ISSN 0012-4966, Doklady Biological Sciences, 2016, Vol. 468, pp. 118–121. © Pleiades Publishing, Ltd., 2016.
Original Russian Text © A.G. Vasil'ev, V.N. Bolshakov, N.G. Evdokimov, N.V. Sineva, 2016, published in Doklady Akademii Nauk, 2016, Vol. 468, No. 1, pp. 000–000.

GENERAL BIOLOGY

Morphological Diversity of Mole Vole Mono- and Polymorphic Populations: Does Chernov's "Compensation Principle" Work within a Population?

A. G. Vasil'ev, Academician V. N. Bolshakov, N. G. Evdokimov, and N. V. Sineva

Received September 29, 2015

Abstract—The ecological "compensation principle" enunciated by Yu.I. Chernov, who suggested a higher level of compensatory diversity in communities depleted in composition, proved to be also applicable to a single population, as demonstrated in a model rodent species, mole vole with mono- and polymorphic coat color, using the methods of geometric morphometrics. The mandible shape diversity was significantly increased in the monomorphic as compared to polymorphic populations, in which the division of foraging activities between animals of different morphs led to a suppression of general morphological diversity.

DOI: 10.1134/S0012496616030030

The "compensation principle," which works in populations, communities, and their constituting species, has been formulated by Academician Chernov [1], who suggested that a decrease in the number of species in the direction from south to north or with increasing altitude is compensated by a higher abundance and diversity of the remaining species. In view of the adverse climatic trends [2, 3], the effects of rapid population transformations related to the "compensation principle" are of great importance, studies on them are expected to move from the purely theoretical area to the applied one.

In this study, we tested the suggestion that Chernov's "compensation principle" works not only at the level of communities and various populations, but also within a population. The main task was to explore the morphological variability and diversity of mono- and polymorphic populations of a model rodent species, the mole vole (*Ellobius talpinus* Pall., 1770), in the southern Urals.

Four mole vole model populations used in our study differed in coat color. The northern Kunashakskaya and the most southern Naursumskaya populations from the Kunashak settlement, Chelyabinsk oblast (19 specimens) and Naursumsky Reserve, Kazakhstan (36 specimens), respectively, were monomorphic in color with solely melanistic northern and brown southern animals. The geographically intermediate populations from Baimak settlement, Bashkortostan (51 specimens) and Troitsk city, Chelyabinsk region (51 specimens) displayed polymorphism of coat color in the form of three color morphs: black, brown, and black-backed (animals with a wide black stripe on the back and a brown belly). All samples consisted of the adult animals.

The mole vole mandible was the object of our study because the animal uses lower incisors when digging the underground tunnels and in foraging. The mandible branch has a relatively flat structure; therefore, the mandible diversity can be studied by the method of geometric morphometrics (GM). GM methods, increasingly used in morphological analysis, make it possible to study the size and shape of the objects separately [4–6].

Using the tpsUtil [7] and tpsDig2 [8] software, 15 landmarks were spread over the mandible images from the right lingual side in order to characterize the mandible shape diversity (Fig. 1a). We used the generalized orthogonal least-squares Procrustes analysis (GPA) [4]. The animal groups were compared by means of the principal component and canonical analyses of Procrustes coordinates.

The intrapopulation morphological diversity was studied using the nearest neighbor point pattern analysis within a diversity polygon [9]. The model of coordinate scattering was characterized by the ratio of R (the mean distance between the neighbor coordinates, *MNND*) to the average distance (μ, determined for the diversity polygon on the basis of the Poisson distribution. If $R < 1$, $R = 1$, or $R > 1$, then coordinate clustering, a random Poisson scattering, or overscattering are observed, respectively. In the latter case, an increase in *MNND* can be interpreted as expansion of the trajectory fan, i.e., as intragroup morphological diversity

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

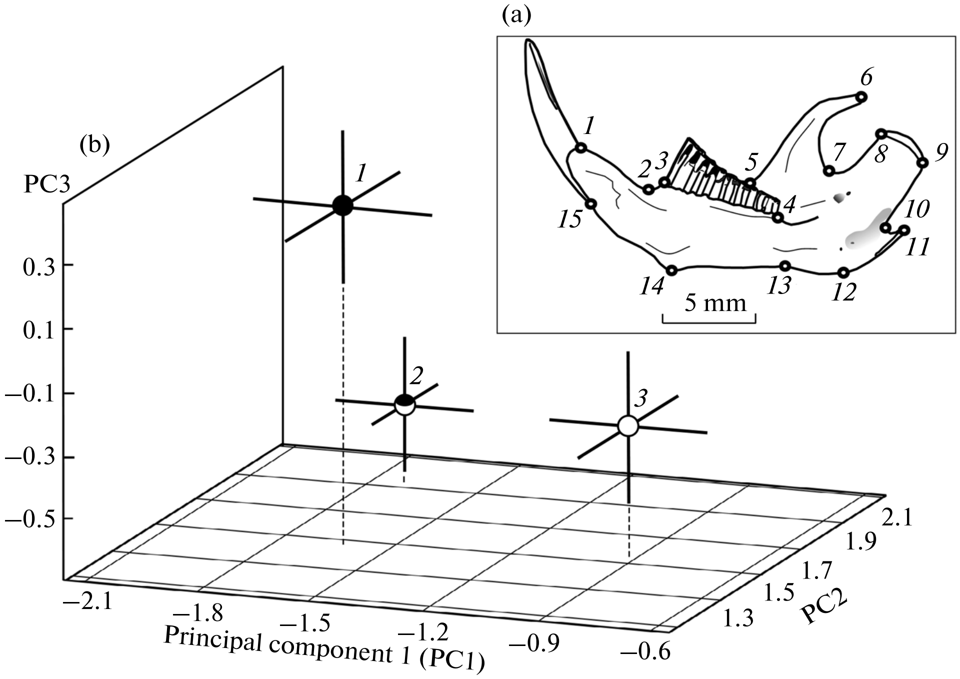

Fig. 1. Layout of (a) the landmarks (*1–15*) over the lingual side of the mole vole mandible branch and (b) centroids of the color morph samples (*1*, black; *2*, black-backed; *3*, brown) in the morphospace of three plrincipal components (PC1–PC3), which characterizes the mandible shape diversity (including the sample centroids and their standard errors, SE).

[9]. All calculations were performed using the TPS [7, 8] and PAST [10] software.

Since no sex-related differences were determined by preliminary analysis, the data on males and females were pooled in the samples. In the Troitsk population polymorphic with respect to coat color, the mandible shape ordination for three morphs (the black, brown, and black-backed) was conducted using the principal component analysis of Procrustes coordinates (Fig. 1b). The figure demonstrates that the centroids of all morphs were separated from one another within the morphospace of the first three principal components. The intrapopulation morph differentiation according to the mandible shape is indicative of their morphogenetic features and functional distinctions related to different mandible functions during digging and foraging in animals of different morphs.

Figure 2 shows the results of canonical analysis of Procrustes coordinates which characterize the mandible shape diversity in four geographically remote mole-vole populations. The intergroup distinctions along all canonical axes were statistically significant. We studied diversity along the first and third canonical variables (CV1, 54.4%; CV3, 14.1% of the variance) significantly associated with the population polymorphism ($r = -0.60$, $p < 0.0001$ and $r = -0.48$, $p < 0.0001$, respectively). Diversity along the second canonical axis (CV2, 31.5% of the variance) was excluded, because it was not associated with population polymorphism ($r = 0.12$, $p = 0.132$). It can be seen from the figure that the diversity polygons of the two monomorphic populations do not overlap, whereas in polymorphic populations, they are superimposed but do not coincide with the polygons of monomorphic populations. Thus, the animal mandible shapes differed significantly in populations monomorphic in coat color (brown and black), whereas in both polymorphic populations, they were similar.

The shadow mandible configurations on this figure correspond to the extreme ordinate values along the canonical variables; hence, one could interpret the general directions of changes in the mandible shape of the compared populations. The mandible configuration typical of the monomorphic brown animals is characterized by a massive masseter part and the upward-shifted articular process, which is indicative of a high potential in crushing of the food objects [11]. The mandibles of the monomorphic black mole voles have a relatively narrowed body, a forward-displaced coronoid process, and a ventral displacement of the articular process, which indicates the possibility of horizontal efforts during food grinding [11]. Unlike the mandibles of the animals from the monomorphic populations, those of the animals from the polymorphic population are hardly capable of the same efforts in vertical or horizontal directions.

Studying the diversity of the intrapopulation mandible shape showed that the mean distances between

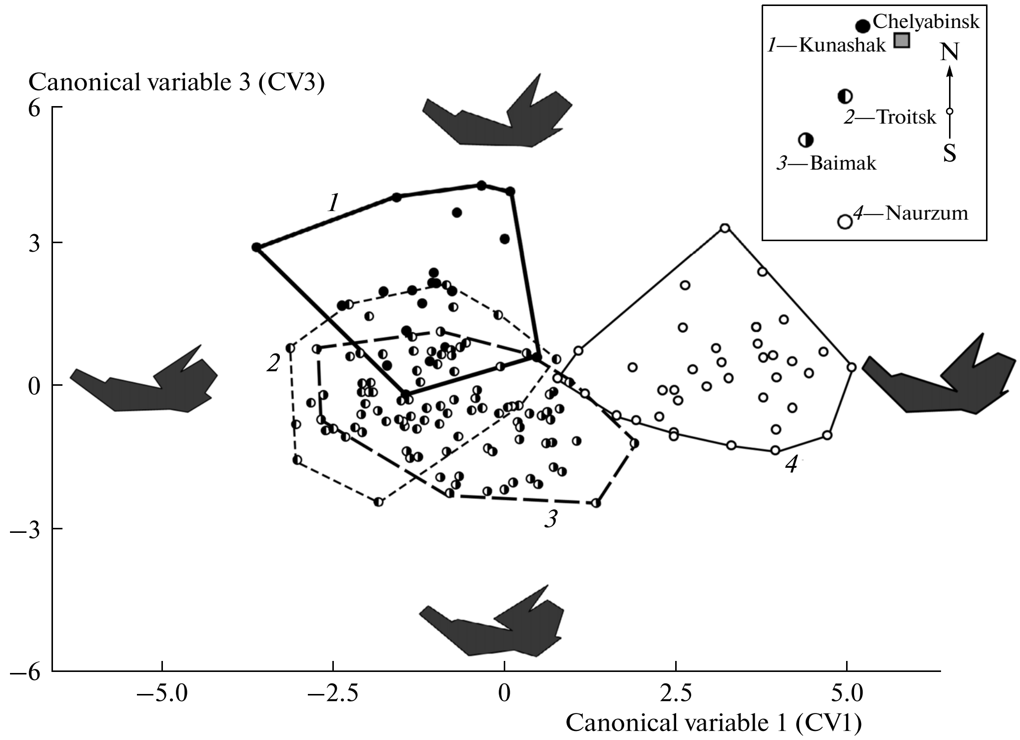

Fig. 2. Canonical analysis of Procrustes coordinates characterizing the mandible shape diversity in four geographically remote mole vole populations: *1*, Kunashakskaya; *2*, Troitskaya; *3*, Baimakskaya; *4*, Naurzumskaya (top right, geographical points of the material collection in the southern Urals). The mandible shadow configurations represent the largest changes in mandible shape along the axes.

the nearest neighbor ordinates (*MNND*) were significantly higher in the monomorphic populations (Fig. 3), where the *R* ratio was significantly greater than 1; i.e., the ordinate overscattering was manifested, whereas in the two polymorphic populations, *R* was almost equal to 1; i.e., the random Poisson scattering was observed.

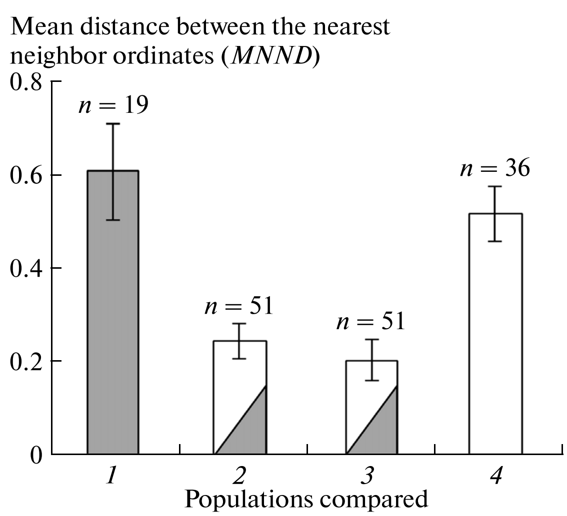

Fig. 3. Comparison of the mean distances (*MNND* ± SE) between the nearest-neighbor ordinates of the canonical axes CV1 and CV3 within the diversity polygons of the monomorphic populations *1* and *4* (Kunashakskaya (melanists) and Naurzymskaya (brown), respectively) and of the polymorphic populations *2* and *3* (Troitskaya and Baimakskaya, respectively).

Thus, in contrast to the monomorphic populations, a decrease in the morphological mandible diversity is observed in the polymorphic populations, where the developing mandible configurations have a lower potential for crushing and grinding of the food objects. The distinctions of the mandible shape among animals of different morphs are clearly manifested when different populations are compared as well as within a single polymorphic population. A kind of "division of labor" is observed between the color morphs within a population, which suppresses a general mandible shape diversity. An increase of the mandible shape diversity (*MNND*) in the monomorphic populations and a sharp diminishing of this index in the polymorphic populations well agree with the Chernov's "compensation principle" not only at the interpopulation level, but also within a single population.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research (project no. 16-04-01831a) and the Program of the Ural Branch of the Russian Academy of Sciences "Living Nature" (project no. 15-12-4-25).

REFERENCES

1. Chernov, Yu.I., *Zool. Zh.*, 2005, vol. 84, no. 10, pp. 1221–1238.
2. Salamin, N., Wuest, R.O., Lavergne, S., et al., *Trends Ecol. Evol.*, 2010, vol. 25, no. 12, pp. 692–698.
3. Sutherland, W.J., Freckleton, R.P., Godfray, H.Ch.J., et al., *J. Ecol.*, 2013, vol. 101, pp. 58–67.
4. Rohlf, F.J. and Slice, D., *Syst. Zool.*, 1990, vol. 39, no. 1, pp. 40–59.
5. Zelditch, M.L., Swiderski, D.L., Sheets, H.D., and Fink, W.L., *Geometric Morphometrics for Biologists: A Primer*, New York: Elsevier Academic, 2004.
6. Klingenberg, C.P., *Hystrix Ital. J. Mammal.*, 2013, vol. 24, no. 1, pp. 43–58.
7. Rohlf, F.J., *tpsUtil. Vers. 1.60*, New York: Depat. Ecol. Evol., State Univ. New York, Stony Brook, 2013.
8. Rohlf, F.J., *tpsDig2. Version 2.17*, New York: Depat. Ecol. Evol., State Univ. New York, Stony Brook, 2013.
9. Hammer, O., *Comput. Geosci.*, 2009, vol. 35, pp. 659–666.
10. Hammer, O., Harper, D.A.T., and Ryan, P.D., *Palaeontol. Electron.*, 2001, vol. 4, no. 1, p. 9.
11. Anderson, Ph.S.L., Renaud, S., and Rayfield, E.J., *BMC Evol. Biol.*, 2014, vol. 14, pp. 85–93.

Translated by A. Nikolaeva