

Volume 27, Number 5

September-October 1996

ISSN: 1067-4136

CODEN: RJOEEW

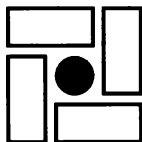
RUSSIAN JOURNAL OF ECOLOGY

Official English Translation of *Ekologiya*

Editor-in-Chief
Vladimir N. Bolshakov

Member of the Russian Academy of Sciences
Director of the Institute of Plant and Animal Ecology,
Ural Division of the Russian Academy of Sciences

A Journal of Original Papers and Reviews on Theoretical and Applied Ecology



Translated and Published by

МАНК ХАЙКА/INTERPERIODICA PUBLISHING

Distributed worldwide by PLENUM/CONSULTANTS BUREAU

Comparison of Migratory and Resident Individuals of the Bank Vole by a Complex of Nonmetric Traits

A. G. Vasil'ev, I. A. Vasil'eva, O. A. Luk'yanov, and L. E. Luk'yanova

*Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences,
ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia*

Received July 27, 1995

Abstract—Comparative analysis of migratory and resident individuals of a population of the bank vole (*Clethrionomys glareolus* Schreber 1780) in saturated habitats (fir–spruce forest) of the middle Urals (Visim reserve) in relation to the phene frequencies of 30 nonmetric cranial traits was performed. The nonreturn trap-line method was used. Sampling was continuously made for many days. Migratory individuals were separated from resident individuals on the basis of the effect of the stabilization of successive catches. Statistically reliable differences between migratory and resident individuals in the complex of phenes of nonmetric skull traits were indirectly revealed, indicating the existence of genetic differences between these two groups of animals. The difference rank between the calculated group of resident and migrating animals approached interpopulational differences (Vasil'ev, 1984a, 1984b).

INTRODUCTION

Biological differences between migratory and resident individuals substantially influence the spatial dispersal of small mammals, including such aspects as the mechanisms, types, and evolutionary changes in dispersal (Stenseth, 1983; Lidicker, 1985). However, since the procedure of separating migrants and residents is very complicated, statistical analysis of these groups of animals had been impossible until recently. The approach based on the long uninterrupted sampling of animals allows the numbers of migratory and resident individuals to be determined. This approach also enables the investigation of various biological characteristics on the basis of changes in the proportion of the number of migrants to the number of residents in successive catches (Berdyugin, 1983; Luk'yanov, 1988, 1994; Shchipanov, 1990; Luk'yanov and Luk'yanova (in press)).

Based on this approach, demographic and morphophysiological features of migratory and resident individuals of the bank vole *Clethrionomys glareolus* Schreber 1780 dwelling in fir–spruce forests of the middle Urals (Visim reserve) were studied (Luk'yanov and Luk'yanova (in press)). It was shown that, among migrants, young individuals predominate in areas with high population density. Migrants reach puberty faster. Resident individuals are distinguished by larger body size and a faster growth rate. It is concluded that resident individuals approximate *K*-strategists, while migratory individuals approximate *r*-strategists. However, the nature of phenotypic differences between the two groups of animals needs clarification.

The goal of the present study was to conduct phenetic analysis of migratory and resident individuals of

the aforementioned population with reference to a set of nonmetric cranial traits that could be interpreted genetically (Yablokov, 1980; Yablokov *et al.*, 1981; Vasil'ev, 1982, 1984a; Hartman, 1980; Sikorski and Bernstein, 1984; Markowski, 1993).

MATERIALS AND METHODS

Sampling was performed in July 1992 for ten days. In total, we analyzed 219 samples of skulls of the bank vole dwelling in the Visim reserve. We placed a line of 160 traps in a fir–spruce forest at 10-m intervals. Pine kernels were used as bait. It should be noted that a large portion of habitats of bank voles was flooded in this season due to excessive precipitation. As a result, at medium abundance of bank voles (23 individuals per 100 trap–days), the population density was high.

To separate migratory individuals and resident individuals, the method of the nonreturn catching of animals, as modified by Shchipanov (1990), was used. This method involves the construction of the curve of daily catches and is based on the effect of the stabilization of successive catches. The presence of resident individuals can be judged by a decrease in the magnitude of successive daily catches, and stabilization of successive catches indicates the presence on this territory of individuals immigrating from other habitats. Thus, once resident individuals have been captured, migratory individuals account for the major portion of caught animals (theoretically up to 100%). Resident individuals, in turn, will predominate among animals that were caught before the beginning of the stabilization of successive catches. Hence, we have two samples in which the proportions of migrants and residents,

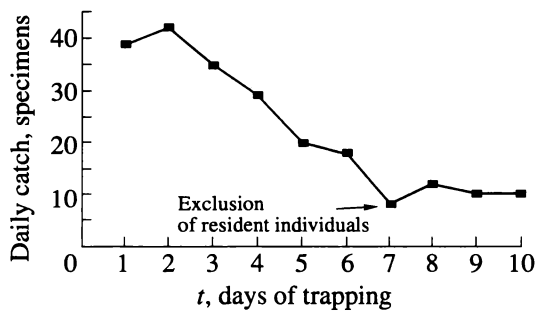


Fig. 1. Dynamics of successive daily catches of the bank vole over ten days (a line of 160 traps were set in the Visim reserve, the Middle Urals, in July 1992).

respectively, are high. Statistical estimates obtained on the basis of these two samples agree closely with estimates that would be obtained on the basis of samples comprising only migrants or residents. This permits biological features of migratory and resident individuals to be compared. Mathematical calculations and the comparison procedure are detailed in a forthcoming article (Luk'yanov and Luk'yanova (in press)). It should be stressed that, in the studied population, the stabilization of successive catches occurred on the seventh day (Fig. 1). Thus, it follows that, from the seventh catch on, all samples comprised only migratory individuals. On the basis of this group, we studied the features of migratory individuals. Among bank voles that were caught during the first six days, resident individuals accounted for about 67%. Therefore, mean statistical estimates of various characteristics obtained on the basis of the second sample approach the "true" values of these characteristics for resident individuals.

The relative age of bank voles was determined according to the recommendations of Olenev (1989). The caught voles were separated into seven age classes depending on the degree of development of the roots of the second upper molar (classes 1–6 correspond to animals of the current year's specimens one to three months in age, and class 7 consists of overwintered animals). The specimens of the current year were, in turn, separated into two groups: *juvenis* (age classes 1–3) and *subadultus* (age classes 4 and 5). The sole adult specimen of the current year belonging to the 6th age class was formally referred to the *subadultus* group.

To analyze phenotypic differences, 30 nonmetric cranial traits representing the appearance of additional foramina for the passage of certain blood vessels and nerves, the loss or appearance of bone fragments, or supplementary bony structures were selected. Some of these traits were described earlier (Vasil'ev, 1984b). Other new features are homologous to traits described for other rodent species by other authors. Since universally accepted Latin names of nonmetric cranial traits are lacking, we had to give these traits working names. The full list of nonmetric traits and their relative position are represented in Fig. 2. Phenotypes of nonmetric

features are designated by numbers in the figures, tables, and the list of variations of features. The appearance or absence of each trait was separately determined on the left and right sides of the skull. The frequency of the occurrence of a trait was calculated on the basis of the total number of sides studied (Hartman, 1980). To exclude potential duplication of information, Spearman rank correlation coefficients between traits were calculated. To find out how the examined traits are related to sex and age, the *G*-test was used. Multiple comparisons of particular samples were made by using the *G*-test (Sokal and Rohlf, 1981) as well.

Standard deviations (*MSD*) and the phenetic distances between the samples (*MMD*) were calculated by the formulas suggested by Hartman (1980). The differences were statistically significant at $p < 0.05$ when $MMD > 2MSD$. Since the distances in the *MMD* matrix do not meet certain metric axioms (for example, the triangle rule), the matrix of phenotypic distances must be "leveled off" before cluster analysis. This procedure can be realized by means of multidimensional nonmetric scaling by using the Kruskal method of minimum "stress" (Kruskal, 1964). We conducted multidimensional nonmetric scaling and cluster analysis (the nearest-neighbor method) with the NTSYS-pc statistical package (Rohlf, 1988).

Statistical treatment of the data obtained was performed with the software packages ECOSTAT (version 1.0) and PHEN (version 3.0), elaborated by Zhigal'skii, Vasil'ev, and Luk'yanov (Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences), and NTSYS-pc (version 1.40/440) (Rohlf, 1988).

RESULTS AND DISCUSSION

Preliminary Analysis and Elimination of Phenotypes

To select traits independent of sex and age and reduce statistical errors, preliminary analysis of correlations between the traits and between the traits and sex, age, and body size was performed, with subsequent elimination of traits linked to these factors.

Six traits (1, 2, 19, 21, 26, and 28) were significantly linked with sex. After eliminating these traits, data on males and females were integrated into a single set. To analyze the relationship between the frequency of the appearance of traits and age, we compared the *juvenis* (age classes 1–3) with the *subadultus* (age classes 4–6) and the specimens of the current year (age classes 1–6) with individuals that survived the winter (age class 7). Statistically significant differences between groups of the current year's specimens were only found for three traits (2, 4, and 29). After eliminating these traits, these two age groups were combined to obtain an integrated sample. Conversely, individuals that survived the winter differed from individuals of the *juvenis* and *subadultus* groups in a great number of traits (1, 2, 4–8, 11, 13, 15, 19, 22, 28, 30). Therefore, specimens of the

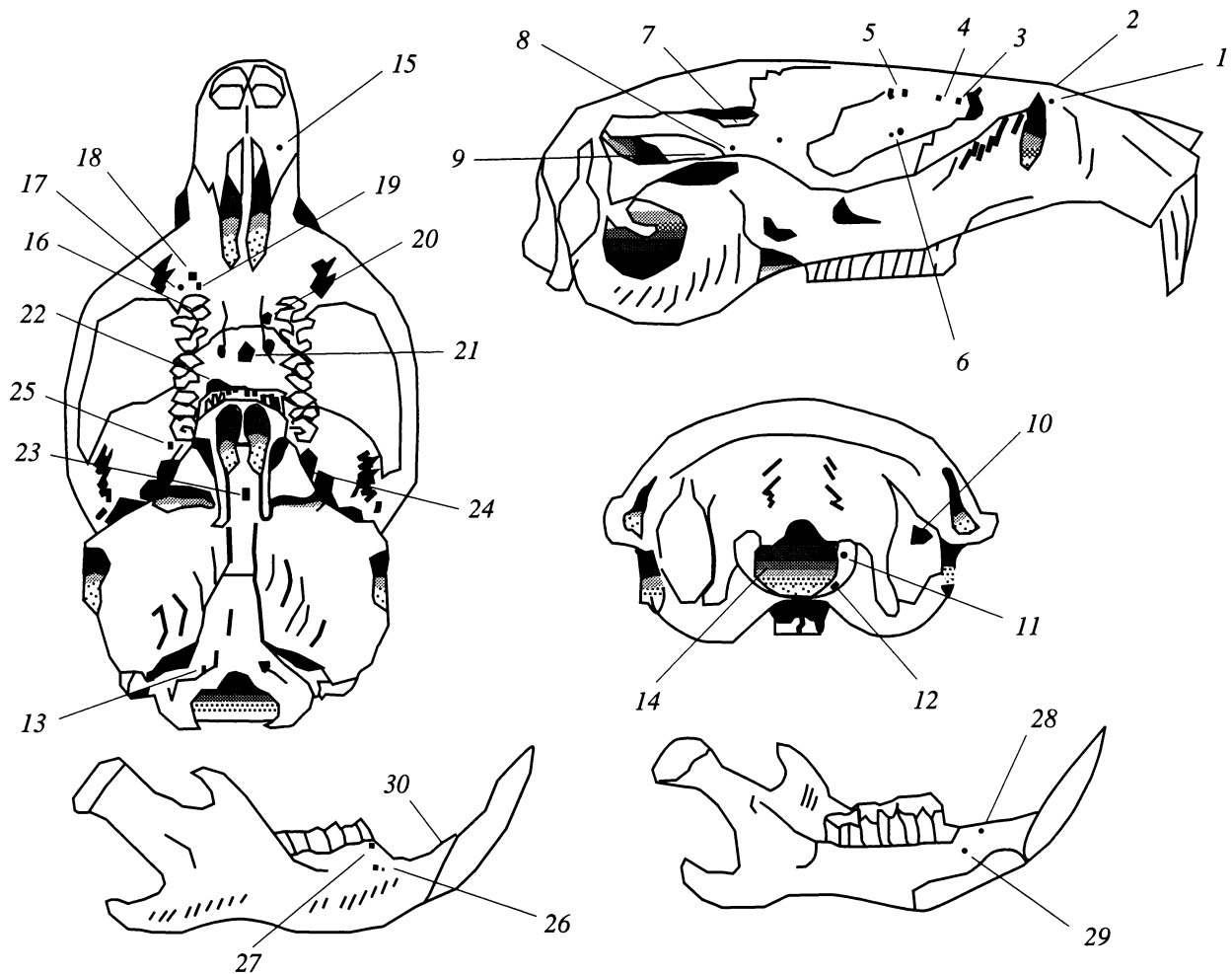


Fig. 2. Scheme of the location of phenes of nonmetric cranial traits on the skull of the bank vole.

(1–30) The numbers of the traits (*U* marks nonbilateral traits; * marks selected traits): (1) doubled *foramen preorbitale* (Berry, 1964); (2) incisure of the aboral edge of *os nasale* (Sikorski and Bernshtein, 1984); (3*) additional anterofrontal foramen; (4) anterofrontal foramen; (5*) doubled frontal foramen; (6*) doubled *foramen ethmoidale*; (7*) loss of a fragment of the parietal bone in the area of the temporal–parietal commissure; (8*) presence of *foramen squamosum*; (9*) absence of *meatus temporale*; (10*) loss of a fragment of the mastoid part of the petrosal bone; (11*) presence of an orifice in the upper part of the occipital condyle; (12) foramen in the lower part of the occipital condyle; (13*) doubled *foramen hypoglossi*; (14*) additional lateral *foramen hypoglossi* (observed through *foramen magnum*); (15*) *foramen premaxillare*; (16*) *foramen maxillare I*; (17*) *foramen maxillare II*; (18*) *foramen maxillare III*; (19) *foramen maxillare IV*; (20*) *foramen palatinum major*; (21*U*) loss of a fragment of the palatine bone; (22*) posterior edge of the palate is not closed; (23**U*) medial foramen in the basisphenoid; (24*) additional bone septum in *foramen ovale*; (25*) additional *foramen rotundum*; (26) doubled *foramen mentale*; (27*) “upper” mental foramen (*foramen mentale I*); (28) “pre-tertiary” mental foramen (*foramen mentale II*); (29) “internal” mental foramen (*foramen mentale III*); (30*) “anterior” mental foramen (*foramen mentale IV*).

current year and individuals that survived the winter were subsequently studied separately.

The Spearman rank correlation coefficients between traits and body size (length) were statistically significant for seven traits (1, 4, 5, 15, 21, 22, and 28). Some of them had already been eliminated, since they were also correlated with sex or age. Three traits (5, 15, and 22) were apparently closely related to body size. Elsewhere, it is shown that resident specimens of the current year have larger body size and grow faster than migratory specimens of the current year (Luk'yanov and Luk'yanova (in press)). Therefore, these three traits

can be used for the comparative study of migratory and resident individuals and should be used in further analysis.

Spearman correlation coefficients were calculated for all pairs of nonmetric traits on the basis of the sample of the current year's specimens in order to preclude duplicate information. All reliable correlations were low and comprised less than 5% of the total number. For this reason, all 12 traits that were weakly correlated (in the range of 0.10–0.18) were included in the set of traits studied. The correlation between traits 18 and 19 was average and negative ($r = -0.429$, $p < 0.001$). However, trait 19 was eliminated at a previous stage; thus,

Table 1. Frequencies of the occurrence of phenes of nonmetric traits of the bank vole sample from a mixed sample predominated by resident specimens and a sample of migrants of various age groups (the middle Urals, 1992)

Trait	Current year's specimens				Overwintered individuals				Multiple comparisons, G-test
	mixed ¹		migrants ²		mixed ¹		migrants ²		
	K/N	K, %	K/N	K, %	K/N	K, %	K/N	K, %	
3	48/263	18.25	8/74	10.81	10/83	12.05	1/8	12.50	
5	160/264	60.61	44/76	57.89	24/84	28.57	0/8	0.39	***
6	7/264	2.65	5/75	6.67	9/84	10.71	0/8	0.39	*
7	10/262	3.82	2/75	2.67	0/84	0.00	0/7	0.51	
8	63/260	24.23	23/75	30.67	11/84	13.10	2/7	28.57	*
9	38/261	14.56	4/76	5.26	13/84	15.48	0/7	0.51	*
10	32/263	12.17	1/75	1.33	5/82	6.10	0/8	0.39	**
11	171/255	67.06	42/75	56.00	59/78	75.64	7/8	87.50	*
13	147/256	57.42	46/74	62.16	31/78	39.74	3/8	37.50	*
14	52/256	20.31	15/74	20.27	15/78	19.23	1/8	12.50	
15	188/264	71.21	57/76	75.00	38/84	45.24	5/8	62.50	***
16	137/264	51.89	34/76	44.74	40/84	47.62	5/8	62.50	
17	183/264	69.32	51/76	67.11	50/84	59.52	0/8	12.11	*
18	189/264	71.59	46/76	60.53	59/84	70.24	5/8	62.50	
20	198/264	75.00	57/76	75.00	56/84	66.67	4/8	50.00	
22	125/256	48.83	29/72	40.28	10/71	14.08	1/5	20.00	***
23	14/130	10.77	0/37	0.02	1/41	2.44	0/8	0.39	*
24	29/262	11.07	5/76	6.58	11/83	13.25	2/7	28.57	
25	34/261	13.03	7/76	9.21	7/84	8.33	1/7	14.29	
27	8/264	3.03	2/76	2.63	1/84	1.19	0/8	0.39	
30	130/264	49.24	22/76	28.95	30/84	35.71	0/8	0.39	***

Notes: K is the sum of the frequencies of the manifestation of a phene on either side of the body; N is the total number of body sides studied. ¹—samples for days 1–6 of trapping. ²—samples for days 7–10 of trapping. * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$.

Table 2. Theoretical frequencies of the occurrence of phenes of nonmetric traits for resident bank vole specimens of the current year (the middle Urals, 1992)

Trait	K/N	K, %	Trait	K/N	K, %
3	40/175	22.86	16	98/176	55.68
5	108/176	61.36	17	126/176	71.59
6	1/176	0.57	18	135/176	76.70
7	8/175	4.57	20	132/176	75.00
8	36/173	20.81	22	91/171	53.22
9	34/174	19.54	23	14/82	17.07
10	31/175	17.71	24	23/175	13.14
11	124/170	72.94	25	26/174	14.94
13	93/171	54.39	27	6/176	3.41
14	34/171	19.88	30	104/176	59.09
15	120/176	68.18			

Notes: K is the sum of frequencies of the manifestation of a phene on either side of the body; N is the total number of body sides studied.

this correlation does not influence the final results. Trait 12 was excluded from further analysis, since it was found in only one case.

Thus, after preliminary analysis, the number of examined traits decreased from 30 to 21. It should be emphasized that we did not find clearly defined directed asymmetry of the samples with respect to these traits.

Phenetic Comparison of Migratory and Resident Individuals

Table 1 shows the frequencies of the occurrence of the phenes of nonmetric traits in individuals from a mixed sample with a predominance of resident individuals and a sample of migrants in groups of the current year's specimens and overwintered specimens. Multiple comparisons revealed reliable differences between these four groups of bank voles in 12 out of 21 traits.

As noted above, migratory individuals account for nearly 100% of the bank voles caught from the seventh through the tenth day. We used this circumstance in estimating the theoretical frequencies of phenes in resident individuals in a mixed sample accumulated in the first six days of trapping. According to the calculations,

Table 3. Phenetic distances *MMD* between mixed samples predominated by resident specimens and samples of resident and migratory specimens of bank voles of various age groups (the middle Urals, 1992)

Age group	Category	1	2	3	4	5
Current year's specimens	1 – migrants ^a	–	0.0307	0.0833	0.1131	0.0734
	2 – mixture ^b	0.0056	–	0.0006	0.1624	0.0822
	3 – residents ^c	0.0063	0.0032	–	0.2093	0.1116
Overwintered individuals	4 – migrants ^a	0.0429	0.0399	0.0405	–	0.0270
	5 – mixture ^b	0.0084	0.0053	0.0059	0.0426	–

Notes: The upper triangle matrix (above the matrix diagonal) shows values of phenetic distances; the lower triangle matrix (below the matrix diagonal) shows averaged standard deviations. (a) Individuals caught during days 7–10. (b) Individuals caught during days 1–6. (c) Calculated values.

the portion of migrants in the total number of animals in the mixed sample was $q = 0.328$. The frequencies of the occurrence of traits can be calculated by the formula $P_r = (P_i - qP_m)/(1 - q)$, where P_r is the frequency of the occurrence of the phene in resident individuals "proper," P_i is the frequency of the occurrence of the phene in a mixed sample, P_m is the frequency of the occurrence of the trait in migrants caught from the seventh through the tenth day, and q is the portion of migrants in a mixed sample (Berdyugin, 1983). The theoretical frequencies of the occurrence of phenes in resident specimens of the current year are represented in Table 2.

Analysis of the matrix of phenetic distances *MMD* between corresponding pairs of the compared groups showed that, in most cases, the selected groups of individuals significantly differed (Table 3). The difference between individuals caught during the first six days (among them, resident individuals predominate) and migratory individuals by the frequencies of the occurrence of phenes of nonmetric traits was statistically reliable for the current year's specimens ($MMD = 0.0307 \pm 0.0056$, $p < 0.01$). For overwintered individuals, the difference between analogous groups of animals was essentially the same. However, since, in this case, the number of migratory individuals was small, the calculated value was not statistically reliable. On the whole, the differences between the current year's and overwintered specimens were the greatest.

The phenetic distance between resident and migratory specimens of the current year by the frequencies of the occurrence of traits was also statistically reliable and much greater than the difference between the current year's specimens caught during the first six days (among them, resident specimens of the current year predominate) and migratory specimens of the current year ($MMD = 0.0833 \pm 0.0063$). These estimates are of special interest, since they indicate that differences between migratory and resident individuals approach the level of interpopulational differences (Vasil'ev, 1984a, 1984b).

"Leveling" of the matrix of phenetic distances (Table 3) was performed by the MDSCALE program with the multidimensional nonmetric scaling procedure. Cluster analysis of the leveled matrix revealed that differences between samples were of two types: ontogenic differences and differences between migrants and residents (Fig. 3). Ontogenic differences occupied the first place, since two large clusters that characterize the phenetic features of the current year's specimens and overwintered individuals were outlined. The differences between migratory and resident individuals occupied the second place, since, in both age groups, subclusters that link migrants and "residents" at nearly equal levels of transformed *MMD* were found. The calculated sample of resident specimens of the current year approaches the mixed sample (the first six days of trapping; among them, resident individuals predominate).

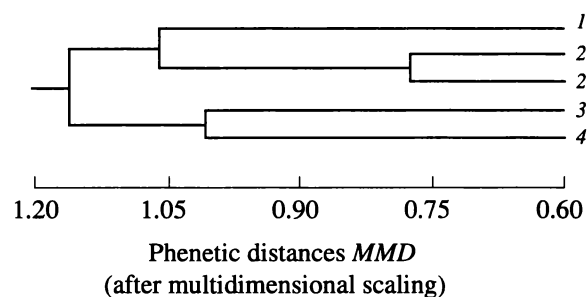


Fig. 3. Cluster analysis of phenetic distances between mixed samples predominated by resident animals and samples of resident and migratory bank vole specimens of different age groups on the basis of the *MMD* matrix, which was leveled off by multidimensional scaling.

(1, 2, 2') Specimens of the current year: (1) migratory individuals caught on days 7–10; (2) individuals caught during days 1–6 (among them, resident individuals predominate); (2') resident individuals (calculated values); (3, 4) overwintered individuals: (3) migratory individuals caught on days 7–10; (4) mixed sample predominated by resident individuals (sample for trapping days 1–6).

CONCLUSION

Preliminarily eliminating traits linked with each other, sex, age, and body size enables the most probable phenetic miscalculations to be avoided. Exclusion of most traits linked to body size essentially decreases the environmental component of variation. All these factors having been removed, the differences between the selected samples in the set of nonmetric traits may be considered to be determined by genetic factors to a significant degree (Hartman, 1980).

Phenetic analysis showed that resident individuals of the bank vole dwelling in areas with high population density substantially differed from migratory individuals in a set of nonmetric cranial traits. This indirectly indicates genetic specificity of the development of individuals in these groups. Cluster analysis revealed that there exists a two-level hierarchy of differences determined by two main factors: (1) ontogenic differences between the current year's and overwintered individuals and (2) differences between migrants and residents. According to statistical estimates, the differences between migratory and resident individuals approximate the level of interpopulational differences (Vasil'ev, 1984a, 1984b). Thus, phenetic comparison of migratory and resident individuals showed that the bank vole population is characterized by phenogenetic heterogeneity, which is manifested in specificity of the territorial behavior of the bank vole. Elsewhere, it was shown that, in the studied bank vole population, resident individuals approximated *K*-strategists by a set of morphophysiological characters; and migratory individuals, *r*-strategists (Luk'yanov and Luk'yanova (in press)). According to the results of the present study, the differences between *K*-strategists and *r*-strategists in murine populations may be attributed to genetic factors.

ACKNOWLEDGMENTS

This study was supported by grants EBR 26/3.4.5 and EBR 26/1.4.7 from the Russian Foundation for Basic Research within the framework of projects 95-04-11041a and 96-04-48013.

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