

Increase in Skull Size of Red Fox (*Vulpes vulpes*) in the Second Half of the XX Century in Northeastern Europe

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Abstract—Based on the skulls of red fox collected in northeastern Europe for 20 years, we obtained new data on directed temporal variation. The increase in skull size is closely related to an increase in the mean annual temperature, i.e., global warming. It was found for the first time that some skull traits increase at different rates, both within and between structural population groups. The phenomenon of increasing skull size with increases in the mean air temperature contradicts Bergmann's rule. The causes of such increase are especially important for an understanding the adaptive role of processes in populations resulting from climate changes.

Keywords: skull, size, *Vulpes vulpes* L., temporal variation, global warming

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Directional changes in body size were observed in a number of animal species in recent decades, or throughout the entire XX century. The size of some species decreased; these are mainly aqueous invertebrates and vertebrates and some terrestrial vertebrates, such as even-toed ungulates and mammals. The reduction in size is mainly related to the effect of hunting [1–6 and others]. In other species, such as passerines [7, 8], three species of *Neotoma* [9], and some voles, mice, and shrews, this tendency is thought to result from global warming, which leads to changes in body size according to Bergmann's rule or, in the case of range fragmentation, the rule of insular reduction [10, 11].

The inverse process, i.e. an increase in size, is typical of many other terrestrial vertebrates. An augmentation of body and skull size in XX century was observed in the large Japanese field mouse *Apodemus speciosus*, cinereus shrew *Sorex cinereus* [12, 13], least weasel *Mustela nivalis* [14], stoat *Mustela erminea* [15, 14], American marten *Martes americana* [16], Eurasian otter *Lutra lutra* [17], European badger *Meles meles* [18], gray wolf *Canis lupus* [19, 20], and red fox *Vulpes vulpes* (at some sites in Europe and Asia Minor, including Denmark, Austria and Israel) [18, 21, 22]. A number of authors suppose that this augmentation is caused by global warming, which is followed by increase in the primary production rate and availability of food resources; this provides a higher growth rate at early stages of ontogeny. The second option, i.e., the consumption of food resources in a warmer climate,

allows the use of some energy intended for thermoregulation and its transformation for growth processes.

The purpose of this study is to describe the phenomenon of changes in skull size in the red fox over two decades and to discuss the possible causes of this phenomenon.

MATERIALS AND METHODS

The study material was collected by N.N. Solomin and S.A. Korytin in a relatively small area in northeastern Europe in the period from 1966 to 1985 and then analyzed by the author. The area does not exceed a square with sides of 200 × 180 km (coordinates: 57°00' N, 47°30' E to 58°50' N, 51°00' E). In 1088 fox skulls with known sex, age, and collection date, we measured the following traits: condylobasal length, facial length, backskull length, malar distance, inter-orbital distance, mastoid distance, and skull height in the area of otic capsule [23]. All animals were caught by hunters, i.e., during the hunting season; thus, the age of young animals varied from 6–7 to 10–11 months; the mean age was 8.5 months. Therefore, we used the skulls of young animals, which have undergone a period of intense growth. Young and adult animals were divided into groups according to the relative width of the canine channel [24]. Samples with a width of 41% or higher were considered to be young [25]; all other samples were considered as adults. The age was determined based on a counting of recording structures in the cement of canines [26].

Table 1. Results of three-factor analysis of variance performed for sex, age, and season and the first principal component

Effect	<i>SS</i>	Degree of freedom	<i>MS</i>	<i>F</i>	<i>p</i>
Absolute term	2.84	1	2.84	1.17	0.279
Sex	1450.91	1	1450.91	600.01	0.000
Age	269.13	1	269.13	111.29	0.000
Number of hunting season	414.63	19	21.82	9.02	0.000
Sex–Age	3.68	1	3.68	1.52	0.218
Sex–Number of hunting season	38.95	19	2.05	0.85	0.650
Age–Number of hunting season	97.81	19	5.15	2.13	0.003
Sex–Age–Number of hunting season	35.15	19	1.85	0.76	0.751

The mean monthly air temperatures were obtained on the site of the Research Institute of Hydrometeorological Information at two meteorological stations (Kumeny and Yaransk) situated in the area of sample collection. In order to synchronize the birth of young animals with temperatures, the mean monthly temperatures were averaged by meteorological stations and transformed to mean annual temperatures in intervals from April to March and from May to April.

For next year statistical treatment of data, we used principal component analysis, regression analysis, and correlation analysis.

RESULTS AND DISCUSSION

The initial principal component analysis included seven skull traits. The first principal component accumulated 69.3% of the dispersion; the eigenvalue of the second component (9.0% of dispersion) was a little lower than unity; therefore, it was not analyzed. The interaction of the first component with target variables is described in Table 1. All variables (sex, age, number of season) had a significant interaction rate with the first principal component. The effect of latitude on skull size in foxes was not analyzed due to the relatively small area of studies. The interaction of concomitant variables was insignificant, except for the pair “age–season,” which results from an increase in mean age by the end of collection period, i.e., an increase in the proportion of adult animals in the total number of samples ($r = 0.43$; $p < 0.05$). The theoretical distribution of adult animals in samples could have some effect on the analysis results. Young animals were coded as “1,” and adult animals were coded as “2”; the real age of adult animals varied from 1+ to 9+. It was found that the absolute age of adult animals does not increase but decreases to the end of collection period ($r = -0.52$; $p = 0.05$; $y = -0.042x + 3.32$; $R^2 = 0.28$).

Due to the number of samples, we could divide samples of each season into four groups: young (0+) and adult (1++) males and females. The pairwise regressions “structural group trait–season” showed that 26 of 28 pairwise regressions were highly signifi-

cant. Changes in two other traits in adult males were close to a 95% significance; these traits were malar width ($p = 0.078$) and mastoid width ($p = 0.057$).

Thus, an increase in skull size from the mid-1960s to the mid-1980s can be proved.

The traits in four structural groups increase at different rates (Tables 2 and 3). An increase in skull size is most significant in young males (by about 0.236% per year). This tendency is especially obvious for interorbital distance and skull height (0.36 and 0.3% per year, respectively). The augmentation rate in females is lower and is almost the same in young and adult animals (0.152 and 0.156% per year, respectively). A small increase in skull trait values was observed in adult males (mean value: 0.113% per year for all traits). The maximal growth in three of four age groups was observed for the same trait, namely skull height in the area of otic capsules. In the fourth group, this trait is second after interorbital distance (Table 3).

Thus, the mean augmentation rate is different in young and adult males and females. The trait values increase to different extents; interorbital distance and skull height have the maximal growth rates. A number of important questions arise.

1. First, why is the rate of changes in skull traits maximal in young males and minimal in adult males, and why is it almost the same in young and adult females?

2. Second, what causes changes in skull proportions?

3. Finally, what causes an increase in all skull trait values in all age and sex groups?

The last question is probably easier to answer than the first two. A number of authors suppose that the most probable cause is climate change. However, the correlations between mean annual temperatures and the first principal component are weak; the level of significance is sufficient (maximal $r = 0.38$; $p = 0.09$; Fig. 1). Analysis of pairwise regressions showed that two of the seven traits in young animals correlate significantly with mean annual air temperature: condylobasal length and facial length. The dependence of

Table 2. Increase in skull trait values in red foxes per year, according to pairwise regression equations, %

Trait	Females 0+	Females 1++	Males 0+	Males 1++
Condilobasal length	0.119	0.146	0.187	0.112
Facial length	0.164	0.197	0.230	0.119
Backskull length	0.065	0.107	0.155	0.083
Malar width	0.191	0.098	0.259	0.065
Interorbital width	0.179	0.126	0.362	0.138
Mastoid width	0.081	0.148	0.148	0.065
Skull height in the area of ear capsules	0.266	0.267	0.300	0.212

Table 3. Increase in skull trait values in red foxes in the period of 20 years (1966–1985), according to pairwise regression equations, %

Trait	Females 0+	Females 1++	Males 0+	Males 1++
Condilobasal length	102.38	102.93	103.75	102.24
Facial length	103.27	103.94	104.59	102.37
Backskull length	101.31	102.14	103.11	101.67
Malar width	103.82	101.96	105.18	101.30
Interorbital width	103.59	102.51	107.25	102.76
Mastoid width	101.61	102.96	102.96	101.29
Skull height in the area of ear capsules	105.33	105.34	106.00	104.24

the latter in young males and females is presented in Fig. 2. Thus, we suppose that augmentation of some skull traits in the red fox is directly or indirectly caused by global warming.

The total increase in the maximal skull length in the red fox in Austria during a period of 100 years was 3.7 and 3.9% in adult males and females, respectively [21]. In Denmark, significant growth was only observed for malar distance, but it closely correlates with body weight, body length, and tail length [18]. Over the last 20 years, condilobasal length in different age and sex groups of foxes in Russia increased from 2.24 to 3.75% (Table 3).

One possible factor of animal growth related to global warming is the development of agriculture [22]. Intense agricultural activities lead to an increase in the number of landfills with agricultural waste, which can serve as additional food resources for foxes. Agricultural development is directly related to increasing human population density.

There are currently no available data on changes in agricultural production over the last 20 years in the area of sample collection. However, there are data on the human population density in regions where the skull size in foxes increased. In 1983 the mean population density was 90 persons/km² in Austria, 116 persons/km² in Denmark, and 291 persons/km² in Israel [27]. Y. Yom-Tov and S. Yom-Tov [22] found that an increase in skull size in foxes in Israel in the XX century coincided with a 16-fold increase in human population density. i.e.,

significant development of the agricultural sphere. At the end of the XIX century (1897), the mean population density in some areas of the Vyatka Governorate (which correspond with the area of sample collection) was 25.3 persons/km² [28]. In the period from 1897 to 1983, the human population density did not increase

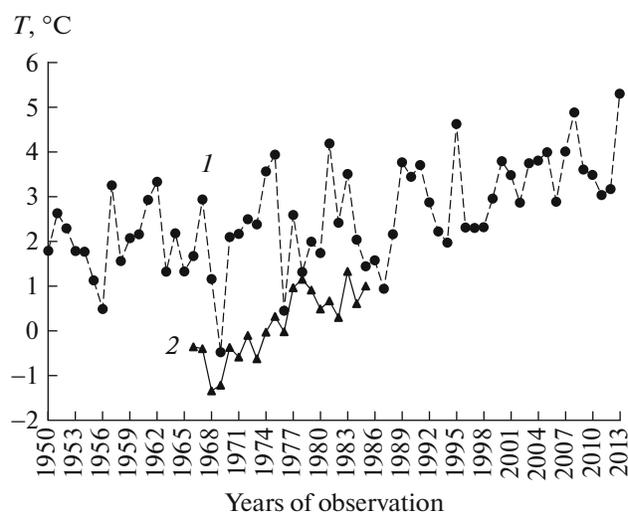


Fig. 1. Changes in mean annual temperature (1) and first principal component (2): (1) $y = -64.14 + 0.034x$; $R^2 = 0.31$; $r = 0.56$; $p = 0.000001$; (2) $y = -211.92 + 0.11x$; $R^2 = 0.68$; $r = 0.82$; $p = 0.00001$.

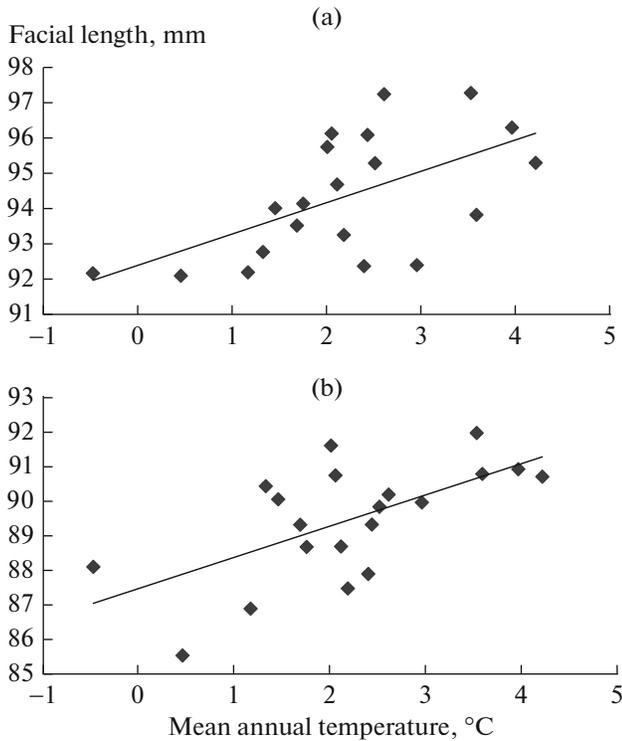


Fig. 2. Dependence of change in mean facial length in young males ($y = 0.88x + 92.39$; $R^2 = 0.34$; $r = 0.58$; $p = 0.01$) (a) and young females ($y = 0.91x + 87.46$; $R^2 = 0.39$; $r = 0.62$; $p = 0.01$) (b) on mean annual air temperature.

and even decreased by almost two times, reaching 13.8 persons/km². In the period from the 1960s to the 1980s, neither the human population density nor the agricultural development rate in the area of sample collection significantly changed. We suppose that any significant effect of agricultural production on changes in skull size in foxes in the area of our study is not as probable as in central Europe and western Asia.

An increase in animal body size with increasing mean annual temperatures contradicts with Bergmann's rule, according to which augmentation is an adaptation to severe climatic conditions, primarily lower mean annual temperatures. Greater body size at higher latitudes allows more effective use of some energy for thermoregulation due to the reduced index "body weight–body surface." Why does the size of the skull and body increase with increasing temperature, when it should decrease, as shown by Bergmann's rule? This question requires further study. This process is most likely affected by a complex of causes, including global warming. Further studies are needed to explain the mechanisms of skull augmentation (whether it results from growth processes, a higher mortality rate of smaller animals, or some other factors).

CONCLUSIONS

The data show that there is a directional trend in the chronographic variability of skull size in red foxes in the period from 1965 to 1985. The rate of increase in seven skull traits differs both within (between traits) and between structural groups of population (young and adult, males and females). The changes in two traits (condilobasal length and facial length) correlates significantly with the increase in mean annual temperature. The same augmentation over a period of 30 years was observed in another region, the middle Urals [29]. The picture of directional changes in the skull size of red fox corresponds with previous data obtained in central Europe and western Asia during much longer time periods [18, 21, 22]. Thus, we observed similar processes of skull augmentation in a huge part of the range of the red fox. This proves the presence of some global factor, which is most likely climate change.

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