



# Body size and craniometry of the herb field mouse from Lithuania in the context of species range

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## Abstract

We present morphometric and craniometric measurements of the herb field mouse (*Apodemus uralensis*) from Lithuania and analyze variation of body and skull size across species range. We suppose species is characterized by high size variability, not following Bergmann's or Murphy's rules. Preliminary, distinct size differences have been registered in the eastern and southern edges of the distribution range, with these populations having largest individuals according to average body and skull size. In terms of tail length and condylobasal length of the skull, Lithuanian mice on the north-western edge of the species range are among the largest, but in terms of body weight, body length, zygomatic skull width and the length of maxillary toothrow, adult *A. uralensis* from Lithuania are small and correspond to those from populations on the western edge of the range. The relative skull width (ratio of zygomatic skull width to condylobasal length) of Lithuanian *A. uralensis* is the smallest across the entire range. In *A. uralensis* from Lithuania, sex dimorphism is weakly expressed, with hind foot length and postorbital constriction larger in adult males, while the height of the mandibula and length of the mandibular diastema is larger in adult females. Juvenile and subadult *A. uralensis* from Lithuania differ in body weight, but not in size.

**Keywords** *Apodemus uralensis* · Species range · Skull and body measurements · Lithuania

## Introduction

The herb field mouse, *Apodemus uralensis* (Pallas, 1811) is widely distributed across Europe and Asia (Kryštufek et al. 2008), though the species distribution is not continuous. New localities for the species have recently been registered in the southern (Darvish et al. 2011), northern (Medvedev and Tretyakov 2014), north-western (Cichocki et al. 2011) and eastern (Shar et al. 2015) parts of the species distribution range.

Analysis of body and skull size changes across the distribution range from south to north has not been done for *A. uralensis* before, and there are no investigations analyzing morphometric variability of *Apodemus* mice in terms of longitudinal aspect, i.e., conformance to Murphy's rule (Meiri et al. 2005). Other *Apodemus* species have been shown to increase in size to the south, such as wood mouse, *Apodemus sylvaticus* (Linnaeus, 1758), where morphological

differences were said to be related to the biology of the species (Alcántara 1991; Jojić et al. 2014) or to isolation as in case of the large Japanese field mouse, *Apodemus speciosus* (Temminck, 1844) (Shintaku and Motokawa 2016). In *A. sylvaticus*, small scale craniometric differences were found to exist in different parts of Slovakia, at least partially based on different altitudes (Čanády and Mošanský 2015). In Slovakia, a positive influence of altitude on body mass and body length of the yellow-necked mouse *Apodemus flavicollis* (Melchior, 1834), *A. sylvaticus* and *A. uralensis* was proved. However, tail length, hind foot length and ear length of these three species decreased at higher altitudes. In striped field mouse *Apodemus agrarius* (Pallas, 1771), all external characters decreased with altitude (Baláž et al. 2012).

The presence of sex dimorphism in *A. uralensis* is questionable, as published results are ambiguous (Spitzenberger and Bauer 2001; Baláž et al. 2012; Čanády et al. 2014; Shar et al. 2015). It was noticed that sex dimorphism in *A. uralensis* from Caucasus Mountains depends on the altitude: while animals in the high altitudes are dimorphic, dimorphism was absent or weak in the lower altitudes (Amshokova 2010). Ambiguous results have also been published regarding the correlation of body size of *A. uralensis* and altitude. In Slovakia, body mass and body length correlate positively with

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altitude, while tail, hind foot and ear lengths are negatively correlated (Baláž et al. 2012), thus Bergmann rule is in power. However, the Caucasus situation is the opposite, as animals from higher altitudes were smaller in five out of the six characters (Amshokova 2010). Differences in body and cranial size were well exhibited between plain and mountain species populations in Slovakia (Čanády et al. 2014).

In Lithuania *A. uralensis* has been known for two decades. Among other species of *Apodemus* present in the country, it can be identified according to the non-overlapping length of the mandibular and maxillary tooththrow (Balčiauskienė et al. 2002). On preliminary material, pooled with no respect to animal age group, female *A. uralensis* in Lithuania were found to be larger in terms of body length, maxillary and mandibular tooth row lengths (Balčiauskienė et al. 2004).

The aim of this paper was to present morphometric and craniometric data on *A. uralensis* from Lithuania in different age groups, to assess size dimorphism of the species in the country and differences in comparison with other populations across the distribution range. As recently published sources show quite a limited selection of such data, the inclusion of the full dataset will expand species knowledge.

## Materials and methods

Our sample of *A. uralensis* consisted of 113 specimens (44 males, 62 females), trapped in 1996–2004 and 2008–2010, mainly in August–October. Trapping was done using standard method: 25 snap traps in a line, 5 m apart from each other, set for 2–3 days, baited with bread and oil, checked once a day (Balčiauskas 2004). All *A. uralensis* sample individuals were trapped in the northern part of Lithuania (Fig. 1). More details about the sample are presented in Juškaitis et al. (2016).

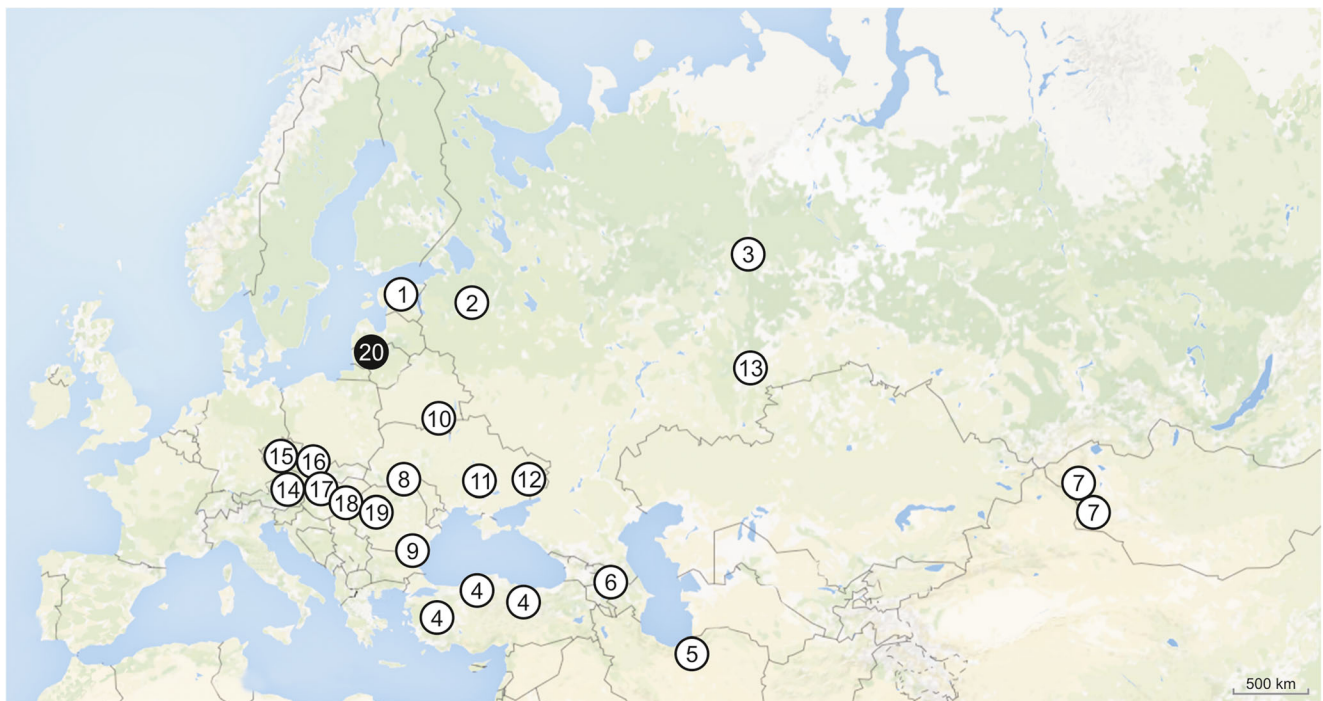
Identification of the species was carried out according to external characters and skull characters, according to Pucek (1981) and Balčiauskienė et al. (2002). Not all individuals were measured for various reasons (destruction of the body by insects and carnivores, destruction of the skull by the trap hammer, etc). Body length, tail length, hind foot length and ear length were measured using a caliper with an accuracy of 0.1 mm. After weighing (with an accuracy of 0.1 g) and dissection, individuals were divided into three age categories: juveniles, sub-adults and adults according to the status of sex organs and atrophy of the thymus, as the latter decreases with animal age (Balčiauskas et al. 2012).

Mice skulls were cleaned using larvae of *Dermestes* sp. beetles. 23 skull characters were measured: X1 – total length of mandibula at *processus articularis*, excluding incisors; X2 – length of mandibula excluding incisors; X3 – height of mandibula at, and including, first molar; X4 – maximum height of mandibula, excluding coronoid process; X5 – coronoid height of mandibula; X6 – length of mandibular

diastema; X7 – length of mandibular tooth row; X8 – length of lower molar M1; X9 – length of *nasalia*; X10 – breadth of braincase, measured at the widest part; X11 – zygomatic skull width; X12 – length of cranial (upper) diastema; X13 – zygomatic arc length; X14 – length of *foramen incisivum*; X15 – length of maxillary tooththrow; X16 – length of upper molar M1; X17 – incisor width across both upper incisors; X18 – condylobasal length; X19 – length of rostrum; X20 – length of the braincase; X21 – interorbital constriction; X22 – postorbital constriction; X23 – height of the braincase (Balčiauskas and Balčiauskienė 2011). Measurements were taken under a binocular microscope with a micrometric eyepiece and digital caliper, both of which have an accuracy of 0.1 mm. Only characters of the right side of the skull were used.

We used published material on morphometric and craniometric data of adult *A. uralensis* across the species range (Fig. 1). Some new locations of *A. uralensis* were out of the species range, as defined by the IUCN (Kryštufek et al. 2008). Recent findings in Poland (Cichocki et al. 2011) shift the former north-western edge of the species distribution westwards. Populations in the central part of the range were represented by Miass, south of Ural (Zagorodniuk 1993), southern Belarus and the northern part of Ukraine (Savickyj et al. 2005), Ukraine (Lashkova 2003), Donetsk in east of Ukraine (Zagorodniuk 2005), the Danube region in Romania and Bulgaria (Zagorodniuk 1993) and the Carpatian region in the west of Ukraine (Zagorodniuk 2005). The southern part of the range was presented by data from Anatolia, Turkey (Kryštufek and Vohralík 2007, 2009), Iran and Azerbaijan (Jangjoo et al. 2011; Darvish et al. 2011) and Caucasus (Amshokova 2010). The northern part was represented by data from Estonia, Valdai and the Ural (Zagorodniuk 2005). For the eastern part of the range, we used data on *A. uralensis* from Mongolia (Shar et al. 2015). The western part was represented by Austria (Steiner 1978; Spitzenberger and Bauer 2001), the former Czechoslovakia (Steiner 1978), Slovakia (Baláž et al. 2012; Čanády et al. 2014), Hungary (Demeter and Lázár 1984), Moravia (Holišová et al. 1962) and Romania (de Mendonça and Benedek 2012). However, such subdivisions are arbitrarily so far.

When measurements were presented separately for males and females in the published sources, we re-calculated the joint sample according to Headrick (2010). For all measurements, we used standard statistical approach (average  $\pm$  SE, minimum and maximum values). We applied Main effects ANOVA for all morphometric and craniometric characters from Lithuania, using gender and age of an individual as categorical predictors, testing for possible influence according Tête et al. (2013). Differences were tested using ANOVA post hoc test (Tukey HSD), also Student's *t*. Minimum significance level was set as  $p = 0.05$ . Calculations were done with Statistica for Windows, ver. 6.0 software (StatSoft 2004). Other samples, based on published data, do not allow ANOVA analysis or clustering, as raw data are not available.



**Fig. 1** Location of the Lithuanian sample (black circle) of *A. uralensis* and data samples from publications (open circles) used for comparison of morphometric and craniometric characters: 1 – Estonia (59.1° N, 28.8° E), 2 – Valdai (57.9° N, 33.2° E), 3 – Ural (60.0° N, 60.0° E), 4 – Anatolia (38.9° N, 28.2° E west; 40.2° N, 32.6° E central; 40.4° N, 36.5° E east), 5 – Iran (36.4° N, 54.3° E), 6 – Caucasus (43.2° N, 42.6° E mountains; 43.4° N, 43.5° E plain), 7 – Mongolia (46.1° N, 91.1° E north, 45.2° N, 90.9° E south), 8 – Carpatian region (48.5° N, 23.2° E), 9 – Danube

region (43.6° N, 28.2° E), 10 – Belarus (51.7° N, 28.4° E), 11 – Ukraine (47.8° N, 34.5° E), 12 – Donetsk (48.0° N, 37.6° E), 13 – Miass (55.1° N, 60.1° E), 14 – Austria (48.2° N, 16.7° E), 15 – former Czechoslovakia (49.9° N, 14.0° E), 16 – Moravia (49.2° N, 16.6° E), 17 – Slovakia (49.0° N, 20.0° E), 18 – Hungary (47.5° N, 21.1° E), 19 – Romania (46.6° N, 21.8° E), 20 – Lithuania (56.2° N, 22.7° E). Coordinates are rounded to the nearest decimal and represent territory, not the locality

## Results and discussion

### Morphometry and craniometry of Lithuanian *A. uralensis*

Juvenile and subadult individuals of *A. uralensis* from Lithuania were found to be similar in body size, but not in body mass which is significantly different between age groups (Tukey HSD,  $p_{\text{ad-sub}} < 0.0001$ ,  $p_{\text{sub-juv}} < 0.0001$ ). Adults are significantly bigger and heavier (Table 1). No dimorphism in external measurements was found in subadult and juvenile animals. In adults only one character, hind foot length, was bigger in males (19.9 vs. 19.1 mm,  $t_{26,12} = 2.26$ ,  $p = 0.03$ ).

We found that the size of several skull characters (length of mandibular tooth row, length of lower molar M1, length of maxillary toothrow, interorbital constriction and postorbital constriction) are not age-dependent (Table 2). However, the other characters were significantly larger in adult animals.

Sex dimorphism in *A. uralensis* from Lithuania was expressed quite weakly (Table 2), as only three skull characters in adults had significant measurement differences. The height of the mandibula including first molar and length of mandibular diastema was larger in females ( $X3 = 3.7$  vs. 3.5 mm,  $t = 2.14$ ,  $p < 0.05$ ;  $X6 = 3.6$  vs. 3.5 mm,  $t = 2.75$ ,

$p < 0.01$ , respectively), while postorbital constriction was larger in males ( $X22 = 3.61$  vs. 3.71 mm,  $t = 2.26$ ,  $p < 0.05$ ). In subadult animals, the length of mandibular tooth row was bigger in males ( $X7 = 2.7$  vs. 2.85 mm,  $t = 3.32$ ,  $p < 0.05$ ). Juveniles of *A. uralensis* were not sex dimorphic.

Sex dimorphism of other *Apodemus* species in Lithuania is expressed differently. In *A. flavicollis*, males are significantly larger in body weight and length (with  $p < 0.05$ ), while in *A. sylvaticus*, females are slightly ( $p < 0.10$ ) larger in body weight, length and maxillary toothrow length (Balčiauskienė et al. 2004). In *A. agrarius*, sex based differences in body size of subadult and adult animals were not registered (Balčiauskienė and Balčiauskas 2016).

### Sex dimorphism in *A. uralensis* populations across species range

Size differences in *A. uralensis* are so marked that sexual dimorphism in this species seems unclear. In subadult *A. uralensis* individuals from Slovakia, males were bigger in all body measures, while in adult animals females were bigger in body mass, body and tail length, with males bigger in the hind foot length (Baláž et al. 2012). In the former Czechoslovakia, body and tail lengths were found to be

**Table 1** Morphometric characteristics (average ± standard error) of *A. uralensis* from Lithuania

Character <sup>a</sup>	Adult ( <i>n</i> = 36, 12♂♂: 24♀♀) <sup>b</sup>		Subadult ( <i>n</i> = 12, 7♂♂: 5♀♀)		Juveniles ( <i>n</i> = 30, 15♂♂: 15♀♀)	
	Avg ± SE <sup>b</sup>	Min–max	Avg ± SE	Min–max	Avg ± SE	Min–max
Q (g)	17.9 ± 0.38 <sup>1</sup>	14.0–22.0	12.6 ± 0.37 <sup>2</sup>	11.0–15.0	11.3 ± 0.32 <sup>3</sup>	6.5–14.6
L (mm)	86.1 ± 0.66 <sup>1</sup>	78.0–94.3	74.9 ± 1.42 <sup>2</sup>	68.5–84.2	73.3 ± 0.90 <sup>2</sup>	63.8–85.0
C (mm)	85.2 ± 0.94 <sup>1</sup>	72.3–96.0	74.3 ± 1.10 <sup>2</sup>	69.0–79.0	72.1 ± 1.62 <sup>2</sup>	43.0–85.5
P (mm)	19.4 ± 0.16 <sup>*1</sup>	17.5–21.3	18.7 ± 0.20 <sup>2</sup>	17.5–19.5	18.8 ± 0.18 <sup>2</sup>	15.8–20.9
A (mm)	14.0 ± 0.14 <sup>1</sup>	11.2–15.5	13.3 ± 0.44 <sup>2</sup>	10.4–15.0	13.1 ± 0.27 <sup>2</sup>	8.8–15.0

<sup>a</sup> Body weight (Q), body length (L), tail length (C), hind foot length (P) and ear length (A)

<sup>b</sup> Values marked with different superscripts in the same line differ significantly at *p* < 0.05. Values marked with an asterisk differ significantly between males and females at *p* < 0.05

significantly bigger in females (Steiner 1978). In Austria, males were larger than females according tail length (*p* = 0.06), hind foot length (*p* = 0.065) and body weight (*p* = 0.09) (re-calculated from Spitzenberger and Bauer 2001). In Mongolia, males were insignificantly larger in body weight

and body length, but significantly larger in terms of tail length and hind foot length (both *p* = 0.03, re-calculated from Shar et al. 2015).

As for dimorphism in skull characters, the situation is similar. According to Steiner (1978), skulls of adult *A. uralensis*

**Table 2** Craniometric characteristics (average ± standard error) of *A. uralensis* from Lithuania

Character (in mm) <sup>a</sup>	Adult ( <i>n</i> = 36, 12♂♂: 24♀♀) <sup>b</sup>		Subadult ( <i>n</i> = 12, 7♂♂: 5♀♀)		Juveniles ( <i>n</i> = 30, 15♂♂: 15♀♀)	
	Avg ± SE <sup>c</sup>	Min–max	Avg ± SE	Min–max	Avg ± SE	Min–max
X1	10.9 ± 0.05 <sup>1</sup>	10.0–11.6	10.6 ± 0.10 <sup>2</sup>	10.2–11.2	10.4 ± 0.07 <sup>c</sup>	9.8–11.2
X2	9.8 ± 0.05 <sup>1</sup>	9.0–10.4	9.5 ± 0.08 <sup>2</sup>	9.2–10.0	9.2 ± 0.08 <sup>2</sup>	8.6–10.2
X3	3.6 ± 0.03 <sup>*1</sup>	3.3–4.0	3.4 ± 0.06 <sup>2</sup>	3.0–3.8	3.3 ± 0.04 <sup>2</sup>	2.8–3.8
X4	5.2 ± 0.04 <sup>1</sup>	5.0–6.0	4.9 ± 0.09 <sup>2</sup>	4.4–5.3	4.8 ± 0.05 <sup>2</sup>	4.3–5.2
X5	5.4 ± 0.04 <sup>1</sup>	5.0–6.0	5.2 ± 0.11 <sup>2</sup>	4.8–5.7	5.0 ± 0.06 <sup>2</sup>	4.3–5.6
X6	3.5 ± 0.02 <sup>*1</sup>	3.3–3.8	3.5 ± 0.04 <sup>1</sup>	3.2–3.7	3.5 ± 0.03 <sup>2</sup>	3.1–3.8
X7	2.8 ± 0.02 <sup>1</sup>	2.6–3.0	2.8 ± 0.03 <sup>*1</sup>	2.6–2.9	2.8 ± 0.02 <sup>1</sup>	2.7–3.1
X8	1.0 ± 0.01 <sup>1</sup>	0.9–1.2	1.0 ± 0.02 <sup>1</sup>	0.9–1.1	1.0 ± 0.01 <sup>1</sup>	0.9–1.1
X9	7.3 ± 0.08 <sup>1</sup>	6.3–8.2	6.8 ± 0.19 <sup>2</sup>	5.5–7.9	6.8 ± 0.09 <sup>2</sup>	5.7–7.9
X10	10.6 ± 0.05 <sup>1</sup>	10.0–10.9	10.5 ± 0.10 <sup>1</sup>	10.0–10.9	10.4 ± 0.05 <sup>2</sup>	10.1–11.1
X11	11.3 ± 0.08 <sup>1</sup>	10.5–12.3	10.5 ± 0.18 <sup>2</sup>	9.9–11.4	10.3 ± 0.15 <sup>2</sup>	8.7–11.5
X12	6.3 ± 0.04 <sup>1</sup>	6.0–6.9	5.9 ± 0.10 <sup>2</sup>	5.4–6.4	5.8 ± 0.06 <sup>2</sup>	5.2–6.4
X13	7.1 ± 0.04 <sup>1</sup>	6.6–7.6	6.9 ± 0.12 <sup>1</sup>	6.1–7.4	6.7 ± 0.07 <sup>2</sup>	6.3–7.5
X14	4.3 ± 0.04 <sup>1</sup>	3.7–4.9	4.0 ± 0.07 <sup>2</sup>	3.7–4.5	4.0 ± 0.06 <sup>2</sup>	3.4–4.4
X15	3.3 ± 0.02 <sup>1</sup>	3.1–3.6	3.4 ± 0.03 <sup>1</sup>	3.1–3.5	3.3 ± 0.02 <sup>1</sup>	3.1–3.6
X16	1.1 ± 0.02 <sup>1</sup>	1.0–1.5	1.0 ± 0.01 <sup>2</sup>	1.0–1.1	1.1 ± 0.01 <sup>2</sup>	0.9–1.2
X17	1.7 ± 0.01 <sup>1</sup>	1.6–1.8	1.7 ± 0.02 <sup>2</sup>	1.5–1.7	1.6 ± 0.02 <sup>2</sup>	1.4–1.8
X18	23.9 ± 0.13 <sup>1</sup>	23.0–25.3	23.0 ± 0.27 <sup>2</sup>	21.6–24.1	22.5 ± 0.22 <sup>2</sup>	21.1–24.8
X19	10.9 ± 0.06 <sup>1</sup>	10.2–11.5	10.5 ± 0.12 <sup>2</sup>	9.9–10.9	10.3 ± 0.09 <sup>2</sup>	9.6–11.5
X20	10.5 ± 0.07 <sup>1</sup>	9.9–11.0	10.0 ± 0.14 <sup>2</sup>	9.2–10.5	9.9 ± 0.10 <sup>2</sup>	9.1–11.2
X21	3.6 ± 0.06 <sup>1</sup>	3.1–4.8	3.5 ± 0.06 <sup>1</sup>	3.3–3.9	3.6 ± 0.05 <sup>1</sup>	3.1–4.0
X22	3.6 ± 0.02 <sup>*1</sup>	3.3–3.9	3.6 ± 0.04 <sup>1</sup>	3.4–3.8	3.7 ± 0.03 <sup>1</sup>	3.4–4.0
X23	8.6 ± 0.06 <sup>1</sup>	8.0–8.9	8.5 ± 0.08 <sup>1</sup>	8.1–8.8	8.4 ± 0.07 <sup>2</sup>	7.7–8.9

<sup>a</sup> Abbreviations for characters are explained in [Material and methods](#) section

<sup>b</sup> Male : female ratio may differ for some characters

<sup>c</sup> Values marked with different superscripts in the same line differ significantly at *p* < 0.05. Values marked with an asterisk differ significantly between males and females at *p* < 0.05



females were larger in postorbital constriction (3.86 vs. 3.77 mm,  $p = 0.02$ ) and in the length of *foramen incisivum* (4.39 vs. 4.31 mm,  $p = 0.05$ ) in the former Czechoslovakia. In Mongolian adult *A. uralensis*, zygomatic skull width is significantly larger in males (12.75 vs. 12.08 mm,  $t = 2.77$ ,  $p < 0.02$ , re-calculated from Shar et al. 2015). In the Caucasus, most of the sex dimorphism in the skull characters were registered at higher altitudes (Amshokova 2010): five characters (condylobasal length, length of rostrum, zygomatic skull width, length of mandibula and biggest skull width) were significantly larger in males, while three (interorbital constriction, length of *foramen incisivum* and height of the braincase) were larger in females. Thus, sex dimorphism in *A. uralensis* is not clearly expressed.

### Variability of *A. uralensis* body measurements

Adult *A. uralensis* from populations in the western part of the range were reported as having the lowest average body mass (17.14–18.58 g) and the Lithuanian sample falls within these limits (Table 1). Significantly heavier individuals were characteristic only for the eastern edge of the range in Mongolia, with  $Q = 21.0$  g (re-calculated from Shar et al. 2015), and the southern edge in Turkey, with  $Q = 20.1$  g (Kryštufek and Vohralík 2007). *A. uralensis* from both of these samples were significantly ( $p < 0.0001$ ) heavier than mice from the western part of the species range (Fig. 2a).

The body length of *A. uralensis* follows the same pattern, reverse to that of Bergmann's rule – the longest mice were registered in the southern and eastern edges of the range, i.e. Turkey and Mongolia (the difference of both to the Central European samples were significant at  $p < 0.0001$ ). Significantly, the smallest mice were found in the northern part of the range, i.e. in the Ural. The body length of adult *A. uralensis* from Lithuania is within the limits of body length of mice from populations in the western and central parts of the range (Fig. 2b).

The tail length of mice from Lithuania is shorter than in Turkey (southern edge of the range), but did not differ from Iran and the Ural, i.e. southern and northern extremes (Fig. 2c). However, tail to body length ratio show differences in longitudinal aspect, with the shortest tails in the east, becoming longer in the west, including the north-western population of *A. uralensis* in Lithuania, where the ratio was the highest. Tail to body length ratio in a south-north direction is consistent (Fig. 2d).

The highest average values of the hind foot of adult *A. uralensis*, over 20 mm (Fig. 2e), were reported from the southern edge populations in Turkey and Iran (Kryštufek and Vohralík 2007; Darvish et al. 2011). Hind foot lengths of 19–20 mm is characteristic for mice from all parts of the distribution range except the most southern. Lithuanian and Mongolian populations are similar in hind foot size (19.4

and 19.2 mm, NS), showing no longitudinal difference. Mice with the smallest hind foot length ( $> 19$  mm) are all from populations in the western part of the range (Fig. 2e).

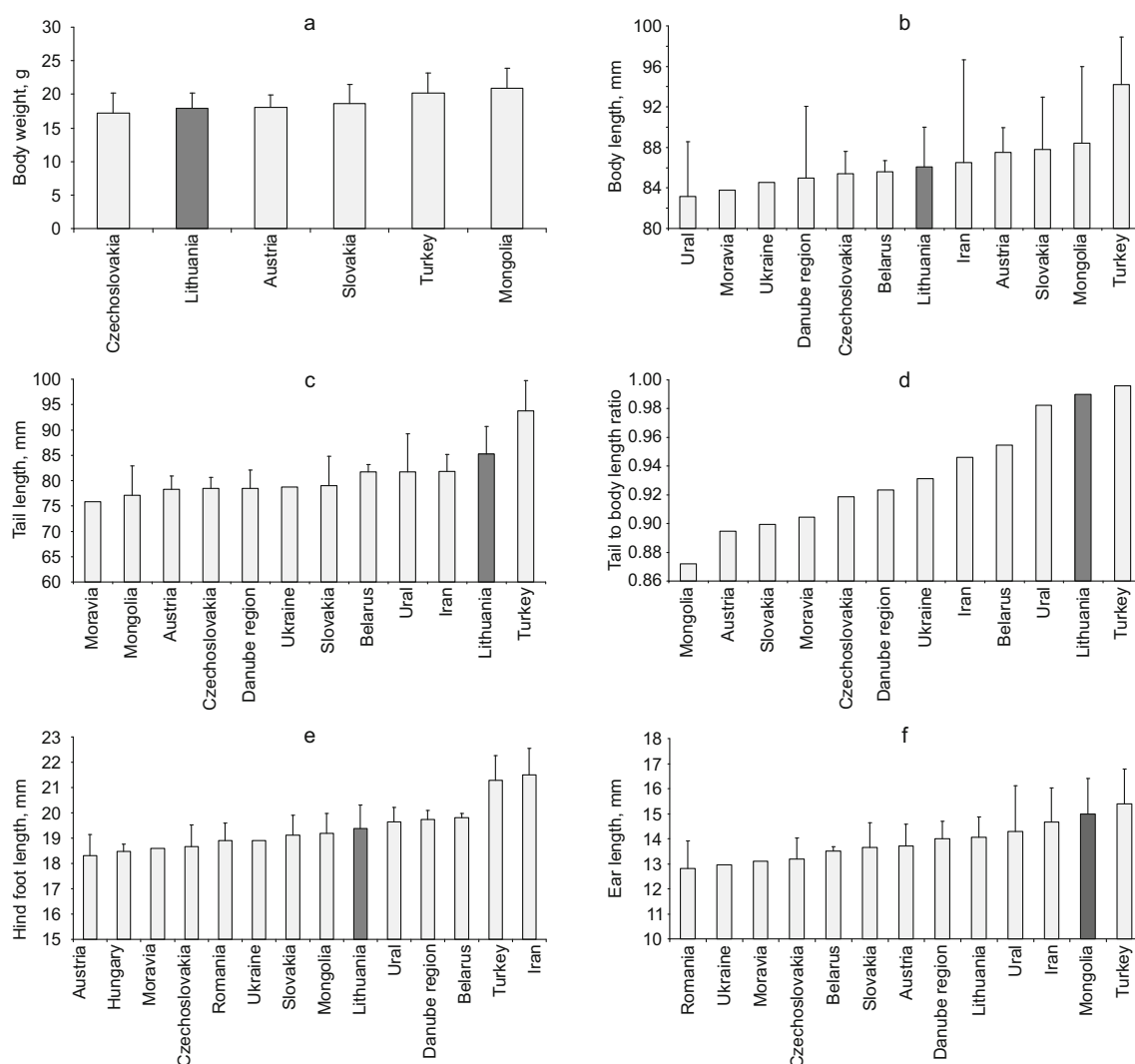
The shortest ears were found in the populations from western and central parts of the *A. uralensis* distribution range (Fig. 2f). An average ear length over 14.5 mm was characteristic only at the southern and eastern extremes of the range, while over 14 mm was characteristic in the northern and north-western parts of the range, i.e. the Ural and Lithuania.

### Variability of *A. uralensis* skull size

The longest skulls of *A. uralensis* are characteristic to edge populations (Fig. 3a), and this parameter is very variable. On the southern edge of the species range (Iran), the condylobasal skull length is over 24 mm (Darvish et al. 2011), while the length is also almost that value in Lithuania in the north-western part of the range (see Table 2, the difference not significant). These two marginal populations differ from the other populations significantly ( $p < 0.001$ ). Condylobasal skull length over 23 mm was characteristic to mice from Caucasus Mountains and Mongolia, and over 22.5 mm to Caucasus plains and Turkey (Kryštufek and Vohralík 2007; Amshokova 2010; Shar et al. 2015). The shortest skulls of adult *A. uralensis* were from Hungary, average 20.6 mm (Demeter and Lázár 1984), Estonia, average 21.08 mm, and Carpatian region, average 21.12 mm (Zagorodniuk 2005).

Populations of mice with the widest skulls, zygomatic width of the skull 12.5 mm and over (Fig. 3b), were characteristic to the eastern and southern edges of the range, specifically Mongolia and Iran (Kryštufek and Vohralík 2007, 2009; Darvish et al. 2011). Quite unexpectedly, according to Baláž et al. (2012), this group also statistically includes *A. uralensis* from Slovakia, though according another author, the zygomatic width of the skull was significantly smaller in this same country, even in mountainous areas (Čanádý et al. 2014). Mice from the Caucasus mountains had zygomatic width of the skull over 12 mm. Average zygomatic width of the skull over 11.5 mm and is characteristic to the Caucasus plain (Amshokova 2010) and Austria (Spitzenberger and Bauer 2001). The narrowest skulls with a zygomatic width of the skull less than 11 mm are from the populations in central and northern parts of the range (Zagorodniuk 2005, Fig. 3b). The Lithuanian sample is characterized by medium zygomatic skull width, and is close to populations from Ukraine and Danube region (Zagorodniuk 1993; Lashkova 2003), Valdai (Zagorodniuk 2005), Slovakia and Belarus (Savickyj et al. 2005; Čanádý et al. 2014).

The pattern of distribution of relative skull width (expressed as the ratio between zygomatic width and condylobasal length) is not clear: relatively short and wide skulls of adult *A. uralensis* are characteristic to western as well as eastern populations, while the skulls of mice from southern,



**Fig. 2** Distribution of morphometric parameters of adult *A. uralensis* in various parts of the species distribution range (average + SD), Lithuania (north-western edge) is filled dark

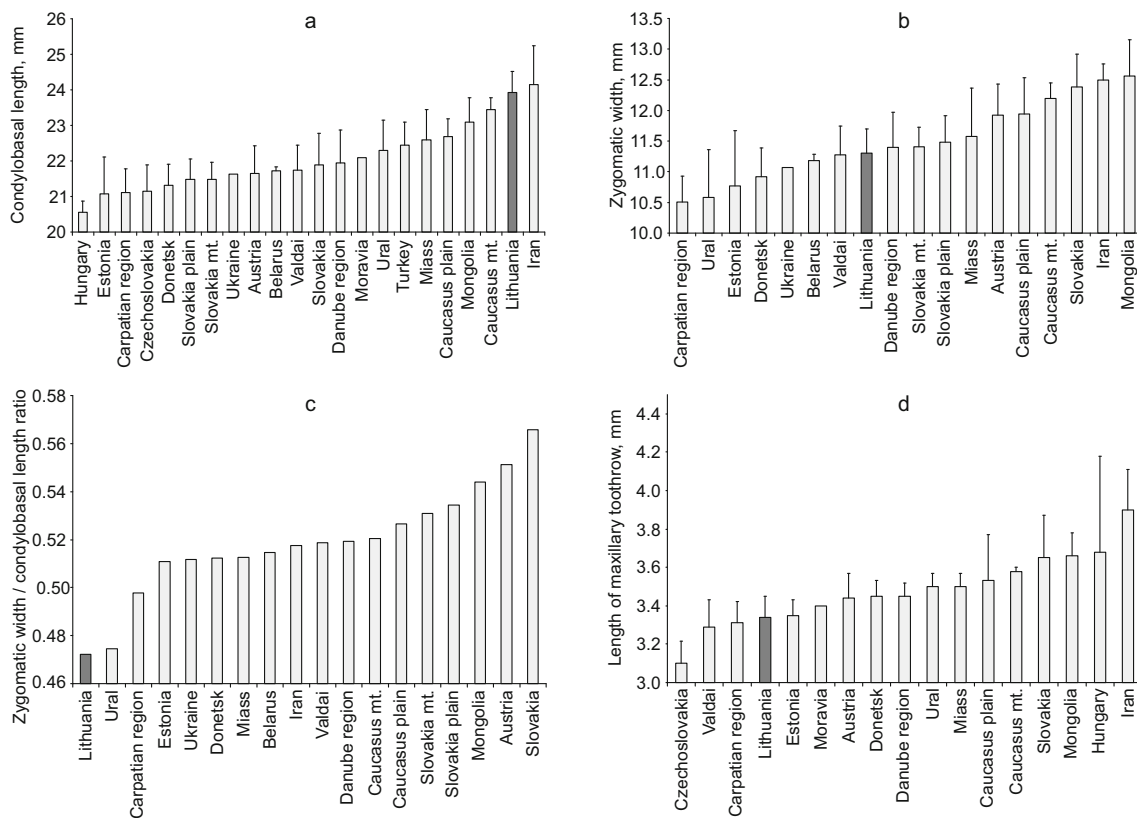
central and northern parts are characterized as medium width (Fig. 3c). Skulls of mice from Lithuania, the Ural and the Carpathian region are the narrowest and longest, with a relative skull width  $< 0.5$ .

The length of maxillary tooththrow has no clear latitudinal or longitudinal distribution either (Fig. 3d), as biggest average values were registered in Iran (3.9 mm), Hungary (3.68 mm) and Mongolia (3.66 mm), i.e., very different parts of the distribution range (Demeter and Lázár 1984; Darvish et al. 2011; Shar et al. 2015). An average length of maxillary tooththrow over 3.50 mm was registered in populations from Slovakia (Baláž et al. 2012), and in the Caucasus mountain range and plains (Amshokova 2010). In the northern populations of adult *A. uralensis*, the average length of the maxillary tooththrow varied from very short in Valdai and Estonia to medium in the Ural (Zagorodniuk 2005). Despite having one of the longest average condylobasal skull length, the average length of the maxillary tooththrow in Lithuania was found to

be one of the shortest (Table 2). The minimum average length of this character was reported from the former Czechoslovakia (3.1 mm, Steiner 1978), differing highly significantly from all neighbouring countries ( $p < 0.001$ , Fig. 3d).

### Geographic aspects of body and skull size in *A. uralensis* confirm extreme variability

Our analysis shows that the geographic variability of body and skull size in *A. uralensis* is quite significant, in general not following Bergmann's rule. Significant differences in external and cranial measurements were found in *A. uralensis* from different regions of the same country, for example in Hungary (Steiner 1978; Demeter and Lázár 1984) and Slovakia (Baláž et al. 2012; Čanádý et al. 2014). The smallest as well as medium and highest average values of the same parameter, such as body length or upper tooththrow length, were characteristic to *A. uralensis* populations from Central Europe.



**Fig. 3** Distribution of skull parameters of adult *A. uralensis* in various parts of the species distribution range (average + SD), Lithuania (north-western edge) is filled dark

We can not attribute these differences to individual measurement errors or biases by different researchers, as high variability of several parameters was also shown in the samples processed by a single author (i.e., Zagorodniuk 2005).

Čanády et al. (2014) already mentioned that *A. uralensis* are smaller in Central Europe than individuals from the eastern part of the distribution range. However, the high variability in *A. uralensis*, as expressed in external as well as in skull characters (see Figs. 2 and 3), was confirmed by different samples from within the same country, specifically in Slovakia (Baláž et al. 2012; Čanády et al. 2014), Hungary (Steiner 1978; Demeter and Lázár 1984) and the former Czechoslovakia (Holišová et al. 1962; Steiner 1978). Thus, significance differences are characteristic to populations even in relatively small areas, inside one country and in the same part of the distribution range of the species.

Even if undoubtedly there were geographical differences in external and skull characters (as shown in Figs. 2 and 3), the high variability camouflages latitudinal and longitudinal clines in body and skull size. We acknowledge that in most characters the largest average values were registered at the southern and eastern edges of the distribution range. As for the eastern part of the range, according to Pavlinov and Lissovsky 2012 it is inhabited by the “semispecies” *A. kastschenkoi*, having a geographical boundary along the

Irtysch River. Thus, the differences of *A. uralensis* from Mongolia, i.e. the eastern edge, may have a genetical base.

Over such a wide territory, many environmental variables are different, and these are of importance in forming a geographical cline (Stillwell 2010). Preferred habitats for *A. uralensis* are different across the range: in central and eastern parts, the preferred habitats are mainly forest edge and open habitats adjacent to woodland (Kryštufek et al. 2008), field boundaries (Baláž et al. 2012), woodlands (Kryštufek and Vohralík 2007) and riparian forests and vegetation (Shar et al. 2015), whilst in south-western part of the range, presence and even dominance of *A. uralensis* in agricultural lands was found (de Mendonça and Benedek 2012; Heroldová and Suchomel 2016). In Lithuania, in the north-western part of species range, *A. uralensis* were mainly registered in “the ecotones of mixed forests and open habitats and in open habitats bordering forests or situated close to them” (Juškaitis et al. 2016).

The relationship between morphological variation and biotic factors was also not clearly identified in another species of the same genus, *A. speciosus* (Takada et al. 2006). A weak correlation between geographic and morphological distances is characteristic also to other small mammal species, for example the water rat *Scapteromys tumidus* (Waterhouse, 1837) (Quintela et al. 2016). The situation is complicated by the fact

that in wood mice, postnatal growth does not stop in most body and skull characters (Frynta and Žižková 1992). According to our data (see Tables 1 and 2), continuous growth is characteristic to most of the characters in *A. uralensis*.

Generalizing, populations of *A. uralensis* inhabiting the eastern and southern edges of the species range are characterized as having the largest individuals in terms of average body and skull size. Data on *A. uralensis* from Lithuania (north-western part of the range) are in accordance with the above, but not in all characters. In terms of tail length and condylobasal length of the skull, Lithuanian *A. uralensis* are among the largest across the distribution range. Most of the body and skull measurements in Lithuanian mice correspond to those from populations of central and western parts of the range.

Skulls of adult *A. uralensis* from Lithuania are different in shape from individuals of other countries, as they could be defined as long and narrow. Most of the skull characters were significantly larger in adult animals, but measurements of five skull characters were not age-dependent.

Sex dimorphism in *A. uralensis* from Lithuania is weakly expressed and uneven: in adult animals, hind foot length and postorbital constriction were bigger in males, while the height of the mandibula and the length of mandibular diastema were larger in females. Younger animals were even less dimorphic.

We conclude, that analysis based on the raw morphometric data is required to find, if these patterns are dependent on the complex of body size and latitude/longitude/height ASL factors.

## Compliance with ethical standards

**Ethical approval** All applicable national, and institutional guidelines for the care and use of animals were followed.

**Conflict of interest** The authors declare that they have no conflict of interest.

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