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GENERAL BIOLOGY

Distinct Features of Intraspecific and Intrapopulation Variability of the Skull Size in the Red Fox

A. M. Gos'kov*, Academician V. N. Bol'shakov, and N. S. Korytin

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Abstract—The range of chronographic variability of the average size of the skull in the red fox (data collected by the authors) from a compact area in the Middle Urals has been assessed for a 30-year period, and the results obtained have been compared with the published data on the geographical variability within the vast species range. The range of changes of the average dimensions of the skull over time spanned almost the entire range of geographical variability. Therefore, the problem of search for factors that determine the morphological diversity arises.

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The species range of the red fox (*Vulpes vulpes* Linnaeus, 1758) is among the largest of those of mammals, this being a clear indication of a high adaptive capacity of the species. Moreover, foxes easily adapt to habitats transformed by human activity and can even occupy seemingly unsuitable "biotopes", such as large urban complexes and the adjacent forest–park areas. The red fox is a species with a complex intraspecific structure. Several studies [1, 2] reported the existence of 16 subspecies in the major part of Eurasian area, whereas the number of subspecies at the area of the former Soviet Union was estimated at 17. On the other hand, polyclinal variability of skull size is characteristic of the red fox [3]. Size and coat color of the animals have always been among the important traits for subspecies identification and retain importance at present.

Continuous clinal variability of body size of the animals hinders the identification of distinct subspecies. Discussion of this problem in scientific publications led the authors of the study [4] to the conclusion that clinal variability of certain traits does not prevent the assignment of an animal to a subspecies according to a set of traits. Coat color, another important systematic trait, does not exhibit a clearly discrete distribution for the red fox as a species (at least in the forest and forest–steppe zones, and partially in the steppe zone). Individuals with dissimilar coat colors can be found in a single subspecies, and the "typical" coat color of the subspecies is only characterized by a slightly higher frequency in this case.

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia
** e-mail: goskov_am@ipae.uran.ru, alexander_goskov@mail.ru*

Chronographic variability of traits is characteristic of the red fox, as well as of many other species. A number of researchers paid attention to the analysis of the relationships between the regularities that control the temporal and spatial variability of morphological traits. For instance, the study of non-metric traits of the bank vole skull performed by Vasil'ev [5] showed that the intrapopulation range of chronographic variability was one order of magnitude less than the geographical variability of the populations. This correlation proves the spatial isolation of the populations and forms the basis for microevolutionary transformations.

Understanding the ratio of chronographic and geographic variabilities of metric traits is of considerable interest; therefore, we performed such a study on the red fox.

The aim of the present study consisted in the analysis of our own data and published data of other authors in order to characterize the ratio between the chronographic and geographic variability ranges for the skull size in the red fox.

Fox skulls from the Museum of the Institute of Plant and Animal Ecology (Ural Branch, Russian Academy of Sciences) were used for the study. The skulls were collected by V.N. Pavlinin, N.S. Korytin, and Yu.M. Malafeev. The skulls were collected between 1960 and 1990 in several neighboring districts of the southeastern part of Sverdlovsk oblast and the neighboring Kataisk raion of Kurgan oblast. The study area extended over the subzones of southern taiga, pine and birch pre-forest–steppe forests, and the north of the forest–steppe zone; thus, the study area was relatively small in comparison with the part of the geographical range of the red fox included in the analysis. The study area corresponded to less than two

Fig. 1. Schematic map of skull size variability in males of the red fox. (*1*) Data from published sources that did not fit into the range of chronographic variability; (*2*) values that fitted into the range of chronographic variability; (*3*) values that exceeded the maximal values of the range; (*4*) the studied area.

degrees of latitude (56.2°–57.8° N) and 4.3° of longitude (59.3°–69.9° E). Information on the sex and the trapping season and site was available for each animal. The age of the animals was determined by counting annular structures in canine tooth cementum. Variation of the condylobasal length (CBL) of the skull was investigated in a sample of 260 skulls of adult foxes. The range of annual variation of average CBL values was compared with the average values of condylobasal length in 43 local samples collected in areas separated by considerable distances [6–13], the characteristics of individual subspecies (four points in total), and the CBL values plotted on the map of clinal variability of the species. Thus, a large part of the living range of the fox, including Europe, Northern Asia (within the borders of the former Soviet Union), and British and Japanese isles, was taken into the analysis.

The minimal value of the average annual CBL was 136.9 mm in the females and 140.18 mm in the males. The maximal values for the females and males were 152.6 and 153.5 mm, respectively. The values for the majority (13 of 16) of fox subspecies identified in Europe and Northern Asia fell within the chronographic variability range of the skull size of the animals from the area under investigation. All average CBL values for 13 subspecies are within the range of variability of the average annual CBL values for the animals from a small area. The values that fell within the chronographic variability range were derived from an area that included the entire forest and forest-steppe zones and a part of the steppe zone (Figs. 1, 2). The number of points that fell within the chronographic variability range of skull sizes was slightly higher in the case of males than in the case of females. The average sizes of foxes from Kamchatka, Northeastern Siberia, south of the Far East, Western Siberia, Northern Kazakhstan, continental Europe, and the British Isles fell within the range of chronographic variability of the Middle Ural sample. Larger males were found in Sweden only [14]. Values for the small foxes of Transcaucasia (subspecies *V. v. kurdistanica*), central Kazakhstan (subspecies *V. v. karagan*), Turkmenistan (subspecies *V. v. flavescens*), and the Japanese Islands (*V. v. japonica*) fell outside the range.

The number of points that fell outside the range of chronographic variability characteristic of females was somewhat larger and included both the points listed above for the males and smaller foxes from the area of the Anadyr Plateau, Northern Kazakhstan, Eastern Transcaucasia, Crimea, Southern Europe, and England.

Thus, one may conclude that the range of chronographic variability in a small area of the Middle Urals exceeded the range of geographical variability of fox skull sizes in the vast area of Europe and Northern Asia. Therefore, it may be assumed that there are virtually no differences in size between 13 of 16 subspecies, since all the values in question fell within the chronographic variability range of a sample collected at a single point. On the other hand, it is completely reasonable to assume that the chronographic variability ranges for all the areas can be similar to that observed in the Middle Urals. In this case, the average skull size in a subspecies can only be assessed if data collected during many years are taken into consideration.

Therefore, the pattern of change of the size parameters of the animals within the living range of the species was presumably very complex: first, it included continuous clinal variability of the sizes in space; second, the oscillating chronographic variability from year to year; third, the presence of distinct intraspecies forms. Therefore, it is important to reveal the mechanisms that underlie spatial and temporal variability of size.

Fig. 2. Schematic map of skull size variability in females of the red fox. (*1*) Data from published sources that did not fit into the range of chronographic variability; (*2*) values that fitted into the range of chronographic variability; (*3*) the studied area.

The demographic parameters of the fox population are under strong influence of external factors. Both the fertility of the animals and the survival rate of all age groups (including the underyearlings) are reduced during the phase of population size decrease. On the other hand, both the fertility of the animals and the survival rate of all age groups increase dramatically during the growth phase [15]. This pattern of birth rate and mortality changes is a clear indication of the more powerful impact of extrinsic factors (both abiotic and biotic) as compared to the contribution of the intrapopulation regulatory mechanisms. For instance, the entire population size and the number of underyearlings decrease if the weather conditions of the summer are abnormal (hot and arid or cold and rainy) and increase if the temperature and humidity conditions are optimal. The weather conditions affect the body size in foxes as well. The analysis of annual changes in seven dimensions of the skulls available to the authors revealed a correlation with the average annual air temperature.

It is extremely important to clarify the mechanism that underlies the annual changes in body size. The variation of size can be related to natural changes in growth rate at early ontogenetic stages or to the variation of fertility and mortality parameters (i.e., variation of the adaptation of the animals). The combined influence of both factors is most likely to control the changes

As a conclusion, we should emphasize that the pattern of chronographic and geographic variability of condylobasal length of the skull of the red fox was very complex. The contribution and the role of specific mechanisms that underlie the spatial and temporal variability of skull dimensions remain uncharacterized.

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