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Variability of Northern Isolated Outpost Population of Lesser White-Toothed Shrew *Crocidura suaveolens* (Pallas, 1811) (Eulipotyphla: Soricidae) in the Southern Urals as an Invasive Synanthropic Species

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Abstract—Geometric morphometrics methods were used to study the manifestations of various forms of variation in the outpost, isolated from the main range of the northern population of the lesser white-toothed shrew *Crocidura suaveolens* (Pallas, 1811) of the Southern Urals using the example of variation in centroid size (CS—centroid size) and the shape of the mandible. Chronographic variability and sexual dimorphism in the Chelyabinsk outpost population were compared with geographical variability in comparison with two remote Kabardino-Balkarian and Krasnodar populations from the central part of the range. The assessment of developmental stability was carried out by analyzing the pattern of the nearest neighboring points of the within-group morphospace (*MNND*—mean nearest neighbor distance). The nutritional features of shrews were assessed by morphofunctional mandibular indices. In the outpost population of the lesser white-toothed shrew, in the years contrasting in climatic conditions (2005–2006), changes in the age structure and sex ratio, instability in the development of mandibles, and changes in their shape and functions during mechanical processing of feed were detected. Significant chronographic variation of the mandible was revealed, which was greater than the range of sex differences in the outpost population. The geographical variation between the isolated Chelyabinsk and two remote populations from the center of the range exceeded the scope of chronographic variation in the Chelyabinsk outpost population. The index of within-group morphological disparity (*MNND*) of mandibles in males and females samples (with the exception of females of 2005) is significantly higher than the expected random values, which proves the manifestation of destabilization of morphogenesis of both sexes in the outpost population in both years. In the rainy year of 2006, the values of the *MI*, *MM*, and *AM* mandibular indexes in males and females differ significantly, indicating that they use different components of the diet during this year, which can reduce trophic competition between the sexes. The revealed high phenotypic plasticity and synanthropic properties of the species make it possible to predict the possibility of further invasion of the lesser white-toothed shrew to the north of the Southern Urals with climate warming, which is important to consider owing to its ability to transmit vector-borne diseases dangerous to humans.

Keywords: *Crocidura suaveolens*, outpost population, variability, mandible, geometric morphometrics, the Southern Urals

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INTRODUCTION

The problem of the formation of rapid adaptations of invasive species to new environmental conditions is one of the most pressing environmental issues in modern ecology (Sakai et al., 2001; Zherikhin, 2003; Dgebuadze, 2014; Saul and Jeschke, 2015). In recent decades, along with global climate change and increased anthropogenic impact on biota, the mass invasion of alien species, leading to changes in the composition and functioning of communities, has been of particular importance in the emergence of biotic crisis phenomena (Parmesan, 2006; Zalasiewicz et al., 2010; Steffen et al., 2011). Many researchers believe that the combined climatic, anthropogenic and invasive impacts on biota can lead to the emergence of regional and global biotic crises (Zherikhin, 2003; Read and Clark, 2006; Huang et al., 2012; Ceballos et al., 2015). The relevance of this problem is primarily due to the need to develop new scientific approaches to preserving the biodiversity of natural biotic communities and studying the adaptive potential of invasive species and advanced forecasting of biotic crisis phenomena (Sutherland et al., 2013; Alberti, 2015; Saul and Jeschke, 2015; Donelan et al., 2020; Vasil'ev, 2021).

The most adequate natural models for studying the problem of adaptation of invasive species to new environmental conditions can be outpost populations of species that, for one reason or another, have populated new territories located outside the boundaries of their main range. Such populations must be exposed to both abiotic and biotic factors and can exhibit adaptive responses to new conditions in the form of changes in morphogenesis and morphofunctional characteristics (Facon et al., 2008; Donelan et al., 2020; Vasil'ev et al., 2022). In this case, long-term observations of outpost populations are important, which will allow us to assess the manifestation of chronographic variability in them (Yablokov, 1966; Schwartz, 1969, 1980). In this case, the phenomenon of chronographic variability makes it possible to identify the potential for developmental modifications in different years in a new environment for the species (Vasil'ev et al., 2022). A comparison of chronographic variability using morphofunctional traits as an example with the scope of their geographic variability (Bolshakov et al., 2013) in populations from the central part of the range also allows us to assess the adaptive capabilities of outpost populations of species when invading new biotic communities living in other abiotic conditions (Sakai et al., 2001).

In recent years, geometric morphometric methods have been increasingly used in morphological studies, the results of which are widely used in ecology (Klingenberg, 2011; Polly et al., 2016; Maestri et al., 2018; Vasil'ev et al., 2018). They allow for separate study of the variability of the sizes and shapes of objects and also allow for a morphogenetic interpretation of changes in shape (Zelditch et al., 2003, 2008; Sheets and Zelditch, 2013; Vasil'ev et al., 2018). The latter allows the use of geometric morphometric methods for the practical solution of the problem of rapid changes in the morphogenesis of outpost populations in new environmental conditions.

Species of small mammals that form numerous populations, carry out 1–3 generations per year, and allow modeling rapid adaptive restructuring of morphogenesis during the invasive colonization of new territories by the species can be used as model objects of research (Vasil'ev, 2021). Such model objects include species of small insectivores of the genus of shrews: the white-bellied (*Crocidura leucodon*) and lesser white-toothed (*Crocidura suaveolens*), which form outpost isolated populations localized outside the northern boundaries of their ranges (Chernousova and Tolkachev, 2006; Vasil'ev et al., 2022). Previously, using geometric morphometric methods, the chronographic variability of the white-bellied shrew in the Southern Urals was studied (Vasil'ev et al., 2022), which made it possible to identify morphogenetic transformations in the shape of the lower jaw associated with a directed change in weather and climatic conditions over the past 40 years. Another species, the lesser white-toothed shrew, which has formed an outpost northern population in the Chelyabinsk Region, has not yet been studied in this regard and can serve as an adequate model for analyzing the phenomenon of chronographic variability of an invasive species in the Southern Urals. To better understand the mechanisms of penetration of invasive species into a new environment, it is necessary to expand such studies under weather conditions of different years. Comparison of the range of sexual, chronographic, and geographical differences in the general morphospace allows us to assess the potential for possible rapid adaptive changes in the morphogenesis of an outpost population outside the main range of the species and to characterize its phenotypic plasticity.

The aim of the work is to study the phenotypic plasticity of the outpost population of the lesser white-toothed shrew in the Southern Urals, isolated from the main range, on the basis of a comparison of the magnitude of sexual dimorphism and chronographic variability, as well as the geographic variability of two remote populations from the central part of the range by geometric morphometric methods using the example of the lower jaw as an organ associated with trophic function.

The design of the study assumed, along with an assessment of the relationship between sexual dimorphism in the size and shape of the lower jaw and chronographic variability in the outpost population of the lesser white-toothed shrew, a comparison of the developmental stability of males and females of the outpost population in ecologically contrasting years according to the index of intragroup morphological diversity *MNND*. At the same time, it was proposed to compare the values of morphofunctional mandibular indices in males and females of the outpost population in these years to assess their probable differences in trophic preferences. A special task was to correlate the range of chronographic and geographic variability in the configuration of the lower jaw using the example of the outpost Chelyabinsk population and two remote populations from the central part of the range.

MATERIALS AND METHODS

A Brief History of the Study of the Lesser White-Toothed Shrew in the Southern Urals

The northern outpost population of the lesser white-toothed shrew was discovered during the joint work of the Central City Sanitary and Epidemiological Supervision (CCSES) no. 71 of Ozersk and employees of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences in 2003 during assesments of the abundance of small mammal species. Later, in the summer and early autumn of 2004–2007, the captures were repeated under the supervision of N.F. Chernousova, Cand. Sci. (Biol.), in seven biotopes within the city limits and in its immediate vicinity. In four of them, samples of the lesser white-toothed shrew were obtained. The invasive species has never been caught outside the city limits. Moreover, it was repeatedly caught together with a typical synanthropic species—the house mouse

(*Mus musculus*) in city buildings, gardens, parks, and shrubbery areas of the forest belt along the road.

The Ozersk population is isolated from the main part of the range and is located at a significant distance to the north of the northern border of the species range (Bolshakov et al., 2005; Chernousova et al., 2005; Chernousova and Tolkachev, 2006). The identification guide to mammals by Bobrinsky et al. (1965) provides information that, according to L.P. Sabaneev, in the Urals, discoveries of the species were noted outside the main range near the cities of Yekaterinburg, Verkhoturye, and Krasnoturyinsk; however, these data have not been verified and are currently not confirmed. There is also information about the probable discovery of the lesser white-toothed shrew in the vicinity of the city of Troitsk in the Chelyabinsk Region (Bobrinsky et al., 1965). The outpost population of the species from the vicinity of the city of Ozersk is located approximately 190–200 km north of this locality. Long-term monitoring of the Ozersk population (2003–2007) proves that, according to existing concepts (Dgebuadze, 2014), it is not just an accidental alien species that has temporarily penetrated into the north of the region in the Southern Urals, but should be considered as a permanently present invasive species. It is still unclear how, where from, and when the species entered the territory of Ozersk.

The staff of the CCSES established that the lesser white-toothed shrew, unlike other small mammals, was a carrier of the HFRS virus—hemorrhagic fever with renal syndrome—and formed a natural focus of this transmissible disease. About 30.4% of all white-toothed shrews examined in the city of Ozersk were infected with the HFRS virus. From published data (Lisovsky et al., 2019), it is also known that the lesser white-toothed shrew in many other places is a carrier of other diseases dangerous to humans—listeriosis, tularemia, leptospirosis, erysipeloid. Therefore, this invasive species in the Southern Urals not only has synanthropic properties but also is a carrier of natural focal infections and, possibly, other transmissible diseases dangerous to humans (Chernousova et al., 2005).

Area of Research and Weather and Climate Conditions upon Collecting Material

The material was previously collected in the vicinity of the city of Ozersk in the Chelyabinsk Region. The area of research is located in the city of Ozersk in different biotopes: (1) forest park area: 55°45′36″ N, 60°42′25″ E; (2) apple orchard: 55°45′10″ N, 60°41′59″ E; (3) forest-shrub belt: 55°45′16″ N, 60°42′06″ E; (4) forest park area on the outskirts of the city between gardens: 55°45′00″ N, 60°42′10″ E; (5) shrub thickets in the floodplain of the stream: 55°45′34″ N, 60°44′02″ E; (6) pine forest with an admixture of birch outside the city: 55°42′33″ N, 60°41′09″ E. The lesser white-toothed shrew was encountered (Chernousova and Tolkachev, 2006) only in the first four.

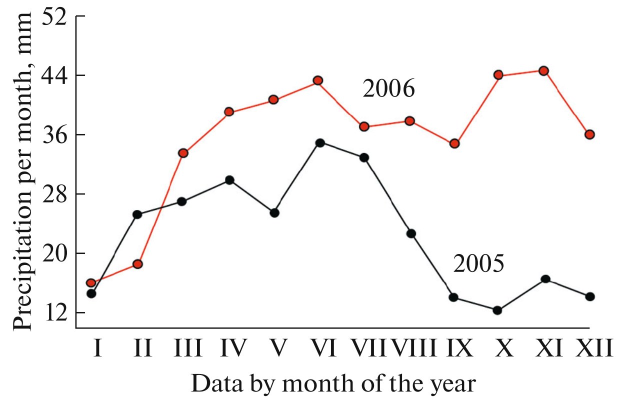

Fig. 1. Smoothed profiles of precipitation dynamics by month in 2005 and 2006 in the Southern Urals.

As the model, we used material collected in the vicinity of Ozersk in 2005 and 2006. Weather conditions in these years could have had different impacts on the lesser white-toothed shrew, directly or indirectly, through changes in the abundance and composition of food items. To compare the weather and climate conditions of these years, annual curves of changes in average monthly temperature and average monthly dynamics of precipitation were constructed (Fig. 1).

The average monthly dynamics of temperature change curves in both years of comparison (2005–2006) turned out to be similar and could not have been a factor differently influencing the morphological development of lesser white-toothed shrews. On the contrary, the average monthly dynamics of the amount of precipitation turned out to be different in the years being compared (see Fig. 1). In this case, we used the method of smoothing successive monthly values. It follows from Fig. 1 that, in 2005 in most spring, summer, and autumn months, there was less precipitation than in 2006. Therefore, if 2005 can be conditionally defined as a relatively "dry" year, then 2006 should be defined as relatively "rainy." It should also be noted that the winter of 2005 saw significantly less precipitation; i.e., there was little snow, which could also have affected the vital activity of the outpost population during the cold season.

The main material used was the collection of the Museum of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences on the lesser white-toothed shrew (*Crocidura suaveolens*). The collection of craniological material taken for this study was carried out in the second half of summer in similar biotopic conditions in an urban environment (Bolshakov et al., 2005; Chernousova et al., 2005; Chernousova and Tolkachev, 2006). In total,

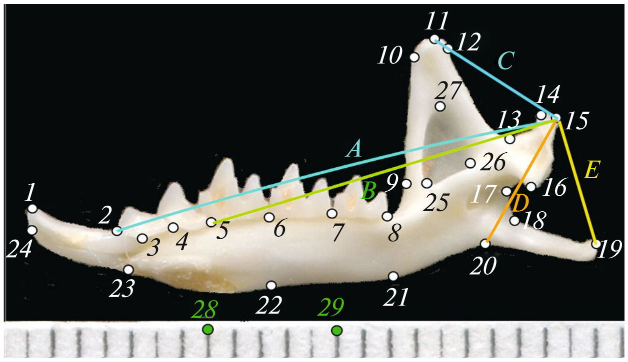

Fig. 2. Placement of landmarks (*1–27*) and two scaling marks (ruler) on the divisions of the measuring ruler (*28–29*) on the lingual side of the lower jaw of the lesser white-toothed tooth and measurements (*A*, *B*, *C*, *D*, *E*) to calculate mandibular indices.

we studied 132 specimens in the Ozersk population in 2005 and 2006. Of these, in 2005, there were 58 (35 males, 23 females), and in 2006, there were 74 (21 males, 53 females).

Unfortunately, we were unable to correlate biotopic variability with chronographic and geographic variability, which was initially assumed, since the material was distributed extremely unevenly across biotopes and locations: the residential area in the forest park, where the species was most abundant, predominated, while in other areas the samples were small. Perhaps this task will be realized in further research.

Additionally, we used two samples of digital photographs of the lower jaw of the lesser white-toothed shrew from the electronic depository of the collection of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), kindly provided to us for comparison. One sample was previously obtained by M.V. Zaitsev in the vicinity of Anapa, Krasnodar Territory: 44°54′52″ N, 37°20′48″ E, n = 15 (11 males; 4 females), and the other was obtained in the mountains on the territory of the Kabardino-Balkarian Republic in the vicinity of the town of Prokhladny: 43°44′60″ N, 44°05′08″ E, n = 9 (5 males; 4 females). The populations inhabit contrasting biotopes and landscapes, but their samples were obtained in the central part of the range. Both samples were collected at a distance of approximately 660 km from each other. Therefore, they allow us to evaluate the ratio of geographical and chronographic forms of variability when compared with samples from different years from the Chelyabinsk outpost population.

Samples of yearlings and overwintered lesser white-toothed shrews of both sexes were compared. Age was determined by the degree of tooth wear. The main material is represented by yearlings. The age structure of allochronic micropopulations was assessed using the χ^2 test.

The lower jaw was used as the main model object of the study to characterize the manifestations of different forms of morphological variability as one of the important organs directly related to food production, nutritional function, and the cenotic role of the species.

The variability of the shape of the lower jaw was studied using geometric morphometric methods (Rohlf, 1999; Zelditch et al., 2004; Klingenberg, 2011; Vasil'ev et al., 2018) on scanned images of the mandibular branches from the lingual side. The photographs of the mandibles were digitized at a resolution of 1200 dpi using the program by F.J. Rohlf tpsUtil and tpsDig2 (Rohlf, 2017a, 2017b). To characterize the variability of the shape of the lower jaw, a configuration of 27 homologous landmarks was used, as well as two scaling landmarks installed on the divisions of a measuring millimeter ruler (Fig. 2).

To assess the stability of the estimates obtained when placing landmarks, the operator repeated the placement of marks and performed a two-way analysis of variance for the factors "sex" (S) and "repetition" (R) using the example of a combined sample from 2005–2006. Calculations were performed in the program *manovaboard* of the IMP application package (Zelditch et al., 2004). The results of the comparison showed that, if the influence of factor S is statistically highly significant (F = 2.766; df1 = 58; df2 = 14790; p = 0.0020), then the influence of the factor of repeated placement of marks by the operator R turned out to be unreliable (F = 1.485; df1 = 58; df2 = 14790; p = 0.1200). Moreover, the interaction effect of these factors S × R was also statistically insignificant (F = 0.528; df1 = 58; df2 = 14790; p = 0.9370). Thus, repeated placement of landmarks does not lead to a significant bias in the estimates and does not require obtaining average values of the coordinates of the marks during their repeated placement to improve the accuracy of the shape comparison results.

The superposition of the landmark configurations was performed using the method of generalized Procrustes analysis—GPA (Rohlf and Slice, 1990; Rohlf, 1999), which includes procedures for image translation (centering), scaling, and rotation using least squares and the calculation of Procrustes coordinates, which characterize the variability of shape. The main data analysis was performed using the MorphoJ program (Klingenberg, 2011). For this program, a template of its contour configuration—an outline—was built in advance to visualize changes in the shape of the mandibles. Mandibular sizes in shrew samples were indirectly estimated on the basis of the centroid size (CS), which was calculated as the square root of the sum of the squares of the distances from the center of the image to each of the landmarks (Rohlf and Slice, 1990).

Since, when assessing the statistical significance of the influence of the factors year (Y) and sex (S) on the variability of a number of traits (centroid size, mandibular indices), we assumed the possibility of interaction between factors (Y × S), we chose for calculations a two-way ANOVA model for nonorthogonal complexes with fixed factors. To carry it out, the conformity of the distribution of variables to the normal law was assessed in advance using the Shapiro–Wilk W-test (Shapiro and Wilk, 1965) and the homogeneity of variances on the basis of the Levene's test for medians. In some cases, the effect size was estimated using Cohen's η^2 index (Cohen, 1992). For multiple comparisons, the Bonferroni correction was used to adjust the significance level of comparisons between three or more groups. Linear regression relationships for individual characteristics were estimated. To identify the strength of the relationship between the features, the Pearson's correlation coefficient and Spearman's nonparametric rank correlation coefficient were calculated. Intergroup differences in mandibular shape were assessed using canonical Procrustes coordinate analysis. To assess the significance of intergroup differences in the factors year (Y) and sex (S) for the total values of all canonical variables, we used a nonparametric multivariate two-way analysis of variance (two-way NPMANOVA) based on permutation testing for 10000 replicates (Anderson, 2001). In assessing the hierarchy of intergroup relations, cluster analysis was applied using the UPGMA method (unweighted pair group method with arithmetic mean), using the matrix of unsquared generalized Mahalanobis distances (*D*).

The assessment of intragroup morphological diversity was carried out using the method of nearest neighbor point pattern analysis within the variability polygon (Davis, 1990; Hammer, 2009). In accordance with this method, the R indicator was estimated—the ratio of the value of the observed average distance between the nearest neighboring ordinates of the variability polygon (*MNND*—mean nearest neighbor distance) to the value of the theoretically expected average distance (*ExpNND*) on the basis of the Poisson distribution. To test the null hypothesis that the observed *MNND* is equal to the value of *ExpNND*, for random dispersion of points with the same density of ordinates within the polygon of variability, the nearest neighbor Z-test was used (Davis, 1990). To remove the edge effect of dispersion of ordinates within a limited polygon of variability, the Donnelly method was used (Donnelly, 1978). The R indicator characterizes the model of dispersion of the ordinates. At $R > 1$, the overdispersion effect appears. Increase in the value of *MNND* when analyzing the variability of the shape of objects can be interpreted as an increase in intragroup morphological diversity (Hammer, 2009), an increase in the fan of morphogenesis trajectories, and an increase in developmental instability (Vasil'ev et al., 2018).

To assess the morphofunctional features of the lower jaw configurations, five measurements were used: *A*—articular-incisor, *B*—articular-molar, *C*—temporal-articular, *D*—articular-masseteric, and *E*—articular-angular (see Fig. 2). On the basis of these measurements, functional mandibular indices were calculated: *TI*—temporal-incisor, *TM*—temporal-molar, *MI*—masseter-incisor, *MM*—masseter-molar, and *AM*—angular-masseteric. The calculation of morphofunctional mandibular indices was carried out using the following formulas (Anderson et al., 2014; Vasil'ev et al., 2022): $TI = C/A$; $TM = C/B$; $MI = D/A$; $MM = D/B$; and $AM = E/D$.

Indices *TI* and *TM* characterize the intensity of longitudinal cutting-chewing movements, and indices *MI* and *MM* characterize the intensity of movements associated with gnawing and crushing food objects (Anderson et al., 2014; Cornette et al., 2015; Vasil'ev et al., 2022). Index *AM* indirectly characterizes the intensity of transverse movements associated with crushing and tearing the food object and/or intercepting the caught prey. The last index is associated with a special phenomenon—active swinging of the jaws when processing a food object while holding it, which Zazhigin and Voyta (2019) defined as swinging. We use the term "swinging" following these authors, who described this phenomenon using the example of specialized genera *Beremendia* and *Blarina* (Soricidae, Soricinae), but it is also true for other groups of shrews, including Crocidurinae.

To identify a possible allometric dependence, i.e., a change in the shape of the mandible depending on a change in size, we estimated a linear regression of the values of the first principal component of shape (PC1) from the values of the natural logarithms of the centroid size lnCS in accordance with existing recommendations (Zelditch et al., 2004). On the basis of regression analysis, it was found that the proportion of the predicted proportion of variance explained by regression for PC1 in all variants of comparison for all samples varied from 1.98 to 12.24% of the total variance. This regression effect was statistically insignificant, since the probability (*p*) of support for the null hypothesis of the absence of regression dependence assessed using the permutation test for 10000 repeated replicates in all variants was large and ranged from $p = 0.1359$ to $p = 0.4144$. Thus, the allometry of the lower jaw was not statistically confirmed and cannot influence the results of the comparison of the chronographic variability of shape in the outpost population of the species in different years.

A preliminary assessment using the 2006 sample as an example revealed significant age differences between yearlings and overwintered ones in the shape of the lower jaw (generalized Mahalanobis distance $D = 6.477$; Hotelling's T^2 jhb = 331.69; $p = 0.0263$), which requires further separate analysis of age groups. Since there were very few overwintered lesser white-toothed shrews in the samples, further comparisons were carried out only on the age group of yearlings.

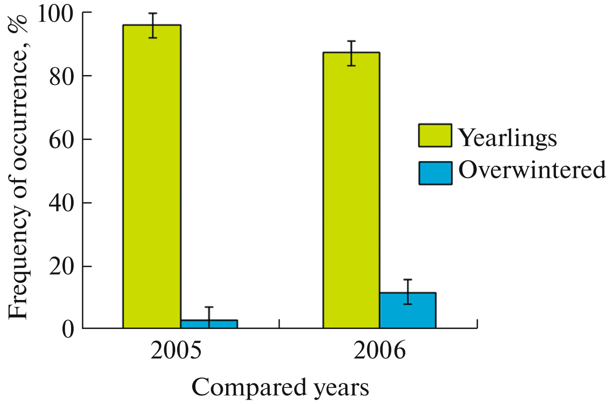

Fig. 3. Age structure of the Chelyabinsk population of the lesser white-toothed shrew in midsummer in the ecologically contrasting years of 2005 and 2006.

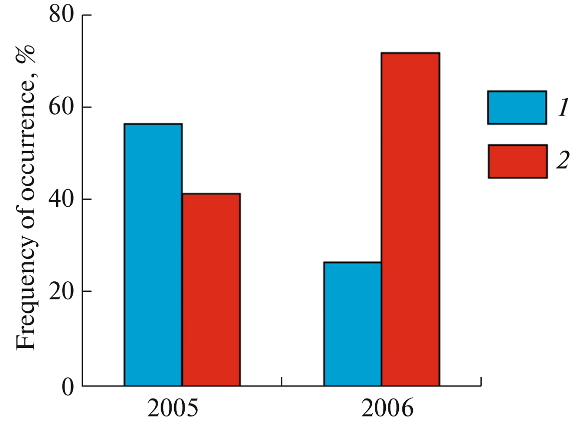

Fig. 4. The ratio of the proportion of males (*1*) and females (*2*) in the outpost population of the lesser white-toothed shrew in the Southern Urals in ecologically contrasting years, %.

The main calculations and statistical analysis of the material were performed using the programs TPS (Rohlf, 2017a, 2017b), PAST 2.17c (Hammer et al., 2001), IMP (Zelditch et al., 2004), and MorphoJ 1.6d (Klingenberg, 2011).

RESULTS AND DISCUSSION

Usually, when analyzing the ecological structure of a population, the abundance according to counts, the distribution of individuals by biotopes, the age structure, the sex ratio, and the characteristics of reproductive processes in the population are compared (Schwartz, 1969, 1980; Bolshakov and Vasil'ev, 1976; Bolshakov et al., 2011). According to the data, Chernousova and Tolkachev (2006) noted that the abundance of animals in natural conditions in the vicinity of the city of Ozersk in 2005 was relatively small and ranged from 0 to 18 specimens per 100 trap-days. The greatest abundance of the species was observed here in synanthropic conditions, and near bodies of water and outside the city limits, the lesser white-toothed shrew was never caught. In the collections of two years—2005 and 2006—the ratio of two age groups—yearlings and overwintered animals—differs (Fig. 3).

A comparison using the chi-square method revealed statistically significant differences between the 2005 and 2006 samples in the ratio of age groups—yearlings and overwintered ones: $\chi^2 = 4.32$; d.f. = 1; $p < 0.05$. The proportion of those who overwintered in the rainy summer of 2006 was significantly higher than in the dry season of 2005. This fact indicates that, in different years, the mortality of those that overwinter in the outpost population may be expressed differently. The winter of 2005–2006 had little snow (see Fig. 1), but this did not affect the proportion and number of overwintering shrews in the catches. It is possible that lesser white-toothed shrews use human structures during the winter. In the summer, during the captures by the sanitary and epidemiological service, shrews were encountered in some buildings and near them within the city limits of Ozersk (Chernousova and Tolkachev, 2006). Comparison of the sex ratio in the 2005 and 2006 samples also revealed significant differences (Fig. 4): $\chi^2 = 12.25$; d.f. = 1; $p < 0.001$. If the proportion of females in the dry year of 2005 was less than that of males and amounted to 41.1%, then in the rainy year of 2006 it reached 71.6%. The sharp drop in the proportion of males in 2006 can be explained by various reasons—trophic, weather, epizootic, or a combination of these. However, it is important to note that representatives of different sexes in the outpost population may be vulnerable to varying degrees in different years, living in environmental conditions that are new to the species. This case shows that males were less adapted to the conditions of the summer of 2006, unlike females.

Thus, the dynamics of the elements of the ecological structure of the outpost population in contrasting years reflected contradictory phenomena. If in the dry year of 2005, under typical hot summer conditions for the species, the proportion of those who overwintered was extremely low, indicating high mortality in this age group, but the sex ratio was close to 1 : 1, then in the rainy year of 2006, on the contrary, the proportion of those who overwintered was several times higher, and the sex ratio shifted towards the predominance of females. All this indirectly indicates insufficient adaptation of structural and functional groups—males and females of different ages in an outpost population that arose relatively recently.

In the lesser white-toothed shrew, as shown by the comparison carried out on the centroid sizes of the lower jaw, its sizes in males and females were close in both years of comparison. The results of the two-way analysis of variance (two-way ANOVA) of centroid sizes (CS) taking into account the factors "year" (Y)

Table 1. Results of a two-way analysis of variance (two-way ANOVA) of the centroid sizes (CS) of the lower jaw of males and females of the lesser white-toothed shrew in different years (2005–2006) in the northern outpost population of the Southern Urals (Chelyabinsk Region)

Source of variability (factors)	Sum of squares (SS)	Degrees of freedom (d.f.)	Mean square (MS)	F	Significance level (p)
Year (Y)	1.050	1	1.050	1.83	0.1790
Sex (S)	0.865	1	0.865	1.50	0.2223
Interaction (Y × S)	0.311	1	0.311	0.54	0.4631
Intragroup	72450	126	0.575		
Total	74676	129			

and “sex” (S), as well as their interaction (Y × S), are presented in Table 1.

From Table 1, it follows that no significant differences were found for any of the factors or for their interaction. Consequently, the centroid dimensions of the lower jaw did not show either sexual dimorphism or chronographic variability.

The assessment of the manifestation of sex differences in the shape of the lower jaw without taking into account chronographic variability was carried out on the basis of a linear discriminant analysis of Procrustes coordinates. Differences in the shape of the mandibles were significant (Hotelling’s $T^2 = 167.146$; $p = 0.006$). The generalized Mahalanobis distance between the sexes in this case was $D = 2.401$ ($p = 0.0055$). The assessment of the correctness of gender discrimination on the basis of the shape of the lower jaw was 88.2%. In cross-validation testing, the discrimination accuracy decreased slightly, indicating instability of sex differences in mandible shape.

We previously presented the results of a multivariate two-factor analysis of variance of the Procrustes coordinates of the lower jaw for the factors “sex” S and “repeated placement of marks” R. Let us recall that, for the factor S (sexual dimorphism), the differences were statistically highly significant ($p = 0.0020$). The latter is in good agreement with the results of discriminant analysis and indicates the presence of well-defined sexual dimorphism in the shape of the mandibles in the lesser white-toothed shrew. Thus, the factor “sex” should be taken into account in further comparisons, and possible biases in estimates due to sex differences and sexual variability in the configuration of the mandibles should be kept in mind.

Chronographic Variability of Mandible Shape in the Northern Outpost Population of the Lesser White-Toothed Shrew

At the next stage of the study, we conducted a canonical analysis of the Procrustes coordinates characterizing the variability of the shape of the mandibles, while simultaneously comparing samples of males and females caught in 2005 and 2006 (Table 2, Fig. 5).

Table 2 and Fig. 5 show that intergroup differences are the greatest between the 2005 and 2006 samples, which are expressed mainly along the first canonical variable CV1, which accounted for about 63% of the total intergroup variance. Positive values along the first canonical variable correspond to the centroids of the 2005 samples, and negative values correspond to the centroids of the 2006 samples (see Table 2). Along the second canonical variable, sex differences were clearly evident (about 21% of the variance): positive centroid values correspond to samples of males, and negative ones to samples of females. It also follows from Fig. 5 that the dispersion ellipsoids of all samples are separated in the morphospace along the first and second canonical variables and hardly overlap (recall that each ellipsoid characterizes 95% of the dispersion of the ordinates of individuals). Chronographic differences thus appeared along the first canonical axis, and gender differences appeared along the second; i.e., judging by the ratio of intergroup dispersions of variables, gender differences are expressed approximately 3 times weaker than chronographic differences. Along the third canonical variable, judging by the values and signs of the centroids of the samples (see Table 2), an interaction between the factors “year” and “sex” is observed: certain features of the configuration of the mandibles of males and females manifest themselves in opposite ways in different years. Since CV3 accounted for approximately 16% of the intergroup variance, it can be concluded that this direction of variability in the general morphospace of canonical axes approaches the level of chronographic variation itself in terms of the magnitude of variation. From Table 2, it also follows that the variability along all canonical variables is highly statistically significant ($p < 0.0001$). As a result, it can be concluded that the chronographic variability in the Chelyabinsk outpost population significantly exceeds the sexual variability.

Thus, the interannual differences turned out to be very large and indicate a rapid modification switch of the process of morphogenesis to development according to a different program, and not the effect of strict selection. During the winter period at the end of 2005, selection could not have led to the manifestation of a certain (according to Darwin) variability, whereas the

Table 2. Results of canonical analysis of Procrustes coordinates characterizing the variability of the shape of the lower jaw in samples of males and females of different years (2005–2006) from the northern outpost population of the lesser white-toothed shrew

Sex, year	Canonical variable		
	CV1	CV2	CV3
Centroids of samples (±*SE*)			
Males, 2005	2.419 ± 0.156	1.205 ± 0.158	0.926 ± 0.198
Females, 2005	2.575 ± 0.241	−1.844 ± 0.230	−1.141 ± 0.200
Males, 2006	−1.517 ± 0.241	1.721 ± 0.176	−1.818 ± 0.254
Females, 2006	−1.957 ± 0.134	−0.611 ± 0.150	0.600 ± 0.122
Results of canonical analysis			
Wilks' Λ	0.0331	0.1841	0.4632
Eigenvalues	4.7332	1.6286	1.1486
Proportion of variance, %	63.02	21.68	15.29
Criterion χ^2	427.66	212.39	96.59
Degree of freedom (d.f.)	108	70	34
Level of significance, *p*	<0.0001	<0.0001	<0.0009

developmental modification, developed and stored in the genome during the existence of the species, could well have been realized. Therefore, there is every reason to believe that, in this case, high phenotypic plasticity of the species (Pigliucci, 2001) was manifested in new ecological conditions as a modification change in the process of morphogenesis (West-Eberhard, 2005).

It is interesting to note that the shape of the mandibles, judging by the outline configurations of the mandibles shown in Fig. 5, inscribed in the deformation

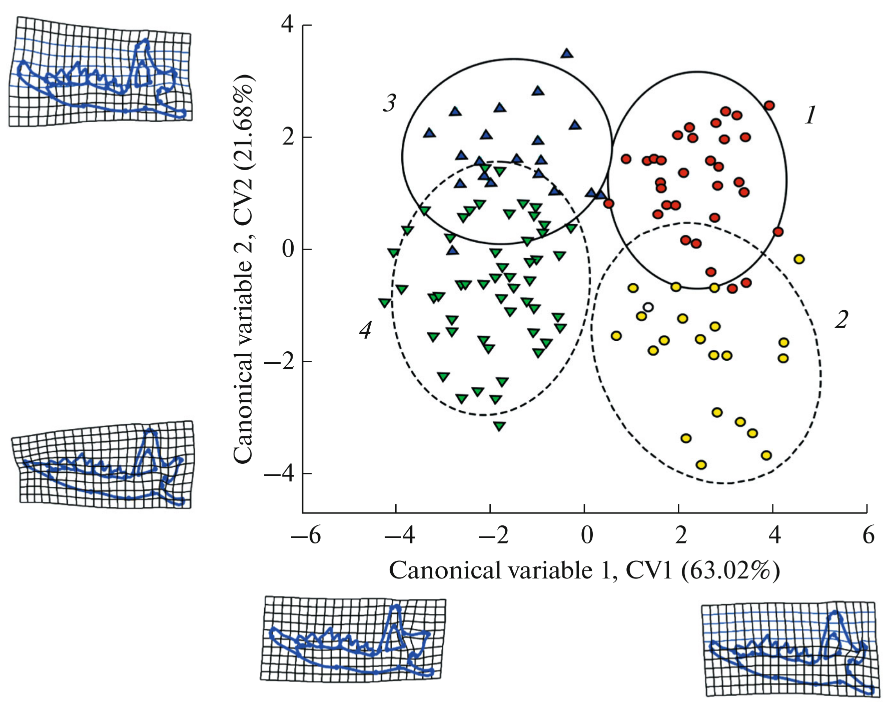

Fig. 5. Results of the canonical analysis of Procrustes coordinates characterizing the variability of the shape of the lower jaw of males (*1*, *3*) and females (*2*, *4*) of lesser white-toothed shrew in samples of different years from the northern outpost population of the Southern Urals (Chelyabinsk Region): (*1*, *2*) 2005; (*3*, *4*) 2006.

Table 3. Nonparametric multivariate two-way analysis of variance (PERMANOVA) of canonical variable values (CV1–CV3) in assessing the influence of year (Y), sex (S), and their interaction (Y × S) on the variability of the lingual mandible shape of the lesser white-toothed shrew in the northern outpost population on the basis of 10000 permutations

Source of variability	Sum of squares	Degree of freedom, d.f.	Mean square	F	Level of significance, *p*
Year (Y)	578.050	1	570.050	160.77	<0.0001
Gender (S)	252.590	1	252.590	71.24	<0.0001
Interaction (Y × S)	19.988	1	19.988	5.64	<0.0001
Residual	446.770	126	3.546		
Total	1289.398	129			

Table 4. The generalized Mahalanobis distance matrix (*D*) and the mean measure of uniqueness (*MMU*) between samples of males and females of the lesser white-toothed shrew in 2005 and 2006 in the outpost northern population of the Southern Urals (Chelyabinsk Region)

Sample	Males, 2005	Females, 2005	Males, 2006	Females, 2006	MMU*
Males, 2005	0.000	3.526	4.827	4.784	4.379
Females, 2005	3.526	0.000	5.108	4.724	4.453
Males, 2006	4.827	5.108	0.000	3.408	4.448
Females, 2006	4.784	4.724	3.408	0.000	4.305

* Mean Measure of Uniqueness (*MMU*).

lattices, is different. In the rainy year of 2006, phenotypes of individuals with a relatively narrowed temporal process but an enlarged articular process were realized. On the contrary, in the dry year of 2005, the angular process moves away to a greater extent in the ventral direction from the articular process, the articular process is relatively reduced and the coronoid process is expanded. It can also be concluded that in males the mandible body is somewhat higher than in females, the coronoid process is shifted in the cranial direction, and the incisor and angular process are relatively thickened. In females, the mandible is gracile and relatively more elongated.

It was of interest to more accurately estimate quantitatively the contribution of the factors "year" (Y) and "sex" (S), as well as their interactions (Y × S), to the canonical variables obtained from the above-mentioned canonical analysis of the Procrustes coordinates of the mandibles of males and females from the 2005 and 2006 samples. To obtain an integrated estimate of the contributions of the above factors and their interactions to the overall intergroup variability of all three canonical variables in their combination, we used a nonparametric multivariate two-way analysis of variance (two-way PERMANOVA) of the values of the canonical variables (CV1–CV3), the results of which are presented in Table 3.

As a result of the calculations, a generalized characteristic of the significance of the contribution of the factors "year," "sex," and their interaction in the variability of the shape of the lower jaw of the lesser white-toothed shrew was obtained. The "year" factor influences the variability of the shape of the mandibles almost 2 times more than the "sex" factor. The share of variance due to the "year" factor accounted for 67.7%, while the share of variance associated with the "sex" factor accounted for 30.0%. In different years, different directions of change in the shape of the mandible in males and females are also significantly manifested, as evidenced by the significant interaction of the factors "year × sex" (2.4% of variance). Consequently, in the isolated northern outpost population of the lesser white-toothed shrew, chronographic intergroup variability is expressed twice as strongly as sexual differences (sexual dimorphism). The manifestation of a significant interaction between the factors "year × sex" probably reflects the effect of insufficient adaptation of animals of both sexes of this outpost population to new local habitat conditions outside the species range.

As a result of the canonical analysis, the matrix of generalized Mahalanobis distances was obtained (*D*) between all pairs of samples being compared, characterizing their morphological uniqueness (Table 4). Table 4 also shows the values of the mean measure of uniqueness of samples (MMU) as the average sums of the distances of a specific sample from all other samples.

From Table 4, it follows that the differences between the sexes in form (manifestations of sexual dimorphism) within each year are approximately close in magnitude and fluctuate from $D = 3.408$ to $D = 3.526$. Generalized Mahalanobis distances (*D*) between samples of different years are consistently

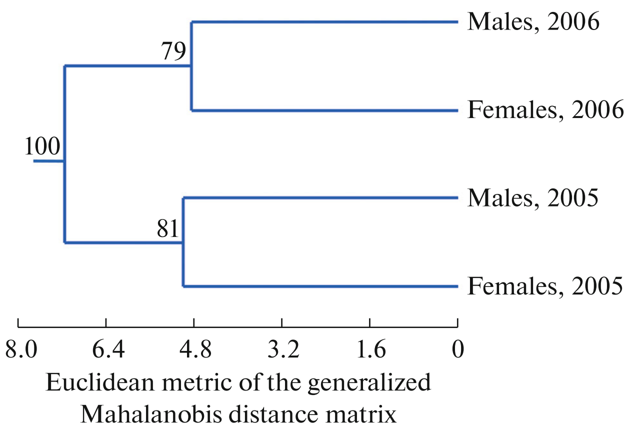

Fig. 6. Results of cluster analysis (UPGMA) of the Euclidean metric of the generalized Mahalanobis distance matrix (*D*) between samples of males and females of the lesser white-toothed shrew of different years (2005–2006) from the northern outpost population of the Southern Urals (Chelyabinsk Region).

higher in magnitude and fluctuate from 4.724 to 5.108. All distances are statistically significant ($p < 0.001$). It is noteworthy that the MMU values for each sample are close in magnitude, which indirectly indicates that all samples are almost equally distant from each other in the general morphospace and the morphological differences between them are, on average, approximately comparable in magnitude. We performed a cluster analysis of the generalized Mahalanobis distance matrix using the unweighted pair group method with arithmetic mean (UPGMA) and revealed a hierarchical structure of relationships between samples in the outpost population of the lesser white-toothed shrew (Fig. 6).

The final cluster is represented by two subclusters, each of which combines samples of males and females of the corresponding year. This hierarchical structure directly confirms the revealed fact that chronographic differences (chronographic variability) are more pronounced than sex differences. Usually, sex differences, being a species trait, exceed short-term chronological differences, especially between closely adjacent years. Only when comparing samples collected over tens of years can chronographic variability, reflecting the trend of long-term directional changes associated with climate change and the development of morphological adaptations to them, be expressed more strongly than sex differences (Vasil'ev, 2021, Vasil'ev et al., 2022). Since in our case the chronographic differences are greater than the sex differences when comparing samples from adjacent years, this reflects the high sensitivity of the morphogenesis of individuals of the outpost population to weather conditions in different years far beyond the main range of the species. Overall, it can be concluded that the results obtained, including the results of cluster analysis, reflect a sharp switch in the process of morphogenesis, and not the consequences of selection. This case should apparently be attributed to a case of certain modification variability in response to a sharp change in weather and climate conditions. It demonstrates a high level of phenotypic plasticity of the outpost population of the lesser white-toothed shrew in the north of the Southern Urals.

Index of Intragroup Morphological Diversity (MNND) as an Indirect Measure of Destabilization of Development

Of particular interest is obtaining information on the magnitude of intragroup morphological diversity, which indirectly characterizes the level of developmental destabilization (Vasil'ev et al., 2018). It is well known that, for this purpose, fluctuating asymmetry (FA) indices of bilateral traits are often used, which were previously proposed by various authors in the second half of the 20th century (Palmer and Strobeck, 1986; Zakharov, 1987, 1992; Palmer, 1994; Gelashvili et al., 2004). Since the assessment of intragroup diversity reflects the same phenomenon as FA indices, but is supplemented by appropriate statistical assessment methods that allow us to identify the characteristics of the dispersion of ordinates within the group polygon of variability, including the "overdispersion" effect, we used this approach (Davis, 1990; Hammer, 2009; Vasil'ev et al., 2018). The results of the assessment of intragroup morphological diversity indicators (*MNND*) by the values of the first two canonical variables and the theoretically expected value (*ExpNND*) are given in the Table 5.

Intragroup diversity index (*MNND*) of mandibles in all samples of males and females (except for females in 2005) is significantly higher than the corresponding values expected for a random Poisson distribution of average nearest distances (*ExpNND*) between adjacent ordinates. The latter indirectly indicates a significant increase in the destabilization of the morphogenesis of the lower jaw in males and females in this outpost population in both years of comparison. At the same time, the values of the R indicator (ratio *MNND*/*ExpNND*) in all cases exceeded 1.0, and according to the Z criterion, all these deviations are statistically significant. This means that all samples of this population show statistically significant overdispersion effects of the ordinates.

If in the dry year of 2005 differences between the sexes in terms of intragroup morphological diversity (*MNND*) did not appear ($t = 0.697$; $p > 0.05$), then in the rainy year of 2006 they were statistically highly significant ($t = 3.363$; $p < 0.001$). The greatest value of *MNND* in males appeared in 2006, but at the same time in this year, the minimum value of the indicator was also observed in females (see Table 5). Since the indicator indirectly reflects the level of destabilization of morphogenesis (Vasil'ev et al., 2018), one can, with some caution, assume that the conditions of the rainy

Table 5. Comparison of intragroup morphological diversity indicators (*MNND*) by the values of the first two canonical variables and their theoretically expected value (*ExpNND*) taking into account standard errors (±*SE*) between samples of males and females of different years (2005–2006) taken from the northern outpost population of the lesser white-toothed shrew in the Chelyabinsk Region

Samples: sex, year	*MNND* ± *SE*	*ExpNND* ± *SE*	*R* (*N* samples)	*Z*	Level of significance, *p*
Males, 2005	0.352 ± 0.042	0.267 ± 0.004	1.321 (33)	3.52	0.00043
Females, 2005	0.412 ± 0.075	0.311 ± 0.007	1.325 (24)	3.05	0.00233
Males, 2006	0.505 ± 0.060	0.305 ± 0.008	1.653 (20)	5.58	<0.00001
Females, 2006	0.293 ± 0.020	0.241 ± 0.002	1.216 (53)	3.01	0.00262

Table 6. Values of mandibular indices taking into account their standard errors (±*SE*) in samples of males and females of different years from the outpost population of the lesser white-toothed shrew in the Chelyabinsk Region

Sex, year (samples)	Morphofunctional mandibular indices				
	TI ± *SE*	*TM* ± *SE*	*MI* ± *SE*	*MM* ± *SE*	*AM* ± *SE*
Males, 2005 (33)	0.285 ± 0.002	0.498 ± 0.003	0.280 ± 0.002	0.490 ± 0.003	0.858 ± 0.005
Females, 2005 (24)	0.285 ± 0.003	0.497 ± 0.004	0.284 ± 0.002	0.495 ± 0.004	0.859 ± 0.004
Males, 2006 (20)	0.282 ± 0.003	0.492 ± 0.005	0.289 ± 0.003	0.502 ± 0.004	0.839 ± 0.005
Females, 2006 (53)	0.281 ± 0.002	0.490 ± 0.003	0.280 ± 0.001	0.489 ± 0.002	0.847 ± 0.004

year 2006 were unfavorable for the males of this population (their relative abundance and share in the catch were low), but, on the contrary, were favorable for females (their abundance and share in the catch were many times higher). Judging by the indicator *MNND*, the drier year of 2005 was generally more favorable for both sexes, although females showed some (albeit insignificant) $t = 1.539$; $p > 0.05$) tendency for it to increase compared to males.

As a result, it can be concluded that, since overdispersion was demonstrated in both males and females in both years and its significant manifestation was proven (see Table 5), the data indirectly indicate a general destabilization of morphogenesis in the outpost northern population of the lesser white-toothed shrew. Moreover, in ecologically contrasting years, males and females showed opposite morphogenetic responses to the conditions of the rainy year of 2006: for males they were unfavorable, but for females they were relatively favorable. At the same time, in the dry year of 2005, conditions were approximately equally favorable for both sexes, which perhaps reflects the greater adaptability of the species to living in warmer and sometimes drier southern regions within its main range. Probably, 2005, in terms of conditions of development, differed little from the conditions typical for the species.

Mandibular Indices and Analysis of Trophic Preferences of the Lesser White-Toothed Shrew in Different Weather and Climatic Conditions

Comparison of the average values of five morphofunctional mandibular indices potentially allows us to assess the characteristics of trophic preferences in males and females in the outpost population of the lesser white-toothed shrew in years with different weather and climate characteristics—2005 and 2006 (Table 6).

From the average values of the indices given in Table 6, it follows that, for such of them as *TI* and *TM*, associated with cutting and sawing movements of the lower jaw, no differences were found between the samples ($p > 0.05$). Two-way ANOVA showed that the other three indices showed significant differences related to the year factor and the year × sex interaction (Table 7).

The interaction effect of the factors “year × sex” by the example of the masseter-incisor index *MI* was clearly evident in males: in 2006, this index was significantly higher than in 2005, while in females, the opposite trend was observed. In 2006, their index tended to be smaller in value than in 2005.

Sex differences in this index in 2006 were highly significant. All this indicates that the gnawing force in the incisor area of males in 2006 was higher than that of females and also significantly higher than that of males in 2005. The index *MM* (masseter-molar) behaves similarly, which reflects the same trends of increased gnawing and crushing of food objects by males in 2006 by the first molar of the lower jaw. By index *AM* (angular-masseteric), general differences between years are evident, regardless of sex (see Tables 6, 7).

In 2005, the value of this index for males and females of the lesser white-toothed shrew was, on average, significantly higher than in 2006. The latter

Table 7. Two-way analysis of variance of the values of morphofunctional mandibular indices (*MI*, *MM*, *AM*) of the lower jaw of the lesser white-toothed shrew when assessing the influence of factors of conditions of year (Y), sex (S), and their interaction (Y × S) in the outpost northern population (2005–2006)

Source of variability	Sum of squares	Degree of freedom, d.f.	Mean square	F	Level of significance, *p*	Effect size, η^2
MI—masseter-incisor index						
Year (Y)	0.000155	1	0.000155	1.498	0.2232	0.0118
Sex (S)	0.000205	1	0.000205	1.985	0.1613	0.0155
(Y × S)	0.001162	1	0.001162	11.249	0.0011	**0.0820**
Residual	0.013014	126	0.000103			
Total	0.014536	129				
MM—masseter-molar index						
Year (Y)	0.000015	1	0.000015	0.048	0.8265	0.0073
Sex (S)	0.000491	1	0.000491	1.589	0.2098	0.0121
(Y × S)	0.002725	1	0.002725	8.821	0.0036	**0.0641**
Residual	0.038930	126	0.000309			
Total	0.042216	129				
AM—angular-masseter index						
Year (Y)	0.006277	1	0.006277	6.421	0.0125	0.0485
Sex (S)	0.000590	1	0.000590	0.604	0.4386	0.0048
(Y × S)	0.000505	1	0.000505	0.517	0.4734	0.0041
Residual	0.123162	126	0.000977			
Total	0.130534	129				

means that, in 2005, in this population, lesser white-toothed shrews actively used the property of horizontal swinging of the branches of the lower jaw (swinging according to (Zazhigin and Voyta, 2019)) when catching prey. With horizontal parallel shifts of the branches of the lower jaw, horizontal crushing and cutting of the tissues of prey is carried out. The results obtained indirectly indicate that the diet of males and females, as well as both sexes in general, was different in different years, which led to a change in the configuration of the mandibles. Of particular interest is the fact that differences in diet were indirectly detected between males and females in the atypical rainy year of 2006. Males more often fed on harder food items, while females fed on relatively softer food items. It is possible that such trophic behavior of males was forced this year, since the number of males was 3 times lower than that of females (females were able, however, to compete for prey). At the same time, the effect of destabilization of the development of males in 2006, judging by the value of the index *MNND*, was the largest in this group, indicating stress of individuals during the process of development.

The Relationship between Geographical, Chronographic, and Sexual Variability in the Shape of the Lower Jaw of the Lesser White-Toothed Shrew

In the final part of the work, we assessed the relationship between three forms of variability (according to (Yablokov, 1966)), geographic, chronographic, and sexual, on the basis of the canonical analysis of Procrustes coordinates. For this purpose, along with samples of males and females from two ecologically contrasting years (2005 and 2006) from the Ozersk outpost population, samples of both sexes from two remote populations isolated by a landscape barrier from the central part of the range of the species—the mountainous Kabardino-Balkarian and the lowland Krasnodar population—were included in the comparison. For greater quantitative comparability, samples of males and females from two ecologically contrasting years in the outpost population were randomly matched in terms of observation volume, 20 individuals each.

The greatest differences, as expected, appeared along CV1 (75.20% of the variance) and were associated with the manifestation of geographic variability between the outpost Chelyabinsk population, on one hand, and samples from the central part of the range,

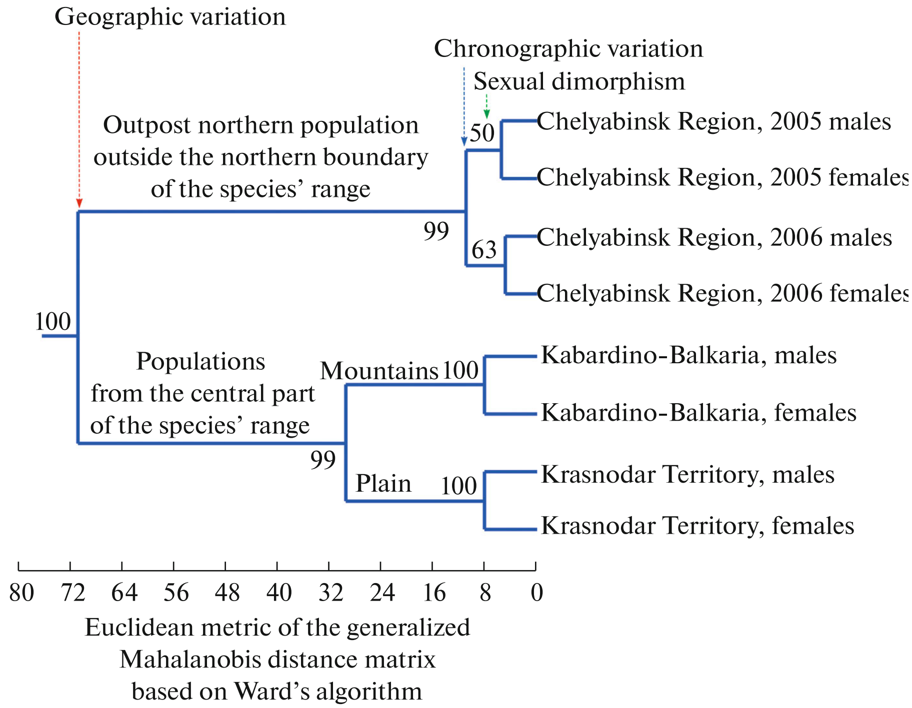

Fig. 7. Cluster analysis (Ward) of the generalized Mahalanobis distance matrix (*D*) between samples of males and females from the Kabardino-Balkarian and Krasnodar populations and ecologically contrasting years (2005–2006) from the Chelyabinsk outpost populations of the lesser white-toothed shrew. The values of bootstrap support, in %, are indicated at the branch nodes. The cophenetic correlation coefficient CCC = 0.991. For geographic coordinates of all sample locations, see Materials and Methods.

on the other hand. Along the second canonical variable CV2 (11.93%), differences were revealed between the last two samples—both landscape-geographical variability of a lower level than along CV1 and a combination of chronographic variability and manifestations of sexual dimorphism in the Chelyabinsk outpost group.

The manifestation of "landscape-geographical" variability between the Kabardino-Balkarian and Krasnodar populations and chronographic variability in the Chelyabinsk outpost population largely coincided along the second canonical axis, but was expressed to varying degrees. The first form of variability was manifested to a greater extent. Landscape-geographical variability and also sex differences and the effect of interaction between the factors "year" and "sex" (Y × S) in the outpost population were also evident along the third canonical variable CV3 (5.48% of variance). According to the generalized Mahalanobis distance matrix (*D*), a final cluster analysis using the Ward method was conducted, which allowed us to evaluate the mutual hierarchy and relationship of the three forms of variability (Fig. 7).

From Fig. 7, it follows that the smallest and approximately equal level of differences in the lengths of the cluster branches appeared when comparing samples of different sexes—the level of sexual dimorphism. The next hierarchical level of differences in terms of sample removal is chronographic variability in the outpost population. The "landscape-geographical" variability when comparing the lowland Krasnodar and mountain Kabardino-Balkarian populations corresponds to an even higher hierarchical level. The maximum level of the hierarchy of morphological differences corresponds to the manifestation of geographic variability of the outpost Chelyabinsk population in comparison with two southern populations from the central part of the species range—Kabardino-Balkarian and Krasnodar.

Thus, it can be confirmed that chronographic variability in the outpost population is expressed more strongly than sexual differences, and the morphological uniqueness of this population, localized far beyond the northern boundary of the range, significantly exceeds the level of "landscape-geographical" variability between geographically isolated populations from the central part of the range.

CONCLUSIONS

An analysis of the variability of the Chelyabinsk outpost population conducted using geometric morphometric methods in comparison with two remote populations from the central part of the range made it possible to evaluate and characterize the level of phenotypic plasticity of the invasive group of the lesser white-toothed shrew. Since the variability of the configuration of the lower jaw—the organ involved in catching prey and the primary processing of food objects—was assessed, the variability of the shape of the mandibles reflects not only their functional characteristics but also differences in the composition of the diet of shrews and their cenotic role in different years.

An initial assessment of the ecological conditions and elements of the ecological structure of the outpost population in 2005 and 2006 made it possible to identify a number of important accompanying circumstances. It is shown that weather conditions in these years differ in the dynamics of average monthly precipitation. If 2005 was dry, then 2006 turned out to be rainy. In the age structure of the outpost population of lesser white-toothed shrews outside the northern border of the range, yearlings completely dominate in different years: in the dry year of 2005, the proportion of those that overwintered was 3.5%, and in the excessively wet year of 2006, it reached 12.2%.

Age differences in the shape of the lower jaw are significant. With age, the length of the incisor shortens and the tips of the premolars and molars are partially erased. Therefore, only yearlings were used in the comparative analysis.

The sex ratio in the outpost population in both years deviates significantly from 1 : 1, with the proportion of females being about 40% in the dry year of 2005 and 81% in the excessively wet year of 2006. Sexual differences in mandible shape are highly significant, and they manifest themselves differently in ecologically different years. However, in terms of the centroid size of the lower jaw, all samples of males and females in 2005 and 2006 do not differ from each other. In other words, in both years of comparison, sexual dimorphism in mandible size is not expressed, but significant sexual dimorphism in their shape is evident. A significant chronographic variability in the shape of the lower jaw was revealed, which was several times greater than the range of sexual differences in the configuration of the mandibles.

In ecologically contrasting years, the values of the functional masseter-incisor, masseter-molar, and angular-masseter mandibular indices in males and females differ significantly, indicating that they feed on different trophic objects in these years, which may reduce potential trophic competition between the sexes in unfavorable years.

The index of intragroup morphodiversity (*MNND*) of the mandibles in the samples of males and females (with the exception of females in 2005) turned out to be significantly higher than the expected random values, and in all samples, the effect of overdispersion of the ordinates of individuals is observed, which indicates a significant increase in the destabilization of the morphogenesis of the lower jaw of lesser white-toothed shrews of both sexes in this outpost population in both years of comparison.

Thus, as a result of the study conducted in ecologically contrasting years, the following was established: a disruption of the age structure and sex ratio in the outpost population of the lesser white-toothed shrew, instability of the development of the mandibles in the years of comparison, and a change in their shape and function during mechanical processing of food in contrasting conditions. Males and females showed opposite morphogenetic responses to the conditions of the rainy year 2006: for males they were unfavorable, but for females they were relatively favorable. On the basis of the set of indicators used, the conditions of the dry year 2005 were more favorable for the outpost isolated population, which corresponds to the typical habitat conditions of the species in the south within its main range.

The geographic variability between the Chelyabinsk outpost and two Kabardino-Balkarian and Krasnodar populations from the center of the range is an order of magnitude (3.5 times) greater than the range of chronographic variability between samples of ecologically contrasting years (2005–2006) in the Chelyabinsk outpost population. The results obtained on the basis of the assessment of the ratio of different forms of variability directly prove the high level of phenotypic plasticity of the lesser white-toothed shrew, which helps explain the stability of the existence of an invasive outpost population of the species far beyond the northern boundary of the range of the species in the Chelyabinsk Region. The high phenotypic plasticity and synanthropy of the lesser white-toothed shrew allow us to predict the possibility of further invasion of the species into the north of the Southern Urals with climate warming, which is important to consider in view of the ability of the lesser white-toothed shrew to transmit vector-borne diseases dangerous to humans.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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