

ORIGINAL ARTICLE

Geographical clines in the size of the herb field mouse (*Apodemus uralensis*)

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Abstract

Patterns of body size variation along geographical gradients have long been searched for and generalized into eco-geographical rules. However, no rodent species has yet been analyzed in relation to the 3 dimensions of latitude, longitude and altitude. We analyzed geographical clines and dimorphism of body and skull size in the herb field mouse (*Apodemus uralensis*) across the species range, based on field data and on data from the literature. Sexual dimorphism in adult *A. uralensis* was not expressed at a large scale, while local patterns were inconsistent. Age-dependent size changes were most expressed in adult individuals: most characters of adults exceeded in size those of subadults, while subadult–juvenile size differences were only significant in body weight and length, zygomatic skull width, length of cranial diastema and breadth of braincase. Despite central morphological niches along the clines being separated, *A. uralensis* populations showed a high degree of size overlap in morphological space. We found the species to be characterized by high size variability, with the largest individuals inhabiting the eastern and southern edges of the distribution range. Tail, hind foot and ear lengths were largest in the southern part of the range, in agreement with Allen's rule. The main measurements that we analyzed, namely body mass, zygomatic skull width and condylobasal skull length, show the presence of 3 clines in the size of adult *A. uralensis*: (i) a decreasing south–north cline, opposing Bergmann's rule; (ii) an increasing west–east cline, in accordance with Murphy's rule; and (iii) an increasing altitudinal cline.

Key words: altitudinal cline, *Apodemus uralensis*, east–west cline, south–north cline, species range

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INTRODUCTION

Variation in key macroecological predictors, such as body size, is undoubtedly characteristic of all animal species. Patterns of size variation have been generalized into ecological/geographical rules, enhancing the understanding of relationships between organisms and

the environmental conditions under which they persist (Nudds & Oswald 2007). As shown by Ashton (2002), intraspecific size–latitude trends are general, and biologically significant. Eco-geographic rules may explain size changes, although they are not necessarily valid for different taxonomic groups and can even be a source of controversy. The mechanisms underlying geographic variations of body size in general are controversial (Chown & Klok 2003) and can be difficult to interpret (Millien *et al.* 2006).

The best known of these rules is Bergmann's rule, according to which within a single species, larger individuals inhabit higher latitudes with colder climate (Gardner *et al.* 2011). Related to Bergmann's rule, Allen's rule states that the size of appendages is smaller in cold climates, thus minimizing body surface area and increasing thermal efficiency (Millien *et al.* 2006). However, exceptions to Bergmann's rule are characteristic to 29% of studied mammals (Millien *et al.* 2006). For example, Bergmann's rule does not apply to Palearctic shrews (Ochocińska & Taylor 2003), nor to Mediterranean water shrews (*Neomys anomalus* Cabrera, 1907), even over short distances (Balčiauskas *et al.* 2014). We analyzed both rules in herb mice [*Apodemus uralensis* (Pallas, 1811)] in relation to the south–north cline.

In Europe, the east–west cline is related to climate differences, which have longitudinal rather than latitudinal expression (Murphy 1985). It has been shown that clinal differences in the east–west direction are characteristic to shrews (Motokawa 2003) and some bird species (James 1970; Meiri *et al.* 2011), but not to carnivores (Meiri *et al.* 2005; 2011). An influence of longitude on the body size of the short-tailed vole [*Microtus agrestis* (Linnaeus, 1761)] was found in Denmark, while the size of the yellow-necked mouse [*Apodemus flavicollis* Melchior, 1834] and the wood mouse [*Apodemus sylvaticus* (Linnaeus, 1758)] “was not significantly related to any of the environmental factors examined” (Yom-Tov *et al.* 2012, p. 59). For other rodent species, Murphy's rule has not been tested so far.

Altitudinal clines in body size have been analyzed for many taxa. Size decreases relating to altitude have been shown in humans (Haas *et al.* 1977), carnivores, rodents and leporids in North America (Zaveloff & Boyce 1988), the skull of Daurian pikas [(*Ochotona dauurica* (Pallas, 1776)] in China (Liao *et al.* 2006; Du *et al.* 2017), many species of birds worldwide (Symonds & Tattersall 2010), Omei treefrogs (*Rhacophorus omeimontis*) in China (Liao & Lu 2011), 361 freshwater fish species in the Yangtze River Basin, China (Fu *et al.*

2004), and in insects, specifically *Dichroplus pratensis* Bruner, 1900 in Argentina (Bidau & Marti 2014). No altitudinal cline in body weight was found in deer mice [*Peromyscus maniculatus* (Wagner, 1845)] (Wasserman & Nash 1979), Anatolian ground squirrels [*Spermophilus xanthoprimum* (Bennet, 1835)] (Gür 2010) or in representatives of the genus *Ctenomys* (Medina *et al.* 2007). By contrast, size increases at higher altitudes have been found to be characteristic in several shrew species (Zaveloff & Boyce 1988).

Among *Apodemus* mice, 2 species, specifically the wood mouse *A. sylvaticus* and the large Japanese field mouse [*Apodemus speciosus* (Temminck, 1845)] do not follow Bergmann's rule, as their size increases to the south (Alcántara 1991; Takada *et al.* 2006; Shintaku & Motokawa 2016). However, analysis of altitudinal size patterns in several species of *Apodemus* has revealed heavier and longer individuals of *A. flavicollis*, *A. sylvaticus* and *A. uralensis* at higher altitudes in Slovakia, this being in line with Bergmann's rule. At the same time, a decrease of tail length, hind foot length and ear length at higher altitudes was observed in these species, this being in line with Allen's rule (Baláž *et al.* 2012). According to Čanádý and Mošanský (2015), there are also altitude-based craniometric differences in *A. sylvaticus* from Slovakia.

None of the *Apodemus* mice have been subjected to longitudinal size change analysis, thus conformance to Murphy's rule is not known.

For the current research, we focused on *A. uralensis*. According to Kryštufek *et al.* (2016), *A. uralensis* is widely, but non-continuously, distributed across Europe and Asia. The species has recently expanded in the north-western, southern, northern and eastern parts of its range (Cichocki *et al.* 2011; Darvish *et al.* 2011; Medvedev & Tretyakov 2014; Shar *et al.* 2015; Balčiauskas *et al.* 2018).

Published regional data on the size of *A. uralensis* are ambiguous, as even the presence of sex dimorphism is not clear (Spitzenberger & Bauer 2001; Baláž *et al.* 2012; Čanádý *et al.* 2014; Balčiauskas *et al.* 2018) and may be amplified by altitude (Amshokova 2010). It is also unclear what the relationship is between body size and altitude: both positive (Baláž *et al.* 2012; Čanádý *et al.* 2014) and negative relations (Amshokova 2010; Baláž *et al.* 2012) have been shown.

Our aim was to assess the geographic variability of *A. uralensis* body and skull size across the species range, analyzing the presence and conformance to south–north,

west–east and low–high altitudinal clines. The relationships in these size parameters and the clines have not been analyzed in any rodent species so far (Balčiauskas *et al.* 2018).

MATERIALS AND METHODS

The sample of *A. uralensis* consisted of 594 specimens that we trapped in the field between 1964 and 2013. In detail, the sample size included 152 individuals from Romania, 135 from the Kabardino-Balkar Republic, 113 from Lithuania, 103 from Slovakia, 35 from Moldova, 29 from Austria and 27 from Mongolia. In total, 260 females and 326 males were analyzed (sex was missing in 8 cases). Adult mice prevailed (388 individuals), with subadults represented by 82 individuals and juveniles by 49 individuals (age was not determined in 71 cases). Species, sex, body weight and size were determined in the laboratory or in the field. We supplemented our field data with raw data from publications (Table S2).

Localities and cline variables

We obtained raw material from 44 trapping locations (Fig. 1 and Table S1), with 1 to 58 individuals captured at each. To this sample, we added literature data from 14 localities (Fig. 1 and Table S2). Geographically, the sampling localities were attributed to each of the 3 axes of the south–north cline (testing Bergmann’s rule and

Allen’s rule), the east–west cline (testing Murphy’s rule) and the low–high cline. In addition to absolute latitude, longitude and altitude (m a.s.l.) values (<http://www.mapcoordinates.net/en> or <https://www.freemaptools.com/elevation-finder.htm>), localities were referred to as being southern (S), central (C) or northern (N), western (W), central (C) or eastern (E), and low (L), medium (M) or high (H). Climatic variables (annual mean temperature [AMT, °C], mean temperature of the warmest quarter [MTW, °C], mean temperature of the coldest quarter [MTC, °C] and annual precipitation [AP, mm]) for trapping localities (Table S1) were obtained from WorldClim (<http://www.worldclim.org/bioclim-aml>).

Measurements and indices

According to body mass, development of the sex organs and the degree of atrophy of the thymus and tooth wear, individuals were categorized as juveniles, subadults or adults (males with visible testicles and females with open genitalia or visible mammae). In Romania, in addition, the difference between juveniles and subadults was checked using fur color (juveniles being grey, with almost no tinge of brown). Some Romanian specimens had to be identified molecularly (de Mendonça & Benedek 2012)

We used 5 body and 43 cranial measurements for this study, taken as in (Balčiauskienė 2007; Amshokova 2010; Čanády *et al.* 2014). Measurements were performed by several authors/collectors; therefore, we

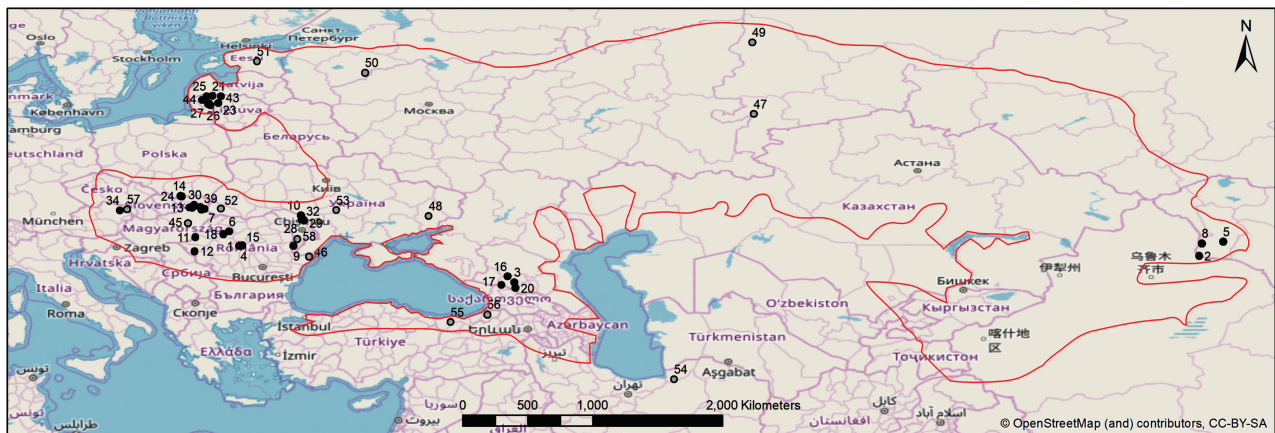


Figure 1 Location of the *Apodemus uralensis* samples; full circles represent trapping locations, while empty circles refer to data from publications. Species distribution range (according to Kryštufek *et al.* 2016, modified) denoted by red line. Coordinates of sampled localities are presented in Supplementary Tables S1 and S2. Location 54 (Touskahestan, Iran) is based on Darvish *et al.* (2010).

checked graphic representations of the measurements, not only description, to ensure they had been conducted in a uniform way. From measurements, 4 body and 2 skull indexes were calculated. However, many characters were underrepresented (Table S3).

Three measurements were selected as best representing the body size of the mice: body mass (Q, g), zygomatic skull width (ZW, mm) and condylobasal length of the skull (CBL, mm). Body mass is a good proxy not only for body size but also for many other parameters of mammalian biology (i.e. Damuth 1981; Lindstedt *et al.* 1986; Medina *et al.* 2007), while the other 2 measurements characterize size and also the form of the skull.

Four standard body measurements and 4 body indexes, as well as the 6 other most numerous skull measurements and 2 skull indices were selected for further statistical analyses for the clines. These were body length (L), tail length (C), hind foot length (P), ear length (A), (all in mm, to an accuracy of 0.1 mm), tail length index, $TLI = C/L \times 100$, hind foot length index, $HFI = P/L \times 100$, ear length index $ELI = A/L \times 100$ and body condition index based on the ratio of body weight and body length, $BCI = (Q/L^3) \times 10^5$, as in Moors (1985). For the skull, we used the width of the interorbital constriction (WIC), breadth of braincase (BB), length of *foramen incisivum* (LFI), length of maxillary tooththrow (LMT), length of cranial (upper) diastema (LCD), and skull height at the braincase (SHB), as well as indexes of relative skull width, $RSW = ZW/CBL \times 100$ and skull height, $RSH = SHB/CBL \times 100$ (Table 1).

Statistical analyses

We tested whether there were significant differences in body and skull measurements depending on the animal age (Table S3) and, in a selected subset of measurements, depending on the sex of animals, using Student's *t* for independent samples. The normality of the selected measurements was tested using Kolmogorov–Smirnov's test (Table 1). For the average values of the characters presented separately for males and females in the published sources, re-calculation according to Headrick (2010) was carried out.

We tested sex-based size differences and, due to the absence of sexual dimorphism (Table 1), measurements from both sexes were pooled. Because age-based size differences between adult animals and subadults were highly significant, while subadult–juvenile differences were poorly expressed (Table S3), only characters of adult *A. uralensis* were used for cline analysis. A standard statistical approach (average \pm SE) was used. The

minimum significance level was $P = 0.05$.

Cline analysis was performed at the locality level, averaging the raw data for every trapping locality, including those from the literature, resulting in a sample size of $N = 58$ (Tables S1 and S2). At the level of the indi-

Table 1 Frequency of best-represented measurements and indices of adult *Apodemus uralensis*, differences between males and females, and normality of distribution

Character [†]	<i>N</i>	Male–female	<i>D</i>
Q	342	NS	0.039 ^{NS}
L	341	NS	0.044 ^{NS}
BCI	338	NS	0.107 ^{**}
C	299	NS	0.057 ^{NS}
P	342	NS	0.093 ^{**}
A	329	NS	0.090 [*]
TLI	298	NS	0.058 ^{NS}
HFI	340	NS	0.055 ^{NS}
ELI	327	*	0.072 ^{NS}
ZW	321	NS	0.051 ^{NS}
WIC	311	NS	0.083 [*]
BB	317	NS	0.126 ^{**}
LFI	308	NS	0.078 [*]
LMT	362	NS	0.104 [*]
LCD	344	NS	0.073 ^{NS}
CBL	343	NS	0.064 ^{NS}
SHB	301	NS	0.073 ^{NS}
RSW	311	NS	0.088 [*]
RSH	299	NS	0.089 [*]

Frequency of best-represented measurements and indices of adult *Apodemus uralensis* (data from raw material and literature sources, presenting raw data), differences between males and females ($*P < 0.05$, NS, not significant), and normality of distribution (Kolmogorov–Smirnov's *D*, difference from normal distribution, $**P < 0.01$, $*P < 0.05$, NS, not significant). [†]A, ear length; BB, breadth of braincase; BCI, body condition index; C, tail length; CBL, condylobasal length of the skull; ELI, ear length index; HFI, hind foot length index; L, body length; LCD, length of cranial (upper) diastema; LFI, length of *foramen incisivum*; LMT, length of maxillary tooththrow; P, hind foot length; Q, body mass; RSH, relative skull height; RSW, relative skull width; SHB, skull height at the braincase; TLI, tail length index; WIC, width of interorbital constriction; ZW, zygomatic skull width.

vidual, we grouped raw measurements ($N = 298\text{--}362$, depending on the character) into categories: south–central–north, west–central–east and low–medium–high.

Linear regression analysis was performed on ungrouped data with coordinates at the level of the individual.

Cline analysis was conducted for all selected characters and indices. Based on the normality of distribution, main effects ANOVA and Wilks' λ were applied to find the cumulative effect of latitude, longitude and altitude (as in Shelomi & Zeuss 2017). Differences between groups were tested using the ANOVA post-hoc test (Tukey's honest significant difference [HSD] for unequal sample sizes). Calculations were conducted using Statistica for Windows, version 6.0 software (StatSoft 2004).

Morphometric niches were calculated as central ellipses for pairs of characters in SIBER (Jackson *et al.* 2011) using R ver. 3.5.0 (<https://cran.r-project.org/bin/windows/base/rdevel.html>). We presume that non-intersecting ellipses show full separation of populations on the south–north, east–west or low–high gradients. A degree of overlap may be interpreted as a similarity measure, while central ellipses correspond to central (core)

morphometric niches.

RESULTS

Sexual dimorphism and age-based size differences in *Apodemus uralensis*, including local aspects

In the pooled sample, most of the measurements of adult *A. uralensis* significantly exceeded those of subadult animals. Exceptions were found for BCI, LCD, WIC, BB, the length of the mandibular diastema and the length of the lower molar M1, as well as TLI and ELI. The HFI and RSH index were significantly larger in subadult animals. Subadult *A. uralensis* were significantly larger than young animals in Q, L, BB, ZW, LCD and RSW, as well as in the length of the mandibula, the maximum height of the mandibular and the length of the *nasalia*. Other differences were not significant (Table S3).

Sexual dimorphism in adult *A. uralensis* was not unambiguous. The main body size characters, Q, ZW and CBL, did not differ significantly between males and fe-

Table 2 Local aspects of the sexual dimorphism in adult *Apodemus uralensis*

Country	Male > female	Female > male
Lithuania	P,* HFI* Postorbital constriction*	Height of mandibula at, and including, first molar* Length of mandibular diastema*
Romania	RSW**	CBL,*** SHB,** ZW,* LCD,* LMT* Coronoid height of mandibula* Length of mandible from the lower anterior part to posterior edge of articular process*
Moldova	Q*	ELI*
Mongolia	C,* ZW*	
Kabardino-Balkar Republic	CBL**	RSW*
Austria	BCI*	
Slovakia	WIC,*** SHB,** P,* ZW,* LCD,* CBL* Interbular width* Occipital width* Length of palatal bone*	

Best-represented characters and indices abbreviated. Characters with significant male–female differences are listed by country (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$). BCI, body condition index; C, tail length; CBL, condylobasal length of the skull; ELI, ear length index; HFI, hind foot length index; LCD, length of cranial (upper) diastema; LMT, length of maxillary tooththrow; P, hind foot length; Q, body mass; RSW, relative skull width; SHB, skull height at the braincase; WIC, width of interorbital constriction; ZW, zygomatic skull width.

males. However, adult females significantly exceeded adult males in the height of the mandibula at and including the first molar, the coronoid height of the mandibula, the length of the mandibular diastema, the interbulbar width and ELI, while males significantly exceeded females in WIC, the length of the mandibular tooth row, occipital width and the length of the palatal bone (Table S3).

We checked sexual dimorphism in adult *A. uralensis* by country to investigate local differences. Results are not consistent: body size was found to be bigger in males from Moldova, Kabardino-Balkar Republic and Mongolia, and in females from Romania (Table 2). These differences are related to the variability of the species body and skull sizes (averages in Table S3).

Significance of geographic clines in *Apodemus uralensis* size

Main effects ANOVA confirmed the presence of 3 geographic clines of Q, ZW and CBL in *A. uralensis*. The south–north cline (Wilks' $\lambda = 0.411$, $F = 126.1$), the west–east cline ($\lambda = 0.886$, $F = 11.4$) and the altitudinal cline ($\lambda = 0.884$, $F = 5.6$) were all highly significant ($P < 0.001$). These 3 clines explained 12.4% of variation of Q, 17.9% of variation of ZW and 27.8% of variation of CBL.

South–north cline in *Apodemus uralensis* size

A decreasing south–north cline, as shown by regression and ANOVA (Fig. 2), opposing Bergmann's rule, was characteristic to the main body size characters Q (16.9%; Tukey HSD, $P < 0.001$), ZW (11.6%, $P < 0.001$) and CBL with some exceptions. Namely, Q showed no trend based on trapping coordinates, while CBL had higher values in the south and north, decreasing in central latitudes (5.3%, $P < 0.001$) (Figs S1 and S4).

At the individual level, the south–north cline was highly significant for all selected characters and indices (ANOVA, Table S4). An expressed decrease was also characteristic to LCD (4.9%; Tukey HSD, $P < 0.001$), LFI (5.5%, $P < 0.001$) and LMT (8.4%, $P < 0.001$). Decreased values in central populations were characteristic to C, P, A, BCI, CBL, SHB, TLI, HFI and ELI, while the highest values in central populations were characteristic to L, BB, WIC and RSW.

At the locality level, the south–north cline was significant in 7 characters and 4 indexes (ANOVA, Table S5). LMT clearly decreased from south to north ($P < 0.001$). The other characters, namely C, A and P, as well

as indexes TLI, HFI and ELI, had the highest values in the south, decreasing in central latitudes and the north. Thus, Allen's rule was confirmed.

West–east cline in *Apodemus uralensis* size

An increasing west–east cline, in accordance with Murphy's rule, was significant (ANOVA and regression analysis, Fig. 3) in the main body size characters Q (26.4%, Tukey HSD, $P < 0.001$), ZW (7.3%, $P < 0.01$) and CBL (2.3%) (Figs S2 and S5).

At the individual level, the west–east cline was highly

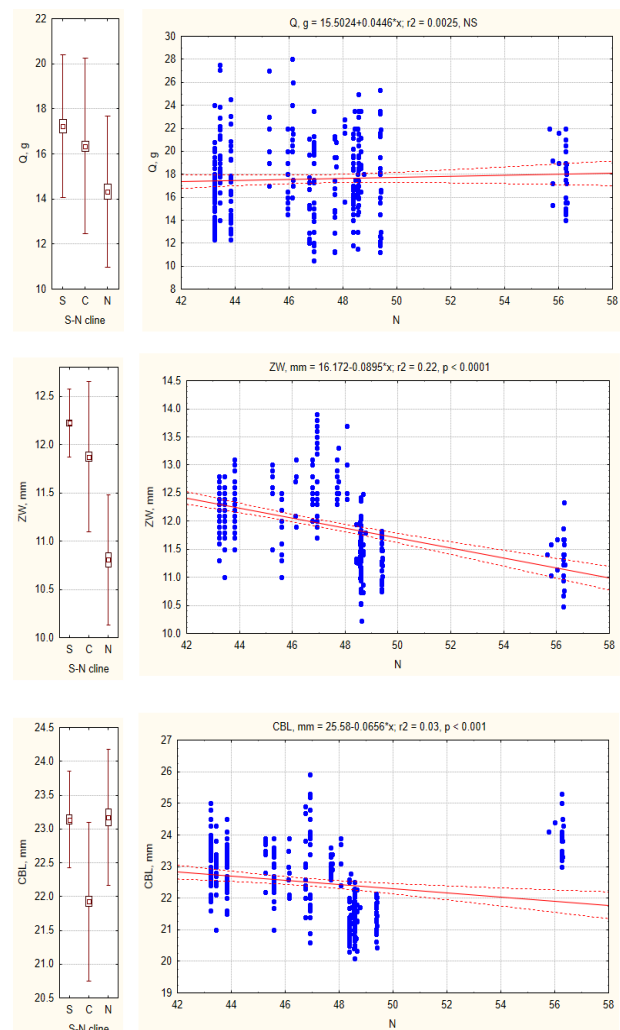


Figure 2 Representation of the south–north cline in *Apodemus uralensis* size using grouped (left) and raw (right) data of body mass (Q), zygomatic skull width (ZW) and condylobasal skull length (CBL).

significant for all characters and indices, excluding RSH (Table S4). An expressed increase was also characteristic to LFI (8.4%, $P < 0.001$), while a trend was observed in RSW (4.7%, $P < 0.1$). An increase of LCD (2.9%, $P < 0.01$) and SHB (4.5%, $P < 0.001$) was both observed from the western to the central part of the range, while a decrease in WIC (11.6%, $P < 0.001$) was noted again from the western to central part. Decreased values in central populations were found in L and BB, while the highest values in central populations were characteristic to L, C, P, A, BCI, LMT, TLI, HFI and ELI (Fig. S2).

At the locality level, the west–east cline was significant in 7 characters and 3 indexes (ANOVA, Table S6).

An increase from west to east was registered in A, LMT, CBL and ZW. Other characters and indices exhibited an increase in the middle longitudes: LFI, P, TLI, HFI and ELI. WIC decreased significantly from western to middle longitudes, but this character was not measured in the eastern part of the range (see Shar *et al.* 2015).

Altitudinal cline in *Apodemus uralensis* size

Increasing altitudinal cline was significant (ANOVA and regression analysis, Fig. 4) in the main body size characters Q (6.0%; Tukey HSD, $P < 0.001$), ZW (5.9%, $P < 0.001$) and CBL (4.6%, $P < 0.001$). However, the increase in Q was even higher (13.2%, compared

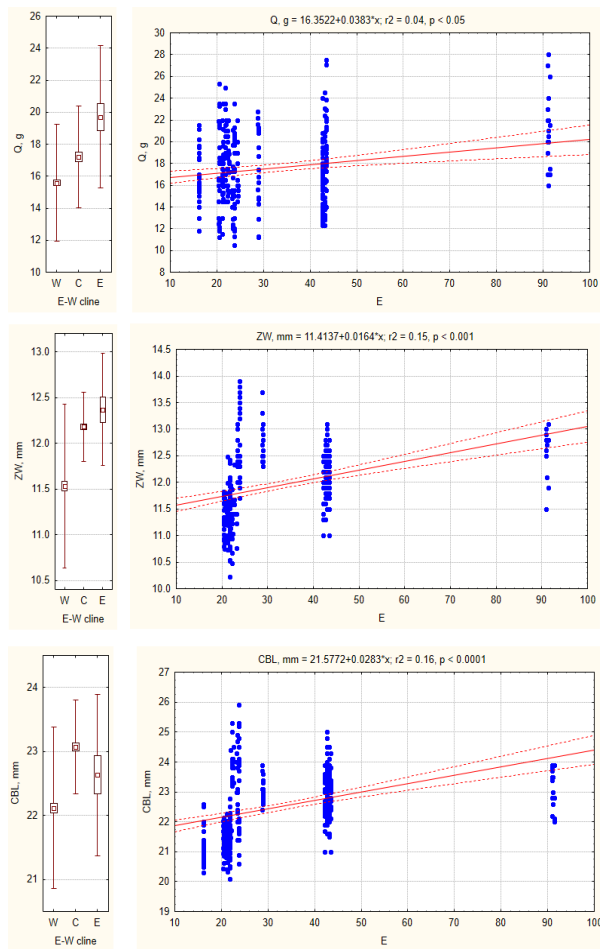


Figure 3 Representation of the west–east cline in *Apodemus uralensis* size using grouped (left) and raw (right) data of body mass (Q), zygomatic skull width (ZW) and condylobasal skull length (CBL).

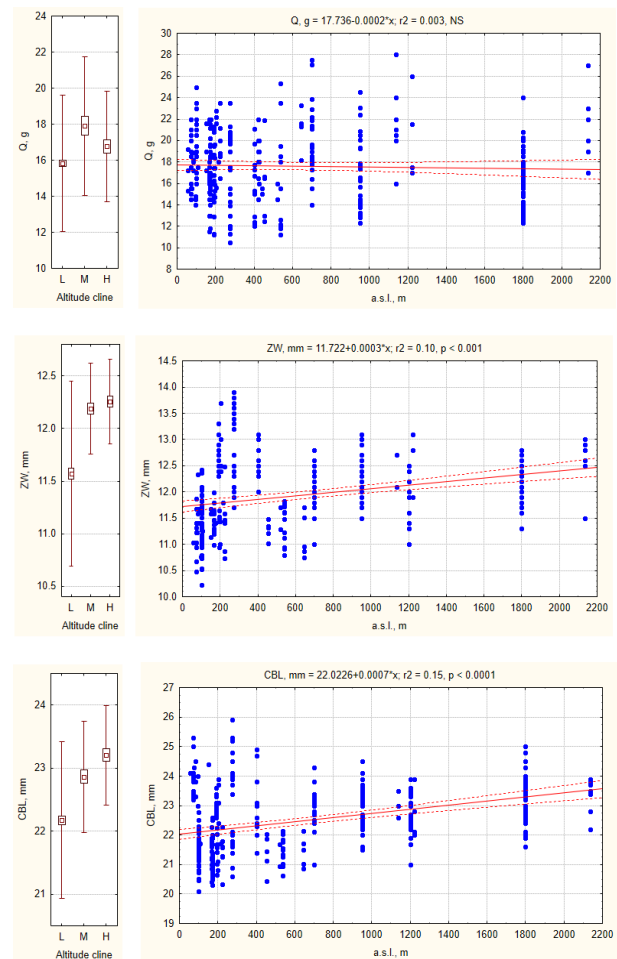


Figure 4 Representation of the altitude dependent cline in *Apodemus uralensis* size using grouped (left) and raw (right) data of body mass (Q), zygomatic skull width (ZW) and condylobasal skull length (CBL). L, low; M, medium; H, high range.

to lowland) in populations located at medium altitudes (Figs S3 and S6).

An altitudinal cline was also expressed at the individual level; just differences in L and RSH were not significant, (Table S4). An expressed increase was characteristic to C (10.2%, $P < 0.001$), A (14.7%, $P < 0.001$), SHB (5.1%, $P < 0.01$) and TLI (9.1%, $P < 0.001$), while WIC decreased (13.1%, $P < 0.001$). Highest values in central populations were characteristic to BCI, LFI, LMT, ELI and RSW, while decreased values in central populations were found in P, BB and HFI (Fig. S3).

Differences in size depending on altitude were significant for 5 of the selected characters and 1 index also at the locality level (ANOVA, Table S7). Increases in A, ZW, CBL and ELI were registered at the higher altitudes. LMT increased from low to middle altitude, then decreased at high altitude. WIC decreased from low to middle altitudes, again increasing at high altitudes. Some other measurements (C, P, LFI and TLI) had a tendency to increase with altitude but did not reach the

significance threshold ($P < 0.10$ in all cases, Table S7).

Separation of populations according to geographic clines

Testing separation of populations in morphological space of skull length and width according to geographic clines revealed that despite statistical differences in average values (Figs 2–4 and Suppl. Tables S4–S7), the morphological space of the main skull size characters showed overlap along geographical clines (Fig. 5). However, the central ellipses were separated in the S–N and W–E clines but partially overlapped in the altitudinal cline between medium and high altitude populations.

Overlap of other characters in 2-dimensional space was even higher. The central ellipses in body length and tail length were separated in the S–N and W–E clines, but partially overlapped in the altitudinal cline between low and medium altitude populations (Fig. 5).

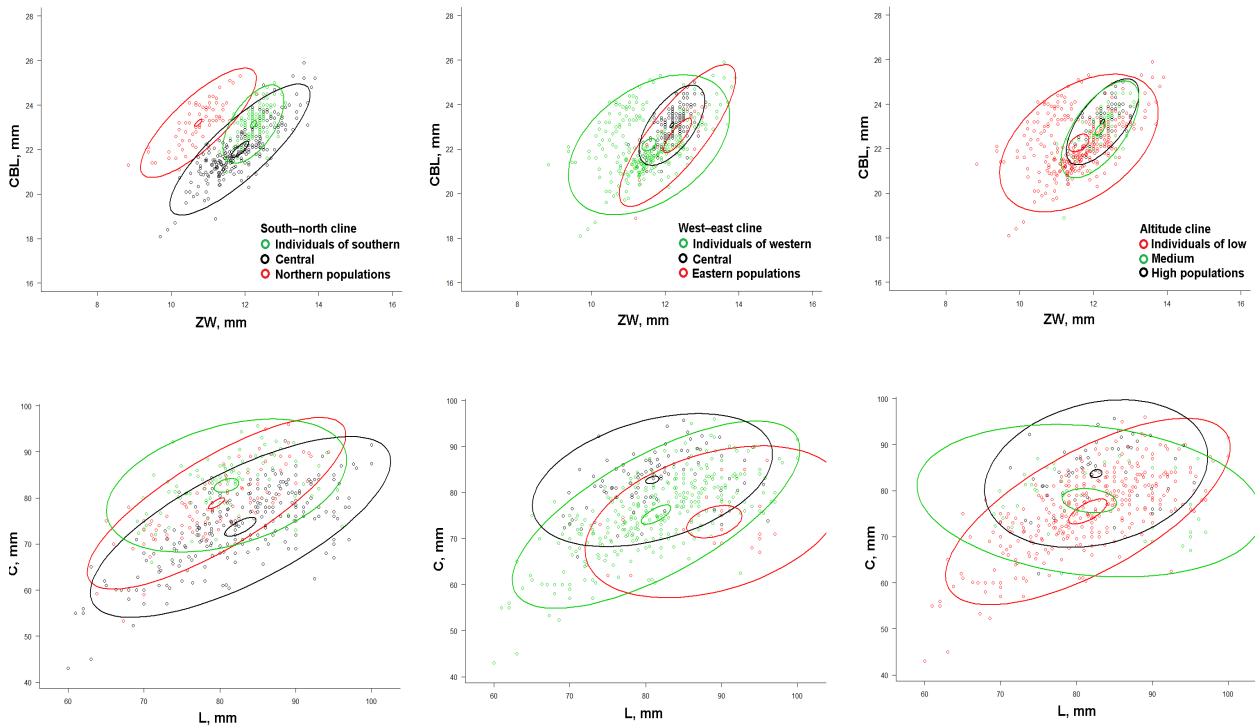


Figure 5 Separation of *Apodemus uralensis* populations along north–south (left), west–east (middle), low–high (right) geographic clines in condylobasal length (CBL) and zygomatic width (ZW) (upper), tail length (C) and body length (L) (lower) morphological space. Central ellipses represent central morphological niches of populations.

DISCUSSION

Our study represents the first evaluation of body and skull size changes according to south–north, west–east and altitudinal clines for *A. uralensis*, accounting also for sexual dimorphism and age-based size differences in this species. Our results show the presence of 3 geographic clines in body and skull size, and also the high variability of characters.

Dimorphism of *Apodemus uralensis* body and skull size

Dimorphism of *Apodemus uralensis* body and skull size is not expressed. In general, sexual dimorphism was not found in the main body size characters (see Table S3). However, there were many local differences which were not related to altitude: body size was found to be bigger in males from Moldova (average m a.s.l. = 194 m), Kabardino-Balkar Republic (m a.s.l. = 1280 m) and Mongolia (m a.s.l. = 1554 m), and in females from Romania, with an average m a.s.l. of 354 m (see Table 2).

Former investigations also revealed the varying degree of sexual dimorphism in *A. uralensis*. However, these data were limited to the local scale and only a few characters were dimorphic with no clear conclusion about whether males or females were bigger in size (Steiner 1978; Spitzenberger & Bauer 2001; Baláž *et al.* 2012; Shar *et al.* 2015; Balčiauskas *et al.* 2018). Males were bigger in all body measures only in subadult *A. uralensis* individuals from Slovakia (Baláž *et al.* 2012). Similarly, no clear expression of sex dimorphism in *A. uralensis* skull characters was shown (Steiner 1978; Amshokova 2010; Shar *et al.* 2015; Balčiauskas *et al.* 2018).

While it has been stated that male-dominated dimorphism is characteristic to many species of *Apodemus* (Montgomery 1989), a clear indication of dimorphism has been shown only in *A. sylvaticus* (Harrison *et al.* 2010) and *A. speciosus* (Ueda & Takatsuki 2005; Kageyama *et al.* 2009). Sexual dimorphism in *A. agrarius* and *A. flavicollis* is not unambiguous (de Mendonça 1999; Velickovic 2006; Chassovnikarova & Markov 2007).

Adult *A. uralensis* significantly exceeded subadult and young animals in Q, ZW, CBL and most other measurements, except LCD, WIC and BB. Subadults exceeded juveniles only in some measurements (Q, L, ZW, BB and LCD). In our opinion, the ontogenetic trajectory of juveniles and subadults and the static allometry of

the adults in *A. uralensis* may be masked by growth factors. There are no data on the growth of *A. uralensis*, although in *A. sylvaticus* postnatal growth does not stop in most body and skull characters (Frynta & Žižková 1992). However, information on changes in the growth rate is lacking for *A. sylvaticus* or *A. agrarius* (Frynta & Žižková 1992; Balčiauskienė 2007). We conclude that *A. uralensis* is not sexually dimorphic, while age-dependent size changes are most expressed in adult individuals.

Geographic clines of *Apodemus uralensis* body and skull size across the species distribution range

Geographic clines of *Apodemus uralensis* body and skull size across the species distribution range have not been analyzed before. Body mass, skull width and length of the species decrease from south to north; thus, we found disagreement with Bergmann's rule. In some other characters, the decrease from southern to northern populations was marked by even lower values in central populations. This is against the expectation that the heaviest and largest individuals should inhabit the central part of the climatic range of the species (Virgós *et al.* 2011). Lengths of tail, hind foot and ear were highest in the southern populations, decreasing towards central and northern range parts, in agreement with Allen's rule.

Agreement with Murphy's rule, with increase of size in a west–east direction across the range, was characteristic to body mass, zygomatic width and skull length, as well as length of *foramen incisivum*. A few more characters increased from the west to the central part of the range but were not measured in the eastern sample. In some characters, an increase from the west to central part of the range was followed by a decrease in the east.

Increase in body size of *A. uralensis* along with altitude was also significant. The abovementioned peculiarities of the geographic clines in the size of *A. uralensis* result in the separation of the central morphological niches in the main skull size characters (see Fig. 5).

Our findings are confirmed by data of other authors relating to local populations of *A. uralensis*. Individuals with the largest body mass and body length were characteristic to the eastern and southern extremes of the range: Turkey and Mongolia (Kryštufek & Vohralík 2007; Shar *et al.* 2015). In adults, the biggest hind foot lengths are found in the southern populations of Turkey and Iran (Kryštufek & Vohralík 2007; Darvish *et al.* 2011).

Variability of skull size and shape in *Apodemus uralensis*

Variability of skull size and shape in *A. uralensis* was apparent. In general, in the southern part of the species range, *A. uralensis* skulls are wide and long, while in the north they are not only smaller (contrary to Bergmann's rule), but relatively narrower. In the western part of the species' range, skulls are short and narrow, while in the east the increase of the skull size is most noticeable in the increase of its relative width (skulls become broader).

High variability of morphometric and craniometric characters is also characteristic to local populations of *A. uralensis* in different countries, as confirmed by several authors for the western part of the range; namely, in the former Czechoslovakia, Slovakia and Hungary (Holišová *et al.* 1962; Steiner 1978; Demeter & Lázár 1984; Vohralík 2002; Baláž *et al.* 2012; Čanády *et al.* 2014). Extremes in condylobasal length have been recorded in the south (Kryštufek & Vohralík 2007; Darvish *et al.* 2011) and also in the northwestern part of the range (Balčiauskas *et al.* 2018), Caucasus (Amshokova 2010) and Mongolia (Shar *et al.* 2015). The shortest skulls are found in localities across the south–north gradient, from the Carpathian Mountains (Zagorodniuk 2005) and Hungary (Demeter & Lázár 1984) to Estonia (Zagorodniuk 2005). The largest zygomatic widths have been reported in the eastern (Shar *et al.* 2015) and southern (Darvish *et al.* 2011) range extremes, as well as in Slovakia (Baláž *et al.* 2012) and the Caucasus Mountains (Amshokova 2010).

Pavlinov and Lissovsky (2012) pointed out that the “semi-species” *A. kastschenkoi* may be present in the region of Irtysh River, posing the possibility that the size of *A. uralensis* from Mongolia may be influenced by genetic factors.

Increase in values of both skull length and width from low to high altitude is interesting because presence of an isolated population of the species in the Liptovské Tatry mountains (Western Tatra Mountains) was described in Slovakia. These individuals had a smaller body size compared to populations living in the highland and lowland areas of Slovakia. A. Mošanský in 1963 and 1995 predesignated these individuals as a new species or subspecies (nomen nudum) of *A. microps* under the working name “*Apodemus parvulus*” (Čanády *et al.* 2014).

Clines in various *Apodemus* species and other organisms

In other *Apodemus* species, the clines are not unidirectional. Latitude-dependent correlations of external and skull measurements were found in the Korean field mouse [*Apodemus peninsulae* (Thomas 1907)], the South China field mouse [*Apodemus draco* (Barrett-Hamilton, 1900)], and the large-eared field mouse (*Apodemus latronum* Thomas, 1911) (Kaneko 2015). However, in the other eastern species, such as the small Japanese field mouse [*Apodemus argenteus* (Temminck, 1845)], the relationship between size and latitude is negative (Millien 2004). This is also in contrast with Bergmann's rule, and in accordance with our results.

Is the situation with geographic clines in *A. uralensis* common with other groups of organisms? Selected publications show geographic clines in body size or other traits being both characteristic and/or non-characteristic to many endotherm and ectotherm animal groups and species: body mass and length, various cranial measurements and hair length in mammals (Wasserman & Nash 1979; Wigginton & Dobson 1999; Medina *et al.* 2007; Du *et al.* 2017), body mass and wing length in birds (Ashton 2002; Nwogu *et al.* 2018), body length in lizards (Angiletta *et al.* 2004), frogs (Liao *et al.* 2011), fish (Fu *et al.* 2004) and spiders (Entling *et al.* 2010), and the length of the body plus other characters in insects (Chown & Klok 2003; Bidau & Marti 2014; Shelomi & Zeuss 2017).

Factors explaining size variability in *Apodemus uralensis*

It has been shown that the effect of population density on body mass and body length in rodents is not unidirectional or is influenced by altitude (McCain 2006; Petrová *et al.* 2018). We have no data on the densities of *A. uralensis* in the analyzed locations, so density effect was not tested. In *P. maniculatus*, increased insulation (longer and thicker hair instead of increase in body mass) was found as an altitudinal cline but not a change in body size (Wasserman & Nash 1979). Du *et al.* (2017, p. 8) found different altitudinal patterns of head–body length and tail/body index in Muridae and Cricetidae along the altitudinal gradient. They concluded that adaptation (in the case of tail index, thermoregulation) “to the local environment is a complex response occurring at multiple functional axes” (Du *et al.* 2017, p. 8). The same explanation (intercorrelation of environmental variables) was given to associations of latitude, ele-

vation and temperature with body size in bobcats (*Lynx rufus* Schreber, 1777) by Wigginton and Dobson (1999).

“Field-based measurements of body size can no doubt be influenced by plasticity of species” and by many different environmental variables (Stillwell 2010, p. 1387). According to Nudds and Oswald (2007, p. 2839), conformance or nonconformance to ecological rules enhances potential “to understand how organisms are restricted to the environmental conditions under which they persist.” We accept the explanation of Millien *et al.* (2006) that interpretations of latitudinal, longitudinal and altitudinal patterns of body size are difficult, because many environmental factors in the species range are interrelated. Besides, recent changes in the distribution range of *A. uralensis* are still occurring and the species is found in a variety of habitats (Balčiauskas *et al.* 2018), being thus exposed to a range of ecological conditions.

In addition, across the species range, altitude is not completely independent of latitude and longitude (i.e. mountains are positioned in the south and east). To overcome this shortcoming of geographic coordinates, further studies on size variation in *A. uralensis* should also consider climatic variables, especially mean temperature (the underlying factor of Bergmann’s rule) and temperature seasonality (the underlying factor of Murphy’s rule). Combining geographic position and climate data would bring insight regarding the mechanisms behind the variations in size across the range of *A. uralensis*. Preliminary climate data (Hijmans *et al.* 2005) allow the implication of the influence of climatic (see Table S1) differences on the clinal changes in body size.

We conclude that body and skull size of *A. uralensis* are related to 3 geographical clines (decreasing northward, increasing eastward and to higher altitude). However, variability in this species is very high. Sexual dimorphism is not expressed and its direction varies in different parts of the range. Further analysis of the interplay of the observed geographical clines in species size and environmental variables may be useful for predicting the influence of climate change on the size of *A. uralensis*.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found in the online version of this article at the publisher's website.

Table S1 Sample size and coordinates of the *Apodemus uralensis* trapping localities

Table S2 Sample size and position of the localities with published data on *Apodemus uralensis*

Table S3 Averaged body and skull measurements and indices of *Apodemus uralensis*

Table S4 South–north, west–east and altitudinal cline presence in selected characters of *Apodemus uralensis* size at the individual level, based on the raw data

Table S5 South–north cline in selected characters of *Apodemus uralensis* size, based on the averages from 37–45 localities

Table S6 West–east cline in selected characters of *Apodemus uralensis* size, based on the averages from 37–45 localities

Table S7 Altitudinal cline in selected characters of *Apodemus uralensis* size, based on the averages from 35–45 localities

Figure S1 Representation of the south–north cline in *Apodemus uralensis* size at the individual level (mean, SE and SD given): C, central; N, northern; S, southern part of the range

Figure S2 Representation of the west–east cline in *Apodemus uralensis* size at the individual level (mean, SE and SD given): C, central; N, northern; S, southern part of the range

Figure S3 Representation of altitudinal cline in *Apodemus uralensis* size at the individual level (mean, SE and SD given): H, high; L, low; M, medium range

Figure S4 Representation of the south–north cline in *Apodemus uralensis* size (regression on raw data)

Figure S5 Representation of the west–east cline in *Apodemus uralensis* size (regression on raw data)

Figure S6 Representation of altitudinal cline in *Apodemus uralensis* size (regression on raw data)