between related individuals; and (3) genetic correlation between genes coding for altruism and phenotypic traits that can be identified. When one or more of these conditions are met, cooperation can evolve if the cost-to-benefit ratio of cooperative acts is greater than a threshold value.

Another conceptual model to explain the evolution of cooperation was developed by van Veelen *et al.* (2010). In this model, grouping and cooperative tendencies were coded as polygenic traits. The authors of the model assume that (1) cooperation increases total group productivity, but lowers the relative fitness of cooperators within their group; (2) the number of offspring produced by an individual is a function of the size of the group it is in, of the cooperativeness of the other group members, and of the cooperativeness of the individual itself; (3) this function is hump-shaped with respect to the size of the group. The model shows that the tendency to form groups and the tendency to cooperate interact, and that the shape of the functions that describe the number of offspring of an individual makes a difference for how changes in parameters change equilibrium outcomes. The first characteristic they share is that, for constant levels of cooperation, they all are hump-shaped with respect to group size. Therefore, there is an optimal group size for the performance of a task. The second common characteristic is that for small groups, it pays off for an individual to cooperate, while cooperating becomes unfavorable if an individual finds itself in a large group.

The founders of behavioral ecology (Davies *et al.*, 2012) proposed four different hypotheses for the evolution of cooperative behavior. The first is kin selection, which explains altruistic cooperation among relatives. The other three all rely on cooperation providing some direct benefit to the cooperator: by-product benefits, reciprocity, and enforcement. In these cases, cooperation ends up not being altruistic, and is instead mutually beneficial. The way in which cooperation can provide a direct benefit can be complex, involving delayed benefits that only accrue in the long term or active enforcement mechanisms (Davies *et al.*, 2012).

The Mongolian gerbil (*Meriones unguiculatus* Milne-Edwards, 1867) is a diurnal social rodent inhabiting typical steppe and semi-desert areas of Central Asia (Bannikov, 1974; Ågren *et al.,* 1989a; Gromov, 2022). The most common social units of this species are extended family groups composed of one adult male, one or two adult females and their male-female offspring (up to four litters, averaging 5–6 young in each litter). The number of individuals in large family groups can amount to 28. The Mongolian gerbil displays characteristics of monogamy such as shared home ranges and nests even beyond the breeding season, selective aggression against strangers but not toward the social partner, and shared parental care. However, the mating system of this species may not be defined as genetically monogamous, because, along with male-female pairs, there are polygynous social units where a male lives with two or even three breeding females. Moreover, both sexes were found to mate not only with their social partners, but also with neighbors and strangers (Ågren *et al*., 1989a; Gromov, 2022). Hence, the Mongolian gerbil has a variable mating system that could be defined as a combination of behavioral (social) monogamy and polygyny. Besides, the Mongolian gerbil is a cooperative breeding species. Cooperation in breeding is related to biparental care of young. Moreover, young gerbils that remain in the natal area become non-breeding helpers assisting in the rearing of their younger sisters and brothers. Behavioral monogamy and cooperative breeding (in terms of alloparental care displayed by elder offspring) may have evolved as an adaptation to harsh environment. Mongolian gerbils act cooperatively defending and marking their territories, digging underground tunnels, maintaining nests, hoarding food, and raising young. Therefore, the Mongolian gerbil is a species with high cooperative abilities (Gromov, 2022).

Thus, the Mongolian gerbil is one of the rodent species with the most complex social organization, which can be used as a model species to test some hypotheses in socioecology and behavioral ecology. The aim of this article is to examine whether the generally accepted conceptual models predicting causal mechanisms for the evolution of sociality and altruistic and cooperative behaviors are relevant to the Mongolian gerbil.

The evolution of sociality

Such a criterion of sociality as group size is not quite appropriate for rodents (Burda *et al*., 2000; Gromov, 2008, 2011a, 2014, 2017, 2018), because the most complicated social structure is characteristic of those rodent species that form rather small family groups, with the only exception — the naked mole-rat *Heterocephalus glaber* (Rüppel, 1842) (Jarvis *et al*., 1994). In other words, a core trait defining social systems and social complexity in rodents is not group size, but group structure or group composition, and the evolution of sociality among rodents means the transition from solitary living to a family-group lifestyle (Gromov, 2008, 2011a, 2014, 2017, 2018).

Considering spatial relationships and group structure, it is important to realize that rodents are primarily sedentary animals, and every adult individual or family group possesses a home range used for basic requirements: foraging, digging of burrows or construction of other shelters to avoid predators and reproduce, interaction with conspecifics, etc. A pronounced sedentary lifestyle distinguishes rodents from the much more mobile primates, ungulates and carnivores. Formation of aggregations and cohesive groups in rodent populations, with rare exceptions, results from more or less tolerant interactions between conspecifics and subsequent overlap of their home ranges. To account for the formation of aggregations or family groups in different rodent taxa, a number of conceptual models have been proposed, but most involve predation pressure and spatial distribution of food resources.

Effects of predation

In rodents, predation pressure is often viewed as a selective force favoring group living (Hoogland & Sherman, 1976; Hoogland, 1979, 1981; van Schaik, 1983; Krause & Ruxton, 2002). Members of larger groups may benefit from dilution (Hamilton, 1971), confusion, and enhanced vigilance (Yáber & Herrera, 1994). However, predation pressure is difficult to quantify, and even though many rodent species are preyed upon by numerous aerial and terrestrial predators, there is no data on the frequency of this predation. Moreover, no methods are developed to evaluate the general effect of predation to compare rodent species with different levels of sociality.

A commonly cited benefit of aggregations is the ability for individuals to reduce their vigilance (i.e., time spent scanning for predators) as group size increases — the so-called ‘group size effect’, or ‘many eyes effect’ (Hamilton, 1971; Pulliam, 1973; Berger, 1978; Lipetz & Bekoff, 1982; Holmes, 1984; Elgar, 1989; Lima, 1990; Roberts, 1996). The results of studies on some gregarious murid rodents (Madison *et al*., 1984; Getz *et al*., 1990; Hakkarainen *et al*., 1992; Jędrzejewski *et al*., 1992; McGuire *et al*., 2002) provide conflicting information suggesting that predation may prevent formation of large groups (i.e., gregariousness), and that single individuals may be most successful in avoiding predation.

It is also important to realize that any cohesive social unit of rodents, especially a family group, does not form immediately or at least in a short period of time. The formation of family groups is preceded by pair bonding. Until a family (i.e. a breeding pair with reared offspring) is actually formed, it is pointless to consider any group effects associated with reduced predation risk.

The so-called group size effect has not been studied in natural populations of Mongolian gerbils. However, an attempt has been made to assess this effect in other gerbil species, *Rhombomys opimus* (Lichtenstein, 1823), which also lives in family groups (Tchabovsky *et al*., 2001). In that study, time budgets of solitary females and females living in male-female pairs were compared. It was shown that females of both categories spent similar time in high-cost upright postures that manifest a high level of alertness (overt scans, after Lima & Bednekoff, 1999). This finding contradicts the hypothesis that vigilance, and especially its high-cost component, should decrease with increasing group size. In paired females, upright postures can be attributed to within-group vigilance, masking the group size effect. The authors of this study suggested that upright posture in *R. opimus* is associated with nonspecific behavior to gain information about the environment whether it is social (potential presence of conspecifics) or ecological (potential presence of predators). In other words, vigilance or scanning can be considered as a general process of acquisition of information, which may be aimed equally at scanning for a predator, competitor, partner, or resources (Desportes *et al*., 1991; Slotow & Rothstein, 1995; Bekoff, 1996; Gould *et al*., 1997; Treves, 2000). This conclusion is also true for such a diurnal species as the Mongolian gerbil living in family groups.

In general, there is no convincing evidence that predation pressure could really promote the evolution of sociality (i.e., the transition from solitary living to a family-group lifestyle) in rodents. A group size effect and other similar effects are characteristic of both gregarious species and species with a family-group lifestyle such as the Mongolian gerbil, and thus cannot explain the formation of family groups (Gromov, 2017).

Effects of food resources

It is generally accepted that the overall abundance and spatial distribution of food resources affect composition and size of social units in populations of mammals, including rodents (Crook, 1970a,b; Alexander, 1974; Jarman, 1974; Crook *et al*., 1976; Macdonald, 1979, 1983; Carr & Macdonald, 1986). It has been particularly shown that the abundance of food resources can influence the spatial distribution of individuals in some rodent species (de Vos & Gillespie, 1960; Johns & Armitage, 1979; Ims, 1987). Furthermore, it is suggested that the spatial distribution of food resources is of great importance in the evolution of social systems, and relevant conceptual models have been proposed to rodents. In particular, the resource dispersion hypotheses (RDH) describes ecological circumstances under which groups could evolve (Slobodchikoff, 1984; Ostfeld, 1990; Johnson, 2002): when resources are patchy, females should form groups to defend the patches, whereas when resources are uniform, females should not clump; males should associate with a group of females (the case of polygyny), when resources are patchy, but only with a single female, when resources are uniform (the case of monogamy). The RDH predicts that polygyny will only prevail under circumstances that favor the defense of resources by groups of more than two individuals. These groups are thought to consist of one male and several females, with the latter taking on the primary role in the resource protection. Conversely, monogamy is expected to persist where much lower levels of resource protection is required, and under such circumstances the male in a breeding pair assumes the role of territorial defense preventing the incursion of rival males (Slobodchikoff, 1984).

A research to test the RDH predictions has been conducted, in particular, on the Gunnison’s prairie dog *Cynomys gunnisoni* (Baird, 1855) (Travis & Slobodchikoff, 1993). It was shown that a more uniform distribution of food resources resulted in a greater number of monogamous family groups versus polygynous. However, the patterns of space use and social structure in the colonies of *C. gunnisoni* were found to be the result of individual responses to the resource abundance and distribution and were not due to male mating strategies, such as resource defense or female defense polygyny (Verdolin, 2007). The results of these studies are somewhat contradictory and only partially support the RDH.

The results of several studies, conducted in populations of the prairie vole, *Microtus ochrogaster* (Wagner, 1843), appear to support the RDH. In a moist habitat, typically abundant with preferred food plants, prairie voles are monogamous cooperative breeders living in family groups formed from breeding pairs maintaining a common territory and sharing parental responsibilities (Carter et *al*., 1995; Carter & Roberts, 1997). In a drier habitat of grasses, with scarce food resources and ephemeral moisture, prairie voles are not monogamous, and home ranges of the males overlap those of several females (Danielson & Gaines, 1987; Getz *et al*., 1993). However, there is a generally accepted view on the prairie vole as a species with a family-group lifestyle exhibiting social monogamy (Carter & Getz, 1993; Carter *et al*., 1995; Insel *et al*., 1995; Roberts *et al*., 1998; Ophir *et al*., 2008; Ahern *et al*., 2011; Barrett *et al*., 2013). Actually, there is much confusion regarding the mating system and structure of social units in populations of the prairie vole (Getz & McGuire, 1997; Roberts *et al*., 1998; Mahady & Wolff, 2002; McGuire *et al*., 2002; Solomon *et al*., 2004; Lucia & Keane, 2012), so the relationship between the distribution of food resources and the composition and size of social units in *M. ochrogaster* remains unclear.

As for the Mongolian gerbil, both monogamous and polygynous family groups were found in habitats with high and low population densities regardless of the spatial distribution of food resources, and the ratio of monogamous and polygynous family groups was the same in different habitats (Gromov, 2022). Generally, the RDH is not universal and cannot explain the evolution of social monogamy in rodents such as Mongolian gerbils. The RDH might predict group composition and size in some gregarious rodents, such as, for example, commensal mice and rats (Gromov, 2018), but not composition and size of family groups in highly social rodent species.

To summarize, one can conclude that the generally accepted socioecological models related to predation pressure and spatial distribution of food resources have low predictive value in explaining the evolution of sociality (i.e., the transition from solitary living to a family-group lifestyle) in rodents, including the Mongolian gerbil.

The evolution of helping and cooperation

In species with a family-group lifestyle, such as the Mongolian gerbil, young individuals delaying dispersal and remaining philopatric may gain direct or indirect fitness benefits staying within their natal groups (Stacey & Ligon, 1987, 1991; Kokko & Johnstone, 1999; Solomon & Keane, 2007). In these groups, offspring participate in care of subsequent litters born to their mothers. It is hypothesized that the formation of extended family groups reflects a compromise between the cost of dispersal versus the cost of foregoing reproduction and staying within the natal group (Nunes, 2007). However, this hypothesis is not entirely applicable to rodents, since juveniles involved in caring for younger siblings may reproduce successfully later, i.e. after dispersal (Gromov, 2023).

As for family groups of Mongolian gerbils, the number of potential offspring of several helpers is not less than the number of their mother’s offspring, and this does not correspond to the conditions under which ‘Hamilton's rule’ applies. The evolution of helping in the Mongolian gerbil is much more than intriguing because estrus females can visit adjacent territories to mate with neighbors or strangers (Ågren *et al*., 1989a; Gromov, 2022), resulting in multiple paternity. Hence, the offspring from an older litter may be related to succeeding litters only as half-siblings. Benefits that helpers might accrue by assisting parents in the rearing of younger siblings would, therefore, proportionately reduced. Thus, it is difficult, if possible at all, to calculate the ratio of benefits and costs of helping in the Mongolian gerbil in terms of ‘Hamilton’s rule’.

According to the inclusive fitness theory (Hamilton, 1964), alloparental care for younger siblings by older juveniles (i.e. helping) may alter both the indirect and direct fitness. In particular, helpers may benefit indirectly if breeders that receive assistance subsequently produce more offspring. In laboratory studies on Mongolian gerbils, however, neither the presence of helpers nor their larger numbers affected litter size at weaning (Ostermeyer & Elwood, 1984; French, 1994). Moreover, it was found that infants may suffer a retarded growth in the presence of helpers (Ostermeyer & Elwood, 1984). Salo & French (1989) carried out a supplementary study to examine a hypothesis that young Mongolian gerbils that remained in their natal family group, and gained experience with younger siblings, would be more successful in raising their own litters than were individuals that did not have such experience. It was shown that early experience with younger siblings influenced reproductive performance, pup development, and parental behavior. The effects of early experience with younger siblings were more influential for males. Measures of pup body mass gain and eye opening both indicated that males that received early experience with younger siblings were better sires, as reflected in advanced pup development. Thus, the presence of an experienced male was directly beneficial for pup development. Besides, both the latency to reproduce the first litter and the proportion of pairs giving birth within 50 days suggest that individuals receiving experience with younger siblings enjoy a reproductive advantage compared to those pairs not receiving such experience. This finding supports the hypothesis that extended residence by non-breeding helpers in family groups of the Mongolian gerbil contributes to the eventual individual, direct reproductive success of these individuals. It is important that these benefits for individual reproductive effort may overweight any potential contribution to the indirect component of inclusive fitness. Overall, the results of these studies support the hypothesis that alloparental care yields direct benefits to helpers by providing experience that allow them to become more successful parents. Moreover, helping may contribute to the individual direct reproductive success of the helpers (Salo & French, 1989).

In general, it seems unlikely that alloparental care in the Mongolian gerbil evolved merely to kin selection under 'Hamilton's rule'. A more appropriate explanation is that helping behavior is a by-product of the evolution of sociality (i.e., the transition from solitary living to a family-group lifestyle; Gromov, 2017, 2018). Extended family groups with helpers arise due to delayed dispersal of offspring, and the latter may gain direct or indirect fitness benefits just staying within their natal groups. In the Mongolian gerbil, alloparental care is not a reproductive altruism and could be considered a form of cooperation due to which both breeding pairs and their older offspring being helpers may gain direct fitness benefits. Some forms of helping, such as brooding and grooming pups, can be stimulated by the physiological mechanisms related to epigenetic (re)programming of the behavior (Gromov, 2011a, 2020). Future studies in this direction would be very useful for better understanding of the helping phenomenon.

As mentioned above, the Mongolian gerbil is a cooperative breeding species. Cooperation in breeding, first of all, is related to biparental care of the young: the adult male engages in all care-taking activities observed in the female, except for nursing (Elwood, 1975, 1979; Gromov, 2009, 2011b). Moreover, both adults were reported to cooperate via their synchronized presence with the young, i.e. temporal coordination or time sharing in the nest (Weinandy & Gatterman, 1999).

Field studies and observations under semi-natural conditions have shown that the Mongolian gerbil is a species with a complex social organization, characterized by cooperation in different activities (Gromov, 2008, 2014, 2018, 2022). It has been already noted that the gerbils act cooperatively to defend and mark their territories, and such cooperative maintenance of territories is typical of this species. In autumn, animals of both sexes and all age classes actively hoard winter stores (Bannikov, 1954). Behavioral observations show that all group members take part in hoarding of a common food supply (Ågren *et al.*, 1989b; Gromov, 2022), so there is clear reason for all animals not to desert their natal burrow. The food-hoarding season (September-October) is reported to be a crucial life-history stage in the Mongolian gerbil for successful over-winter survival (Deng *et al.*, 2017a,b). One can suggest that individuals acting cooperatively to hoard food and defend winter stores benefit more than solitary foragers and thus increase their chances of survival during the severe season. In other words, the fitness of members of family groups might be higher than the fitness of solitary foragers, and thus natural selection has promoted formation of family groups in populations of the Mongolian gerbil, like in some other rodent species belonging to the Palearctic fauna (Gromov, 2017, 2018).

With regard to the conceptual framework developed by Lehmann & Keller (2006), behavioral observations of Mongolian gerbils show that the conditions considered necessary for the evolution of cooperation, such as direct benefits to the focal individual performing a cooperative act, as well as preferential interactions between related individuals, are only partially met. The key point is that the founders of family groups are primarily breeding pairs of unrelated individuals. However, these unrelated individuals exhibit diverse and complex cooperative activities, such as digging common burrows, scent marking and defending territories, as well as care for young. Kin selection (Hamilton, 1964) does not explain the evolution of such cooperative behaviors in breeding pairs. There is also no evidence of genetic correlation between genes encoding cooperative behaviors and phenotypic traits in the Mongolian gerbil.

It can be assumed that females benefit most from pair bonds, especially through cooperative interactions with males in the territory defense and care for offspring. Once a male and female begin to live together as a breeding pair, the subsequent evolution of social behavior may enhance the initial advantage of group living. The group augmentation as a result of reproduction and delayed offspring dispersal promotes complication of the social organization, as well as contributes to intensifying cooperation. Concurrently, the family group members seem to achieve greater fitness due to the cooperation and thus more successfully compete with solitary dwellers for their territories and food resources. Therefore, cooperation should be considered the core trait of the family-group lifestyle, and biparental care along with alloparenting seem to play a key role among other forms of cooperative behavior through which members of the family group gain essential benefits.

Cooperation is much more likely between mates than between unrelated same-sex individuals, at least because of proximate (neuronal and hormonal) mechanisms suppressing aggression between sexual partners. As a result, less aggressive interactions and more affiliative behaviors towards individuals of the opposite sex compared to individuals of the same sex can be expected (Wolff & Sherman, 2007). One of the important forms of affiliative behaviors is social grooming that maintains and enforces pair bonds. Grooming functions in particular to relax the groomee or groomer as it stimulates beta-endorphin release (Keverne *et al.*, 1989). It is not surprising that grooming is a commonly observed behavior typical of interactions between members of family groups in many social rodents, including the Mongolian gerbil (Gromov, 2011a,b).

The conceptual model developed by van Veelen *et al.* (2010) predicts a hump-shaped function reflecting levels of cooperation with respect to group size. According to this prediction, one can expect that in species with a family-group lifestyle two unrelated individuals (e.g., a breeding pair) as well as individuals in family groups of very large size (compared to some optimal group size thought to be typical of the species) would be less inclined to cooperate or even avoid cooperation. However, behavioral observations of Mongolian gerbils do not support this assumption. First, there is no optimal group size typical of family groups of this species (Gromov, 2008, 2022). Second, both in breeding pairs and large family groups, cooperation does not become unfavorable (Gromov, 2022). Therefore, the conceptual model developed by van Veelen *et al.* (2010) is not applicable to the Mongolian gerbil.

Regarding the hypotheses explaining the evolution of cooperative behavior within the framework of behavioral ecology (Davies *et al.*, 2012), the first of them, associated with kin selection, does not account for the evolution of altruistic cooperation such as alloparental care, as shown above. As for other three hypotheses (Davies *et al.*, 2012), cases where cooperation would provide a benefit as a by-product or automatic consequence of an otherwise ‘self-interested’ act of cooperation, or examples of so-called reciprocal helping, were not recorded in family groups of the Mongolian gerbil.

Behavioral observations of Mongolian gerbils both in nature and semi-natural conditions do not support the hypothesis that cooperation could be evolved through ‘punishment’ of group members (Davies *et al.*, 2012). As for other rodent species, it was found that lactating females of *Lasiopodomys brandti* (Radde, 1861) (Gromov, 2005) and *Microtus arvalis* (Pallas, 1779) (Gromov, 2013), as well as males of *Microtus guentheri* (Danford et Alston, 1880) (Libhaber & Eilam, 2002) exhibited unusual behavior that could be called ‘policing’ or ‘coercion’ to cooperation, because they forced their mates to remain with the pups in the nest while they left the nest to feed. In the Mongolian gerbil, as it mentioned above, such a behavior was not recorded.

The most intriguing cooperative behavior characteristic of the Mongolian gerbil is paternal care. According to the fitness-enhancing hypotheses (Trivers, 1972; Maynard-Smith, 1977), paternal care evolved because there was an initial direct benefit to offspring, fathers and/or mothers. The prevailing paradigm assumes that a male’s fitness can increase through providing care if his offspring survive and reproduce, and certainty of paternity is presumably a contributor to the evolution of paternal care. However, multiple mating by female Mongolian gerbils results in multiple paternity. It means that many male Mongolian gerbils provide care for both own offspring and young sired by other males. In other words, ‘careful fathers’ promote distribution of not only their own but alien genes as well. Therefore, the fitness-enhancing hypotheses do not adequately explain the evolution of paternal care in the Mongolian gerbil. A possible explanation of this phenomenon is that paternal care being typical of this species is a by-product of a family-group lifestyle. Cohabitation of breeding partners and nest attendance exhibited by males results in additional tactile stimulation of pups by ‘careful fathers’ that in turn stimulates paternal responsiveness of males in adulthood (Gromov, 2009, 2011a). This phenomenon is also related to epigenetic (re)programming of parental behaviors (Gromov, 2020).

In summary, neither the theory of kin selection nor other generally accepted conceptual models developed in behavioral ecology provide a satisfactory explanation for the evolution of helping and other forms of cooperative behavior in the Mongolian gerbil. The same applies to the socioecological hypotheses explaining the evolution of sociality in rodents. According to the proposed conceptual model (Gromov, 2014, 2017, 2018), the evolution of sociality in the Mongolian gerbil, as well as in other rodent species, is closely related to a family-group lifestyle. Family groups are formed through pair bonding, which in turn stimulates cooperative behaviors, especially care of offspring. Extensive cooperation in family groups maximizes the fitness of their members. This process could be called ‘stimulation of similar with the similar’. Therefore, cooperation can be considered one of the important driving factors promoting the formation of family groups in rodent populations. This evolutionary process can occur under any ecological conditions, irrespective of predation pressure or resource distribution, as long as solitary individuals are less competitive than breeding pairs and, especially, family groups. In the latter, due to cooperation, the efforts of several individuals are successfully combined in construction of complex burrow systems, food hoarding, defending and marking the territory, and care for young. Harsh environments typical of the Palaearctic zone can create preconditions for the transformation of social structures into more complex ones, and it is the complicated family-group social organization suppressing intra-specific aggression or, at least, minimizing its negative effects and promoting social bonds that is necessary for successful cooperation.

Conclusion

The Mongolian gerbil is a highly social and cooperative breeding species with the complicated social organization and biparental care of offspring. Young gerbils remaining in the natal area become non-breeding helpers assisting in the rearing of the infants. Mongolian gerbils act cooperatively defending and marking their territories, digging underground tunnels, maintaining nests, hoarding food, and raising young. Therefore, the Mongolian gerbil is a species with high cooperative abilities. Behavioral monogamy, cooperative breeding (in terms of alloparental care displayed by elder offspring), and complex forms of cooperation may have evolved as an adaptation to harsh environments and extreme climate of Central Asia.

The generally accepted conceptual models relevant to the evolution of sociality among mammals do not explain the evolution of sociality in the Mongolian gerbil. Predation pressure and spatial distribution of food resources cannot be considered selective forces promoting the formation of family groups in this species. Alloparental care in the Mongolian gerbil is not reproductive altruism, and it seems unlikely that this behavior evolved merely due to kin selection under 'Hamilton's rule'.

The evolution of cooperation is closely related to the processes associated with pair bonding and the formation of family groups, suggesting that cooperative behaviors in the Mongolian gerbil are a by-product of the evolution of sociality. In fact, cooperation is an immanent attribute of pair bonding and a family-group lifestyle of the Mongolian gerbil. Complex forms of cooperation, in turn, contribute to the evolution of sociality. This evolutionary process can be thought of as some kind of 'stimulation of similar with the similar': pair bonding stimulates cooperation, and cooperation in turn contributes to the formation of extended family groups typical of this species.

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