

Morphogenetic Effects of Resettlement of Mole Voles (*Ellobius talpinus* Pall., 1770) from the Southern Population to the Northern Boundary of the Species Range

A. G. Vasil'ev*, Academician V. N. Bol'shakov, I. A. Vasil'eva, N. G. Evdokimov, and N. V. Sineva

Received September 26, 2017

Abstract—Geometric morphometry has been used to reveal transformations of mandible morphogenesis in the offspring of mole voles resettled to the northern part of the species range from a southern population. The transformations were new compared to both the original (southern) and the aboriginal (northern) populations. A significant increase in the intragroup morphological disparity estimated by the mean nearest neighbor distance (MNND) in the resettled animals compared to both aboriginal populations is an indirect indication of an increased developmental instability in the resettled animals exposed to new climatic conditions.

DOI: 10.1134/S001249661801009X

Experimental modeling of intraspecies reactions of animals to a rapid change in climatic conditions is a relevant task due to the expected negative trends of climate change and the need to predict biotic rearrangements related to these changes [1, 2]. Experiments in evolutionary ecology, such as breeding of different intraspecies forms in animal vivaria, revealed distinctive features of morphological deviations from different laboratory colonies and the original natural populations [3, 4]. These “experiments” with animals are difficult to perform under natural conditions; therefore, they have been performed extremely seldom, restricted to a small number of economically important species introduced into new areas [5]. The mole vole (*Ellobius talpinus* Pall., 1770) is a burrowing rodent. The coat color is brown in southern populations of this species and black in the northern populations; therefore, the mole vole is a promising model for resettling experiments, as the offspring of resettled individuals can be distinguished from aboriginal animals by coat color in field studies [6].

The aim of the present study was to assess the results of resettling several families of the model species (the mole vole) from a southern population to the northern border of the species range. We tested the hypothesis of dissimilarity of morphogenetic reactions in geographically remote intraspecies groups formed under different climatic conditions and placed into the same environment. Comparative analysis of morphological intragroup diversity (disparity) in the offspring of animals from the southern population resettled to

the northern boundary of the species range and aboriginal southern and northern animals was of especial interest.

The initial plan of the study included reciprocal resettling, i.e., capture of all animals from three families of each of the two (northern and southern) populations and cross-transfer of these families between burrows of animals from a different population. The fate of the resettled animals could be inferred from coat color upon regular captures of animals with subsequent return to the family colonies. Southern mole voles (the brown morph) reproduced successfully and gave rise to offspring at the northern boundary of the species range, whereas a colony of melanistic northern animals (the black morph) did not survive in the south. We compared three craniological series of adult specimens from the Zoological Museum of the Institute of Plant and Animal Ecology (Ural Branch, Russian Academy of Sciences) that included samples from the northern (Kunashak settlement, Chelyabinsk oblast, 68 spec.) and southern (town of Kuvandyk, Orenburg oblast, 38 spec.) populations and a sample of offspring of resettled animals from the southern population (28 spec.). All samples were collected in August 2005, three years after the release of the southern founder individuals at the territory of the northern population. The aliens characterized by brown coat color formed autonomous family colonies and avoided communities of aboriginal melanistic animals. The aliens' progeny did not form mixed couples (the reasons for prolonged segregation of individuals from different populations remain unclear).

Geometric morphometry [7–9] has been used to analyze variability and disparity of the mandible shape. The lower jaw was selected for analysis because

*Institute of Plant and Animal Ecology, Ural Branch,
Russian Academy of Sciences, Yekaterinburg, Russia*
*e-mail: vag@ipae.uran.ru, vag2591@yandex.ru

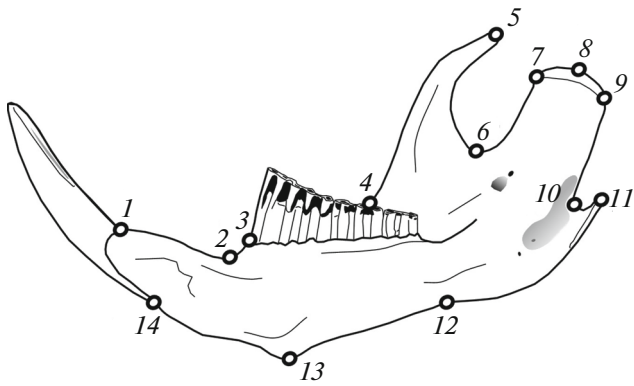


Fig. 1. A scheme of landmark (1–14) placement at the lingual side of the mandible branch of the mole vole.

the mole vole uses the mandibular incisors for burrowing and mandible configuration is related to mechanical composition of soil and the processing of food objects [10].

A set of 14 landmarks was placed on the lingual side of the right mandible branch using the tpsUtil [11] and tpsDig2 [12] software. These marks were used to study the variability of mandible shape (Fig. 1). Generalized Procrustes analysis (GPA) and the least squares method were used to superimpose the mark configuration [7]. Procrustes coordinates that characterized shape variability were used to perform intragroup

comparisons based on canonical analysis. Intrapopulation morphological diversity (disparity) was inferred from the values of mean nearest neighbor distance (MNND) between ordinates within the variability polygon [13]. The ratio (R) of the empirical MNND to the value of mean distance (μ) expected according to the Poisson distribution characterized the pattern of ordinate dispersion. Ordinate aggregation was observed at $R < 1$, Poisson dispersion, at $R \sim 1$, and overdispersion, at $R > 1$. MNND increase in the third case could be interpreted as expansion of the morphogenetic fan and morphological disparity [10, 13]. The TPS [11, 12], MorphoJ 1.06d [9], and PAST 2.17c [14] software was used for statistical analysis. Preliminary statistical testing did not reveal a significant effect of sex on the variability of the mandible shape; therefore, animals of both sexes were pooled for each sample.

Canonical analysis of Procrustes coordinates characterizing the variability of mandible shape showed that there was almost no overlap between the ordinate variability polygons for the two aboriginal populations, since these polygons were located in different areas of the morphological space (Fig. 2). The intergroup difference was statistically significant along both axes. The proportion of variance along the first canonical variable was 62.5%.

The polygon of resettled animals was shifted relative to that of the original southern group, even though

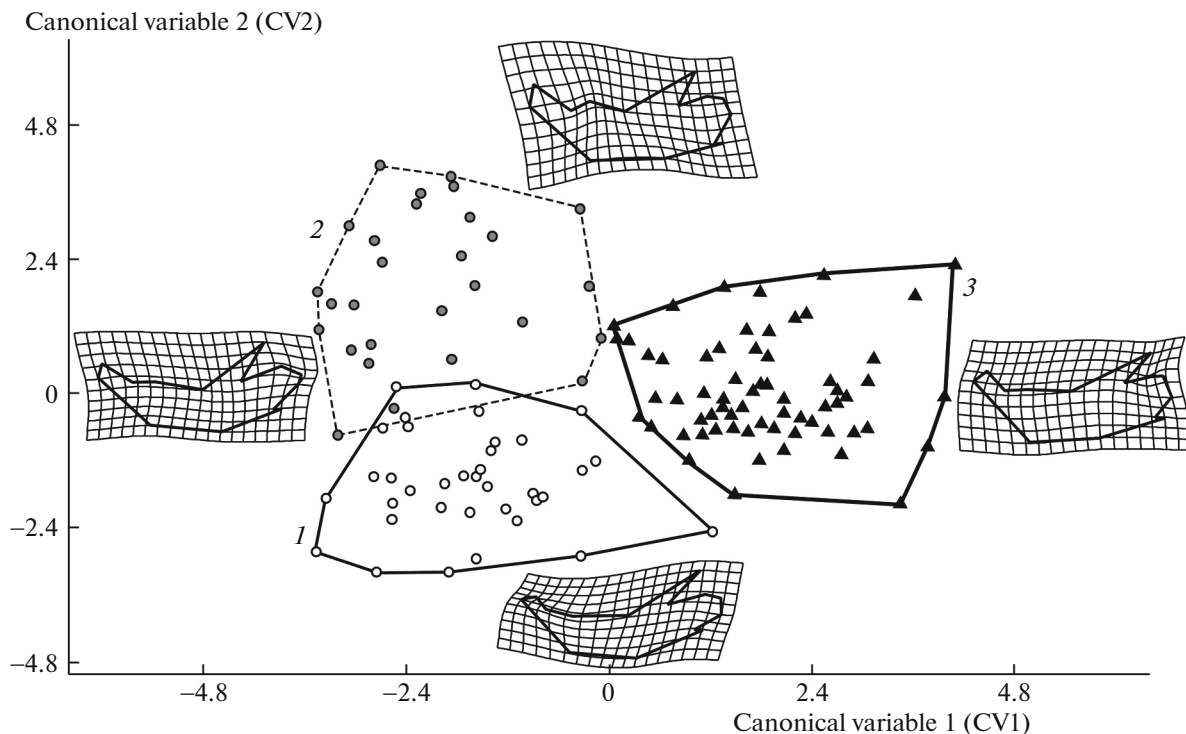


Fig. 2. Results of canonical analysis of Procrustes coordinates that characterize mandible shape variability in samples from the southern population (1), offspring of resettled southern animals (2), and the northern (3) population in the common morphological space along the first two canonical variables (CV1, CV2). Projections of mandible configurations on the deformational grids reflect the most pronounced changes of jaw shape along the respective canonical axes.

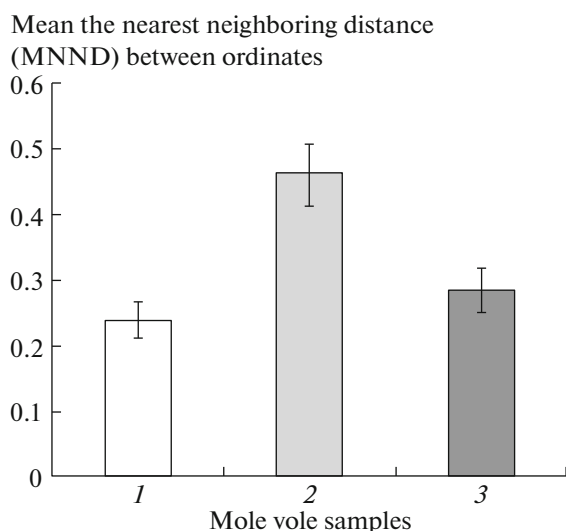


Fig. 3. Comparison of the MNNDs (with the standard error (*SE*) values taken into account) between the nearest neighboring ordinates for samples from the southern population (1), offspring of resettled southern animals (2), and the northern (3) population after random rarefaction of the data to obtain equal numbers of individuals in all samples.

some morphological features specific for the parent population were conserved. However, this shift did not bring the polygon closer to that of the aboriginal animals from the northern population. Therefore, one can conclude that mandible morphogenesis processes are different in the resettled animals and the aboriginal northern animals, despite the similar living conditions. On the one hand, this is indicative of genetic dissimilarity of the two original populations, and on the other hand, this demonstrates the capacity for rapid reorganization of morphogenesis in the resettled animals.

The rarefaction procedure was used to test the hypothesis of increased ordinate dispersion (morphological disparity) in the sample of resettled animals' progeny: all sample sizes were reduced to the minimal sample size in a random manner. Intragroup morphological disparity (MNND) of the jaw shape was indeed significantly higher in the group of resettled animals than in the original populations (Fig. 2); moreover, significant ordinate overdispersion ($R = 1.28$, $Z = 2.46$, $p = 0.014$) was observed in the former group. On the other hand, ordinate dispersion in the aboriginal samples had a random pattern (southern population: $R = 1.02$, $Z = 0.27$, $p = 0.786$; northern population: $R = 1.13$, $Z = 1.40$, $p = 0.16$). The increase in MNND (Fig. 3) and ordinate overdispersion in the group of resettled animals can be interpreted as expansion of the morphogenetic reaction fan and modification variability in a new environment (the northern part of the species range). The shift of the normal value for the group with regard to mandible shape is indicative of the possibility of rapid morphogenetic rearrange-

ments upon the colonization of an area with new climatic and cenotic characteristics by the population. One can conclude that the resettled animals and their progeny acquired new morphogenetic features observed neither in the animals of the parent (southern) population nor in those of northern population within a small number of generations exposed to the novel conditions of the north. Thus, we revealed dissimilar morphogenetic reactions of distant populations to the same natural conditions and demonstrated the possibility of rapid morphogenesis rearrangement to form morphological features that enabled the resettled animals to thrive under new climatic and cenotic conditions along with individuals of the northern population.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research (project no. 16-04-01831) and the Integrated Program of Basic Research of the Ural Branch of the Russian Academy of Sciences (project no. 18-4-4-28).

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Translated by S. Semenova