Morphogenetic Effects of Drought and Nonselective Elimination in Population of Bank Vole (*Clethrionomys glareolus*) in Southern Taiga Subzone

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Abstract—Methods of geometric morphometrics have been used to estimate the influence ratio of nonselective elimination and drought factors on variation in the shape and size of the mandible in the population of bank vole (*Clethrionomys glareolus* Schreb.) in the southern taiga subzone. Nonselective elimination of rodent populations for medical and sanitary purposes was carried out in a felling site located in a focus of hemorrhagic fever, in the spring of a climatically normal year and of a dry year. The summer samples of mature young of the year from control bank vole colonies and impact colonies (i.e., recovered after deratization) in adjacent years have been compared. The results show that drought, nonselective elimination, and the interaction of these factors have significant effects on the size and shape of the mandible. Changes in its shape under drought conditions are largely due to allometry. Morphogenetic effects of nonselective elimination are highly repeatable between climatically different years. A significantly higher level of within-group morphological disparity (*MNND*) of the undisturbed control cenopopulation in a dry year has been revealed, which indirectly indicates a stronger destabilization of morphogenesis upon exposure to the autecological factor. Every ecological factor contributes to the development of specific configurations of the mandible; i.e., it induces certain changes in morphogenesis in response to aut- and synecological effects and their combination.

Keywords: population, nonselective elimination, drought, variation, mandible, bank vole, allometry, geometric morphometrics

The phenomenon of nonselective elimination as an evolutionary ecological factor that leads to the reduction in genetic diversity after a population passes through a bottleneck, followed by a random selection of the founders of a new population [1–3], has been discussed for many years [4–6], and the hypothetical mechanism of microevolutionary transformation of populations is widely used by geneticists to interpret the results of phylogeographic reconstructions of intraspecific structure and species ranges [3, 7, 8]. At the same time, the ecological and population morphological effects of the mechanism of nonselective elimination have not been studied sufficiently [4–6].

Since nonselective elimination initially leads to an abrupt decrease in abundance, which concerns not only the population of a certain species but also the entire community (in a given case, cenopopulations of sympatric rodent species), with subsequent recovery on account of immigrants and their reproduction in vacant areas, this factor acts at the cenotic rather than at the intrapopulation level. Therefore, morphogenetic changes in local species colonies recovered after nonselective elimination should primarily reflect the effect of removal of initial cenotic limitations. In other words, one should expect the manifestation of a morphogenetic response to an extremely low density of a community at the first stages of recovery and the almost complete absence of individuals of competing species in the nearest environment. Against this background, interannual comparisons make it possible to assess the manifestation of chronographic variation [2, 5, 9] determined mainly by climatic and phenological factors.

In our previous study [6], the morphogenetic responses to nonselective elimination were compared in two closely related sympatric species, the bank vole and northern red-backed vole, in different seasons of the same year. Using the methods of geometric morphometrics, we found that the dominant species (bank vole) and the subdominant species (northern red-backed vole) colonizing a vacant area had similar changes in the shape of the mandible; i.e., the two species showed parallel morphogenetic responses [6]. Seasonal changes in the shape of the mandible were also almost parallel in these species, but this between-group variation and the variation revealed by comparing voles from control and impact colonies after non-

selective elimination were differently directed in morphospace. To assess the repeatability and stability of the morphogenetic effect of nonselective elimination, it is necessary to compare its consequences in different years and compare the chronographic (climatogenic) and population cenotic components of between-group morphological variation with respect to their range and direction. It is also relevant to estimate probable changes in the process of morphogenesis in the impact area in a dry year compared to a normal year.

Therefore, the purpose of this study was to test the hypothesis of a possible combined influence of nonselective elimination and drought on morphological variation in the model population of the dominant rodent species, the bank vole (*Clethrionomys glareolus* Schreb.), in the southern taiga subzone of the Udmurt Republic. It was particularly interesting to compare the range and direction of the between-group variation associated with both factors and estimate the repeatability of morphogenetic effects of nonselective elimination in climatically different years.

MATERIAL AND METHODS

The study was performed with craniological collections from the Zoological Museum of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences. As an adequate model, we used the series of bank vole skulls collected in the southern taiga of the Udmurt Republic in July 1975 during a severe drought, which also affected other Russian regions [10], and in the previous, climatically normal year (1974). The situation was complicated by the fact that, in both years, the study area (endemic for hemorrhagic fever) was treated with rodenticides in spring to reduce the risk of human infection during timber harvesting in the focus of the disease. This resulted in nonselective elimination of rodents [6], after which the rodent community recovered due to in-migration and reproduction of animals from the surrounding areas, as well as the annual reproduction of these migrants. In July 1974 and 1975 (2 months after nonselective elimination), Evdokimov [24] collected samples of rodents from the control and impact (rodenticide-treated) site. Both sites in 1975 were displaced for 400−500 m relative to their location in the previous year. Rodents were caught with lines of 100 wooden crush traps exposed for 10 days in similar southern taiga biotopes. Unlike in the previous study [6], the 1974 material for comparative analysis consisted of only one species, the bank vole, and was collected during the same summer season. We compared the samples of mature young of the year (males and females) from control and impact bank vole colonies taken in the adjacent years. The total amount of the material studied in 1974 was 126 ind., including 98 ind. from the control and 28 ind. from the impact site; in 1975, 45 ind. (18 and 27 ind., respectively).

Variation in the mandible shape was studied by methods of geometric morphometrics [11−13] in scanned images of the left mandibular rami. Images of the mandible from the lingual side were digitized at 1200 dpi with the tpsUtil and tpsDig2 software [14, 15], and the arrangement of 15 homologous landmarks was analyzed to describe variation in the mandible shape (Fig. 1a). Variation in the mandible size in the samples was assessed based on the size of the mandibular ramus area (SM) within the contour drawn through the landmarks, which was calculated using tpsUtil [14]. This indicator was chosen because the centroid size, which is commonly used for indirect assessment, depends not only on the overall size of the object but also on the degree of indentation of its contour [12].

The configurations of the landmarks were superimposed by the method of generalized least-squares Procrustes analysis (GPA) [16] with calculation of Procrustes coordinates reflecting variation in shape. It should be noted that the methods of geometric morphometrics, which allow analysis of variation in the shape itself of digitized objects, excluding the influence of variation in their size, leave open the possibility of morphogenetic interpretation of the observed differences [12, 13, 17].

To reveal possible bias in estimates depending on operator errors or sex-related differences, landmark placements were repeated twice and two-way analysis of variance (ANOVA) was carried out. Since the differences in both cases lacked statistical significance, we combined the male and female samples and used the results of one-time landmark placement of in subsequent calculations.

To reveal possible allometric dependence [18], i.e., the dependence of changes in shape on size, we estimated the regression of the first principal component of shape (PC1) on the natural logarithm of centroid size, lnCS (Fig. 1b). The figure clearly shows the negative correlation between the PC1 and lnCS values, which is accompanied by characteristic changes in the configurations of mandible (shadow contours inscribed into deformation grids). As found by one-way ANOVA, PC1 explained 54.71% of the total variance of regression. The regression effect proved to be statistically significant: the probability of the null hypothesis of no regression was estimated using a permutation test with 10000 iterations and proved to be negligible ($p < 0.0001$). This result showed that further analysis of the material and interpretation of observed differences should be performed taking into account allometric changes in the shape of mandible due to different relative growth rates of its individual parts. Therefore, to remove the expected allometric effect [18], the Procrustes coordinates were standardized by regression to the natural logarithm of centroid size (lnCS) using the Standard7 module from the IMP software package [12].
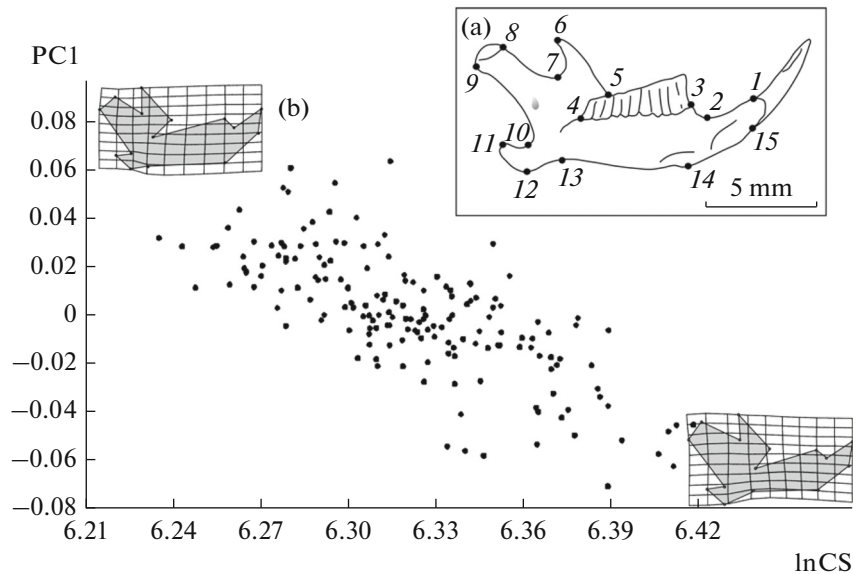
Fig. 1. (a) Locations of landmarks (1–15) on the lingual side of bank vole mandible and (b) regression dependence of the first principal component (PC1) values characterizing variation in the mandible shape on the natural logarithm of centroid size (lnCS). Top left and bottom right insets are shadow configurations of mandibles that are inscribed into deformation grids and correspond to the minimum and maximum PC1 values.

Between-group differences in the mandible shape were assessed using canonical analysis of unstandardized and standardized Procrustes coordinates. The hierarchy of between-group differences was evaluated by UPGMA cluster analysis of the matrix of generalized non-squared Mahalanobis distances (*D*).

Using the manovaboard software module from the IMP software package [12], we performed a two-way ANOVA of Procrustes coordinates to estimate the proportion of variance and the significance of influence for the factors of drought and nonselective elimination and for their interaction.

The levels of within-group morphological disparity were estimated by analyzing the pattern of mean nearest-neighbor distances (*MNND*), with standard errors, between ordinates within the variation polygon [19, 20]. The edge effect of ordinate scattering was leveled off as described [21]. The significance of differences in *MNND* between the control and impact samples was estimated by one-way ANOVA and Tukey's post hoc *Q* test.

Basic calculations and statistical analysis of the material were performed with the TPS [14, 15], PAST 2.17c [22], IMP [12], and MorphoJ 1.6d software [13].

RESULTS

Comparing the area of the lingual projection of mandibular rami (SM) in the samples collected in two climatically contrasting years, we revealed similar changes in voles from the impact sites relative to voles from the control sites (Table 1). Levene's test con-

firmed uniformity of SM variances within the samples ($p = 0.341$). This allowed us to use one-way ANOVA for the multiple comparison of the samples, which revealed significant between-group differences in this parameter ($F = 17.96$; d.f.1 = 3, d.f.2 =167; $p \ll 0.0001$). The statistical significance of differences in the average SM values between the samples was estimated by Tukey's post hoc *Q* test. The mandible area in animals from the impact groups did not differ significantly between years ($Q = 0.13$, $p = 0.9997$) but was significantly greater than in the control groups in both years ($Q = 5.27$, $p = 0.0011$ for 1974; $Q = 9.38$, $p \ll 0.0001$ for 1975). It is noteworthy that the value of this parameter was significantly lower in the control group in the dry year than in the climatically normal year ($Q = 4.25$, $p = 0.014$), which indirectly indicates that the growth of young of the year in the control site was somewhat inhibited in the drought period.

Canonical analysis of the standardized Procrustes coordinates characterizing variation in shape showed that the configuration of the mandible in voles from the control groups significantly differed between in 1974 and 1975, while voles from the impact groups were largely similar in this respect (Fig. 2, Table 2). In Fig. 2, which shows ellipsoids covering 95% of the ordinates of individuals and sample centroids with standard errors along each canonical axis, it is clearly seen that differences between the control samples are mainly manifested along the first axis (CV1), which accounts for 58.91% of the total variance. Since these samples were taken in the years with contrasting weather conditions, it can be assumed that differences

Table 1. Comparison of landmark-bounded area of mandibular ramus (SM with standard error, *SE*), between bank vole samples from control and impact sites in climatically normal year (1974) and dry year (1975)

Parameter	Samples being compared			
	1974		1975	
Site	Control	Impact	Control	Impact
Number of animals, *n*	98	28	18	27
SM ± *SE*	35985.3 ± 191.5	37844.2 ± 290.9	34486.5 ± 520.3	37798.2 ± 389.2

between them are largely due to the direct or indirect influence of drought in 1975 on morphogenesis. Shadow configurations in the figure characterize deformations of the mandible relative to its consensus configuration for each group centroid. These configurations really differ significantly between the control groups but are almost identical in both impact samples. In addition, the variation ellipsoids of both impact samples largely overlap with each other, thereby transgressing in the plane of the first (CV1) and second (CV2) canonical axes accounting for 91.75% of the between-group variance.

The UPGMA cluster analysis of the matrix of generalized Mahalanobis distances (*D*) between the sample centroids confirmed similarity between the impact samples and, on the other hand, divergence between the control samples taken in different years (Fig. 3). It
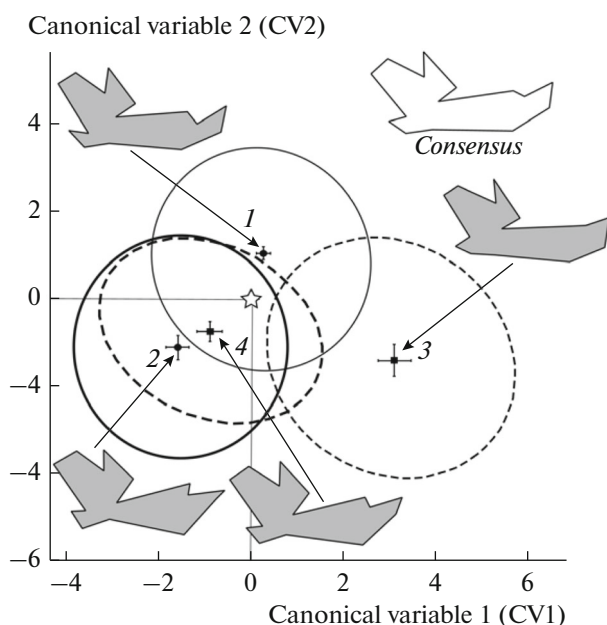

Fig. 2. Results of canonical analysis of standardized Procrustes coordinates characterizing variation in mandible shape in (1, 3) control and (2, 4) impact samples of bank voles collected in (1, 2) climatically normal and (3, 4) dry years in the southern taiga of the Udmurt Republic. Sample centroids are shown with standard errors (*SE*). Ellipsoids cover 95% ordinate scattering. Shadow configurations of mandibles correspond to the centroids, with the asterisk indicating the location of consensus configuration.

is noteworthy that the generalized Mahalanobis distance between the impact samples of different years was minimal (*D* = 1.712) and significantly lower (by 2.2-tuple) than the distance between the control samples (*D* = 3.774). In other words, the effect of drought on change in the mandible shape proved to be twice as strong as that of nonselective elimination.

In view of regression dependence of changes in the mandible shape with respect to the PC1 values on the size of their centroids (lnCS), i.e., an allometric effect, we compared the results of canonical analysis performed with the standardized and unstandardized Procrustes coordinates. The resulting estimates of between-group differences proved to be almost identical, and the coefficient of correlation between the two generalized Mahalanobis distance matrices according to the Mantel's test was $R = 0.9987$ ($p = 0.038$). Thus, the between-group differences in the mandible shape revealed by canonical analysis are highly stable and, at first sight, not directly related to the allometric effect.

To estimate the proportions of variance and the significance of the influence of nonselective elimination and drought, we carried out additional two-way ANOVA of unstandardized and standardized Procrustes coordinates of the mandible for the four bank vole samples using the manovaboard module from the IMP software package [12]. As noted above, the calculations were made taking into account two repeated landmark placements that were necessary for estimating the significance of the influence of each factor with regard to random operator error. As a result, the size of samples compared was doubled. The significance of group variances was estimated using the permutation test with 100 iterations. The results showed that the influence of operator was negligible and statistically insignificant ($F = 0.14$; d.f. = 26, 8866; $p = 1.000$).

In both variants of calculation, it was found that the factors of drought (Y) and nonselective elimination (E) and their interaction (Y × E) had a statistically significant influence on variation in the mandible shape. When analyzing unstandardized data, the proportion of group variance explained by the drought effect (Y) was estimated at 50.15% ($F = 18.93$, d.f. = 26, 8866; $p < 0.01$); according to the analysis of standardized data, this proportion was 29.48% ($F = 9.28$, d.f. = 26, 8866; $p < 0.01$). The proportion of the variance explained by nonselective elimination (E) was 33.69%

for the unstandardized data (F = 12.69, d.f. = 26, 8866; $p < 0.01$) and 36.08% for the standardized data (F = 11.37, d.f. = 26, 8866; $p < 0.01$). As estimated for the effect of factor interaction (Y × E), the respective proportions were 16.16% ($F = 6.08$, d.f. = 26, 8866; $p < 0.01$) and 34.43% ($F = 10.81$, d.f. = 26, 8866; $p < 0.01$).

Interpreting the initial unstandardized data, it can be concluded that the drought factor has a relatively higher effect on morphogenesis than the nonselective elimination factor. In turn, analysis of standardized data makes it possible to supplement this conclusion with the point that the basic mechanism of morphogenetic changes is the allometric effect (see Table 1). In contrast, nonselective elimination leads to the fixation of a certain route of morphogenesis that is associated with an increase in the mandible size (see Table 1) and reflects a narrow range of possible mandibular proportions in the spectrum of potential allometric states of the shape. Therefore, while the proportion of the variance determined by the drought factor decreased from 50 to 29% after standardization, the proportion of the variance associated with nonselective elimination remained almost the same: 33 and 36%, respectively. Another noteworthy fact is the proportion of variance explained by the interaction of factors sharply increases after standardization, from 16 to 34%. This is direct evidence that allometric effects partially counterbalance the manifestation of the interaction, thereby disguising actual developmental rearrangements resulting from different morphogenetic responses of the control and impact groups to the effect of the dry year.

As shown in our previous studies [5, 23], the *MNND* value increases significantly under unfavorable conditions, which reflects increasing ordinate scattering in the morphospace of a sample and can be interpreted as destabilization of morphogenesis. Therefore, we used this approach to estimate within-group morphological disparity in all the four bank vole samples, calculating *MNND* in two ways: based on the initial numbers of observations and after for the initial observation volumes and after random sample alignment to the minimum size, i.e., after the rarefaction procedure (Table 3). The comparison showed that the two control bank vole samples differed significantly with respect to this parameter (Tukey's *Q* test = 5.365, $p = 0.0009$ after rarefaction), with the *MNND* value reaching a peak in the dry year and decreasing to a minimum in the climatically normal year. The values of this parameter in the impact samples were almost identical (Tukey's *Q* test = 0.074, $p = 0.9999$ after rarefaction).

The comparison of *MNND* values in the control and impact samples in the dry year showed that its value was lower in the impact group (Tukey's Q test = 3.776, $p = 0.0381$ after rarefaction). Since the impact samples did not differ in this parameter, it can be assumed that the voles of this group did not exhibit a
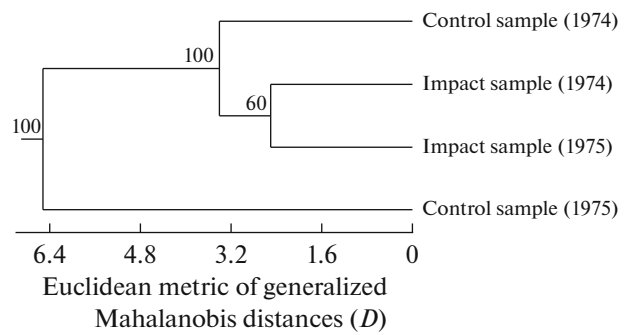

Fig. 3. Results of UPGMA cluster analysis of a matrix of generalized non-squared Mahalanobis distances (*D*) between the centroids of control and impact samples in climatically normal year (1974) and dry year (1975).

morphogenetic response to drought, unlike the control group.

DISCUSSION

Although no bias in estimates was revealed by comparing between the results of canonical analysis with the unstandardized and standardized Procrustes coordinates, these two variants of two-way ANOVA provided additional data on the general pattern of variation in the shape of mandible, revealing a significant contribution of allometric effects to between-group differences. Consequently, data standardization can be regarded not only as a method for excluding allometric effects acting as an hindrance [18], but also as a way to obtain useful alternative information providing a deeper insight into actual morphogenetic changes

Table 2. Results of canonical analysis of standardized Procrustes coordinates of bank vole mandible and values of centroids of control and impact cenopopulations in climatically normal year (1974) and dry year (1975)

Centroids of samples and estimated significance of between-group differences	Canonical variables		
	CV1	CV2	CV3
Control group, 1974	0.000509	0.003336	0.000195
Impact group, 1974	−0.00625	−0.00478	0.002415
Control group, 1975	0.01229	−0.00593	0.000366
Impact group, 1975	−0.00356	−0.0032	−0.00346
Eigenvalues	1.5718	0.8768	0.2204
Wilks' Λ-test	0.1950	0.4864	0.8689
Number of degrees of freedom	78	50	24
Proportion of variance, %	58.91	32.84	8.25
Level of significance	$p < 0.0001$	$p < 0.0001$	$p = 0.0047$

Table 3. Comparison of levels of within-group morphological disparity (*MNND* with standard error, *SE*) based on the values of the first two canonical variables (CV1 and CV2) characterizing between-group variation in the mandible shape in bank voles from the control and impact sites in climatically normal year (1974) and dry year (1975)

Samples compared, year	Initial observations	After rarefaction
	MNND $\pm$ *SE*	*MNND* $\pm$ *SE*
Control group, 1974	0.1713 ± 0.0099 ($n = 98$)	0.1943 ± 0.0302 ($n = 18$)
Impact group, 1974	0.2753 ± 0.0336 ($n = 28$)	0.2413 ± 0.0336 ($n = 18$)
Control group, 1975	0.3607 ± 0.0356 ($n = 18$)	0.3604 ± 0.0355 ($n = 18$)
Impact group, 1975	0.2456 ± 0.0204 ($n = 27$)	0.2436 ± 0.0267 ($n = 18$)

occurring under the effect of certain ecological factors.

The results of canonical analysis directly indicate that, despite the influence of drought, both impact groups newly formed upon local recovery ("reload") show a unidirectional switch in morphogenesis that is specific for this kind of synecological processes. The principal possibility of characteristic switches in morphogenesis in rodents during changes in cenotic conditions (the completeness of species composition of the community) and population abundance has been recently demonstrated in our study on a bank vole population in the Middle Urals [17].

Of particular interest are the results of comparing the values of *MNND*, the parameter independently characterizing within-group morphological disparity. Their analysis shows that within-group morphological disparity in the control site significantly increased under drought conditions. In other words, the scattering of ordinates and the average nearest-neighbor distance between them increased, providing indirect evidence for increasing destabilization of morphogenesis in this group [17]. A similar level of *MNND* values in the impact groups (despite the drought factor) is more likely to be indicative of repetitiveness in the morphogenetic response of young of the year to the recurrence of synecological conditions created every year as a complex of population and cenotic consequences of nonselective elimination. Therefore, these characteristic directional switches in morphogenesis in response to a certain population and cenotic situation can be justly regarded as historically shaped compensatory modifications of development that may be implemented within the "norm of reaction" of the species and/or its local population [17]. In turn, in the undisturbed control groups, a sharp climatic deviation such as drought also proves to be a strong stress factor of development that influences the process of morphogenesis and contributes to its switching in the direction that is historically determined by the species norm of reaction for dry years.

On the whole, the analysis of morphological variation in the bank vole mandible showed that, in the control vole group, the influence of autecological factor (drought), leads to certain retardation of growth processes, as well as significant, largely allometric changes in the mandible shape, and contributes to increase in between-group morphological disparity (i.e., induces morphogenetic destabilization). In other words, there is a characteristic switch of the morphogenetic program, and the range of morphogenetic trajectories increases. On the whole, the effect of drought as an autecological factor on variation in the mandible shape is more significant than the effect of the synecological factor of nonselective elimination. At the same time, the population and cenotic consequences of nonselective elimination prove to be more significant as an organizing, limiting, and guiding factor, leading to the recurrence of morphogenesis, acceleration of mandible growth, and more rapid maturation of animals from the impact groups [24], despite the effect of drought. The necessity for the local population of the dominant species (bank vole) to recover after nonselective elimination under conditions of the emerged "ecological vacuum" and parallel recovery of other constituent species of the rodent community is a more important stimulus causing a unidirectional switch in the morphogenetic program, compared to the draught factor that influenced bank vole morphogenesis only in the undisturbed rodent community in the control area.

CONCLUSIONS

Comparative analysis performed in this study has shown that the mandible size changes (increases) to a greater extent under the effect of the factor of nonselective elimination (i.e., when cenotic relationships change in the course of recovery of the rodent community) rather than under the effect of autecological climatic factor, i.e., drought. It can be assumed that the acceleration of the growth and maturation of voles and the directional switch in their morphogenesis in the impact area are determined by the compensatory population-ecological mechanism of the emergency recovery of cenopopulations and rodent community. In addition, a significant combined interaction of factors of drought and nonselective elimination was revealed. This interaction was reflected in the variation in the shape of mandibles, which was partially compensated by allometric effects and manifested

itself as a significant independent factor only after their preliminary exclusion. In this case, the interaction of the factors implies that different directions of variation in the mandible shape were manifested in the control and impact vole groups under the contrasting conditions of the adjacent years. Thus, sensitivity of morphogenesis to autecological factor was found to be high in the undisturbed control cenopopulations and low in the impact cenopopulations, which show a similar morphogenetic response to the effect of nonselective elimination.

The proposed approach based on the use of methods of geometric morphometrics makes it possible to supplement the population-ecological and cenotic aspects of analysis with data on changes in the course of morphogenesis of certain cenopopulations in response to the effect of autecological and synecological factors and their combination. This approach offers prospects for studies on the morphogenetic consequences of the effect of adverse climatogenic aut- and synecological factors at the level of populations and communities.

ACKNOWLEDGMENTS

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Translated by D. Zabolotny