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Interactions between intruders and residents in the mole vole Ellobius talpinus *

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Abstract We studied the behavioral and endocrine responses of the fossorial social rodent , mole vole *Ellobius talpinus* Pall. , to intrusions of strangers into burrow systems that were occupied by intact families. Both in reproductive and non-reproductive seasons , all intruders disappeared from the burrow systems of residents within two days of introduction , whereas 4 of 7 individuals introduced into empty burrows remained there at least for two days. Introduction of strangers led to the concentration of residents at the point of release and to an increase of plasma corticosterone in both residents and intruders. During the breeding season , introduction of strangers was also accompanied by an increase of plasma testosterone of residents on the day of introduction. Thus , simulation of intrusion of strangers demonstrated the efficient social fence of resident mole voles that seems to be an important mechanism of stabilization of size and structure of mole vole families. Encounters of residents and intruders resulted in activation of physiological mechanisms of stress , especially during the breeding season [*Acta Zoologica Sinica* 50 (1) : 19 - 26 , 2004].
Key words Fossorial rodents , Mole vole , Familiarity , Social fence , Stress

鼹形田鼠入侵鼠和留居鼠之间的相互作用 *

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摘 要 我们研究了营掘地生活的社会性啮齿类——鼹形田鼠 (*Ellobius talpinus* Pall.) 对陌生鼠入侵完整家庭所占据洞穴系统后的行为和内分泌反应。在繁殖期和非繁殖期, 所有的入侵鼠都在进入洞穴 2 天内从留居鼠的洞穴系统内消失; 而在引入空洞穴的 7 只鼹形田鼠中, 有 4 只至少在该洞穴中停留了 2 天。引入陌生鼠导致留居鼠在释放地的集中, 并引起留居鼠和入侵鼠血浆中皮质酮水平的增加。在繁殖期, 在引入陌生鼠的当天, 也伴随着留居鼠血浆中睾酮增加的现象。所以, 对陌生鼠入侵的模拟表明了留居鼹形田鼠有效的社会性防范, 这可能是该物种家庭大小和结构稳定的一个重要机制。留居鼠和入侵鼠的相遇激活了压力的生理机制, 特别是在繁殖季节更是如此 [动物学报 50 (1) : 19 - 26 , 2004]。
关键词 营掘地生活的啮齿类 鼹形田鼠 熟悉程度 社会性防范 压力

Kinship and familiarity of individuals play an essential role in establishing the social structure of animal populations. Social units in many species consist of genetically related individuals (Jarvis , 1981 ; Sherman and Holmes , 1985 ; Pfenning and Sherman , 1995) . Agonistic reaction to introduction of unfamiliar conspecifics seems to be an important mechanism of both regulation of the local density (Charnov and

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Finerty, 1980; Hestbeck, 1982, 1988) and behavioral defense against parasites that could be brought by newcomers (Loehle, 1995; Lewis, 1998; Moshkin et al., 2000). Indeed, social isolation can provide protection from novel infections, on one hand, but kin breeding as an inevitable consequence of isolation often results in a substantial decline in fitness due to inbreeding (Shields, 1982; Fletcher and Michener, 1986; Jarvis et al., 1994). Moreover, aggression towards the intruders could be detrimental for both residents and intruders due to stress and/or injuries.

Among vertebrates, the highest degrees of sociality are known in fossorial rodents (Jarvis et al., 1994). In some of these species breeding is restricted to one female and one to three males (Jarvis, 1981). Sociality, as the consequence of high risk of dispersion, leads to the high degree of kinship between colony members (Reeve et al., 1990). The self-restraint model (Snowdon, 1996) proposed that inbreeding avoidance is one of the main reasons of reproductive suppression in cooperatively breeding animals. In damaraland mole-rats, *Cryptomys damarensis*, presence of non-related partner seems to be an essential condition for successful reproduction (Bennet et al., 1996; Clarke et al. 2001). Even in the naked mole rat, *Heterocephalus glaber*, a species with extremely low dispersion (O'Rian et al., 1996), preference of unfamiliar mates has been described (Clarke and Faulkes, 1999). On the other hand, in laboratory conditions this species is highly xenophobic to foreign conspecifics: residents attacked unfamiliar animals immediately after their introduction (Lacey and Sherman, 1991; O'Rian and Jarvis, 1997). In another colonial fossorial rodent, the mole vole, *Ellobius talpinus*, dispersion in nature is a common phenomenon, especially in the young-of-the year cohort (up to the 70%), but only few immigrants (less than 10%) become members of unfamiliar colonies and take part in reproduction (Evdokimov, 1997, 2001). This species occupies a wide range of steppe and forest steppe landscapes from Eastern Europe to central Asia and has rather stabile social units, i.e., families. Each family has discrete burrow system and consisted of 2 - 15 individuals. Among them there are several mature males, but only one reproductively active female (Evdokimov and Pozmogova, 1993; Evdokimov, 2001). Experimental studies of mole voles in the laboratory revealed a low level of intraspecies aggression. Encounters of two or of six unfamiliar mole voles led to only few agonistic interactions (Bolshakov et al., 1989; Moshkin et al., 1991). In contrast to terrestrial rodents, encounters induced weak stress responses as assessed by the increase of plasma corticosterone (Bolshakov et al., 1989). In another experiment we placed two unfamiliar groups (each group consisted of individuals from the same family) of four mole voles for 48 hours in different parts of three connected cages where a central cage was divided by a screen. Removal of the screen led to an aggregation of the voles in a common group with no signs of aggression (Petrovski, unpublished data). These data are not necessarily indicative of the nature of agonistic reactions of mole voles towards foreign conspecifics in nature; behavioral responses to strangers in an unfamiliar laboratory environment may differ from those occurring under natural conditions.

In order to elucidate the role of familiar conditions, which include habitual space and odor, in resident response to intruders we simulated intrusion of strangers in the burrow systems that were occupied by mole vole families. Since only one point of a given burrow system was used for introduction, we propose that concentration of residents around this hole can reflect the behavioral response to intrusions. Also we predict the changes of plasma corticosterone and testosterone to be indicators of stress reaction of both residents and intruders.

1 Materials and methods

1.1 Area, trapping and sampling

We studied mole voles in field conditions in August 17 - 25, 1996 and in April 19 - 26, 1997. The examined population occupied the North-Eastern boundary of the species' range - 54°36′N, 82°43′E (Novosibirsk region, Russia). According to literature (Evdokimov and Pozmogova, 1993; Evdokimov, 2001) and our unpublished data, in northern populations mole voles reproduce in late winter and spring. Summer and fall is the period of active food storage. Thus, our two experiments included both reproductive (April) and non-reproductive (August) periods in the annual cycle of mole voles.

Since each family occupies an isolated burrow system that is easily detected visually by the hills of soil dragged out on the surface (Evdokimov, 2001), we considered individuals captured in a burrow as members of the same family. Distance between studied families was no less than 200 m. List of family groups, number of trapped individuals and family structures are presented in Table 1. For ethical reasons and in adherence to "Rules of Scientific Experiments Conduction" approved by the decree of the Presidium of Russian Academy of Sciences from 2.04.80 No. 12 000 - 496, we minimized the number of trapped animals to samples size just sufficient for the robust statistics. We trapped animals simultaneously in 4 - 6 families with live-traps that were constructed by B. A. Golov for trapping of mole voles (Golov,

1954). It consists of steel springs with 30-mm diameter (close to diameter of mole vole tunnel) and 200 - 250 mm length. One end of spring is closed and other end has wire door that open in one direction inside the spring. We inserted traps up to 150 - 200 mm into mole vole tunnels at 3 or 4 points of the burrow system, where recent burrowing activity had been detected by fresh hills of soil. The construction of the trap allows recognizing immediately the act of capture by appearance of a fresh soil in the trap and the sound of gnawing. Additionally we inspected the traps each 4 min but there were no occasions of undetectable captures. Trapping sessions lasted from 15:00 h to 20:30 h local time. Trapped individuals (both males and females) were removed immediately for collection of a blood sample. We collected blood samples (about 300 μl) in heparinized capillary via puncture of the retroorbital sinus. In order to limit the effect of handling on the hormone concentrations we spent less than 2 min for blood sampling. In rodents, rise of blood glucocorticoids was recorded only 3 - 5 min after beginning of stress impact (Kiohisa et al., 1977; Kugler et al., 1988). Blood samples were centrifuged (3 000 r/min, 15 min) and plasma was collected in small plastic vials (Eppendorf) and stored in - 20 ℃ until analysis. After collection of blood samples we weighted all the animals, individually marked them by toe clipping, detected sex and (if possible) reproductive status of the individual. In reproductive season we considered pregnant or lactated females to be reproductively active and distinguished mature and non-mature males by anal-genital distance. In non-reproductive period testes mass of males dramatically decreases (Evdokimov, 2001) so mature and immature males become undistinguished. We placed individuals captured in the same family in a common cage (plastic bax 50 cm ×30 cm ×25 cm) with the pieces of turf and carrot. After the finishing of the trapping session we released them at the points they were captured in given session, in the case of the intruders in second trapping session (see below) 3/in the burrow of the novel family. Then we covered the open hole by the piece of turf.

Table 1 Structure of the families and protocol of the experiment

Family	Season of trapping	Number of animals			Source of intruders
		Initial	Removed	Released	
1	August 1996	7(4 + 3)	7	0	
10A	Same above	20(13 + 7)	15	7 (4 + 3)	1
10B	Same above	24(11 + 13)	0	10(7 + 3)	10A
11	Same above	11(7 + 4)	7	0	
12	Same above	11(8 + 3)	0	7(4 + 3)	11
7A	April 1997	13(7 + 1 + 1 + 4)	10	0	
7B	Same above	14(7 + 0 + 1 + 6)	0	10(6 + 1 + 1 + 2)	7A
13A	Same above	12(6 + 0 + 1 + 5)	6	0	
13B	Same above	6(3 + 0 + 1 + 2)	6	0	
14A	Same above	7(3 + 0 + 2 + 2)	0	6(3 + 0 + 1 + 2)	13B
14B	Same above	12(9 + 0 + 1 + 2)	0	6(3 + 0 + 1 + 2)	13A

Data in breakers means males + females in August and mature males + immature males + mature females + immature females in April. "Source of intruders" means the colony where the intruders were removed.

1.2 Introduction of strangers

We trapped mole voles in three successive sessions with 1-day intervals. In the first session we treated individuals at all the families under the standard protocol, described above. Before the second session we randomly chose half of the families to be used as intruders. For intruders a second trapping session was begun at 11:00. Trapped animals were caged with individuals from the same family until 14:30 when they were introduced in one of the rest (resident) families. For releasing of intruders we opened a tunnel at the point nearby the geometrical center of the burrow system of residents. Only one point in each resident burrow system colony was used for releasing of the intruders. We measured the distances from the point of introduction to the points of capture of the residents as an indicator of the behavioral response of residents to intruders. The number of intruders released into the same burrow system varied from 6 to 10 depending on the size of the resident colony. We also tried to introduce a similar proportion of males and females and to release at least one mature female in reproductive condition (Table 1). In resident colonies we began the second trapping session at 15:00 and treated under the standard protocol all the captured individuals including intruders (regardless of the way of recapture). After the end of the trapping session we released them at the points of their trap-

ping in this session. In the third session we trapped mole voles only in resident colonies and treated them under standard protocol. In the August 1996, we additionally captured seven individuals in family 1 and introduced them in the empty burrows of the family 10A two days after the removal of majority of the residents. In this family we performed two trapping series, one and two days after release of intruders. We additionally inspected families of residents treated in August 1996 by means of 1-day trapping sessions in October 1996 and in April 1997.

1.3 Steroid assay

The concentrations of corticosterone and testosterone in blood plasma were measured by radioimmunoassay using Sigma antibodies (Rabbit Anti-Corticosterone and Rabbit Anti-Testosterone) and Amersham labeled hormones ([1,2,6,7-H^3]-Corticosterone and [1,2,6,7-H^3]-Testosterone). Excluding extraction analysis was made according to manufacture's instruction. A uniform procedure of extraction preceded radioimmunoassay: 3 ml ethyl ether was added to glass tubes containing 30 - 50 μl plasma and vortexed. Then we removed 2 ml extracts, transferred to new tubes, dried at 55 ℃ under vacuum, and added 100 μl of phosphate buffer (pH = 7.0). Extraction yield checked for every set of assay using ^3H labeled steroids varied from 85 % to 95 %. Sensitivities of the assay determined from 95 % confidence limit of zero standards were 30 pg/tube for corticosterone and 5 pg/tube for testosterone. To determine parallelism, we constructed a five-point, two-fold dilution series of plasma samples in phosphate buffer and compared them with standard curve of each steroid. There were no significant differences between slope of standard curve and slope of line generated by plasma samples of assayed mole voles. As males and females showed no differences in corticosterone concentrations we analyzed them together. Testosterone concentrations we measured in males only.

1.4 Statistical analysis

Since concentrations of corticosterone showed asymmetrical distribution, we normalized the data by extraction of square roots. Effects of the trapping session, sex and season of the year on hormone concentrations we estimated by Two-way and three-way ANOVA. We also calculated Two-way ANOVA for the study of the influence of trapping session and season on the distance from the point of introduction to the points of capture of the residents. We used LSD test for multiple comparison of means. Comparisons of the same index in different seasons (April vs August series) we performed by Student *t*-test. Since the testosterone titers in some individuals were below the level of detection, for the comparison of these data we used non-parametric tests: Kruskal-Wallis test, Mann-Whitney test and rank order Spearman correlation. Differences in the trapping probabilities we estimated by Yates corrected χ^2. To exclude the effect of circadian fluctuations of physiological parameters, we compared data of hormones with the time of the day as covariance.

2 Results

2.1 Probability and spatial distribution of recaptures

We calculated trapping probability as ratio of the individuals captured in a given session to the number of all individuals captured in the family during the entire three sessions. In resident families trapping probability was 40 % - 70 % in both fall and spring (Fig. 1). In August 1996 during the first day of release (session II) we re-captured only two of 17 intruders and one of them was captured above ground one hour after the introduction into burrow system of the family 10B. In family 12 one intruder jumped out from the hole near the point of introduction immediately after it's opening before setting of a live-trap. Two days after introduction (session III), one more intruder was captured on the area of family 12 in his own isolated burrow, which had no a connection with the burrow system of the residents. When we trapped the resident families two months later (in October 1996) we did not re-capture any newcomers. In April 1997 there were no signs of burrowing activity in family 10b. In family 12, however, among three marked individuals we captured one former intruder (Table 2). Among 7 individuals released in the empty burrow system of family 10A, after the removing of the majority of the dwellers, we re-captured 4 individuals in the two successive trapping series. This recapture rate was significantly higher in comparison with the re-capture rate of mole voles intruded into occupied burrow system (Yates corrected $\chi^2 = 3.89$; $P < 0.05$).

In April 1997 on the first day of introduction (session II) we re-captured 11 of 22 (50 %) intruders. Among them, nine intruders were trapped in resident burrow systems; one was captured on the surface, and one in a new burrow, which did not connect with the resident burrow system. Intruder males and females were re-captured in the same proportion as released, but none of the mature females was re-captured. Re-capture rate on the day of introduction was significantly higher for the intruders in April than in August (Fig. 1, Yates corrected $\chi^2 = 7.88$; $P < 0.005$). Two days after introduction (session III) we re-captured only one intruder (Fig. 1).

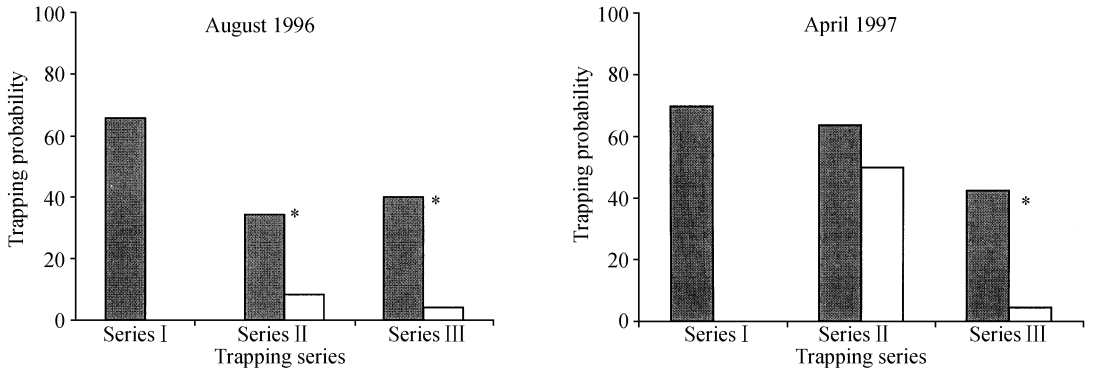

Fig. 1 Trapping probability of residents and intruders in the colonies of release
For residents, calculated as percentage of individuals captured in a given session to all residents captured in the colony, for intruders, as percentage of individuals re-captured after introduction. Here and in Figs. 3 and 4, closed bars denote residents, open bars denote intruders. Asterisks indicate significant differences between the respective values in residents and intruders (Student *t*-test, $P < 0.05$).

Table 2 Number of individuals captured in the resident's families two and eight month after introduction of the strangers

Trapping series	Family 10B			Family 12		
	Residents	Intruders	Non-marked	Residents	Intruders	Non-marked
October 1996	9	0	1	5	0	0
April 1997	0	0	0	2	1	4

Invasion of intruders led to the crowding of the residents at the point of introduction (Fig. 2). Two-way ANOVA (trapping session and season as factors) revealed statistically significant effects of both factors and their interaction on the distance from the point of introduction to the points of capture of the residents ($F = 10.73$, $P < 0.0001$ for trapping session; $F = 5.45$, $P < 0.05$ for season and $F = 12.32$, $P < 0.00001$ for interaction of the factors). The average distance in both seasons was minimal (6.0 ±1.5 m) on the day of release (session Ⅱ), in comparison with session Ⅰ, performed two days before (12.0 ± 2.4 m) and session Ⅲ, performed two days after release of the intruders (14.0 ±1.8 m; $P < 0.05$, LSD-test).

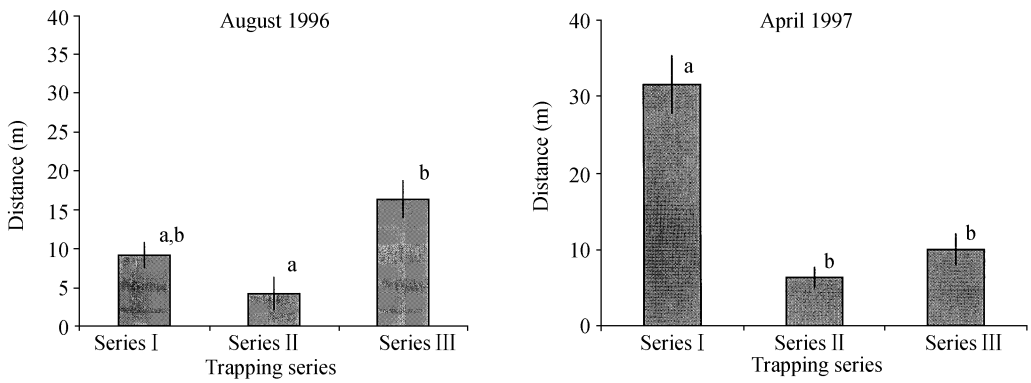

Fig. 2 Distances (Mean ± SE) from the points of the captures of the residents to the points of intruder releasing
Here and in Fig. 3 bars with different letters are significantly different (LSD-test, $P < 0.05$)

2.2 Plasma corticosterone and testosterone

To study the effects of season, sex and trapping session on plasma corticosterone in mole voles we treated all the data collected in session Ⅰ, and data of residents collected in sessions Ⅱ and Ⅲ by Three-way ANOVA. Season and sex did not affect individual values of plasma corticosterone ($F = 3.21$, $P = 0.08$ and $F = 0.82$, $P = 0.36$, respectively), but trapping session did ($F = 4.78$, $P < 0.01$).

Taken together the data of both seasons and sexes we showed that concentration of corticosterone significantly increased on the day of introduction (session Ⅱ, mean = 71.48 ±4.39 ng/ml) in comparison with concentration of corticosterone two days be-

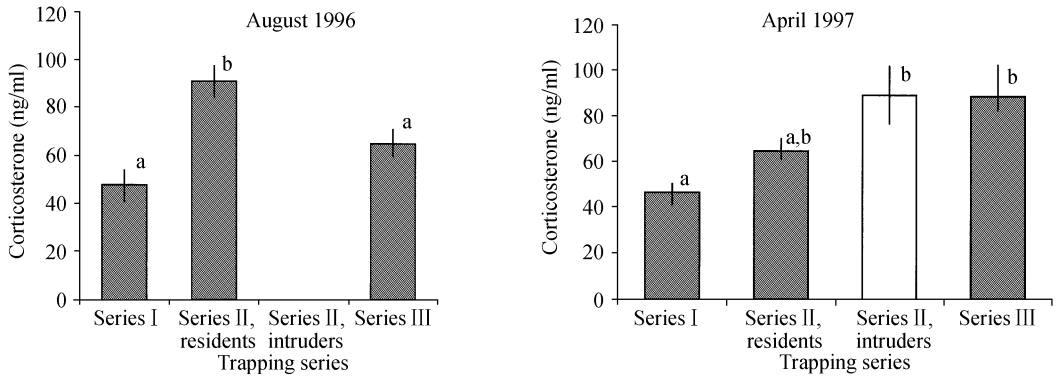

Fig. 3 Plasma corticosterone (Mean ±SE) in mole voles before and after release of the intruders
Data for males and females are combined. One-way ANOVA revealed a significant effect of the day of trapping on corticosterone concentrations.

fore releasing (session Ⅰ, mean = 47.02 ±3.28 ng/ml; $P < 0.05$, LSD-test) (Fig. 3).

We could collect only 8 blood samples in intruders trapped on the day of release in April 1997. Concentration of plasma corticosterone in intruders (89.05 ±12.79 ng/ml) was significantly higher than in residents (64.60 ±5.44 ng/ml) trapped on the same day ($t = 2.09$, $P < 0.05$).

In August, concentration of plasma testosterone in males was below the threshold of detection. In April (reproductive season), concentration of testosterone exceeded undetectable level in 65.1% of samples (Fig. 4). Trapping session affected significantly on plasma testosterone in resident males (Kruskal-Wallis test, $H = 6.5$; $P < 0.05$). In session Ⅰit was significantly ($P < 0.05$; Mann-Whitney test) lower than in session Ⅱ (0.075 ±0.041 ng/ml and 0.184 ±0.037 ng/ml respectively). Plasma concentration of testosterone did not correlate significantly with concentration of corticosterone ($r_s = -0.24$, $P = 0.16$).

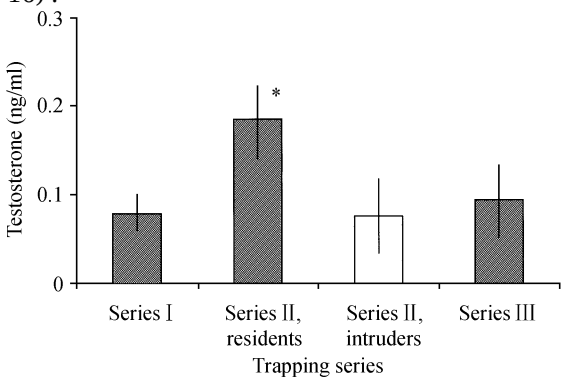

Fig. 4 Plasma testosterone (Mean ±SE) concentrations in mole vole males before and after release of the intruders in April
Asterisk indicates significant differences between day of introduction and pre-releasing day ($P < 0.05$, Mann-Whitney test).

3 Discussion

Social structure of the mole vole population was similar to those described by Evdokimov (2001). Typically, a family group consisted of one-two dozens of individuals occupying common burrow system. Sex ratio was biased to males (Table 1). Most families, with two exceptions, had one reproduced female. The emigration rate in mole voles is relatively high, but only few immigrants succeed in joining a strange family (Evdokimov, 1997, 2001). But, as in other colonial rodents (Clarke and Faulkes, 1999; Clarke et al., 2001), mole vole immigrants had more chances to take part in reproduction in comparison with residents (Evdokimov, 1997, 2001). In laboratory conditions probability of successful reproduction in pairs formed from unrelated partners was higher than in pairs formed from individuals from the same family (Evdokimov, pers. com.). Nevertheless, in native families absence of newcomers does not prevent reproduction. As in naked mole rat (Jarvis, 1981; Jarvis et al., 1994) death of the "queen" leads to the maturation of one of the related females. High longevity of mole voles (up to 6 years) provides an opportunity for the majority of the resident colony members to take part in reproduction (Evdokimov, 1997, 2001).

Data of our field experiments show that, in contrast to the relatively constant re-capture rate in residents, mole voles experimentally transferred into an unfamiliar family displayed a dramatic reduction in re-capture probability two days after release (session Ⅲ). Captures of intruders on the surface and in new burrowed tunnels indicated that at least some of them abandoned the burrows in which they were released. Both the concentration of residents around the points of release and the high rate of re-captures of mole vole intruders in resident-free burrows (family 10A) suggests that intruders, regardless of the sex and reproductive status, were banished by residents rather than

voluntarily abandoning unfamiliar burrow systems. This conclusion is in contradiction to the direct observation of the behavioral response to strangers that we studied under laboratory conditions. Encounters of the unfamiliar conspecifics in a neutral arena or co-using area by previously isolated family groups of mole voles did not provoke an agonistic reaction (Petrovski, unpublished data). Discrepancy of field and laboratory studies indicated that familiar conditions, which include habitual space and odor, are important factors regarding the behavioral response of mole voles to intruding strangers. Naked mole rats kept in laboratory similarly displayed strong aggression towards intruders (Lacey and Sherman, 1991; O'Rian and Jarvis, 1997). Introduction of laboratory-maintained mole voles into the home cages of other families (Novikov et al., unpublished data) also provoked sharply aggressive reaction of residents. It seems that long-term caging in artificial burrow systems is sufficient for simulation of the environmental conditions that are necessary for "normal" behavioral response to intruders.

In both seasons, invasion of strangers induced a stress reaction in resident mole voles. In August concentration of plasma corticosterone increased on the day of release (session II) and declined two days later (session III) to a level recorded before release (session I). In April, however, plasma corticosterone significantly exceeded basal level two days after release of strangers. Seasonal differences in the recovery of adrenocortical activity were accompanied by a different rate of the intruder banishment. Since in August the percentage of the re-trapped intruders dramatically declined on the day of release, we can propose that most of them were banished within the first hours after release. In April, residents spent more time banishing strangers. Recapture rates of intruders on the day of release were similar to those of residents and were significantly higher in comparison to recapture rates of intruders in August. According to the April data, intruder mole voles also were stressed on the day of release. In contrast to a uniform adrenocortical response to social stressors, plasma testosterone could increase or decrease in stressful conditions. Direction of androgen response to social conflicts is hierarchy dependent (Sapolski, 1982; Huhman et al., 1991). In our study we have found a different androgen reaction to social stimuli in the paradigm resident $\mathcal{S}$ intruder. During breeding season (April 1997) plasma testosterone increased in resident males on the day of release, but it did not change in intruders.

In naked mole rats urinary cortisol and testosterone strongly correlated with social rank. Since dominant females of this species are aggressive, stress of subordinate females is considered an essential factor in reproductive suppression (Clarke and Faulkes, 1997, 1998). However there is no relationship between female reproductive status and urinary testosterone or cortisol in colonies of damaraland mole rats with low aggressive rate (Clarke et al., 2001). Thus, there is a correlation between social rank and hormonal status in fossorial rodent with high level of both intra- and intercolonial aggression, but not in non-aggressive species. We have no direct observations on aggressive conflicts in mole voles in nature, but in our study we have found a different androgen reaction to social stimuli in the paradigm resident $\mathcal{S}$ intruder. During breeding season (April 1997) plasma testosterone increased in resident males on the day of release, but it did not change in intruders.

In conclusion, simulation of invasion of strangers demonstrated the efficient social fence of resident mole voles. This phenomenon seems not to be in contradiction with the demands of inbreeding avoidance. Successful immigration in nature may depend of the stability of the family, increasing when the family size is decreased. Disappearance of the some members of colony 12 during the winter of 1996 - 1997 seems to be a reason of successful introduction of one former intruder 6 month after its release. Thus, the agonistic reaction towards strangers could be an important mechanism of stabilization of size and structure of mole vole families. At the same time encounters of residents and intruders result in activation of physiological mechanisms of stress, especially during the breeding season.

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