

The Ratio of Biotopic and Interannual Variability of Bank Voles in Windfall- and Fire-Transformed Forest Biotopes of the Middle Urals

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Abstract—Manifestations of biotopic and interannual variability in the bank vole (*Clethrionomys glareolus*) were assessed in biotopes that appeared after windfall followed by forest fire in the territory of the Visim Nature Reserve (the Middle Urals). The methods of geometric morphometrics were used to compare variations in the mandible shape and morphofunctional mandibular indices in even-age youngster samples taken in climatically different adjacent years in the windfall and burnt-out areas. Significant morphogenetic differences between them and the functional peculiarities of mandibles were revealed. Interannual climatogenic variations are comparable in value with biotopic ones but are differently directed in the common morphospace. At burnt-out sites, the spread of climatogenic variability of mandibular shape is higher than in the windfall area. In a year with a rainy summer, the morphofunctional differentiation of bank voles from both biotopes associated with the trophic preferences of animals increased. High phenotypic plasticity revealed in different years in restoring biotopes directly indicates the presence in the animals of cenopopulations of historically emerged pre-adaptations of individual development as a range of adaptive modifications of morphogenesis to particular climate fluctuations and biotopic consequences of natural disasters: windfall and fire.

Keywords: windfall, forest fire, bank vole, population, variability, morphogenesis, geometric morphometrics

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INTRODUCTION

In recent years, the long-term consequences of different anthropogenic impacts on the variability of local populations of model species have been frequently assessed [1–8]. At the same time, the problem of indirect consequences of natural disasters on variability has not been sufficiently studied [9–11]. In contrast to anthropogenic and technogenic impacts, whose natural populations have hardly encountered throughout their existence, natural disasters such as hurricanes, floods, windfalls, fires, etc., on the contrary, have repeatedly affected species habitats and are considered to be natural factors. Animal species must have historically formed systemic adaptive responses to many of them at the cenotic [10], population [2, 6] and individual [12, 13] levels, which primarily affect the processes of individual development. Therefore, it can be expected that, in contrast to anthropogenic impacts, natural catastrophic events should cause quite definite developmental modification switches compensating for negative environmental changes, the

change in the vegetation composition of biotopes, and forming adaptive rearrangements of morphogenesis.

Windfall leads to dramatic changes in the initial biotopic conditions: plant communities composition is changed, numerous shelters for small mammals are temporarily formed, and wood-destroying fungi, insects, and microorganisms are attracted, which contribute to utilization of the fallen timber. Dried out wood is largely responsible for forest fires on the site of windfall in subsequent years (dry thunderstorms, anthropogenic causes). Fire leads to indiscriminate elimination of vegetation and local population of many animal species, including small mammals. Subsequently, along with vegetation recovery, small mammals enter the burnt area due to irruption from the adjacent areas unaffected by fire, and their local community is formed anew. A similar process is observed after mass nonselective deratization [11].

Previously, we have more than once found individual developmental switches in populations in response to different community completeness [14], to nonse-

lective elimination [11], and to different phases of population dynamics (different density and stress levels, respectively). Such stress-induced switches of the developmental program can manifest themselves during the recovery of local populations as an adaptive morphogenetic response to new ecological conditions.

Such effects can be found not only in rodents and are more general in nature, since they have also been revealed in another group of small mammals: shrews (Soricidae). A.V. Badyaev et al. [15, 16], have shown that the members of local communities of shrews (*Sorex*) experience severe stress in modified open biotopes after local clear-cutting of overmature forest in Montana (United States) with the subsequent burning of remaining forest debris, which increases embryonic mortality, decreases the population size, and causes abnormal and unstable development (including increased fluctuating asymmetry (FA) of the mandible). V.M. Zakharov et al. [17], also revealed a relationship between the level of FA and the dynamics of population of the common shrew in Finland: the developmental instability marked by FA increased during population declines under unfavorable conditions. Thus, the stress of individual development of small mammals under dramatic changes in the living conditions in local habitats can significantly influence the state, size, and stability of development of animal populations as a general biological factor, and its effect can increase under climatic and anthropogenic changes, as well as due to natural disasters. Further study of this problem in the model species of small mammals can potentially shed light on the problem of mechanisms of mosaic evolution [16, 18].

It would be interesting to assess the manifestations of morphogenetic effects in natural model cenopopulations under the conditions of modified natural biotopes formed after natural catastrophic impacts. It is still unclear how biotopic variability is manifested in climatically different years: are inter-annual morphogenetic changes directed similarly in cenopopulations of different biotopes or does biotopic specificity appear first and foremost? The natural model cenopopulations of rodents, which inhabit contrasting biotopes that appeared after natural disasters such as windfall and wildfire, provide an opportunity to solve these problems.

The variability in the shape and size of biological objects can be assessed by the methods of geometric morphometrics [19–23], which provide a possibility of morphogenetic interpretation of the detected differences in shape [23–25] and using this approach to assess the effects of certain climatic or biotopic conditions on morphogenesis.

The present study was aimed at analyzing the morphogenetic effects of a disturbed habitat of the bank

vole (*Clethrionomys glareolus* Schreber, 1780) in forest biotopes (mainly the changes in vegetation composition) under the influence of two natural catastrophic events: the windfall (1995) and the subsequent fire (1998) in the Visim Nature Reserve in the Middle Urals. The mandible was chosen as a research object, because the variability of its shape and size is closely related to the functional loads when treating food objects and trophism of the rodents [14, 26, 22]. As has been shown previously [11, 14, 27], the latter allows estimation of morphofunctional differences between bank vole cenopopulations associated with their trophic preferences.

Special attention was paid to the study of morphogenetic and functional responses to the contrasting environmental conditions of two adjacent years in two cenopopulations of the species inhabiting transformed biotopes: a windfall area and a pyrogenic area (overgrowing burnt-out place). In this case, it is not about the long-term morphological consequences of changes in biotopic conditions but the assessment of Darwinian definite variability and phenotypic plasticity reflecting the manifestation of characteristic modifications of morphogenesis under different environmental conditions.

MATERIALS AND METHODS

The craniological material for studying the biotopic and climatogenic effects on mandibular morphogenesis in a bank vole population is represented by the samples collected in the Visim State Nature Biosphere Reserve (Middle Urals, Sverdlovsk Region: 57°28' N, 60°00' E) in August 2003 and 2004 in the area of windfall that occurred in June 1995, and in the pyrogenic area: a burnt-out area after the wildfire in June 1998.

Animals were captured by L.E. Lukyanova by the method of standard trap lines with 100 wire traps per transect at a distance of 10 m from each other within 5 days. The traps were checked daily in the morning hours. The relative abundance was estimated in terms of 100 traps per day. Weather conditions of different years were characterized on the basis of the Visim weather station data.

The craniological collections from the Museum of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, were used in the study. All of the studied samples are represented by youngsters of both sexes (juvenile and over-wintered individuals were excluded). The studied material included 70 specimens (the area of windfallen trees (W): 11 specimens in 2003, 16 specimens in 2004; pyrogenic area (P): 33 specimens in 2003, 10 specimens in 2004).

The shape and size of the mandible were compared by the methods of geometric morphometrics using

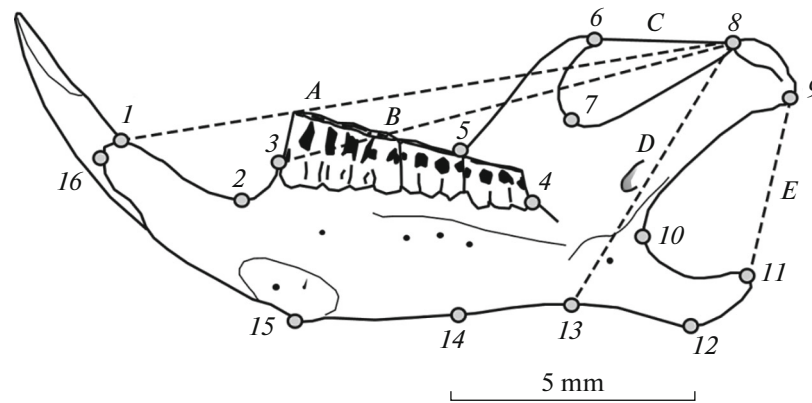


Fig. 1. The placement of landmarks (1–16) on the lingual side of the mandible of the bank vole and five initial measurements (A–E) for calculations of the mandibular morphofunctional indices (*TI*, *TM*, *MI*, *MM*, *AM*) [according to 27, 30].

photographs of the right branches of the mandible of a bank vole from the lingual side obtained with a flatbed scanner at an optical resolution of 1200 dpi. Sixteen landmarks characterizing the variability of mandible shape were placed on each image using the tpsUtil [28] and tpsDig2 [29] programs (Fig. 1).

Five measurements were made to assess the morphofunctional features of the mandible: *A*, articular–incisive; *B*, articular–molar; *C*, temporomandibular; *D*, articular–masseter; and *E*, articular–angular (see Fig. 1). These measurements were used to calculate the morphofunctional mandibular indices [see 27, 30, 31]: *TI*, temporal–incisive; *TM*, temporal–molar; *MI*, masseter–incisive; *MM*, masseter–molar; and *AM*, angular–masseter. The indices were calculated according to the formulas [23, 27]: $TI = C/A$; $TM = C/B$; $MI = D/A$; $MM = D/B$; and $AM = E/D$. Note that the *TI* and *TM* indices characterize the intensity of longitudinal cutting–chewing movements, and the *MI* and *MM* indices characterize the intensity of movements associated with gnawing, crushing, and braking of food objects. The previously proposed *AM* index indirectly characterizes the intensity of transverse chewing movements related to transverse feed grinding [26, 30].

The Procrustes coordinates were calculated using the Generalized Procrustes Analysis (GPA) [19] based on the least squares method. The centroid size (CS) indirectly characterizing the object size was calculated as a square root of the sum of the squares of the distances from the object center to each landmark [19]. Preliminary double rearrangement of the landmarks did not reveal any significant shifts in estimates due to operator errors [32].

The intergroup differences in mandibular shape were assessed by the canonical Procrustean coordinate analysis. Multiple intergroup comparisons of the centroid size and individual canonical variables were performed by One-Way ANOVA. Possible allometric

effects of the changes in mandible shape were assessed by the principal component analysis of Procrustes coordinates in each of the four samples, with estimation of regression relationships between the centroid size and PC1 values in the respective samples.

The contributions of canonical variables to intergroup differences associated with weather conditions and biotope affiliation were assessed by the multivariate nonparametric two-way analysis of variance PERMANOVA. The significance of intergroup differences was assessed by the year (*Y*) and biotope (*B*) factors, taking into account their interaction ($Y \times B$). The calculation was made in the PAST 4.06 software [33] using the Euclidean metric and the permutation test with 10,000 replicates. The effect of each environmental factor on mandible shape was assessed by the linear discriminant analysis with calculation of its significance based on Hotelling's T^2 test. Procrustes distances *d* and their significance levels were calculated pairwise in parallel.

The intragroup morphological disparity was calculated on the basis of the nearest neighbor point pattern analysis within sample variability polygons (convex hulls) [34, 35] for the first two canonical variables (CV1 and CV2). The *R* index, i.e., the ratio of the mean nearest neighbor distance (MNND) to the expected nearest neighbor distance (ExpNND) was estimated. If $R < 1$, then there is a marked ordinate clustering; if $R = 1$, there is Poisson's dispersion; if $R > 1$, there is overdispersion. The latter case with the increasing MNND was interpreted as an increase in intragroup disparity [35] and, in terms of geometric morphometrics, as an expansion of the fan of morphogenetic trajectories of individuals in the morphospace: the effect of developmental stress leading to its instability [23]. The null hypothesis of MNND equality to ExpNND with an equal density of variability polygon ordinates was assessed on the basis of the

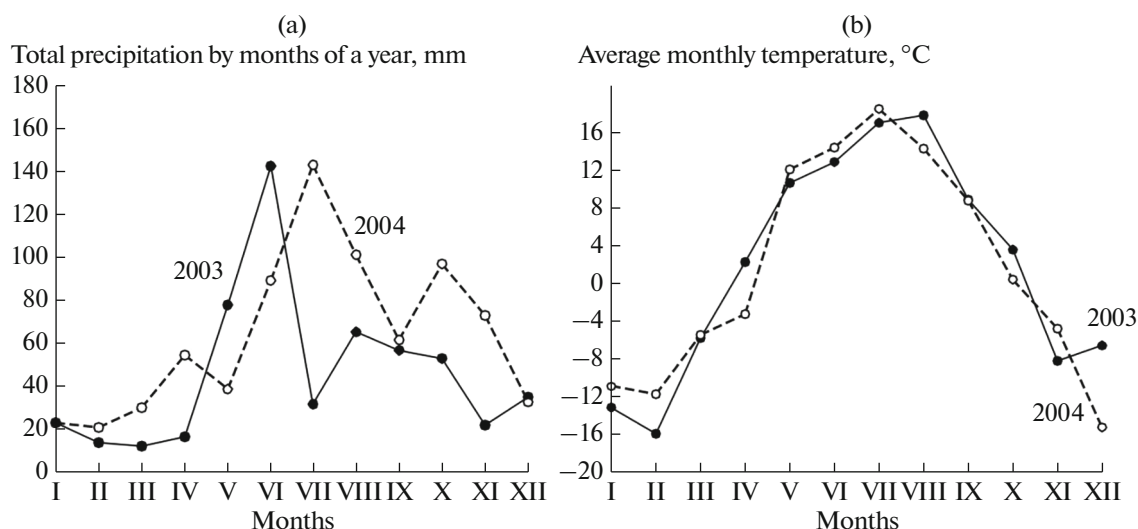


Fig. 2. The dynamics of total precipitation by months (a) and the average monthly values of temperature (b) in the Visim Nature Reserve in the Middle Urals in 2003 and 2004.

nearest neighbor Z-score [34]. The probable marginal effects of ordinate scattering for variability polygons were compensated by the Donnelly method [36].

Statistical calculations, including the methods of geometric morphometry, were performed using TPS [28, 29], MorphoJ 1.6d [22], and PAST 4.06 [33].

RESULTS

The ecological specificity of the years of comparison is due to different dynamics of precipitation in the spring and summer of 2003 and 2004, against the background of similar dynamics of the average monthly temperature (Fig. 2). In 2003, there was a significant amount of precipitation in May and June, while July and August were dry; the next year, the amount of precipitation in May was twice less, but all summer months were rainy. At the same time, the dynamics of the average monthly temperatures in these years was almost the same (see Fig. 2).

The CS of mandibles in the studied groups of youngster bank voles at different sites and in different years were similar and were not statistically different (Welch's F-test = 1.86; d.f. = 24,74; $p = 0.1063$). Sex differences in the CS of the mandible were also insignificant (Welch's F-test = 3.07, d.f. = 67,42; $p = 0.0843$) and hence the samples could be combined by sex when using CSs. The special preliminary discriminant analysis of the Procrustes coordinates of the mandibles of male and female bank voles in combined samples of different years revealed no significant differences between sexes (Hotelling's $T^2 = 67.77$; $F = 1.15$; $p = 0.3368$), which also allows further investigation in the samples combined with respect to sex. We have also shown the

absence of sex differences in mandible shape in 2003 during the high abundance phase in the neighboring Sylva population of bank voles localized 70 km southwest of the Visim Nature Reserve [14].

The canonical analysis of the Procrustes coordinates characterizing the variability of mandibular shape included the samples of 2003 and 2004 combined by sex from both the windfall and pyrogenic areas. The results of the comparison are presented in Table 1 and Figure 3. Significant differences were shown along the first two canonical variables: CV1 and CV2 (see Table 1). The differences along the third canonical axis are formally statistically significant, but only at the first level of significance, so they have poor statistical substantiation. The intergroup variance along the first two canonical axes is 85.24% of the total value, which allows us to interpret the differences along these two variables quite reliably.

The polygons of variability of all four samples occupy their own regions in the morphospace along the first two canonical variables (see Fig. 3). The sample of 2003 from the pyrogenic area is most distant from other samples.

In 2003, the cenopopulations from the windfall and burnt-out areas differed to the greatest extent. In 2004, the intergroup differences are less pronounced, but the variability polygons of samples from both cenopopulations are significantly shifted in the morphospace. This is observed to a greater extent for individuals inhabiting the burnt-out area. It is interesting to note that the directions of shifts of the polygons are significantly different in the years compared and in both cenopopulations. In Figure 3, the arrows show different directions of centroid shifts depending on

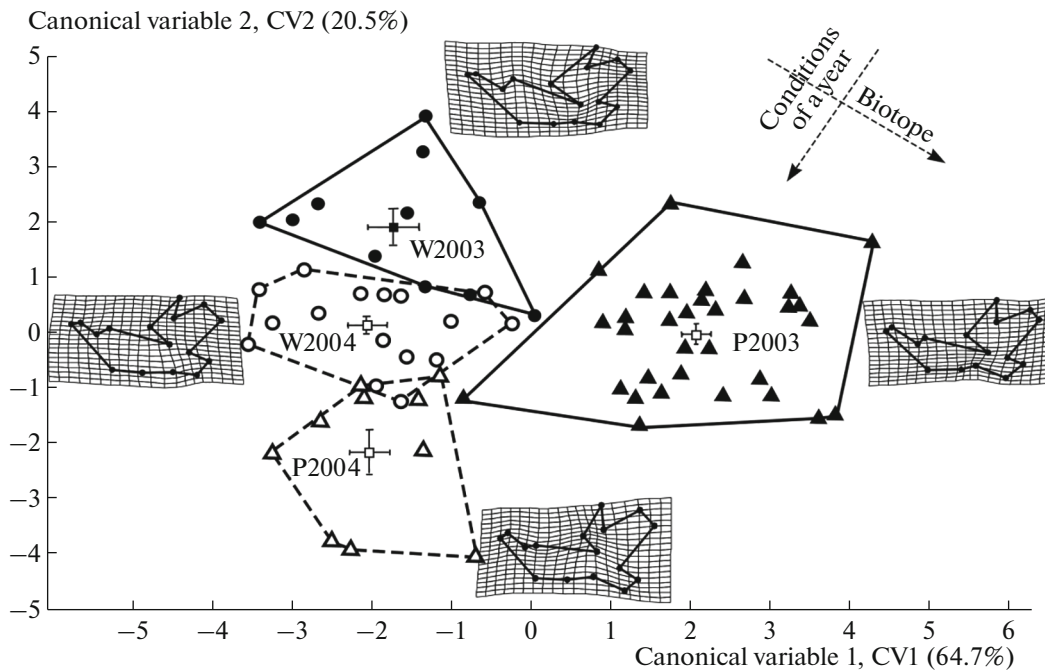


Fig. 3. The results of canonical analysis of the Procrustes coordinates characterizing variability in the shape of the mandible of bank voles in the Visim Nature Reserve in different years (2003–2004) in the windfall area (W2003, W2004) and pyrogenic area (P2003, P2004). Here and in Figs. 4 and 5, the contours of landmark configurations in the deformation grids correspond to the minimum and maximum values along the axes.

environmental conditions of different years and for samples belonging to the cenopopulations of different biotopes. The polygons of variability for both samples of 2003 from different biotopes are localized in the upper and right regions of the morphospace, while the samples of 2004 are shifted downwards and to the left. On the other hand, if we draw a secant diagonal from the lower left corner to the upper right corner, the pairs of samples from the same biotopes but of different years will be localized on different sides (the left and the right) of the common morphospace.

The multivariate nonparametric analysis of variance PERMANOVA based on the values of three canonical variables (CV1–CV3) made it possible to estimate their mutual contribution to intergroup differences taking into account the effects of two environmental factors: conditions of the year and belonging to the biotope (Table 2). The table shows that, with respect to the sum of all three canonical variables, the factors of conditions of the year (Y), belonging to the biotope (B), and their interaction ($Y \times B$) have a significant effect on intergroup variability in the mandible shape of the bank vole. The fractions of intergroup variance determined by the effects of both main factors have similar values: the effect of conditions of the year accounts for 25.6%, while the effect of biotope conditions accounts for 25.2%. Since there is almost no interaction between the factors (2.5% of variance),

the directions of intergroup variability caused by the year (Y) and biotope (B) factors are almost orthogonal in the morphospace plane, as is shown by the arrows in Figure 3. It means that they affect intergroup variability independently of each other.

The direct estimation of intergroup differences related to the effects of the above-mentioned environmental factors was performed by the linear discriminant analysis. As a result, it was established that interannual differences manifested themselves to the greatest extent (the Procrustes distance $d = 0.0162$; the generalized Mahalanobis distance $D^2 = 8.940$; Hotelling's $T^2 = 146.08$; $p = 0.0004$). The differences between the samples from two contrasting biotopes (windfall and burnt-out areas) are slightly less pronounced ($d = 0.0135$; $D^2 = 8.845$; $T^2 = 146.73$; $p = 0.0004$). The interannual (Fig. 4) and biotopic (Fig. 5) differences in mandible shape are to some extent opposite in the direction of changes in mandible configuration. The splines of mandible configurations on the deformation grids shown in the figures correspond to the extreme, the maximum (on the right) and the minimum (on the left) values of the discriminant function.

In 2003, the mandible of bank voles has a relatively wide body, a horizontally elongated angular process, and a thinned coronoid process shifted to the back (see Fig. 4). In 2004, it is characterized by greater gracility, has a relatively narrow body, an upward deflection in

Table 1. The results of canonical analysis of the Procrustes coordinates characterizing the variability in the mandible shape of bank voles in the samples of 2003 and 2004 from cenopopulations of sites of windfalls and burnt areas of the Visim Nature Reserve

Biotope, year, parameter	Canonical variable		
	CV1	CV2	CV3
Centroids of the samples ($\pm SE$)			
Windfall area, 2003	-1.646 ± 0.315	1.911 ± 0.329	-1.255 ± 0.279
Windfall area, 2004	-1.978 ± 0.243	0.137 ± 0.167	1.458 ± 0.230
Pyrogenic area, 2003	2.098 ± 0.183	-0.047 ± 0.175	0.036 ± 0.175
Pyrogenic area, 2004	-1.947 ± 0.245	-2.167 ± 0.408	-1.072 ± 0.369
Results of canonical analysis			
Wilks' Λ	0.0497	0.2491	0.6188
Eigenvalues	4.1746	1.3267	0.8523
Canonical correlation	0.87	0.71	0.62
Proportion of variance, %	64.70	20.54	14.76
Criterion χ^2	159.04	73.66	28.08
Number of degree of freedom (d.f.)	84	54	15
Level of significance, p	<0.0001	0.0002	0.0211

Table 2. Two-way nonparametric multivariate analysis of variance (PERMANOVA) of the effects of the factors of year conditions (Y), biotope (B) and their interaction ($Y \times B$) on the variability of the lingual side of the mandible of bank voles in the Visim Nature Reserve in the Middle Urals (2003–2004)

Source of variability	Sum of squares	Number of degrees of freedom, d.f.	Mean square	F	Level of significance, p
Year (Y)	0.75553	1	0.75553	36.17	0.0001
Biotope (B)	0.74473	1	0.74473	35.65	0.0001
Interaction ($Y \times B$)	0.07349	1	0.07349	3.52	0.0001
Residual	1.37970	66	0.02089		
Total	2.95245	69			

the masseter region at the junction with the angular process deflected downward, and an anterior displacement of the coronoid process. The latter was also typical of another species, the pygmy wood mouse living under unfavorable conditions [5]. When comparing the biotopic differences in the shape of the mandible (see Fig. 5), the similar variants of structure, i.e., the relatively thickened mandible body with the horizontally directed angular process and the backward shift of the coronoid process, were observed in animals from the windfall area.

Previously it has been shown [27, 28, 30] that the complex of morphofunctional mandibular indices can be used to estimate the peculiarities of rodent foraging activity. Therefore, it was interesting to assess the mor-

phofunctional features of mandibles in the rodents of both cenopopulations and their transformations in different years, which are associated with the changes in local foraging conditions.

The values of mandibular indices were compared in the same two allochronous pairs of syntopic samples of bank voles from the windfall and pyrogenic areas using the same digitized images of the lingual side of the mandibular branches. The results of the comparison are shown in Table 3 and partially in Figure 6. It follows from Table 3 that the index values in the intrapopulation groups are little different with respect to the *MI* and *MM* indices, i.e., in the degree of gnawing activity. For the *TI*, *TM*, and *AM* indices associated with different manifestations of chewing activity,

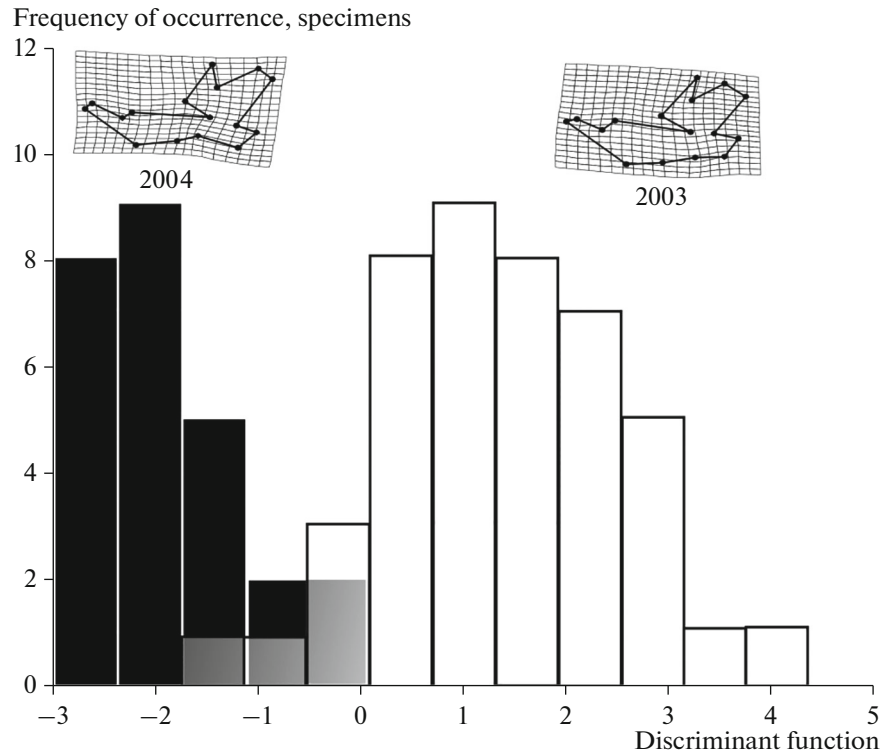


Fig. 4. The results of linear discriminant analysis of the Procrustes coordinates, which characterize the variability of mandible shape of bank voles in the Visim Nature Reserve in 2003 and 2004.

the differences are more pronounced. In particular, when comparing the intergroup differences in the variability of the *TI* and *AM* indices (see Fig. 6), the *AM* index increased significantly from 2003 to 2004 in the windfall area, i.e., the capacity for lateral chewing activity increased. At the same time, the mean values of *TI* and *TM* indices increased significantly in the pyrogenic area from 2003 to 2004, i.e., the longitudinal chewing activity increased in this biotope of voles.

In conclusion, the manifestation of intragroup morphological diversity was assessed with respect to

the *MNND* indicator in the compared cenopopulations of the bank vole in adjacent years (Table 4). Note that *MNND* was calculated based on the values of the first two canonical variables (CV1 and CV2). Since the canonical analysis characterizes the variability of the features that are least variable but maximally distinguish the samples from each other, in this case there is an opportunity to assess the stability of morphogenesis by the example of variability of the mandible shape in the morphospace for each of the compared groups of animals [see 23, 25].

Table 3. The values of morphofunctional mandibular indices with allowance for their standard errors ($\pm SE$) in the allochronous samples (2003–2004) of bank voles in the windfall area (W) and pyrogenic area (P) of the Visim Nature Reserve in the Middle Urals

Sample, year (spec.)	Morphofunctional mandibular indices				
	<i>TI</i> $\pm SE$	<i>TM</i> $\pm SE$	<i>MI</i> $\pm SE$	<i>MM</i> $\pm SE$	<i>AM</i> $\pm SE$
W2003 (11)	0.220 \pm 0.005	0.284 \pm 0.007	0.553 \pm 0.007	0.714 \pm 0.006	0.586 \pm 0.008
W2004 (16)	0.231 \pm 0.003	0.295 \pm 0.004	0.557 \pm 0.003	0.713 \pm 0.005	0.610 \pm 0.006
P2003 (33)	0.224 \pm 0.003	0.287 \pm 0.003	0.559 \pm 0.002	0.717 \pm 0.003	0.595 \pm 0.005
P2004 (10)	0.242 \pm 0.006	0.308 \pm 0.007	0.555 \pm 0.004	0.707 \pm 0.005	0.596 \pm 0.006

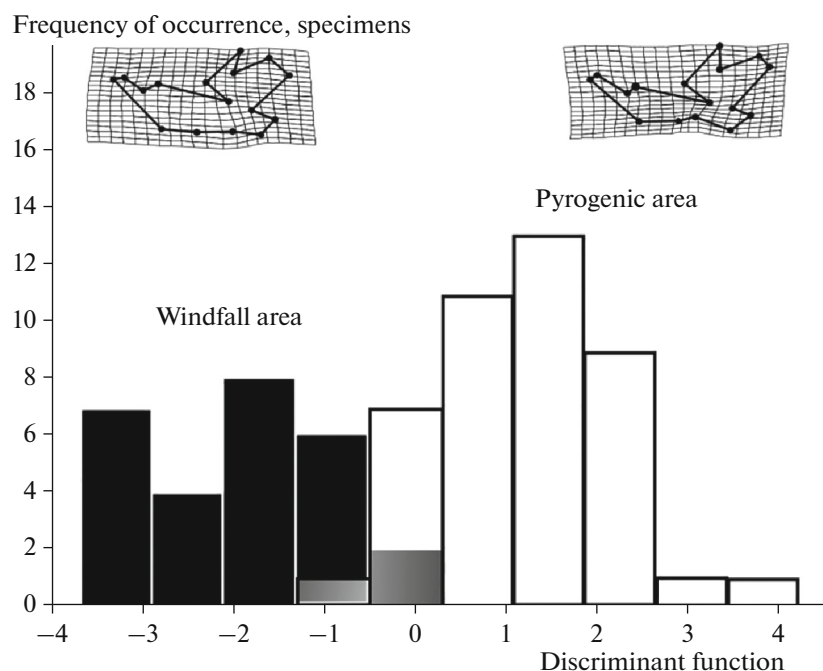


Fig. 5. The results of linear discriminant analysis of the Procrustes coordinates, which characterize the variability of the mandible shape of bank voles in the Visim Nature Reserve in the windfall and burnt-out areas.

According to the data of Table 4, the *MNND* parameter characterizing the morphological diversity of local groups of the bank vole with respect to mandible shape is significantly higher ($t = 2.1$) in animals from the windfall area than from the burnt-out area in the same year. The *R* ratio for the samples from the windfall area in both adjacent years was significantly higher than 1.0 (see Table 4), indicating overdispersion of the ordinates in the morphospace. On the contrary, in the samples from the burnt-out area in both adjacent years, the *R* ratio does not statistically differ from 1.0 (see Table 4), i.e., formally corresponds to the random Poisson distribution. Thus, the development in the burnt-out area occurs randomly within the normal range, in contrast to the windfall area, where voles were probably stressed in ontogeny.

DISCUSSION

The relatively dry summer of 2003 and rainy summer of 2004 (see Fig. 2) in the Visim Nature Reserve were responsible for the differences in the seasonal dynamics of vegetation cover in these years. Accordingly, these circumstances should have also been manifested in the dynamics of species abundance in the compared years: in 2003, the population as a whole was at the peak of abundance; in 2004, there had been some decline [37]. In 2003, the peak of the species abundance was observed in the Middle Urals and in the neighboring Sylva population in the vicinity of the village of Shigayevo near the settlement of Sylva [14].

Previously we have shown [14] that sex differences in bank vole underyearlings in the Middle Urals are almost not marked in favorable years with the high species abundance and the multispecies composition

Table 4. The intragroup morphological diversity in the allochronous (2003–2004) samples of bank voles in the two typical biotopes in the Visim Nature Reserve: windfall (W) and pyrogenic (P) areas

Sample	<i>MNND</i> ± <i>SE</i>	<i>ExpD</i> ± <i>SE</i>	<i>R</i>	<i>Z</i>	<i>p</i>	<i>n</i>
Windfall area						
W2003	0.782 ± 0.205	0.478 ± 0.015	1.63	3.51	0.0005	11
W2004	0.454 ± 0.052	0.336 ± 0.006	1.35	2.38	0.0174	16
Pyrogenic area						
P2003	0.347 ± 0.048	0.303 ± 0.002	1.15	1.45	0.1461	33
P2004	0.616 ± 0.218	0.483 ± 0.016	1.28	1.45	0.1474	10

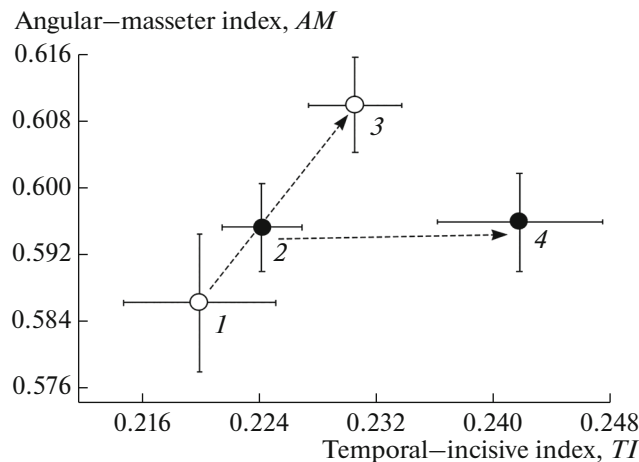


Fig. 6. The ordination of mean values taking into account standard errors (\pm SE) of morphofunctional mandibular indices *TI* (temporal–incisive) and *AM* (angular–masseter) for the allochronous samples of bank voles from the windfall area (1—2003; 3—2004) and the pyrogenic area (2—2003; 4—2004) in the Visim Nature reserve (the Middle Urals).

of the rodent community but increase in unfavorable years with the low abundance and oligospecies composition of the community, i.e., with the numerical predominance of a species in the community. We demonstrated the absence of sex differences in CS of the mandible in the same year 2003 [14] in the neighboring Sylva population at a distance of 70 km to the southwest, with a relatively high abundance. Therefore, the absence of pronounced sex differences in underyearlings of the Visim bank vole population is not a special case and indirectly indicates relatively favorable conditions for the species development in the years compared.

The calculation of linear regression of the first principal component (PC1) computed by the Procrustes coordinates relative to the logarithms of the CS showed no significant dependence between these variables for the sample from the windfall area (the proportion of predicted variability is 5.48% at $p = 0.2250$). However, regression dependence was shown for the sample from the pyrogenic area (the proportion of predicted variability is 45.62% at $p < 0.0001$). The findings directly indicate the absence of significant effects of allometry on the mandible shape variability in the windfall area but its presence in the pyrogenic area. It is possible that this allometric growth mechanism, which influences the characteristic nonlinear change in the shape of the mandible with the increase in its size, is associated with the increased migration of the group of rapidly maturing and growing youngsters to the restoring burnt-out area. Such ecological effect of habitat filtering of this group of underyearlings [38] is quite probable but requires further studies to be verified.

The previous studies of this species conducted in a similar biotope near the village of Shigayevo, the Shalinsk district of the Sverdlovsk oblast, have shown [14]

that the polygons of mandible shape variability almost do not overlap in the morphospace in case of different abundance levels, as well as complete and incomplete composition of the rodent community. The latter is consistent with the data obtained for the Visim Nature Reserve. In this case, the polygons of variability are so greatly separated from each other in the morphospace that it is possible to suggest a marked modification switch of mandibular morphogenesis in bank voles from the cenopopulations compared.

The gracile variant of the mandible with the anteriorly displaced coronoid process is predominant in the bank vole from the pyrogenic area. It has already been noted that this variation is characteristic of impact settlements of this species, as well as of the little wood mouse in anthropogenically modified habitats [5, 11]. Both variations of the mandible structure considered above (both in the windfall area and in the pyrogenic area) can be interpreted as characteristic biotopic modifications of mandibular morphogenesis of the bank vole. In other words, certain switches of morphogenesis implementing the characteristic phenotypic traits of mandibles take place in local settlements of the species in different habitats and in years with different weather conditions.

Since windfalls and subsequent forest fires are typical natural catastrophic phenomena, natural adverse environmental factors, which this forest species has encountered many times throughout its existence, the bank vole seems to be able to switch morphogenesis in a certain way at the early stages of ontogenesis. Here, it uses a historically established pool of inherited modifications adequate to the emerging environmental conditions.

In the “Annals of Nature of the Visim State Nature Biosphere Reserve for 2003” it is noted that in the windfall area of that year there was a high yield of spruce, ashberry, and hips. At the same time, the total cover of herbaceous vegetation increased up to 70–80% at the early stages of overgrowing of the burnt-out area in the reserve after the fire of 1998 (1998–2002) [39]. In 2003–2004, its area did not decrease; the fireweed, or rosebay willowherb (*Chamaenerion angustifolium*), the reed grass (*Calamagrostis obtusata*) and Langsdorf's reedgrass (*Calamagrostis langsdorffii*) were predominant in herbage composition of different years, i.e., in both years the burnt-out area had a dense grass cover (mainly represented by cereals) and had no tree layer (mature trees). It can be supposed that the above-mentioned (see Table 4) intensification of the transverse masticatory function in rodents from the windfall area in 2004 was due to the possibility of feeding on spruce seeds and berries. On the contrary, the increase in longitudinal chewing activity in animals from the burnt-out area could be explained by the feeding of bank voles mainly on parts of dominant herbaceous plants (using mostly cereals for food). The dense grass cover due to two reed grass species (*C. obtusata*, *C. langsdorffii*) and the absence of developed tree stand in these years resulted in the high availability of shelters and protective remises for the bank vole over the relatively open unforested territory of the pyrogenic area. It is possible that this additional circumstance contributed to an increase in the relative abundance of the species in this area, which performed the function of positive ecological filtering [38] and enhanced the immigration of actively growing and maturing youngsters to this biotope during their dispersal from adjacent territories.

Judging by the value of the *MNND* parameter (see Table 4), developmental instability was significantly manifested in the windfall area in both adjacent years, in contrast to the relatively stable mandibular morphogenesis in the burnt-out area (the ordinates have a random Poisson distribution, the *MNND* value is low, and the interannual differences are insignificant). The above also leads to a conclusion that ecological conditions in the restoring burnt-out area with dense herbaceous cover are not only attractive for dispersing youngsters but also relatively more favorable for their morphogenesis, which also indirectly confirms the effect of ecological filtering into this biotope of dispersing bank vole youngsters.

Earlier, A.V. Badiaev et al. [16], also found a similar effect by the example of four species of shrews of the genus *Sorex*: the level of FA of mandible measurements increased significantly in the forest biotopes modified by logging compared to the control unaffected areas. All the above indicates similar responses of different repre-

sentatives of small mammals to the developmental stress resulting from habitat transformation.

The rapid interannual changes in morphogenesis that we have revealed are probably caused by particular directed modifications in the function of the population epigenetic system [40, 41]. Similar effects associated with different manifestations of epigenetic variability in local populations of the common shrew (*Sorex araneus*) in contrasting forest biotopes of the Bialowieza Forest (Poland) were discovered previously by J.M. Wujcik et al. [42]. In particular, different biotopes were shown to have different levels of epigenetic variability estimated by a set of bilateral non-metric traits of the cranium and the mandible. We have already mentioned the study by V.M. Zakharov et al. [17], demonstrating an increase in developmental instability (epigenetic variability) of the same species on the basis of bilateral non-metric cranial traits, with its low abundance in unfavorable years. The reality of rapid epigenetic changes in the mandible of linear mice foraging the feeds of different consistency has been proven in a number of experimental studies [27, 43]. Manifestations of biotopic variability can be different in scope not only in rodents but also in insectivorous mammals. For example, for the common shrew (*Sorex araneus*) there is a known case when the effects of local conditions of different altitudinal belts of the Ural Mountains on the development of animals can be so great that the range of biotopic variability of the species settlements at different heights can exceed the morphological differences between representatives of different chromosome races inhabiting the plain [44]. During the historical formation of such altitudinal biotopic variability, there could also be initial epigenetic rearrangements that allowed the species to colonize new extreme biotopes.

The above suggests that the stress-induced epigenetic mechanisms of morphogenesis switching toward certain specific developmental modifications and their possible further transgenerational inheritance [40, 45, 46] may contribute to the development of adaptive morphogenetic changes within a short period of time. Since forest fires and clear cutting, in contrast to windfalls, are rather frequent events, further studies in a series of model species samples collected under appropriate conditions can verify the hypothesis of specificity of morphogenetic responses to particular constellations of environmental factors, which appear after fire or clear-cutting, based on the methods of geometric morphometrics. Further analysis of epigenetic variability in the same samples, with respect both to the set of bilateral non-metric skeletal traits [11, 42] and to individual and group-wise manifestation of the FA of morphological structures [2, 15, 17], is a real way to identify the characteristic phenotypes emerging in response to a particular complex of developmental

stress factors. Such studies will make it possible to assess the role of epigenetic variability in the formation of certain modifications of morphogenesis resistant to stress and enhancing the survival of these phenotypes, which can affect the stability and dynamics of the population as a whole.

CONCLUSIONS

The research results lead to the following conclusions. The biotopes that appeared in the Visim Nature Reserve after the windfall and subsequent fire are quite suitable for normal existence of the bank vole. It has been established that morphogenetic variability of the bank vole mandible is almost equally affected by both climatic (abiotic) factors and ecological features of the new biotopes (biotic). It has been shown that mandibular morphogenesis is labile and capable of switching at the early stages of development in response to the habitat conditions being formed. There are grounds to suppose that, due to common natural events such as forest windfalls and fires, the model species since its origin has accumulated a pool of potentially available developmental modifications (permissible trajectories of morphogenesis), which are adequate to the natural ecological conditions being formed both after natural catastrophic events and during the subsequent demutational succession of local communities.

Based on the resultant estimates, it can be assumed that the conditions in the windfall area are generally less favorable for the bank vole compared to the recovering burnt-out (pyrogenic) area. When the species inhabits both biotopes, characteristic configurations of the mandible are formed, which are largely related to different morphofunctional loads due to different ranges of feeds in these biotopes. During the relatively dry summer of 2003, at the peak of the species abundance in the pyrogenic area, there were great biotopic differences in morphogenesis of the mandible, but their morphofunctional specialization was absent. Perhaps, the latter was due to the availability and abundance of feeds (the yield of spruce, mountain ash, and dog rose). In 2004, at the high level of precipitation in the spring–summer period that influenced vegetation, the morphogenetic differences between inhabitants of different biotopes decreased but their morphofunctional specialization increased, being accompanied by characteristic changes in mandible configuration. In the windfall area, the function of transverse masticatory forces of the mandible increased when feeding on solid food objects, grains, and seeds. The function of longitudinal forces of the mandibles related to longitudinal cutting and chewing of vegetable food, most likely, the green parts of herbaceous plants, increased in the burnt-out area.

Thus, high phenotypic plasticity, labile morphogenesis, and the historically formed pool of potentially available developmental modifications ensure the high stability and rapid adaptation of bank vole cenopopulations to the biotopes formed under the exposure to natural catastrophic events such as windfalls and forest fires.

The studies in model rodent species have demonstrated a close relationship between the changes in local climatic and biotopic conditions and the variability of mandible shape, as well as the adaptive morphofunctional rearrangements of postnatal morphogenesis. All the above opens up the prospects of using ecomorphological approaches in combination with the methods of geometric morphometrics to obtain additional monitoring estimates of stability, adaptability, and the ecological state of cenopopulations of the model species of small mammals.

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