

Red Fox Skull Size Variability Along the Ural's Meridian: Bergmann's Rule or the Optimum Rule?

N. S. Korytin^{a, *} and A. M. Goskov^{a†}

^a Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia

*e-mail: nsk@ipae.uran.ru, nikkor@olympus.ru

Received June 8, 2023; revised September 26, 2023; accepted September 30, 2023

Abstract—Changes in the skull size of the red fox (*Vulpes vulpes* L.) along the eastern macroslope of the Ural Range from the forest-tundra to the steppe are analyzed. The sizes varied from minimum in the north to maximum in pre-forest-steppe pine-birch forests. Further south, the size of the skull decreased again. The average fox population density changed similarly. Based on these data, it was concluded that the sizes change in accordance with the optimum rule, and not with Bergman's rule. Probably, microevolutionary adaptations to living conditions are influenced by general factors that influence both body size and the population density of the species.

Keywords: biogeographical patterns, intraspecific variability, geographic variability, sexual dimorphism, population density

DOI: 10.1134/S1067413624010041

INTRODUCTION

The red fox is a species that occupies a huge home range, probably one of the largest among mammals, and exhibits significant geographic variability. There are up to 45 subspecies throughout the whole area [1]. According to various reports, 14–17 subspecies are known on the territory of the former Soviet Union, grouped into three groups: *vulpes*, *karagan*, and *caucasica* [2–4], and on the territory of Russia, 12 subspecies [5]. Subspecies of the group *vulpes* inhabit the forest zone, *karagan*, forest-steppe, steppe, and desert, and *caucasica*—mountains.

V.G. Geptner et al. [2], and A.A. Aristov and G.F. Baryshnikov [4], when describing the subspecies of foxes, indicate that the largest animals inhabit the forest zone both within the European part of Russia and in Siberia: *vv vulpes*, *vv tobolica*, *vv jakutensis*, *vv beringiana*, and *vv daurica*. Also, the large ones include controversial subspecies, which are not recognized by all taxonomies: *vv kamtschadensis*, *vv shantaricus*, *vv dolichocrania*, and *vv schrencki*. Authors highlighting *vv diluta*, a forest-steppe fox [2, 3, 6–8], indicate the same large size of this form. Smaller sizes are characteristic of steppe foxes *vv stepensis* and *vv karagan*, even smaller foxes live further south, in the semi-deserts and deserts of Central Asia (*vv flavescens*). In general, we can assume that the change in the size of a fox according to the above description corresponds to Bergmann's rule. The largest animals

live in the north and northeast of the range; further south their sizes decrease.

On the isoline map of the total length of the fox skull published by P.V. Terentyev [9], the sizes of foxes change somewhat differently and, according to the author's conclusion, are more consistent with the optimum rule. In the western part of the range, within the former Soviet Union, the length of the skull increases from the southern part of the deserts of the Turan Lowland to the north-northwest to approximately the southern taiga forests of the Russian Plain. Further to the north and west, the size of the skull decreases slightly. In the eastern part of the range, the picture is less clear: from a minimum on the Central Siberian Plateau, the size of foxes increases to the southeast and northeast, in turn, the main isolines go in the northeast direction approximately to the Kolyma basin.

Based on materials from V.G. Yudin [10], the largest form in the Far East (*dolichocrania* [6]), is living in Primorye, Lower, and Middle Amur region (in the forest zone). Further to north, the size of foxes decreases. On the Chukotka Peninsula, in the Anadyr River basin and, probably, in the Indigirka River basin, a relatively small fox lives (the condylobasal length of males is 141.9 mm, females 135.3 mm) [10], i.e., in the northeast of the range in Eurasia it is not large form, as would be expected in accordance with Bergmann's rule, but a relatively small fox. There is no information on the size of foxes from other parts of the range where the fox lives in forest-tundra or tundra.

[†] Deceased.

Table 1. Sample structure and size

| Region | Males | | Females | | Total |
|--------------------------------|-------|-----|---------|-----|-------|
| | 0+ | 1++ | 0+ | 1++ | |
| Sverdlovsk oblast | 426 | 184 | 259 | 159 | 1028 |
| Chelyabinsk oblast | 36 | 20 | 29 | 15 | 100 |
| Kazakhstan | 6 | 2 | 9 | | 17 |
| Kurgan oblast | 50 | 15 | 37 | 25 | 127 |
| Yamalo-Nenets Autonomous Okrug | 11 | 5 | 11 | 3 | 30 |
| Bashkiria | 3 | 5 | 1 | | 9 |
| Tyumen oblast | 23 | 13 | 27 | 8 | 71 |
| Orenburg oblast | 14 | 18 | 34 | 18 | 84 |
| KHMAO | 2 | 4 | | 1 | 7 |
| Total | 571 | 266 | 407 | 229 | 1473 |

Analysis of the animal size geographical variability shows that the body sizes of most species, both among poikilotherms and among homeotherms, change following Bergmann's rule. M.V. Mina and G.A. Klevezal [11], using a large number of examples, discussed in detail the influence of various factors on the growth of animals, explaining the nature of geographical variability, which can manifest itself in accordance with Bergmann's rule. In particular, these authors described the results of experiments by Barnett et al., showing "that mice raised in the cold, when selected for high rates of reproduction (this is exactly the kind of selection that occurs in nature), after 10–12 generations reached larger sizes than individuals from normal conditions, and these growth characteristics were retained at any growing temperature" (quoted from: [11], page 152).

A revision of Bergmann's rule on a large number of species shows that, for example, 72.34% of birds follow Bergmann's rule, and 27.66% do not [12]. The same authors found that among the 149 species of mammals analyzed, only 65.1% followed this rule, including the fox. A more detailed examination of size variability in representatives of the order Carnivora (46 species) revealed that only 50% of species (including the fox) change in size in accordance with Bergmann's rule [13].

Some authors [14] associate an increase or decrease in the body weight of mammals with the productivity of food items, and a change in the size of predators with the mass of the main prey species, in particular the wolf [15] and the fox [16]. The fox was also larger in regions where agriculture was more developed [17].

The revision of Bergman's rule has been carried out more than once over a period of more than a century and a half since its publication; there are both supporters and opponents of this postulate. Work carried out in recent decades on a large number of species of birds

and mammals [12, 13] indicates that half or more species follow Bergmann's rule, including the species of interest to us, the red fox.

In the Urals and surrounding areas, the fox lives from the northern to the southern extremity of the Ural Mountains, including the southern tundra, forest-tundra, taiga, forest-steppe, and steppe. In the Urals a conditional border is drawn between *vv vulpes* and *vv tobolica*, however, there is no information on the size of the Ural foxes themselves.

In general, based on currently known information about the size of foxes within the range in the territory of the former Soviet Union, it is impossible to say unambiguously according to which of the geographical rules the sizes change, Bergmann's or the optimum of the range (abundant center hypothesis). In this regard, it seems relevant to study the change in the size of the fox in a fairly extended meridian area of the range, from the forest-tundra to the steppe. This approach to analysis will make it possible to neutralize to some extent the possible influence on the dimensions of the latitude and altitude of the area.

Objective—To fill the gap in the missing information about the sizes of Ural foxes and try to identify a possible pattern of changes in their sizes along the Ural meridian.

MATERIALS AND METHODS

The material for the analysis was skulls from the collections of the Museum of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences and the Arctic Research Station, Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, collected (including by the authors) for the periods 1955–1990 and 2012–2019 among hunters during the harvesting season, which lasts from November to early March. A total of 1473 fox skulls were used, obtained mainly in the Sverdlovsk, Chelyabinsk, Kurgan, and Orenburg oblasts (Table 1), i.e., from the eastern macroslope of the Ural Mountains and the adjacent territory.

The analysis included skulls for which the sex, season, and location of harvest were known. If possible, the approximate coordinates of the recovery site were determined. In cases where only the hunting area was known, the animal was assigned coordinates close to the central one for the administrative region. The study area extends from south to north, 51.4°–68.4° N and from west to east 56°–73.6° E. In the meridional direction, the extreme points are spaced from each other at a distance of about 2000 km.

The age of the foxes was determined using several methods. At the first stage, the width of the canal and the diameter of the upper canine were measured, and the relative width of the canine to the diameter of the canine itself was calculated [18]. When the relative channel width was more than 45%, the animals were

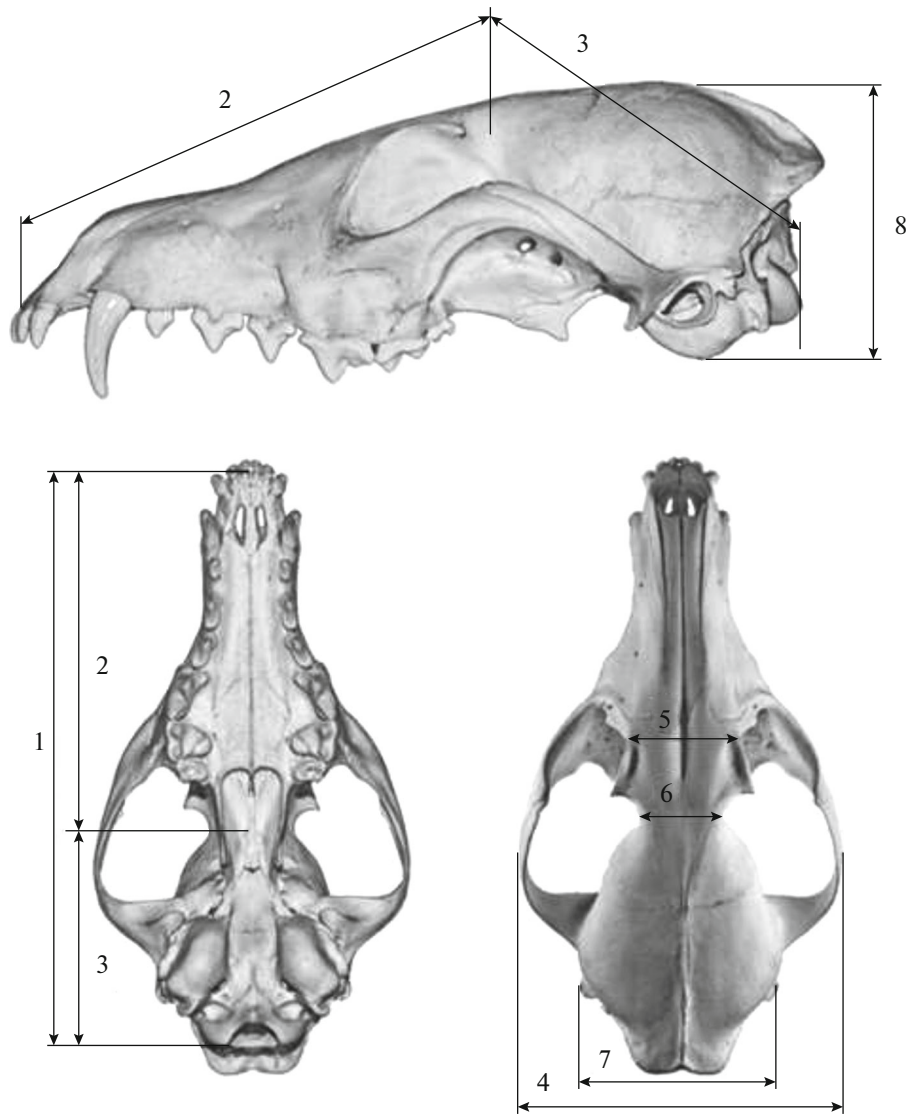


Fig. 1. Scheme for measuring skull features: (1) condylobasal length, (2) length of the facial region, (3) length of the brain region, (4) zygomatic width, (5) interorbital width, (6) postorbital width, (7) mastoid width, (8) height of the skull in the area of the auditory capsules.

considered young [19], the others were classified as adults, whose age was determined by counting the number of annual layers in the canine cementum according to the standard method [20, 21]. In the absence of canines, the suture between the main sphenoid bone and the anterior sphenoid bone (sutura presphenoid-basis phenoidalis) was studied. This suture is open and clearly visible in underyearlings, but in the second year of life it closes completely and becomes indistinguishable on the skull [22–24]. Changes in the size of characters were analyzed in four groups: young males and females; adult males and females.

The following features of the skull were measured (by [7]), taken using a ShTs-II-250-0.05 caliper with an accuracy of 0.05 mm (Fig. 1): condylobasal skull length (CSL), length of the facial region, length of the

brain region, zygomatic width, interorbital width, postorbital width, mastoid width, height of the skull in the area of the tympanic chambers, and diameter of the canine. It was assumed that changes in skull length reflect changes in body length.

Changes in characteristics were considered both in the latitudinal range and in groups corresponding to certain natural zones according to botanical-geographical zoning maps [25–28]. As can be seen from Table 1, the material at our disposal is distributed extremely unevenly among administrative districts and, accordingly, among natural zones and subzones. A small number of skulls was obtained from the forest-tundra and northern taiga, and therefore, they were combined into one group. On the other hand, a sufficient amount of material from the southern taiga and

Table 2. Changes in the condylobasal length of the skull of young (0+) foxes in natural areas

| Vegetation zone (subzone) | Males | | Females | |
|--------------------------------|----------|---------------|----------|---------------|
| | <i>n</i> | <i>M</i> ± SE | <i>n</i> | <i>M</i> ± SE |
| Forest-tundra + northern taiga | 10 | 144.22 ± 1.25 | 10 | 136.43 ± 1.42 |
| Southern taiga | 30 | 146.41 ± 0.92 | 32 | 139.34 ± 0.87 |
| Pre-forest-steppe | 351 | 148.08 ± 0.26 | 201 | 141.18 ± 0.33 |
| Forest-steppe | 125 | 145.79 ± 0.46 | 93 | 139.64 ± 0.54 |
| Steppe | 27 | 143.17 ± 0.87 | 50 | 138.55 ± 0.58 |

Table 3. Changes in the condylobasal length of the skull of adult (1++) foxes in natural areas

| Vegetation zone (subzone) | Males | | Females | |
|--------------------------------|----------|---------------|----------|---------------|
| | <i>n</i> | <i>M</i> ± SE | <i>n</i> | <i>M</i> ± SE |
| Forest-tundra + northern taiga | 9 | 148.79 ± 0.97 | 3 | 137.58 ± 1.86 |
| Southern taiga | 34 | 147.86 ± 0.84 | 23 | 140.91 ± 1.01 |
| Pre-forest-steppe | 137 | 149.21 ± 0.38 | 124 | 142.16 ± 0.35 |
| Forest-steppe | 52 | 147.86 ± 0.74 | 47 | 140.70 ± 0.46 |
| Steppe | 19 | 145.56 ± 1.11 | 21 | 139.66 ± 1.06 |

forest-steppe made it possible to identify the pre-forest-steppe subzone (or the subzone of aspen-birch or pine-birch subtaiga forests) [25, 26], located in the southeastern part of the Sverdlovsk oblast and characterized by high mosaic nature, into separate group habitats, significant anthropogenic transformation, and low levels of average annual precipitation.

When comparing fox population densities in different natural zones, the average yield of pelts per 10,000 ha was used. We have previously shown [29] that this indicator better describes the dynamics of the fox population than the population indicator obtained using winter route census. We used information for a 10-year period, from 1961 to 1970, when fox hunting was well developed. The average number of harvested skins was calculated in the administrative regions of Sverdlovsk, Kurgan, Chelyabinsk, and Tyumen (which at that time included the Yamalo-Nenets and Khanty-Mansi Autonomous Okrugs) oblasts. Administrative districts were classified as a particular natural zone (subzone) if more than 50% of the area of the district was located within the zone.

When statistically processing the material, variance and regression analyses were used. Processing was carried out in Statistica 8.

RESULTS

The results of measuring the main feature characterizing the size of the skull, condylobasal length, are given in Tables 2 and 3. This character is used for analysis by most authors studying the geographical variability of the fox, and in this regard, it allows comparison of changes in size across the species' range.

In three of the four groups (replications) we see a naturally changing result in five categories of vegetation zones, a gradual increase in the value of the CSL from the forest-tundra and northern taiga to the pre-forest-steppe and a smooth decrease in the southern direction. And only the size of the skull of adult males from the forest-tundra and northern taiga somewhat violates the obtained result, it turned out to be larger when compared with other groups. In general, changes in the CSL depending on belonging to a natural area turned out to be highly significant ($F(4, 1378) = 17.83; p = 0.000$). There is no correlation between mean values and standard deviations, and the variances are homogeneous. An similar result was obtained with a slightly different comparison, a change in the CSL depending on the latitude of the area (Figs. 2, 3). The largest average sizes are typical for latitudes from 56.7° to 57.5°. It is in this latitude range that the pre-forest-steppe area is located. To the north and south of it, the average sizes decrease.

Similar to the condylobasal length, the length of the facial region, the length of the brain region, the zygomatic width, the interorbital width, the mastoid width, and the height of the skull in the area of the auditory chambers change in all four groups (Appendix 1).

There is a close negative relationship between the latitude of the area and vegetation zones (subzones) ($r = -0.81, p = 0.000$), which is quite expected. However, we did not limit ourselves to providing only one parameter. In the latitude gradient, a smooth increase in the size of the fox skull was found from north to south to the pre-forest-steppe subzone and then a smooth decrease to the steppe zone. Estimating the average value of CSL within one vegetation zone makes it possible, using a definitely objective parameter, to compare the obtained values with other regions.

When analyzing Fig. 3, attention is drawn to the narrowing of the distance between the curves (the value of the CSL in adult males and females) from high to low latitudes. This fact indicates a clear decrease in the degree of sexual dimorphism from northern to more southern latitudes. Note also that in Fig. 2, reflecting changes in the CSL of young males and females, the curves run parallel, i.e., in young animals from different parts of the range, sexual dimorphism remains the same.

In order to understand which relative size category (large, medium, small) the CSL values we obtained from different natural zones belong to, we collected literature information on the sizes of foxes [2, 6, 10,

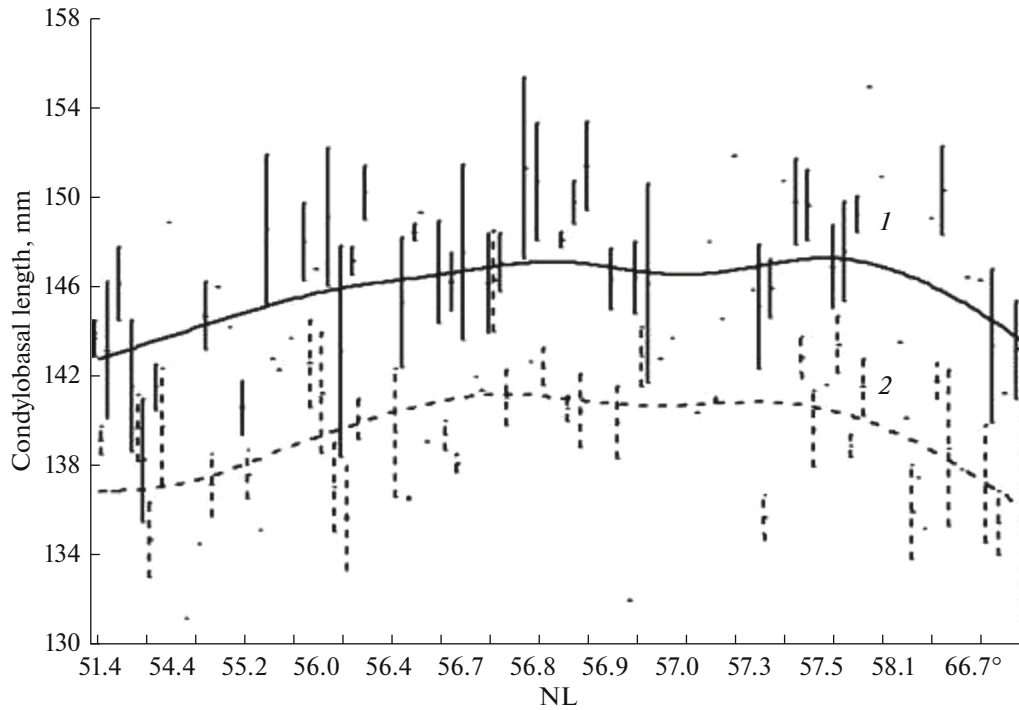


Fig. 2. Changes in the condylobasal length of the skull of young males (1) and females (2) in the latitude gradient: line—approximation of the mean using the weighted least squares method; points—single observations; dots and vertical lines—mean \pm SE. Males $F(63;407) = 1.89$; $p = 0.0001$; females $F(48;293) = 1.57$; $p = 0.0119$.

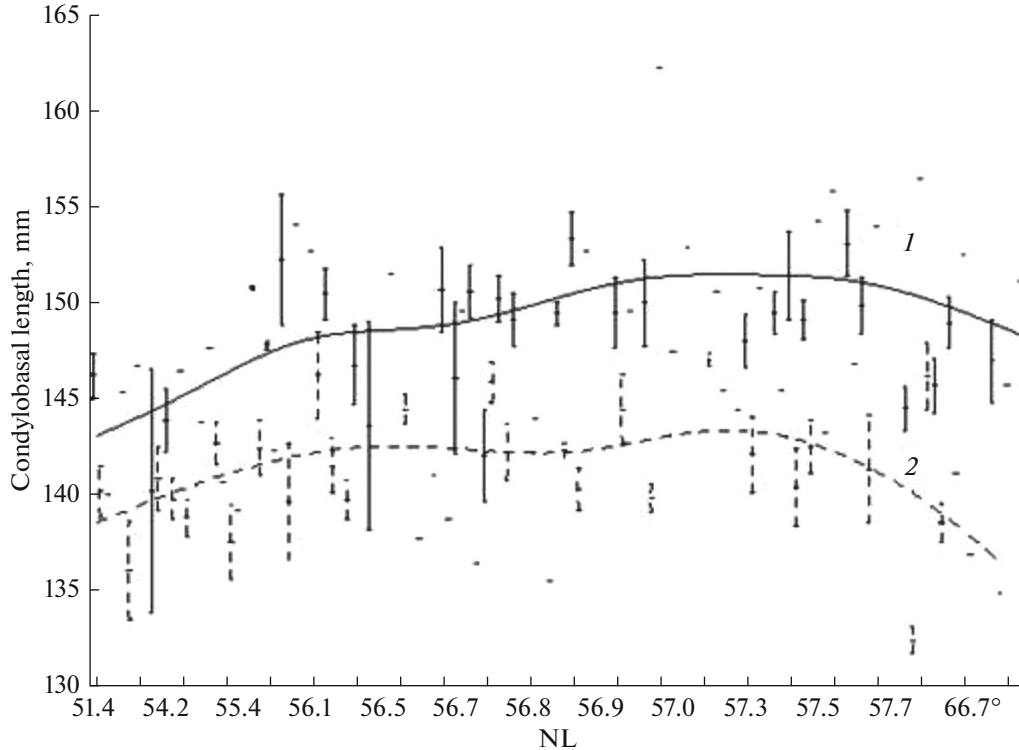


Fig. 3. Changes in the condylobasal length of the skull of adult males (1) and females (2) in the latitude gradient: line—approximation of the mean using the weighted least squares method, points—single observations; dots and vertical lines—mean \pm SE. Males $F(51;170) = 1.8$; $p = 0.0027$; females $F(44;158) = 1.95$; $p = 0.0015$.

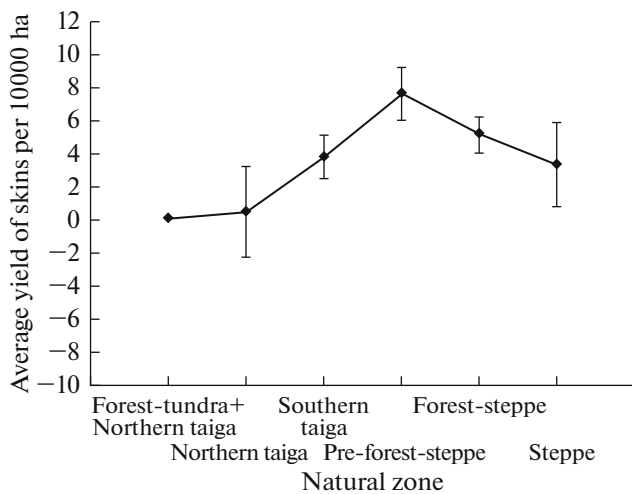


Fig. 4. Changes in the average fox population density, expressed in the average yield of pelts per 10000 hectares of habitat, in different natural zones and subzones. Mean \pm SE. $F(5; 91) = 5.67; p = 0.00013$.

30–44]. In total, there were 45 average CSL values for males and 41 for females. The points cover almost all of Europe and part of the area in Asia, located within the former Soviet Union. The entire range of values was divided into three equal parts: the large category included values of CSL of males equal to 148.6 mm or more; in the medium category, from 148.5 to 144.6 mm; in the small category, 144.5 mm or less. A similar division for females is as follows: large, more than 142.1 mm; medium, from 142.0 to 138.0 mm; small, less than 137.9 mm. Males and females of Ural adult foxes from the steppe and forest-steppe fell into the category of medium in size, and foxes from the southern taiga should also be classified as medium. Large foxes inhabit the pre-forest steppe.

A relatively contradictory situation emerged for adult foxes from the northern regions, forest-tundra, and northern taiga: females fell into the small category, males into the large category. Young animals from these subzones turned out to be the smallest. It should be noted that the sample size is small from the northern regions; accordingly, the average estimates are not reliable enough. Nevertheless, we suppose that there is more evidence indicating the small size of foxes from these regions than the opposite. According to our data, young males and females, as well as adult females, turned out to be smaller than animals from the southern taiga and more over smaller than animals from the pre-forest steppe.

Thus, the largest sizes of foxes are characteristic of the middle part of the range; to the north and south the sizes decrease. The results coincide with the data of V.G. Yudin [10] about the small size of foxes living in Chukotka, as well as part of the data on the map published by P.V. Terentyev [9]. The map shows a

slight decrease in size north of the central zone of the European part of Russia.

The change in the fox skull size occurs in accordance with the optimum rule. There is clearly no compliance with Bergmann's rule; in colder climates the sizes decrease.

In parallel with the change in skull size, the average fox population density in different natural zones was compared. It turned out that the curve of density changes behaves identically to the curve of changes in skull size (Fig. 4). The minimum population density is typical for the northern regions, then it gradually increases to the pre-forest-steppe, and further to the south, in the forest-steppe and steppe, the yield of skins per 10000 hectares decreases ($p = 0.000$). The difference in density between the forest-tundra, northern taiga, and pre-forest-steppe reaches 2–7 multiplicity orders, between the latter and southern taiga the difference is almost twofold. Further to the south, the density decreases not so significantly, by 1.5–2.3 times.

So, in the pre-forest steppe we observe not only the maximum sizes of foxes, but also the highest density of the species, i.e., the optimum rule is confirmed not by one parameter (size), but by two, size and population density.

DISCUSSION OF THE RESULTS

The relatively high population density of foxes is a consequence of increased survival and (or) birth rates, which, coupled with body size, suggests that pre-forest steppe conditions are most favorable for this species. Living conditions both in the forest-tundra and northern taiga, and in the steppe, are less favorable, which is expressed not only in lower population density, but also in the size of animals. Probably, not only temperature make life conditions more pessimal but some another factors. These include the small volume of the ecological niche, which is smaller both in the north part of the area, but also in the steppe zone.

A simultaneous decrease in the average population density and skull size indicates that both in the north, in the forest-tundra and northern taiga subzones, and in the south, in the steppe, the fox is exposed to a complex of unfavorable factors that affect not only the size of the animals, but also fertility and survival rate.

Our results are very similar to data obtained when studying the size and body weight of the European badger [45]. The length and body weight of a badger from a population living west of 40° E changes in accordance with the optimum (*or abundant centre hypothesis*) rule, and not with Bergmann's rule. The largest badgers live in the central part of the range of this population; to the north and south their sizes decrease.

We suppose that in the north and south of the fox's range, the dominant factors determining some reduc-

tion in size may be factors of a different nature: in some places the determining factor may be or, most likely, abiotic factors, in others factors of a biotic nature. Probably, the advantages that Bergmann's rule (the physical meaning of which is determined by Rubner's rule) gives to larger individuals due to the reduction of heat loss in northern latitudes are offset by some more powerful factor, leading not to an increase, but to a decrease in body size. The level of heat loss is largely determined by the heat-protective properties of the hair, the density and height of which in winter is significantly higher in the northern forms of many widespread species [46]. In general, it is likely that in the center of the fox's range, the influencing factors are such that the balance between energy consumed and expended is more favorable than in the north and south.

The fact that we discovered a change in the size of the skull (body) of a fox in accordance with the optimum rule, and not Bergmann's rule, suggests that the microevolutionary differentiation of fox populations in the area is influenced by factors other than those that determine the change in the ratio of surface area to body volume. Therefore, a detailed analysis of the body size of the fox is necessary as one of the most important species characteristics within the entire range, and a study of the dependences of size changes on potential impact factors.

SUPPLEMENTARY INFORMATION

Supplementary materials are available for this article at <https://doi.org/10.1134/S1067413624010041> and are accessible for authorized users.

FUNDING

The work was carried out within the budget framework (state task No. 122021000084-4).

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The work was carried out using museum material, without conducting experiments on live animals. Fox carcasses were collected from hunters who had special permission to hunt them.

CONFLICT OF INTEREST

The authors declare that they do not have any conflicts of interest.

REFERENCES

1. Wilson, D.E. and Reeder, D.M., *Mammal Species of the World*, Wilson, D.E. and Reeder, D.M. Eds., Maryland: JHU, 2005.
2. Geptner, V.G., Naumov, N.P., Yurgenson, P.B., et al., *Mlekopitayushchie Sovetskogo Soyuza. T. 2. Morskije korovy i khishchnye* (Mammals of the Soviet Union. Vol. 2. Sea Cows and Carnivores), Moscow: Vyssh. Sh., 1967.
3. Baryshnikov, G.F., Garrut, V.E., Gromov, I.M., et al., *Katalog mlekopitayushchikh SSSR (pliocen-sovremennost')* (Catalogue of Mammals of the USSR (Pliocene–Today)), Leningrad: Nauka, 1981.
4. Aristov, A.A. and Baryshnikov, G.F., *Mlekopitayushchie fauny Rossii i sopredel'nykh territorii. Khishchnye i lastonogie* (Mammals of the Fauna of Russia and Neighboring Regions: Carnivores and Pinnipeds), St. Petersburg, 2001.
5. Abramov, A.V. and Khlyap, L.A., Order Carnivora, in *Mlekopitayushchie Rossii: sistematiko-geograficheskii spravochnik* (Mammals of Russia: Systematic and Geographical Reference Book), Pavlinov, I.Ya. and Lisovskii, A.A., Eds., Moscow: KMK, 2012, vol. 52, pp. 313–382.
6. Ognev, S.I., *Zveri Vostochnoi Evropy i Severnoi Azii. Khishchnye mlekopitayushchie* (Mammals of Eastern Europe and Northern Asia: Carnivorous Mammals), Moscow: Gos. Izd., 1931.
7. Novikov, G.A., *Khishchnye mlekopitayushchie fauny SSSR* (Mammals of Eastern Europe and Northern Asia: Carnivorous Mammals), Moscow: Akad. Nauk SSSR, 1956.
8. Pavlinov, I.Ya. and Rossolimo, O.L., *Sistematika mlekopitayushchikh SSSR: dopolneniya*. (Systematics of the Mammals of the USSR: Additions), Moscow: Mosk. Gos. Univ., 1998.
9. Terent'ev, P.V., Methodological considerations for studying intraspecific geographic variation, in *Mater. Vsesoyuz. soveshch. "Vnutrividovaya izmenchivost' nazemnykh pozvochnykh zhivotnykh i mikroevolyutsiya"* (Proc. All-Union Conf. "Intraspecific Variability of Terrestrial Vertebrate Animals and Microevolution"), Shvarts, S.S., Ed., Sverdlovsk, 1966, pp. 3–20.
10. Yudin, V.G., *Lisitsa Dal'nego Vostoka SSSR* (Fox of Russian Far East of the USSR), Vladivostok: Dal'nevost. Nauchn. Tsentr Akad. Nauk SSSR, 1986.
11. Mina, M.V. and Klevezal', G.A., *Rost zhivotnykh. Analiz na urovne organizma* (Animal Growth. Analysis at the Organism Level), Moscow: Nauka, 1976.
12. Meiri, S. and Dayan, T., On the validity of Bergmann's rule, *J. Biogeogr.*, 2003, vol. 30, pp. 331–351.
13. Meiri, S., Dayan, T., and Simberloff, D., Carnivores, biases and Bergmann's rule, *Biol. J. Linn. Soc.*, 2004, vol. 81, pp. 579–588.
14. McNab, B.K., Geographic and temporal correlations of mammalian size reconsidered: a resource rule, *Oecologia*, 2010, vol. 164, pp. 13–23. <https://doi.org/10.1007/s00442-010-1621-5>
15. Geist, V., Bergmann's rule is invalid, *Can. J. Zool.*, 1987, vol. 65, pp. 1035–1038.
16. Kolb, H.H., Variation in the size of foxes in Scotland, *Biol. J. Linn. Soc.*, 1978, vol. 10, pp. 291–304.
17. Yom-Tov, Y., Yom-Tov, Sh., Barreiro, J., et al., Body size of the red fox *Vulpes vulpes* in Spain: the effect of agriculture, *Biol. J. Linn. Soc.*, 2007, vol. 90, pp. 729–734.
18. Smirnov, V.S., Age determination and age structure of the Arctic fox population in Yamal, *Tr. Salekhard. Statsionara Ural. Fil. Akad. Nauk SSSR*, 1959, vol. 1, pp. 220–238.

19. Korytin, N.S. and Endukin, A.Yu., Comparison of two methods for determining the age of a red fox, *Inf. Mater. Inst. Ekol. Rast. Zhivotn.*, 1982, p. 17.
20. Klevezal', G.A. and Kleinenberg, S.E., *Opređenje vozrasta mlekopitayushchikh po sloistym strukturam zubov i kosti* (Age Determination of Mammals by Layered Structure in Teeth and Bones), Moscow: Nauka, 1967.
21. Klevezal', G.A., *Printsipy i metody opredeleniya vozrasta mlekopitayushchikh* (Principles and Methods of Determining of Mammals Age), Moscow: KMK, 2007.
22. Churcher, C.S., Cranial variation in the North American Red Fox, *J. Mammal.*, 1960, vol. 41, no. 3, pp. 349–360.
23. Johnston, D.H. and Beauregard, M., Rabies epidemiology in Ontario, *Bull. Wildl. Dis. Assoc.*, 1969, vol. 5, no. 3, pp. 357–370.
24. Harris, S., Age determination in the Red fox (*Vulpes vulpes*)—an evaluation of technique efficiency as applied to a sample of suburban foxes, *J. Zool.*, 1978, vol. 184, pp. 91–117.
25. Kolesnikov, B.P., *Lesorastitel'nye usloviya i tipy lesov Sverdlovskoi oblasti: prakticheskoe rukovodstvo* (Forest Conditions and Forest Types of the Sverdlovsk Region. A Practical Guide), Sverdlovsk: Ural. Nauchn. Tsentr Akad. Nauk SSSR, 1973.
26. Kapustin, V.G. and Kornev, I.N., *Sverdlovskaya oblast'. Priroda, naselenie, khozyaistvo, ekologiya* (Sverdlovsk Oblast: Nature, Population, Economy, and Ecology), Ekaterinburg: Ural. Univ., 1998.
27. Yurkovskaya, T.K., Vegetation map, in *Natsional'nyi atlas pochv Rossijskoi Federatsii* (National Atlas of Soils of the Russian Federation), Shob, S.A., Ed., Moscow: Astrel', 2011, pp. 46–47.
28. Kulikov, P.V., Zolotareva, N.V., and Podgaevskaya, E.N., *Endemichnye rasteniya Urala vo flore Sverdlovskoi oblasti* (Endemic Plants of the Urals in the Flora of the Sverdlovsk Region), Mukhin, V.A., Ed., Ekaterinburg: Goshchitskii, 2013.
29. Korytin, N.S., Reliability of estimates of the abundance of large mammals obtained by different methods, *Materialy III Mezhdunarodnogo simpoziuma "Dinamika populyatsii okhotnich'ikh zhivotnykh Severnoi Evropy"* (Proc. II Int. Symp. "Population Dynamics of Game Animals in North Europe"), Danilov, P.I., et al., Eds., Petrozavodsk: Inst. Biol. Karel. Nauchn. Tsentra Ross. Akad. Nauk, 2003, pp. 117–118.
30. Gidayatov, Yu.Kh., Nasibov, S.B., and Aliev, R.A., Cranial features of foxes in various natural regions of Azerbaijan, in *Mater. IVs'ezda Vsesoyuz. teriol. o-va* (Proc. IV Congr. All-Union Theriol. Soc.), Moscow, 1986, pp. 120–121.
31. Danilov, P.I., Rusakov, O.S., and Tumanov, I.L., *Khishchnye zveri Severo-Zapada SSSR* (Carnivorous of the North-West of the USSR), Leningrad: Nauka, 1979.
32. Lebedeva, N.I., Morphological features of the common fox (*Vulpes vulpes* L., 1758) of the lower Dnieper region, *Visn. Zaporiz'kogo Derzh. Univ.*, 2000, no. 2, pp. 210–214.
33. Poleshchuk, E.M. and Sidorov, G.N., *Morfofiziologicheskaya i kranilogicheskaya kharakteristika lisitsy i korsaka Zapadnoi Sibiri* (Morphophysiological and Craniological Characteristics of the Fox and Corsak of Western Siberia), St. Petersburg: LiSS, 2004.
34. Sidorovich, A.A. and Orlov, I.A., The influence of feeding conditions on the growth and development of young red foxes (*Vulpes vulpes* L.) in central Belarus, *Vestn. Fonda Fundam. Issled.*, 2012, vol. 62, no. 4, pp. 60–70.
35. Sludskii, A.A. Varshavskii, S.N., Ismagilov, M.I., et al., *Mlekopitayushchie Kazakhstana. Khishchnye (sobach'i, medvezh'i, enotovyie), lastonogie (nastoyashchie tyuleni)* (Mammals of Kazakhstan. Carnivores (Canids, Bears, Raccoons), Pinnipeds (True Seals)), Alma-Ata: Nauka KazSSR, 1981.
36. Chernyavskii, F.B., *Mlekopitayushchie Krainego Severo-Vostoka Sibiri* (Mammals of Extreme Northeastern Siberia), Moscow: Nauka, 1984.
37. Shevchenko, L.S., Craniometric characteristics of the common fox of the European part of the USSR, *Vestn. Zool.*, 1987, no. 3, pp. 63–71.
38. Korablev, N.P., Korablev, M.P., Korablev, A.P., et al., Factors of polymorphism of craniometric characters in the red fox (*Vulpes vulpes*, Carnivora, Canidae) from the center of European Russia, *Biol. Bull.*, 2018, vol. 46, pp. 946–959. <https://doi.org/10.1134/S0044513418090064>
39. Amaike, Y., Oishi, T., Uruguchi, K., et al., Geographical variation in skull morphology in the Hokkaido population of the Red Fox, *Vulpes vulpes*, *Mammal Study*, 2015, vol. 40, no. 4, pp. 245–256. doi <https://doi.org/10.3106/041.040.0405>
40. Ansoerge, H., Intrapopular skull variability in the red fox, *Vulpes vulpes* (Mammalia: Carnivora: Canidae), *Zool. Abh.*, 1994, vol. 48, no. 6, pp. 103–123.
41. Fairley, J.S. and Bruton, T., Some observations on a collection of fox skulls from North-East Ireland, *Irish Nat. J.*, 1984, vol. 21, no. 8, pp. 349–351.
42. Hartová-Nentvichová, M., Anděra, M., and Hart, V., Cranial ontogenetic variability, sex ratio and age structure of the Red fox, *Cent. Eur. J. Biol.*, 2010, vol. 5, no. 6, pp. 894–907.
43. Hell, P., Paule, L., Shevchenko, L.S., et al., Craniometrical investigation of the Red fox (*Vulpes vulpes*) from the Slovak Carpathians and adjacent lowlands, *Folia Zool.*, 1989, vol. 38, no. 2, pp. 139–155.
44. Huson, L.W. and Page, R.J.C., A comparison of fox skulls from Wales and South-East England, *J. Zool.*, 1979, vol. 187, no. 4, pp. 465–470.
45. Virgo's, E., Kowalczyk, R., Trua, A., et al., Body size clines in the European badger and the abundant centre hypothesis, *J. Biogeogr.*, 2011, vol. 38, pp. 1546–1556.
46. Scholander, P.F., Evolution of climatic adaptation in homeotherms, *Evolution*, 1955, vol. 9, pp. 15–26. <https://doi.org/.tb01510.x> <https://doi.org/10.1111/j.1558-5646.1955>

Publisher's Note. Pleiades Publishing remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.