

Structure of Colonies in the Northern Mole Vole, *Ellobius talpinus* (Rodentia, Cricetidae)

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Abstract—The structure of two northern mole vole colonies from northern Chelyabinsk oblast (the Kunashak colony, 1981–1983) and southern Kurgan oblast (the Kurtamysh colony, 1985–1999) has been analyzed with respect to the number and composition of families, seasonal and annual population dynamics, age and sex composition and sex ratio, individual life span, migrations, breeding, and reproductive potential. The Kunashak colony is at the northwestern boundary of the species range, and its population is monomorphic (all animals are of the black color morph). The Kurtamysh colony is located in an optimal habitat, and its population is polymorphic, consisting of animals of three color morphs (black, brown, and transitional). Consideration is given to certain specific features of northern mole voles belonging to different color morphs.

Keywords: northern mole vole, marking, family, colony, age structure, sex ratio, reproduction, migrations, polymorphism

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INTRODUCTION

The northern mole vole (*Ellobius talpinus* Pall., 1770) belongs to a special life form, subterranean rodents. Unlike burrowers, they permanently live and feed underground, except for a short migration period. The northern mole vole is a zonal species of steppes 1 2 and semideserts in the south of Russia; in the Ural 3 region, it expands to the mountains (in Bashkortostan and Chelyabinsk Region) and forest–steppe (in northern areas of Chelyabinsk and Kurgan regions).

In the course of evolutionary transition of the northern mole vole from aboveground to subterranean mode of life (Orlov, 1978), some groups of animals segregated from others and established long-term families with permanent home ranges. Such a family life pattern of the northern mole vole has long been known to researchers (Kirikov, 1952; Slastenina, 1959; Shubin, 1961; Dubrovskii, 1965; etc.). In suitable habitats, these animals form colonies consisting of a variable number of relatively isolated families, depending on habitat size and population density. In rare cases, some families may live 800–900 m apart from the colony.

The northern mole vole is one of a few species in the Russian fauna whose coat color is highly variable 2 and depends on the location of habitat. In the Ural region and neighboring areas, it varies from light brown to black (Evdokimov and Pozmogova, 1984).

The purpose of this study was to analyze the structure of individual mole vole families and family groups (colonies) by means of total mark–recapture and, on

this basis, to reveal specific features of monomorphic and polymorphic colonies.

MATERIALS AND METHODS

Studies were performed in the Southern Urals and Transural region by the mark–recapture method, using modified Golov’s live traps (1954). Attention was focused on observations of individual mole vole colonies consisting of a certain number of families (their number was determined from mark–recapture data). The trapped animals were marked by finger clipping, which provided the possibility of monitoring each individual throughout the period of its presence in the family range or in the territory of the colony. All members of each family were trapped to reveal the actual composition of the families and the colony.

The first mark–recapture experiment (1981–1983) was performed in the hunting enterprise located west of Shugunyak Lake in the Kunashak district of Chelyabinsk Region, at the northwestern boundary of the northern mole vole range. The Kunashak population is monomorphic, i.e., represented only by the black (melanist) color morph. The colony under study occupies a 6-ha area of a steppified hay meadow with a small aspen–birch forest island. The animals were captured, marked, and recaptured four times in 1981 (in April, June, August, and October), four times in 1982 (in April, May, August, and October), and three times in 1983 (in April, June, and September). Nine families were observed, 237 animals were

marked, and each marked individual was recaptured 2–10 times. The next month after the last recapture (for emigrants) or the month of the first recapture (for immigrants) was considered as the date of migration for young animals. For animals of older age, the next month after the last recapture was considered as the date of death.

The second experiment was performed in the Kurtamysh district of Kurgan Region. The Kurtamysh mole vole colony is polymorphic and contains three color morphs: black, brown, and intermediate. It occupies a territory of about 8 ha in the forest–steppe zone, which includes grain crop fields and hay meadows with aspen–birch forest islands. The animals were marked and recaptured two times per year (in April to May and in August to September) in 1985 to 1999. A total of 25 families were observed, 817 animals were marked, and each marked individual was recaptured 2–13 times. Marked young or older animals absent from catches in spring were regarded as having emigrated or died, respectively, in the previous autumn, and those absent in autumn, as having emigrated (died) in the spring of the same year; new (unmarked) individuals appearing in spring or autumn were considered immigrants beginning from the moment of their capture.

For comparative analysis of family composition, the families from the two colonies were divided into groups according to the number of members: (I) 2–3 ind., young families consisting of one female and one or two males; (II) 4–6 ind., parents with young of the year; (III) 7–10 ind., parents with yearlings and young of the year; (IV) 11–15 ind., parents with their offspring of previous years and young of the year; and (V) families with the maximum possible number of members (more than 15).

Northern mole voles in the studied populations may live to an age of up to 4, 5, or over 6 years. Seven groups were distinguished in their age structure: group 1, young of the year; group 2, yearlings; group 3, 2-year-olds; group 4, 3-year-olds; group 5, 4-year-olds; group 6, 5-year-olds; and group 7, 6-year-olds. The animals were considered adult after the first wintering, i.e., beginning from age group 2. Five to seven groups consisting of migrant and resident animals were permanently represented in the colonies. Migrants contributed to the first three age groups. This category included not only individuals leaving the colony (emigrants) or coming to the colony and remaining there (emigrants) but also those moving from one family to another within the colony (intermigrants). The term “residents” was applied to animals that were born in a given family and lived there for no less than a year. Disappearing individuals of older age groups (4–7) were considered dead of natural causes. Each population could contain up to three generations of young of the year per season, i.e., the early spring, spring, and summer generations.

RESULTS AND DISCUSSION

Data on the quantitative composition of mole vole families showed that families of groups III and II prevailed in both Kunashak and Kurtamysh colonies; then followed groups I and IV, and families of group V were rare (Fig. 1). Since studies in the two colonies were performed in different years and with different numbers of marked families, their comparative analysis was performed with regard to relative population abundance (the average number of animals per family) and the ratio of family groups. Data on the Kurtamysh colony were selected for the period when the general dynamics of its population had the same pattern as in the Kunashak colony (1988–1990) (Fig. 2). As animal abundance (density) in the colonies increased, the proportion of group I families proved to decrease both in spring and autumn, with the proportion of group III families increasing in spring and that of group IV families, in autumn.

Thus, seasonal and annual changes in the size of family groups in both colonies proved to have a similar pattern. This is evidence for common trends in the dynamics of quantitative and qualitative composition of their populations, which are accounted for by regular inflow and outflow of family members (birth of the young and dispersal of mature individuals, death of old animals, and immigration).

The number and quantitative composition of families determine the total abundance of animals in the colony. This parameter is relatively stable, with its seasonal and annual fluctuations (Table 1, Fig. 2) being much lower than in other murine rodents. The lowest abundance is observed in April to May, since a large number of overwintered young animals disperse by that time, but it then increases as the new offspring (spring and summer generations) are born and reaches a peak in August to September (Fig. 2a). A slight decrease in abundance takes place in autumn (August to October) due to the dispersal of young and death of old animals. During the wintering period (November to March), until the onset of spring migrations and the birth of the young, the abundance of families (the numbers of family members) remains almost unchanged. However, the autumn census counts of mole voles distinctly vary by years (Fig. 2b).

Stationary observations on marked families allow highly accurate evaluation of the age structure and sex ratio in mole vole colonies. In the Kunashak colony, for example, all animals captured and marked in 1981 (except young of the year) fell into the group consisting of animals born in previous years. Marked young of the year (age group 1) born in 1981 entered group 2 in 1982 and group 3 in 1983; young of the year born in 1982 entered age group 2 in 1983; and those born in 1983 represented age group 1. Thus, the age structure of the Kunashak colony in September 1983 consisted of groups 1 (born in 1983), 2 (1982), 3 (1981), and a

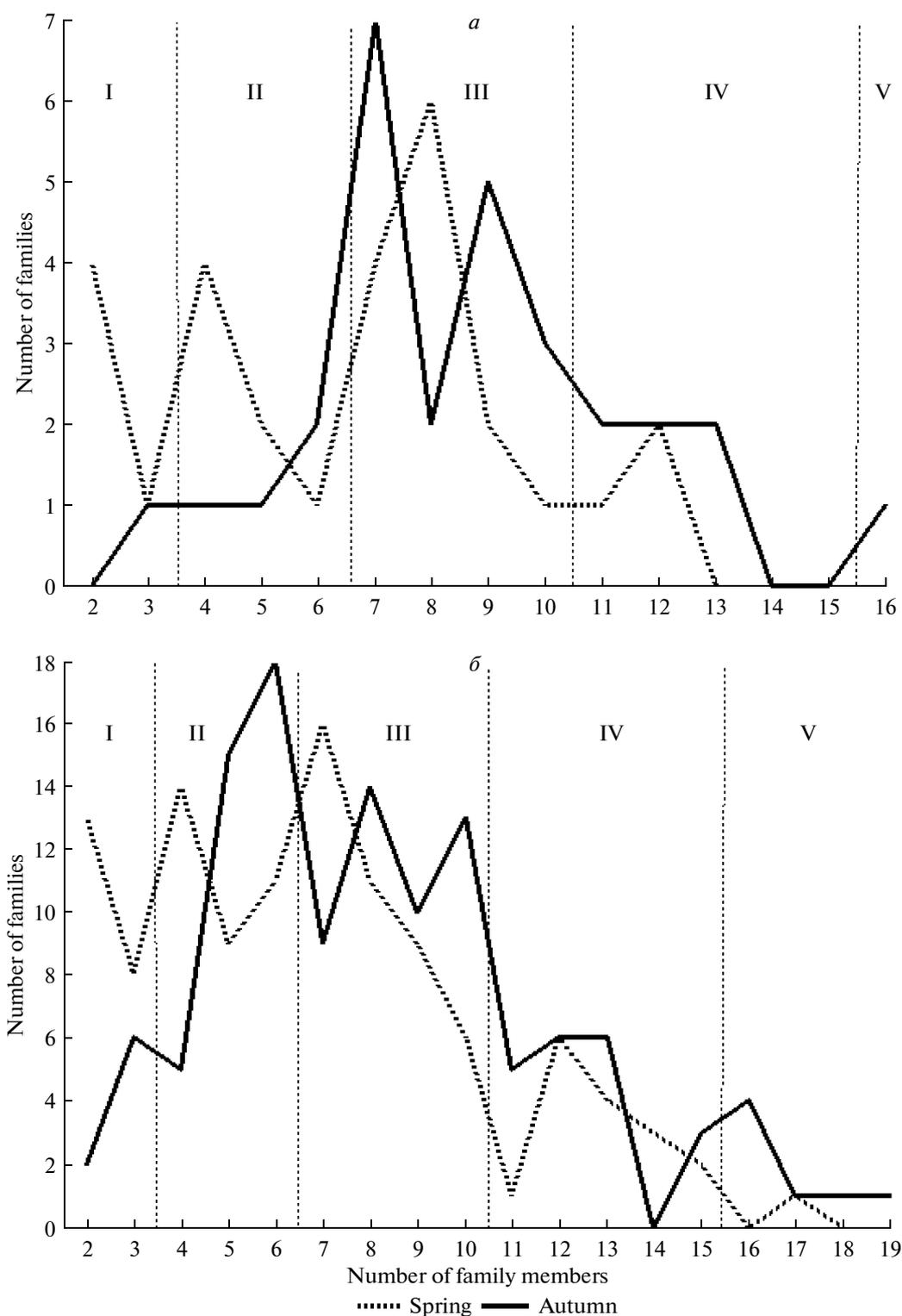


Fig. 1. Quantitative composition of mole vole families in (a) Kunashak and (b) Kurtamysh colonies in spring and autumn. Roman numerals (I–V) designate groups of families.

mixed group (Fig. 3a). The age of mole voles in the mixed group was determined from the degree of first molar root development (Evdokimov, 1997). The results showed that they were of age groups 4 and 5

(born in 1980 and 1979). Thus, the population of this colony consisted of five age groups, and the families included different proportions of animals from these groups.

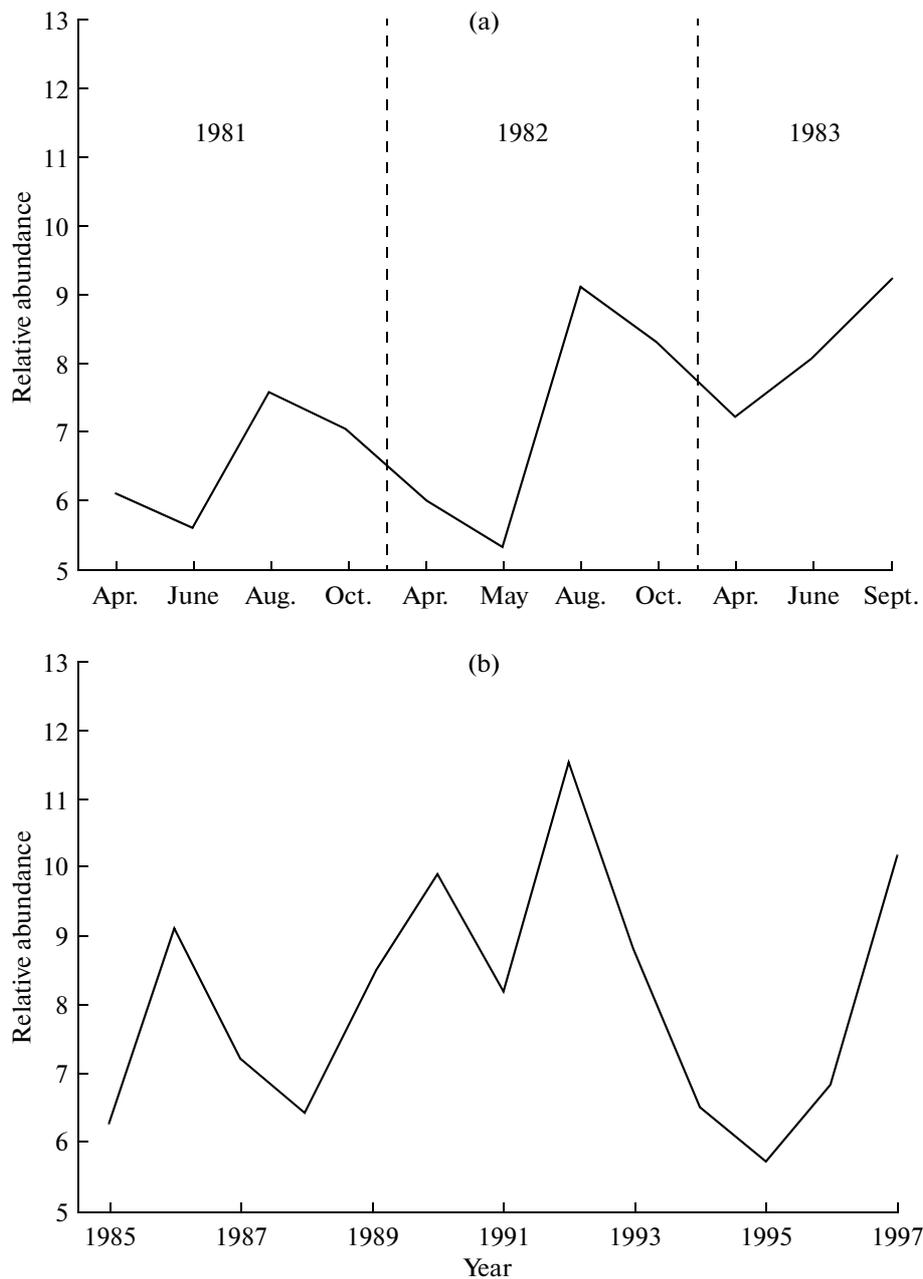


Fig. 2. Dynamics of the relative abundance of mole voles: (a) seasonal dynamics in the Kunashak colony and (b) annual dynamics in the Kurtamysh colony.

Long-term observations on marked animals in the Kurtamysh colony made it possible to evaluate the life span of mole voles, the age structure of the local population, and its dynamics (Fig. 4). Beginning from 1988, when the colony already consisted of animals with known birth years, five to seven age groups were represented in it every year. Thus, its population in 1988 consisted of five groups (1–5, born 1984–1988); in 1989, of six groups in spring (1–6, born 1984–1989) and of five groups in autumn (1, 3–6), animals of group 2 (born 1985) perished; in 1990, of five groups (3–7); in 1991 and 1992, of six groups (3–8, 4–9). In

1993, the mole vole population in spring included seven age groups (4–10), but the last animals born in 1988 (group 5) died by autumn. In 1994, animals born in 1987 (group 4) died by spring, and the population consisted of six age groups (6–11). From 1995 to 1997, seven age groups were represented in the colony (6–12, 7–13, and 8–14, respectively).

The results of numerous one-time catches and observations on marked animals showed that males prevail in northern mole vole populations of the Ural region (Evdokimov and Pozmogova, 1984). In catches

Table 1. Seasonal and annual dynamics of the composition of northern mole vole families

Group of families	Kunashak colony						Kurtamysh colony					
	1981		1982		1983		1988		1989		1990	
	Spring	Au-tumn	Spring	Au-tumn	Spring	Au-tumn	Spring	Au-tumn	Spring	Au-tumn	Spring	Au-tumn
I (2–3)	40.0	10.0	11.1	0	0	0	22.2	25.0	8.3	8.3	0	0
II (4–6)	10.0	30.0	44.4	22.2	33.3	11.1	55.6	25.0	25.0	41.7	25.0	8.3
III (7–10)	30.0	60.0	33.3	55.6	66.7	44.4	22.2	41.7	33.3	16.7	50.0	50.0
IV (11–15)	20.0	0	11.1	22.2	0	33.3	0	8.3	33.3	25.0	35.0	41.7
V (>15)	0	0	0	0	0	11.1	0	0	0	8.3	0	0
<i>n</i>	10	10	9	9	9	9	9	12	12	12	12	12
AA	61	70	54	75	65	92	44	77	100	101	101	119
RA	6.1	7.0	6.0	8.3	7.2	10.2	4.9	6.4	8.3	8.4	8.4	9.9

Figures in parentheses show the number of animals per family; *n* is the number of families; AA, absolute population abundance (number of animals); RA, relative abundance (the ratio of absolute abundance to the number of families captured).

Table 2. Proportions of males and females (%) in mole vole families (nos. 1, 4–11) of the Kunashak colony

Sex	Family									Total	
	1	4	5	6	7	8	9	10	11	<i>n</i>	%
Males	67.0	63.6	38.2	55.6	59.0	58.8	61.9	83.3	37.9	142	57.3
Females	33.0	36.4	61.8	44.4	41.0	41.2	38.1	16.7	62.1	106	42.7
<i>n</i>	24	33	34	27	39	17	21	24	29	248	100.0

n is the total number of males and females.

from different parts of the species range (a total of 2060 ind.), the proportion of males averaged $59.5 \pm 1.1\%$. In the Kunashak colony, this proportion over three years was 57.3 %, but the sex ratio varied from family to family (Table 2). Variation in this parameter was also observed in the Kurtamysh colony (1985–1997), where the proportion of males was 58.8% of the total population (1233 ind.).

These data provide evidence that the prevalence of males over females is a common phenomenon in mole vole populations. As observed in different parts of the species range (the Southern Urals, Transural region, and Western Siberia), this prevalence is especially distinct in older age groups; the proportion of males among adult animals averaged $63.9 \pm 1.5\%$ ($n = 687$), compared to $54.6 \pm 1.6\%$ ($n = 538$) among young of the year. Figure 3b shows data on changes in the proportion of males in individual dated age groups during three years of observations on the Kunashak colony. Their proportion reaches a peak in the older mixed group, but its sharp increase is observed beginning from age group 3 (to 69.0% in the Kunashak colony and 72.2% in the Kurtamysh colony). This increase is probably explained by the process of dispersal (migration) involving mainly the animals of age group 2, in which females prevail (Fig. 5).

A relatively small proportion of females in older age groups does not mean that they are in deficit. Thus, participation in reproduction was observed for only 17 out of 106 females (16.0%) over 3 years in the Kunashak colony and for 39 out of 256 females (15.2 %) over 12 years in the Kurtamysh colony. As a rule, only one (“queen”) female per family participates in reproduction (Table 3), and the number of families in a colony (population) is strictly regulated. During the study period, the population of the Kurtamysh colony (8 ha) in a given moment consisted of no more than 12 families, and that of Kunashak colony (6 ha), of no more than 10 families.

The long-term existence of relatively isolated families within a limited area with limited food resources forage supply implies the necessity of regular seasonal emigration of the excess part of the family (colony). This is confirmed by the dynamics of the overall population size and the number of emigrants in the Kunashak colony (Fig. 6a).

The dispersal (emigration) of mole voles begins in spring and involves animals of the first three age groups, which successively leave their families (colonies) as they grow and mature. In the Kunashak colony, the dispersal of animals born in 1981 began in the autumn of the same year and, after wintering, contin-

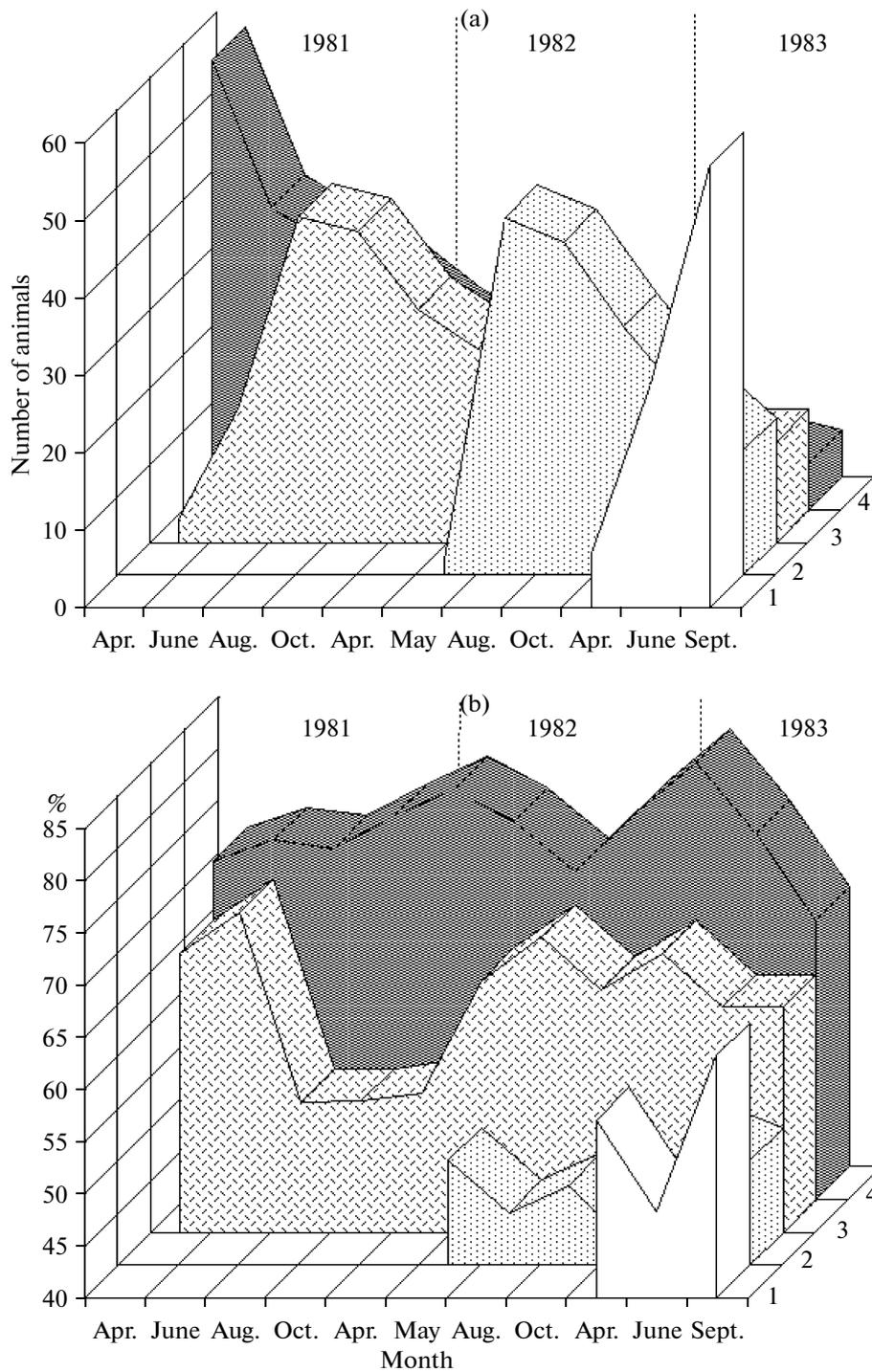


Fig. 3. Dynamics of (a) age structure and (b) sex ratio (proportion of males) by age groups (1-4) in the Kunashak mole vole colony: (1-3) groups born in 1983, 1982, and 1981, respectively; (4) mixed group.

ued throughout the spring, summer, and autumn of 1982. Some of them dispersed on the second year of life (after the second wintering), in the spring and summer of 1983. During 3 years, 34 out of 42 animals born in 1981 (80.9%) emigrated from the colony.

The dispersal of mole voles born in 1982 ($n = 46$ ind.) proceeded in a similar way but was more active:

73.9% of these animals emigrated within the first two years.

Observations on mole voles in the Kurtamysh colony showed that, in each age group (generation), active dispersal of animals takes place during the first two years of their life (Fig. 4). During the observation period, emigrants of age group 1 accounted for 0 to

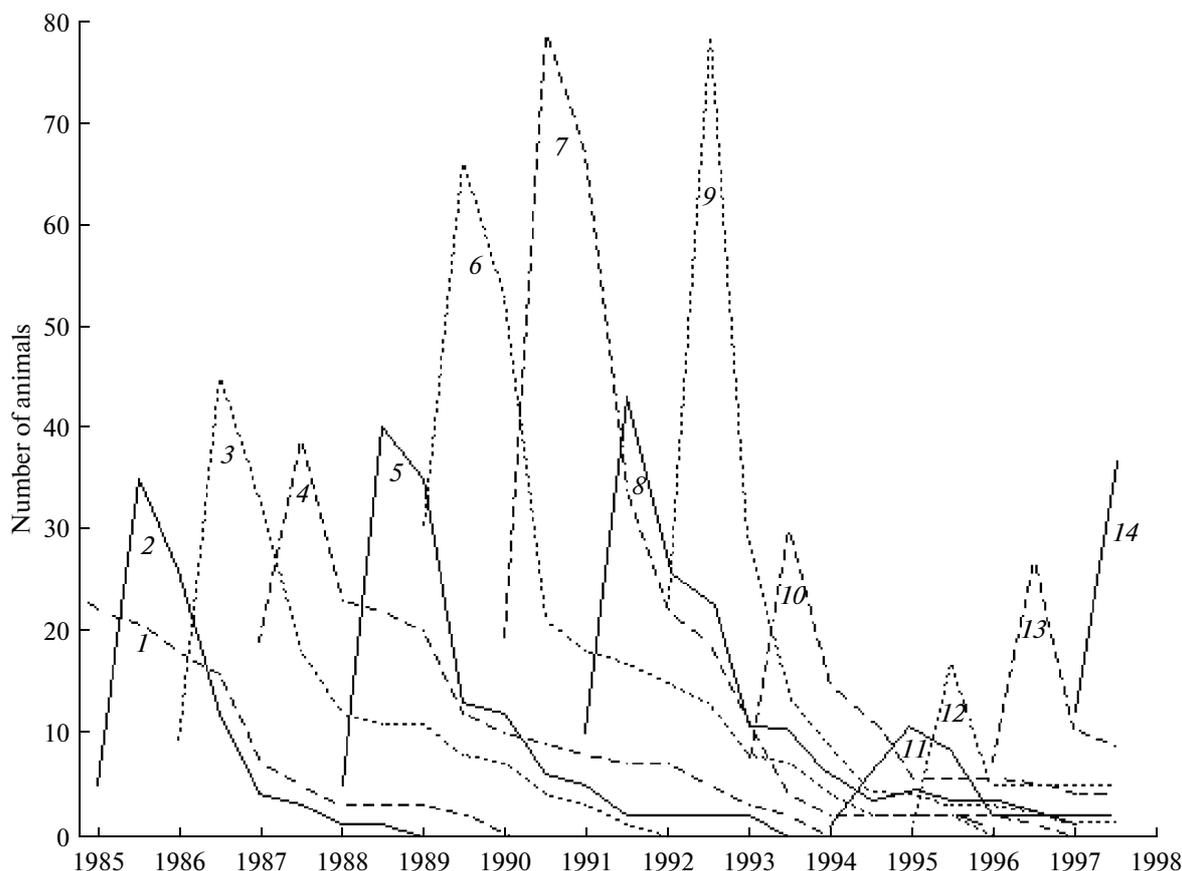


Fig. 4. Age structure and life span of mole voles from the Kurtamysh colony in the period from 1985 to 1998 (according to spring and autumn censuses); (1–14) age groups born in 1984 to 1997.

40% (on average, 15.5%) of their total number; of group 2, for 42.5–87.5% (66.7%); and of group 3, for 0 to 35.7% (17.8%). Over 12 years, 86.5% of a total of 556 male and female mole voles emigrated from the

Kurtamysh colony. Every year, animals of age group 2 (born in the previous year) comprised the greater part of emigrants. Therefore, the total number of emigrants in a given year depends mainly on the number of animals born in the previous year (Fig. 6b).

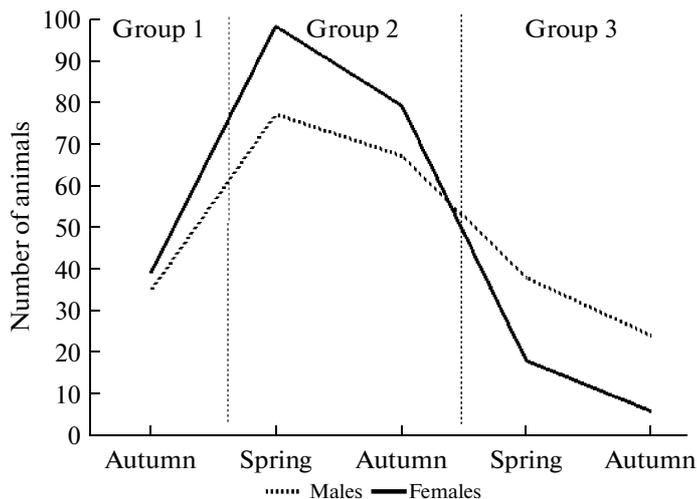


Fig. 5. Dynamics of emigration of male and female mole voles by age groups and seasons in the Kurtamysh colony.

Although the composition of families in the northern mole vole is variable, one female per family usually participates in reproduction. Only a few exceptions to this rule were observed in more than 300 families marked during the study. Thus, among nine families recorded in the Kunashak colony, family no. 7 was the only one where two females (nos. 70 and 126) participated in reproduction simultaneously (Table 3). Both young females (except immature young of the year) and females of older age group produce one litter during the first breeding season and two or three litters during the subsequent seasons. Inbreeding in mole voles is practically excluded, because families are formed of resident animals and migrants from neighboring families or colonies (Table 3).

As noted above, migrating mole voles include not only emigrants but also immigrants and intermigrants, which play a major role in the maintenance of homeostasis and reproductive potential of a colony (Table 4). The renewal of reproductive population in the

Table 3. Composition of parents in mole vole families and participation of females in reproduction (the Kunashak colony)

Family no.	Animal number, sex, and status	Year of birth	1981				1982				1983		
			Apr.	June	Aug.	Oct.	Apr.	May	Aug.	Oct.	Apr.	June	Sept.
1	>10, female	1979	4	+	+	+	5	+	+	†	0	0	0
	9, male	1981	+	+	+	+	+	+	+	+	+	+	+
	11 >122, female	1982	0	0	0	0	0	0	0	0	+	3	+
4	7 >59, female	1981	0	0	0	0	+	3	+	+	6	5	+
	53, male	1978	+	+	+	+	+	+	+	+	+	+	†
5	58, female	1978	5	+	†	0	0	0	0	0	0	0	0
	54, male	1977	+	+	†	0	0	0	0	0	0	0	0
	>41, female	1979	0	0	0	+	4	+	+	†	0	0	0
	>56, male	1978	0	+	+	+	+	+	+	+	+	+	†
	>57, male	1978	0	+	+	+	+	+	+	+	+	+	†
	60, female	1981	0	0	+	+	+	+	+	+	5	+	+
6	94, female	1980	4	+	+	+	4	3	+	+	5	4	+
	61, male	1979	+	+	+	+	+	+	+	+	+	+	+
7	67, female	1978	5	4	+	†	0	0	0	0	0	0	0
	68, male	1977	+	+	+	†	0	0	0	0	0	0	0
	5 >70, female	1981	0	0	0	0	0	0	+	+	5	4	+
	81, male	1981	0	+	+	+	+	+	+	+	+	+	+
	96, male	1981	0	0	+	+	+	+	+	+	+	+	+
	>126, female	1982	0	0	0	0	0	0	+	+	3	+	+
8	76, female	1978	3	+	+	†	0	0	0	0	0	0	0
	75, male	1978	+	+	+	+	+	+	+	+	+	†	0
	1 >2, female	1980	0	0	0	0	+	4	+	+	4	3	+
	78, male	1981		+	+	+	+	+	+	+	+	+	+
9	>84, female	1980	5	+	+	+	5	+	+	+	5	4	+
	>85, male	1979	+	+	+	+	+	+	+	+	+	+	+
10	10.1, female	1978	4	3	+	†	0	0	0	0	0	0	0
	11.1, male	1979	+	+	+	+	+	+	†	0	0	0	0
	11 >20, female	1981	0	0	0	0	0	5	+	+	4	3	+
	>12.1, male	1980	0	0	+	+	+	+	+	+	+	+	+
11	46.1, female	1979	5	+	+	+	5	4	+	†	0	0	0
	4.1, male	1978	+	+	+	+	+	+	+	†	0	0	0
	>215, female	1982	0	0	0	0	0	0	0	0	+	4	+
	105, male	1982	0	0	0	0	0	+	+	+	+	+	+

(+) animal present, (0) animal absent, †, animal died; figures show the number of offspring produced by a female. In the second column, ordinal numbers of marked animals in the first series (2–215) and the second series (4.1, 10.1, 11.1, and 46.1) are indicated. Animals designated 11 >122, 5 > 70, 7 > 59, and 1 > 2 are intermigrants from corresponding families (11th, 5th, 7th, and 1st) of their own colony; animals designated >10, >41, >56, >126, etc. are immigrants from neighboring colonies; animals 9, 53, 58, 54, etc. are resident.

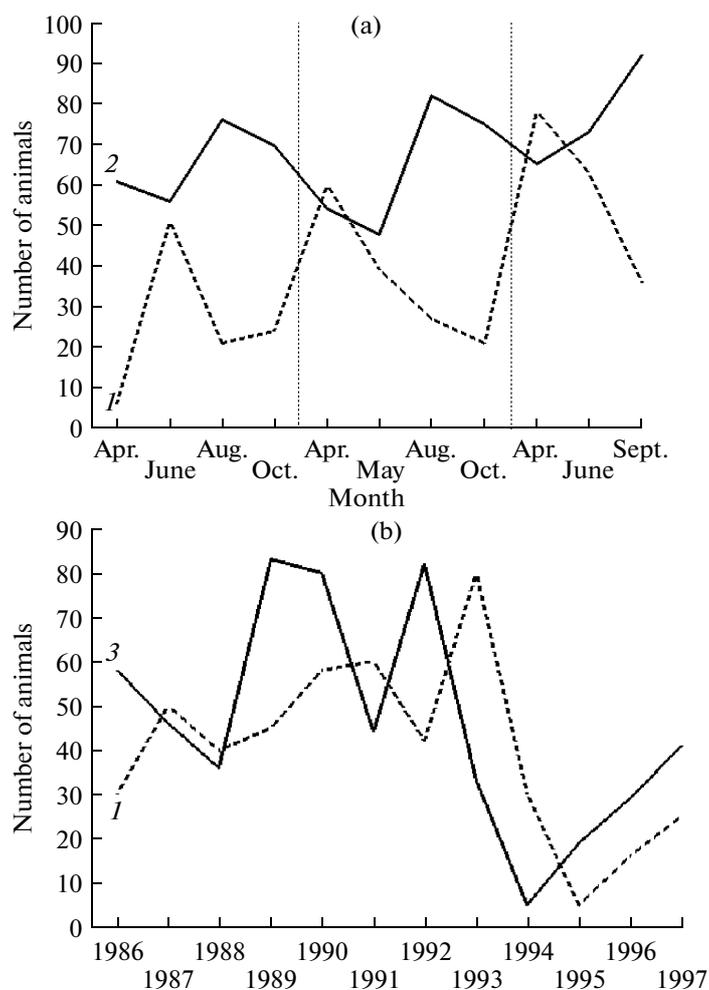


Fig. 6. Relationships between (1) the number of emigrants and (2) the total number of mole voles and (3) the number of young of the year in (a) Kunashak and (b) Kurtamysh colonies.

Kunashak colony was accounted for by relatively small numbers of resident animals (3.8% of the total population), intermigrants (0.9%), and immigrants (1.5%); taken together, they comprised 6.2% of the total population, with its probable reproductive potential being 44.7% (Table 4). The reproductive population of the Kurtamysh colony also consisted of residents, intermigrants, and immigrants, which accounted for 5.3% of the total population; its probable reproductive potential was 37.9% (Table 4).

The two colonies differ in parameters of demographic composition and reproductive potential, since the Kunashak colony is located at the northwestern boundary of the species range (northern Chelyabinsk Region), whereas the Kurtamysh colony occupies a favorable habitat in the southern Kurgan Region. Therefore, the Kunashak colony requires a greater amount of reproductive resources.

Another difference between them is that the Kurtamysh colony, unlike the Kunashak colony, is polymorphic (Table 5). Coat color polymorphism is a fairly rare phenomenon among numerous externally uni-

form species. It largely contributes to population heterogeneity and has adaptive significance, allowing local populations to develop a wide spectrum of adaptations (Altukhov, 1983).

Let us consider the migration process in three color morphs of mole voles from the Kurtamysh colony (Table 6). The greater part of black animals (50.8%) migrate before and after wintering, i.e., in late autumn and early spring; the proportion of migrants in the warm period (from spring to autumn) is markedly smaller (33.0%). Conversely, the majority of animals of the brown and transitional morphs migrate in the period from spring to autumn: 47.5 and 50.0%, compared to 33.1 and 24.3% in the cold period, respectively. Evidence that the black color morph is better adapted to cold is provided by the results of previous study on the energetics of tissue (mitochondrial) oxidative metabolism in mole voles of the black and brown morphs (Bol'shakov et al., 1982).

Each color morph of the northern mole vole has its specific features and functional significance (Evdokimov, 2005), which provide the possibility for local

Table 4. Demographic composition and probable and actual reproductive potentials of the Kunashak (1981–1983) and Kurtamysh (1988–1990) colonies

Colony composition	Total population		Participation in reproduction					
			males		females		males + females	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Kunashak colony								
Young of the year	155	29.2	—	—	—	—	—	—
Emigrants	123	23.2	—	—	—	—	—	—
Residents / adults	168	31.7	12	2.3	8	1.5	20	3.8
Intermigrants	47	8.9	—	—	5	0.9	5	0.9
Immigrants	22	4.1	4	0.8	4	0.8	8	1.5
Dead	15	2.8	—	—	—	—	—	—
Total	530	100.0	16	3.0	17	3.2	33	6.2
Kurtamysh colony								
Young of the year	199	34.0	—	—	—	—	—	—
Emigrants	147	25.1	—	—	—	—	—	—
Residents / adults	209	35.7	7	0.7	11	1.4	18	3.1
Intermigrants	9	1.5	8	1.4	1	0.2	9	1.5
Immigrants	4	0.7	1	0.2	3	0.5	4	0.7
Dead	17	2.9	—	—	—	—	—	—
Total	585	100.0	16	2.7	15	2.6	31	5.3

“Dead” refers to resident animals of older age groups that died of natural causes; *n* is the number of animals.

Table 5. Percent ratios of color morphs in the Kurtamysh colony

Morph	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Black	38.5	37.5	38.1	41.8	42.7	48.6	49.3	49.0	50.7	51.2	48.4	55.0	62.1	50.8	58.7
Brown	44.8	40.8	41.3	40.3	39.8	34.7	34.4	34.3	35.9	27.4	32.3	28.8	18.5	21.2	22.4
Transitional	16.7	21.7	20.6	17.9	17.5	16.7	16.3	16.7	13.4	21.4	19.3	16.2	19.4	28.0	18.9
<i>n</i>	96	152	160	134	206	245	221	210	223	84	62	80	103	118	143

n is the number of animals.

Table 6. Pattern of animal emigration from the polymorphic Kurtamysh colony

Age group	Black morph				Brown morph				Transitional morph			
	from spring to autumn		from autumn to spring		from spring to autumn		from autumn to spring		from spring to autumn		from autumn to spring	
	%	<i>n</i>										
1	—	—	35.0	89	—	—	23.0	32	—	—	10.0	7
2	27.1	69	13.4	34	40.3	56	5.8	8	40.0	28	5.7	4
3	5.9	15	2.4	6	7.2	10	4.3	6	10.0	7	8.6	6
Total	33.0	84	50.8	129	47.5	66	33.1	46	50.0	35	24.3	17

(—) Young of the year (age group 1) do not migrate in spring; *n* is the number of animals.

populations to colonize zones with different landscape–climatic conditions in the Cisural region, Southern Urals, Transural region, and Western Siberia. Thus, the species is represented by polymorphic

populations in the southern Kurgan Region and Bashkortostan and by monomorphic populations along the northwestern boundary of its range: the transitional morph in Tatarstan, the black morph in the north of

Chelyabinsk and Kurgan regions, and the brown morph in the Omsk Region.

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SPELL: 1. semideserts, 2. Ural, 3. Bashkortostan