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Abstract. We studied 468 museum specimens of the common hamster (387 skins and 204 skulls) collected in Belarus, Ukraine, Russia and Kazakhstan. Besides a standard tricolour type which prevailed, we identified six colour variants: *stavropolicus* with reduced white spots, and a bicolour entirely devoid of spots, white, piebald, dark-black (atypical melanistic) and intense dark (melanistic). The overall proportion of variant hamsters was estimated at 4.3 %. Colour variants were significantly more diverse and more frequent in Europe. The presence of melanistic hamsters was positively associated with high temperatures and high levels of precipitation. Cranial traits were largely invariant and the only significant trend was a slight increase in zygomatic width with longitude. We found no evidence of geographically contiguous clusters of populations which would be homogeneous enough or distinct from other similar clusters to be formally recognized as a distinct subspecies. The western segment of the common hamster's range (to the west of the Carpathian Mts.) is the most diverse genetically and morphologically while the populations to the east of the Carpathians are rather uniform. This homogeneity is further intensified on the eastern side of the Urals.

Key words: colour polymorphism, geographic variability, melanism, Russia, Siberia, subspecies, Ukraine

Introduction

The common hamster *Cricetus cricetus* (Linnaeus, 1758) is a widespread Palaearctic rodent of prominent external appearance. Its range stretches across 5500 km of steppes and farmland from the Low Countries of western Europe to the River Yenisei in Siberia. As one can expect for a wide-ranging small mammal, a considerable interpopulation variation was documented in the common hamster, formalised in recognition of about nine subspecies (Niethammer 1982, Berdyugin & Bolshakov 1998). Several studies meticulously elaborated patterns of regional variation in molecular markers (Neumann et al. 2005, Banaszek et al. 2010, Schröder et al. 2013), colour polymorphism (Gershenson 1945, 1946, Vorontsov 1982, Schröder et al. 2013), and morphometric traits (Ognev 1924, Stefen 2013). The western part of the range is genetically structured at different scales. The estimated times of divergence between phylogroups vary between 10 kya and about 150 kya (Neumann et al. 2005), i.e. the phylogeographic architecture is largely the outcome of the Last Glacial Maximum

(LGM). Size varies among regions but with no obvious trend (Berdyugin & Bolshakov 1998). In addition, morphometric dimensions of hamsters were reported to contrast at different time scales, both centennial (Stefen 2013) and millennial (Smirnov & Popov 1979). Colour polymorphism attracted particular interest. While the hamster is one of the most colourful European mammals (Niethammer 1982), it is also quite variable in this respect. A wide range of colour variants have been reported (Kayser & Stubbe 2000), in addition to very high local proportions of black hamsters in central (Niethammer 1982) and eastern Europe (Vorontsov 1982, Berdyugin & Bolshakov 1998).

Studies regarding the intraspecific diversity in the common hamster have intensified over the last years, being motivated by the necessity to establish significant units for conservation management. Gone are the times when hamsters were considered a major pest to agriculture with bounties paid for destroyed animals (Weissenborn 1839) or when they were killed in hundreds of thousands annually to meet the demands
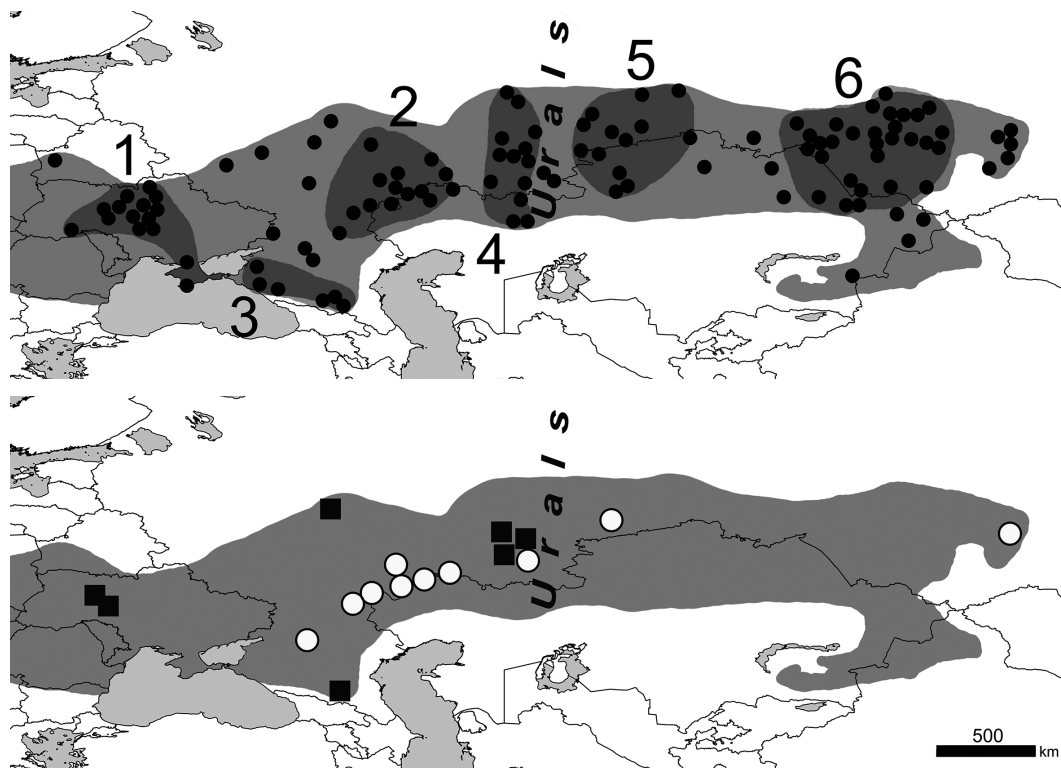
Fig. 1. Locations of common hamster samples used in this study. Samples were pooled into six populations (shaded dark grey): 1 – Ukraine and Crimea, 2 – south-central Russia and adjacent north-western Kazakhstan, 3 – Ciscaucasia, 4 – Cis-Urals, 5 – Trans-Urals, 6 – Siberia (top inset). Bottom inset shows distribution of two colour variants (traits): intense black hamsters (black squares), and the presence of white chest spot (circles). The tentative range of the common hamster is shaded light grey. The Urals delimit Europe (west) from Asia (east).

of the fur trade (Gershenson 1945, Popov 1960, Sludskiy et al. 1977). Today, the hamster is probably the fastest declining European mammal (Surov et al. 2015) and is classified as a species of conservation concern in many parts of its range (Weinhold 2008). The decline first became evident in the west (Libois & Rosoux 1982) and has by now reached eastern Europe (Rusin et al. 2013).

We address spatial variability in phenotypical traits in the common hamsters in the east, i.e. in Ukraine, Belarus, Russia, and Kazakhstan. Contrary to western Europe (Schröder et al. 2013, Stefen 2013), this issue attracted little attention in eastern Europe and western Asia beyond traditional taxonomic studies (e.g. Ognev 1924, Vinogradov et al. 1936) and frequency assessments of "melanistic" hamsters in presumably dimorphic populations (Gershenson 1945). There are several good reasons for exploring geographic variability more in detail. The hamster is a polytypic species and the range covered in our study is believed to be occupied by seven distinct subspecies (Berdyugin & Bolshakov 1998). Recognition of morphologically diagnosable subspecies presumes discontinuities in variation (e.g. Corbet 1978) and therefore signals the existence of substantial morphological variability. We searched for patterns in spatial variability in various morphometric traits in the common hamster and tested whether the gaps in a continuous variability are genuine. Variability may be either a legacy of evolutionary history or a short term response to environment, or both. A pattern in size variation in particular may demonstrate adaptation to ecological variation. Namely, optimal body size maximizes the potential for growth and reproduction and changes with varying climatic conditions and with quality of diet (Porter et al. 2000). Furthermore, colour dimorphism was frequently explained by variability in climatic conditions (Berdyugin & Bolshakov 1998), although the predictions were never tested.

Hamsters from eastern Europe are not of interest merely on their own. Populations in Ukraine and southern Russia were probably the main source for repeated westward recolonizations during the LGM (Neumann et al. 2005). Understanding phenotypic variation in the east can therefore also shed light on the patterns uncovered further west.

For these reasons we looked for a pattern of variability in the common hamster and tested whether such a pattern, if at all present, is associated with climatic variables. We were particularly interested

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in geographic contiguity of discrete clusters of populations which would be identifiable by a particular trait. Such populations, if uncovered, might be suitable targets for conservation management.

Material and Methods

We studied 468 museum specimens (387 skins and 204 skulls) housed in the following collections (abc): BMNH – Natural History Museum, London (formerly British Museum (Natural History)), U.K. (12); NMW – Natural History Museum, Vienna, Austria (3); SZM – Siberian Zoological Museum, Institute of Systematics and Ecology of Animals, Russian Academy of Sciences, Siberian Branch, Novosibirsk, Russia (132); ZFMK – Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (3); ZIN – Zoological Institute and Zoological Museum, Russian Academy of Sciences, St. Petersburg, Russia (318). For further details on samples see supplementary information. Among voucher specimens we distinguished between standard museum skins and pelts. The former were done as round skins, more rarely as carded skins or flat skins (Hangay & Dingley 1985), retained ears, lips, paws and the tail, had attached label with information on the site, date, collector, sex and external measurements, and were frequently accompanied by a skull. Pelts, on the other hand, resulted from case skinning for the fur market by hamster trappers. Pelts therefore lacked parts which add no value to the fur (paws etc.) and detailed information, and were never accompanied by a skull. We presumed that museum skins originated from randomly collected hamsters and that pelts were selected for a museum collection from larger random samples due to unusual colouration. For example, among the 15 pelts in ZIN, 13 were colour variants.

Hamsters were collected in Belarus (1), Ukraine (37), Russia (336), and Kazakhstan (94). The year of collection was recorded for 447 individuals (= 95.5 %) and ranged from 1836 to 2009. Half of specimens were sampled between 1927 and 1956 (median year = 1932). We divided samples into those of European and Asiatic origins with the Ural Mts. set as the delimiting point (Fig. 1). There were 224 hamsters from Europe and 220 from Asia; the remaining individuals (4) lacked detailed information on geographic origin. Next, we pooled individuals from a landscape of geomorphological and climatic continuity into six groups hereafter referred to as "populations". These populations were (Fig. 1): 1 – Ukraine and Crimea, 2 – south-central Russia and adjacent north-western Kazakhstan, 3 – Ciscaucasia, 4 – Cis-Urals, 5 – Trans-Urals, 6 – Siberia.

Scoring data

Each skin was photographed in lateral and ventral views. We recorded any deviations from the standard tri-colour pattern (figured in Niethammer 1982). Furthermore we measured four fur traits (to the nearest millimetre): SpL – chest spot length, SpW – chest spot width, StL – chin streak length, and CuL – cuff length (for definitions see Schröder et al. 2013). The length of the head and body (HB) was obtained from the specimen tags. When HB was not recorded, it was estimated from the museum skin to the nearest centimetre (cf. Schröder et al. 2013). We calculated three indices (I) to quantify relative sizes of white fur traits: $SpotI = HB^{-1} \times \sqrt{100} \times (SpL \times SpW)$; $StreakI = (StL/HB) \times 100$; $CuffI = (CuL/HB) \times 100$ (Schröder et al. 2013). Similar to the results of Schröder et al. (2013), the StreakI and the CuffI varied independently of sex in our samples as well.

Three linear measurements were scored from each skull using a Vernier calliper adjusted to the nearest 0.1 mm: CbL – condylobasal length, ZyW – zygomatic width, and MxT – length of maxillary tooth-row (on alveoli) (Stefen 2013). The relative width of the skulls

Table 1. Factor loadings obtained from the principal components analysis of 19 z-standardized climatic variables. Only character loadings > 0.7 are shown.

Climatic variable		CPC1	CPC2
BIO1	Annual mean T	0.859	
BIO2	Mean diurnal T range		
BIO3	Isothermality		
BIO4	T seasonality (CV)	0.840	
BIO5	Max. T of warmest month		0.923
BIO6	Min. T of warmest month	0.938	
BIO7	T annual range	–0.944	
BIO8	Mean T of wettest month		
BIO9	Mean T of driest month	0.747	
BIO10	Mean T of warmest month		0.801
BIO11	Mean T of coldest month	0.934	
BIO12	Annual P	0.740	
BIO13	P of wettest month		–0.863
BIO14	P of driest month	0.928	
BIO15	P seasonality (CV)		
BIO16	P of wettest quarter		–0.865
BIO17	P of driest quarter	0.916	
BIO18	P of warmest quarter		–0.919
BIO19	P of coldest quarter	0.901	
Eigenvalue		9.71	5.40
Variance (%)		51.3	28.6

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were expressed as a quotient ZyWI = (ZyW/CbL) × 100. Two age classes (juvenile *vs.* adult) were assessed on the basis of the overall size (Sludskiy et al. 1977), skull shape, and molar wear (Vohralík 1975, Stefen 2013). Only adults were used in craniometric analyses to minimize the effect of ontogenetic growth.

Spatial and environmental patterns in morphometric datasets

Pooling samples into populations can obscure the configuration of spatial variation in morphometric data, specifically by producing an artificial stepwise pattern where a smooth cline actually occurs. To avoid this trap, we used a single specimen in regression analysis as the sampling unit.

For each locality we obtained latitudinal and longitudinal coordinates using ArcGIS 9.3 (ESRI 2010) base maps (coordinate system WGS84). Climatic variables (BIO; taken for the 1950-2000 period; WorldClim database available at http://www.worldclim.org/) represented annual trends (e.g. mean annual temperature, annual precipitation), seasonality (e.g. annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g. temperature of the coldest and warmest month, and precipitation of the wet and dry quarters) (Table 1). Additionally, a geospatial bioclimatic database was developed using ArcGIS Spatial Analyst tools (ESRI 2010) by attributing all variables to the location points representing each sample.

Because climatic variables may be correlated, we performed a Principal Components Analysis (PCA) on these data. To prevent dominance in the PCA by large values at the expense of small ones, data were z-standardized using the formula: $z = (x − μ) σ^{-1}$, where x is an individual raw score, μ is the mean of the population and σ is the standard deviation of the population. Note that z-scores can be defined without assumptions of normality. The first two Climatic Principal Components (CPCs) had eigenvalues > 5 and explained 80 % of the variance in the original dataset. The eigenvector matrices showed that CPC1 was primarily loaded with high eigenvectors for temperature variables and for precipitation. CPC2 was loaded with high positive eigenvectors for temperature of the warmest period and high negative values for precipitation in the wettest and warmest period (Table 1).

Statistical tests

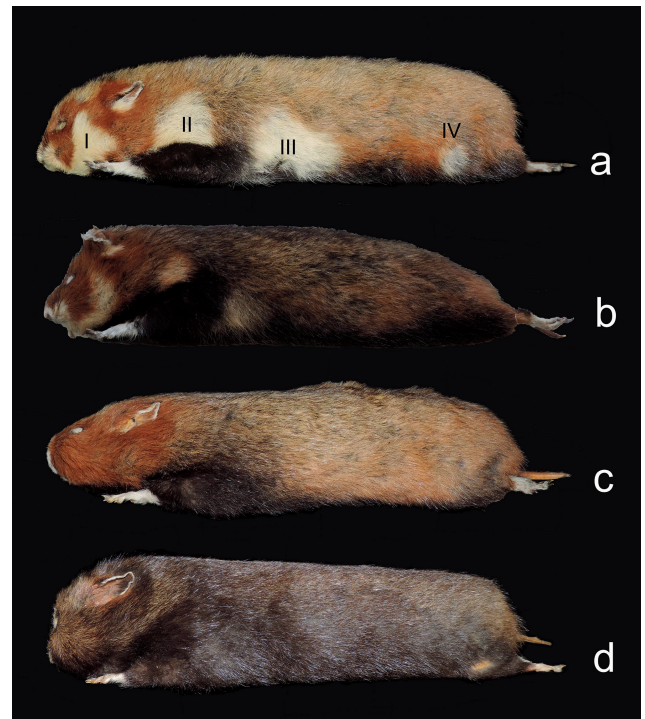Measurements and indices were transformed to logarithms in order to decrease differences in

Fig. 2. Colour variation in common hamsters from Russia and Ukraine: a – standard tricolour from Pokrovka in Kurganskaja oblast', western Siberia (ZIN 16275); b – *stavropolicus* type from Vladikavkaz, North Ossetia-Alania, European Russia (BMNH 26.2.2.20); c – bicolour type from Kislovka in Tomskaja oblast', western Siberia (SZM 3106); d – black (atypical melanistic) hamster from Novaja Chertoryja in Zhitomirskaja oblast', Ukraine (ZIN 23559). Light patches: I – cheek, II – neck, III – axillary, IV – thigh.

variance between variables. The normal distribution and homogeneity of the variances were tested by Kolmogorov-Smirnov and Bartlett tests, respectively. No substantial departures (*p* > 0.05) from normality and/or homoscedasticity were found in our data sets which legitimized the application of parametric

Fig. 3. Variation in piebald hamsters from Bashkortostan, European Russia. The underlying colour is standard tricolour (a – Mesjagutovskij rajon; ZIN 25263) and intense black in two pelts from Ufa (b – ZIN 25257, c – 25265). Shown are dorsal (a-c) and ventral side (a', b').

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Table 2. Descriptive statistics (mean ± standard deviation) for two indices expressing relative size of white fur traits (StreakI – chin streak index, CuffI – white cuff index), three skull measurements (CbL – condylobasal length of skull, ZyW – zygomatic width, MxT – length of maxillary tooth-row), and relative width of skull (ZyWI) in six populations (Pop.) of common hamsters. Measurements are in millimetres, indices are given as percentages. For definition of populations see text and Fig. 1. Sample sizes (n) are given separately for pelt trains/cranial variables. Sexes are pooled.

Population	n	StreakI	CuffI	CbL	ZyW	Mxt	ZyWI
1 Ukraine	27/10	10.8 ± 3.55	3.2 ± 0.29	47.6 ± 0.89	27.0 ± 0.65	7.97 ± 0.11	57.0 ± 5.1
2 S-cent. Russia	49/27	13.5 ± 3.84	4.6 ± 0.21	48.8 ± 0.55	28.0 ± 0.39	8.22 ± 0.07	57.3 ± 3.0
3 Ciscaucasia	20/13	13.6 ± 4.59	4.4 ± 0.38	46.9 ± 0.79	26.2 ± 0.52	8.28 ± 0.10	56.2 ± 4.2
4 Cis-Urals	52/17	11.8 ± 3.30	4.2 ± 0.22	49.3 ± 0.69	29.0 ± 0.49	8.31 ± 0.08	58.4 ± 3.8
5 Trans-Urals	47/10	11.8 ± 4.08	3.9 ± 0.23	50.1 ± 0.90	28.8 ± 0.69	8.20 ± 0.11	57.0 ± 5.4
6 Siberia	111/55	9.0 ± 5.82	4.3 ± 0.14	49.0 ± 0.38	28.3 ± 0.28	9.20 ± 0.05	57.5 ± 2.2

statistical tests. Variation in continuous variables and association between morphometric traits and environmental variables (geographic coordinates and CPCs) was assessed using analysis of variance (one-way ANOVA and factorial ANOVA) and regression analyses (simple and multiple regressions). Differences in proportions between samples were compared using χ^2 test. Statistical analyses were performed using STATISTICA (StatSoft, Version 5.5, Tulso, OK, U.S.A. 1999).

Results

Colour

A significant majority of the hamsters we examined were of standard tricolour type (cf. Niethammer 1982) with brownish buff upper parts and a black belly and with contrasting light patches on the contact between the brown and black areas. These patches were, in anterior-to-posterior direction, the cheek, neck, axillary, and thigh patches (Fig. 2a). Obvious deviations from the standard pattern were observed in 29 skins, 13 of which were pelts. The average frequency of colour variants was therefore estimated at 4.3 %. Only one single variant was recorded to the east of the Urals, and the difference between the proportions of variant hamsters on the each side of the mountain chain (8.1 % in Europe *vs.* 0.6 % in Asia) was highly significant ($p < 0.0001$).

An adult female from western Siberia lacked all light spots (Fig. 2c) and is classified as a bicolour type. Two adults from North Ossetia-Alania were intermediate between the tri- and the bicolour types in lacking the thigh spot entirely and showing a reduction in the remaining blotches (Fig. 2b); these hamsters were classified as *stavropolicus* morphotype (the name is based on "subspecies" *C. c. stavropolicus* Satunin, 1907). One of these individuals was darkened (Fig. 2b) while the other was normally bright.

Three pelts from Bashkortostan collected between

1928 and 1930 had prominent irregular white patches and were classified as piebald. The underlying colour was either a standard tricolour (Fig. 3a) or black (Fig. 3b, c). A further two pelts were white (both from Bashkortostan), and 19 skins (incl. 8 pelts) were intense black throughout except for white paws, ears and snout ("melanistic" sensu Kayser & Stubbe 2000). The majority of melanistic hamsters were from Bashkortostan (10 skins), following by Ukraine (5), Nizhniy Novgorod (2), and Ciscaucasia (1) (Fig. 1). A further three skins, one each from Ukraine (Fig. 2d), Ciscaucasia (Adygea), and Kazakhstan (no locality) were blackish but retained rufous tints dorsally, on the rump, and the head ("atypical melanistic" sensu Kayser & Stubbe 2000). Not a single black individual was accounted for in samples collected to the east of the Urals and the difference between the two major regions was significant ($p < 0.001$). ANOVA retrieved significantly higher CPC1 scores for localities which contained melanistic hamsters (F = 17.746, df = 1, 136, $p = 0.00005$) as compared to sites where this variant was not recorded in our study. Melanistic hamsters were therefore associated with high temperatures and high precipitation.

A thigh spot was present in 336 hamsters (= 86.8 %), and this proportion did not differ significantly ($p = 0.396$) between the populations in Europe (87.7 %) and Asia (86 %). A white chest spot was rare, recorded in 15 skins (3.9 %) and the majority of such hamsters (n = 8) were from the middle Volga region (Fig. 1). Although the spot was significantly more frequent ($p = 0.04$) to the west of the Urals (6.5 % in Europe *vs.* 1.1 % in Asia), a single incidence was observed at the very eastern edge of the species' range in the Krasnoturanskij district. The chest spot was on average small (SpotI = 4.92 ± 2.181) and frequently diffused (8 skins).

Indices for two white fur traits, the StreakI and the CuffI, loosely correlated (r = 0.14, $p = 0.02$). A streak

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was more frequently absent (StreakI = 0) in Asia (15.8 %) than in Europe (0.7 %) and the difference was highly significant ($p < 0.0001$). There was significant heterogeneity in StreakI among the populations (F = 8.622, df = 5, 298, $p < 0.0001$). The StreakI was the shortest in Siberia and the longest in Cisaucasia and in south-central Russia (Table 2). Forward stepwise regression on climatic variables (CPCs) and geographic coordinates yielded significant results (F = 7.266, df = 3, 291, $p = 0.0001$) but regression fit was very low (6 %). Beta and F-to-enter values were significant (at $p < 0.05$) for both climatic variables and CPC2 had the highest explanatory power. Therefore, the chin streak tended to be longer in regions of hot warm season and low precipitation.

The Cuff was absent in 4.1 % of individuals but we found no difference between the two main regions. There was significant heterogeneity among populations (F = 4.375, df = 5, 299, $p = 0.0008$) with Ukrainian hamsters having the shortest CuffI (Table 2). Forward stepwise regression on coordinates and CPCs resulted in a significant model (F = 11.760, df = 4, 315, $p < 0.00001$). Of the three environmental variables included in the regression model, Beta and F-to-enter values were by far the highest for latitude. Only a small fraction of variance (5 %) was explained by latitude alone.

Cranial data

Factorial ANOVA (population and sex as factors) retrieved no significant variation in any of the three linear parameters and in the quotient. The two factors were not in interaction. Regression of variables onto geographic coordinates and the two climatic variables retrieved significant associations only for both measures of skull width, ZyW (F = 9.877, df = 1, 158, $p = 0.002$) and ZyWI (F = 7.242, df = 1, 159, $p = 0.008$). In both models, the longitude was the only variable with a reasonably high Beta and F-to-enter values. The correlation between zygomatic width and longitude was positive, i.e. hamsters tend towards wider skulls in the east, the fit however was very low (5.5 % for ZyW and 4.2 % for ZyWI).

Discussion

Our results confirmed significant regional variation in colour types and colour traits among hamsters occupying eastern Europe and western Asia. Colour variants were significantly more diverse and more frequent in Europe. Similarly, two white fur traits (the white chin streak and the chest spot) were more frequently present in Europe. Furthermore, the StreakI attained the lowest mean in Siberia, and the CuffI showed significant deviations only in European populations. Differences between means were slight however, the overlap in ranges was wide and spatial trends were weak. Interpopulation differentiation in the two indices is more the statistical phenomenon than the evidence of the existence of discrete colour types. Cranial measurements proved even more inert than colour traits and only zygomatic width showed a slight trend of west-to-east increase. There was nothing in our results to evidence discrete morphotypes.

Obviously we found no evidence of geographically contiguous clusters of populations which would be homogeneous enough on one hand and distinct from other similar clusters on the other to be formally recognized as a distinct subspecies. Our results therefore offered little hope for meeting the established "75 % rule" threshold as a guideline for good practice in delimiting subspecies (e.g. Amadon 1949). Instead, we repeatedly came across slight differentiation with no proof of discontinuity. Division of the common hamster into subspecies therefore does not create entities which would be "recognizably different" (Corbet 1978), i.e. would allow for the allocation of each specimen, or a majority of them, into the actual subspecies. Since this criterion was not met in our study we conclude that division of the common hamster into a subspecies is not congruent with the pattern in morphological variability (or lack of it) and thus obscures reality. Our conclusion matches that already expressed by Novikov (1935) and Popov (1960) who believed that the number of subspecies in the common hamster is grossly exaggerated.

Colour polymorphism is the most prominent feature of individual and population variability in the common hamster. The list of variants includes black (atypical melanistic and melanistic), piebald, white, albino, yellow (flavistic), red, sand, and "iron grey" coloured hamsters (Petzsch 1936, Kayser & Stubbe 2000). Yellow, red, sand, and iron grey were not represented in our material. The only variant we encountered in Siberia (bicolour) has thus far not been detected in Europe. Colour variants were frequently detected in very low proportions, e.g. < 0.1 % in Germany and 0.3-1.0 % in Austria (reviewed in Kayser & Stubbe 2000). We tentatively estimated the overall proportion of colour variants at 4.3 % what is remarkably close to 3.08 % as the average percentage of "melanistic" hamsters in Ukraine and European Russia estimated from nearly two million skins (Gershenson 1946). Local proportions of black hamsters, usually reported as melanistic, attain values of up to 50 % in Thuringia (Zimmermann 1969)

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and > 80 % in Ukraine and Bashkortostan (Berdyugin & Bolshakov 1998). The last two regions also emerged on our map (Fig. 1) as areas with a relatively abundant presence of black hamsters. The phenomenon however was inadequately documented in the museum material available to us. For example, all black hamsters from Bashkortostan were pelts while the museum skins (n = 41) were of a standard tricolour type.

Considering the overall low proportion of variants it is not surprising that the main source of information on colour polymorphism in different periods of the 20th century was the fur market which was supplied by hundreds of thousands hamster pelts annually. Kayser & Stubbe (2000) had at their disposal records of more than 73 thousand hamsters trapped between 1915 and 1980 in the Harz Mts., Germany, and Gershenson (1946) was dealing with summary statistics based on 1.97 million hamster skins collected in Ukraine and Russia between 1931 and 1939. Museum collections, with up to a few hundred skins at the best, are dwarfed when compared to samples which were a by-product of commercial trapping. While we accept the limitations of our material in studying the phenomenon, we nevertheless stress the importance of museum vouchers as reality checks. In the records of hamster trappers the colour variants frequently lack clear description (Kayser & Stubbe 2000) what may oversimplify reality. Gershenson (1945) regarded hamsters in eastern Europe as "dimorphic with respect to an easily classifiable trait" (i.e. melanistic vs. tricolour). As concluded by Kayser & Stubbe (2000) and shown also in our study, a standard tricolour pattern may be connected to the melanistic extreme through a gradation in darkening, across a slightly darker, with remnants of the normal colouration (dark *stavropolicus* in Fig. 2b) and a much darkened "atypical melanistic" which still retains a rusty wash to a various degree (Fig. 2d). The category "melanistic" as used in Gershenson (1945, 1946) most probably contains a diversity of dark and black variants which may not necessarily share the same genetic background. Due to the fact that only a few dozens of pelts from a huge fur market have been saved as museum vouchers, an enormous wealth of information has been irretrievably lost. This concern does not hold only for black hamsters but may have wider connotations. Popov (1960) wrote of three white skins from Bashkortostan which were deposited in ZIN, and were evidently the only ones ever recorded in the region. We examined these vouchers and found that one of them (ZIN 51959) is not a hamster, but a white russet souslik *Spermophilus major*.

Skull dimensions were surprisingly stable throughout the entire region especially when considering the wide range of climatic diversity, with a range in annual mean temperature of 12.8 °C (from –0.9 °C to 11.9 °C) and the annual precipitation varying from a low 160 mm to a moderately high 875 mm. Also surprisingly, we detected no secondary sexual dimorphism in size, although this phenomenon is widespread in the species, being reported from various populations (Popov 1960, Vohralík 1975, Sludskiy et al. 1977, Niethammer 1982). Cranial samples available to us were small, which possibly posed undesirable bias on statistical tests by creating a type II error. Similarly, as previously stressed in the account on colour variants, museum samples are hardly sufficient to allow testing of variation in natural populations. The times when collecting hamsters was easy are over, and the gaps in museum collections will most likely never be filled. Considering a general decay in natural history collections in many European countries (Andreone 2015, Kryštufek et al. 2015a) it will already be an achievement to save the existing museum vouchers for future generations.

Our results, in concert with published information, make it possible to propose a wider picture of morphological variability across the entire range of the common hamster. The most divergent are the westernmost populations (to the west of the River Rheine) which are characterized by smaller size (Niethammer 1982), a high incidence of large chest spot, a longer chin streak and a white cuff on the forepaws (Schröder et al. 2013). Henceforth, this morphotype is referred to as the Western. Its cranial uniqueness was further confirmed in a multivariate analysis of linear skull dimensions (Stefen 2013). Hamsters from the area between central Europe and the eastern margin of their range on the banks of the River Yenisei are of fairly uniform size (cf. Table 2 and data in Niethammer 1982). The chest spot is rarely present and is small or diffused and the cuff and chin streak are shorter (Eastern morphotype). Populations from the Upper Rheine in Germany show intermediate characteristics (Schröder et al. 2013). Although the hamsters occupying vast areas of central and eastern Europe and western Siberia are fairly uniform, some regional variations are also obvious. Asiatic populations were the least variable in nearly all studied traits. Proportion of colour variants seems to be higher in eastern Europe than in central Europe (Kayser & Stubbe 2000). Furthermore, the prevalence of the tricolour type is locally punctuated by a high proportion of black hamsters, again coming

from central and eastern Europe (Gershenson 1945, Niethammer 1982). Part of this variation was perhaps due to local environment. It was stressed in the past (Gershenson 1945, 1946, Popov 1960, Vorontsov 1982) and shown in our study, that melanistic hamsters are associated with high (> 500 mm) annual precipitation. This can at least partly explain their absence from Siberia, where the average precipitation is < 300 mm annually (Gvozdetskiy & Mikhaylov 1963). The reality however may be more complex since the proportion of melanistic hamsters (Berdyugin & Bolshakov 1998) and of other colour variants (Kayser & Stubbe 2000) also correlates with population densities. One of the possibilities for the interplay between the population context and deviations from the standard colour type may be population stress (Potapov et al. 1998).

The overall pattern of morphological variability is only partly concordant with the genetic architecture of the common hamster (Banaszek et al. 2010), possibly due to different rates of molecular and morphological evolution (cf. Kryštufek et al. 2012, 2015b). Namely, of the three evolutionary lineages in Banaszek et al. (2010), the North lineage includes both morphotypes and the transitional populations, while the remaining lineages, the Pannonian and the East lineages, contain only the Eastern morphotype. The most diverse is the western segment of the species' range (to the west of the Carpathian Mts.) which contains two of the three genetic lineages, and both main morphotypes. Populations occurring to the east of the Carpathians are rather uniform, containing a single phylogeographic lines and only one morphotype. The morphological uniformity is further exacerbated on the eastern side of the Urals.

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Supplementary online material

Supplementary information – list of specimens (URL: http://www.ivb.cz/folia_zoologica/supplemetarymaterials/krystufek_et_al._supplementary_information.docx).