

Types of Narrow-skulled Vole (*Lasiopodomys gregalis*) Colonies in Northern Kulunda and Seasonal Dynamics of Their Demographic Composition

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Received May 16, 2014

Abstract—Demographic structure and its seasonal dynamics have been studied in colonies of narrow-skulled voles (*Lasiopodomys gregalis* Pall.) in Northern Kulunda. Three types of colonies have been distinguished: (I) true colonies (large, complex families), (II) simple families (nuclear or incomplete), and (III) all-male colonies. Changes in their sex, age, and functional composition (based on animal migration activity) during the breeding season have been analyzed.

Keywords: narrow-skulled vole, colony structure, demographic composition, seasonal dynamics

DOI: 10.1134/S106741361601015X

A major foundation for population homeostasis is provided by regularity in the spatial distribution of individuals and the system of relationships between them, which determine the formation of spatial-ethological population structure (Shilov, 1977, 1991; Gromov, 2008). Moreover, parameters that are vitally important for the existence of a population in the changing environment are optimized at the level of familial triad (a male, a female, and their offspring), which is an elementary structure at the population level of biological organization (Potapov and Evsikov, 2000; Evsikov et al., 2008; Evsikov and Potapov, 2011).

The formation of family groups in mammals, including rodents, is based primarily on three types of nuptial relationships: promiscuity, monogamy, and polygamy (Pianka, 1981). Polygamy in rodents exists mainly in the form of polygyny; polyandry has been described only in the naked mole-rat *Heterocephalus glaber* (Jarvis, 1981). A complete family group represents a simple, or nuclear family typical for monogamy. If the offspring remain in such family and start breeding there, a complex family (colony) is formed. In case of promiscuity or polygyny, males do not participate in parental care, and the family composition remains incomplete.

The narrow-skulled vole *Microtus gregalis* (Pallas, 1779) or, according to recent taxonomy, *Lasiopodomys (Stenocranius) gregalis (Mlekopitayushchie Rossii...*, 2012) inhabits mainly open landscapes in several isolated parts of its range. The validity of its segregation into a new genus, different from *Microtus*, is confirmed by the results of combined analysis of morpho-

logical and molecular genetic data (Kovaleva et al., 2012).

Elementary (familial) population groups of this species are classified as colonies (Pal'chekkh et al., 2003; Gromov, 2008). Published data are available on the structure of their burrow systems, seasonal and annual population dynamics, and spatial population structure (Mal'kova et al., 2004; Sokolova, 2004; Dupal, 2010), but variation in organization of local colonies and seasonal dynamic processes occurring in them have not been studied in detail.

Parameters characterizing the demographic structure of an animal settlement include primarily the size of local population and its sex and age composition. In colonial species (*L. gregalis* in particular), of special importance is the ratio of migrant (dispersing) and settled animals. The latter refers to individuals that permanently live in the colony and move only within the part of its territory corresponding to their home range (Mal'kova et al., 2004). Several variants of animal movements are distinguished: emigration refers to dispersal from the native (parent) colony; immigration, to settling in a new colony (*Animal Dispersal...*, 1992; Ims and Yoccoz, 1997); and nomadism, to traveling between colonies without staying there for long (Caughley, 1979; Evdokimov and Pozmogova, 1992). Thus, migrant animals are differentiated into several groups. In studies on the northern mole vole *Ellobius talpinus*, Evdokimov (2001) distinguished the category of intermigrants, i.e., animals that migrate from one family to another and subsequently start breeding there. Apparently, such animals are emigrants in rela-

tion to their native colony and immigrants in relation to the new colony.

MATERIAL AND METHODS

Studies on the demographic composition of local settlements of narrow-skulled voles were performed in the forest–steppe zone of Northern Kulunda in the southwest of Novosibirsk oblast, near the Karasuk Research Station of the Institute of Animal Systematics and Ecology.

Inhabited settlements were identified by traces of animal life activities near the burrow systems, such as fresh gnaw marks, food remains, excavated earth, and the state of entrances to the burrows.

The voles were caught with Sherman traps baited with bread moistened with vegetable oil. To prevent them from death, pieces of fresh vegetables were placed in each trap. Five traps were set within the territory of each settlement on trails and near burrow entrances and examined every 2 hours. Trapping was conducted in May to August 2009, 2010, and 2012 in series lasting several days to 1.5 months.

Each animal trapped for the first time was assigned an individual number, marked by finger clipping (White et al., 1982; Karaseva and Telitsina, 1996), weighed, and examined for gender by measuring the anogenital distance, which is markedly greater in males than in females (Tupikova, 1964), as well as for external characters such as body size and the state of fur coat and reproductive organs. On this basis, the animal was included in one of three age groups: overwintered, immature young of the year, or mature young of the year (Klevezal, 2007). Puberty in young of the year was assessed by vaginal opening in females and by the anogenital distance (Nazarova, 2011) and the degree of development of the testes (estimated visually) in males. Pregnancy at late stages was diagnosed by palpation; early stages were determined only in dead females during autopsy.

On the basis of migration activity, the voles were classified into the following functional groups: residents (the founders of the colony and their nonmigrant offspring), emigrants (the offspring of the founders that disappeared from catches after a certain time), immigrants (animals that joined the colony), and nomads (animals that were trapped in the colony only once). An individual group of transmigrants was not distinguished, because only one marked male had moved from one colony to another during the study period. It was included in the group of emigrants in the former colony and in the group of immigrants in the latter colony.

The animals trapped on the last day of the series or recorded only once and found dead in the trap were included in the group with an indeterminate migrational status. The proportion of the dead did not exceed 15% of the total number of trapped animals.

They were autopsied by the standard procedure, and females were examined for placental scars to estimate their reproductive status.

On the whole, the sex and age composition of 21 colonies was analyzed, and 322 voles were marked in this course. The seasonal dynamics of demographic structure were considered using the example of 12 colonies in which trapping was conducted most thoroughly.

RESULTS AND DISCUSSION

During autopsy, placental scars from two previous pregnancies were found in an overwintered female trapped in late May 2009. This fact is in agreement with available data that the breeding period in narrow-skulled voles from steppe populations starts in late March to early April (Sokolova, 2004). A total of 15 female young of the year were found dead during the study period. Among them, six females showed signs of previous breeding (on average, 6.3 ± 0.64 placental scars per animal), seven were pregnant (7.0 ± 0.65 embryos per animal), and only two (died in the first 10-day period of June) had a closed vaginal orifice, but the state of the uterus provided evidence that they were approaching puberty. The minimum and maximum body weights of a mature nonpregnant female recorded over the study period were 8.8 and 40.0 g; the maximum weight of a male, 44.1 g.

Base on analysis of demographic composition, three types of narrow-skulled vole colonies were distinguished:

Type I. Large (true) colonies: complex families consisting of resident animals belonging to different sex and age groups and differing in reproductive status. Up to 36 animals were recorded in such a colony during the summer season, and up to 13 animals could be simultaneously found within its territory. Females numerically prevailed over males. This was the most frequent type (11 out of 21 colonies, 52.4%).

Type II. Small colonies formed by nuclear or incomplete families (without a mature male) that included up to four resident animals (as a rule, a breeding pair or a single mature female and the last-generation offspring), with females prevailing over males (7 out of 21 colonies, 33%).

Type III. Colonies consisting only of males (overwintered and young of the year) that appeared to be not involved in breeding for some reason. One such colony was found each year (3 out of 21 colonies, 14.3%).

Certain general features can be noted in the dynamics of vole population composition during the study period. Thus, the bulk of the population at the onset of the breeding season consists of overwintered animals and immature young of the year of the first spring generations, but overwintered animals almost disappear by the end of the season, yielding domi-

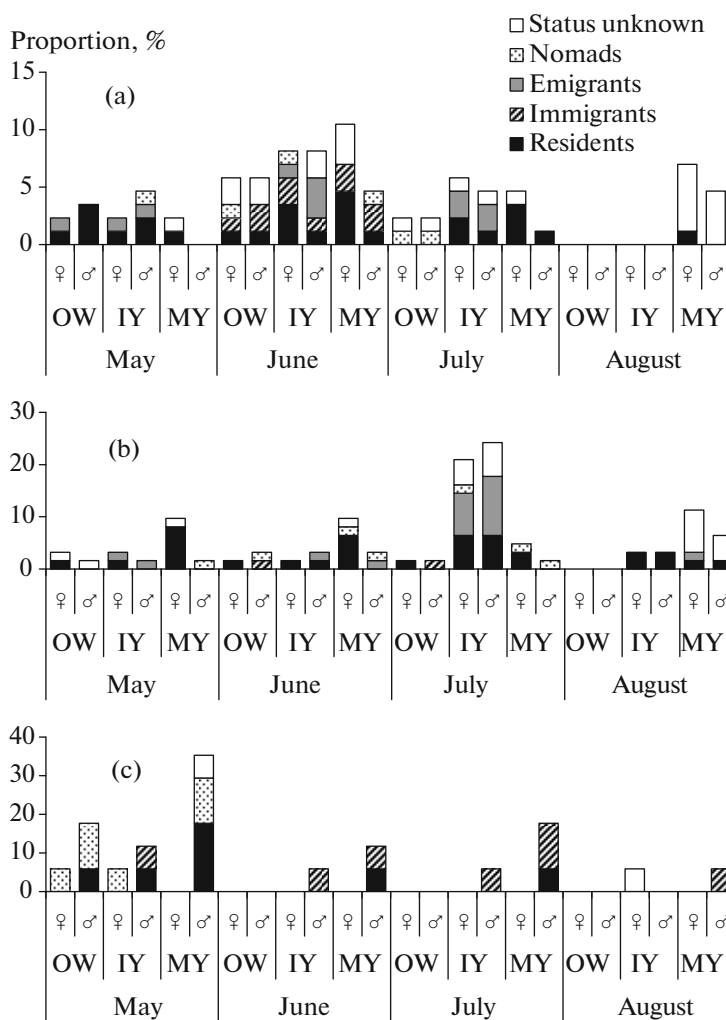


Fig. 1. Seasonal changes in the demographic composition of vole colonies: (a) type I (complex families), (b) type II (simple and incomplete families), type III (male colonies); (OW) overwintered animals, (IY) immature young of the year, (MY) mature young of the year.

nance to mature young of the year. At the same time, the demographic ratio of individuals in functional groups proved to differ between colony types.

In large colonies (type I), the majority of residents are females, mainly mature young of the year (Fig. 1a). Overwintered animals are a component of different functional groups in May–June, but in midsummer they occur only among nomads. A colony is usually founded by a pair of overwintered animals, and then its population grows due to breeding within the colony (Silk, 2007) and immigration. Colony size markedly increases from May to June on account of both residents and migrants but decreases abruptly from July to August.

In type II colonies, females are also more prevalent among residents. This group includes females of all age groups until midsummer, but overwintered individuals disappear from catches by the end of the sea-

son (Fig. 1b). Unlike in type I colonies, colony size does not increase during the first half of the breeding season, probably because mature males are short in numbers. In July, immature animals predominate in the population, but a large proportion of them subsequently leave the colony.

The group of emigrants in colonies of both types is represented in all seasons mainly by immature young of the year that appear to be born in the colony and disperse from natal groups.

Type III (all-male) colonies are low populated. At the beginning of the season, they consist of resident and immigrant males, with nomadic males appearing periodically. Only three visits of females (two nomads and one with an indeterminate status) were recorded at the end of the season (Fig. 1c).

Type III colonies are not reproductive, but they have been recorded in representatives of different taxa,

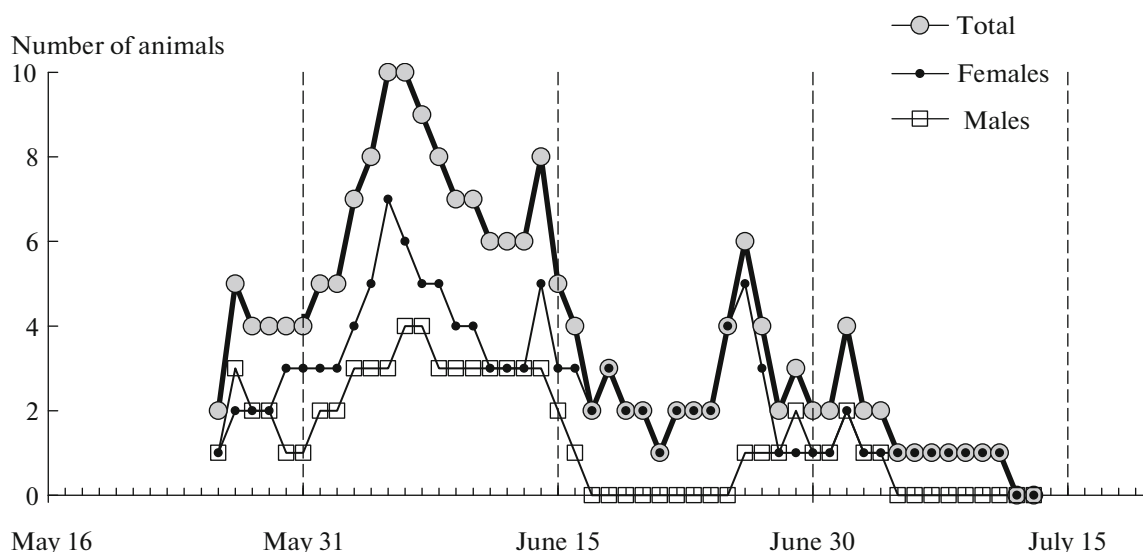


Fig. 2. Time course of change in the number of voles in catches during the breeding season in colony no. 3 (large type I colony).

including primates (Henzi and Barrett, 2003; *Reproduction...*, 2006) and rodents (Kuz'min, 2009). Hence, their role in the population is of special interest. According to Bateman's (1948) principle, almost all females participate in breeding, while males sharply differ in reproductive success depending on their competitiveness. Since females are receptive only during the short period between pregnancies, the effective sex ratio—of the number of estrous females to that of reproductively active males (Michener and McLean, 1996)—highly varies during the breeding season (Rogov, 1999). As shown in studies on water voles (Evsikov et al., 1997), a numerical and functional excess of males results in a strong aggravation of competition among them and provides abundant material for effective natural selection, which may give rise to mobile microevolutionary transformations. When males predominate, many of them are excluded from breeding (Potapov and Evsikov, 2000) and, being displaced from native colonies by competitors, establish new “bachelor” colonies (Bragin, 2003). The existence of all-male colonies also suggests that part of males in the population constitute a kind of its functional reserve that, under certain conditions, is mobilized to be involved in breeding (Rogov, 1999; Rogov et al., 1999).

The time course of change in the numerical composition of the large reference colony no. 3 (Fig. 2) provides evidence for the existence of several stages in the life of the colony (namely, rapid population growth and gradual decline) and restrictions on its life span. As the number of the young in the colony increases, food resources in its vicinity are depleted, and this apparently forces the animals to disperse, with consequent disintegration of the colony. It should be noted,

however, that the formation and seasonal dynamics of demographic structure of narrow-skulled vole colonies beyond the breeding season (during wintering) have not yet been studied.

The size of intrapopulation groups in social animals is maintained at the species-specific optimal level through the regulation of breeding intensity (Silk, 2007). The colonial narrow-skulled vole has mechanisms for accelerating the growth of family size, including endogamy (breeding within the family) described in this species previously (Zadubrovskaya, 2011; Zadubrovskaya et al., 2011; Potapov et al., 2012). However, it has not developed mechanisms for limiting the rate of reproduction, which are characteristic of several other colonial species (Silk, 2007), and the size of narrow-skulled vole colonies is apparently regulated by means of animal dispersal.

ACKNOWLEDGMENTS

This study was supported by the Basic Research Program of State Academies of Sciences (2013–2020), project no. VI.51.1.6.

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Translated by N. Gorgolyuk