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*Full Length Research Paper*

# Biparental care, tactile stimulation and evolution of sociality in rodents

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**Sociality in rodents means a family-group mode of life. Factors promoting pair-bonding and biparental care appear to be of crucial importance for evolution towards sociality. Social species differ from solitary ones because of a higher rate and lasting duration of tactile contact between mates (brooding and grooming) and direct care of young exhibited by both parents (especially brooding, huddling over and grooming pups). The results of my studies support the hypothesis that additional tactile stimulation of pups by parents, as well as limitation of such stimulation, can lead to substantial alteration of their subsequent behavior, especially parental one. Behavioral alteration caused by limitation of tactile stimulation was found to be expressed by weakening of pair-bonds and reduced paternal care. Tactile stimulation is considered a proximate mechanism promoting pair-bonding and a higher rate of paternal care. Paternal investment expressed by direct care of young seems to be an essential factor responsible for the evolution towards sociality in rodents.**

**Key words:** Rodents, sociality, tactile stimulation, evolution.

## INTRODUCTION

The problems posed by the evolution of the diverse forms of animal sociality are among the most important and fascinating in evolutionary biology. Over the last several decades, numerous studies concerning the phenomenon of sociality in various mammal communities, including those of rodents, have been carried out. Traditional views of evolution of sociality focus on ecological factors such as predation risk and physical resources integrated into models of the causes and consequences of sociality (Crook, 1970; Alexander, 1974; Clutton-Brock, 1974; Hoogland and Sherman 1976; Hoogland, 1981; Carr and Macdonald 1986; Jarvis et al., 1994; Ebensperger, 1998; McGuire et al., 2002). Unfortunately, very little is known about proximate causation of sociality, especially in rodents.

In the general sense, sociality means group-living, that in turn may be viewed as a life-history tactic increasing the fitness of group members (Armitage, 1981, 1999). The evolution of sociality requires that individuals both get together in groups and cooperate within them. Among rodents, the most social species like alpine marmots, beavers, musk-rats, naked mole-rats, some voles and gerbils, live in family groups. Hence, the high sociality, and even eusociality, in rodents could be considered as family-group mode of life. Families in turn are defined by the continuing interaction of offspring with their parents (Emlen, 1994; Jarvis et al., 1994), so family groups usually are composed of close kin, and breeding within the groups is restricted mainly to one female and one male (monogamous families). However, there are some exceptions, for example, among musk-rats *Ondatra zibethicus* (Marinelli and Messier, 1995), prairie voles *Microtus ochrogaster* (Roberts et al., 1998), Brandt's voles *Lasiopodomys brandti* (Gromov, 2003), Mongolian gerbils *Meriones unguiculatus* (Ågren et al., 1989; Gromov 2008), and some other rodent species with female-biased populations, where family groups include two or three reproducing females (polygynous families). Besides, there are polyandrous families with two or three males mating with one female like in the naked mole-rat *Heterocephalus glaber* (Jarvis et al., 1994).

As a rule, families occur when grown offspring delay dispersal and continue to reside with parents. Emlen (1994) supposed that the critical step in understanding the evolution of the family is to understand the causes of such delayed dispersal. But it is also important to understand the main factors promoting pair-bonding because the first step to formation of a monogamous pair or even an extended family group is long-term association between female and the male mate. Another major factor that also seems to be involved in evolution towards sociality in rodents is participation of males in care of their offspring (Gromov, 2011). Among rodents, sole maternal care is the most frequent pattern associated with promiscuity, while biparental care is associated, although not always, with monogamy (Kleiman, 1977; Wang and Insel, 1996). Biparental care is relatively uncommon (Kleiman, 1977; Kleiman and Malcolm, 1981), hence for males this is an unusual partitioning of reproductive effort. The purpose of this paper is to show the role of parental care, especially biparental one, as a factor promoting pair-bonding and evolution towards family-group mode of life (that is, the highest category of sociality) in rodents belonging to Myomorpha (mice, hamsters, voles, gerbils, etc). Environmental factors and ultimate mechanisms promoting pair-bonding and a higher level of parental care are out of consideration in this article, but proximate mechanisms underlying the inter-specific differences related to various aspects of social organization, seem also play an important role in evolution towards sociality, and thus deserve special attention.

## THE SPATIAL- AND- ETHOLOGICAL POPULATION STRUCTURE, PAIR-BONDING, AND PARENTAL CARE

Rodents belonging to Myomorpha are known to have particular differences in their mating systems and the spatial-and-ethological population structure (SEPS). According to previously developed classification (Gromov, 2005a, 2008), SEPS could be divided into four main types. Type I means lack of social groups in solitary dwellers (except of temporary and unstable aggregations of males competing for receptive females during the reproductive season only) with promiscuous mating and consequently very weak pair bonds like, for example, in the Tamarisk gerbil *Meriones tamariscinus* (Gromov et al., 1996; Gromov, 2001) or the gray hamster *Cricetulus migratorius* (Vasilieva and Surov 1984; Gromov, 2008). Type II represents multi-male–multi-female breeding colonies existing due to overlapping home ranges and also characterizing of promiscuous mating, weak pair bonds and early offspring dispersal like in bank voles *Clethrionomys spp.* (Mihok, 1976, 1979; West 1977; Viitala, 1977; Kawata, 1985, 1988), the meadow vole *Microtus pennsylvanicus* (Madison, 1980a, b; Ostfeld et al., 1988) or the Midday gerbil *Meriones meridianus* (Popov et al. 1989). Type III is characteristic of species with relatively stable reproducing pairs or weakly consolidated family groups with early offspring dispersal like in the common vole *Microtus arvalis* (Boyce and Boyce III, 1988; Zorenko, 1994; Langsdale and Young, 1999), the social vole *M. socialis* (Kasatkin et al., 1998; Shilova and Kasatkin, 2000), the Libyan gerbil *Meriones libycus* (Daly and Daly, 1975; Ågren, 1979; Gromov, 1997) or the steppe lemming *Lagurus lagurus* (Gromov, 2008). Type IV represents structural family groups with biparental care, strong pair bonds (behavioral monogamy), delayed offspring dispersal, and complicated social organization related particularly to differentiation of behavioral roles, hierarchy of subordination, suppression of reproduction in offspring, etc., like in the Mongolian gerbil *M. unguiculatus* (Ågren et al., 1989; Gromov, 2008), the mandarin vole *Lasiopodomys mandarinus* (Smorkatcheva, 1999) or the Brandt's vole *L. brandti* (Zhang and Zhong, 1981; Fang and Sun, 1991; Wan et al., 1998; Zöphel, 1999; Gromov, 2008). These types of SEPS could be considered as four categories of sociality among rodents.

Cross-species comparison (Gromov, 2008, 2011) showed that there is a pronounced tendency towards both reinforcement of pair bonds and increasing rate of direct parental care (brooding and grooming pups), especially paternal one, when solitary or gregarious species (Types I and II) are compared with those living in family groups (Types III and IV). In solitary dwellers (Type I), like many hamsters or some voles and gerbils, spacing behavior only operates among adult individuals that are usually intolerant of conspecifics of both sexes. Non-aggressive interactions between males and females occur during relatively short mating periods only, and males usually do not contact with pregnant and lactating females (Gromov, 2008). A very high proportion (up to 95%) of agonistic behaviors (attacks, chases, wrestling, offensive and defensive postures, avoidance) in dyadic encounters of opposite-sex individuals reflects the weakest pair-bonds in essentially solitary species. Cross-species comparison of four *Meriones* gerbils with different types of SEPS (*M. tamariscinus, M. meridianus, M. libycus, M. unguiculatus*) revealed that this proportion declines when solitary (*M. tamariscinus*) or gregarious species (*M. meridianus*) are compared with those living in family groups (Gromov, 2008): maximum values (76 to 95%) were found in *M. tamariscinus* (Type I) and minimum ones (9 to 11%) – in *M. unguiculatus* (Type IV) (Figure 1). In other words, a lower proportion of agonistic acts in male-female interactions could be used as a suitable predictor of pair-bonding.

For estimation of the reinforcement of pair-bonding in rodents one can use some other behaviors, for example, nest cohabitation of parents rearing the young, and grooming of their mate. Cross-species comparison of seven cricetid rodents (*C. migratorius, Clethrionomys rutilus, M. arvalis*, *M. socialis, Lagurus lagurus, L. brandti* and *M. unguiculatus*) with different types of SEPS shows that time spent in the nest by both parents (Figure 2) as well as duration of grooming (licking) of the mate (Figure 3) significantly correlated with the type of SEPS: for all three variables, Spearmen $R > 0.546$, $t_{(N-2)} > 5.408$, $p < 0.001$. The minimum values of these variables were

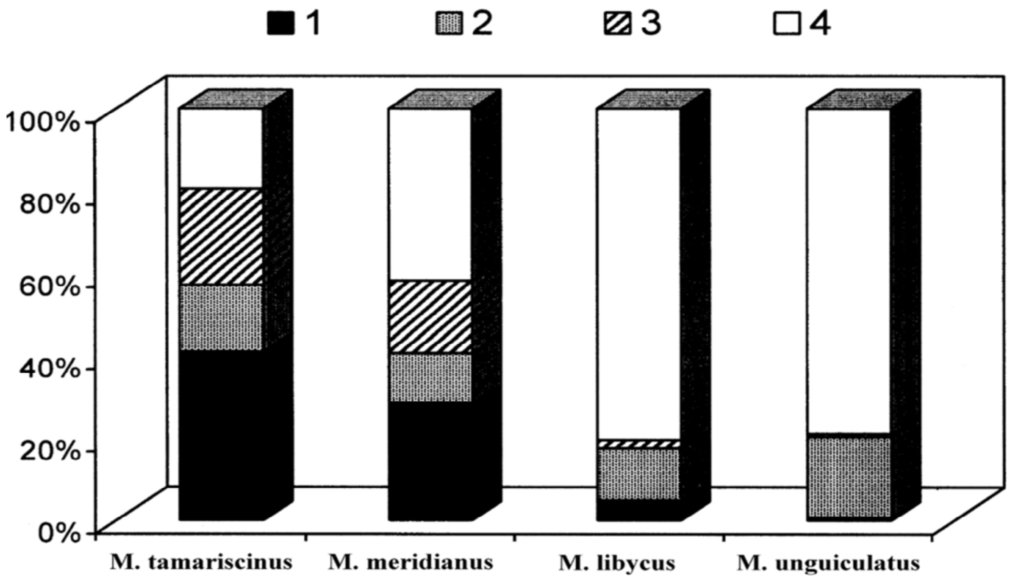

**Figure 1.** Proportions (%) of overt aggressive, (1) ritualized agonistic (2) and peaceful interactions (4) as well as avoidance (3) in dyadic encounters of males and females of four *Meriones* species with different types (I-IV) of the spatial-and ethological population structure. The data are obtained due to visual observations of the animals in the natural habitats and the large outdoor enclosures (Gromov, 2008).

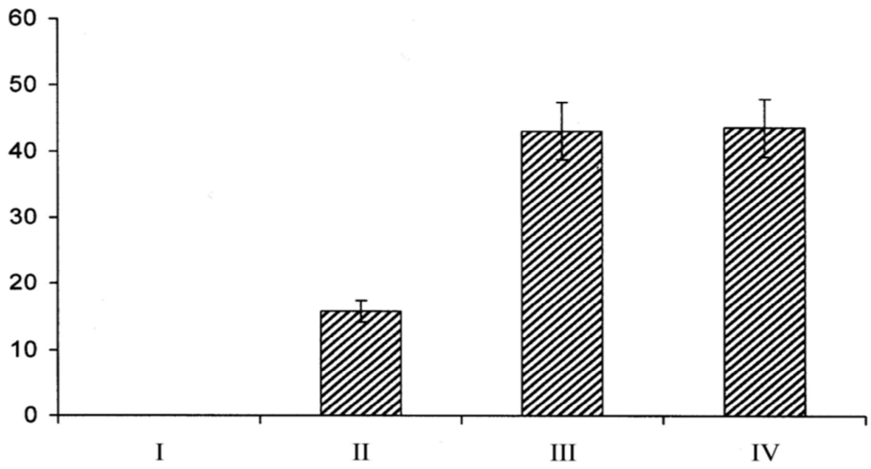

**Figure 2.** Variation in time spent in the nest with the mate (mean duration in minutes per 1 h ± SE) among rodents with different types of the spatial-and-ethological population structure (I-IV). To carry out this comparative analysis, samples of species belonging to the same type of SEPS (that is, *M. arvalis, L. lagurus* and *M. socialis*, type III, as well as *L. brandti* and *M. unguiculatus*, type IV) were united.

found in *C.rutilus* (Type II) and the maximum ones – in *L. brandti* and *M. unguiculatus* (Type IV). In other words, the weakest pair bonds are characteristic of *C. migratorius* (Type I) in which males nearly do not have contact with pregnant and lactating females. Males of species living in family groups (especially that ones belonging to Type IV like *M. unguiculatus*) display a higher rate of activity related to the female mate's grooming than do males of *C. rutilus* (Type II). Besides, the breeding pairs of species living in family groups (Type III and Type IV) spend significantly longer time together in the nest than do males and females of *C. rutilus* (Type II). These interspecific differences reflect reinforcement of pair bonds in rodents living in family groups (Types III and IV) compared to solitary (Type I) or gregarious ones (Type II).

Perhaps, for such a cross-species comparison it would be better to use samples of closely related species of one systematic group, for instance voles of family Arvicolinae

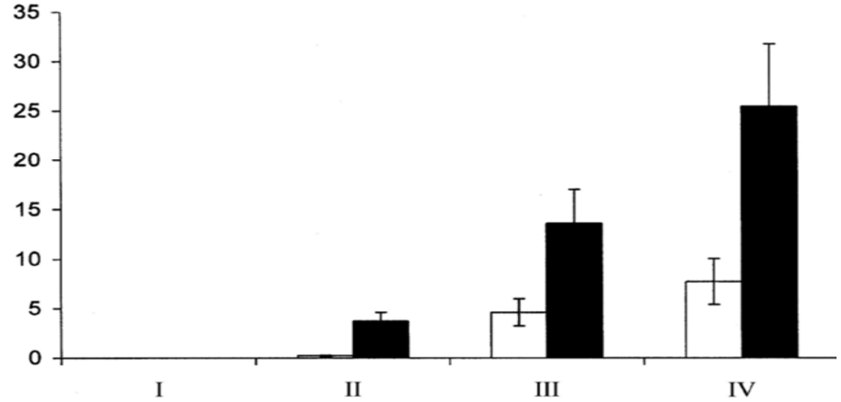

**Figure 3.** Variation in the mate grooming (mean duration in seconds per 1 h ± SE) exhibited by females (open bars) and males (closed bars) among rodents with different types of the spatial-and-ethological population structure (I-IV).

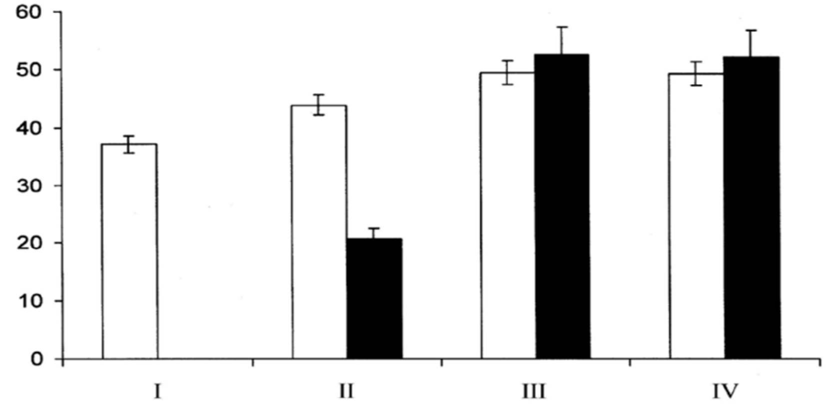

**Figure 4.** Variations in total nest attendance (mean duration in minutes per 1 h ± SE) in females (open bars) and males (closed bars) among species with different types of the spatial-and ethological population Structure (I-IV).

(for example, the montane vole, the meadow vole, the common vole, and the Brandt's vole). Unfortunately, I do not have the baseline data for the first two species collected under uniform conditions, using uniform sampling methods, like for the last two ones.

Direct parental care seems also to play an essential role in evolution towards sociality among rodents. Cross-species comparison showed that such direct care-giving activities as nest attendance of both parents related to a higher rate of brooding pups (Figure 4), as well as pup grooming (Figure 5), especially the ones exhibited by males, were also expressed in a significantly larger extent in species with family-group mode of life (*M. arvalis, M. socialis, L. lagurus, L. brandti,* and *M. unguiculatus,* Types III and IV) compared with *C. rutilus* (Type II) or *C. migratorius* (Type I). This tendency is clearly supported by the correlation analysis that revealed a pronounced relationship between the types of SEPS and nest attendance in females (Spearmen R = 0.454, $t_{(N-2)}$ = 4.232, $p < 0.001$) and males (Spearmen R = 0.624, $t_{(N-2)}$ = 6.636, $p < 0.001$). Besides, males of species with family-group mode of life (Types III and IV) were found to groom their pups much longer than do males of gregarious ones (Type II). This conclusion is also supported by the correlation analysis: Spearmen R = 0.690, $t_{(N-2)}$ = 7.910, $p < 0.001$. On the contrary, the relationship between the types of SEPS and pup grooming by females was revealed to be insignificant.

The present findings show that there is an obvious relationship between the four aforementioned categories of sociality and both pair-bonding and parental responsiveness, especially that one related to the direct paternal care. In essentially solitary dwellers (Type I) like the gray hamster, males do not display care-giving activities. The same seems to be typical of many other representatives of subfamilies Cricetinae, for example, the golden hamster *Mesocricetus auratus* (Rowell, 1961; Daly, 1972), and Microtinae, for example, the montane vole *Microtus*

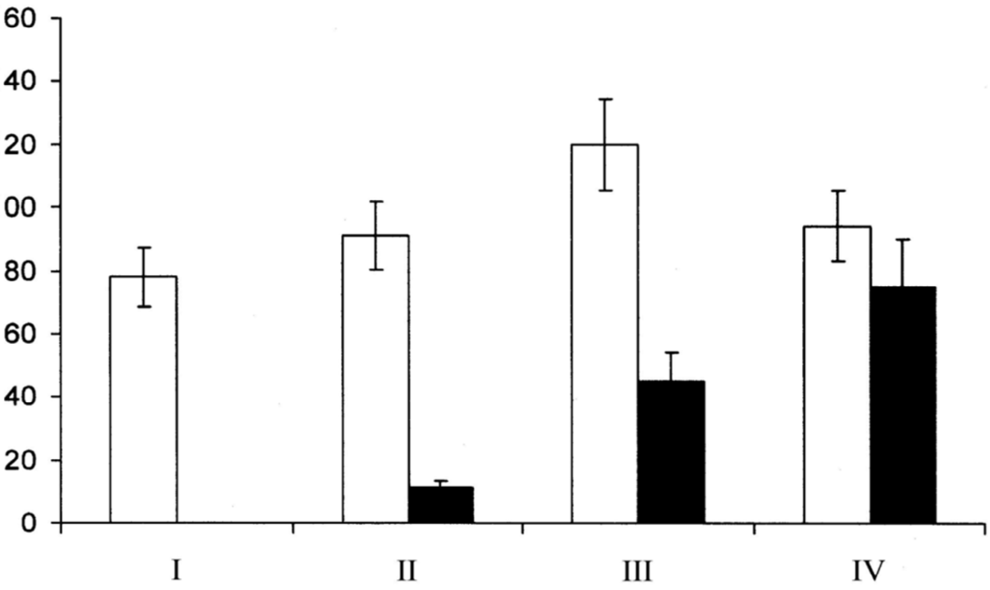

**Figure 5.** Variations in pup grooming (mean duration in seconds per 1 h ± SE) in females (open bars) and males (closed bars) among species with different types of the spatial-and ethological population structure (I-IV).

vole *Microtus montanus* (McGuire and Novak, 1986). Primarily uniparental care is also characteristic of gregarious rodents (Type II) like *C. rutilus* (Gromov, 2009a) as well as *Peromyscus leucopus* (Xia and Millar, 1988), *M. pennsylvanicus* (McGuire and Novak, 1984; Oliveras and Novak, 1986) or *C. gapperi* (McGuire, 1997) in which males display parental responsiveness partially or occasionally only; besides, males of gregarious species exhibit maximum variability of direct parental care (Hartung and Dewsbury, 1979; McGuire, 1997; Gromov, 2009a, 2011). Among rodents living in family groups, there are species with relatively weak pair bonds and a medial level of paternal responsiveness (Type III) like *M. arvalis* and *L. lagurus* (Gromov, 2010, 2011) or, for example, *Peromyscus californicus* (Gubernick and Alberts, 1987). Species with structural family groups (Type IV), like *L. brandti* or *M. unguiculatus* (Gromov, 2005b, 2009b), exhibit resistant pair bonds and a higher level of biparental care. The same seems to be characteristic of the prairie vole *Microtus ochrogaster* (McGuire and Novak, 1984; Oliveras and Novak, 1986; Solomon, 1993), pine vole *M. pinetorum* (McGuire and Novak, 1984; Oliveras and Novak, 1986) and mandarin vole *L. mandarinus* (Smorkatcheva, 2003).

Thus, one can say about a continuum of pair-bonding and care-giving activities associated with the four main types of SEPS, that is, four categories of sociality. This continuum reflects progressive reinforcement of pair bonds and an increase of level of direct parental care, especially paternal one providing for a higher rate of tactile stimulation of pups due to huddling over them, side-by-side contacts, brooding and grooming (licking).

## Behavioral and physiological effects of biparental care and tactile stimulation

A study carried out by McGuire (1988) has shown that young of the meadow vole reared by prairie-vole parents received more parental contacts than pups fostered to meadow-vole parents. When tested in adulthood, cross-fostered females spent more time in the nest and exhibited more brooding and grooming pup than in-fostered females, cross-fostered males often entered the natal nest and engaged in more pup contact behavior than in-fostered males, in that number brooding and grooming pups. In terms of sociality, experimental groups of the meadow vole, in which males exhibited paternal care, could be regarded as more social ones.

In my recent study (Gromov, 2009b) young males of the Mongolian gerbil reared in incomplete family groups (without sires) exhibited a lower rate of subsequent parental responsiveness related to nest attendance and hence a lower rate of brooding pups as well as grooming pups; besides, these males groomed their female mates significantly less frequently than the males of the control group. In terms of sociality, the experimental groups of the Mongolian gerbil, in which both males and females exhibited a lower rate of pair-bonding and parental behaviors, could be considered as less social ones.

The results of both studies suggest that pair-bonding and development of parental behavior, especially paternal one, are subjects to influence by characteristics of the early environment, or, in other words, is very important for acquiring patterns of paternal care. It is evident that young males can 'inherit' to an extent the stereotype of parental behavior of their sires: if the adult male exhibits increased parental care, the 'careful father' behavioral stereotype is in a manner fixed in young males, and vice versa (McGuire, 1988; Roberts et al., 1998). In my experiments with Mongolian gerbils (Gromov, 2009b), a quite expected effect was obtained: young males that had no contact with their sires, after reaching sexual maturity, cared for their own pups to a lesser degree than "normal" males that grew in families with both parents. Similar transformation of parental behavior that occurs not only in males but in females also can fix and intensify within generations. This phenomenon undoubtedly has an epigenetic nature: variations in parental behavior related to different levels of tactile stimulation of offspring appear to serve as a mechanism for the nongenomic transmission of individual differences in parental responsiveness across generations.

Tactile stimulation is known to be an important influence in ontogeny of rodents (Russell, 1971; Vandenbergh, 1967). Licking young, which are considered as part of grooming (McGuire and Novak, 1984, 1986; Solomon, 1993), facilitates blood circulation of infants and in turn supports thermoregulation and activates the infants (Eilam and Smotherman, 1998). Besides, physical contact may affect parent-infant bonding and subsequent social interactions (Gubernick and Alberts, 1987). Although pup grooming decreased during postnatal development, it did not disappear entirely at weaning in species with the family-group mode of life (Gromov, 2005b, 2007, 2009b), when the aforementioned functions were no longer required. Therefore, pup grooming probably plays an additional, social role, in maintaining the bond between parents and their offspring. The direct parental care of males is mainly related to brooding and licking pups that provide additional tactile stimulation of infants.

The role of tactile stimulation in the formation of complicated social organization of rodents has almost not been studied. However, the data concerning neurobiological basis of parental care indicate the critical importance of tactile stimulation for understanding inter-specific differences in parental behavior and pair bonds. In particular, numerous thermoregulatory behaviors that are typical of some gregarious species during the non-breeding season and especially of species living in family groups suggest that huddling by the male with his mate and young may be an important factor in the evolution of social monogamy (Rathbun and Rathbun, 2006).

Recent research showed that female offspring or adopted, cross-fostered pups that had early experiences with mothers who licked and brooded a lot showed higher levels of licking as adults as compared to females raised with mothers who licked and crouched less (Francis and Meaney, 1999; Francis et al., 1999). This research additionally highlights the role of tactile stimulation as a major factor contributing to normal development of physiological, behavioral and neuroendocrine responses in the rat neonate and perhaps neonates of other rodents.

Another recent study assessed the effects of complete maternal deprivation and the 'replacement' of maternal behaviors by the addition of simulated maternal-licking (with a soft paint brush) on the development of adult maternal behaviors (Gonzalez et al., 2001). The results of this study indicate that, how infants were reared can affected both later maternal and emotional behavior. In comparison to mother-reared females, artificially reared animals showed fewer frequencies and shorter durations of a number of maternal responses towards their pups after they gave birth in adulthood, artificially reared animals showed reduced levels of retrieving, licking, and crouching over pups; besides, they spent less time in the nest. But artificially reared neonates that were provided with additional tactile stimulation that mimicked the effects of mothers' licking have shown patterns of behavior more similar to mother-reared females. Hence, additional licking-like stimulation was able to ameliorate the effects produced by maternal deprivation.

Other recent cross-fostering studies using populations of female laboratory rats that naturally vary in their maternal behavior indicated that the maternal behavior of adopted offspring is highly correlated with that of adoptive mothers (Francis et al., 1999) although the adopted mothers did not gestate the offspring and had no genetic relationship to them. The mechanism through which this early experience affects the animal's later maternal behavior is not known yet. However, there are a number of potential mechanisms. Maternally deprived animals do not receive the same olfactory and somatosensory stimulation that is necessary for normal development of responses to social cues later on. Under normal circumstances, the young learns about mother's odors and that learning along with tactile stimulation can influence later behavior. This early experience of olfactory-somatosensory associations is encoded by the brain and produces long-lasting changes in brain. In particular, formation of the association between licking and maternal odor produces changes in the olfactory bulbs, altering their neurochemical and structural properties (Wilson and Sullivan, 1994; Najbauer and Leon, 1995), and depends on the activation of the noradrenergic system that originates in the midbrain locus coereleus and terminates in the olfactory bulbs (Wilson and Sullivan, 1994). Besides, additional environmental manipulations during the preweaning period, including somatosensory stimulation, produce changes in cortex, hippocampus, and other limbic areas, and considerably affect the development of the hypothalamic-pituitary-adrenal axis (Cramer, 1988; Pascual and Figueroa, 1996; Rosenzweig and Bennett, 1996; Liu et al., 1997; Post et al., 1998). Early deprivation from the mother seems to alter the development of the medial preoptic system or its afferent (amygdala, bed nucleus of stria terminalis) or efferent (midbrain tegmentum) connections (Numan, 1994). Or, more likely, that it alters the development of receptor systems and related neurotransmitter systems that reside in the maternal circuit such as oxytocin and dopamine (Noonan et al., 1994; Numan, 1994; Bridges, 1996; Insel, 1997; Nelson and Panksepp, 1998; Panksepp et al., 1994; Stern and Keer, 1999; Keer and Stern, 1999; Numan et al., 2006).

Maternal deprivation, which effects negatively on the hypothalamic-pituitary-adrenal axis, is also known to produce pups that have enhanced corticosterone response to various stressors, increased c-Fos expression in the paraventricular nucleus, altered metabolism, down regulation of mineralocorticoid and glucocorticoid mRNA receptors in the hippocampus, and serum growth decreases. However, by reinstating critical components of the dams' nurturing behavior some of the negative physiological responses due to maternal deprivation can be reversed (Suchecki et al., 1993; Vasquez et al., 1996; Kuhn and Schanberg, 1998; Van Oers et al., 1998).

Thus, maternal behavior is critical, not only because the mother provides nutrients, warmth, and protection to the altricial pups, ensuring that the pups can survive past weaning, but it also serves to provide the offspring with experiences that promote their behavioral development and the appropriate expression of their maternal behavior when they grow up. The current evidences suggest that tactile stimulation that effects on the development of receptor systems and related neurotransmitter systems such as oxytocin, dopamine, and vasopressin, also contributes to regulation of different aspects of pair-bonding (Numan and Insel, 2003). These neuropeptides and dopamine are known to be released by the activation of somatosensory afferents in response to social contact and grooming. For example, experimental studies carried out primarily on the prairie vole show that mating induces dopamine release, and released dopamine acts in a region- and receptor-specific manner to regulate pair-bonding behavior (Liu and Wang 2003). Arginine vasopressin increases the time spent grooming, contacting, and brooding pups, and vasopressin gene expression increases in both males and females of the prairie vole postpartum (Wang et al., 2000). Besides, central oxytocin manipulation also alters partner preference formation in both male and female prairie voles (Cho et al., 1999). In addition, a specific role for the ventral tegmental area, the bed nucleus of the stria terminalis, the lateral septum, and the medial nucleus of the amygdala in partner preference formation is confirmed (Wang and Aragona, 2004; Curtis and Wang, 2005). The results of these studies suggest that tactile stimulation might be expected to have specific physiological effects in the infant with predictable outcomes on development of their parental responsiveness as well as pair-bonding behavior.

Moreover, these effects might be expected in the infants of both sexes.

## Additional tactile stimulation and evolution towards sociality in rodents

Studies carried out on a number of species with a family-group mode of life (Elwood, 1975, 1983; McGuire and Novak, 1984; Solomon, 1993; Clark et al., 1997; Smorkatcheva, 2003; Gromov, 2005b, 2007, 2009b, 2010) indicate that infants reared by two parents receive additional tactile stimulation from males, whereas the offspring nourished by female only in essentially solitary rodents is devoid of such extra stimulation. Bearing in mind the results of the experiments on artificial rearing and cross-fostering of infants (McGuire, 1988; Roberts et al., 1998; Gonzalez et al., 2001), as well as the experiments with Mongolian gerbils (Gromov, 2009b), one may conclude that participation of males in rearing their offspring is the important factor of subsequent development in individuals of the same sex of the ‘careful father’ behavioral stereotype that is so typical of many rodent species with a family-group mode of life. Moreover, additional tactile stimulation of infants promotes reinforcement of social bonds and peaceful relationships in family groups. Although experimental studies indicate the special role of grooming (licking) pups in formation of their subsequent parental behavior, the tactile stimulation of pups with the participation of the male provides the combined effect of grooming and brooding.

I think that the role of supplementary tactile stimulation in evolution towards sociality among small rodents could be clearer if compare with paternal responsiveness, for example, social vole or the Mongolian gerbil with that of social marmots. Current knowledge suggests that, for instance, the Olympic marmot (*Marmota olympus*) is highly social, living in extended family groups usually composed of one adult male, two females and their offspring (Barash, 1973, 1974; Armitage, 1981, 1999). Group members live in a common home range and always hibernate together in one hibernaculum. The Olympic marmot is referred to as highly tolerant concerning interactions between members of the family group, but pregnant and lactating females are known to occupy separate nest burrows and aggressively respond to approach of the adult male to the burrow until weaning of the young. Thus, in spite of the family-group mode of life, sole maternal care is rather typical of the Olympic marmot, and males do not exhibit direct paternal care like huddling over or grooming young before weaning as it is characteristic of many social mice, voles and gerbils. Primarily aggressive interactions of pregnant and lactating females with the male mate in family groups of the Olympic marmot suggest relatively weak pair bonds in this species as well.

The difference in paternal responsiveness and pair-bonding in the Olympic marmot and some voles or gerbils living in family groups is in accordance with my hypothesis of the fundamental role of the supplementary tactile stimulation in evolution towards sociality among rodents. Infants of the Olympic marmot do not receive extra stimulation from their fathers that is necessary for adequate transformations in the neurobiological basis of parental responsiveness and social bonds. Consequently, weak pair bonds and lack of direct paternal care (that is, brooding and grooming infants) are typical of the species. Nevertheless, the Olympic marmot as many other representatives of the genus *Marmota*, for example, *M. marmota*, *M. sibirica* and *M. bobac*, live in family groups (Barash, 1976; Suntsov, 1981; Arnold, 1990; Rymalov, 1994). But, in contrast to many social mice, voles and gerbils, marmots are relatively large rodents. It is hypothesized that prolonged toleration of offspring is a means of preventing dispersal of undersized young (Barash, 1974) or continued parental investment (Armitage, 1981, 1987). For example, Olympic marmots achieve less than 25% of their adult weight during the year of birth, and the young of this species need to remain in the family with their mothers. As yearlings, Olympic marmots are still only 30% mature and, accordingly, they remain closely associated with their mothers until they are 2 years old. At this point, having achieved 70% of adult weight, the Olympic marmots finally disperse and bear their first litter following (their third) year (Barash, 1974). Similar peculiarities of offspring development are characteristic of the alpine marmot, after emerging from hibernation, yearlings averaged about 40% and 2 year-olds about 80% of adult mass (Arnold, 1990a). The large body mass and some other factors (for example, short active season, long developmental time, benefits from the subordinates' presence for rearing young, fitness effect of social hibernation) seem to establish the main basis for the evolution of sociality in marmots (Barash, 1974; Arnold, 1990a, b; Armitage, 1999). This basis, however, does not include such a proximate mechanism as biparental care providing the additional tactile stimulation of infants, and this appears to be true for other large rodents whose males do not exhibit the direct paternal care.

## Conclusion

Field and experimental studies suggest that evolution towards sociality in rodents is under control of various ultimate and proximate mechanisms and factors. I hypothesize that in small rodents, like many representatives of Myomorpha, biparental care and additional tactile stimulation of pups by means of brooding and grooming, play an essential role in evolution of sociality that in turn could be imagined as transition to family-group mode of life, or in other words a progressive evolutionary transformation of SEPS of Type I into Type IV. The significance of such a proximate mechanism in the evolution of sociality of rodents is underestimated so far.

I would like to emphasize that evolution of family-group mode of life do not means evolution of monogamy, but evolution of various types of families – monogamous, polygamous or extended ones, because formation of any of them starts from a reproducing pair. Ultimate factors that promote pair-bonding and biparental care – a special topic that deserves separate consideration (not in this article). I do not consider the effect of paternal care on the general fitness and survival of offspring as well, because this is also a special topic. Moreover, experimental studies on different rodent species provide conflicting information concerning the effect of presence of the sires on the development and survival of the offspring. For example, male parental investment has been found to increase pup survival in *P. californicus* (Gubernick et al., 1993; Cantoni and Brown, 1997; Gubernick and Teferi, 2000) or *M. unguiculatus* (Gerling and Yahr, 1979), and to accelerate pup development in *M. ochrogaster* (Wang and Novak, 1992, 1994) and *M. pennsylvanicus* (Storey and Snow, 1987) but no effect was revealed in some other species or under different environmental conditions (Elwood and Broom, 1978; Priestnall and Young, 1978; Wuensch, 1985; Shilton and Brooks, 1989).

Considering the phenomenon under study, I would like to note that there is no definite, 'standard' level of sociality that would be characteristic of any rodent species. Experimental studies show that a relatively high level of intra-specific variability is typical of the pair-bond and parental behaviors (McGuire, 1997; Gromov, 2007, 2009a). It means that within populations of any gregarious or polygamous as well as so-called monogamous rodent species there are breeding pairs or family groups that could be regarded as more social and less social (Roberts et al., 1998). These intra-specific differences in social attachment between members of particular breeding units, as well as in their parental responsiveness, according to my hypothesis, could be explained by the influence of the early environment, or, in other word, by the degree of participation of males in care of their offspring. Ultimate causation of the family-group mode of life is out of consideration in this article, but I can assume the ecological circumstances whereby family groups could evolve are evidently the ones promoting cooperation in foraging, territory defense or communal care of offspring, so that individuals living in family groups will have higher fitness than those living as solitary dwellers. Direct paternal care by means of tactile stimulation of young is one of the factors (mechanisms) promoting formation of long-lasting pair bonds as well as development of paternal behaviors in offspring. This phenomenon has an epigenetic nature and could be considered as 'stimulation of similar to the similar'.

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