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Altruism and cooperation in rodents: Insights from analysis of conceptual models and empirical data

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ABSTRACT. Conceptual models explaining the evolution of altruistic and cooperative behavior, as well as empirical evidence from rodents are reviewed in this article. Alarm calling and helping (alloparental care) are well-known altruistic behaviors in rodents. In behavioral ecology, alloparental care is considered reproductive altruism, which is costly to the actor and benefits the recipient. The evolution of helping is thought to be predicted from the theory of kin selection. Among rodents, however, helping is unlikely to evolve simply through kin selection. A more appropriate explanation is that helping is a by-product of the evolution of sociality (i.e., the transition to a family-group lifestyle). The same applies to the evolution of different cooperative behaviors, most typical of the species living in family groups. Kin selection does not explain the evolution of cooperative behaviors between unrelated individuals, especially in breeding pairs that form family groups. An alternative idea for the evolution of altruistic and cooperative behaviors in rodents is proposed.

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Альтруизм и кооперация у грызунов: выводы на основе анализа теоретических концепций и эмпирических данных

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РЕЗЮМЕ. В статье рассматриваются концептуальные модели, объясняющие эволюцию альтруистического и кооперативного поведения, а также эмпирические данные, относящиеся к грызунам. Сигналы тревоги и помощничество — наиболее известные формы альтруистического поведения у грызунов. В поведенческой экологии помощничество считается репродуктивным альтруизмом, который дорого обходится инициатору этого поведения и приносит пользу только реципиенту. Полагают, что эволюция помощничества может быть предсказана теорией родственного отбора. Однако маловероятно, что у грызунов помощничество является исключительно результатом действия родственного отбора. Более подходящее объяснение состоит в том, что помощничество — побочный продукт эволюции социальности (т. е. перехода к семейно-групповому образу жизни). То же самое относится и к эволюции различных кооперативных форм поведения, наиболее типичных для видов с семейными группами. Родственный отбор не объясняет эволюцию кооперативного поведения между неродственными особями, особенно в размножающихся парах, являющихся основателями семейным групп. Предложена альтернативная идея эволюции альтруистического и кооперативного поведения у грызунов.

КЛЮЧЕВЫЕ СЛОВА: грызуны, кооперация, альтруизм, родственный отбор, эволюционные модели.

Introduction

The origin and persistence of intra-specific altruism and cooperation as specific forms of social behavior is one of the enduring puzzles in socio-ecology and behavioral ecology. Social behaviors have been studied extensively in the laboratory and field in many species of rodents. Hamilton (1964) has shown how social behaviors could be defined according to their fitness consequences for the actor and recipient. A behavior is social if it has fitness consequences for both the individual that performs that behavior (the actor) and another individual (the recipient). Further, social behaviors are classified according to whether the consequences they entail for the actor and recipient are beneficial (increase fitness) or costly (decrease fitness). A behavior which is beneficial to the actor and costly to the recipient is selfish; a behavior which is beneficial to both the actor and the recipient is mutually beneficial; a behavior which is costly to the actor and beneficial to the recipient is altruistic. Selfish and mutually beneficial behaviors can be explained from the perspective of individuals maximizing their reproductive success. As for altruistic behavior, according to Hamilton (1964), it can only be explained by also taking account of the indirect consequences of the behavior.

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.*, 2007a; Davies *et al.*, 2012). Different forms of cooperation may evolve once individuals live in groups. Theoretically, cooperation can evolve through several mechanisms, including kin selection, reciprocity, by-product mutualism, and some other ones, that are considered below.

When considering altruistic and cooperative behaviors in rodents, it is important to realize that rodents are primarily sedentary animals, and every adult individual 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. 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.

The formation of groups and the evolution of cooperation within them are considered the two essential components of sociality, or group living (Alexander, 1974). The social structure and, subsequently, social units in rodent populations may be classified as follows: solitary dwellers, aggregations (multi-male–multi-female breeding colonies), and family groups (Gromov, 2008, 2017, 2018). Solitary dwellers, especially of the same sex, use primarily exclusive home ranges and display nonsocial behaviors, such as activity and feeding patterns, like in many hamsters, ground squirrels, some voles and gerbils (Gromov, 2008, 2017, 2018). Many ground squirrels form colonies, but adults however lead solitary lives within these colonies (Armitage, 1981).

In fact, there are two main types of social groups in rodent societies (Gromov, 2017, 2018): (1) multi-male–multi-female breeding colonies that are characteristic of gregarious species, such as bank voles, *Clethrionomys glareolus* (von Schreber, 1780) [Bujalska & Saithoh, 2000], wood mice, *Apodemus sylvaticus* (Linnaeus, 1758) [Garson, 1975; Montgomery, 1980], Wagner's gerbils, *Gerbillus dasyurus* (Wagner, 1842) [Gromov *et al*., 2000], midday gerbils, *Meriones meridianus* (Pallas, 1773) [Popov *et al*., 1989; Gromov, 2008, 2024a], commensal mice and rats (Brown, 1953; Calhoun, 1963; Sage, 1981; Waterman, 2007) or capybaras, *Hydrochoerus hydrochaeris* (Linnaeus, 1766) [Macdonald *et al*., 2007; Herrera *et al*., 2011]; and (2) family groups, like in beavers (Brady & Svendsen, 1981; Busher *et al*., 1983; Dezhkin *et al*., 1986), African mole-rats, *Heterocephalus glaber* Rüppell, 1842 (Jarvis, 1981; Honeycutt, 1992), prairie voles, *Microtus ochrogaster* (Wagner, 1843) [Getz & Carter, 1980; Getz & Hofmann, 1986; Getz *et al*., 1993], Mongolian gerbils, *Meriones unguiculatus* (A. Milne-Edwards, 1867) [Ågren *et al*., 1989a; Gromov, 2022], social voles, *Microtus socialis* (Pallas, 1773) [Kasatkin, 2002; Gromov, 2023b], and Brandt's voles, *Lasiopodomys brandtii* (von Radde, 1861) [Gromov, 2023c].

In multi-male–multi-female breeding colonies of muroid rodents, adult females tend to maintain exclusive home ranges during the breeding season; adult males occupy much larger and unprotected home ranges located corresponding to the location of the females' ranges. In species with a family-group lifestyle, interactions within family groups markedly differ from those between groups with the former being to include affiliative, cooperative, and nepotistic social acts; spatially, members of a family group exhibit considerable overlap, including sharing a nest burrow or other shelter. Family groups occupy nearly exclusive and protected home ranges and exhibit, as a rule, aggressive interactions with neighbors and strangers (Gromov, 2008, 2022, 2023b).

The evolution of group living among rodents proceeded (and, perhaps, proceeds at presents) in two general directions: (1) towards formation of aggregations (breeding colonies) and (2) towards formation of family groups, but it is the latter that is characterized by the most complex social structure (Gromov, 2008, 2017, 2018). Hence, the evolution of sociality in rodents means transition not towards gregariousness or coloniality, but towards a family-group lifestyle, and every colonial, such as ground squirrels, or gregarious species has to be regarded less social than any species living in family groups.

Cooperative and altruistic behaviors appear to vary significantly in dependence on the social structure of the species, i.e., the composition of social groups. Unfortunately, published data on cooperative and altruistic behaviors of rodents are scattered, and a general and comprehensive analysis of such behaviors is lacking. The aim of this review is to fill this gap and to examine the consistency between empirical data on rodents and conceptual models, including kin selection theory, explaining the evolution of altruistic and cooperative behaviors. This review also focuses on behavioral differences among rodent species with various social structures.

Conceptual models explaining the evolution of cooperative and altruistic behaviors

It is well known that natural selection designs individuals to behave in their own selfish interests, but not for the good of their species or for the good of the group in which they live. However, individuals do not behave selfishly all the time and often cooperate with others. In some cases, cooperation provides an immediate or delayed benefit to the survival and reproduction of the actor that outweighs the cost of performing the behavior. In other cases, cooperation is mutually beneficial and can be explained by selfish interests. However, more troubling for evolutionary theory are examples where cooperative behaviors provide no benefit to the actor and are altruistic. But, how one can explain altruistic behaviors?

According to the theory of natural selection, a gene can increase its transmission to the next generation either by increasing the reproductive success of the individuals in which it is in or by increasing the reproductive success of other individuals who carry copies of that gene. These different ways of passing a copy of a gene to the next generation are termed direct and indirect, respectively. Hamilton (1964) showed that when these indirect effects are taken into account, natural selection on genes will lead to individuals behaving in a way that maximizes their inclusive fitness rather than their own or direct reproductive success. Inclusive fitness is defined as the sum of direct and indirect fitness, where direct fitness is defined as the component of fitness gained from producing offspring, and indirect fitness is defined as the component of fitness gained from aiding related individual, both descendant and non-descendant. The impact of the actor's behavior on its reproductive success is the direct fitness effect. The impact of the actor's behavior on the reproductive success of the social partners weighted by the relatedness of the actor to the recipient is the indirect fitness effect. Maynard-Smith (1964) coined the term kin selection to describe the process by which characteristics are favored due to their effects on relatives.

Conceptual models relevant to altruism

When interacting individuals are related, 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.*, 2007a). According to Hamilton (1964), groups of closely related individuals are a necessary condition for the evolution of altruism and cooperative behaviors via kin selection. Another important point is that kin selection requires a sufficiently high relatedness between interacting individuals (Davies *et al.*, 2012).

One of the well-known phenomena 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 exhibits parent-like (helping) behavior towards young of a single brood (Koenig & Pitelka, 1981). According to Solomon & Keane (2007), cooperative breeding means care of young by individuals other than the genetic parents. Cooperative breeding groups are either extended families or groups with multiple breeding females, i.e. kin clusters (Solomon & Keane, 2007). In cooperatively breeding mammals, young individuals assist in rearing offspring that are not their own through activities such as feeding, carrying, babysitting, and pup thermoregulation. These activities are defined as helping, or alloparenting (Emlen, 1991; Emlen *et al.*, 1991; Solomon & French, 1997).

In the conceptual framework of 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. If the individual was faced with the alternative of rearing its own offspring or helping its sister to produce offspring, then the expression becomes $B/C > 2$ (0.5/0.25). In this case helping behavior would evolve only if it resulted in two or more extra offspring produced by the sister for every one offspring lost by the individual providing alloparental care. These examples show that kin selection is not just about genetic relatedness; it is also about the ecological factors that determine the cost and benefit of behaviors (Davies *et al.*, 2012).

According to a recent review on kin selection (Bourke, 2014), studies parameterizing Hamilton's rule with data from natural populations of cooperatively breeding birds, mammals, and eusocial insects demonstrate that (1) altruism occurs even when sociality (i.e., grouping) is facultative; (2) in most cases, altruism is under positive selection via indirect fitness benefits that exceed direct fitness costs; and (3) social behavior commonly generates indirect benefits by enhancing the productivity or survivorship of kin. Unfortunately, this review did not cover any rodent species.

Conceptual models relevant to cooperation

The problem of cooperation is why should an individual carry out a behavior that benefits another individual? In other words, cooperative behaviors can be exploited by “free riders” (cheats) who benefit from others cooperating whilst avoiding the cost of cooperating themselves. This is famously illustrated by the Prisoner’s Dilemma model showing that while an individual can benefit from mutual cooperation, it can do even better by exploiting the cooperative efforts of others (Axelrod & Hamilton, 1981). This model predicts that cooperation is not an evolutionary stable strategy (ESS), because in a population of cooperators a mutant that defected (i.e., free rider) would spread. Defect, however, is an ESS: in a population “all defect” a mutant cooperator does not gain an advantage. Any population with a mixture of heritable strategies will, therefore, evolve to “all defect”. It is important to realize that the Prisoner’s Dilemma model is just an illustration of the problem of cooperation, and not a solution. A possible solution to this problem is thought to be that cooperation can be favored by kin selection when it is directed towards relatives, and therefore provides indirect fitness benefits (Davies *et al*., 2012).

A number of theoretical models have been proposed to explain the origin and persistence of intraspecific cooperation and altruism, but there is much confusion about the relationship between these models. 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, altruism or cooperation can evolve if the cost-to-benefit ratio of altruistic and cooperative acts is greater than a threshold value.

This conceptual model assumes so-called green-beard effect (Hamilton, 1964; Grafen, 1984): the carrier of an altruism gene (or a specific allele) is essentially recognizing copies of the same gene (or a specific allele) in other individuals. Whereas kin selection involves altruism to related individuals who share genes in a non-specific way, green-beard alleles promote altruism toward individuals who share a gene that is expressed by a specific phenotypic trait. However, such green-beards are unlikely to be common or generally important (see Davies *et al*., 2012). One problem is that they would need to be complex, doing three things: signal, recognition, and cooperation. It is hard enough to imagine a gene that completely encodes for one behavior, let alone three! Another problem is that they could be easily invaded by “falsebeards” that displayed the beard, without performing the altruistic behavior. Consistent with this, only a very small number of green-beards has been discovered, and no one among rodents (Davies *et al*., 2012). There is also no evidence of genetic correlation between genes encoding altruism and phenotypic traits in rodents. As it was explained above, altruistic cooperation, such as alloparental care, can be favored between related individuals by kin selection. However, this form of cooperation can also take place between non-relatives. Cooperation between non-relatives needs special consideration – in this case cooperation must provide some direct fitness benefit to the cooperator. According to West *et al*. (2007a), direct benefits explain mutually beneficial cooperation, whereas indirect benefits explain altruistic cooperation. Therefore, cooperation is not just about kin selection.

Some authors suppose that there are many ways to enforce cooperation, which has been referred to by terms such as “punishment”, “policing”, and “coercion” (Frank, 2003; van Veelen *et al*., 2010). An essential point here is that if there is a mechanism that rewards cooperators and/or punishes free riders, then this can alter the benefit/cost ratio of helping, and hence favor cooperation. Davies *et al*. (2012) used specific examples on meerkats, birds and fish to illustrate how some enforcement mechanism can work, but these mechanisms are not relevant to rodents, and there are no known examples of enforcement of cooperation via punishment among Rodentia.

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 of these is kin selection, which explains altruistic cooperation between relatives. The other three hypotheses 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 number of empirical studies supporting kin selection theory has been growing in the recent decades, possibly due to genetic screening techniques becoming more accessible, opening new opportunities to obtain appropriate data (Gardner *et al*., 2010; Bourke, 2011, 2014). Nevertheless, there is no agreement about the extent of explanations that kin selection theory can tackle (Nowak *et al*., 2010; Abbot *et al*., 2011; Allen *et al*., 2013; Bourke, 2014). At present, kin selection is thought to separate natural selection into its direct and indirect components simply (Frank, 2013; Bourke, 2014).

In some cases, cooperation can provide a benefit as a by-product or automatic consequence of an otherwise "self-interested" act. The idea here is that cooperation is always the best option from an individual or selfish perspective, but that this may also provide a benefit to others. Some forms of this cooperative behavior are called by-product mutualism, in which an individual's behavior maximizes its own immediate fitness and any positive effects on the fitness of other individuals are coincidental (Clutton-Brock, 2002).

Some authors (Lima, 1995; Bednekoff & Lima, 1998; Rodriguez-Gironés & Vásquez, 2002) consider that two interacting animals do better by cooperating together compared to each acting individually and both parties achieve rewards without sacrificing anything for the other. For example, two ground squirrels forage together in the field, where each of them spends time scanning the environment for predators and hence losing foraging time. In this case, if predator detection by one animal is almost instantly sensed by the non-vigilant animal, then sharing the vigilance of other ground squirrels, i.e. cooperating at looking out for any danger around them, would increase each other's foraging time, while anti-predator vigilance would not diminish it. Hence, two ground squirrels that share vigilance (so at any time there is one subject watching for predators) are more efficient at detecting predators, even if they diminish their individual rate of vigilance while in groups. In other words, the two ground squirrels will certainly do better by using a cooperative vigilance behavior.

A case of reciprocity was proposed by Trivers (1971) who argued that if individuals preferentially help those that have helped them (reciprocal helping), then any short-term cost of helping another individual can be more than repaid by the help that is returned in exchange at a later point. The problem for the evolution of reciprocity is the possibility of free riding because of the time delay between one individual gaining and the other doing so. Reciprocity has been suggested to be important in numerous cases (Davies *et al*., 2012). In these cases, cooperation however can be explained by a more simple mechanism, such as by-product benefit (Clutton-Brock, 2009). Consequently, whilst it used to be assumed that reciprocity was of widespread importance, it is now thought to be rare or even absent in animal societies (Davies *et al*., 2012). Moreover, cooperation based on direct reciprocity seems to be inherently unstable from an evolutionary viewpoint unless subjects' interactions are repeated after they first encounter each other (Trivers, 1971; Axelrod & Hamilton, 1981; West *et al*., 2007b; Vásquez, 2016).

Below, some well-known cases of altruistic and cooperative behaviors of rodents are considered in relation to the conceptual models explaining the evolution of altruism and cooperation, as well as the conformity of the behaviors with these conceptual models.

Altruistic behaviors in rodents

Alarm calling is thought to be a form of altruistic behavior in some rodent species. In diurnal rodents, such as ground squirrels (*Spermophilus* spp.) living in colonies, as well as marmots (*Marmota* spp.), prairie dogs (*Cynomys* spp.), great gerbils [*Rhombomys opimus* (Lichtenstein, 1823)], Mongolian gerbils or Brandt's voles living in family groups, individuals often act as sentinels, watching for predators while the rest of the group forages (Dunford, 1977; Sherman, 1977; Hoogland, 1983; Blumstein, 2007; Gromov, 2008). When the sentinel spots an approaching predator (a raptor or carnivorous mammals), it gives an alarm, and everyone rushes to safety (Neill & Cullen, 1974; Sherman, 1977, 1985; Blumstein & Armitage, 1997). If, by calling, individuals exposed themselves to a greater risk of predation than non-callers, then calling behavior would be a phenotypically altruistic behavior (Alexander, 1974).

Explaining why animals emit potentially costly alarm calls to help others has been a topic of considerable interest (Maynard-Smith, 1965; Charnov & Krebs, 1975; Sherman, 1977; Blumstein *et al*., 1997; Blumstein, 2007). If calling increases predation risk then such signals should be produced only if calls carry relatively long distances, callers can accurately assess their own vulnerability, and callers benefit from communicating alarm to someone. Understanding the adaptive significance of alarm calling has often focused on investigating its costs.

Calling may have three types of fitness costs: energy, opportunity, or predation (Blumstein, 2007). No studies have been conducted on the energy costs of alarm signaling in rodents. Opportunity costs (i.e., the costs of not engaging in other important behaviors) are experienced by both the signaler and the receiver. From the signaler's perspective, alarm calling seems to preclude foraging and engaging in activities other than vigilance. While analyses of time budgets may be used to contrast the opportunity costs of calling (i.e., the cost of not engaging in an alternative behavior), the link between opportunity costs and fitness is unstudied. From the receiver's perspective, responding to calls modifies current behavior (Baack & Switzer, 2000). Typically, individuals immediately increase vigilance, but, over time, receivers habituate to tonic signals, that is individuals assess that the danger has passed and return to what they were doing previously (Loughry & McDonough, 1988; Nikol'skii, 2000; Hare & Atkins, 2001; Blumstein & Daniel, 2004). Again, the fitness consequences of this opportunity cost have not been studied in any rodent species.

Is alarm calling in fact a risky behavior? Unfortunately, evidence for predation costs of calling is difficult to obtain. Predation events are rare and hard to observe, and there have been no experimental studies focusing on predator's responses to alarm calls (Lima, 2002). However, Sherman (1977) found that when a terrestrial predator appeared, Belding's ground squirrels [*Urocitellus beldingi* (Merriam, 1888)] emitting calls were tracked and killed more often than non-callers, whereas calling in response to an aerial predator enhanced an individual's likelihood of escape over that of non-callers who probably were unaware of the raptor's presence (Sherman, 1985). This finding makes it even more difficult to assess alarm calling in terms of the cost and benefits for the caller.

Dunford (1977), Sherman (1977), and Hoogland (1983) argued that alarm calls in ground-dwelling sciurids could be explained, in part, by kin selection, because the emission of alarm calls is more common when emitters are in the presence of kin. Studies demonstrating the ability of kin recognition provided further indirect support to the role of kin selection (Holmes & Sherman, 1982, 1983; Holmes, 1984, 2004; Mateo, 2003; Holmes & Mateo, 2007). Specifically, it was found that female Belding's ground squirrels were much more likely to give alarm calls than males and, furthermore, females with close relatives nearby were more likely to give calls than females without. This finding shows that individuals are more likely to incur the cost of calling when relatives are nearby to gain a benefit. Other studies however provided evidence that individuals gave alarm calls even in situations when there were no relatives nearby (see, for example, Hoogland, 1995). Moreover, the above studies did not constitute a quantitative test of Hamilton's rule. Indeed, it would be difficult to assess the costs and benefits of alarm calling in terms of offspring lost and gained.

There is the commonly held belief that callers may obtain indirect fitness benefits by increasing the survival of collateral kin. However, there is some controversy over the relative importance of warning descendent versus collateral kin for explaining the adaptive significance of alarm calling. Sherman (1977) and Dunford (1977) independently reported that, by calling, some Belding's ground squirrels and round-tailed ground squirrels [*Xerospermophilus tereticaudus* (Baird, 1857)] were alerting descendent and non-descendent kin. Callers therefore received nepotistic fitness benefits from calling. Calling to increase indirect fitness has been also reported to occur in chipmunks (Smith, 1978; Burke da Silva *et al*., 2002), prairie dogs (Hoogland, 1995, 1996), as well as other ground squirrels (Schwagmeyer, 1980; Davis, 1984; MacWhirter, 1992). Sherman's (1977) study quantified the frequency of calling when animals were surrounded by relatives and non-relatives, but many other studies did not, and evidence for kin-selected benefits from calling often was based on a caller being surrounded by relatives. Accordingly, most researchers suggested that calling was nepotistic (Blumstein, 2007). It should be noted also that enhancing indirect fitness might be more essential to some species than others, and not all species have evolved alarm calling behavior in the same way (Holmes, 2001).

It would seem that sentinels behave altruistically, risking their own welfare for the sake of the conspecifics. However, Bednekoff (1997) in his theoretical model showed that sentinel behavior could arise through individual actions that are obviously selfish. The key assumptions of this model are that individuals are only likely to behave as sentinels when they are satiated, and that such a behavior may be beneficial to the sentinel itself because it can detect a predator in due time. Besides, alarm calling may reduce the likelihood of attack because the predator loses the advantage of surprise. Subsequently, there may be a series of changeovers in the group, as sentinels become hungry and are replaced by satiated individuals. In short, each individual is simply choosing the best option for itself, depending on its own state and the behavior of others in the group. Moreover, even solitary individuals may become sentinels when they satiated, because sentinel behavior may benefit both groups and solitary individuals. Thus, alarm calling is not a case of altruism but rather of mutualism: both caller and responders may gain a benefit from group living (Davies *et al*., 2012). So, there is still no complete clarity regarding the nature of selective forces promoting the evolution of alarm calling in rodents, and this behavioral phenomenon needs further studies.

As for alloparental care, or helping, it is known that in some species with a family-group lifestyle young individuals delay dispersal and remain philopatric because they 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. Alloparental care includes feeding, retrieving, and huddling over pups, as well as pup grooming (Emlen, 1991; Solomon & French, 1997; Gromov, 2023a).

It should be noted that in many social muroid rodents, the number of potential offspring of several helpers in the sum 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 among social muroid rodents is much more than intriguing because in some species exhibiting social monogamy (e.g., *M. unguiculatus, M. ochrogaster, M. socialis*) estrus females can visit adjacent territories to mate with neighbors and strangers (Solomon *et al*., 2004; Ågren *et al*., 1989a; Gromov, 2022, 2023b). As a result, multiple paternities have been found in many litters (Gromov, 2024b). Therefore, 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 alloparental care in social muroid rodents in terms of "Hamilton's rule".

According to the inclusive fitness theory (Hamilton, 1964), alloparental care for younger siblings by older juveniles 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, however, neither the presence of helpers nor their larger numbers affected litter size at weaning in several species, including *M. unguiculatus, Microtus pinetorum* (Le Conte, 1830), and *M. ochrogaster* (Ostermeyer & Elwood, 1984; Solomon, 1991; Powell & Fried, 1992; French, 1994; Hayes & Solomon, 2004). The only study on Oldfield mice [*Peromyscus polionotus* (Wagner, 1843)] provided evidence that increased survival of offspring in the presence of helpers might affect lifetime reproductive success (Margulis *et al.*, 2005) suggesting a direct fitness effect for breeding pairs.

Helpers may also benefit the breeders by increasing the quality of offspring produced. Specifically, alloparental care may result in increased offspring size relative to offspring reared by a single female, as it was shown in a study on prairie voles (Solomon, 1991). However, this effect has not been found in other muroid rodents (Gromov, 2023a). In some muroid rodents, helpers may decrease the workload of breeders, but the effects of alloparental care were found to be slight and often mixed (Gromov, 2023a).

The results of some studies support the hypothesis that alloparental care yields direct benefits to helpers by providing experience that allow them to become more successful parents (Salo & French, 1989; French, 1994; Smorkatcheva & Smolnyakova, 2004; Margulis *et al.*, 2005; Stone *et al.*, 2010; Wu *et al.*, 2013; Rymer & Pillay, 2014; Pillay & Rymer, 2015). Helping may also contribute to the individual direct reproductive success of the helpers (Salo & French, 1989; French, 1994; Margulis *et al.*, 2005; Stone *et al.*, 2010; Rymer & Pillay, 2014; Pillay & Rymer, 2015). Thus, direct and indirect fitness effects of alloparental care in rodents appear to be species-specific or dependent on the experimental conditions (Gromov, 2023a).

In general, it seems unlikely that alloparental care in rodents 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 to a family-group lifestyle; Gromov, 2017, 2018, 2023a). Extended family groups with helpers form due to delayed dispersal of offspring, and the latter may gain direct or indirect fitness benefits just staying within their natal groups (Stacey & Ligon, 1987, 1991; Kokko & Johnstone, 1999; Gromov, 2017, 2018). In rodents, alloparental care is not 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 or indirect fitness benefits depending on species-specific life history traits. The expression of both parental care and helping might be governed by the same underlying genetic mechanisms (Linksvayer & Wade, 2005). Moreover, some forms of helping in rodents like brooding and grooming pups were found to be stimulated by the physiological mechanisms related to epigenetic (re) programming of the behavior (Gromov, 2011, 2020). Future studies in this direction would be very useful for better understanding of this phenomenon, especially in plural-breeding species, such as, for example, the Brandt's vole (Gromov, 2023c).

Regarding the differences in reviewed behaviors in species with various social structures, it should be noted that alarm calling evolved both in essentially solitary rodents, such as ground squirrels, and species living in family groups, such as marmots, prairie dogs, great gerbils or Brandt's voles, that is independently on the composition of social units. It is very likely that alarm calling is an adaptation of diurnal rodents to open habitats, such as steppes, prairies, and deserts. As for helping, this behavior evolved exclusively in species with a family-group lifestyle.

To summarize, one can conclude that in rodents both alarm calling and alloparental care (helping) are not so much altruistic as cooperative behaviors, which are a by-product of colonial (in ground squirrels) or a family-group lifestyles. The role of kin selection in favoring alarm calling and alloparental care is questionable. Anyway, these two behavioral phenomena in rodents need further studies.

Cooperation in rodents

Different rodent species exhibit various forms of cooperation. Sherman (1981a, b) described some kind of cooperation between breeding females and their progeny in Belding's ground squirrels. In this species, a female establishes a territory surrounding its nest burrow and produces a single litter. At the time of weaning, the juvenile females tend to remain near their natal area. As a result, most female Belding's ground squirrels spend their whole lives surrounded by close female kin. It was found that closely related females (mother and daughters, sisters) seldom fight for nest burrows and seldom chase each other from their territories. Furthermore, they cooperate to defend each other's young against infanticidal conspecifics. Such cooperation among close relatives, in contrast to the conflict among unrelated individuals, could be predicted from the theory of kin selection.

Potentially nepotistic behaviors that may contribute to greater reproductive success for female ground squirrels living in kin clusters include, in particular, reduced aggression among relatives (Michener, 1979; Charnov & Finerty, 1980; Sherman, 1980; McClean, 1982), sharing of space (Sherman, 1981a, b; Vestel & McCarley, 1984; Mappes *et al*., 1995; Lambin & Yoccoz, 1998), cooperative defense against predators or conspecifics (Sherman, 1980, 1981a, b; Wolff, 1993). A positive effect of the presence of additional group mates has been documented also in marmots (e.g., *Marmota caudata aurea*, *M. marmota*; Arnold, 1993; Blumstein & Arnold, 1998). In these marmot species, subadults warm related juveniles in the hibernacula during winter, that results in increased overwinter survival of young individuals. By remaining in the family group, reproduction of subadults is delayed, and a direct fitness cost is incurred. However, by hibernating with other family members, the subadults have an opportunity to recoup some of the fitness loss by gaining indirect fitness through alloparental care directed to close kin (Armitage, 2007).

Caviomorph rodents exhibit a range of diverse cooperative behaviors, some of which could be the result, at least partially, of kin selection. For instance, degus [*Octodon degus* (Molina, 1782)] showed longer vigilance scans when foraging in the company of siblings, compared to degus in non-genetically related groups (Vásquez, 2016). Another example of cooperation, probably not related to kin selection, is that degus in trios spontaneously dug burrows in the same site; under these conditions, diggers may alternate their burrowing activity by replacing each other, although in some occasions they excavate at the same site simultaneously (Ebensperger & Bozinovic, 2000). In some of those cases, degus established digging chains with two or three individuals removing soil in the same direction in a coordinated fashion. It is suggested that a family-group lifestyle in degus evolved as a necessity to cooperate in construction of burrows (Ebensperger & Bozinovic, 2000; Vásquez, 2016).

Several caviomorph rodents exhibit communal breeding, but such a behavior has been studied only in a few species (Hayes, 2000; Vásquez, 2016). Degus, in particular, showed allomothering, in some cases biased to kin, under certain circumstances (Ebensperger *et al*., 2004; Jesseau *et al*., 2009). Ebensperger *et al*. (2014) have found that the effect of number of females per group on the per capita number of offspring produced was more positive during years with lower mean degus density and mean food abundance. However, communally breeding degus did not attain short-term fitness benefits compared with solitarily breeding degus (Ebensperger *et al*., 2007), and group living did not enhance the survival of offspring (Hayes *et al*., 2009; Ebensperger *et al*., 2011).

Perhaps the greatest paradox of communal breeding is communal nursing (or allonursing), i.e. the sharing of milk with young produced by another female (König, 1994, 1997; Hayes, 2000). Given the physiological costs of lactation (König *et al*., 1988), mothers should avoid suckling offspring other than their own. Jesseau *et al*. (2009) conducted a study on degus, using a radionuclide (phosphorus-32) to track milk transfer from mothers to their young in nests occupied by two mothers and their litters. Mothers housed with a genetically unrelated pair nursed their own two-week-old offspring preferentially, although not exclusively, compared to their co-nesting partner's offspring, whereas mothers housed with a sister nursed indiscriminately, delivering roughly equal amounts of milk to their own offspring and their nieces and nephews. It was suggested that discriminative nursing as a function of relatedness between co-nesting female degus could be an adaptation to communal nesting when mothers shared a burrow containing many young of different degrees of genetic relatedness (Jesseau *et al*., 2009).

Packer *et al*. (1992) and Roulin (2002) summarized several functional and non-functional hypotheses to explain why mothers sometimes nurse alien offspring. Their comparative analysis of the published data revealed that non-offspring nursing is most common in polytocous species that form small groups, and this is consistent with models of cooperation based on kin selection, reciprocity or mutualism (Packer *et al*., 1992). A review of empirical data showed that observations were consistent with predictions of three hypotheses explaining why females nurse alien offspring (Roulin, 2002): the misdirected parental care, kin selection, and milk evacuation hypotheses.

According to the first hypothesis, a female would nurse an alien offspring, because she did not notice that it is not her own or because allosucklers steal her milk (Packer *et al*., 1992). Since allonursing is common in species that live in dense groups like, for example, in prairie dogs (Hoogland *et al*., 1989) or house mice (Manning *et al*., 1995), this breeding activity would persist as a by-product of group living where the benefits of breeding close to each other are greater than the costs, including those associated with allomaternal care (Pusey & Packer, 1994; Manning *et al*., 1995). However, even if the misdirected parental care hypothesis can explain some instances of allonursing, it cannot account for all the variation in the female propensity to nurse allosucklers. For example, females of the common yellow-toothed cavy, *Galea musteloides* Meyen, 1833, selectively nurse some alien offspring over others indicating that allonursing is not always due to an error (Künkele & Hoeck, 1995).

The kin selection hypothesis proposes that a mother nurses alien offspring only if they share genes by common descent allowing her to spread those genes in her population (Packer *et al*., 1992). This hypothesis therefore predicts that females preferentially nurse closely over distantly or unrelated offspring when their own mother does not provide them with sufficient high-quality milk. In communally breeding species, groups are often composed of related individuals (Hayes, 2000). In such species, females preferentially form a communal nest with a closely related partner (Wilkinson & Baker, 1988; Hoogland *et al*., 1989; Manning *et al*., 1992). This implies that females direct allonursing activities towards related individuals, and hence allonursing may provide inclusive fitness benefits. In line with this proposition, a laboratory study (König, 1994) showed that female feral mice, *Mus musculus* Linnaeus, 1758, mixing their pups in a common nest achieved higher reproductive success if they did so with a sister rather than an unrelated female. Data reported by König (1994) are consistent with the kin selection hypothesis, since mice achieved a greater lifetime reproductive success when sharing a nest with a sister than with an unrelated female or by reproducing alone.

Finally, the milk evacuation hypothesis advocates that mothers nurse allosucklers to evacuate surplus milk that their own offspring did not consume (Wilkinson, 1992). Under this scenario, mothers that constantly or momentarily produce more milk than their offspring can consume should be more willing to nurse alien offspring. This hypothesis, however, does not apply to rodents.

Group living provides many other opportunities for cooperation. For instance, group living can improve foraging through cooperation (Rutte & Taborsky, 2007; Davies *et al*., 2012). In particular, it has been shown that by remaining philopatric and associating with conspecifics, African mole-rats, *H. glaber*, living in extended family groups can act cooperatively to find food patches, thereby increasing their chances of survival (Jarvis, 1981; Honeycutt, 1992).

Experimental studies also showed that naïve individuals could learn from experienced individuals about the location of food. Galef & Wigmore (1983) trained Norway rats [*Rattus norvegicus* (Berkenhout, 1769)] to search for food in a three-arm maze. Each arm had food with a different flavor. In the first part of the experiment the rats learned that on any particular day only one of the three sites contained food, but the site was unpredictable. Then on the days of the actual experiment each of the test rats was allowed to sniff a "demonstrator" rat in a neighboring cage. The demonstrator had been allowed to feed on whatever randomly chosen food was available for that day, and some of the test rats, having sniffed the demonstrator, went to the correct site on their first choice of the day. "Sniff" is the operative word because other experiments showed that the cue the test rat picks up from the demonstrator is the smell of the food it has eaten. Thus, individuals in groups of Norway rats benefit from communication, and the exchange of information facilitates the search for food and contributes to cooperative foraging, as a form of by-product mutualism.

Other notable examples of cooperation in rodent societies include cooperative breeding in *Peromyscus* Gloger, 1841 (Sherman *et al*., 1995; Solomon & French, 1997), *Rattus* Fischer, 1803 (McClintock, 1984), as well as other muroid rodents (Gromov, 2023c), thermoregulatory huddling in *Microtus pennsylvanicus* (Ord, 1815) and *Peromyscus maniculatus* (Wagner, 1845) [Madison *et al*., 1984; Andrews & Belknap, 1986]. These forms of cooperation also can be defined as by-product mutualism.

Behavioral observations show that within breeding colonies of gregarious rodent species adult individuals lead solitary lives, like in essentially solitary rodent species (such as most ground squirrels), and usually do not cooperate, with some exceptions, e.g., in Belding's ground squirrels (Sherman, 1981a, b), commensal mice and rats (Galef & Wigmore, 1983; Hayes, 2000) and a number of other muroid rodents (see above), as well as in cavies (Künkele & Hoeck, 1995) and capybaras (Macdonald *et al*., 2007; Ebensperger & Hayes, 2016). As for family groups in highly social rodents, their members engage in diverse and complex cooperative activities (Gromov, 2017, 2018). No doubt, adults and their offspring are relatives, suggesting that kin selection may facilitate the evolution of cooperative behavior. But 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 and constructing other shelters (like in beavers), scent marking and defending territories, as well as care for young. Kin selection does not account for the evolution of such cooperative behaviors, and this form of cooperation can be defined by-product mutualism. Except for biparental care, the male and female in a breeding pair act independently from each other when digging underground tunnels, marking and defending the territory or hoarding food, like, for example, in Mongolian gerbils (Gromov, 2022), but their activities are beneficial for both of them.

Cooperation is much more likely to be expected between mates than between unrelated same-sex individuals at least because of the operation of proximate (neuronal and hormonal) mechanisms suppressing aggression between heterosexual partners. One would expect less aggressive interactions and more affiliative behaviors toward an opposite-sex conspecific than toward conspecific of the same sex (Wolff & Sherman, 2007). One of the important forms of affiliative behavior is social grooming that is referred to as maintaining pair bonds. Social grooming functions in particular to relax the groomee or groomer as it stimulates beta-endorphin release (Keverne *et al*., 1989). Social grooming is a commonly observed behavior in breeding pairs and family groups of many social rodent species and facilitates social bonding and cooperation (Gromov, 2011).

The conceptual model of 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., breeding pairs) 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, this assumption is not supported by field and laboratory studies on rodents living in family groups. First, there is no optimal group size typical of any rodent species with a family-group lifestyle (Gromov, 2000, 2008, 2017, 2018). Second, even in species with large family groups, such as *M. unguiculatus* (Gromov, 2022) or *H. glaber* (Jarvis, 1981; Honeycutt, 1992), cooperation does not become unfavorable, as the conceptual model of van Veelen *et al*. (2010) predicts. Therefore, the conceptual model explaining the evolution of cooperation developed by van Veelen *et al*. (2010) is not applicable to rodent societies.

The most specialized cooperative societies are found among herbivorous rodents, in which the distribution of their food supply and the energetic requirements of individuals allow the formation of relatively large and stable social groups, like in so-called eusocial rodents (Jarvis, 1981; Alexander *et al*., 1991; Honeycutt, 1992; Lacey & Sherman, 2007; Clutton-Brock, 2009; Gromov, 2017, 2018). In many rodent species with a family-group lifestyle, cooperative behaviors include scent marking and protecting the territory, constructing nest burrows or other shelters, digging underground tunnels, food cashing, and some other activities (Gromov, 2017, 2018). Cooperative maintenance of territories, as well as thermoregulation, has been suggested as the main benefit of grouping and monogamy in large-sized rodents, such as many marmot species (Arnold, 1993; Armitage, 2007), as well as Cape porcupines, *Hystrix africaeaustralis* Peters, 1852 (Corbet & van Aarde, 1996).

The most familiar example of an individual giving aid to another is parental care. The young will have copies of their parent's genes, so parental care is one of the ways in which parents can increase their genetic contribution to the next generation. Females are more predisposed to care for the young, since the offspring often have a prolonged period of gestation inside the female, during which the male can do little direct care (though he can protect and feed the female). Once the young are born they are fed on milk and only the female lactates. Because of these constraints on the opportunity to care for offspring, and also because, with internal fertilization, the male can desert first, it is not surprising that most rodents have parental care by the female alone, with the male deserting to seek further matings. Accordingly, biparental care associated with social monogamy occurs in not so many rodent species, where the male contributes to direct care for the young, implying cooperation with the female (Gromov, 2017, 2018).

In species with persistent pair bonds, cooperation could be selected if it would enhance fitness of both the male and female. However, contrary to the conceptual models explaining biparental care (Trivers, 1972; Maynard-Smith, 1977), in rodent species with a family-group lifestyle and social (biparental) monogamy potential reproductive success (and thus individual fitness) is usually lower than in solitary or gregarious species for which cooperation is not so typical (Gromov, 2021). This phenomenon has no explanation yet. Nevertheless, in species with a family-group lifestyle, cooperative activities are much more diverse and complex than in solitary or gregarious species (Gromov, 2017).

Considering the behavior of breeding pairs, it can be assumed that females receive the greatest benefit from pair bonds, especially through cooperative interactions with the preferred sexual partners. The formation of family groups promotes complication of the social organization that, in turn, results in extending and intensifying cooperation when the size of family groups increases due to delayed offspring dispersal (i.e., group augmentation); concurrently, the family group members seem to achieve greater fitness due to cooperation and thus more successfully compete with solitary foragers. Cooperation undoubtedly should be considered the core trait of a family-group lifestyle, and biparental care along with helping are the most important forms of cooperative behaviors, due to which members of the family group may gain benefits. These benefits may be derived, in particular, from increased survival of the young, potential breeding opportunities as a subordinate, acquisition of better parental experience, as well as the potential for territory inheritance and higher reproductive success associated with becoming a territory holder. Therefore, the evolution of cooperative behaviors in rodent societies cannot be considered apart from the processes associated with the evolution of sociality, i.e. the transition from solitary living to a family-group lifestyle.

It should be noted that cooperation in family groups of rodents is not necessarily associated with coordination of actions of the group members, although it does not exclude it, as shown in African mole-rats (Jarvis & Sale, 1971) and degus (Ebensperger & Bozinovich, 2000), coordinating their actions when digging underground tunnels. Along with some representatives of Hystricomorpha, coordination is also typical of parental care in some muroid rodents, such as the Mongolian gerbil (Waring & Perper, 1980; Weinandy & Gatterman, 1999), the prairie vole (McGuire & Novak, 1984), the Brandt's vole (Gromov, 2005), the steppe lemming, *Lagurus lagurus* (Pallas, 1773) [Gromov, 2010], and the social vole (Gromov, 2007): male and female rearing a litter coordinate arrivals and departures at the natal nest such that young are rarely left unattended.

However, when beavers are busy constructing lodges, dams, and larders (Dezhkin *et al*., 1986; Busher, 2007), or when gerbils and voles living in family groups defend and mark their territories, as well as hoard food (Ågren *et al*., 1989b; Gromov, 2008, 2018, 2022, 2023c), coordination is usually not observed, and members of the family group act independently of each other. Nevertheless, the results of the actions of each individual undoubtedly benefit the entire family group. Cooperation in this case can be considered as a by-product effect of independent actions of group members, as suggested by some authors (Lima, 1995; Bednekoff & Lima, 1998; Rodriguez-Gironés & Vásquez, 2002; Clutton-Brock, 2009). Therefore, such cooperation that is typical of most rodent species living in family groups can be defined as by-product mutualism.

As mentioned above, there is no evidence that cooperation in rodent societies could be evolved through punishment, like, for example, in meerkats (Davies *et al*., 2012). However, some lactating females of *L. brandtii* (Gromov, 2005) and *Microtus arvalis* (Pallas, 1779) [Gromov, 2013] housed in pairs with males exhibited unusual behavior that could be called "policing" or "coercion" to cooperation. Specifically, in behavioral observations of *M. arvalis* breeding pairs, some females were housed with males reared in single-mother family units; these males exhibited a lower rate of paternal care. In the four out of ten such pairs, the females exhibited a behavior that could be called "forced babysitting": the female aggressively drugged the male back to the nest to remain with the pups while she has been leaving the nest. In females housed with males reared in biparental family units, such a behavior has not been noted (Gromov, 2013). Surprisingly, in other species of social voles, *Microtus guentheri* (Danford et Alston, 1880), males exhibited similar behavior, forcing their mates to baby-sit (Libhaber & Eilam, 2002). The results of these observations also show that many forms of cooperation in breeding pairs and family groups of rodents couldn't be predicted from the theory of kin selection. However, it is difficult to predict such "coercion" to cooperation under natural conditions, and this behavior, described above, may simply be an effect of captivity.

Conclusion and future directions

The present review shows that empirical data from field and laboratory studies on rodents are inconsistent (at least partially) with conceptual framework developed for understanding the evolution of altruism and cooperation. Specifically, the behavior that is thought to be a case of altruism in rodents (in particular, alarm calling) is difficult to recognize as truly altruistic. Some behavioral observations, as well as theoretical models (e.g., Bednekoff, 1997), suggest that sentinel behavior could arise through selfish individual actions. As for alloparental care, or helping, numerous studies provide evidence that this behavioral phenomenon is not reproductive altruism. Generally, it seems unlikely that alarm calling and alloparental care in rodents evolved merely to kin selection under "Hamilton's rule". A more appropriate explanation is that both alarm calling and helping are by-product mutualism.

The evolution of sociality in rodents means the transition from solitary living to a family-group lifestyle characterized by diverse and complex forms of cooperation (Gromov, 2011, 2017, 2018). In essentially solitary and gregarious species, cooperative behaviors are usually lacking or manifested to a very limited extent. In other words, the evolution of cooperation is closely related to the processes associated with pair bonding and the formation of family groups, suggesting that cooperation in rodent societies is a by-product of the evolution of sociality.

Pair bonding facilitates the cooperation between founders of family groups regarding establishment, scent marking and defending territories, as well as providing care for young. In family groups, social bonding also promotes cooperation in different activities associated with digging underground tunnels and construction of burrows and other shelters, foraging, scent marking and defending home ranges, hoarding, as well as alloparental care exhibited by older offspring towards younger siblings. In fact, cooperation is an immanent attribute of pair bonding and a family-group lifestyle in rodents. Complex forms of cooperation, in turn, contribute to the evolution of their sociality. This evolutionary process can be thought of as some kind of "stimulation of similar with the similar".

The theory of kin selection can not explain the evolution of cooperation in rodent societies. The most complex forms of cooperation are characteristic of the species with a family-group lifestyle, but the founders of family groups are predominantly breeding pairs of unrelated individuals. Thus, relatedness is not a major factor of the evolution of cooperative behaviors. An alternative idea proposed for understanding the evolution of altruistic and cooperative behaviors in rodents should be developed as a conceptual model incorporating not only recent findings supporting the assumption of the above-mentioned behaviors as a by-product of the evolution of sociality, but also the results of research on epigenetic factors (re)programming behavior of rodents (Gromov, 2020).

Many conceptual models explaining the evolution of cooperation in animal societies, including kin selection, reciprocity, enforcement, punishment, and some other ones, are not entirely applicable to rodent societies. Among the generally accepted concepts, the hypothesis of by-product mutualism seems to be most credible.

Cooperation as an important part of social behavior is a fundamental attribute of the socio-ecology of many rodent species and has been the focus of extensive research by scientists from multiple disciplines (Blumstein *et al.,* 2010). Although the diversity of studies focused on cooperative behaviors in rodents is not abundant, the number of these studies has been increasing in recent years (see reviews in Gromov, 2017, 2018). By carrying out studies on diverse species and populations, and in particular adding new scarcely studied species and environments to modern research, we will certainly accomplish useful knowledge in diverse rodent taxa, contributing to fully understand the richest mammalian order, Rodentia.

Future studies on cooperative behaviors in rodents should try to disentangle the mechanisms that explain observed cooperative behaviors. It is possible that some cooperative behaviors only occur under specific ecological and social conditions. Particular target behaviors to be further assessed comprise parental care, helping, cooperative activities associated with establishment, scent marking and defending territories, as well as food hoarding in different rodent species. Interspecific comparisons would also be very welcome in order to infer evolutionary trajectories of cooperative behaviors.

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