

Chernov's Compensation Principle and the Effect of Rodent Community Completeness on the Variability of Bank Vole (*Clethrionomys glareolus*) Population in the Middle Urals

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Abstract—Using methods of geometric morphometrics, significant differences have been revealed in manifestations of variability and morphological disparity in allochronous samples from the population of model species, the bank vole (*Clethrionomys glareolus* Schreb. 1780), in the Middle Urals at different levels of rodent community (taxocene) completeness in different years. Two states of the taxocene—oligospecific (two species) and polyspecific (five species)—and the level of relative abundance of bank voles (high or low) have been taken into account. Comparative analysis of variation in the size and shape of the mandible in same-aged (late-summer) young of the year has shown that significant morphogenetic differences exist between the animals sampled from the rodent taxocene at its different states (oligospecific and polyspecific) and, to a lesser extent, at high and low levels of abundance. The level of variation and the parameter of intragroup morphological disparity (*MNND*) in the mandible shape reach a maximum when the community has a reduced composition and decrease to a minimum when its composition is complete (i.e., in the oligo- and polyspecific taxocene). A parallelism is observed in the manifestation of morphofunctional changes of the mandible in male and female voles under conditions when the taxocene has high abundance and oligospecific composition or low abundance but polyspecific composition. Different morphogenetic responses of the population to oligo- and polyspecific composition of the community are considered as a compensatory increase of morphological disparity in the dominant species (the bank vole) under conditions of incomplete composition of the taxocene and low population density, in accordance with Chernov's ecological compensation principle.

Keywords: rodents, community composition, variability, morphological disparity, Chernov's compensation principle, geometric morphometrics

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Differences in the completeness of species composition of a biotic community should have an effect on the manifestation of variation of its constituent species [1–6]. According to the ecological compensation principle formulated by Chernov [7], when some of closely related species are absent from the community, other species should take on the functions of the absentees, which may result in a compensatory increase in their abundance, variability, and morphological disparity. This principle usually manifests itself in the increasing abundance of dominant species against the background of abrupt decline of subdominant species in unfavorable years and also in the compensatory numerical strength of individual taxonomic groups and species in northern or mountain communities upon reduction of their species diversity [7]. Therefore, it is of interest to study manifestations of variability in a certain species in ecologically different years, at different completeness of the community in which this species is usually numerically prevalent.

Based on Chernov's compensation principle, we hypothesize that the variability and morphological disparity of the dominant species should increase when the abundance of other species drops abruptly and the community becomes mono- or oligospecific, and, conversely, these parameters should decrease to a minimum when the species composition of the community is complete and the numerical prevalence of the dominant over other species is relatively low [6]. In the latter case, subdominant species perform their own functions in the community, and the compensatory increase in the morphological disparity of the dominant is “not required.”

The search for such natural ecological models potentially makes it possible to solve the problem of integrity of taxocene, a community comprising closely related species [8]. If there is no interdependence of variability between the species components of the taxocene, then its functional integrity as a fragment of biotic community is not manifested. Therefore, this

ecomorphological problem is of fundamental nature, pertains to the field of evolutionary ecology, and its analysis may help to gain an insight into the phenomenon of diffuse coevolutionary rearrangements in the morphology of species within the community [2, 3].

Long-term research on manifestations of variability and morphological disparity in the same local population of the dominant species, with regard to changes in its abundance and completeness in the composition of the taxocene, is conducive to solving this problem. Geometric morphometrics appears to be the most effective methodological tool for this purpose [9–11], the more so that allows morphogenetic interpretation of the observed differences [12, 13].

In this study, methods of geometric morphometrics were used in an attempt to estimate the actuality of Chernov's compensation principle as applied to the pattern of morphological variability and disparity in the population of dominant species, the bank vole (*Clethrionomys glareolus* Schreb. 1780), in the Middle Urals in years with different levels of animal abundance and completeness of the species composition of rodent taxocene: from overdominance of a single species (*mono-* or *oligospecific* taxocene) to the stage where this species is a member of multicomponent community (*polyspecific taxocene*).

MATERIAL AND METHODS

The study was performed with the series of bank vole skulls selected from the collections kept at the Zoological Museum of the Institute of Plant and Animal Ecology (Ural Branch, Russian Academy of Sciences). Three allochronous samples were included in analysis. They consisted of animals trapped at different phases of abundance and different species completeness of the rodent taxocene in a birch–aspen forest near Shigaevo, 5 km northwest of the village of Sylva (Shalinskii raion, Sverdlovsk oblast) (below, referred to as the Sylva population). The first sample (48 males and 32 females, 1988) was collected by A.G. Vasil'ev when the bank vole was highly abundant and almost absolutely dominant, i.e., under conditions of oligospecific community composition (97 bank voles and 2 northern red-backed voles per 200 trap–days). The second sample (45 males and 39 females, 2003) was collected by N.L. Dobrinskii at high abundance and polyspecific composition of the rodent community, which included five species: the bank vole, northern red-backed vole, root vole, field vole, and pygmy wood mouse. The abundance of bank vole in this case was close to that of subdominant northern red-backed vole. The third sample (16 males and 16 females, 2006) was taken by Dobrinskii when the abundance of rodent community was low but its species diversity was relatively high, as in the previous case. All these samples were collected in late summer and comprised young of the year of approximately the same age (juveniles were excluded).

Variation in the shape of the mandible as a structure directly connected with the trophic function of species in the community was used as a morphological model. It was assumed that this function should vary depending on the level of species completeness of the community.

Analysis was performed by methods of geometric morphometrics [9–11], which allow variation in the size and shape of test objects to be evaluated separately. They also provide the possibility to visualize changes in shape of these objects [14]. Electronic images of the right mandibular rami were digitized with the tpsUtil and tpsDig2 software [15, 16] and analyzed with respect to the arrangement of 16 landmarks characterizing variation in the mandible shape. Moreover, it has been shown [17, 18] that morphofunctional features of the mandible shape associated with differences in the mechanics of food processing can be estimated from the indices based on four measurements: A , B , C , D (Fig. 1). We calculated four indices proposed by Anderson et al. [17]: temporal-incisor (TI) = C/A ; temporal-molar (TM) = C/B ; masseter-incisor (MI) = D/A ; and masseter-molar (MM) = D/B .

Variation in the mandible size was evaluated indirectly, from the centroid size (CS) in pixels calculated as the square root from the sum of squared distances from the center of the image to each of the landmarks. The superimposition procedure was performed by the method of generalized orthogonal least-squares Procrustes analysis (GPA) [9]. The resulting Procrustes coordinates (characterizing variation in the mandible shape) were used for between-group comparisons by means of canonical analysis. The hierarchy of between-group relationships was evaluated using UPGMA cluster analysis.

Morphological disparity within the groups was evaluated by nearest neighbor point pattern analysis within the variation polygon [19]. In accordance with this method, index R was calculated as the ratio of the observed mean nearest neighbor distance ($MNND$) between ordinates to the theoretically expected mean distance (μ) calculated for the variation polygon based on the Poisson distribution. The null hypothesis that the observed $MNND$ is equal to μ value for random point scattering at the same density of ordinates within the polygon was evaluated using the nearest neighbor test (Z score) [19]. The method proposed by Donnelly [20] was used to eliminate the edge effect of ordinate dispersion within the limited polygon.

Index R characterizes the model of ordinate dispersion: $R < 1$ indicates ordinate clustering; $R = 1$, Poisson dispersion; and $R > 1$, overdispersion. In the last case ($R > 1$), an increase in $MNND$ value in analysis of variation in the shape of test objects may be interpreted as evidence for increasing morphological disparity within groups [21] or, in terms of geometric

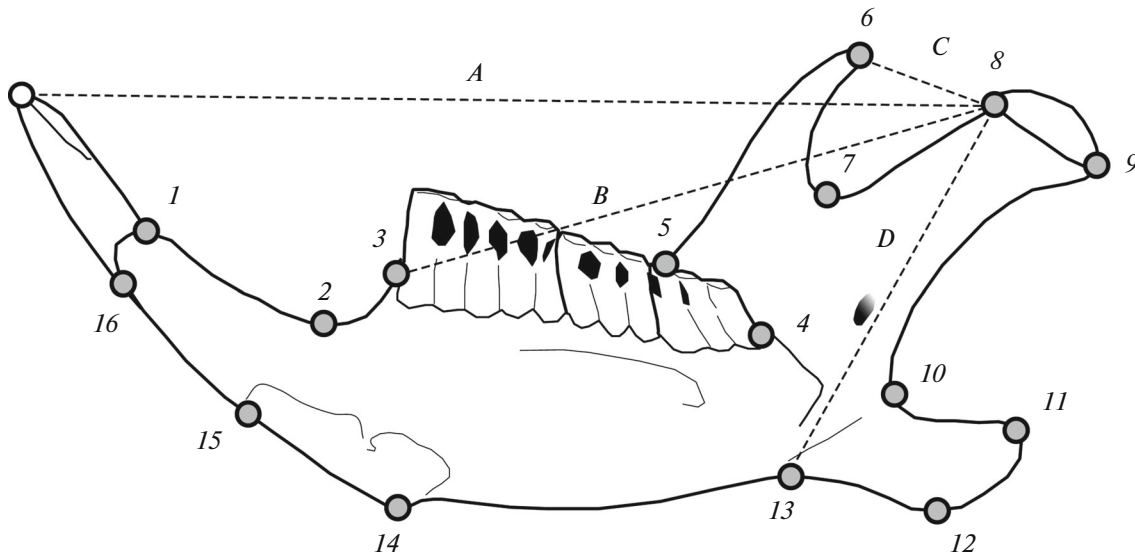


Fig. 1. Locations of 16 landmarks characterizing variation in the shape of the bank vole mandible on its lingual side and measurements (*A–D*) for calculating mandibular morphofunctional indices: (*A*) incisor, (*B*) molar, (*C*) temporal, (*D*) masseter (according to [17]). The unnumbered landmark (top left) was used as accessory for making measurements.

morphometrics, for a wider “fan” of individual morphogenetic trajectories within the sample [8, 22, 23].

All calculations by methods of geometric morphometrics and other multivariate ordination and classification methods were performed with programs MorphoJ 1.6d [11] and PAST 2.17c [24].

RESULTS AND DISCUSSION

A comparison of the centroid size (CS) characterizing the size of the mandible in allochronous samples from the bank vole population revealed significant differences between the sample taken in 1988, when the rodent community had an oligospecific composition, and the samples taken in 2003 and 2006, when its composition was polyspecific. The CS (i.e., the mandible size) was the smallest in animals from the 1988 sample (965.34 ± 2.32 ; $n = 80$) and the largest in animals trapped in 2003 at high abundance and species completeness of the community (977.70 ± 2.65 ; $n = 84$). An intermediate value (974.17 ± 5.33 ; $n = 32$) was determined for the 2006 sample taken when animal abundance was low but the level of community completeness was high. The Mann–Whitney *U*-test with Bonferroni correction confirmed statistical significance of the difference between the maximum and minimum CS values ($U = 2441$, $Z = 3.022$; $p = 0.0025$). The 2003 and 2006 samples did not differ in CS ($U = 1302$, $Z = 0.256$; $p = 0.7977$) and were therefore pooled into a single sample characterizing the polyspecific state of the taxocene. Its comparison with the 1988 sample confirmed that CS (the mandible size) was significantly greater in bank voles from the

taxocene in the polyspecific state ($U = 3459$; $Z = 3.024$; $p = 0.0025$).

Between-group comparisons of variation in the mandible shape in three samples of bank voles from the Sylva population were made using canonical analysis of Procrustes coordinates. As seen in Fig. 2, the polygons of variation within the samples show almost no overlap in the common morphological space. Between-group differences along the axes of both canonical variables (CVs) are statistically significant. The between-group variance along the CV1 axis amounts to 75% of the total variance and reflects differences between the samples corresponding to the polyspecific state (on the left) and oligospecific state of the taxocene (on the right). Differences along the CV2 axis (25% of the total variance) concern the level of population abundance, with the 2006 sample (low abundance) being at the top and the 1988 and 2003 samples (high abundance) at the bottom.

To take into account specific manifestations of sex-related differences in different years, canonical analysis of Procrustes coordinates characterizing the variability of mandible shape in allochronous samples of bank voles from the Sylva population was performed in a different variant, with the samples divided into males and females. The results are shown in Fig. 3 and Table 1. The proportion of between-group variance along the axes of the first four CVs amounts to 96.6%, with the CV1 axis accounting for 56.74% (data statistically significant). As seen from Fig. 3, the variance along this axis, as in the first variant, reflects significant differences in the shape of mandibular rami between samples from the taxocene in the polyspecific state (2003 and 2006) and in the oligospecific state (1988): cen-

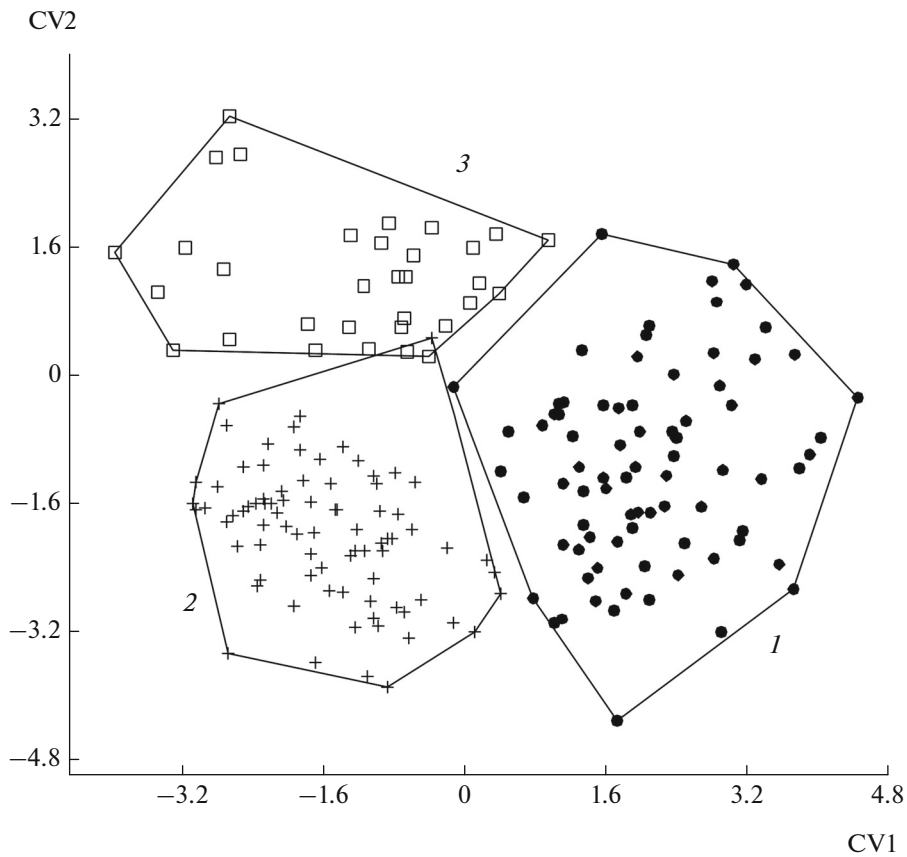


Fig. 2. Results of canonical analysis of Procrustes coordinates characterizing variation in the shape of the mandible in three allochronous samples of bank voles from the Sylva population, the Middle Urals: (1) 1988, (2) 2003, (3) 2006.

troids of the former are located on the left, and those of the latter, on the right.

Between-group differences along the CV2 axis are related to phases of high and low animal abundance (top and bottom centroids, respectively). This axis accounted for 19.19% of the total between-group variance. Along the CV3 axis (12.5% of the total variance), opposite directions of differences between males and females in the mandible shape were revealed for the 2003 sample versus the 1988 and 2006 samples, while the direction of these differences (the sign of the centroids) in the latter two samples was the same (Table 1). Sex-related differences manifested themselves mainly along the CV4 axis ($r_{sp} = 0.54$, $p < 0.0001$), which accounted for 8.22% of the total variance. As follows from Table 1, the values of male centroids on this axis are negative, while those of female centroids are positive. Between-group variation along the CV5 axis lacks statistical significance.

The shaded contours of the mandibular rami in Fig. 3 characterize the extreme states of their shape corresponding to the minimum and maximum values along the CV1 and CV2 axes. It can be seen that they markedly differ between the animals that developed at different levels of species completeness of the commu-

nity or animal abundance. In particular, bank voles from an oligospecific community show an increase in the size of the coronoid and angular processes and the relative tooth row length. The opposite situation is observed when the community has a polyspecific composition: the coronoid process is shortened and displaced anteriorly, with the relative lengths of the tooth row and angular process decreasing as well. The level of animal abundance also has an effect on variation in the mandible shape: at high abundance, the coronoid process is displaced anteriorly, and the body of the mandible becomes thinner and more gracile; at low abundance, the depth of the mandible body markedly increases, and the coronoid process is displaced posteriorly. It should be noted, however, that the results obtained by visualizing variation in the mandible shape should not be taken literally, because they reflect only general tendencies of variation in the configuration of landmarks [14]. In comparisons of allochronous samples, all pairwise between-group differences in the mandible shape were statistically significant ($p < 0.001$).

UPGMA cluster analysis of the matrix of generalized Mahalanobis distances (D) between allochronous samples of male and female voles revealed segregation

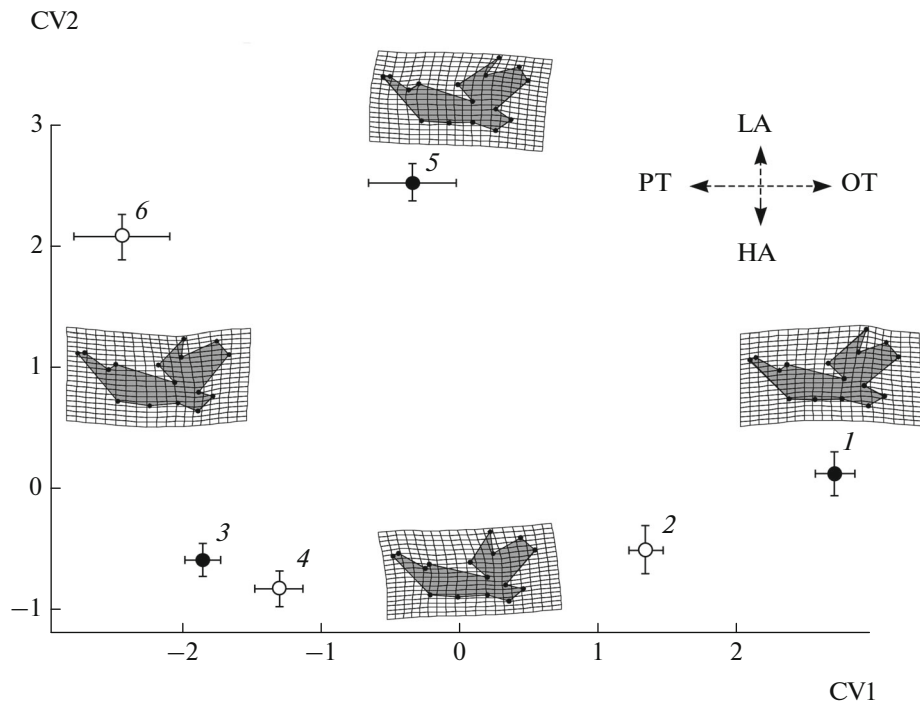


Fig. 3. Results of canonical analysis of Procrustes coordinates characterizing variation in the shape of the mandible in male (odd numbers) and female (even numbers) bank voles in three allochronous samples from the Sylva population, the Middle Urals: (1, 2) 1988; (3, 4) 2003; (5, 6) 2006. Centroids of the samples are shown with standard errors. Arrows indicate directions of between-group variation: PT, polyspecific taxocene; OT, oligospecific taxocene; LA, low abundance; HA, high abundance.

of animals trapped in 1988 (both males and females) from the two other samples (Fig. 4). In turn, the cluster formed by the 2003 and 2006 samples divided into two subclusters comprising males and females trapped in the same year. It should be noted that in 1988 and 2003, when the abundance of animals was high, differences in the mandible shape between males and females were relatively low, almost half those at low abundance in 2006.

Thus, at different completeness levels of the rodent taxocene and abundance levels of its constituent model species (the bank vole), these animals in allochronous samples show differently directed morphogenetic changes. Such switches in morphogenesis in response to the current population-cenotic situation may be regarded as compensatory modifications of development that the species has acquired during the period of its existence. They may be related to different morphofunctional requirements for the structure of the mandible as a food-procuring and processing organ under different ecological conditions. In our previous study, similar compensatory modifications of the mandible structure were revealed in the impact plot during natural recovery of bank vole population after rodent extermination in a natural focus of hemorrhagic fever in the Udmurt Republic, against the background of high abundance and species completeness of the rodent taxocene in the control plot [23].

To verify the probable functional nature of these morphogenetic changes, we calculate four morpho-

functional indices (Table 2) that allow indirect estimation of the biomechanical efficiency of food processing from the proportions of the mandible (see [17]). In the allochronous samples of both males and females, the greatest between-group differences were revealed in the values of temporal-incisor (*TI*), temporal-molar (*TM*), and masseter-molar (*MM*) indices.

Coupled between-group differences in the *TI* and *MM* indices are illustrated in Fig. 5. Their values proved to be the lowest in males and females from the 2003 sample, which was collected at high population abundance and complete species composition of the taxocene. Sex-related differences in these values lack statistical significance. In contrast, sex-related differences in the 1988 and 2006 samples were well manifested: in both cases, *TI* values were higher in males, whereas *MM* values were higher in females, especially in the 2006 sample. Sex-related differences in the mandibular indices were most clearly manifested in the 2006 sample taken at a low abundance of the bank vole population in the polyspecific rodent taxocene. The specific mandible configuration observed in males is typically formed as a result of intensive horizontal jaw movements during mastication, which lead to an increase in the *TI* index [see 17], while the mandible structure formed in females reflects prevalence of the vertical occlusal pressure used for chopping up the food, which is accompanied by an increase in the *MM* index.

Table 1. Canonical analysis of Procrustes coordinates characterizing variability of mandible shape in male and female bank voles in three allochronous samples from the Sylva population, the Middle Urals

Sample (year, animal sex) and parameters of differences	Canonical variables				
	CV1	CV2	CV3	CV4	CV5
	Sample centroids				
1988, males	2.531	-0.076	-0.127	-0.417	0.417
1988, females	1.425	-0.325	0.763	1.010	-0.619
2003, males	-1.914	-0.367	1.074	-0.619	0.071
2003, females	-1.338	-1.124	-1.296	0.237	-0.045
2006, males	-0.136	2.431	-0.867	-1.025	-0.859
2006, females	-1.702	2.267	0.007	1.365	0.762
	Parameters of differences				
Eigenvalue	3.3834	1.1442	0.7437	0.4903	0.2018
Percentage of variance	56.74	19.19	12.47	8.22	3.38
Wilks' Lambda	0.034	0.149	0.320	0.558	0.832
χ^2	601.53	338.47	202.70	103.73	32.72
Number of degrees of freedom	140	108	78	50	24
Significance level	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p = 0.1101$

Comparisons of the mean values of the above indices allow the conclusion that the morphogenetic response observed at the low density of bank vole population in the polyspecific taxocene and at its high density against the background of almost complete absence of other species in the taxocene is similar and

manifests itself in the unidirectional increase of sex-related differences in the shape and specific morpho-functional features of the mandible.

The samples were also compared with respect to within-group morphological disparity by calculating the mean nearest neighbor distances (*MNND*)

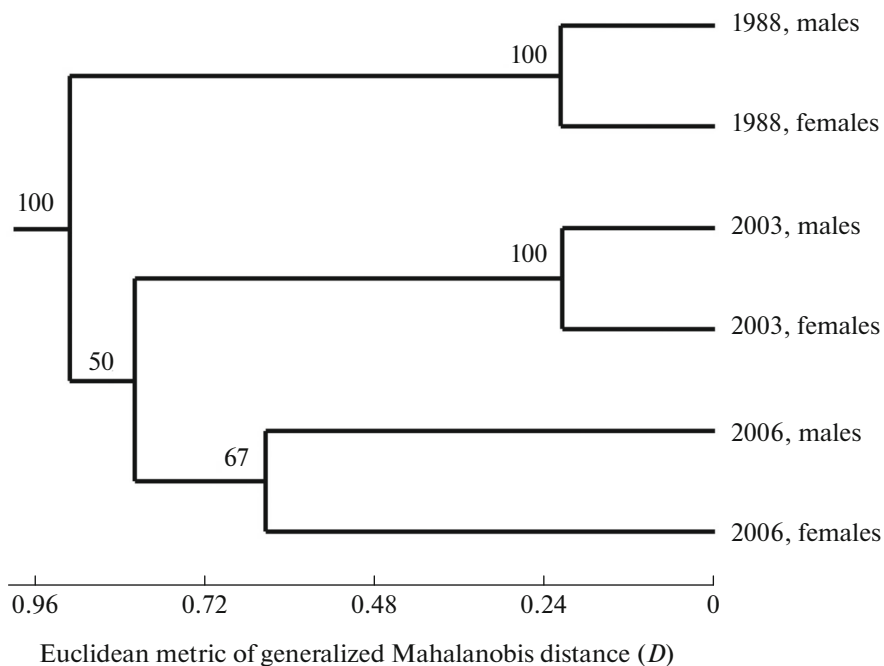
**Fig. 4.** Results of UPGMA cluster analysis of a matrix of generalized Mahalanobis distances (*D*) between samples of male and female bank voles taken in different years.

Table 2. Morphofunctional mandibular indices of male and female bank voles in three allochronous samples from the Sylva population, the Middle Urals

Sample (year, animal sex)	Mandibular indices				<i>n</i>
	<i>TI</i>	<i>TM</i>	<i>MI</i>	<i>MM</i>	
1988, males	0.217 ± 0.003	0.278 ± 0.003	0.691 ± 0.002	0.886 ± 0.002	48
1988, females	0.204 ± 0.003	0.263 ± 0.004	0.692 ± 0.003	0.891 ± 0.002	32
2003, males	0.205 ± 0.004	0.262 ± 0.005	0.692 ± 0.004	0.886 ± 0.004	44
2003, females	0.203 ± 0.006	0.259 ± 0.007	0.693 ± 0.004	0.885 ± 0.005	40
2006, males	0.221 ± 0.004	0.283 ± 0.005	0.691 ± 0.003	0.884 ± 0.003	16
2006, females	0.207 ± 0.005	0.269 ± 0.005	0.692 ± 0.005	0.898 ± 0.004	16

between ordinates and their variance on the basis of CV1 and CV2 values (see Fig. 2). The results (Table 3) show that both *MNND* and its variance in the population of the dominant species (bank vole) sharply increased in 1988, when its abundance was high and the taxocene was in the oligospecific state, and decreased in 2003, when its state was polyspecific, with the abundance of this population being also high. The *MNND* value at low population abundance and the polyspecific state of the taxocene in 2006 was significantly higher than in 2003 (the same level of species completeness but high population abundance), but its variance remained low. Thus, it can be concluded that the level of morphological disparity in the Sylva population is the highest under conditions of high animal abundance and oligospecific composition of the taxocene (1988), intermediate at low abundance

and polyspecific composition of the taxocene (2006), and the lowest at high animal abundance in the polyspecific taxocene (2003). It is noteworthy that the variance of *MNND* between ordinates reaches a maximum when the taxocene has oligospecific composition but is relatively low when its composition is polyspecific, whether the population abundance of the dominant species is high or low. In other words, this parameter can be used, with some caution, as a potential indicator of instability in the functioning of the rodent taxocene.

Comparisons of the empirical and theoretically expected nearest neighbor distances between ordinates (*MNND* and μ) showed that overdispersion of ordinates manifested itself in the 1988 sample ($Z = 3.872$, $p < 0.0001$), unlike in the 2003 and 2006 samples where a Poisson distribution was observed (Table 3). Index *R* also reflected this effect: for the 1988 sample, $R = 1.396$ (significantly higher than 1.0), while its values for the 2003 and 2006 samples are close to 1.0. Thus, the above results also confirm that morphological disparity in the population of the dominant species sharply increases when the species diversity of the taxocene drops but this species reaches high abundance, indicating that conditions for it are relatively favorable. Morphological disparity in this population also increases and remains high (the nearest neighbor distances between ordinates are consistently large) under conditions of its low abundance and polyspecific composition of the taxocene. Finally, when the abundance of the dominant species is high and the composition of the taxocene is polyspecific, both the level of morphological disparity and its variance are low (the nearest neighbor distances between ordinates are consistently small), in accordance with our hypothesis.

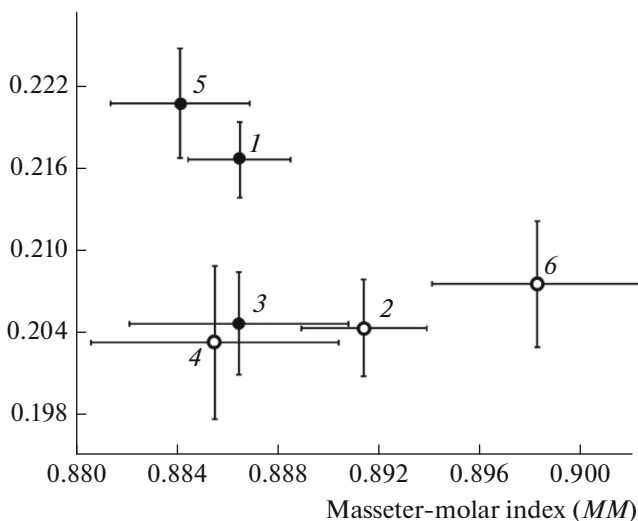
Temporal-incisor index (*TI*)

Fig. 5. Coupled comparison of mean values (with standard errors) of the masseter-molar and temporal-incisor morphofunctional indices of the mandible in male (odd numbers) and female (even numbers) bank voles in three allochronous samples from the Sylva population, the Middle Urals: (1, 2) 1988; (3, 4) 2003; (5, 6) 2006.

CONCLUSIONS

In the classic study by Jablonski and Sepkoski [4], the authors metaphorically formulate the concept of close interrelationship between species within communities, defining it as “ecological locking.” Cavender-Bares et al. [25] conclude that the level of variabil-

Table 3. Comparison of parameters characterizing between-group morphological disparity in the mandible shape based on values of the first two canonical variables in allochronous samples of bank voles from the Sylva population, the Middle Urals

Parameter	Samples		
	1988	2003	2006
Empirical mean nearest neighbor distance between ordinates (<i>MNND</i>)	0.50 ± 0.05	0.28 ± 0.03	0.37 ± 0.03
Theoretically expected mean distance between ordinates calculated on the basis of Poisson distribution (μ)	0.36 ± 0.05	0.25 ± 0.06	0.32 ± 0.05
Variance of nearest neighbor distances between ordinates	0.089 ± 0.011	0.036 ± 0.004	0.030 ± 0.004
Z score (nearest neighbor test)	3.872	1.421	1.496
Probability of random dispersion (<i>p</i>)	0.0001	0.1553	0.1346
Index of ordinate dispersion pattern (<i>R</i>)	1.396	1.146	1.154
Number of individuals after rarefaction (<i>n</i>)	32	32	32

ity of species cohabiting in the same community depends on their mutual influence on each other. The results of our study are in agreement with these views. They show that the size of the mandible in the model species, the bank vole, is significantly smaller if the species composition of rodent community is impoverished, compared to animals from the community with polyspecific composition. Under conditions of different species completeness of the taxocene and different abundance levels of the bank vole as its constituent species, differently directed morphogenetic changes are observed in animals from allochronous samples. The range of morphological disparity within the population increases both upon reduction in the species composition of the taxocene and at low population abundance (in the latter case, to a smaller extent), i.e., in the ecological situation that is adverse or not optimal for the community. When this situation is favorable (i.e., at high species diversity of the taxocene and abundance of the dominant species), the level of morphological disparity remains low. Therefore, *MNND* can serve as an indirect indicator of adverse ecological conditions for both the population of the dominant species and the taxocene as a whole [26].

When the species composition of the taxocene is impoverished, the main load of utilizing the resources of cenosis falls on the dominant species (in our case, the bank vole). This leads not only to compensatory switches in morphogenesis (manifested as changes in the shape and functional properties of the mandible in males and females) but also to an abrupt increase in the level of morphological disparity, which involves the realization of a fan of morphogenetic trajectories that are atypical under other ecological conditions. At low abundance and/or incomplete species composition of the taxocene (adverse and/or nonoptimal conditions), modification of morphogenesis takes place in the population, leading to change in the shape of the mandible and emergence of distinct sex-related differences in its structure, which have certain morpho-functional significance. At such a constellation of

population-cenotic conditions, males and females in the population behave almost like distinct biotypes or morphs specialized for consuming different food resources.

Therefore, the results of this study may be directly interpreted as an example of the compensation effect in the dominant species [7, 23], which takes upon itself the functions of other species when they are absent from the community or population abundance is low.

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