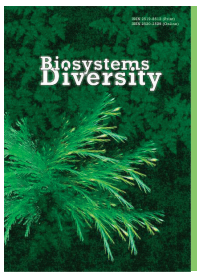

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The colour phases of the European red squirrel in Ukraine: Similarities and differences by craniometric characters

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The different colour phases of the European red squirrel occuring in Ukraine were analysed in a morphological context. They are indicated in the literature as different subspecies of *Sciurus vulgaris* L. and described only based on their coat colouration. In Ukraine, at least three colour phases occur: dark (black and brown), red, and light red, which in natural habitats occur separately from one another. These phases co-occur in human settlements and at different altitudes, in particular at the boundary of the lowland and piedmont zones and of piedmont and mountainbelts. The aim of the present study was to find some other morphological differences between the red squirrel's phases in Ukraine beyond their coat colouration and to reveal the possible interaction between colouration and morphological variation of the squirrels. Eighteen craniometric and four external characters were measured and analysed. Results have shown that the squirrel's colour phases differ among themselves by some characters, although the most visible differences were revealed when all measurents were analysed together. It has been revealed that the three colour phases are stabilized types (populations) manifested in a multidimensional space as different populations with minimal overlap (up to 10%). The population of dark squirrels in Ukraine is morphologically the most distant from the light red phase and less so from the red one. The dark phase significantly differs from the red phase by 9 of 18 craniometric characters with Mayr's coefficient of divergence (CD_{min} = 0.62, CD_{max} = 0.96). The dark phase significantly differs from the light red phase by two craniometric characters according to ANOVA, but only by one character according to Mayr'scoefficient of divergence (CD = 0.96). The red and light red phases significantly differ by four parameters having CD_{min} = 0.64 and CD_{max} = 0.76. The geographically transitional red phase is morphologically intermediate according to the results of discriminant analysis.

Keywords: red squirrel; colour phase; morphological variation; craniometric character; discriminant analysis.

Introduction

About 10 of more than 40 known subspecies of the European red squirrel (Miller, 1912; Bosch & Lurz, 2012; Koh et al., 2015) were described mainly based on morphology and coat colouration (Sidorowicz, 1961). In Ukraine, several subspecies are known distinguished by the colour of the fur as well (Zizda, 2005). It has been repeatedly described in the literature that colouration polymorphism of squirrels has a taxonomic component (Lurz et al., 2005) and is related to morphologic differentiation (Sidorowicz, 1958), geographical and genetic variation (Barratt et al., 1999; Hale et al., 2004; Paulauskas, 2006; Dozières, 2012), and isolation (Wauters et al., 1994; Delin and Andrén, 1999; Grill et al., 2009; Wauters et al., 2010; Madsen et al., 2015). However, attempts to find morphological (Sidorowicz, 1958, 1961) and genetic differences between close subspecies (Bilokon et al., 2014) in order to explain their heterogeneity due to adaptation (Zawidzka, 1958; Voipio & Hissa, 1970; Tonkin, 1983; Wauters et al., 2004) or ecological and biogeographic patterns (Cott, 1940; Burtt, 1981; Caro, 2005, 2013) did not give reliable results. Therefore, considering different colour phases of the squirrel as geographic morphs would be more reasonable since their diversity has still been insufficient to clearly distinguish the different subspecies from one another.

The squirrel's geographic variation on a large scale and under various conditions with the absence or weak isolation of different populations reveals interdependence between the genetic diversity of these populations (Trizio et al., 2005). In a narrow geographic region with high isolation effects, morphological variability and genetic diversity between close populations of the squirrel are practically absent (Sidorowicz, 1958; 1961). In the Ukrainian Carpathians, the effects of isolation between squirrel populations are blurred and genetic differences between close phases are weak or practically absent (Bilokon et al., 2014). Since Ukraine has a large terrritory having various geographic conditions in different regions, morphological differences between the squirrel's colour phases could be expected here.

Thus the aim of this research is to find some other morphological differences between the red squirrel's phases in Ukraine beyond their coat colouration and to reveal the possible interaction between colouration and morphological variation in the samples. In Ukraine, at least three colour phases of red squirrel occur, including a dark (black and brown squirrels), a red, and a light red phase (Zizda, 2005). We possess a unique material on the variability of squirrels from Ukraine, where three colour phases converge.

The colour phases of the squirrel and their distribution in Ukraine. According to research conducted, four subspecies of the red squirrel occur in Ukraine, such as *Sciurus vulgaris carpathicus*, *S. v. fuscoater*, *S. v. kessleri*, and *S. v. ukrainicus*. Each subspecies is represented by a distinct colour phase: *S. v. carpathicus* – black, *S. v. fuscoater* – brown, *S. v. kessleri* – red, and *S. v. ukrainicus* – light red (Zizda, 2008). The colour phases shown in Figure 1 are: 1) light red (LPh), the most lightly coloured squirrels with red tails; 2) red (RPh), intermediately coloured squirrels having red coat and red or brown tail; and 3) dark (DPh) – the two righthand examples, the most darkly coloured squirrels varying from dark brown to black both in the coat and tail.

The subspecies occuring in Ukrainie have a high geographical and individual variability similarly to other subspecies of *Sciurus vulgaris* within its range. When dealing with only a single specimen from the population it is practically impossible to determine to which subspecies it belongs thus when observing single individuals of the squirrel it is easier to describe the colour phase rather than the subspecies. In addition, the analysis of records of the squirrel by questionaires gives rather blurred

results regarding subspecies since an observation of a darkly coloured individual can be interpreted differently (brown, black, dark, etc.). Such data can lead not only to incorrect interpretation of distribution of subspecies, but also of colour phases (e.g., light red and red). Accordingly, studying variability of red squirrels can be complicated since it becomes necessary to analyse a sufficient sample from different populations in order to determine subspecies.

Fig. 1. The colour phases of the European red squirrel: light red, red and dark (brown and black), collection of the Zoological Museum of Ivan Franko Lviv National University

When studying specimens from distinct squirrel populations in Ukraine, three colour phases can be distinguished.

1. Dark phase. The colouration of these squirrels, especially in summer, varies from black to coffee coloured with a rufous tincture. In winter such shades remain on the back, tail, and feet, while the ears can have a slighly lighter colour than the back or be the same as the ear-tufts. The sides of the winter coat are dark grey, although dark brown tones with rufous shade prevail, while the back is dark, black or brown, without a rufous tinct, and the tail remains black. Regarding subspecies, two of them belong to the dark phase: *S. v. carpathicus* is represented by black squirrels, while specimens of *S. v. fuscoater* are brown.

2. Red phase. It can be easily confused with the light red form, especially when these two phases do not co-occur. The coat is red and rusty, the tail in summer is also rusty and rufous. In winter the colouration of the back and feet does not change, while the ear-tufts become rather brown or coffee coloured with a rusty shade. Grey colour in the winter coat is present only on the sides, as in the dark phase. The red phase represents the subspecies *S. v. kessleri*.

3. Light red phase. It is the lightest form of the squirrel, which can be identified when compared to other light forms or when finding them in lowland regions of Ukraine. These are rufous and light rufous squirrels without rusty shade having an almost entirely grey winter coat, except a narrow ligh rufous stripe on the back and the tail, which remains rufous. The light red phase represents the subspeies *S. v. ukrainicus*.

The subspecies *S. v. carpathicus* (black phase) is common in the upper forest zone of the Carpathians above 600 m a.s.l. It occurs in coniferous and mixed coniferous-deciduous forests. According to our studies conducted in 2005–2018, it occurs in natural forests and protected areas, also in human settlements located in highland districts of Transcarpathia, including Mizhhiria, Tiachiv, and Rakhiv raions. These squirrels are the darkest, almost black. They have low abundance in the region and are the most isolated from other colour phases and neighbour with the subspecies *S. v. fuscoater* in mountain mixed forests and human settlements.

The subspecies *S. v. fuscoater* (brown phase) occurs in Ukraine in piedmont and mountain zones below 600 m a.s.l. in mixed coniferous-deciduous and mixed deciduous forests of Prykarpattia, including also human settlements. It is also common in forests at the border of piedmont and lowland zones, where it often co-occurs with the subspecies *S. v. kessleri*. This subspecies is less isolated from *S. v. kessleri* than from *S. v. carpathicus* and has a wider distribution occuring often in synanthropic conditions at the lower edge of its altitudinal range.

The subspecies *S. v. kessleri* (red phase) is common in lowland broad-leaved forests of Western and partly of Central and Northern Ukraine (to the west of the Dnipro River). This subspecies is weakly isolated and occurs mainly in large city parks or protected areas. It neighbours with the subspecies *S. v. ukrainicus* in Central and Northern (to the west of the Dnipro river) Ukraine.

The subspecies *S. v. ukrainicus* is common in Northern, Eastern, and partly in Central Ukraine (to the east of the Dnipro river). In the north, it neighbours with other light coloured subspecies (*S. v. ognievi* and *S. v. formosovi*), while in the east and south it neighbours with *S. v. exalbidus*.

Transitional forms can be distinguished within each subspecies mentioned, namely dark and light variations within each of the subspecies. The analysis of colour variation in squirrels conducted in 2005–2018 allowed us to conclude that subspecies cannot be identified during field research in natural conditions without the presence of a considerable sample of the subspecies investigated. Having the knowledge and experience of observations on the squirrels' distribution, however, it is possible to distinguish four colour forms, such as black, brown, red, and light red, within a wider geographic region. At the same time, to identify subspecies is rather complicated and requires the examination of large samples from distinct populations. Therefore, searching for approaches which enable one to distinguish between different colour phases in small samples from large territories remains a topical issue, especially in a morphological and genetic context.

Materials and methods

Samples from different zoological museums of Ukraine, including the State Museum of Natural History (Lviv), Zoological Museum of Ivan Franko Lviv National University, Zoological Museum of Taras Shevchenko Kyiv National University, Zoological Museum of Uzhhorod National University, National University of Forestry of Ukraine (Lviv), and the Zoological Museum of Mykola Gogol State University of Nizhyn, were analysed. For the analysis, 18 craniometric characters (Fig. 2) and 4 body measurements of 59 specimens were taken (after Zagorodniuk (2012) with additions).

The following skull measurements were taken: 1) total skull length (TL); 2) condylobasal length (CBL); 3) upper tooth row length (UTL); 4) length from the last molar to the proximal end of the skull (MBCL); 5) interorbital width (IOW); 6) length of the upper diastema (DILU); 7) coronal length of the upper molars (CML); 8) zygomatic width (ZB); 9) braincase width (BBC); 10) width of postorbital constriction (PC); 11) frontal length (FL); 12) mandibular length (LM); 13) length of the lower diastema (DILL); 14) mandibular height (MH); 15) coronal length of the lower molars (CmL); 16) width of auditory bulla (BW); 17) maximal diameter of auditory bulla (BLD); 18) braincase height (HBC).

The following body measurements were analysed: 19) head and body length (HB); 20) tail length (T); 21) hind foot length (HF); 22) ear length (EL).

Only specimens providing complete data were included in the analysis: damaged or beaten skulls were neglected as well as specimens without clear indication of record localities.

To compare craniometric characters in various colour phases, ANOVA, Mayr's coefficient of divergence (CD), and discriminant analysis were used. The distance between populations of different colour phases was shown with help of the Mahalanobis distance (Zagorodniuk, 2007; McDonald, 2014).

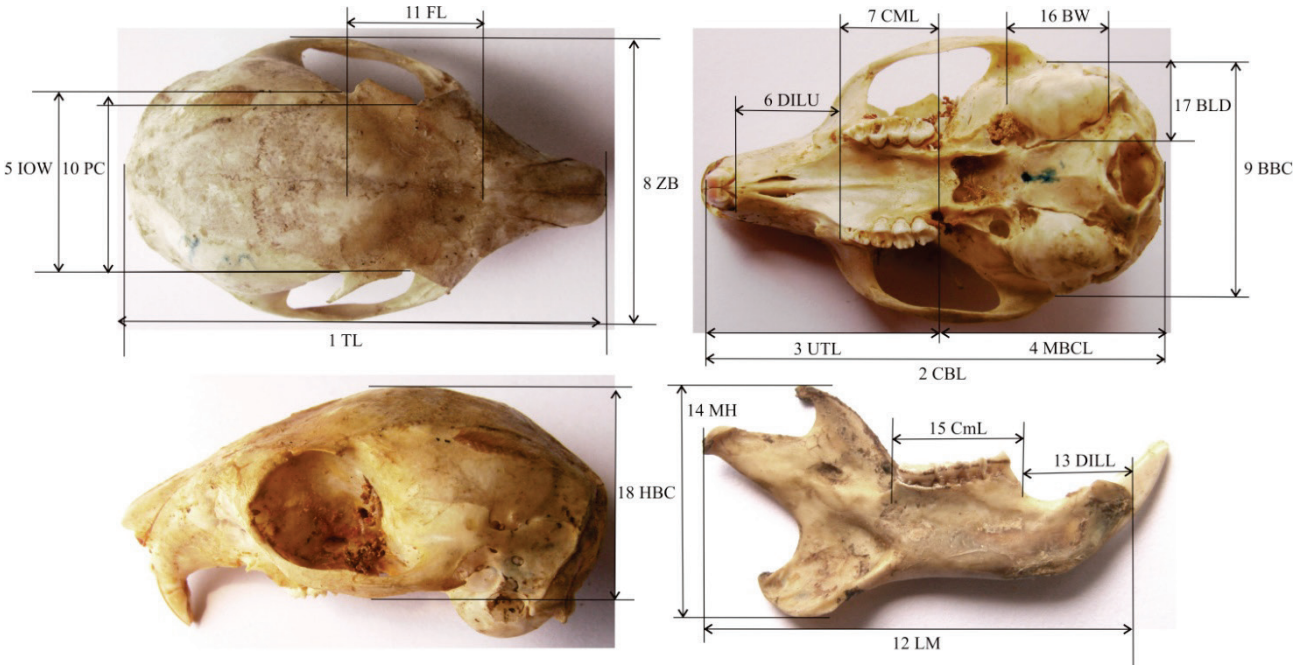

Fig. 2. Skull measurements used in the analysis

Results

A total of 18 craniometric characters of the three colour phases of the squirrel were compared with the help of ANOVA and Mayr's coefficient of divergence (CD) (Table 1). CD indices for the analysed 18 characters with values of reliability of $P < 0.10$ are not present. If the value of a character is reliable with $P < 0.05$ for one colour phase, then for the other two it is reliable only with $P < 0.10$ or the phases do not differ significantly at all. Two reliable values with $P < 0.05$ in different colour phases were not observed. The value of characters with different degrees of certainty for two different colour phases is present in the case of ZB, MH, BW, and HBC (Table 1).

Table 1
The variation of craniometric measurements in the colour phases of the European red squirrel according to ANOVA and Mayr's coefficient of divergence (CD)

Parameter	Colour phase			ANOVA analysis			Coefficient of divergence (CD)		
	Dark (1)	Red (2)	Light red (3)	1/2	1/3	2/3	1/2	1/3	2/3
1 *(TL)*	50.58 ± 2.03	52.48 ± 0.20	51.34 ± 2.40	–2.85*	–1.10	–1.32	–0.81*	–0.34	–0.45
2 *(CBL)*	46.67 ± 1.91	47.77 ± 2.65	46.89 ± 2.24	–1.68**	–0.34	–1.04	–0.48	–0.11	–0.36
3 *(UTL)*	25.02 ± 1.00	24.37 ± 2.16	25.54 ± 0.92	1.43	–1.67	1.96**	0.41	–0.54	0.76*
4 *(MBCL)*	21.69 ± 1.09	22.51 ± 1.57	21.80 ± 1.22	–2.20*	–0.32	–1.46	–0.62*	–0.10	0.51
5 *(IOW)*	16.43 ± 2.35	17.55 ± 0.86	16.96 ± 2.51	–2.09*	–0.70	–1.00	–0.70*	–0.22	–0.35
6 *(DILU)*	12.95 ± 0.93	14.06 ± 3.09	13.32 ± 1.73	–1.82**	–0.91	–0.84	–0.55	–0.27	–0.31
7*(CML)*	9.61 ± 0.52	9.64 ± 0.34	9.72 ± 0.47	–0.23	–0.67	0.57	–0.07	–0.22	0.19
8 *(ZB)*	30.76 ± 0.98	31.78 ± 1.69	31.44 ± 1.70	–2.68*	–1.68**	–0.59	–0.76*	–0.51	–0.20
9 *(BBC)*	21.88 ± 3.12	22.92 ± 1.43	22.91 ± 1.10	–1.42	–1.23	–0.03	–0.46	–0.49	–0.01
10 *(PC)*	16.84 ± 2.97	16.43 ± 3.20	17.02 ± 3.28	0.47	–0.18	0.54	0.13	–0.06	0.18
11 *(FL)*	13.09 ± 0.99	12.97 ± 0.78	13.19 ± 0.66	0.47	–0.34	0.88	0.14	–0.12	0.30
12 *(LM)*	29.81 ± 1.00	31.36 ± 2.33	30.15 ± 2.25	–3.22*	–0.71	–1.56	–0.93*	–0.21	–0.53
13 *(DILL)*	7.47 ± 0.83	8.00 ± 1.50	7.65 ± 0.79	–1.58	–0.70	–0.80	–0.45	–0.22	–0.30
14 *(MH)*	16.36 ± 2.06	18.45 ± 2.51	16.77 ± 2.63	–3.23*	–0.57	–1.94**	–0.92*	–0.18	–0.65*
15 *(CmL)*	9.40 ± 0.39	9.40 ± 0.41	9.29 ± 0.30	0.05	0.94	–0.81	0.02	0.31	–0.28
16 *(BW)*	10.77 ± 0.98	11.33 ± 0.72	10.85 ± 0.77	–2.23*	–0.29	–1.91**	–0.66*	–0.10	–0.64*
17 *(BLD)*	8.09 ± 0.83	8.34 ± 0.92	8.18 ± 0.52	–1.00	–0.38	–0.61	–0.29	–0.13	–0.22
18 *(HBC)*	20.33 ± 1.53	20.90 ± 0.94	21.46 ± 0.82	–1.50	–2.66*	1.87**	–0.46	–0.96*	0.64*

Notes: * – values with reliability $P < 0.05$, ** – with $P < 0.10$.

The variability between DPh and RPh with $P < 0.05$ is determined by TL: CD = –0.81; MBCL: CD = –0.62; IOW: CD = –0.70; ZB: CD = –0.76; LM: CD = –0.93; and BW: CD = –0.66. The variability between DPh and LPh is determined with $P < 0.05$ in the following characters: HBC: CD = –0.96; and ZB: CD = –0.76. The differentiation between RPh and LPh with $P < 0.05$ is determined by the following measurements: UTL: CD = –0.76; MH: CD = –0.65, BW: CD = –0.64; HBC: CD = 0.64.

Consequently, DPh and LPh are significantly different by two craniometric characters according to CD. These characters are the brain case height (HBC, $P < 0.05$) and brain case width (BBC, $P < 0.10$). RPh and LPh differ by four characters with $P < 0.10$, among which two belong to the upper jaw and one to the lower jaw with CD = 0.64 and CD = 0.76. The DPh and RPh differ by 9 characters, 8 of which differ with a coefficient of reliability $P < 0.05$, and CD = 0.62 to CD = 0.96. According to the discriminant analysis, the best distinction between the colour phases is found in the combined analysis of all measurements: 18 craniometric characters and four body measurements. The results are shown in Figure 3.

The three groups (clouds) of data show 10 % overlap between all colour phases. Figure 2 shows that the light red and dark phases are distributed relatively far from each other. The red phase squirrels occupy an intermediate position between the dark and light red phases. The clouds of the dark and red phase overlap more than those of the dark and light red squirrels. However, there is a greater difference in the distance of clouds between different populations (Fig. 3) than within a population of a single colour phase. In conclusion, it is a similar situation to the way in which various colour phases are distributed in nature.

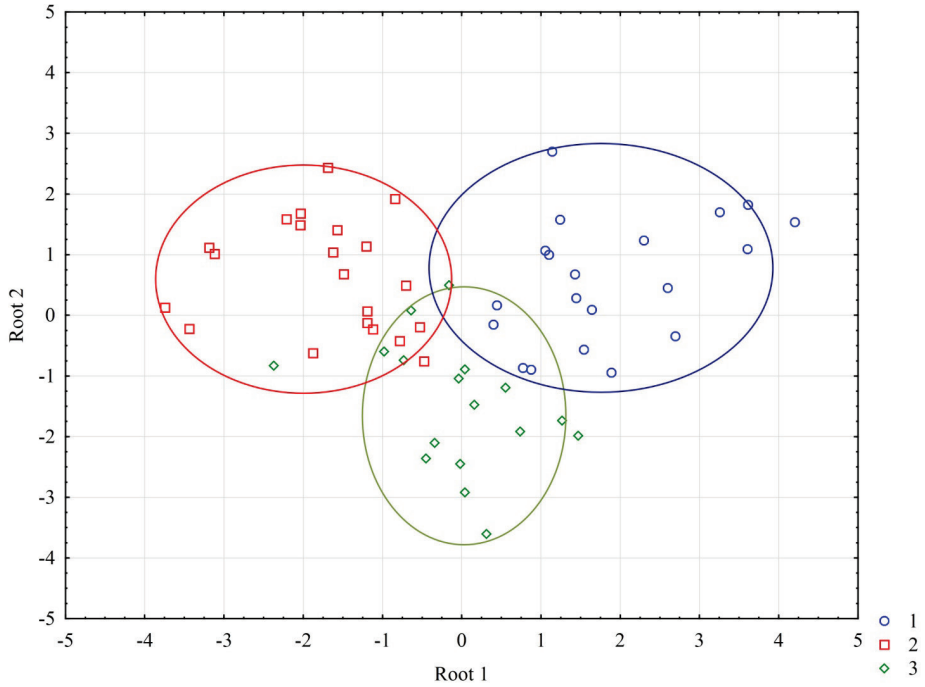

Fig. 3. Differences between the squirrel's colour phases according to discriminant analysis of 22 characters: *1* – dark phase, *2* – light red phase, *3* – red phase

In order to find out whether the distance between populations varies more than within separate populations, analysis of the Mahalanobis distances was conducted. Accordingly, the distance between the dark and red phases is 8.16, between the dark and light red phases is 10.69, while between the red and light red phases it is 10.53. Consequently, the existing differences and the nature of distances between the colour phases showed that the darkly coloured squirrels have the smallest distance from the red squirrels (the Mahalanobis distance is 8.16), although morphologic measurements indicate the largest difference between these two phases (by 9 characters, according to ANOVA). The red phase of the squirrel showed an intermediate position between the dark and light red phases. According to the Mahalanobis distance, red squirrels are more similar to the dark ones than to the light red phase. The Mahalanobis distances between the pairs of Dph – LPh and RPh – LPh are close. These colour phases have a visible difference by only two cranial characters.

Discussion

The study of different morphometric characters using discriminant analysis showed that the best result between colour phases are observed when all characters are considered together. In order to see the differentce between populations of the squirrel, different numbers of parameters were needed.

1. The dark and light red phases demonstrate the least overlap of clouds with minimal number (2) of characters. In the Carpathian region of Ukraine, these two colour phases spatially occur far from each other. Dark squirrels are widespread in the mountains, including urban green zones as well, while the light red phase is common in the lowland area, including city parks and other green zones. In other lowland regions of Ukraine, only the light red phase of the squirrel is distributed.

2. The red and light red phases of the squirrel differ well by four characters and their clouds overlap to 10%. Geographically these phases are separated in the region of the Ukrainian Carpathians, and meet only in piedmont areas. They are also common in urban areas of these altitudes. In other regions of Ukraine, the light red and red phases are distributed separately.

3. The red and dark squirrels differ by 9 characters. In natural habitats of the Ukrainian Carpathians, they occur in the foothills and often up to the upper piedmont region. They can be seen in the green zones of mountain settlements as well. These two colour phases of the squirrel are distributed only in the Carpathian region of Ukraine.

The general tendency is the following: the closer colour phases exist geographically, the more morphological parameters are needed for their differentiation. Therefore, considering the results of this study, the difference between the brown and black phases of the squirrel would be manifested with a total difference when at least 12 characteristics of the 18 studied are analysed, which would mean that, at this stage, it is impossible to see significant differences between the most similarly coloured phases of the squirrel. If this hypothesis is true, then it can be explained by the fact that no differences were found between closely coloured phases of the squirrel (black and brown) in the mountains of Poland and Ukraine in the course of genetic and morphological studies (Zawidzka, 1958; Sidorowicz, 1958, 1961; Belokon et al., 2014).

In the light of the obtained results, we can assume the further differentiation of the black phase of the squirrel by colouration and morphology, considering that the black phase in the Carpathian region is confined to mountains and higher elevations in general and occurs in relative isolation from other colour phases.

Conclusions

Analysing morphometric characters of three different colour phases of the European red squirrel in Ukraine, a larger distance was revealed between populations of different phases than within a single population of each phase. Morphologically, the population of dark squirrels in Ukraine is the most distant from the light red phase and less so from the red phase. The dark phase differs from the red one by 9 of 18 craniometric characters with their CD = 0.62 to 0.96. The dark form differs from the light red phase only by two craniometric characters, one of which has CD = 0.92. The red and the light red phases differ by four parameters having CD = 0.64 to 0.76. The geographically transitional colour phase (red) is morphologically intermediate as well.

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