Population response of rodents to control with rodenticides

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Abstract We summarize theoretical approaches and practice of rodent pest control in Russia and former USSR during last 50 years. We review literature as well as original data to understand mechanisms of rodent populations recovery after chemical control campaigns in urban areas, agricultural lands and natural foci of plague. Laboratory and field experiments indicate that inherent individual variation in behavioural, physiological and life-history traits provides survival of heterogeneous mix of individuals in residual population with increased resistance to poisonous baits and high reproductive potential that leads to fast recovery of a population. In a series of field experiments with various rodent and lagomorph species (Mus musculus, Rattus norvegicus, Meriones unguiculatus, M. meridianus, M. tamariscinus, Ochotona pallasi) we have shown that patterns of recolonization of depopulated area and mechanisms of population recovery vary among species and depend on species-specific social organization. After control territorial and group-living species demonstrated an increase in mobility and affiliative and marking behaviour and a decrease in intraspecific aggression. The rate of recolonization of treated areas was high due to redistribution of survived individuals and immigration by neighbors. Population recovered to original level due to increased breeding performance and fecundity of both survived residents and immigrants. In contrast, socially-independent species exhibited minor changes in behaviour. Recolonization was mainly due to better survival and recruitment of youngs so the rate of recolonization was low. Species-specificity of behavioural compensation mechanisms to control should be considered when developing ecologically based rodent management strategies [Current Zoology 55 (2); 81 – 91, 2009].

Key words Rodent control, Compensation mechanisms, Rodenticides, Field experiments

Significant progress has been achieved in developing rodent pest control strategies during last three decades. Both practice and fundamental ecological and population studies contributed significantly to better understand and predict rodent population dynamics and to make control more effective, economically beneficial and environmentally benign (Prakash, 1988a; Leirs et al., 1996; Wang and Zhang, 1996; Xia, 1996; Zhang and Wang, 1998; Singleton et al., 1999, 2003; Aplin and Singleton, 2003; Zhang et al., 2003; Shilova, 2005). Integrative and multidisciplinary approach to rodent pest control allowed developing modern Ecologically-based Rodent Management (EBRM) strategy (Singleton et al., 1999). The model of EBRM suggests incorporating of both extrinsic (density-independent) and intrinsic (density-dependent) factors as fundamental principles of population regulation (Krebs, 1995, 1999; Leirs et al., 1997; Julliard et al., 1999) to develop efficient control strategies with environmental and economic concern (Stenseth et al., 2001, 2003).

However, despite significant progress in the theory of EBRM, so far only a few effective ecologically-based strategies have been suggested and successfully applied (e.g. Leirs et al., 1996; Zhang et al., 1999; Stenseth et al., 2001, 2003), and rodent pests are still a problem in many countries (Singleton et al., 1999). Studies of compensation mechanisms contributed significantly to our understanding of low efficiency of control by rodenticides (Prakash, 1976; Shilova, 1993; Singleton et al., 1999; Hinds et al., 2003; Cowan et al., 2003). However, case studies rarely progressed beyond descriptive level, and we are still lacking both field experimental data and comprehensive knowledge of proximate (behavioural and physiological) mechanisms to explain population resistance to chemical control and quick population recovery after application of rodenticides and to provide effective management strategies (Leirs et al., 1999; Krebs, 1999; Singleton et al., 1999).

Traditionally, rodent ecological studies in Russia focused on population patterns in areas treated with rodenticides (Naumov et al., 1972; Shilova and Shilov, 1977; Komeev and Karpov, 1983; Shilova, 1991, 1993). Extensive rodent control campaigns in the former Soviet Union were organized and performed at governmental level. This provided numerous data on rodent population response to rodenticides. In addition, this determined strong government-supported demand for fundamental and applied studies to develop control strategies on the other hand. Here, we summarize theory and practice of rodent control in Russia to understand the mechanisms of (a) resistance of rodent populations to rodenticides and (b) population recovery after rodenticide applications.
1 Rodent control in Russia

As elsewhere, in the former USSR and later in Russia, the main goals of rodent control are (1) to control rodents in urban and rural areas and in animal husbandry facilities to improve the sanitary state and to reduce economic losses (main target species are rats of genus Rattus and mice Mus musculus, M. domesticus; (2) to control rodents in agricultural lands to reduce damage to crops (target species are some species of susliks Spermophilus and voles Microtus; and (3) to control rodents in foci of natural rodent-borne infections (mainly plague) (main targets are great gerbils Rhombomys opimus, jirds Meriones and little susliks Spermophilus pygmaeus). Until present, the common practice is chemical control by applying both acute rodenticides (zinc phosphide, glyfluorine) and anticoagulants (warfarin, diphacinone, difenacoum, brodifacoum) by spreading poisonous baits.

Extensive and non-selective treatment of buildings with rodenticides without any pre-assessment of rodent population, epizootic situation or economic damage caused by rodents was the distinctive feature of urban rodent control campaigns in the countries of the former USSR. “Complete Systematic Deratization” was carried out all year round everywhere in the USSR (Polezhayev and Kirin, 1956). All communal buildings such as hospitals, warehouses or places of public catering were treated by dry baits with anticoagulants (mainly warfarin) at least twice a month (Toshchigin, 1983). By the end of the 1980s, the total area of buildings systematically treated with chemical agents attained several billion square meters.

In modern Russia, the former strategy of communal rodent control has been considerably revised (Rylnikov, 2006; 2007, 2008). It is recommended to pre-assess the abundance and distribution of brown rats in buildings as well as to consider urban structure before applying rodenticides. Control measures are carried out only in buildings inhabited by rodents and taking into account demographic and spatial structure of rat population. Applying of rodenticides during breeding season proved to extend the effect (Rylnikov, 2006).

The control of rodents in agricultural lands in the former USSR covered enormous areas. At the end of the 1970s in Kazakhstan 10 – 12 millions ha of fields were treated with zinc phosphide annually to control populations of the little suslik (Kryltsov and Zaleskii, 1979). In Western Siberia, the red-cheeked suslik Spermophilus erythrogenys considered to be agricultural pest was a target species of control in vast areas (Skalov and Gagina, 2004). To reduce competition with livestock, social voles Microtus socialis were controlled on pastures of Southern Russia (Yakovlev and Babich, 2002). To combat water voles Arvicola terrestris on crops, over 100000 ha were treated with rodenticides annually (Maksimov and Ivanov, 1974). In the late 1970s, chemical control of murid rodents was performed annually in total area of 6.8 millions ha of agricultural lands (Belov and Suvorova, 1979). At present, more than 3 millions ha of crops in Russia are annually treated by acute rodenticides and anticoagulants (Klimchenko et al., 2004).

Even more striking control efforts were made in natural focci of plague. In early 1930s, the method of “complete cleaning” of areas populated by the little suslik, the reservoir of plague, was introduced by governmental Antiplague Service. Areas treated with acute rodenticides (zinc phosphide) covered about 60 millions ha. Extremely large areas (over 2 millions ha) were treated with rodenticides in deserts to control gerbil main reservoirs of the plague pathogen (Bibikov et al., 1968).

The control campaigns against great gerbils in the Central Asian natural focus of plague in 1960s had become a model for developing rodent control strategy which took into consideration structural organization of rodent populations (Naumov, 1963; Naumov et al., 1972). “Elementary” foci of infection were defined as corresponding to “elementary” (local) populations of host species of rodents. Control measures were recommended to be applied within such “elementary” populations which were considered as the lowest level unit of the population structure that provided continuous circulation of the plague pathogen and its spreading over the surrounding areas.

In the last decade in Russia, control strategy in the foci of rodent-borne diseases has been redesigned to meet both economic and environmental demands and became more environmentally benign and less costly. This modern strategy involves local control of risk zones instead of large-scale extensive campaigns. Analysis of biological and social factors that affect risk of human infection demonstrated that very limited areas only within the vast areas of a plague focus (sometimes not more than 1% – 2% of the entire focus area) have potential epidemiological danger (Matrosov, 2007). Thus, it was recommended to control gerbils only in these “risk zones”. Similar approach was recommended by Popov (2002) to control the little suslik in the plague foci.

2 Efficiency of control

As early as 60 years ago, Davis (1951) noted that control of brown rats in buildings produced only short-term effect, and a treated population quickly recovered to the origin level. Later, short-term effect of spreading poisonous baits and quick population recovery after initial crash caused by treatment were reported for a variety of rodents in a variety of landscapes in many countries all over the world (Bayomi et al., 1976; Advani and Prakash, 1987; Rowe and Swiney, 1988; Prakash, 1988a; Huang and Feng, 1998; Gunuprasad, 1992;
Similarly, in Russia, occasional local control measures (so-called “focal deratization”) applied to rats and mice in buildings was shown to produce only a short-term effect (Kuzyakin, 1963). These observations stimulated development and application of control techniques with multiple large-scale extensive chemical treatments of buildings in urban and rural areas at regular intervals (at least twice a month).

In agricultural lands, level of suslik control after treatment with acute rodenticide achieved 80%. However, population recovered to original level of abundance as fast as in two years and even reached higher abundance than populations in untreated areas (Gladkina, 1958).

After applying rodenticides (zinc phosphide) to the little susliks in the plague foci, their abundance decreased by 80% – 90%, but this effect was extremely short (Popov, 2002). Quick full recoveries of populations of susliks in vast treated areas were reported for Central Asian, Volga-Ural, Transcaucasian, and Central Caucasian foci of plague, i.e., in highly diverse natural landscapes—deserts, dry steppes, foothill plains, and high mountains (Popov, 2002). Popov (2002) noted that large-scale extensive control of susliks did not decrease epizootic activity and thus the attempts to reduce risk of infection in the natural foci of plague by extensive control of reservoir species appeared to have no prospects. Short-term effect of large-scale rodenticide application was also shown in foci of plague carried by great gerbils in Kara-Kum desert where control measures failed to terminate epizootic activity (Naumov et al., 1972).

In other cases, control measures produced low effect. Annual treatment of 300000 ha with zinc phosphide in the Volga-Ural plague focus resulted in the decrease of abundance of midday gerbils Meriones meridianus and tamarisk gerbils M. tamariscinus by 2% to 31%: only and produced no effect on epizootic activity, which was as intense as prior to rodenticide treatment (Kuznetsov, 1985).

Concluding, even large-scale extensive applications of rodenticides commonly practiced in the former USSR produced low or short-term effect on rodent pest populations.

3 Causes of rodent population resistance to rodenticides

World-wide practice of chemical control of rodent populations showed that efficiency of rodenticides whatever method of spreading poisonous baits had been used never achieved 100%. Usually, mortality does not exceed 80% – 90% and some individuals resistant to control by either reason always survive and remain in treated areas (Prakash, 1988a; Shilova, 1991; Singleton et al., 1999; Rylnikov, 2007). Understanding physiological and behavioural mechanisms responsible for rodent resistance to toxicants may contribute to make control strategies more efficient.

3.1 Physiological resistance to poisons

In a series of experimental studies, individual rodents were shown to vary in their sensitivity to rodenticides due to individual differences in neurophysiology or behaviour (Kamenov and Zolotarev, 1979: Kamenov, 1980: Kamenov et al., 1980: Shilova, 1993). In house mice, accumulation of warfarin in the liver was correlated with learning abilities of an individual. After consuming poisonous bait, mice that exhibited fast development of a conditioned response to light and sound (see details in Kamenov, 1980) accumulated less poison in their liver and survived better than mice with slow and poor abilities of learning. Moreover, “well-learning” excreted warfarin from their organisms faster than in “poor-learning”. Consequently, all “well-learning” mice survived rodenticide treatment, whereas 50% of “poor-learning” did not (Kamenov et al., 1980). Since mice with high learning abilities were more likely to occupy high social rank, accumulation of poison in the liver appeared to be correlated negatively with the social rank: the concentration of warfarin in the liver of dominant individuals was only 0.06 – 0.15 mg/kg as compared to 0.50 – 0.76 mg/kg (P < 0.05) in subordinate individuals.

Sensitivity to rodenticides was shown to depend also on age and reproductive state of an individual. For example, young Microtus arvalis, Microtus socialis and Microtus gregalis were more susceptible to warfarin and glyflurinore than conspecific adults (Pelagman and Ivanova, 1973). Pregnant females of brown rats, black rats, house mice, and midday gerbils were shown to be generally more sensitive to anticoagulants than non-breeding females, although some of them successfully produced and raised offspring (Kazakevich et al., 1970: Shilova, 1993).

Variation in sensitivity to rodenticides may be very high even among individuals of the same sex and/or age under the same conditions. As shown by Bolokhovets (1978), lethal doses of warfarin for laboratory mice of the same sex and age varied from 10 to 3000 mg/kg.

Thus, high variation in sensitivity to rodenticides among different categories of individuals (sex, age, neurophysiology, reproductive status, social rank) may explain why some of members of a rodent population always survive in areas treated with rodenticides. Furthermore, variation in sensitivity to toxins within these categories of individuals ensures surviving of diverse assemblage of individuals with increased resistance to rodenticides that form persistent residual population.

Sensitivity to rodenticides may vary not only at individual, but also at group or population level
neophobia as well as field experiments. Behavioural and experimental data are of key importance when effective rodent control strategies should be developed (Singleton et al., 1999).

In our earlier studies, we observed cautious response to baits during the first days of field experiments in almost all rodent species studied, including mongolian gerbils Meriones unguiculatus and midday gerbils, little suslikss and long-tailed susliks S. undulatus, house mice, brown rats, bank voles Myodes glareolus (Shilova, 1993). The only exception from this rule was Spermophilus pygmae that showed no neophobic response to unknown food.

Laboratory experiments demonstrated that the rate of bait consumption depended on the structure of social groups, being significantly higher in stable groups than in newly formed groups (Krasnov and Khokhlova, 1988; Shilova, 1991). In stable social groups, group metabolic rate in individuals living in stable social groups was, on average, significantly higher than that in individuals kept in isolation. Moreover, mice living in stable social groups excreted warfarin faster than isolated mice so mortality in the former was lower than in the latter (Table 1).

Table 1 Metabolic rate and sensitivity to warfarin (260 mg/kg) in house mice kept in stable groups and in isolation (after Shilova, 1991).

<table>
<thead>
<tr>
<th>Experimental conditions</th>
<th>Consumption of ( O_2 ) per 100 g of body mass (( n ))</th>
<th>Content of warfarin in liver, mg/kg (( n ))</th>
<th>Mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isolation</td>
<td>583.0 ± 12.5 (28)</td>
<td>0.30 ± 0.14 (30)</td>
<td>25.0</td>
</tr>
<tr>
<td>Group</td>
<td>745.8 ± 21.2 (19)</td>
<td>0.03 ± 0.02 (22)</td>
<td>8.3</td>
</tr>
</tbody>
</table>

In rodents, sensitivity to rodenticides may also vary in dependence of the phase of their population cycle. For example, the effect of fluoracetamide on great gerbils was higher in years of population increase when new groups were formed (Korneev and Karpov, 1983) and individuals likely suffered an increased stress level (Rogovin et al., 2008).

Thus, sensitivity to rodenticides and survival of rodents after control are related not only to some individual traits but may vary among groups of individuals and be associated with population dynamics. As a result, some individuals or the whole colonies resistant to toxin survive after chemical control application and form sustainable residual populations.

### 3.2 Behavioural resistance to poisons

In addition to physiological and biochemical resistance to poisons, behavioural resistance to rodenticides, i.e., avoidance of poisonous bait, is another factor that allow rodents to survive chemical control (Singleton et al., 1999). Cautious response to baits is a manifestation of repeatedly demonstrated general neophobic rule (see Mathur and Prakash, 1980; Prakash, 1988b; Brigham and Sibly, 1999; Pryambodo and Peltz, 2003). However, case studies of behavioural response to baits in rodents have rarely been carried out. This is especially true for studies of factors affecting response to baits during the first days of field experiments in almost all rodent species studied, including mongolian gerbils Meriones unguiculatus and midday gerbils, little suslikss and long-tailed susliks S. undulatus, house mice, brown rats, bank voles Myodes glareolus (Shilova, 1993). The only exception from this rule was Spermophilus pygmae that showed no neophobic response to unknown food.

Laboratory experiments demonstrated that the rate of bait consumption depended on the structure of social groups, being significantly higher in stable groups than in newly formed groups (Krasnov and Khokhlova, 1988; Shilova, 1991). Indeed, house mice in newly-formed social groups consumed significantly less proportion of offered bait than whereas mice in long-established groups consumed (14.8% ± 0.9% versus 39.8% ± 1.9%, respectively; Khokhlova, 1987).

Another factor affecting the manifestation of cautious response to bait is familiarity with the surroundings. Animals invading unfamiliar area are usually under stress; they show low response to novel food and, consequently, consume baits poorly (Shilova, 1991, 1993). In midday gerbils, cautious response to bait differed significantly in dependence of animal being in familiar or unfamiliar place (Shilova and Derviz, 1987). Sedentary individuals readily consumed novel food (oats). However, after the entire colony (29 individuals) had been moved to a similar but unfamiliar habitat previously vacated from resident population, the gerbils showed cautious response to pre-acclimated bait (Fig.1). Consumption rate decreased significantly despite the fact that all moved gerbils settled in new habitat, exhibited typical space-use pattern and lived under density similar to that in their native habitat.

![Fig.1 Response to baits in native colony (solid line) and after transferring to unfamiliar habitat (dashed line) in midday gerbils (after Shilova and Derviz, 1987)](image)
chemical control practice. This may be illustrated by an example with house mice in the natural focus of plague of Kalmykia. Some mice are commensal but other mice live in natural habitats surrounding human buildings. However, these “wild” mice invade buildings rarely due to aggression from commensal conspecifics (Khoikhlova, 1987; Krasnov and Khoikhlova, 1988; Shilova, 1993). Application of rodenticides in buildings resulted in almost complete extermination of local resident mice who readily consumed poisonous bait. Buildings vacated from resident mice were immediately occupied by mice from surrounding “wild” colonies. Moreover, since mice in newly formed groups and in unfamiliar surroundings show cautious response to bait, control efficiency of newcomers reached 40% only. The epidemiological situation appeared to be even more complicated after control measures, since “wild” mice brought from nature to buildings a flea Nosopsyllus mokrzerkii which is a plague vector species that previously has never been found in human buildings.

The cautious response to poisonous bait seems to be favoured by natural selection. In Kazakhstan, an area of 2.5 millions ha was annually treated with oat grain poisoned with zinc phosphate during 7 years to control the little susliks. Initially, susliks consumed 55% – 70% of grain whereas after six years of control the bait consumption rate was only 11% of bait. Individuals born in the treated area did not eat oats at all. The increase in percentage of susliks cautious to bait was correlated with changes in some of their morphological traits such as the size of two temporal openings (Kryltsov and Zaleskii, 1979).

To persist, animal populations should represent a heterogeneous assemblage of individuals that vary in their ecological, physiological, life-history and behavioural traits (Shilov, 1985, 2006). This natural inherent population heterogeneity determines variation among individuals and among colonies of individuals in both sensitivity to rodenticides and in response to baits, which in turn guarantees survival of some individuals or groups of individuals after chemical control. Heterogeneity of survived individuals and colonies with increased resistance to poisons combined with cautiousness to baits ensures persistence of residual populations resistant to chemical control and high potential for quick recovery.

4 Compensation mechanisms of rodent population recovery after control

4.1 Behavioural mechanisms

Various forms of communicative behavior of animals play important role in the process of self-organization of biological systems (Zhang, 2002). Communication and social behaviour is a key factor in integrating population into a sustainable biological system (Panov, 2001). However, proximate behavioural mechanisms underlying population recovery after control are poorly studied.

Individuals that survive in residual populations in treated with rodenticides areas find themselves lacking familiar social environment in general and familiar partners, in particular. Moreover, invading of stranger conspecifics from neighboring untreated sites into recently depopulated area contributes to social unpredictability shown to increase stress level (Popov, 2006). These intruders suffer not only from unfamiliar social environment but from strange non-social environment as well (e.g. increased predation risk or poor familiarity with food distribution). To reduce costs of novel situation and to form stable reproductive units both survived residents and newcomers should establish new relationships and integrate.

In a series of field experiments with rodents and lagomorphs (target species of chemical control in the natural foci of plague) we studied whether changes in individual or social behaviour after population crash were complementary with species-specific patterns of social organization and how these changes contributed to population recovery.

4.1.1 Pallas’s pika (Ochotona pallasi Gray 1867)

Pallas’s pikas, inhabiting high-mountain areas of Mongolia and Tuva, are characterized by strict territoriality, non-overlapping home ranges and high level of aggression towards neighbors and strangers. This behaviour guarantees individual pikas an exclusive access to scarce food resources which is especially important under severe conditions of high mountains. Affiliative behaviour is rarely observed in this species (Tarasov, 1950).

We modeled recolonization of depopulated area by releasing pikas to an experimental plot vacated from all residents (Orleny et al., 1982; Shilova and Orleny, 2004). The frequency of aggressive contacts among pikas released to unfamiliar depopulated area was significantly lower than among residents in intact colony (0.03 ± 0.02 and 1.1 ± 0.7 per 100 min, respectively). No territory defense by newcomers was recorded, and their home ranges fully overlapped. Pikas in the experimental plot allocated as much as 10.2% of activity time to exploratory behaviour, whereas this proportion was as low as 4.1% in pikas from the intact colony.

Similar changes in the behavior of Pallas’s pikas were observed in another experiment when 70.7% of resident population was removed from the colony (Shilova and Orleny, 2004). In residual population, the exploratory activity of individuals increased by 4.7 times and the frequency of marking behaviour increased by almost 10 times (0.5 and 4.9 acts per 100 min before and after removal, respectively). Territorial behaviour was not observed in pikas even within their own home ranges and the frequency of agonistic interactions with neighbors and strangers decreased from 1.4 to 0.6 per
100 min of observation. On the contrary, frequency of familiarization contacts (naso-nasal and naso-anal sniffings) and tactile contacts combined significantly increased (0.60 and 1.57 per 100 min of observation before and after removal, respectively).

Thus, Pallas’s pikas in residual populations or when colonizing vacated areas switch from separating to integrating behaviour. This likely contributes to reestablishment of social relationships and reproductive units and stimulates population recovery.

4.1.2 Mongolian gerbil (Meriones unguiculatus Milner-Edwards 1867)

Mongolian gerbils are highly social, live in family groups actively defending common territory, exhibit delayed dispersal and socially induced suppression of maturation of youngs, and maintain stable within-group relationships and pair bonds (Payman and Swanson, 1980; Agren et al., 1989; Goltsman et al., 1994).

In our experiment, an area of 50 ha occupied by the colony of individually marked gerbils was treated with acute rodenticide (monofluorurate) by spreading poisonous baits (Orlenev and Pereladov, 1981; Orlenev, 1987; Shilova and Orlenev, 2004). Mortality of gerbils was as high as 86% (194 of 226 previously marked gerbils died). Immediately after application of rodenticide (on the next day) survived gerbils started moving extensively and chaotically over their own as well as strange vacant or still occupied home ranges, while family groups adjacent to treated area fissioned and their members, including adult males and females dispersed into depopulated plot. During next 2 weeks, percentage of transient individuals (recaptured only once in contrast to multiply recaptured residents) was much higher in treated area than in intact colonies (72% and 20%, respectively). Time allocated to exploratory activity increased by 3 times and frequency of full erect “post” postures acting to search surroundings for partners and predators increased by almost 10 times. Density of well-visible sand marks (“heaps” containing urine, feces or ventral gland secretion; see Agren et al., 1989) was four times higher in treated than in untreated area while resident population reached only 17% of pretreatment level. Within a month, 45% of newcomers resided in treated area so that the population achieved 39% of the original abundance (66% of animals were immigrants from control colonies, whereas 34% were survived residents).

Decomposition of intact groups combined with search-for-contacts behaviour and wide ranging resulted in recolonization of depopulated area by gerbils within the first 2 post-treatment weeks (Orlenev and Pereladov, 1981; Orlenev, 1987). New groups of gerbils composed of reproductive individuals were formed in the treated area. However, interactions of gerbils in these newly formed groups were still significantly different from those in intact colonies (Fig.2). These gerbils performed more affiliative and less aggressive behaviour toward both new partners and strangers as compared with gerbils from intact colonies. As a result, newly formed groups were more “opened” to accept new members.

Thus, in this “socially dependent” (Goltsman et al., 1994) species sudden and drastic decrease of density and transformation of familiar social environment produced immediate behavioural response. Under “social vacuum” caused by treatment, motivation for search for contacts and information overbalanced integrating mechanisms that normally maintain stability and integrity of family groups (Goltsman et al., 1994; Shilova and Orlenev, 2004). Such “seeking for lost” response allowed quick redistribution and recombination of survived gerbils and, as a result, quick recolonization of depopulated area and formation of new breeding units.

4.1.3 Midday gerbil (Meriones meridianus Pall. 1773)

In contrast to Mongolian gerbils, midday gerbils are characterized by a low social activity (Popov et al., 1989) and are recognized as “socially independent” species (Goltsman et al., 1994). In particular, they

Fig.2 Proportion of different behavioral contacts in mongolian (A) and midday (B) gerbils in treated and untreated colonies
show no stress hormones response to variation of population density (Kuznetsov et al., 2004), while avoiding contacts with conspecifics is a distinctive feature of their social organization.

Series of removal experiments with midday gerbils (Tchabovsky, 1993) indicated that animals survived after treatment (from 0 to 7% of original population) as well as their neighbors from adjacent intact colonies did not increase movements or exploratory activity and showed no tendency for immediate recolonization of depopulated area. In 2 months after treatment, from 10% to 29% of neighbors (depending on season) only dispersed into vacated plots. These were adult males and dispersing subadults (both males and females), whereas no one breeding females were found among immigrants.

Changes in behaviour of midday gerbils in treated area were not as pronounced as they were in Mongolian gerbils (Fig. 2). They performed more familiarization and less agonistic behaviour than in intact colonies; however, unlike in Mongolian gerbils, the rate of affiliative behaviour in midday gerbils did not increase. Frequency of marking was also similar in treated area and in intact colonies (0.77 ± 0.53 and 1.04 ± 0.41 acts per 10 min, respectively; NS).

Treated populations attained 8% - 41% of pre-treatment level within 2 months, and the full recovery occurred 4 - 8 months post-treatment. Both dispersing youngs from neighboring colonies and locally born individuals contributed to population recovery. Indeed, 88% of juveniles born in treated unsaturated area were recruited in contrast to 33% in intact saturated colonies.

Thus, in “socially independent” midday gerbil unlike in “socially dependent” mongolian gerbils, depopulation did not trigger immediate and strong behavioural response among survived residents or neighbors. They demonstrated conservative space use pattern and strong philopatry and showed no tendency for quick colonization of vacated habitat or reestablishment of lost social bonds. The rates of recolonization of treated area and population recovery were low and occurred mainly due to immigration of dispersing youngs and recruitment of locally born individuals. These fundamental between-species differences in response to depopulation were used to classify target species as having either “slow” or “rapid” type of population recovery after population crash (Shchipanov, 2000, 2001).

4.2 Patterns of reproduction

In species with density dependent mechanisms of population regulation a population quickly recovers after application of rodenticide, attaining 80% - 90% of pre-treatment level due to compensation mechanisms of better survival and/or better reproduction of individuals from residual population as it occurs after natural depressions (Christian and Davis, 1966; Leis et al., 1997; Krebs, 1999; Singelton et al., 1999). Beginning from pioneering studies of Davis (1951), this phenomenon has been repeatedly described for brown rats and other rodents. For example, high reproductive potential of residual rat population after control in London was described by Twigg (1988). Kozlov (1981) reported that all female rats survived after chemical treatment in husbandry farms of Russia were pregnant. In Brandt’s voles Lasiopodomys brandti quick population recovery after chemical control on pastures was shown to be caused by higher breeding performance of survived individuals and by earlier reproduction as compared with individuals in untreated populations (Yang et al., 1979; Zhou et al., 1992; Zhong et al., 1999). Density-dependent and density-independent (environmental) factors of population regulation in the multimammate rat Mastomys natalensis were incorporated in a model for the development of new effective ecologically-based strategy of pest control (Stenseth et al., 2001). Between-species and seasonal variation in density-dependent and density-independent effects and in their combination determine species-specific short-term and long-term population dynamics and specific case-sensitive requirements for control strategies to make them efficient (Stenseth et al., 2003).

In Russia, compensation mechanisms of population recovery such as reproductive patterns in residual populations were studied in details in various gerbil species which are the main target of control in the natural foci of plague. Species-specific patterns of compensation mechanisms appeared to be well explained by species-specific social systems (Popov and Tchabovsky, 1995).

Group-living socially great gerbils demonstrate socially induced suppression of maturation and reproduction of youngs (Naumov et al., 1972; Goltsman et al., 1977) and density dependent variation in stress level (Rogovin et al., 2008). In this species, control measures were followed by earlier maturation and reproduction of young females and by increased fecundity (Yakovlev, 1967; Yakovlev and Radchenko, 1968). Increased reproductive performance caused population recovery in the treated area of 500000 ha within one year with contribution of immigrants being minor (if at all).

Mongolian gerbils are polygynous and are characterized by socially induced suppression of maturation and reproduction of youngs (Orlenev, 1987; Payman and Swanson, 1980; Agren et al., 1989). Males maintain stable pair bonds with females, mate usually with familiar females from their family group and like in great gerbils, only family group founders reproduce. Breeding and reproductive patterns of Mongolian gerbils in treated with rodenticides depopulated areas in the plague focus in Tuva significantly differed from those in untreated areas (Orlenev, 1987; Shilova, 1993; Shilova and Orlenev, 2004). After treatment of an area of 200 ha with zinc phosphide, 90% of animals died. Young dispersing females started to arrive to treated
area from adjacent colonies immediately after treatment. They demonstrated obvious signs of maturation and were either ready for mating or already fertilized. Average body mass of breeding females was almost two times lower than that of females in the untreated colony (Table 2). Similar pattern was observed in residual populations of mongolian gerbils in another geographic location: after control with 88% kill rate, mean body mass of primiparous females decreased from average 58 g to 35 – 50 g (Wang et al., 1998).

Table 2 Reproductive patterns of female Mongolian gerbils in treated and intact colonies before and after treatment with zinc phosphide (after Orlènev, 1987)

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Before</th>
<th>Intact</th>
<th>After</th>
<th>Intact</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage of breeding females</td>
<td>24.0</td>
<td>29.1</td>
<td>76.5</td>
<td>14.7</td>
</tr>
<tr>
<td>Average body mass of pregnant females g (range)</td>
<td>71.5 (58.0 – 91.0)</td>
<td>69.6 (59.0 – 88)</td>
<td>55.3 (31.0 – 96)</td>
<td>116</td>
</tr>
<tr>
<td>n</td>
<td>159</td>
<td>83</td>
<td>68</td>
<td>116</td>
</tr>
</tbody>
</table>

* No pregnant females recorded

Survived or dispersing into depopulated area males lacked familiar female partners, so they ranged widely and mated opportunistically with females in estrus (Orlènev, 1987; Shilova, 1993; Shilova and Orlènev, 2004). In contrast to intact colonies, young males in treated areas actively participated in reproduction. In 92% of examined males, the epididymis and seminal vesicle were enlarged (the average size of the epididymis and seminal vesicle was 12.2 mm ± 1.1 mm and 14.7 mm ± 2.8 mm, respectively, in treated area and 11.9 mm ± 0.6 mm and 9.0 mm ± 2.4 mm, respectively, in the untreated area). In 4 weeks, the percentage of pregnant females reached 91.4%, while gerbils in intact colonies already terminated reproduction by this time (late August). Thus, mongolian gerbils started breeding immediately after treatment, i.e., before stable family groups or even stable home ranges were established.

Similar compensation mechanism was observed in solitary tamarisk gerbils. This species do not form stable family groups or pair bonds, however younger females delay dispersal and breeding in the presence of their mothers (Tchabovskiy and Bazynk, 2004). As a result, certain part of potential female breeders in saturated habitats do not reproduce and start breeding after density decline. Kuznetsov and Matrosov (1985) showed that after control percentage of pregnant females significantly increased, so that population quickly recovered due to increased reproductive rate and fecundity.

On the contrary, in close-related solitary midday gerbils, that do not exhibit socially induced suppression of maturation or reproduction (Goltsman et al., 1994) and show no density dependent variation in stress hormones (Kuznetsov et al., 2004) population crash after control did not stimulate reproduction, and population recovery occurred due to increased survival of young animals (Kuznetsov and Matrosov, 1985). These observations support results of our removal experiments with this species that demonstrated higher recruitment of young in treated with rodenticide areas.

5 Conclusions

Rodent control practice is among the most strong human impacts that affect animal abundance and distribution and provides us with unique opportunity to study compensation mechanisms of recovery and sustainable functioning of populations after unpredictable and sharp external damaging impact. Under “catastrophic” event such as control measures, adaptive mechanisms of population regulation, masked under normal conditions can be uncovered and ultimate impact under which populations can persist and recover can be revealed (Shilova, 1993; Shatunovskii and Shilova, 1995; Shilova and Shatunovskii, 2005).

Field and laboratory experiments on rodent population response to control by rodenticides revealed important intrinsic factors determining population recovery and sustainable functioning after damaging extrinsic impact:

— inter-individual variation in physiological and behavioural traits which contributes to population heterogeneity as a major factor determining survival of residual population with high potential for recovery;

— communicative behaviour as a major integrating force driving individuals in residual population to integrate and re-establish damaged social system and reproductive units;

— behavioural and physiological species-specific compensation mechanisms as a major driving force stimulating quick recovery of residual populations after damage by better reproduction or survival.

Significance and contribution of intrinsic factors and proximate (physiological or behavioural) mechanisms to population resistance and recovery after damage vary between and within species and may be interlinked in some compensatory way. For example, resistance to poisons in brown rats was shown to be correlated negatively with cautious response to bait (Rylnikov and Roslavtseva, 1990). In house mice living in stable groups in contrast to isolated ones or those from newly formed
groups, toxins were excreted from organism more rapidly due to higher metabolic rate, although they consumed bait more readily and ingested more poison due to suppressed neophobic behaviour.

Role of integrative and communicative behaviour in re-establishment of social bonds in residual populations varies among species depending on species-specific social relationships. In territorial or group-living species, depopulation results in quick and strong behavioural response such as increased mobility, affiliative and marking behaviour and decreased aggression. Switching from separating to integrating behaviour results in quick recolonization of depopulated habitats and re-establishment of pair bonds and reproductive units. In socially independent species, depopulation does not affect significantly behavioural patterns of survivors or neighbors and recolonization goes on slowly.

Similarly, species-specific pattern of social system affects mechanisms of population recovery. In socially dependent species with density dependent reproduction and reproductive skew due to suppression of reproduction of subordinate or young individuals, there is always certain “reserve” of potential breeders. Consequently, population recovers to original level due to early maturation and recruitment of previously non-reproducing potential breeders and increased fecundity. In socially independent species, population recovery is mainly due to better survival of youngs and their recruitment in residual population. Thus, species-specificity of compensation mechanisms should be incorporated in ecologically based rodent management to make control strategies more effective.

Combined effect of inherent physiological and behavioural population heterogeneity and species-specific compensation mechanisms results in survival and quick recovery of residual population after control by rodenticides. Moreover, such post-control populations may retain and accumulate increased resistance to poisons favored and fixed by selection. Thus, application of rodenticides as poisonous food baits may significantly decrease the abundance of pest species but it is not an irreversible damaging impact that precludes recovery and persistence of the controlled population (Shilova, 1993; Shilova and Shatunovski, 2005). This problem is unlikely to be overcome by traditional chemical control strategies since resistance and potential for recovery after damaging impact are inherent biological features of any biological system in general and an animal population in particular. Rational land use and management of habitats may seem being more promising and worth approach especially in already transformed ecosystems.

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