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COMPARATIVE CRANIOMETRIC ANALYSIS OF RED FOX (*VULPES VULPES*) POPULATIONS FROM DIFFERENT ALTITUDINAL ZONES OF TRANSCARPATHIA

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Abstract

This study examines cranial variation in the red fox (*Vulpes vulpes*) across three ecological zones of Transcarpathia (lowland, premontane, and montane). We examined 134 skulls, of which 78 were adults and 56 were subadults. All specimens originated from the Zoological Museum of Uzhhorod National University. Only specimens with a recorded locality (district) and sex were included. Twenty-six cranial measurements were taken with 0.1 mm precision, and each skull was assigned to one of the three zones. Morphological differences were detected among the populations. Lowland foxes generally exhibited larger skull measurements than montane individuals, particularly in skull lengths, suggesting that ecological factors may influence cranial development. Among adult individuals, montane foxes had shorter skulls and a narrower neurocranium compared to lowland foxes. The observed pattern supports the notion that the red fox exhibits notable plasticity in response to local ecological pressures. In addition to regional comparisons within Transcarpathia, our dataset was evaluated against published measurements from neighboring countries and other regions of Ukraine. When comparing our data with those from other countries and regions, the premontane males differed only from Romanian individuals in total length and Hungarian individuals in maximum zygomatic width, while females differed only from individuals from the Ukrainian Carpathians. Lowland males differed from most other populations except the Ukrainian Carpathian and Steppe ones, while females differed from all those reported in the literature. Montane males showed differences in total length, maximum zygomatic width, basal length, and neurocranium width compared to the Slovakian, Ukrainian Carpathian, Polissia, Hungarian, Steppe, and Romanian populations, whereas females were less variable and differed only from the Slovakian, Ukrainian Carpathian, Polissia, and Steppe populations. Premontane population showed the least variation compared to published data, whereas lowland and montane populations exhibited greater sex- and population-specific cranial differences across the neighboring fox populations.

Cite as

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Порівняльний краніометричний аналіз популяцій лиса рудого (*Vulpes vulpes*) з різних висотних поясів Закарпаття

Іштван Желіцькі

Резюме. У цьому дослідженні проаналізовано краніологічну мінливість у лиса рудого (*Vulpes vulpes*) у трьох зонах Закарпаття (низовинна, передгірська та гірська). Досліджено 134 черепів, з яких 78 від дорослих особин, а 56 — недорослі. Черепи вимірювали у колекції Зоологічного музею Ужгородського національного університету. До аналізу включали лише ті зразки, на яких було зазначено місце збору (адміністративний район) та стать. Проведено 26 краніальних промірів з точністю 0,1 мм після чого кожен череп віднесено до однієї з трьох зон. Серед популяцій виявлено краніологічні відмінності. Лисиці низовини загалом мали більші розміри черепа порівняно з гірськими особинами, особливо за довжиною черепа, що свідчить про можливий вплив екологічних факторів на розвиток черепа. Серед дорослих особин гірські лиси мали коротші черепи та вужчу мозкову коробку у порівнянні з низовинними. Виявлена закономірність підтверджує, що лис рудий проявляє значну пластичність у відповідь на локальні екологічні умови. Окрім регіональних порівнянь у межах Закарпаття, ми порівнювали свої дані з опублікованими для сусідніх країн та інших регіонів України. Такий аналіз показав, що популяція лиса з передгір'їв відрізнялися лише від румунських особин за загальною довжиною та від угорських за виличною шириною, тоді як самки відрізнялися лише від особин українських Карпат. Самці низинних районів Закарпаття відрізнялися від більшості інших популяцій, за винятком українських Карпат та Степу, тоді як самки від усіх інших даних, опублікованих у літературі. Гірські самці демонстрували відмінності за загальною довжиною, виличною шириною, базальною довжиною та шириною мозкової коробки порівняно з популяціями зі Словаччини, українських Карпат, Полісся, Угорщини, Степу та Румунії, тоді як самки відрізнялися від популяцій зі Словаччини, українських Карпат, Полісся та Степу. Передгірська популяція показала найменші відмінності відносно опублікованих даних, тоді як низовинні та гірські демонстрували більш виражені статеві та міжпопуляційні відмінності краніальних показників відносно сусідніх популяцій лисиць.

Ключові слова: лис рудий, краніометрія, морфологія черепа, статевий відбір, географічна варіація.

Introduction

The red fox (*Vulpes vulpes*) is the most widely distributed terrestrial carnivoran on Earth. Its exceptional adaptability allows it to thrive in regions ranging from the Arctic to North Africa, and from North America to the Japanese islands [Heltay 1989]. Examining skull measurements provides important insights into geographic variation, ecological adaptations, and morphological differences between populations. This extensive range has also led to the recognition of around 44 subspecies [Larivière & Pasitschniak-Arts 1996].

Red foxes inhabit a wide variety of geographic regions, each with distinct climatic and ecological conditions. Such diversity can result in notable differences in morphology among populations, making it particularly valuable to study the cranial characteristics of foxes across the different zones of Transcarpathia.

Studies from around the world show a variety of patterns in cranial variation. In the Czech Republic, five out of 21 measured skull traits differed significantly between males and females [Brudnicki *et al.* 2009]. In Hungary, these differences were most pronounced in sexually mature individuals, though younger foxes showed less variation; even so, female skulls remained clearly distinct from those of males [Csányi *et al.* 2023]. Pronounced sexual dimorphism has also been reported in fox populations in Australia [Forbes-Harper *et al.* 2017], the Czech Republic [Hartová–Nentvichová *et al.* 2010], Slovakia, Romania, and Ukraine [Hell *et al.* 1989].

This dimorphism is thought to result from sexual selection and the need to reduce competition between males and females [Lynch 1996]. Male competition often involves aggressive encounters, with larger males generally enjoying greater reproductive success than smaller ones [Abramov & Puzachenko 2005].

Bergmann's rule, a widely recognised ecogeographical principle, states that animals tend to be larger in colder regions. Interestingly, in red foxes, skull and body size appear to decrease with increasing altitude [Yom–Tov *et al.* 2006].

Turyanin [1975] suggested that the varied environmental conditions of Transcarpathia could potentially support multiple subspecies. Yet, information on red fox populations in this region remains scarce. Korchynskyi et al. [1993] reported that between 1946 and 1992, only 10.5% of studies on the Carpathian mammalian fauna addressed red foxes, underlining the need for more detailed and systematic research. Craniometric analysis is a key method for investigating these populations [Zagorodniuk 2012; Gomes & Valente 2016].

While some studies document reproduction and foraging of red foxes in Transcarpathia, craniological investigations are limited to just a few sources [Hell *et al.* 1989; Zhelitski 2002]. In the present study, we aim to explore cranial differences among three populations—lowland, premontane, and montane—by examining skulls preserved in the Zoological Museum of Uzhhorod National University, which was established in December 1945 [Kron *et al.* 2019].

Materials and methods

In a recent study we measured 134 skulls of red foxes (56 subadult, 78 adult) from the scientific collections of the UzhNU Zoological Museum. The fox skulls included in the study were collected in Transcarpathia between 1951 and 1976, with some additional specimens collected in 2015. To assess interpopulational variations we examined all the skulls which were signed by site and sex. Measurements were taken using a calliper with an accuracy of 0.1 mm. We also determined the age of the individuals [Heltay 1989] and classified them into two categories: subadult and adult.

In this study, we measured only those skulls for which the sex and collection locality were known. In most cases, however, only the administrative district was recorded. Since the administrative boundaries of districts never precisely follow geographic features, we assigned to the lowland and montane zones only those areas that clearly belonged to them.

Accordingly, the lowland zone includes the Uzhhorod, Berehove, Vynohradiv, and Mukachevo districts, whereas the montane zone comprises the Rakhiv, Tiachiv, Mizhhiria, Velykyi Bereznyi, and Perechyn districts (Volovets would belong to the montane zone, but no data are available). The remaining districts were therefore assigned to the premontane zone.

The assignment of these zones was based on the geographical classification according to the altitudinal gradient. This classification allows for meaningful comparisons of local populations with those of directly adjacent countries. The lowland area borders Hungary and Slovakia, whereas the montane zone borders Romania and Poland.

The territory of the Transcarpathia region is located in western Ukraine and shares borders with Hungary, Poland, Slovakia, and Romania. Despite its relatively small area (12 800 km^2), the region exhibits remarkable environmental diversity. Approximately four-fifths of its territory is occupied by montane ranges interspersed with valleys and depressions, while only one-fifth constitutes lowland areas. The region is conventionally divided into lowland, premontane, and montane zones.

According to Herenchuk [1981], winter lasts longer in the montane zone, summers are shorter, and temperatures are generally cooler. Summer temperatures, as well as the average monthly temperatures in January, correspond to winter daily means ranging from –5 to 0 °C. On the lowlands, temperatures in this range occur for about 15 days, while in the montane they persist for 27 days. Days with a daily mean temperature of 20–25 °C number around 43 in the lowlands, but only one in the montane. Precipitation is more than twice as high (1411 mm) in the montane zone, due to the Carpathians' geographic features. Temperature also drops by roughly 1.1 °C for every 100 m of elevation.

For each of the three zones, we calculated descriptive statistics, including the minimum (min), maximum (max), and mean (M) values, as well as the standard deviation (SD). The results are presented separately for males and females, and are compared with data from other neighbouring countries. The Shapiro–Wilk test was then used to assess the distribution of the data. According to the results of the normality tests, only the traits TL, BL, GLN, MPL, LMR, LC, GMB, GBOC, MWN, ZYG, LBS, GPB, LPB, BCA, and LN were included in the subsequent analyses.

The variation in the linear traits was further examined using multivariate ordination methods, including discriminant analysis. In addition, three-way and two-way MANOVA were also performed. First, we analysed all of our data, including subadult specimens. Afterwards, we focused only on adult skulls to avoid the effects of age classes. For the purpose of comparison with previously published studies, analyses were restricted to adult individuals; accordingly, only these specimens are presented in the tables. Comparisons with literature data were carried out using a one-sample t-test. For statistical analysis, we utilised SPSS, PAST 5.3, and Microsoft Excel.

The following cranial measurements were recorded (Fig. 1).

Results and discussion

The three-way MANOVA revealed that sex had a significant effect on cranial morphology ($p = 0.00$), and differences among populations and age groups were also significant ($p = 0.02$ and $p = 0.00$, respectively). These results indicate that cranial morphology varies systematically across populations and age classes, rather than reflecting only individual-level or purely environmental variation.

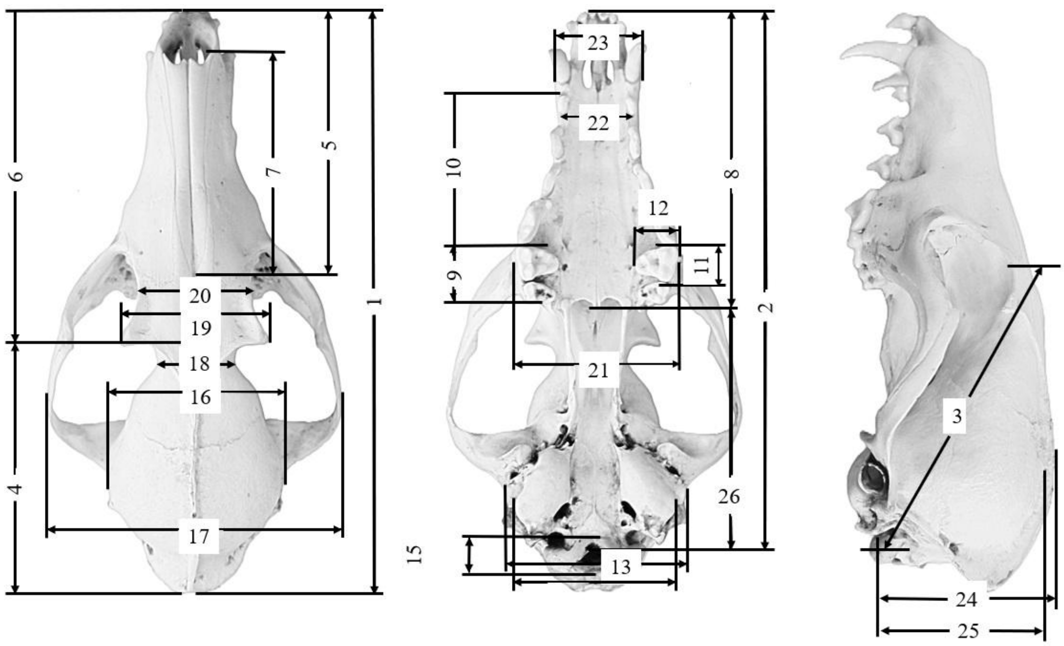


Fig. 1. Studied cranial measurements.

Рис. 1. Досліджені черепні виміри.

1) Total length (TL): akrokranion to prosthion. 2) Basal length (BL): basion to prosthion. 3) Neurocranium length (NL): basion to nasion. 4) Upper neurocranium length (UNL): akrokranion to frontal midpoint. 5) Viscerocranial length (VCL): nasion to prosthion. 6) Facial length (FL): frontal midpoint to prosthion. 7) Greatest length of the nasals (GLN): nasion to rhinion. 8) Median palatal length (MPL): staphylion to prosthion. 9) Length of the molar row (LMR). 10) Length of the premolar row (LPR). 11) Length of the carnassial (LC): measured at the cingulum. 12) Greatest breadth of the carnassial (LBC). 13) Greatest mastoid breadth (GMB): otion to otion. 14) Greatest breadth of the occipital condyles (GBOC). 15) Height of the foramen magnum (HFM): basion to opisthion. 16) Maximum width of the neurocranium (MWN): euryon to euryon. 17) Zygomatic width (ZYG): zygion to zygion. 18) Least breadth of the skull (LBS): at the postorbital constriction. 19) Frontal breadth (FB): ectorbitale to ectorbitale. 20) Interorbital width (IOR): entorbitale to entorbitale. 21) Greatest palatal breadth (GPB): across the outer borders of the alveoli. 22) Least palatal breadth (LPB): measured behind the canines. 23) Breadth at canine alveoli (BCA). 24) Skull height without the sagittal crest (SHSC). 25) Skull height (SH). 26) Length of neurocranium (LN): staphylion to basion.

Although morphological divergence among populations is moderate, the statistical evidence shows that population membership contributes meaningfully to cranial variation. Ecological conditions and geographic structuring thus influence cranial morphology, and these effects are consistently detectable in multivariate analyses.

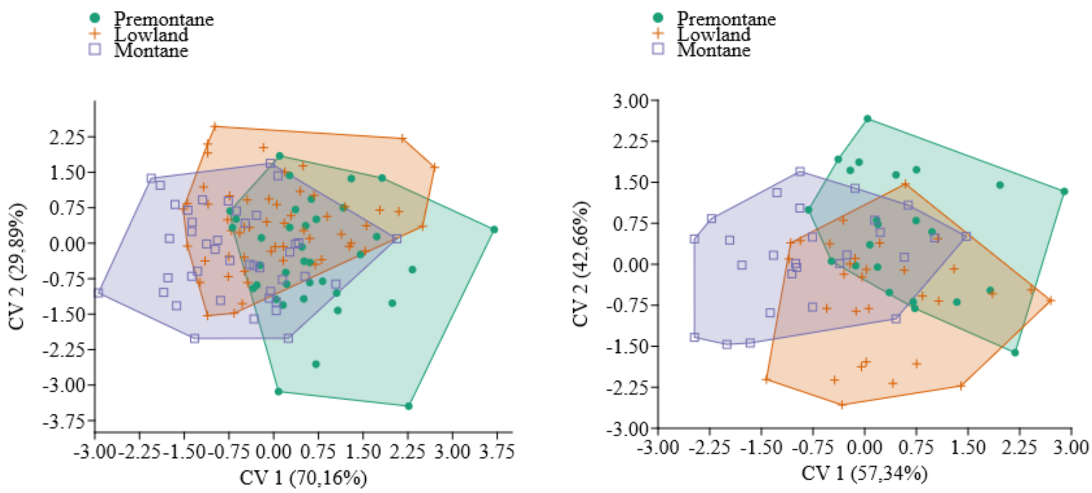
A two-way MANOVA focusing on adult individuals further confirmed the influence of sex on cranial morphology ($p = 0.03$) and detected statistically significant population differences ($p = 0.04$), along with a significant interaction between population and sex ($p = 0.04$). These findings highlight that a substantial portion of the observed variation reflects geographically structured differences rather than individual-level variation alone. Overall, our results confirm pronounced sexual dimorphism in this regional population, likely resulting from a combination of sexual selection and ecological adaptation, where larger males may have advantages in territory defence, mating, and prey handling.

Based on the adult dataset, CV1 captures the main morphological differences among the populations (57.34% of the variance), while CV2 represents secondary differences (42.66%). The premontane population exhibits an intermediate morphological pattern between the lowland and montane groups, whereas the lowland and montane populations are well separated along the two primary canonical variates (Fig. 2). We summarised the minimum, maximum, mean, and standard deviation of normally distributed cranial traits for adult individuals included in the analysis (Table 1).

Comparisons with data from other countries and regions (Table 2) revealed distinct patterns at the population level. In the case of total length, montane males differed significantly from the Slovakian, Hungarian, and Romanian individuals reported in the literature, whereas premontane males differed only from the Romanian individuals. Lowland males differed from all other populations except the Ukrainian Carpathian and Steppe males (Fig. 3). Montane females differed only from the Ukrainian Carpathian individuals, and the same pattern was observed for premontane females. Lowland females differed from all other populations reported in the literature (see Fig. 3).

For maximum zygomatic width, montane males differed from the Slovakian and Hungarian populations, whereas montane females did not differ from any literature data (no data were available from Romania). In the premontane population, only the males differed from the Hungarian individuals. Lowland males differed from the Slovakian and Hungarian populations, while lowland females differed from the Polissia and Steppe individuals.

Regarding basal length, montane males did not differ only from the Polissia individuals (no data were available from Romania and Hungary), whereas montane females did not differ only from the Polissia and Steppe individuals.



a *b*

Fig. 2. Discriminant analysis of all data of red fox individuals: with subadults (*a*) and adults only (*b*).

Рис. 2. Дискримінантний аналіз усіх особин лиса рудого: разом з напівдорослими (*a*), тільки дорослих (*b*).

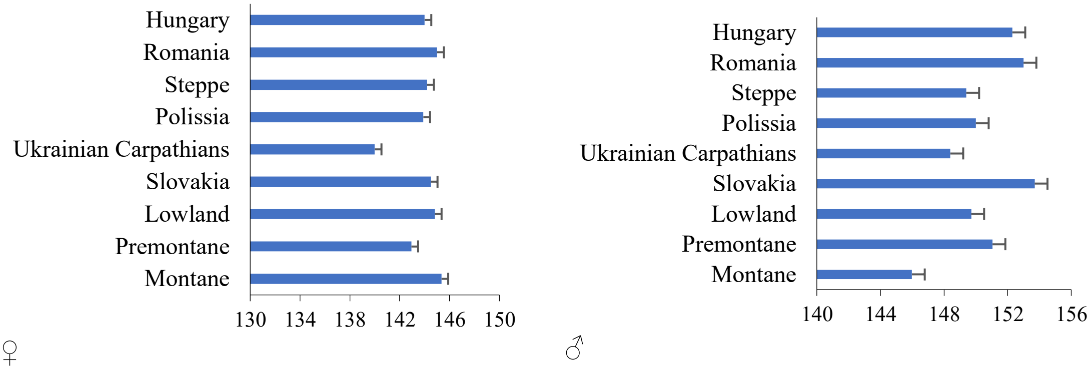


Fig. 3. Variation in total length of skull among countries and regions (Mean + SE): female (♀) and male (♂).
Рис. 3. Зміни загальної довжини черепа між країнами і регіонами (Mean + SE): у самок (♀) і самців (♂).

Table 1. The craniometric measurement values of the red fox from Transcarpathia (min–max / M ± SD)
Таблиця 1. Краніометричні показники лиса рудого із Закарпаття (min–max / M ± SD)

Measures	Montane		Premontane		Lowland	
	male, n = 20	female, n = 7	male, n = 10	female, n = 5	male, n = 28	female, n = 8
TL	137.5–156.0 145.9 ± 5.2	142.0–148.5 145.3 ± 2.1	143.5–157.0 151.0 ± 5.3	138.8–144.7 142.9 ± 2.3	138.5–161.0 149.7 ± 5.9	135.0–158.8 144.8 ± 8.1
BL	126.6–141.3 133.5 ± 4.0	130.2–136.6 133.6 ± 2.3	129.7–144.8 138.0 ± 5.8	126.5–132.7 131.2 ± 2.6	126.5–145.7 136.5 ± 5.2	125.3–145.2 133.5 ± 7,2
NL	71.8–83.8 77.3 ± 3.6	74.0–81.0 77.9 ± 2.1	72.0–83.4 79.8 ± 3.7	74.5–80.0 77.2 ± 2.0	74.8–85.0 79.4 ± 2.6	71.0–84.0 77.3 ± 4.8
GLN	49.7–63.0 54.9 ± 3.7	49.0–56.0 53.9 ± 2.5	55.4–66.5 58.9 ± 3.4	50.2–56.7 53.5 ± 2.7	50.8–64.0 56.6 ± 3.7	51.7–59.5 53.9 ± 2.6
MPL	69.5–79.5 74.4 ± 2.7	72.0–76.0 73.5 ± 1.6	73.0–80.5 77.8 ± 2.7	68.3–71.5 70.5 ± 1.3	69.0–81.0 75.8 ± 3.4	69.0–78.6 72.8 ± 3.6
LMR	12.5–14.8 13.5 ± 0.5	12.0–15.5 13.6 ± 1.2	13.0–15.2 13.9 ± 0.7	12.8–14.1 13.4 ± 0.5	12.4–15.5 13.9 ± 0.7	12.5–14.7 13.7 ± 0.7
LC	12.2–15.5 13.6 ± 1.0	12.3–14.3 13.8 ± 1.2	11.7–15.6 13.5 ± 0.9	12.2–15.9 12.9 ± 0.7	12.0–15.4 13.7 ± 0.9	12.3–14.8 13.1 ± 0.6
GMB	43.0–48.8 45.7 ± 1.5	44.0–48.8 46.0 ± 1.5	44.2–49.6 47.1 ± 1.8	44.1–47.5 46.7 ± 1.4	43.2–50.5 46.3 ± 1.5	41.3–47.9 44.6 ± 2.2
GBOC	23.0–27.5 26.0 ± 1.2	25.0–27.6 26.1 ± 0.9	24.7–29.0 26.4 ± 1.4	23.5–27.0 25.6 ± 1.3	24.5–27.7 26.1 ± 0.8	24.0–27.1 25.7 ± 0.9
MWN	45.2–49.0 47.2 ± 1.2	46.5–48.7 47.3 ± 0.8	46.7–50.5 48.5 ± 1.5	46.4–49.0 47.6 ± 1.0	44.5–51.0 48.1 ± 1.6	45.5–49.8 47.0 ± 1.7
ZYG	71.0–85.0 76.6 ± 3.6	72–79.5 76.0 ± 2.9	69.7–84.9 77.7 ± 4.9	70.7–81.0 75.5 ± 5.0	71.8–83.0 77.4 ± 2.9	71.5–80.6 76.2 ± 3.6
LBS	19.8–23.9 22.0 ± 1.0	21.0–23.7 22.3 ± 0.9	20.5–26.7 23.6 ± 1.7	21.2–23.9 22.2 ± 1.1	18.0–27.0 22.3 ± 1.9	19.5–23.0 21.3 ± 1.2
GPB	35.5–44.5 39.3 ± 2.0	36.7–43.0 39.7 ± 2.0	37.6–41.5 40.0 ± 1.1	38.1–43.5 40.5 ± 2.5	32.6–42.4 38.9 ± 2.0	37.1–40.5 38.5 ± 1.0
LPB	19.5–23.8 21.7 ± 1.1	20.0–25.5 22.0 ± 1.8	21.0–23.8 22.4 ± 0.9	19.0–24.8 22.2 ± 2.33	20.0–25.0 22.0 ± 1.4	20.1–23 21.4 ± 1.0
BCA	20.0–26.2 23.5 ± 1.3	23.0–24.2 23.5 ± 0.3	22.2–26.2 24.2 ± 1.5	21.0–26.7 24.1 ± 2.5	22.0–27.3 23.7 ± 1.2	22.1–25.0 23.2 ± 1.1
LN	55.6–63.0 59.1 ± 1.9	57.0–62.0 59.4 ± 1.8	52.5–64.0 59.2 ± 3.7	58.0–61.3 60.3 ± 1.3	55.8–66.1 60.0 ± 2.5	56.0–66.0 59.4 ± 3.5

Table 2. The craniometric measurement values of the red fox (*Vulpes vulpes*) from different countries and regions
Таблиця 2. Краніометричні показники лиса рудого (*Vulpes vulpes*) із різних країн та регіонів

Region	TL ♂ / ♀	BL ♂ / ♀	MWN ♂ / ♀	ZYG ♂ / ♀	References
Transcarpathian Montane zone	146.0 145.4	133.5 133.6	47.2 47.4	76.6 76.0	this study
Transcarpathian Premontane zone	151.1 142.9	138.0 131.2	48.5 47.7	77.8 75.5	this study
Transcarpathian Lowland zone	149.7 144.8	136.5 133.6	48.1 47.1	77.4 76.3	this study
Slovakia	153.7 144.5	139.5 129.5	47.2 47.8	80.3 75.7	Hell *et al.* 1989
Ukrainian Carpathians (montane zone)	148.4 140.0	135.9 128.7	48.6 47.5	77.1 76.6	Hell *et al.* 1989
Polissia (Ukraine)	150.0 143.9	137.1 131.7	48.7 47.9	77.3 73.9	Hell *et al.* 1989
Steppe (Ukraine)	149.4 144.2	136.5 132.4	48.6 47.8	77.1 74.5	Hell *et al.* 1989
Romania	153.0 145.0	– –	– –	– –	Hell *et al.* 1989
Hungary	152.3 144.0	– –	– –	81.2 76.7	Csányi *et al.* 2023

The premontane population did not differ from any literature data (see: Table 2). Lowland males differed only from the Slovakian individuals, while lowland females did not differ only from the Ukrainian Carpathian literature data.

In the case of maximum width of the neurocranium, montane males did not differ only from the Slovakian males (no data were available from Romania and Hungary), whereas montane females did not differ only from the Ukrainian Carpathian individuals. In the premontane and lowland populations, only the males differed from the Slovakian literature data.

Overall, these patterns suggest that the premontane population exhibits the least differences compared to published data from other regions, while the lowland and montane populations show more pronounced morphological differentiation, especially among males. Similar population-level variation has been reported in Ukraine for raccoon dogs, where differences were attributed to heterogeneous climatic conditions [Lazariev 2024], and in red foxes, environmental effects have also been documented [Parsons *et al.* 2020].

Some of the larger skull sizes observed in the premontane zone may result from uncertainty regarding the exact collection sites. To improve reliability, additional specimens should be collected from clearly defined zones—for instance, Berehove for the lowland, Rakhiv or Mizhhiria for the montane, and the Irshava region for the premontane population. Overall, craniometric analyses indicate significant differences among populations, particularly in skull length. The differences among local populations are unlikely to result from gene flow with neighbouring countries, as connectivity toward Romania and Hungary is limited by the Tisza River. Male-mediated dispersal plays a key role in maintaining population connectivity, as males move on average six times farther than females, covering approximately 37.8 km [Walton *et al.* 2018, 2021]. While males facilitate gene flow between populations, females tend to retain locally advantageous genes within their natal areas. Differences observed between neighbouring countries may result from restricted gene flow, local environmental conditions, or sexual selection.

Conclusions

The present study provides new craniometric data on red fox (*Vulpes vulpes*) populations inhabiting different altitudinal zones of Transcarpathia. The results reveal that both geographic variation and sexual dimorphism significantly influence skull morphology.

Morphometric differences among lowland, premontane, and montane populations likely reflect ecological and environmental adaptation. The observed gradient in skull dimensions supports the assumption that local climatic conditions, prey availability, and habitat structure may contribute to morphological diversification within the region.

Sexual dimorphism was expressed in nearly all cranial traits, with males showing consistently larger and more massive skulls than females. This pattern is in line with findings from other parts of Europe and the world, suggesting that sexual selection and intraspecific competition play an important role in shaping red fox morphology.

Overall, the study highlights that the red fox of Transcarpathia exhibits notable morphological plasticity, influenced by both environmental heterogeneity and biological factors.

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Declarations

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