

Factors of Polymorphism of Craniometric Characters in the Red Fox (*Vulpes vulpes*, Carnivora, Canidae) from the Center of European Russia

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Abstract—Craniometry was investigated in four samples of the red fox (*Vulpes vulpes* L. 1758) ($n = 403$) from Tver oblast. Factors affecting the metric polymorphism of the fox skull can be presented in the following order according to their significance: age, sex, geographic, and chronographic variability. The geographic and chronographic factors are correlated with the jaws and teeth. An analysis of the time interval from the early 1990s to the present shows a weak trend toward an increase in some cranial structures. However, the inclusion of material from the 1980s reveals a more complex trend in the chronographic variability with size fluctuations. This may be due to the high rate of mortality which determines the stochastic nature of the chronographic size variability. The spatial variability of odontological and craniometric characters can be of adaptive functional significance.

Keywords: red fox, morphological variability, European part of Russia

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INTRODUCTION

The variability of organisms is a complex phenomenon. From the point of view of evolutionary biology, the variability of organisms is one of the main prerequisites for the process of natural selection (Mednikov, 1969; Timofeev-Resovskii et al., 1978). If we consider this phenomenon from the standpoint of population biology, it should be stated that it is important for the stability and integrity of the population as a biological system (Yablokov, 1987). The following factors of polymorphism should be considered important: age, sex, and spatial and temporal variability of animals.

We continue the series of publications devoted to the intrapopulation analysis of the morphological characters of mammals of the order Carnivora inhabiting the center of the European part of Russia.

The fox (*Vulpes vulpes* Linnaeus 1758), a species of the Canidae family, occupies an area of about 70 million km², covering five continents and at least 83 countries (Sillero-Zubiri et al., 2004). Such a spread range and the gradient of environmental factors

formed within its borders, as well as the long phylogenetic history of the species populations, predetermined the pronounced phenotypic variability. Modern taxonomists distinguish 45 subspecies of *Vulpes vulpes* (Wozencraft, 2005). The European subspecies *Vulpes vulpes crucigera* Bechstein 1789 dwells within the geographic region considered in this paper. It is sympatric with two members of the Canidae family: the gray wolf (*Canis lupus* Linnaeus 1758) and the raccoon dog (*Nyctereutes procyonoides* Gray 1834)—an introduced species the number of which significantly exceeds that of native predators (Makarov et al., 2009). From the morphological point of view, the red fox is well studied, including the metric and discrete variability of its skull (Huson and Page, 1980; Helle et al., 1989; Ansorge, 1994; Szuma, 2007, 2008; Hartová-Nentvichová et al., 2010, 2010a; etc.). A significant part of the morphological papers is devoted to study of the species across a large part of the range in the Old and New Worlds (Churcher, 1960; Davis, 1977; Szuma, 2007, 2008; etc.), and only a few publi-

Table 1. Characteristics of the material used

Sample no.	Collection site in Tver oblast	Males	Females	Total	Collection period
1	Southwest	70	80	150	1982–2006
2	Center	52	43	95	1995–2005
3	Northeast	33	39	72	2003–2006
4	Southeast	48	38	86	1996–2010

cations deal with the metric variability of the species at the level of individual populations and subpopulations (Huson and Page, 1980). The few (Yudin, 1986) studies of the chronographic variability of foxes have recently attracted the interest of theriologists (Yom-Tov, Y. and Yom-Tov, S., 2012; Goskov and Korytin, 2016; etc.).

Geographically, the closest points of study of the craniometric variability of the species are the northwestern European part of Russia (Danilov et al., 1979) and Moscow oblast (Szuma, 2008). In Tver oblast and the neighboring regions, no such studies have been performed.

The fox is a traditional object of hunting, so representative osteological material have been collected, covering various geographic locations of Tver oblast over a long period; data have been accumulated on the ecological and demographic characteristics, which creates prerequisites for performing fundamental morpho-ecological studies of the species.

The aim of this work is to study the craniometric variability of the red fox and assess how the morphological diversity of the skull is influenced by the age and sex of individuals, and geographical and chronographic variability.

MATERIALS AND METHODS

Information on the number of species in the study area was obtained in the regional bodies of Rosprirodnadzor (Ministry of Natural Resources of Tver oblast). For the period of collection of the analyzed sample, according to the winter route accounting from 1976 to 2008, the average number of species in Tver oblast amounted to 8500 ± 800 individuals (minimum 5500, maximum 12800).

The sex, location, and date of hunting of animals were indicated by the corresponding hunters who participated in the collection of the material. The geographic coordinates of the capture sites in degrees and minutes were obtained as geographic centroids of the samples in each administrative district in the MapInfo GIS-Russia desktop mapping system.

The age of each individual was determined visually according to the degree of development of the relief structures of the skull (sagittal crest, orbital processes), obliteration of the nasal and intersectional

sutures, the state of the dental system (Habermehl, 1986; Klevezal, 2007), and by using instrumental techniques on layers of cement for decalcified and dyed preparations of the apical part of the canine (Klevezal and Kleinenberg, 1967). By the combination of external characters, a group of the oldest individuals was selected ($\approx 7\%$ of the sample) from the canines of which preparations were made. Among the individuals classified as “old,” 20% were animals aged 3+ years; 25%, 4+ years; 25%, 5+ years; 15%, 6+ years; and 15%, 7–8+ years. In general, the ratio of age groups in the sample of foxes from Tver oblast corresponded to that of animals inhabiting Wales (Great Britain) (Huson and Page, 1980), and is close to that obtained in the Czech Republic (Hartová-Nentvichová et al., 2010a). In the subsequent calculations, the skulls were divided into two groups: young individuals, prereproductive age individuals, and adults aged 1+ and older.

The measurement scheme included 17 measurements of the skull and mandible, including the measurement of bilaterally symmetrical characters. The scheme is largely unified with that proposed by Ansoerge for the red fox (Ansoerge, 1994) (Fig. 1). Measurements with an accuracy of 0.01 mm were made with a Sylvac S_Cal Work digital caliper synchronized with a computer using an optical cable.

The total amount of material studied was 403 specimens. The skulls of the animals were distributed across the conventionally designated areas of collection, covering all of Tver oblast (Table 1, Fig. 2).

The processed material is in the collections of the Craniological laboratory of the Central Forest Reserve (samples 1–3) and at the Department of Biology of Tver State University (sample 4).

The analysis included all the skulls that preserved the integrity of the overall structure. To compensate for the measurements that cannot be obtained on damaged skulls, a linear regression method was used. To do this, the correlation links of the measured signs between each other were determined for fully complete specimens ($n = 153$). The measurement that correlated the most with the desired attribute was a predictor (x), and the “response” measurement (y) was the desired variable. An equation of the form $y = a + b \times x$ was obtained. To assess the quality of prediction of the trait, the coefficient of determination R^2 and the level

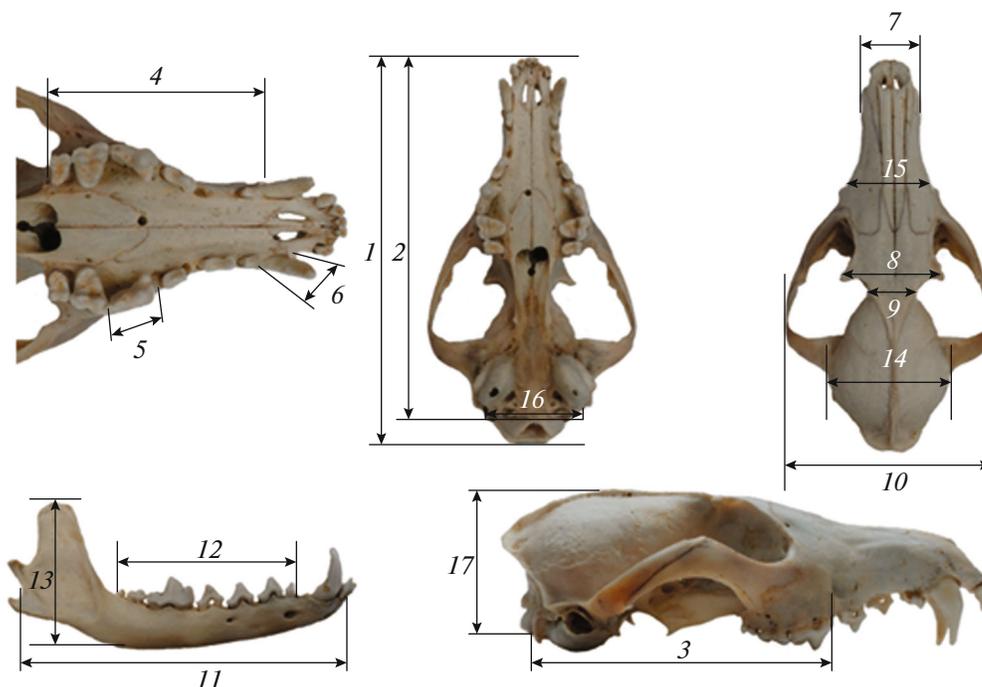


Fig. 1. Scheme of fox skull measurements: (1) condylbasal skull length, (2) distance from the rear edge of the drum chambers to the front edge of the incisal bone, (3) distance from the rear edge of the drum chambers to the rear edge of the infraorbital foramina, (4) length of the upper molar teeth, (5) coronary length P⁴, (6) width of the upper canine at the base, (7) width of the upper jaw above the canines, (8) distance between the lateral edges of the postorbital processes, (9) width of the postorbital constriction, (10) zygomatic width, (11) length of the lower jaw from the front edge of the neck neutral incisal alveoli to the notch between the articular and angular processes, (12) length of the lower row of molars, (13) the greatest height of the coronoid process, (14) the width of the cerebral capsule (maximum), (15) rostrum width at the level of the infraorbital foramina, (16) width at the level of the jugular processes, and (17) the maximum height of the skull.

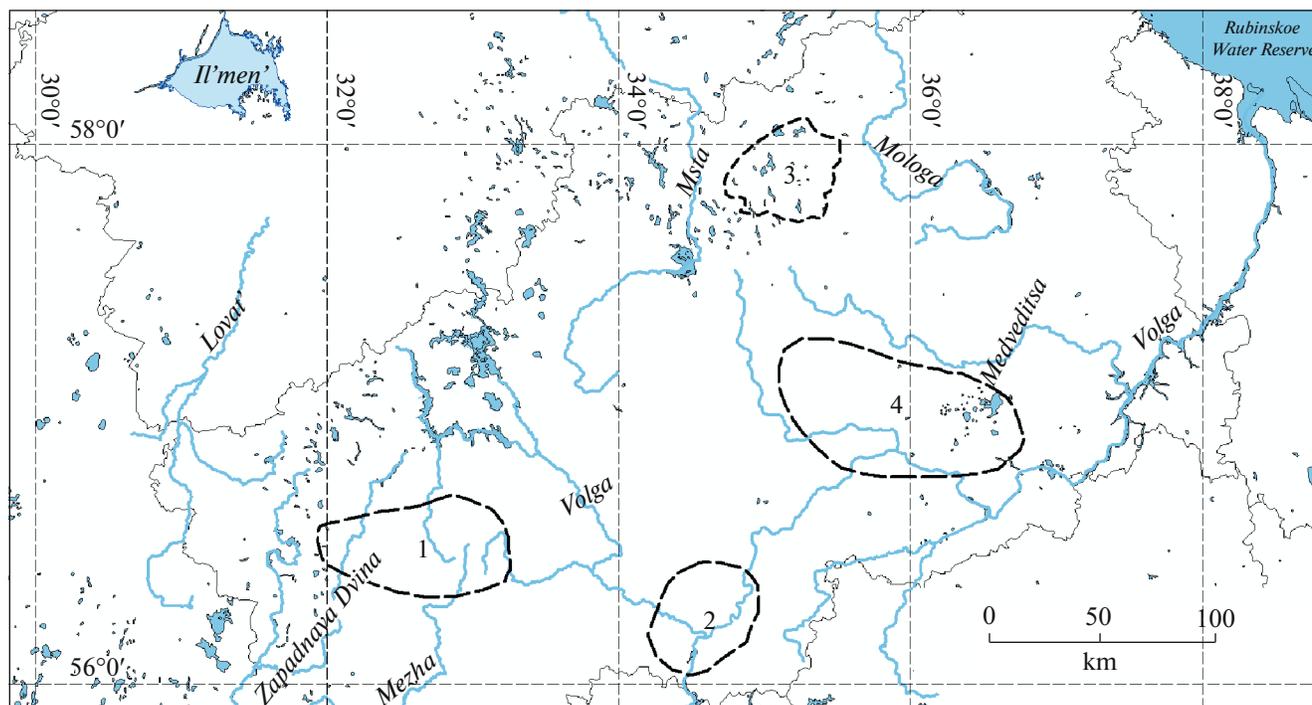


Fig. 2. Map of the collection sites. The dashed line shows the collection areas, and their numbers correspond to the numbers given in Table 1.

of statistical significance of the assessment p were used. The filling of the gaps was carried out taking into account the sexual and territorial affiliation of the animals.

To study sexual dimorphism, we used the methodological approach described by us earlier (Korablev et al., 2013). The sexual dimorphism index (SDI) was calculated by the formula: $SDI = 100 \times (X\delta - X\varphi)/X\varphi$, where SDI is the percentage of sexual dimorphism; $X\delta$ and $X\varphi$ are the average values of characters for males and females. Discriminant analysis was applied to highlight the characters that are most significant in the description of intersexual differences. The scale of morphological differences was estimated by the magnitude and statistical significance of the Mahalanobis distance between samples (D^2) (Rozhnov and Abramov, 2006), and the qualitative assessment of differences was performed by the percentage of correctly classified individuals in a priori defined classes: males and females (Hartová-Nentvichová et al., 2010). To further characterize the morphological variability of males and females, the coefficient of variation (CV) was used (Mednikov, 1969; Mieri et al., 2005), evaluating the significance of differences between the sexes using the Wilcoxon nonparametric test (Mieri et al., 2005). Analysis of the sexual size dimorphism was carried out for the entire sample, without geographic separation.

In order to obtain virtual independent factors (macro variables) describing the variation of all craniometric variables, nonmetric multidimensional scaling was performed. The logarithms of the initial dimensions of the skull had preliminarily been taken using the formula $b = \log x_{ij}$ and the decimal logarithm, where b is the measured sign and x_{ij} is the measured value of the sign for each individual. The need for data normalization is dictated by the fact that the physical value of the logarithm is determined by the relations in the system in accordance with the function $y = a \times x^b$ (Puzachenko, 2004). From the biological point of view, the effect of allometric age-related changes is thus manifested, as individuals of different ages are present in the sample. To build ordination, the Euclidean distance was used; as a result of calculations at 1000 iterations, we stopped at three axes of multidimensional scaling (AMS), the stress value was 0.108. The share of variability explained by the axes was AMS-1 = 65.3%, AMS-2 = 16.5%, AMS-3 = 12.1%, in total, 93.9%.

Biological interpretation of the obtained AMS macro variables was carried out taking into account their correlation, first, with the craniometric characters and, second, with the tested factors of metric polymorphism. A nonparametric Spearman rank correlation coefficient was used as a measure of conditionality. Taking into account the conditionality of the AMS variability, they were analyzed. To assess the nature of the influence of the factors studied on macro

variables, a general model of multivariate regression analysis was used.

As reference methods, for the cross-validation of results and elimination of statistical errors of the first and second kind (we assume the presence of space–time variability a priori), discriminant and permutation multivariate analysis of variance (PERMANOVA) (Anderson, 2001) of the measured characteristics was used, in which the predictors were the following tested factors: collection region, sex, and age of the animals. A comparison of the results obtained using various methods of multivariate statistical analysis significantly increases the reliability of the findings (Nuzzo, 2014).

Multidimensional nonmetric scaling and PERMANOVA (Euclidean distance, 999 iterations, Bonferroni correction) were performed in the statistical environment R (R Core Team, 2016). The IBD program (Bohonak, 2002) was used to estimate the effect of isolation by distance on morphological variability using the Mantel test (1000 iterations). All other statistical calculations were performed in the Statistica 12.0 software package.

RESULTS

Description of the Macro Variables Used

The morphometric diversity of the red fox with the measurement scheme used is described by three AMS. Using the Spearman correlation criterion, the dependence of variation of the axes on individual variables—the measured characteristics of the skull—was established (Table 2).

As Table 2 shows, the first axis is significantly correlated with all the measured variables, with the exception of the width of the post-orbital constriction. The highest values of the correlation coefficients (≥ 0.70) were determined for the skull characters, reproducing the total dimensions of its cerebral and visceral parts (characters 1–3, 6, 7, 10–13). For the second axis, low correlations with many craniometric characters were revealed, but it describes the variability of characters 8 (the distance between the lateral edges of the post-orbital processes) and 9 (the width of the post-orbital constriction) to the greatest extent. The third axis of multidimensional scaling correlates with the minimum number of measurements, among all axes. Nevertheless, it contains an important piece of information characterizing the variability of the characters: 15 is the width of the rostrum at the level of the infra-orbital foramina, 5 is the coronary length of the fourth premolar, and 6 is the width of the canine at the base. The axes are orthogonal with respect to each other, and there is no correlation between them ($r_{\text{Spearman}} \geq 0.001, p > 0.05$).

Further, it follows from the above calculations that the variation of AMS-1 is due to two factors: the sex and age of animals. AMS-2 correlates insignificantly with the age and sex of the animals. AMS-3 statisti-

Table 2. The values of the Spearman correlation coefficient of axes with the variables: the sizes of the skull and predictors

Parameter	AMS-1	AMS-2	AMS-3
1	-0.80	-0.19	0.14
2	-0.85	-0.20	0.13
3	-0.83	-0.23	–
4	-0.69	-0.31	-0.18
5	-0.51	-0.16	-0.36
6	-0.70	-0.11	-0.36
7	-0.74	–	–
8	-0.64	0.57	–
9	–	0.79	-0.21
10	-0.79	–	–
11	-0.87	-0.17	–
12	-0.77	-0.20	–
13	-0.77	-0.11	–
14	-0.65	–	–
15	-0.59	0.15	0.64
16	-0.66	-0.10	0.19
17	-0.61	–	–
	Predictor		
Sex	0.50	0.11	–
Capture period	–	–	-0.34
Age	-0.52	-0.12	–
	Capture site		
Longitude	–	–	-0.45
Latitude	0.12	–	-0.27

Only statistically significant ($p < 0.05$) correlations are shown. A dash indicates the absence of a statistical significance.

cally significantly correlates with three factors: the capture period, the geographic longitude, and the breadth of material collection, in the absence of a significant correlation with the sex and age group of animals. Therefore, the biological meaning of the axes can be summarized as follows: the first axis describes the sex of the animals and their age group. The second axis, to a much lesser extent, describes the sex and age variability. The third axis reproduces the spatial–temporal variability of the red fox. Taking into account the proportions of the variance reproduced by the axes, it is possible to speak about the predominance of the sex–age variability in craniometric data over all other types of variability. The spatial–temporal variability is much less pronounced. However, its manifestation with such a small geographic coverage and time interval in the samples studied deserves attention, of

course. Thus, the performed analysis of the macro variables obtained—the axes of multidimensional scaling—confirms the initial hypothesis about the effect of a priori selected polymorphism factors on the size variability of the fox skull.

Sexual Size Dimorphism

The results of the calculation of SDI are given in Table 3. On average, for all skull characters, SDI amounted to 3.01 with the maximum and minimum values of -0.15 and 5.02 , respectively. Males exceed females in size in all measured characters of the skull, with the exception of the interorbital width. The minimum value of SDI is noted for character 16 (width at the level of the jugular processes). Maximum sexual differences were found in some characters of the dental system and jaw apparatus, among which are the width of the upper canine at the base (6), the length of the mandible, and the height of its coronary process (11, 13). The intersexual differences in the characters characterizing the overall dimensions of the skull, for example, the condylobasal length (1) and some related measurements, are quite significant: the zygomatic width (10) and the width of the upper jaw above the canines (7). In the group of immature animals, the mean value of SDI was significantly lower and amounted to 1.04.

The average coefficient of variation for seventeen characters in females is 4.37 ± 0.39 and in males is 4.62 ± 0.38 ; according to the Wilcoxon criterion, the differences between them are not significant ($p < 0.05$). The values of the coefficient of variation in the group of animals of prereproductive age were slightly lower and amounted to 4.20 ± 0.61 for females, 4.26 ± 0.65 for males, statistically significant differences between them were also absent ($p < 0.05$).

Discriminant analysis allowed us to establish that the correct classification of individuals into the sex groups (males and females) was 76.2 and 75.9%, respectively. The square of Mahalanobis distances (D^2) between them is 1.71, and the differences are statistically significant: $p = 0.000001$. According to discriminant analysis, the following characters have the highest resolution: the width of the upper canine at the base of ($W-\lambda = 0.71$, $F = 5.63$, $p = 0.02$), the width of the rostrum at the level of the infraorbital foramina ($W-\lambda = 0.71$, $F = 4.44$, $p = 0.04$), the distance from the rear edge of the drum chambers to the front edge of the incisal bone ($W-\lambda = 0.71$, $F = 5.33$, $p = 0.02$).

Different methods of statistical processing of the sexual size dimorphism give fundamentally similar results, but slightly differ in details. The best quantitative visual assessment of intersex differences can be determined by the total size of the skull, whereas functionally important characters with small linear dimensions can be identified using the relative size indices of males and females.

Assessment of the Effect of Sex and Age Factors of Metric Polymorphism

Taking into account the conditionality of the variation of AMS-1 by the sex and age variability of animals, using the general model of multifactor regression analysis, we investigated the force and nature of the influence of these factors on the size polymorphism of the skull. The number of individuals involved in the analysis was 333 adults and 63 young. The quality of the regression analysis model is characterized by the correlation coefficient (R) = 0.65, the corrected coefficient of determination (R^2) = 0.43, and the Fisher criterion (F) = 149.8, with a high statistical significance $p > 0.001$. To estimate the contribution of each of the tested factors to the morphological variability of the skull, the Pareto coefficients (α) were used. Graphically, the nature of the influence of the factors on the dynamics of age and sex variability is presented in Fig. 3.

It follows from the graph that males at a young age are larger than females, and with age, these differences remain and increase. Sexual size dimorphism progresses: with age, sex differences increase. Both age ($F = 141.06$, $p = 0.0001$) and sex ($F = 111.10$, $p = 0.0001$) are factors that are almost identical in their influence on the variability of the skull. The values of the coefficients α for the former and the latter were 11.88 and 10.54, respectively.

Chronographic and Geographical Variability

Discriminant analysis of male foxes from various samples allowed us to distinguish two of the most variable craniometric characters: the coronary length P^4 $W\text{-}\lambda = 0.53$, $F = 2.7$, $p = 0.04$ and the rostrum width at the level of the infraorbital foramina $W\text{-}\lambda = 0.59$, $F = 9.78$, $p = 0.00005$. These skull measurements are related to the functioning of the dental apparatus in animals; however, the latter of these characters has the highest resolution in terms of spatial variation.

The classification matrix of discriminant analysis indicates that the average level of recognition of populations is 60.1%. Samples 1 (72.9%) and 4 (70.8%) are recognized best of all, and samples 2 (48.1%), and 3 (36.4%) are slightly worse; in the erroneous classification, they are most often associated with sample 1.

As a result of the analysis of females carried out according to a similar scheme, two craniometric characters were identified with the greatest contribution to the variation of their sizes made by the geographical collection area: the width of the brain capsule $W\text{-}\lambda = 0.58$, $F = 3.00$, $p = 0.03$, and the width of the rostrum at the level of the infraorbital foramina $W\text{-}\lambda = 0.67$, $F = 13.40$, $p = 0.00001$. It is character that, in the two sexes, the width of the rostrum at the level of the infraorbital foramina is subject to spatial variability to a greater degree.

Table 3. Morphometric characterization of adult red fox males and females in Tver oblast

Parameter	Mean \pm error	Min–max	CV	SDI
1	148.59 \pm 0.37	138.31–162.47	3.45	3.63
	143.43 \pm 0.31	134.06–157	2.78	
2	140.62 \pm 0.33	129.71–153.68	3.25	3.94
	135.32 \pm 0.30	126.51–148.92	2.84	
3	89.58 \pm 0.20	81.14–96.53	3.09	3.61
	86.46 \pm 0.21	79.11–95.58	3.02	
4	55.12 \pm 0.21	36.04–66.77	5.27	3.14
	53.44 \pm 0.19	44.48–60.71	4.56	
5	14.94 \pm 0.05	12.59–16.55	4.73	2.56
	14.56 \pm 0.05	12.40–16.22	4.68	
6	7.17 \pm 0.03	5.74–9.20	6.65	5.02
	6.83 \pm 0.04	5.34–8.95	6.51	
7	24.50 \pm 0.10	21.02–28.34	5.70	3.23
	23.72 \pm 0.09	20.68–26.72	5.01	
8	37.75 \pm 0.21	30.94–45.70	7.56	3.43
	36.49 \pm 0.23	29.50–45.10	7.83	
9	22.59 \pm 0.10	19.65–30.12	6.12	–0.15
	22.63 \pm 0.12	19.43–26.72	6.74	
10	80.13 \pm 0.22	72.00–89.24	3.83	3.52
	77.37 \pm 0.23	70.26–95.78	3.85	
11	108.12 \pm 0.24	101.40–116.06	3.06	3.25
	104.73 \pm 0.25	96.16–115.95	3.02	
12	61.36 \pm 0.14	53.62–65.74	3.17	2.43
	59.88 \pm 0.14	54.72–66.34	2.94	
13	39.92 \pm 0.14	34.61–44.20	4.61	4.40
	38.24 \pm 0.15	32.98–44.20	4.95	
14	48.56 \pm 0.10	42.67–52.08	2.79	2.31
	47.46 \pm 0.11	44.07–51.90	2.93	
15	30.11 \pm 0.16	25.04–37.76	7.34	2.66
	29.36 \pm 0.14	25.62–35.62	6.22	
16	47.38 \pm 0.16	36.39–52.17	4.64	1.85
	46.51 \pm 0.13	38.85–50.43	3.64	
17	42.18 \pm 0.10	39.38–48.56	3.22	2.36
	41.19 \pm 0.09	36.68–45.40	2.83	

For each character, males are on the upper line ($n = 183$) and females are on the lower line ($n = 157$). For (1–17) see Fig. 1.

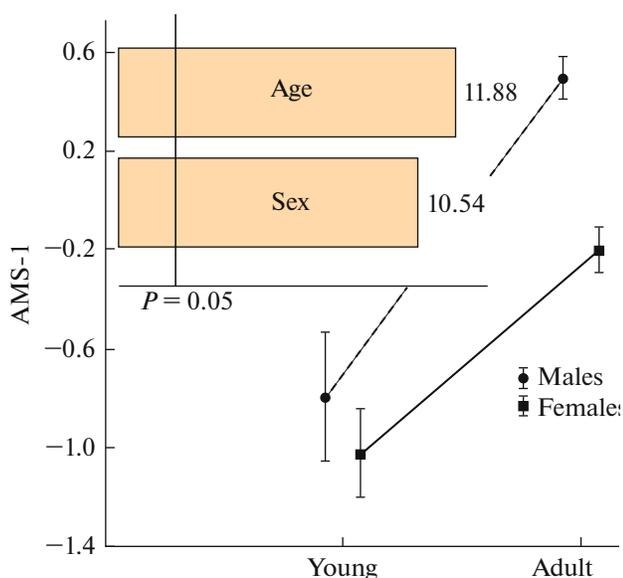


Fig. 3. Dynamics of age and sex variability of the red fox. The histogram shows the factors distributed by the force of influence, and the numbers correspond to the values of α . Vertical lines indicate a 95% confidence interval.

The classification matrix indicates that the average level of recognition of females from different samples is 56.5%. Among the individual samples, the best recognized is sample 1 (75.0%), and sample 4 is slightly worse (52.63%). The most poorly recognizable sample is 2 (39.53%), and as in the case of males, an erroneous classification counts them as sample 1.

The results of permutational multidimensional dispersion analysis of all measured characters without separation by sex and age indicates significant differences between samples 1 and 3 ($F = 4.83$, $p = 0.024$) as well as between 1 and 4 ($F = 8.27$, $p = 0.006$). Adult males and females differ in samples 1 and 4 ($F = 8.51$, $p = 0.006$, the former, $F = 3.71$, $p = 0.02$, the latter). Young animals from different samples under the age of one year did not differ significantly ($p < 0.05$). When used as dependent variable characters 5, 6, and 15, samples without separation by sex and age differ in pairs 1 and 2 ($F = 7.76$, $p = 0.006$), 1 and 3 ($F = 14.44$, $p = 0.006$), 1 and 4 ($F = 26.70$, $p = 0.006$), as well as between 2 and 4 ($F = 6.28$, $p = 0.012$). Males are significantly different in pairs 1 and 3 ($F = 6.75$, $p = 0.018$), 1 and 4 ($F = 19.42$, $p = 0.006$), as well as between 2 and 4 ($F = 6.17$, $p = 0.024$). In females, samples 1 and 2 ($F = 5.61$, $p = 0.006$), 1 and 3 ($F = 9.87$, $p = 0.006$), as well as between 1 and 4 ($F = 11.28$, $p = 0.006$) are different. At the age of one year, only females differ in samples 1 and 4 ($F = 6.03$, $p = 0.036$). Adult males differ significantly in pairs of samples 1 and 3 ($F = 5.96$, $p = 0.006$), 1 and 4 ($F = 15.24$, $p = 0.006$), and 2 and 4 ($F = 4.85$, $p = 0.024$). In adult females, samples 1 and 2 ($F = 4.98$, $p = 0.042$), 1 and 3 ($F = 7.75$, $p = 0.006$), as well as between 1 and 4 ($F =$

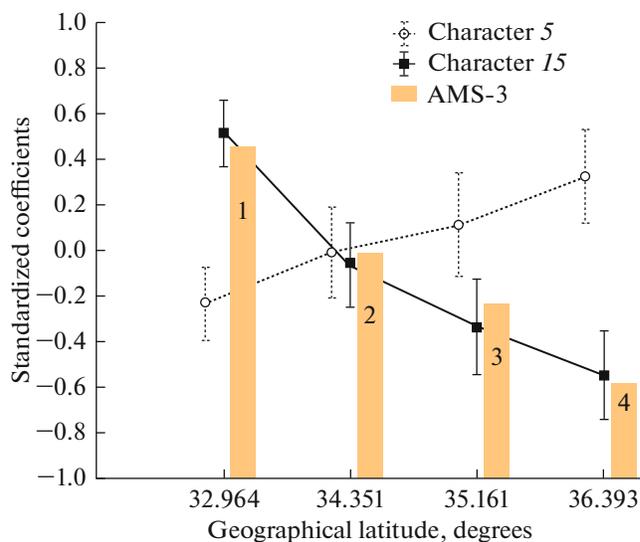


Fig. 4. The variability of the individual sizes of the skull and fox dental system in the context of geographical longitude: the four collection points correspond to the four coordinates on the chart. Vertical lines indicate a 95% confidence interval.

7.41, $p = 0.006$) are different. From the analysis performed, it can be concluded that geographic variability manifests itself in animals of reproductive age, the nature of the variability of both sexes is predominantly symmetrical, except that differences were found not only between the first and other samples, but also between the second and fourth localities in males. The most contrasting differences were found in the foxes from the first and fourth samples when analyzing the three most variable characters.

The analysis performed allows us to assume the more or less pronounced originality of the animals from the first locality and, to a lesser extent, from the fourth one. Given that discriminant analysis distinguishes the width of the rostrum at the level of the infraorbital orifices as the most variable trait of fox males and females, it is possible to use the AMS-3 as a variable that generalizes the spatial and temporal variability of the species. Since this variable is practically devoid of the influence of the sex and age components, discriminant analysis allows us to generalize the trends of spatial variability in the general sample. In this case, with extremely high discrimination power, $W\text{-}\lambda = 1.00$, $F = 14.1$, $p > 0.0001$, the share of correct recognition of sample 1 was 90.0%. For sample 4 it does not exceed 36.8%. The rest are not recognized, and the average level of correct classification is 44%.

The nature of the spatial variability of animals in the context of longitude is presented in Fig. 4.

The graph determines the variation of the fox rostrum width as a decrease in the gradient of geographic longitude from southwest to northeast and southeast of Tver oblast: the maximum differences between sam-

Table 4. Values of the most variable characters of the red fox, mm

Character	Sample no.			
	1	2	3	4
5	14.51 ± 0.06	14.68 ± 0.08	14.76 ± 0.08	14.92 ± 0.08
6	6.93 ± 0.05	6.98 ± 0.05	6.89 ± 0.05	6.96 ± 0.05
15	30.60 ± 0.20	29.40 ± 0.17	28.84 ± 0.18	28.40 ± 0.17

ples 1 and 4 are 2.2 mm, or 7.2%. The variability of the fourth premolar coronary length is characterized by a contrasting trend: the highest values were found for sample 4; the minimum ones, for sample 1. The differences between them are 0.4 mm, or 2.7%. Table 4 shows the average values of the most variable craniometric characters in spatial–temporal terms.

The analysis of the values of the characters presented in the table reveals a general tendency: the wider the rostrum, the shorter the coronary length of the fourth premolars and the smaller the width of the canines; the smaller the width of the canines, the shorter the coronary length of the fourth premolar. However, the apparent trend is not statistically significant. It is, probably, determined by a higher correlation of the odontological characters among themselves, compared with the correlation of the odontological and craniometric characters. Figure 5 shows the anatomical regions of the skull in which the dimensional morphological variability of the fox that inhabits the center of the European part of Russia is the most pronounced.

Figure 6 shows the chronographic dynamics of the fox skull size in Tver oblast over a period of 28 years.

The nature of the chronographic variability of the skull is determined by the variation in the width of the rostrum (15), the coronary length of the fourth premolar (5), and, to a slightly lesser extent, the width of the canine (6). It shows a pronounced fluctuation. The most significant variability covers the period from the early 1980s to the early 1990s (5 = 14.52 ± 0.17 mm; 6 = 7.59 ± 0.30 mm; 15 = 30.71 ± 0.56 mm). After a short period from 1990 to 1995, characterized by a decrease in the value of characters 5 = 14.56 ± 0.11 mm and 6 = 6.97 ± 0.07 mm, but a slight increase in character 15 = 32.28 ± 0.29 mm, from 1996 to 2010 there is a tendency toward an increase in characters 5 = 14.81 ± 0.04 mm; 6 = 7.00 ± 0.03 mm, and a decrease in character 15 = 29.22 ± 0.10 mm. Significant differences for the periods of animal captures were found for character 6: 1982–1989 and 1990–1995, also for the collection years 1982–1989 and 1996–2010 and character 15: 1982–1989, 1990–1995, and 1996–2010.

DISCUSSION

Sexual Size Dimorphism

In exploring the sexual dimorphism of the fox in the population of northeastern Ireland, Lynch (Lynch, 1996) noted that males have a larger, more elongated skull than females, but at the same time are characterized by a relatively narrow interorbital width. Researchers from the Czech Republic came to similar conclusions analyzing the sexual dimorphism of the species in this country (Hartová-Nentvichová et al., 2010). The data obtained in this work confirm the sex characteristics mentioned for the populations of the species of insular and continental Europe. The mean value of sexual dimorphism, calculated as SDI in the fox populations of the Czech Republic, slightly exceeded the figure obtained by us (3.3 Czech Republic, 3.01 our data). Thus, the highest values of sexual dimorphism are characteristic for the following characters: the length of the skull (SDI = 3.7–4), the zygomatic width (SDI = 3.8), and the width of the canine (SDI = 4.7). The interorbital width in males is smaller than that of females (SDI = –0.4). This ratio of the size proportions of the skull of the two sexes, in terms of functional biomechanics, indicates a greater force of compression of the jaws in males and their ability to hunt for larger prey. Using the example of the raccoon dog of the Japanese Islands, a negative correlation was found between the interorbital width and the power of the chewing muscles (Haba et al., 2008). Along with a significant development of the width of the zygomatic arches, this indicates a more developed jaw apparatus of the males, allowing them to reach greater force of compression of the jaws. Such biomechanical advantages are designed to reduce intraspecific competition due to some segregation of the trophic niches. However, they are not the primary cause of sexual dimorphism, the fundamental bases of which are formed by sexual selection.

The ratio of the shares of males and females correctly classified using discriminant analysis also gives an idea of the dynamics of size sexual dimorphism in different parts of the range of the species. In northeastern Ireland, the values varied from 73 to 87% (Lynch, 1996); in Norway they reached 73% (Frafjord, 1993); and in Wales, 88% (Huson and Page,

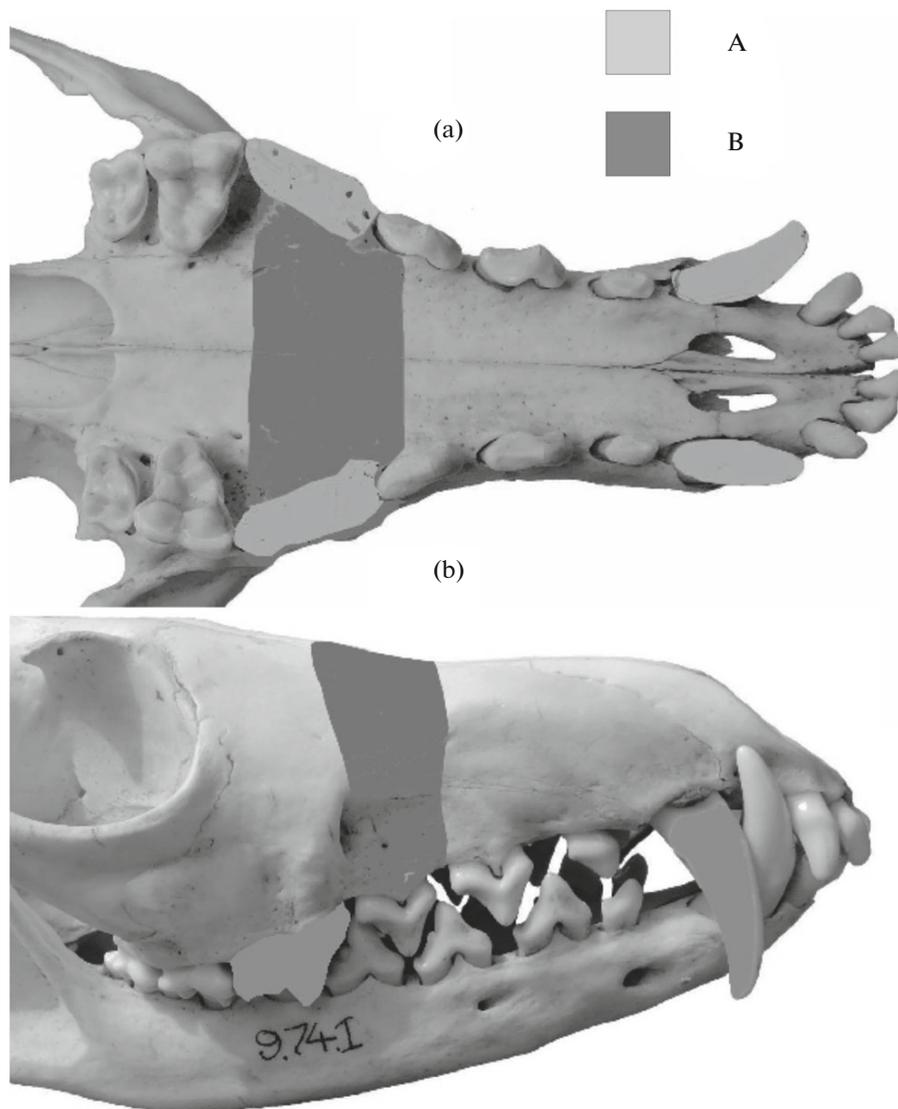


Fig. 5. The most variable anatomical and functional regions of the visceral skull of the red fox: (a) ventral, (b) lateral projection. (A) Characters with a higher correlation value ($r_{\text{Pearson}} = 0.44, p > 0.05$), (B) characters with a lower correlation value ($r_{\text{Pearson}} = 0.25, p > 0.05$).

1979). In the Czech Republic the proportion of correct recognition of males was 65% and that of females was 54% (Hartová-Nentvichová et al., 2010). The values of “recognition” of the sexes obtained by us to a greater extent correspond to the sexual dimorphism of the species in Northern Ireland.

The age dynamics of sexual dimorphism, which manifests itself as progressively increasing differences in the size of the sexes, was also noted in the Czech Republic (Hartová-Nentvichová et al., 2010). In particular, the authors cited established trends toward an increase in the size sexual dimorphism of the condylobasal length and zygomatic width, reaching a peak of values in animals older than one year of age. The interorbital width shows a complex tendency: when females

are of a large size under the age of one year, sex differences are leveled when they reach one year and increase as much as possible in the group of 2+, when females exceed in size the characters of males. If we consider changes in the size sexual dimorphism in ontogenesis, according to Hartov-Nentvichova et al. (Hartová-Nentvichová et al., 2010), the mean SDI in yearlings was 3.2 and for adults, 3.3, which corresponds to our conclusions on the age dynamics of this indicator. These results are consistent with the position of Geodakyan (1991), according to which the intergender differences increase with age.

For the red fox, the fact of the spatial–temporal variability of sexual dimorphism is confirmed. On the scale of the range, the manifestation of sexual differ-

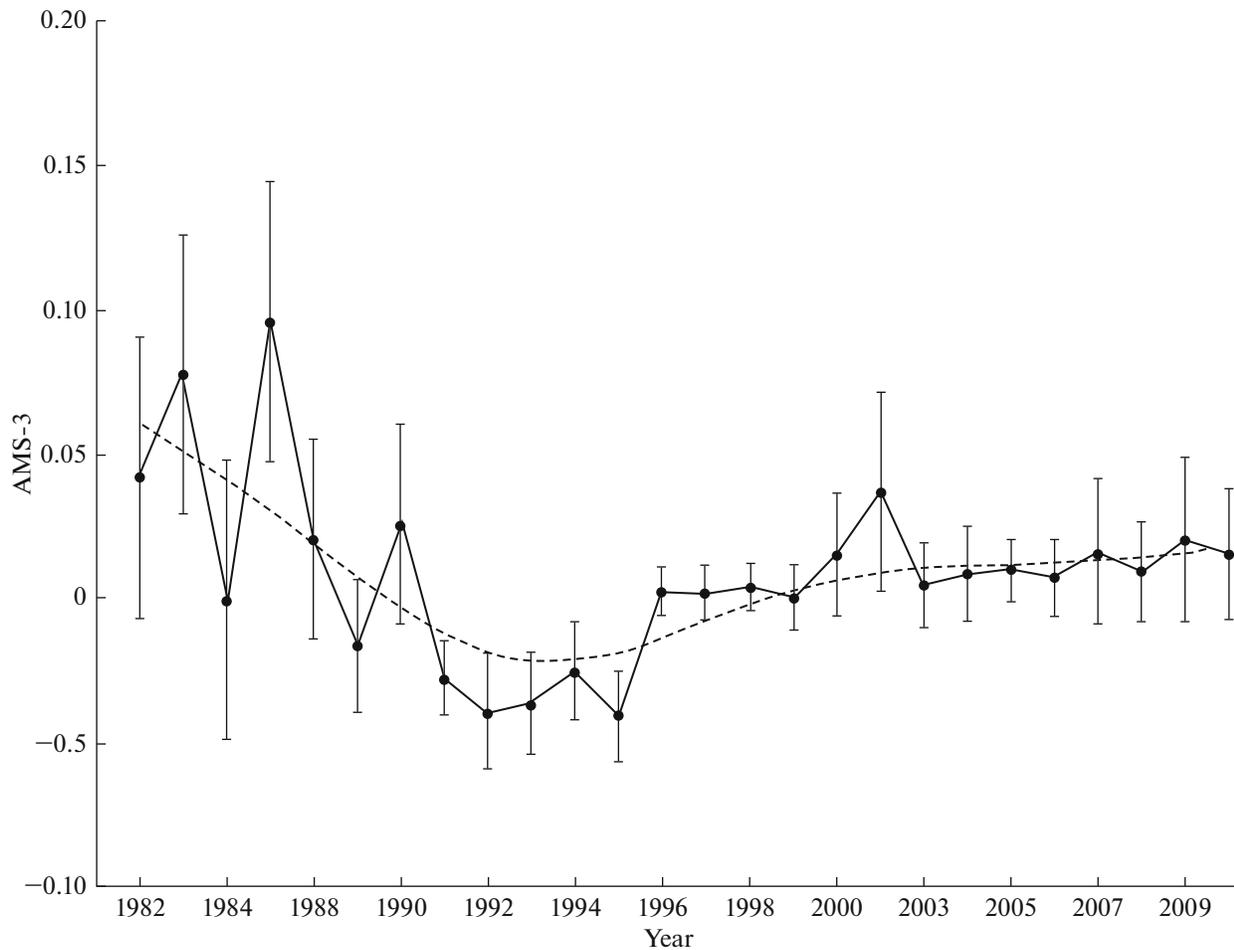


Fig. 6. Chronographic dynamics of the red fox size. Vertical lines indicate a 95% confidence interval.

ences depends, in addition to sexual selection, as well as intra- and interspecific competition, on the density of populations, which determines the variation of the breeding strategy from poly- to monogamy (Szuma, 2008).

Spatial Variability

In the present study, taking into account the geographical coverage of the territory, we study the phenomenon of the intrapopulation variation of the red fox. However, even in a relatively small area, the subpopulations of the species have significant geographical variability of individual craniometric characters. The results of a comparison of similar measurements of fox skulls collected in the Czech Republic (Hartová-Nentvichová et al., 2010) and considered in this study indicate that the animals in the center of the European part of Russia are larger. In some measurements, such as the condylobasal length, fox skulls from Russia are larger by 4.8 (males) and 5.5 mm (females). The zygomatic width is a parameter that hardly changes in the populations under consideration, as is

the width of the interorbital space and the cerebral capsule. The height of the coronoid process of the lower jaw and the length of the upper row of molars are 1.1 and 2.6 mm larger in the animals from the territory of the European part of Russia. The differences between the animals from the southwest (Czech Republic) and the northeast (our data) correspond to the tendency of the latitudinal nature of the size variability noted in the study of fox populations, for example, in the Palearctic (Szuma, 2008). However, in comparing the foxes from the center and northwest of the European part of Russia, they are found to be smaller. Thus, the condylobasal length of the skull is shorter than that of the animals studied by us by 3.5 (males) and 3.4 (females) mm, the zygomatic width by 1.5 and 1.1 mm, but the interorbital width of the northwestern foxes is larger by 0.4 (males) and 1.1 mm (females) (Danilov et al., 1979). This suggests a more complex trend of intraspecific variability, which does not always correspond to the “latitudinal” nature.

The variability of the species on the microgeographic scale, within 70–180 km, found in the popu-

lation of foxes in the British Isles, in Wales (Huson and Page, 1980), may be associated with the influence of the environment in a gradient of complex terrain.

The nature of the size variation of the fox within Tver oblast indicates a pronounced variability of at least two craniometric characters: the width of the rostrum and the coronary length of the fourth premolar. Both characters are associated with functional features of the dental apparatus; therefore, it can be assumed that they are determined both by dietary variability and by social factors implying intra- and interspecies contacts. With the low population density of the red fox in Tver oblast (0.07–0.16, on average, 0.1 individuals/km²), the intraspecific competition in the populations of this carnivore is not high. In addition, in this part of the range, the fox has no direct competitors; aggressive interspecific interactions are observed only when the burrows are shared with a badger or a raccoon dog (Kowalczyk et al., 2008; Drygala and Zoller, 2013).

From the point of view of isolation by distance and the occurrence of morphogenetic originality of individual samples, the influence of this factor in the territory under consideration is leveled by a low, but stable population of the species and the absence of geographical barriers. This is confirmed by the Mantel test when comparing matrices of geographical distances between samples with their morphological distances expressed as D^2 : there was no statistically significant correlation between them ($Z = 7589.56$, $r = 0.54$ at $p \leq 0.16$). Individual fox habitats in continental Europe reach 30 km², and the diurnal travel length is up to 11.8 km (Goszczycki, 2002). Such biological features of the species determine panmixia on a microgeographic scale.

Important predictors of the intraspecific size variability of mammals are food resources, which are characterized by nutritional value, abundance, and structure of individual groups of food, and competitive relationships, exacerbated in interspecific relationships by close ecological niches (Van Valen, 1965; Meiri et al., 2005; Huston and Wolverton, 2011). Therefore, the noted differences in the individual sizes of the skull and the dental system of the fox can be caused by the joint, complementary influence of factors. The range of food available to animals, the adaptive variability of individual morphological structures to the characteristics of the mesoclimate, and, to some extent, the territorial disunity of the sites of material collection at a distance exceeding 300 km, which contributes to the emergence of peculiar morpho-genetic localities, can play a significant role.

Chronographic Variability

With collections of fox skulls covering a long time interval on a limited geographic space, it is convenient

to test the hypothesis of chronographic variability of the species. The results of our study show that, over three decades in Tver oblast, the chronographic variability of the fox is reliably present. In terms of influence, the factor of temporal size variability is inferior to the factors of age, sex, and geographic variability. The chronographic variability of the fox in this part of the range fluctuates and has no directed tendency. It should be noted that for the fox and the wolf, in the second half of the 20th century in many populations of Asia Minor and Europe, including the European territory of Russia up to the Urals and in the populations of the Far East, researchers have noted a tendency to increase in size, primarily the length of the skull (Yudin, 1986; Korytin and Goskov 2016; Yom-Tov, Y. and Yom-Tov, S., 2012; Goskov and Korytin, 2016). According to some authors, chronographic variability of sizes prevailed over the geographic one (Goskov and Korytin, 2015).

A number of hypotheses are intended to explain the observed phenomenon, among them anthropogenic influence, both indirect, i.e., global climate change (Goskov and Korytin, 2016), and direct, through the formation of a large area of agrocenoses (Yom-Tov, Y. and Yom-Tov, S., 2012). The “anthropogenic” hypothesis implies an increase in the primary productivity and quality of ecosystems, which to a certain extent affects the linear and volumetric sizes of the body of consumers of various orders (Huston and Wolverton, 2011). Another explanation has a phylogenetic basis complying with the Cope-Depéret rule, prescribing a tendency to increase in the size of animals in the process of historical development. Such a view was expressed in studies of wolf (Ramensky et al., 1985) and sable (*Martes zibellina* Linnaeus 1758) skulls (Monakhov, 2014). In the latter case, the author notes that changes in the size of animals over decades in many cases are unreliable and multidirectional and do not contradict the species stability.

According to the results of our research, there is no reason to assume the growth of animals over time. Human activities in the area of material collection for the period under consideration were characterized only by increased forest management. Climate changes, manifested in the growth of average annual temperature, were reliable, but even the relatively large increment of this indicator by +2.08°C between 1962 and 2010 (Puzachenko, 2012) did not lead to profound ecosystem transformations and probably did not affect the morphological variability of the fox.

We assume that one of the possible causes of the stochastic chronographic variability of the fox could be the nondirectional elimination of animals: total mortality, as a result of hunting by man and as a result of natural causes. The influence of the anthropogenic factor on microevolutionary processes in the populations exploited by humans has been considered in

detail and summarized for ungulates and carnivorous mammals (Rozhkov and Pronyaev, 1994). In studying a population of raccoon dogs northeast of Tver oblast, we found that high total mortality of individuals can cause deviations from the mean values of the “optimal phenotype” with a plus and a minus sign (Korablev et al., 2012). The variability of the morpho-phenetic appearance of the populations of some species of game animals may indicate not the trends of its change and not the persistent differences between the samples, but random fluctuations in the frequency of the parameters caused by large total mortality. According to the data on the material entering the craniological collection of the Central Forest Reserve, the fox steadily occupies the fourth place, after the American mink (*Neovison vison* Schreber 1777), the raccoon dog, and the pine marten (*Martes martes* Linnaeus 1758). In order to regulate the numbers, fox hunting is permitted year-round. According to special studies, the survival rate in the fox populations in the Urals region is estimated at 33% for yearlings and 56% for adults, indicating intense elimination of animals of all ages (Korytin, 2002).

Since the analysis of the spatial and temporal variability of the fox, as shown by the results of the calculations, is reduced to variation in the size of canines and premolars, as well as the structures of the skull functionally associated with these characters (rostrum width), it can be assumed that the size polymorphism of these characters is related to the diet range of the species in the time aspect. Significant differences found only in groups of adult animals indicate the adaptive nature of size variation. The size of the prey and the predator’s dentition can be correlated. A similar dependence in the predator–prey system was established for the American mink during systematic hunting for the muskrat (*Ondatra zibethicus* Linnaeus 1766) and the water vole (*Arvicola terrestris* Linnaeus 1758) (Zalewski and Bartoszewicz, 2012). However, in order to answer this question, a detailed study of the dynamics of the fox’s nutrition in the geographic region under consideration is required.

The results of the study of the intrapopulation variation of the fox and the previous studies on mustelids and raccoon dogs suggest that the structuring of mammalian populations on a minimum geographical scale is a general pattern. The degree of observed differences is low, does not have a stable relationship with the distance between samples, and is probably determined by a combination of endogenous and external factors. In some cases, the differences between subpopulations can reach the interpopulation scale, which significantly increases the level of requirements for the interpretation of the results of studying intraspecific variability. It is possible to consider morphologically isolated groups such as demes or their consortia existing for a limited number of generations. The mechanisms of their occurrence are temporary violations of pan-

mixia, including as a result of assortative mating and zoo-dominance. Such a phenomenon in a population may be accompanied by the Wahlund effect. At the same time, the noted morphological differences may not be of an obvious adaptive nature, but by reinforcing polymorphism, they form a complex population system that is more resistant to external factors and serve as material for adaptation genesis, the vectors of which are mainly formed by ecological features rather than microevolutionary trends.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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