

Coupled Biotopic Variation in Populations of Sympatric Rodent Species in the Southern Urals

V. N. Bol'shakov, A. G. Vasil'ev, I. A. Vasil'eva, Yu. V. Gorodilova, and M. V. Chibiriyak

*Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences,
ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia*

e-mail: vag@ipae.uran.ru

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Abstract—Using geometric morphometric methods, coupled biotopic variation in the shape of the mandible was revealed in cenopopulations of two sympatric rodent species, the pygmy wood mouse (*Sylvaemus uralensis* Pall., 1811) and bank vole (*Myodes glareolus* Schreb., 1780), in the Southern Urals. As a rule, heterospecific pairs from syntopic samples synchronously taken in cenopopulations of the two species inhabiting contrasting local biotopes displayed similar (parallel and unidirectional) morphological changes. In an unusually arid year, however, differently directed morphogenetic responses were revealed in young of the year from cenopopulations of the two species in broadleaf forest outliers surrounded by steppe vegetation on tops of the Guberlya low hills. Such a local disturbance of the coupled pattern of biotopic variation in *S. uralensis* and *M. glareolus* cenopopulations under ambient conditions sharply deviating from the optimum may be evidence for depletion of their coevolutionary adaptive potential, which is estimated from the range of ecological conditions at which parallelism in the variation of sympatric species is observed.

Keywords: evolutionary ecology, geometric morphometrics, biotopic variation, rodents, sympatric species, cenopopulations, coevolutionary potential

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Evolutionary and ecological trends of coupled variation in the same homologous morphological structure in different sympatric species forming cenoses have not yet been studied sufficiently (Pianka, 1981; Giller, 1988; Vasil'ev et al., 2010; Mouillot et al., 2013). Meanwhile, this aspect is extremely important for resolving a number of problems in evolutionary ecology, because it allows advancement from the population to the cenotic level of research, i.e., makes it possible to consider population–cenotic manifestations of variation (Vasil'ev et al., 2010; Violle et al., 2012; Bukvareva and Aleshchenko, 2013; Bol'shakov et al., 2013). As shown in our previous studies, the coupled morphological variation of sympatric species under different habitat conditions allows their coevolutionary potential to be evaluated: the wider the range of ecological conditions at which parallelism in the variation of sympatric species is observed, the higher the potential of these species for coevolution (Bol'shakov et al., 2013; Vasil'ev et al., 2013). We have indeed observed parallelism of intergroup variation in the majority of situations with coupled morphological variation (in geographic, chronographic, and technogenic forms) in pairs of model rodent species codominant in the community under conditions of their cohabitation under different ecological conditions. It has appeared important to reveal the situation where the coevolutionary potential of the compared species

under altered environmental conditions will be depleted; i.e., parallelism in their morphogenetic responses will not be manifested.

According to our hypothesis, such a possibility may arise when comparing biotopic variation in sympatric rodent species that populate ecologically contrasting biotope in a year with climatic conditions strongly deviating from the norm. It should be reminded that biotopic variation is usually understood as the kind of variation that is accounted for by the influence of specific abiotic and biotic conditions of the environment on the development of even-aged conspecific individuals inhabiting different biotopes (Shvarts, 1969, 1980; Bol'shakov and Vasil'ev, 1975).

The assessment of coupled biotopic variation in sympatric species implies the use of material collected in the same local biotopes during a short period of time (necessarily in the same year and season). The degree of concordance in morphological variation between two or more species in the community can be most rigorously estimated by relying on the comparison of homologous elements in the shape of the objects included in analysis, rather than on their conventional linear measurements.

New digital methods of geometric morphometrics (GM) have been developed during the past few decades, which make it possible to analyze variation in

the shape of objects regardless of their size (Rohlf and Slice, 1990; Zelditch et al., 2004; Klingenberg, 2011). A special advantage of GM is that it deals with coordinates of landmarks (homologous anatomical elements) whose pattern is a reliable criterion for assessing coupled variation of taxonomically close sympatric species in a local community (taxocene). Moreover, GM allows visualization of transformations in the shape of objects, thereby making it possible to directly interpret manifestations of variability in morphogenetic terms (Zelditch et al., 2004; Drake and Klingenberg, 2010; Klingenberg, 2011).

In this study, GM methods were used to analyze coupled biotopic variation in cenopopulations of two sympatric rodent species—the pygmy wood mouse *Sylvaemus uralensis* Pall. and bank vole *Myodes glareolus* Schreb.—in the Southern Urals under conditions of an unusually arid year in order to evaluate their coevolutionary potential. Attention was focused on comparison of the extent and directions of morphogenetic responses manifested in biotopic variation of mandible shape in pairs of *S. uralensis* and *M. glareolus* cenopopulations from contrasting biotopes.

MATERIAL AND METHODS

Coupled biotopic variation in sympatric species can be adequately evaluated only on condition of parallel comparison between syntopic samples synchronously taken from biotopes with contrasting environmental conditions. As a natural model complying with this requirement, we selected three local communities that included cenopopulations of *S. uralensis* and *M. glareolus* from the vicinity of the city of Kuvandyk, Orenburg oblast (the material was collected in the second half of June 2010). Only the group of even-aged animals (young of the year) was included in analysis: 75 ind. of *S. uralensis* (30 from the floodplain, 30 from the forest strip, and 15 from forest outliers) and 69 ind. of *M. glareolus* (30, 5, and 34, respectively). However, the relative abundance of species and local taxocenes (per 100 trap–days) was evaluated with regard to all age groups.

Local communities of the two species inhabited biotopes with contrasting ecological and orographic conditions: a floodplain forest in the Sakmara River floodplain (GPS coordinates: 51°28.939' N, 57°17.122' E); wind protection forest strip of elm, acacia, and ash-leaved maple along the railway (51°28.547' N, 57°17.167' E); and broadleaf forest outliers 1.5–3 ha in area on hilltops in the western part of the Guberlyra low-hill range (51°28.082' N, 57°17.044' E). The animals in these biotopes were trapped in parallel, with the distance between trap lines varying from 0.7 to 1 km.

The two species are often codominant in the rodent community. The bank vole dominated in the floodplain forest; the pygmy wood mouse, in the forest strip; and both species were almost equally abundant in the forest outliers.

These biotopes differed in absolute elevation, forming a gradient from 202 m a.s.l. in the floodplain to 221 m in the forest strip, and 372 m in the forest outliers. Moisture supply decreases along its gradient, being the highest in floodplain forest along the Sakmara River and the lowest in forest outliers on hilltops surrounded by steppe vegetation, where signs of aridization are observed. There also is a gradient of above-zero temperatures: in 2010, when the spring–summer season was unusually hot (up to 42–44°C), average air temperatures in the morning and during the day in forest outliers were 2–4°C higher than in the floodplain and 1–2°C higher than in the forest strip. The hot weather enhanced the contrast in ambient conditions between these biotopes.

The term “cenopopulation” is traditionally used in botanical and geobotanical research (Rabotnov, 1969; Uranov, 1975; Lyubarskii, 1976). Zoologists use terms such as population, micropopulation, colony, community, deme, or, more neutral, locality and group. In our case, local populations of sympatric rodent species could be referred to as micropopulations (Shvarts, 1969, 1980), because all territorial groups confined to different neighboring biotopes are potentially interconnected and exchange migrants. On the other hand, there is relative territorial and landscape isolation of such biotopes, and their rodent communities are spatially separated.

We propose to apply the term “cenopopulation” to micropopulations of sympatric animal species territorially confined to the same biotope (in broad sense, biocenosis), thereby emphasizing their cenotic unity. This term not only indicates that a given group belongs to the local community but also suggest that its representatives potentially acquire common properties (a certain pattern of variation) that differ from certain properties of local cenopopulations in other biotopes.

Since it is difficult to study all species comprising a given community, researchers often concentrate on fragments of communities that consist of taxonomically close sympatric species, or taxocenes, performing a certain function in the community (Hutchinson, 1957; Chernov, 2008; Vasil'ev et al., 2010). A local rodent taxocene is usually confined to a certain biotope (from a landscape facies to a specific tract of land) and comprises cenopopulations of sympatric species, which allows such groups to be used for accomplishing the task set in this study.

Comparisons were made of the right mandibular rami of *S. uralensis* and *M. glareolus*. This object was chosen in view of previous data that the shape of the mandible in rodents varies depending on habitat conditions. The rami were imaged from the lingual side with a pad scanner at a resolution of 1200 dpi. Variation in the shape of the ramus was evaluated based on the pattern of 16 landmarks (Fig. 1) which were digitized using the tpsDig2 program (Rohlf, 2013a). All images were digitized for the second time, and preliminary analysis showed that the displacement of shape

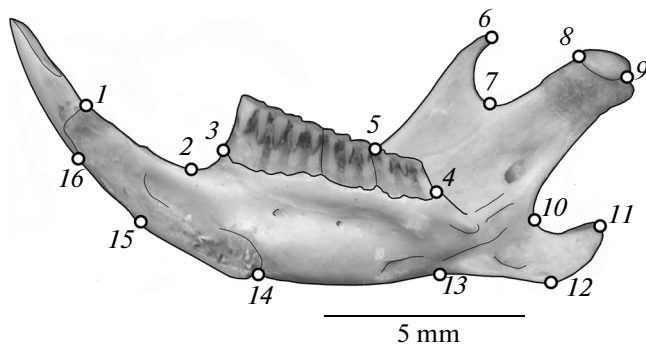


Fig. 1. Positions and designations of homologous markers on the lingual side of the right mandibular ramus in *S. uralensis* and *M. glareolus*: (1) posterodorsal alveolar edge of lower incisor; (2) area of greatest depression of dorsal mandibular edge near diastema; (3) anterior alveolar edge of m1; (4) posterior alveolar edge of m3; (5) point of crossing of projection of crown edge of m3 with anterior edge of coronoid process base; (6) coronoid process apex; (7) point of the greatest depth of coronoid–articular notch; (8) anterior edge of condyle of articular process; (9) posterior edge of condyle of articular process; (10) point of the greatest depth of articular–angular notch; (11) posterior edge of angular process; (12) lower edge of angular process; (13) point of the greatest depth of symphyseal–angular notch; (14) posterior edge of symphyseal tubercle; (15) anterior edge of symphyseal tubercle; (16) posterodorsal alveolar edge of lower incisor.

estimates between the two variants were very small (no more than 1.5% of variance) and usually lacked statistical significance. Therefore, it is sufficient to digitize the images only once.

The data were analyzed by the method of generalized least squares Procrustes superimposition. Centroid size (CS) characterizing the size of a digitized object was calculated as the square root of the summed squared distances of each landmark from the center of the image (Rohlf and Slice, 1990). Procrustes coordinates were used for canonical analysis of the mandible shape. Statistical calculations, including two-way ANOVA, were made with applications program packages TPS (Rohlf, 2013a, 2013b), MorphoJ (Klingenberg, 2011), and PAST (Hammer et al., 2001).

RESULTS AND DISCUSSION

In the arid year 2010, the relative abundance of animals (ind./100 trap–days) was relatively high in all local taxocenes of rodents, averaging 35.3 ± 2.8 in the forest strip, 27.1 ± 0.8 in the floodplain forest, and 22.3 ± 1.7 in the forest outliers. Its values for the two dominant species (*S. uralensis* and *M. glareolus*) and subdominant yellow-necked mouse (*Sylvaemus flavicollis*) differed significantly between the biotopes (Fig. 2). Thus, *M. glareolus* dominated in the floodplain forest and forest outliers, while *S. uralensis* was subdominant in these biotopes but dominated in the forest strip. The yellow-necked mouse occurred sporadically in the

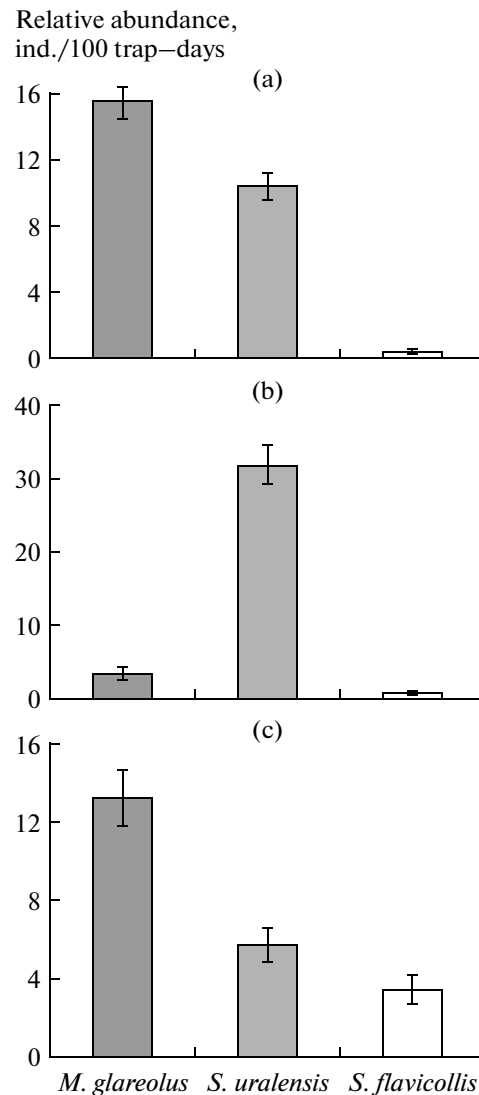


Fig. 2. Comparison of relative abundance of three rodent species most frequently trapped in three contrasting biotopes in the vicinity of Kuvandyk (2010): (a) forest in the Sakmara River floodplain, (b) forest strip, (c) forest outliers. Vertical lines show standard errors.

floodplain forest and forest strip, but its abundance in the forest outliers was only slightly inferior to that of *S. uralensis*.

Special comparisons revealed no significant sex-related differences in the shape of the mandible in biotopic samples of either *S. uralensis* or *M. glareolus* from different cenopopulations, confirming previous data that sex-related differences in young of the year of these two species are very small and usually lack statistical significance (Gorodilova, 2011; Zыkov, 2011; Fominykh, 2011). Hence, materials from males and females in each sample were pooled.

Two-way ANOVA for CS of the mandible (which is proportional to the mandible size) depending on animal species and biotope confirmed the significance of

Table 1. Results of two-way ANOVA for variation in the size of centroid (CS) for the mandible of young of the year *M. glareolus* voles and *S. uralensis* mice from three contrasting biotopes of Orenburg oblast

Variation source (factor)	Cum of squares	d.f.	Mean square	F	Significance level (<i>p</i>)
Species (<i>S</i>)	118000	1	118000	158.2	≤0.0001
Biotope (<i>B</i>)	16700	2	8348	11.19	≤0.0001
Interaction (<i>S</i> × <i>B</i>)	22420	2	11210	15.03	≤0.0001
Within-group	98450	132	745.9		
Total	221100	137			

not only species-specific but also biotope-specific differences and also revealed a statistically significant interaction of these factors (species × biotope), providing evidence for interspecific differences in the growth of animals in different biotopes (Table 1).

Since growth processes indirectly reflect the adequacy of environmental conditions (Mina and Klevezal, 1976), it appears that the floodplain forest along the Sakmara River is the most favorable biotope for *M. glareolus* (animals from this cenopopulation are larger), while conditions for *S. uralensis* are more favorable in the forest strip and forest outliers (i.e., in biotopes with low moisture and even signs of aridity).

The calculated Procrustes coordinates were used to perform canonical analysis of the mandible shape in three pairs of syntopic and synchronous samples of *S. uralensis* and *M. glareolus* from the three biotopes. The results are shown in Fig. 3. Data discrimination along the first canonical axis was based on obvious differences in taxonomic features and trophic specialization of the two species and, hence, was excluded from consideration. Biotopic variation was revealed along the second and third axes. In samples from the floodplain forest and forest strip, the mean values of canonical variables in both species showed parallel changes; i.e., the centroids of these samples were located close to each other in the morphospace formed by the sec-

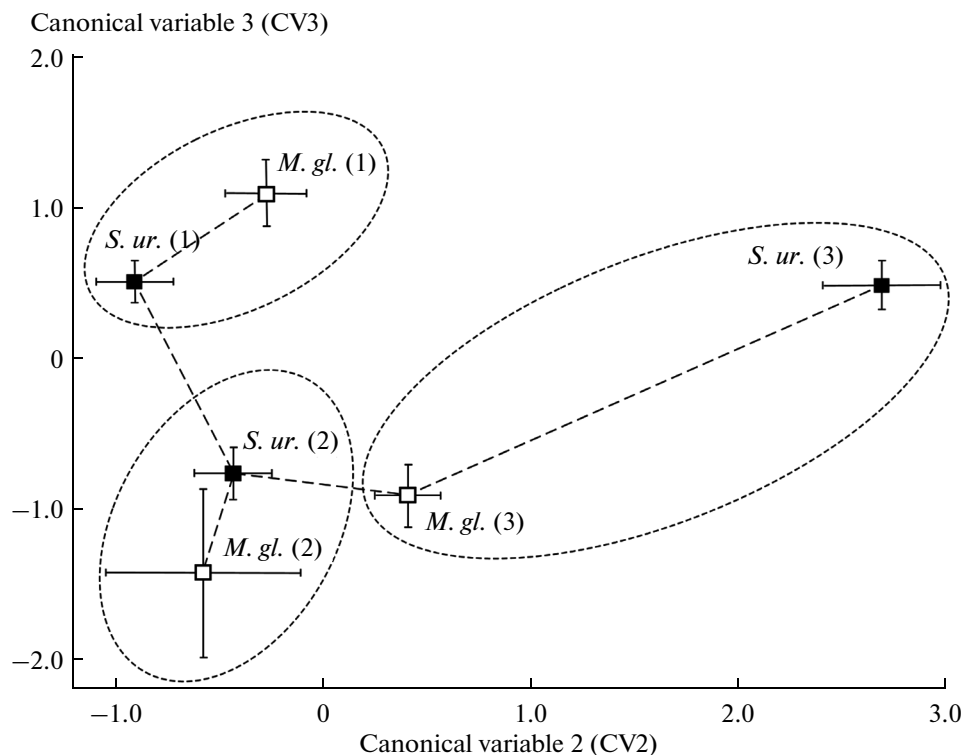
**Fig. 3.** Results of canonical analysis for coupled biotopic variation in the shape of the mandible in sympatric *S. uralensis* mice (*S.ur.*) and *M. glareolus* voles (*M.gl.*) in three contrasting biotopes: (1) floodplain forest, (2) forest strip, and (3) forest outliers. Dashed lines show the minimum spanning tree between sample centroids (with standard errors along canonical axes); ellipsoids enclose centroids for cenopopulations of local taxocenoses.

Table 2. Evaluation of correctness in object classification by means of canonical analysis for the shape of the mandible in comparisons of syntopic populations of *S. uralensis* (1–3) and *M. glareolus* (4–6) from three contrasting biotopes of Orenburg oblast

Species		<i>S. uralensis</i>			<i>M. glareolus</i>			Total in row	Correctness, %
	Biotope/cenopopulation	1	2	3	4	5	6		
<i>S. uralensis</i>	1 – river floodplain	23	7	0	0	0	0	30	76.67
	2 – forest strip	3	25	2	0	0	0	30	83.33
	3 – forest outliers	0	0	15	0	0	0	15	100.00
<i>M. glareolus</i>	4 – river floodplain	0	0	0	26	1	3	30	86.67
	5 – forest strip	0	0	0	0	5	0	5	100.00
	6 – forest outliers	0	0	0	3	2	24	29	82.76
	Total in column	26	32	17	29	8	27	139	84.89

ond and third canonical variables. However, changes in the mandible shape revealed in samples from the forest outliers were not parallel: the centroid of *S. uralensis* sample (*S.ur.3*) proved to be displaced toward the top right corner of the plot, while the centroid of *M. glareolus* sample (*M.gl.3*) was located close to that from the forest strip (*M.gl.2*).

Thus, *S. uralensis* showed a specific morphogenetic response to conditions in the forest outliers, while such a response in *M. glareolus* was almost absent. Differences in the direction of morphological changes were indicative of the effect of factor interaction (species \times biotope). Two-way ANOVA of variation in the mandible shape along the second and third canonical axes confirmed that the effect of this interaction is significant both in *S. uralensis* and *M. glareolus* ($p < 0.001$). It was also found that individual values along these axes did not correlate with CS of the mandible ($p < 0.05$); i.e., intergroup biotopic variation in the mandible shape was not related to the allometric effect.

The results of classification and attribution of individuals to “their own” samples based on canonical analysis of the mandible shape confirm the existence of biotopic variation and show that a characteristic pattern of variation in the mandible shape can be used as a criterion for assigning an animal to the proper cenopopulation with a probability of about 85% (Table 2).

CONCLUSIONS

Biotopic variation in cenopopulations of *S. uralensis* and *M. glareolus* manifested itself in two relatively moist biotopes, but such parallelism of morphogenetic changes, which usually leads to similar modifications of the mandible shape in both species, was not observed in the forest outliers. Our working hypothesis explaining this phenomenon is that the higher morphogenetic plasticity of *S. uralensis* and its specific morphogenetic response to conditions of development in the forest outliers (the most arid of the three

biotopes) are accounted for by the evolutionary preadaptation of this species to living under more arid conditions, compared to *M. glareolus*.

The present-day range of *M. glareolus* lies mainly in the temperate zone, while that of *S. uralensis* extends to arid regions of Central Asia. Hence, *M. glareolus* appears to be historically incapable of such morphogenetic modifications in response to climate aridization. Comparing the ranges of the two species, it may be concluded that the level of their sympatry is the highest in the temperate zone. The range of *S. uralensis* is generally displaced southward relative to the *M. glareolus* range and covers areas located much farther south than the southernmost groups of the latter species. This suggests that the upper temperature limit within the ecological preferendum of *S. uralensis* is higher than in *M. glareolus*. It is probable that exposure to high ambient temperature in the forest outliers had a threshold effect on morphogenesis of *S. uralensis* mice in the corresponding cenopopulation and triggered a specific subprogram of development that had been set up when conditions in habitats of this species were more arid. This is indirectly confirmed by the fact that the shape of the mandible in these animals is most close to that in conspecific mice from the Karkarala population in central Kazakhstan (Gorodilova, 2011).

Such a morphogenetic response of *S. uralensis* in the forest outliers could probably take place only in the arid year 2010, since it was not observed in 8 other years characterized by normal climatic parameters. Therefore, this case is an exception from the rule of parallelism in the geographic and chronographic variation of *S. uralensis* and *M. glareolus* which is indicative of their high coevolutionary potential (Bol'shakov et al., 2013). The fact of violation of this rule is evidence that the coevolutionary potential of the two codominant species in the forest outliers was depleted in the arid year.

Thus, increased aridity and abnormally high temperatures during the spring–summer season of 2010 resulted in modification of morphogenesis in

S. uralensis young of the year, involving change in the mandible shape to the pattern characteristic of conspecific populations inhabiting arid regions of Central Asia. It is probably the high developmental plasticity and capacity for rapid adaptive modifications under effect of high temperatures that provided for the survival of this species in arid regions of Central and Western Asia.

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