ORIGINAL ARTICLE

Changes in size of Baltic field voles over the last 50 years: are they really shrinking?

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Abstract

Using museum materials and recently trapped specimens of field voles (*Microtus agrestis* (Linnaeus, 1761)) from Lithuania and Estonia, we assessed temporal and latitudinal trends in body and skull size, comparing the periods 1980–1996 and 2014–2016. We measured four body and 23 skull characters, size-adjusting them using the geometric mean procedure. A pronounced decrease in the size of *M. agrestis* was noted in Estonia, where 23 out of 27 adjusted body and skull characters had decreased by up to 21.9%, with only the tail length, hind foot length, maximum height of mandibula excluding coronoid process and coronoid height of mandibula increasing significantly. Decreases were less marked in voles from Lithuania – most pronounced were a 6.1% decrease in adjusted body length, an 11.6% decrease in adjusted length of the braincase, a 3.85% decrease in the breadth of the braincase, measured at the widest part, a 2.9% decrease in condylobasal skull length and a 2.2% decrease in the height of the braincase. The coronoid height of the mandibula of Lithuanian individuals showed an 8.4% size increase. In both countries, the confounding effect of sex on the size changes of *M. agrestis* from 1980 to 2016 was much smaller than the effect of time period. Concluding, voles in Estonia became significantly smaller, while changes in the measured characters in Lithuania were heterogeneous.

Keywords *Microtus agrestis* · Body size change · Skull size · Climate warming

Introduction

Ecological responses to ongoing climate change are numerous, diverse and taxonomically widespread (Teplitsky et al. 2008). Rapid climate change imposes selection pressures on traits important to fitness and, therefore, microevolution in response to climate-mediated selection is potentially an important mechanism that could mitigate negative consequences of climate change (Gienapp et al. 2008). In many taxa of organisms, including mammals, there is a trend for warmer areas to be characterized by a smaller body mass (Frelich et al.

2012), and this is commonly interpreted as meaning that climate change could also have a possible influence on the size of individuals (Yom-Tov et al. 2003; Watt et al. 2010): "Responding to climate warming, body size starts to reduce" (Gardner et al. 2011), or "Many species already exhibit smaller sizes and many others are likely to shrink" (Sheridan and Bickford 2011). Warming-induced reductions in body size are greater in aquatic than terrestrial species (Forster et al. 2012), for example in marine fish (Cheung et al. 2013) and salamanders (Caruso et al. 2014). However, body sizes also shrink in endothermic organisms (Angilletta Jr et al. 2004; Daufresne et al. 2009; Forster et al. 2012), including in most bird species (Teplitsky et al. 2008; Van Buskirk et al. 2010; Yom-Tov and Geffen 2011). The opposite however has generally been true among mammals (Yom-Tov et al. 2003, 2008; Yom-Tov and Yom-Tov 2004; Yom-Tov and Geffen 2011 and citations therein). Nevertheless, there are examples of decreasing body mass in woodrats (*Neotoma* sp.), Soay sheep (*Ovis aries* Linnaeus, 1758) and red deer (*Cervus elaphus* Linnaeus, 1758) in responce to milder winters and increasing temperature (Post et al. 1997; Smith et al. 1998; Ozgul et al. 2009). With the exception of rapid morphological

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changes reported in Mexican voles (*Microtus mexicanus* (Saussure, 1861)) and meadow voles (*M. pennsylvanicus* (Ord, 1815)) by Pergams and Lawler (2009) without detail on direction of change, there is no other published information on size change in *Microtus* voles, including the field vole (*Microtus agrestis* (Linnaeus, 1761)).

It is estimated that of terrestrial non-volant threatened mammals, nearly 50% of species are already negatively influenced by recent changes in climate (Pacifici et al. 2017). However, not all mammals respond to climate change as expected, large ones being the most responsive: 41% of assessed species did not respond at all, while 7% responded in an opposite manner to that expected (McCain and King 2014). For example, the body length of small mammals in Denmark over the last 175 years has mostly increased, with the rate of change being high (Schmidt and Jensen 2003). In rodents over four continents, a greater propensity for increasing body size trends has been noted than for decreasing size (Pergams and Lawler 2009).

In the latitudes from 63 to 65 degrees north, there are studies that show organisms have become smaller with increasing temperatures. Smaller individuals are better suited to warmer environments, thus the present trends in climate change should result in further decreases in organism size (Sheridan and Bickford 2011). However, it does remain not proven that observed size changes are related to climate warming. Body size in small mammals may also change due to antropogenic transformation (Lomolino and Perault 2007) or fragmentation of habitat (Millien et al. 2006).

Size reduction is not the only ecological response to climate (Sheridan and Bickford 2011), there has also been a genetic change towards lower body mass. The latter represents an adaptive response to viability selection favoring juveniles growing up to become relatively small adults, i.e. with a low potential adult mass, these presumably completing their development earlier (Kruuk 2017; Bonnet et al. 2017).

M. agrestis is widespread in the Palaearctic, generally common and occurring in a wide range of habitats, though with a preference for damp areas (Kryštufek et al. 2016). In the Baltic States, *M. agrestis* is not rare, but also not a dominant species. In Lithuania, the species accounted for 8.1–9.4% of small mammals trapped in wet forests and swamps in 1980–1981; 6.3% in open areas and meadows in 1983, 2.2% in forests, swamps and meadows in 1981–1990, 4.3–14.3% in various habitats of nature reserves in 1990–1994 and 4.2–20.8% in various habitats of large protected areas in 1990–1997, with a maximum of 23.7% in 1993 (Balčiauskas and Juškaitis 1997). More recently, in 2014–2016, *M. agrestis* individuals accounted for 6.1–8.6% of all small mammals trapped in reedbeds and flooded meadows at Rusnė, west Lithuania (authors data, unpubl.). In the coastal wetlands of Estonia, the proportion of *M. agrestis* was 17.3% (Scott et al. 2008), the species being present in 2/3 of trapping sessions and in at least six habitat types.

Our aim was to assess temporal and latitudinal trends in the body and skull sizes of *M. agrestis* using museum and recently trapped specimens from both Lithuania and Estonia, intending to test whether specimen sizes had changed over last 50 years.

Material and methods

We measured and analyzed data from 428 *M. agrestis* individuals, 283 of which had been trapped in Lithuania between 1968 and 2016 and 145 trapped in Estonia between 1980 and 2016.

As the majority of trapping was conducted in autumn, we expected that the year of collection would reflect the year that the most of the individuals had been born. However, continuous data on body and skull size were not available, thus samples were compared as discrete variables according to Yom-Tov and Geffen (2011), before and after a certain point in time. We set two time periods, 1980–1996 and 2014–2016, resulting in a sample size of 398 individuals (Table 1).

Significant warming of the climate was observed across the Baltic countries in the period 1951–2010. The lowest mean temperatures were observed in Estonia and highest in Lithuania, the average difference between the two being 1–2 K (Jaagus et al. 2014). According to these authors, the increase over the period 1951–2010 was an average 0.30 K/decade in the continental part of the region, with the highest increases of temperature being observed in March, April, May, July and August and the rate of warming being slightly higher in Estonia.

Voles were trapped with snap traps, then weighed and measured, with the age and sex being recorded at dissection as in Balčiauskas et al. (2012). We used five standard body measurements (body mass, Q, body length, L, tail length, C, hind foot length, P and ear length, A). Body condition was evaluated as an index based on the ratio of body weight and body length (Drouhot et al. 2014), namely $BC = (Q/L^3) \times 10^5$, where Q is body mass (g) and L is body length (mm) as in Moors (1985).

Vole skulls were cleaned through boiling or maceration (in the earlier period) or with *Dermestes* beetle larvae (in the more recent period). In the skull and mandible, 23 characters were measured as in Balčiauskienė et al. (2015), using a binocular microscope with a micrometric eyepiece to an accuracy of 0.1 mm, or with digital callipers. Only the characters of the right side of the skull were used. Measurements were: 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 toothrow; X8 – length of lower molar M1; X9 – length of nasalia; X10 – breadth of

Table 1 Sample characteristics of the field vole (*Microtus agrestis*)

Country	Period		Sex		Age [a]		
	1980–1996	2014–2016	Male	Female	Ad	Sub	Juv
Lithuania	191	63	135	145	45	15	30
Estonia	131	13	68	51	79	21	13
Total	322	76	203	196	124	36	43

[a] ad – adult, sub – subadult, juv – juvenile animals

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 toothrow; 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.

All cranial measurements were taken by one author, while body measurements were by several collectors. For museum specimens, some of this latter information was missing. We checked the normality of the measurements using Kolmogorov-Smirnov's test. To assess possible bias, the difference in variation coefficient between the countries was tested using the Levene test for homogeneity of variance.

Due to wide variations in the body size across the vole sample (Online Resource 1), the measured characters were size-adjusted. We used the geometric mean procedure, described in Dumont (2004): cranial and body measurements for each vole were divided by the geometric mean of the corresponding measurements from that individual. ANOVA and Student t-test were used to test if there were latitude and/or time period based differences. The GLM model with the time period as a covariate and sex for confounding effect was used. Though age categories are related to body size, we excluded this by size-adjustment of the characters and thus we did not check age for its confounding effect. All statistics were done in Statistica for Windows ver. 7.

Results

The distribution of most characters in *M. agrestis* was not normal. Differences between the countries were present, with more characters normally distributed in the voles from Estonia. In both countries, the difference from normal distribution was significant for hind foot length and skull characters X3–X6, X8, X16, X17, X21 and X22 (Online Resource 2).

The highest variation was found in body measurements that had been taken by several collectors (Online Resource 1). Significant differences in variation of body length and ear length were found between Estonia and Lithuania. Albeit being much smaller than the variation in body measurements,

variation of several skull characters also differed significantly between the countries. Minimum–maximum ranges of most characters were extensive in both countries (Online Resource 1), thus size adjustment was necessary.

In general, means of the adjusted measurements significantly differed between the countries in the period 1980–1996 (Wilks $\lambda = 0.48$, F = 2.0, $p < 0.002$), but not in 2014–2016 (Wilks $\lambda = 0.003$, NS). In both countries, the means of the adjusted measurements significantly differed between above-mentioned periods (Lithuania, Wilks $\lambda = 0.29$, F = 3.0, $p < 0.001$; Estonia, Wilks $\lambda = 0.00$, F = 10,183, $p < 0.01$).

Changes in adjusted body measures were not consistent between the countries (Fig. 1). A decrease in body length between the periods 1980–1996 and 2014–2016 was significant in Lithuania (Fig. 1a). The length of the hind foot decreased in Estonia (Fig. 1c), while the mean length of the hind foot significantly increased in Lithuania (Fig. 1c), as well as ear length in Estonia (Fig. 1b). Body condition of *M. agrestis* decreased in Estonia by nearly 6% (from BC = 2.61 to 2.46; t = 1.22, df = 68, NS), while it increased by 6% in Lithuania (from 2.91 to 3.09; t = 2.87, df = 251, $p < 0.005$).

Six skull characters decreased between the periods 1980–1996 and 2014–2016 in Estonia and Lithuania (Fig. 2). Of these, condylobasal length (Fig. 2a), height of the braincase (Fig. 2b) and length of the braincase (Fig. 2c) decreased significantly in both countries, while decreases in the length of mandibular diastema, the length of cranial (upper) diastema and the breadth of braincase, measured at the widest part, (Fig. 2d–f) were significant in Estonia.

Two skull characters did not change between the investigated periods in Lithuania, while they were significantly reduced in Estonia – zygomatic skull width (Fig. 3a) and zygomatic arc length (Fig. 3b).

Five skull characters significantly decreased between the periods of 1980–1996 and 2014–2016 in Estonia, but significantly increased in Lithuania: total length of mandibula at *processus articularis* (Fig. 4a) – length of mandibular tooth row (Fig. 4b), length of lower molar M_1 (Fig. 4c), length of maxillary toothrow (Fig. 4d) and length of upper molar M^1. There were more skull characters which exhibited the same pattern, though the increase between 1980 and 1996 and 2014–2016 in Lithuania was not significant, while the shrinking in Estonia was very substantial (Online Resource 3).
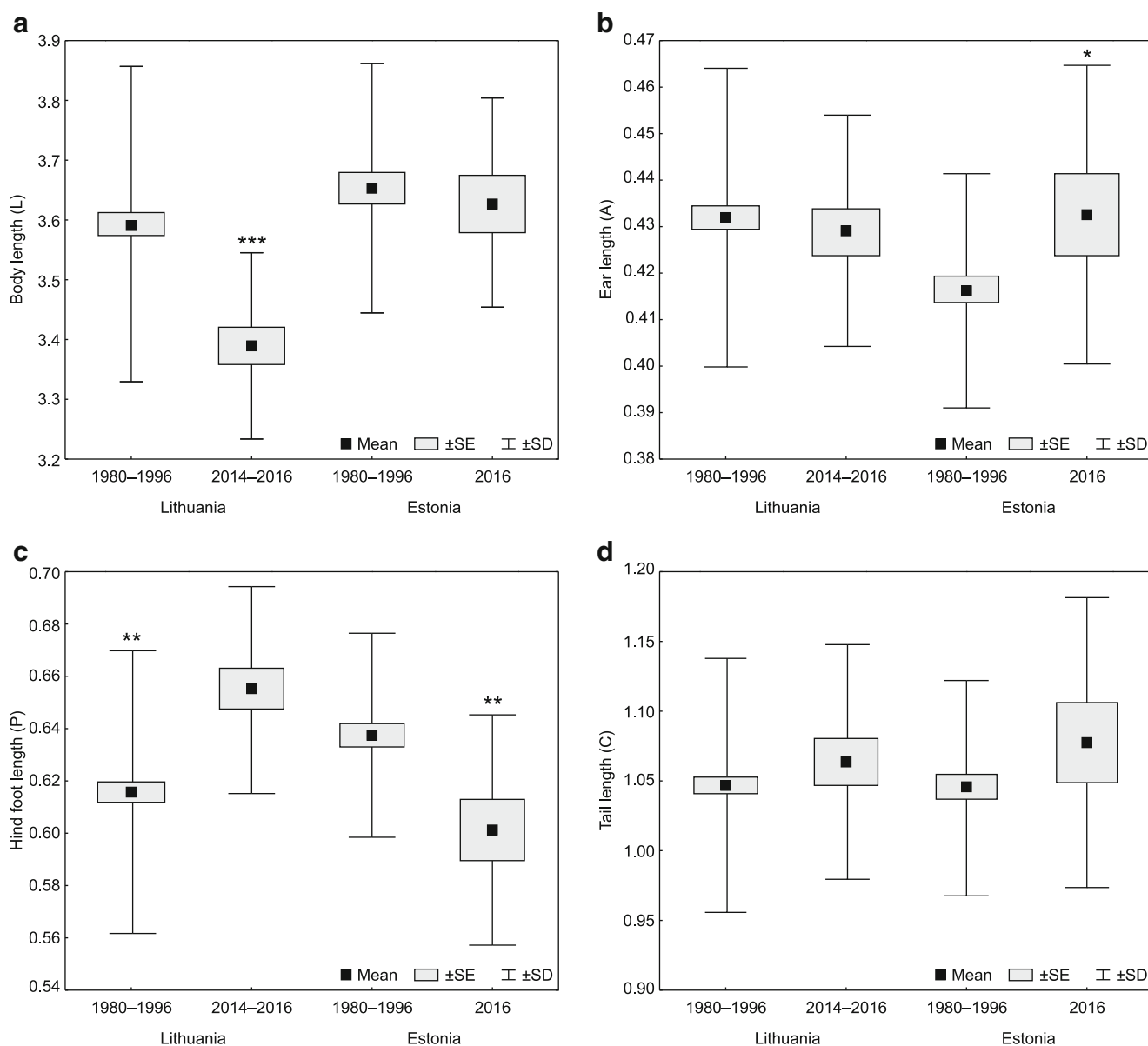
Fig. 1 Changes in adjusted body measurements of *M. agrestis* in Lithuania and Estonia between the periods 1980–1996 and 2014–2016: a – body length, b – ear length, c – hind foot length, d – tail length.

Significance of difference in means between periods in the country: *** $-p<0.001$, ** $-p<0.01$, * $-p<0.05$

Finally, the means of two skull characters significantly increased between the periods of 1980–1996 in both countries. These were the maximum height of mandibula, excluding coronoid process, (Fig. 5a) and coronoid height of mandibula (Fig. 5b).

The decrease in the size of *M. agrestis* was more pronounced in Estonia, where most of the adjusted body and skull characters between the periods of 1980–1996 and 2014–2016 decreased by up to 21.9%. Increases were found only for tail length, hind foot length and height of mandibula – the maximum height of mandibula, excluding coronoid process, increased by 21.9%, while the coronoid height of mandibular by 16.9% (Table 2).

In Lithuania, a decrease was registered in two body measurements: a 6.1% decrease in adjusted body length and 0.7% in ear length. Concerning skull characters, the biggest decrease was in adjusted length of the braincase (11.6%), while lesser decreases were also registered for the breadth of braincase measured at the widest part (3.85%), for condylobasal skull length (2.9%) and for the height of the braincase (2.2%). Increase in character size was most pronounced for the maximum height of mandibula, excluding coronoid process, at 8.4% and coronoid height of mandibular at 7.0% (Table 2).

We tested whether the sex of the voles had any influence on how animal size changed over time, i.e., whether it acted as a
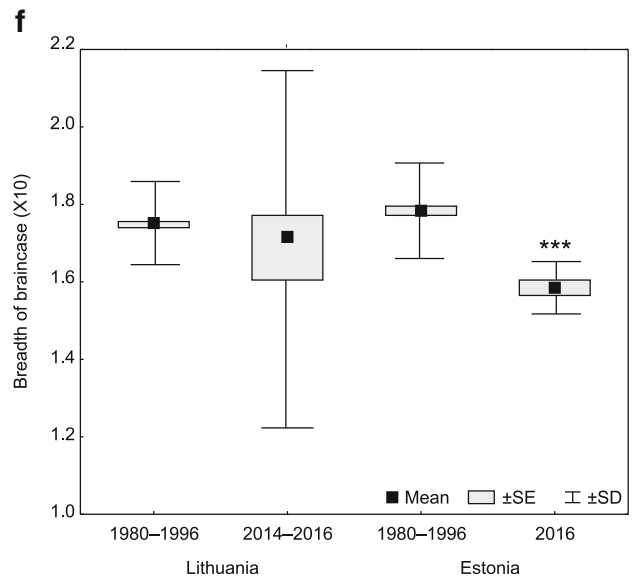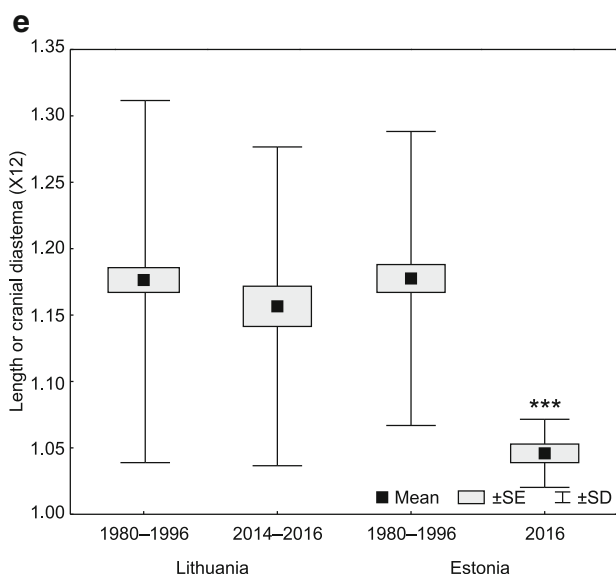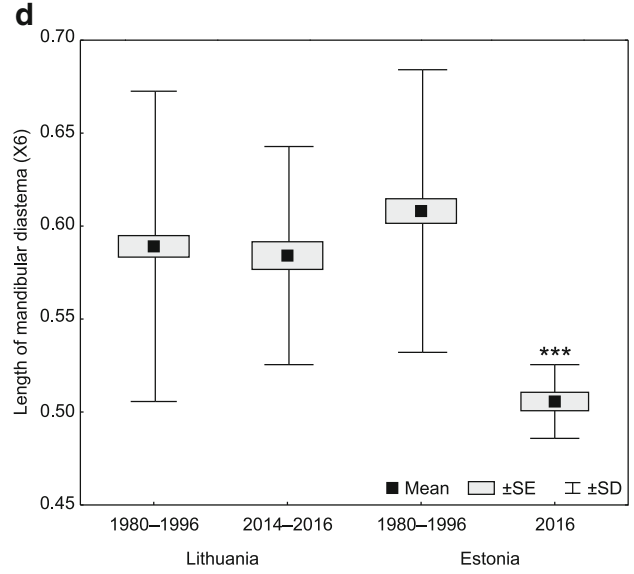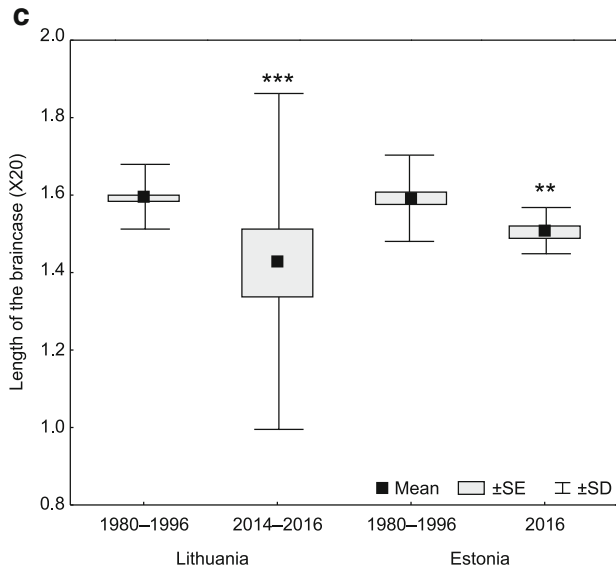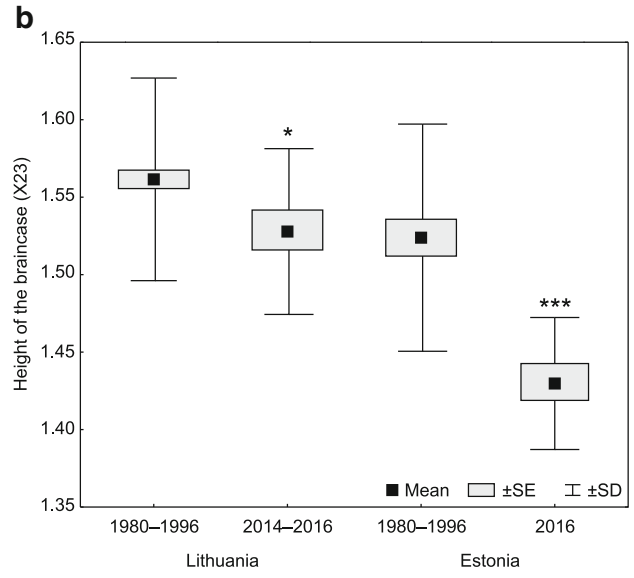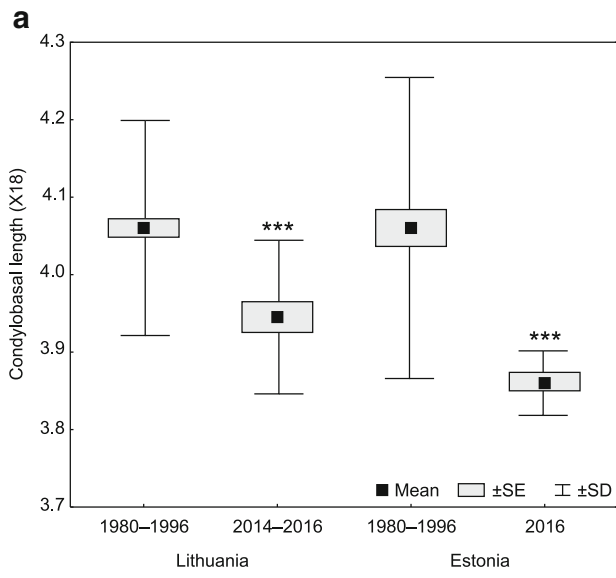
Fig. 2 Decrease in adjusted skull measurements of *M. agrestis* in Lithuania and Estonia between the periods 1980–1996 and 2014–2016: a – condylobasal length, b – height of the braincase, c – length of the braincase, d – length of mandibular diastema, e – length of cranial diastema, f – breadth of braincase. Significance of difference in means between periods in the country: *** – p < 0.001, ** – p < 0.01

confounding factor to the time period for both countries. In Estonia, changes in adjusted body measurements did not depend on sex of animal (Wilk's λ = 0.08, F = 0.64, NS), but were influenced by time period (Wilk's λ = 0.0001, F = 82.17, $p < 0.1$). In Lithuania, the significance of the time period was higher (Wilk's λ = 0.29, F = 5.28, $p < 0.0001$) than that of sex (Wilk's λ = 0.47, F = 2.41, $p < 0.005$). In all cases, the effect of age (using body mass as a proxy) on the observed changes in the size of *M. agrestis* was excluded by adjusting body and skull measurements.

In both countries, time period was the only factor to show significant influence on body condition (Estonia, F = 5.00, $p < 0.05$; Lithuania F = 15.79, $p < 0.0001$). Changes in two size-adjusted body measurements of the voles from Estonia, namely hind foot length and ear length, were also dependent on time period. In Lithuania, changes in body length and tail length were influenced by both period and sex (Online Resource 4).

Concerning changes in skull measurements, the influence of time period was significant for 13 characters in Estonian voles, while sex for only three. In these three cases (total length of mandibula at *processus articularis* excluding incisors, length of mandibula excluding incisors and height of the braincase), the influence of the time factor was stronger than the confounding effect of sex (Online Resource 4).

In Lithuania, changes in two characters (length of the braincase and height of the braincase) were dependent on the confounding effect of sex, not on time period. In change to one further character, the length of mandibular diastema, the effect of sex was stronger that the time factor. However, changes of the other 10 characters depended solely on the time period under consideration (Online Resource 4). Thus, in both countries, the confounding effect of the sex of the animal on size changes of *M. agrestis* during 1980–2016 was much smaller than the effect of time period.

Discussion

Body size is a very important trait in an animal, as it determines other characteristics such as survival, reproduction, growth and migration (Lomolino and Perault 2007; Daufresne et al. 2009; Yom-Tov and Geffen 2011). Body size influences characteristics of species and communities (Gibert and DeLong 2014). Not surprisingly, decreases or increases of organism size under higher temperatures receive wide attention, as they may be very important in the future under conditions of continuing climate change (Sheridan and Bickford 2011; Frelich et al. 2012; Gibert and DeLong 2014).

Though examinations of museum collections worldwide would allow for further quantification of possible size-change trends (Millien et al. 2006; Gardner et al. 2011; Sheridan and Bickford 2011), publications on rodent size change are lacking, with just two vole species, *M. mexicanus* and *M. pennsylvanicus*, having been reported as undergoing morphological changes in the last century (Pergams and Lawler 2009). In a study on common vole (*M. arvalis*
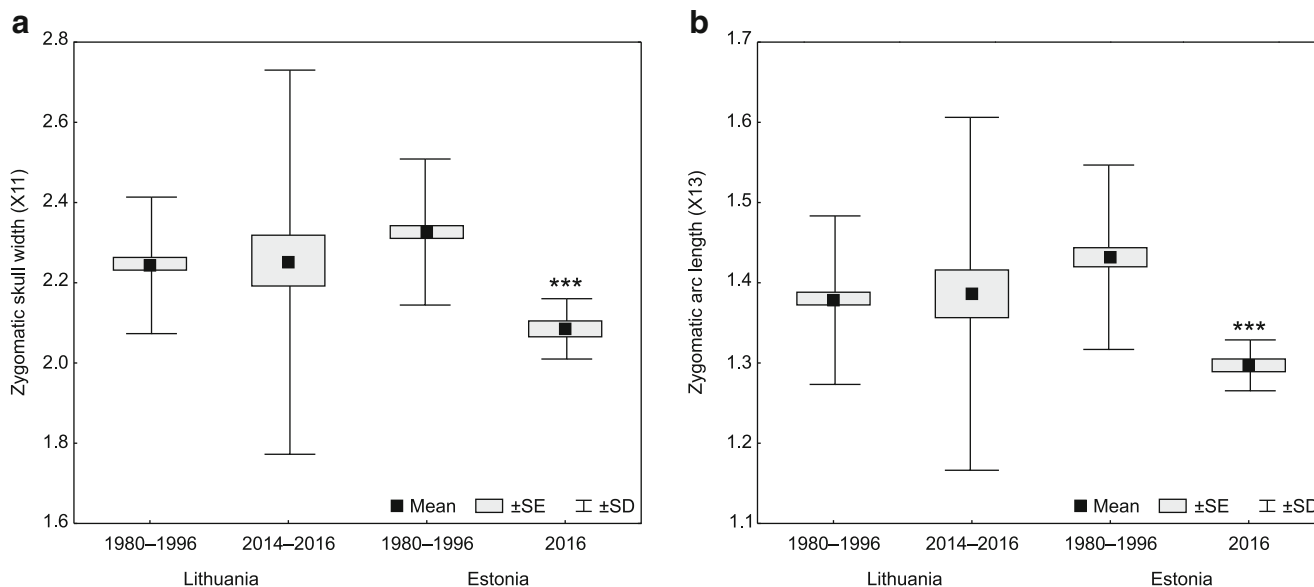

Fig. 3 Changes in adjusted skull measurements of *M. agrestis* in the periods 1980–1996 and 2014–2016, showing no change in Lithuania, but decrease in

Estonia: a – zygomatic skull width, b – zygomatic arc length. Significance of difference in means between periods in the country: *** – p < 0.001
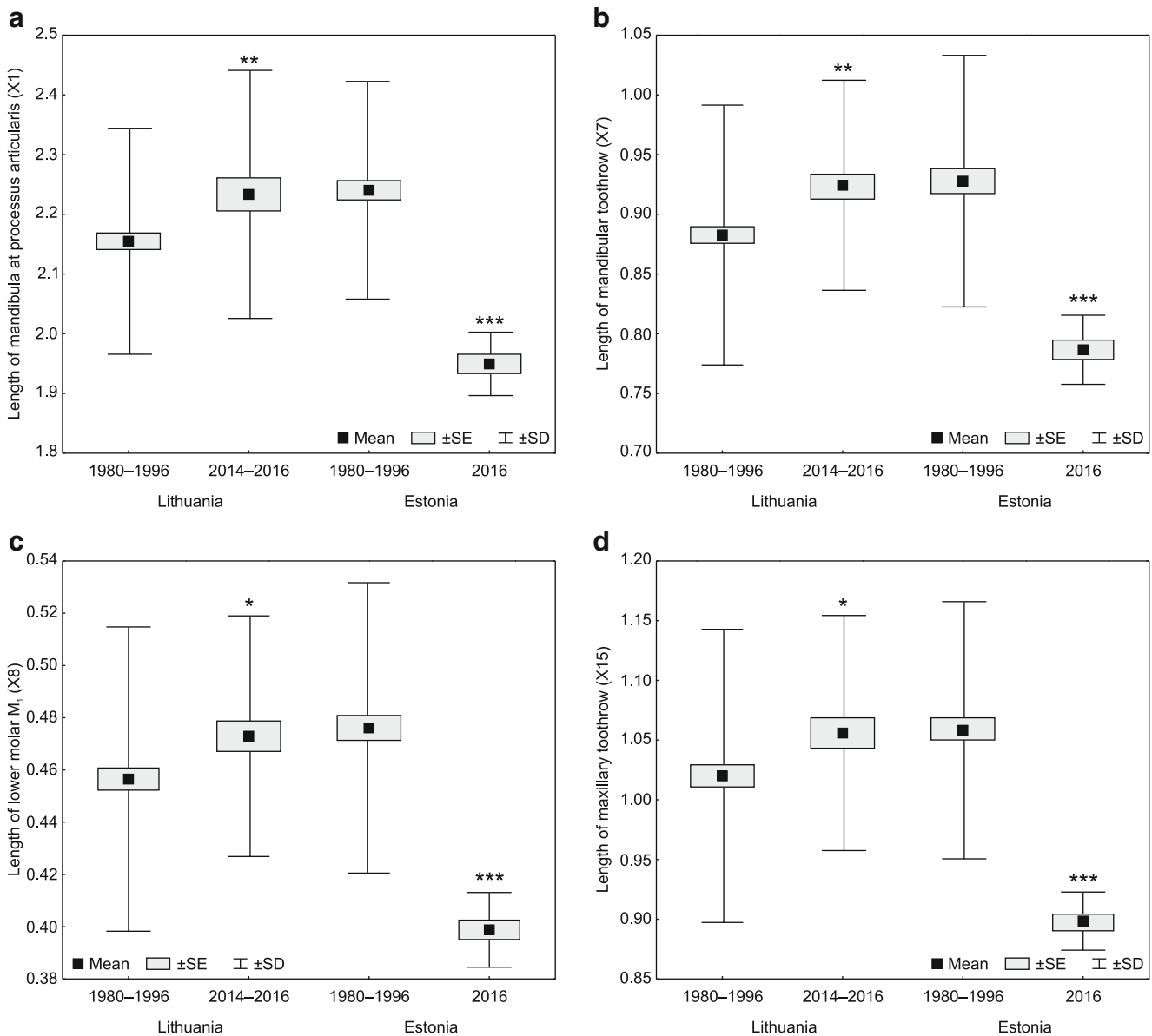
Fig. 4 Changes in adjusted skull measurements of *M. agrestis* between the periods 1980–1996 and 2014–2016, showing skull size decrease in Estonia and increase in Lithuania: a – total length of mandibula at *processus articularis*, excluding incisors, b – length of mandibular toothrow, c – length of lower molar M1, d – length of maxillary toothrow. Significance of difference in means between periods in the country: *** – p < 0.001, ** – p < 0.01, * – p < 0.05

(Pallas, 1778)), it was shown that climate changes do not influence morphological variability, but the investigation was based on molar M_1 only (Renvoisé et al. 2012). To our best knowledge, we present the first data on body and skull size changes of *M. agrestis* in the Baltic countries.

We found that size reduction in *M. agrestis* was better pronounced in Estonia, where 23 out of 27 adjusted body and skull characters decreased by up to 21.9% (average decrease was 13.6%). Against this, tail length and hind foot length significantly increased and, in the skull, the maximum height of mandibula, excluding coronoid process and coronoid height of mandibula increased by 21.9% and 16.9% accordingly.

In the voles from Lithuania, size change was not unambiguous. Significant were a 6.1% decrease in adjusted body length, an 11.6% decrease in adjusted length of the braincase, a 2.9% in condylobasal skull length and 2.2% in the height of the braincase. A decrease of 3.85% in the breadth of braincase, measured at the widest part, was not significant. Significant increases were found in total length of mandibula at *processus articularis*, excluding incisors, maximum height of mandibular (excluding coronoid process), coronoid height of mandibular, length of mandibular tooth row, length of lower molar M_1, length of maxillary toothrow and length of upper molar M^1. The maximum height of mandibula, excluding coronoid
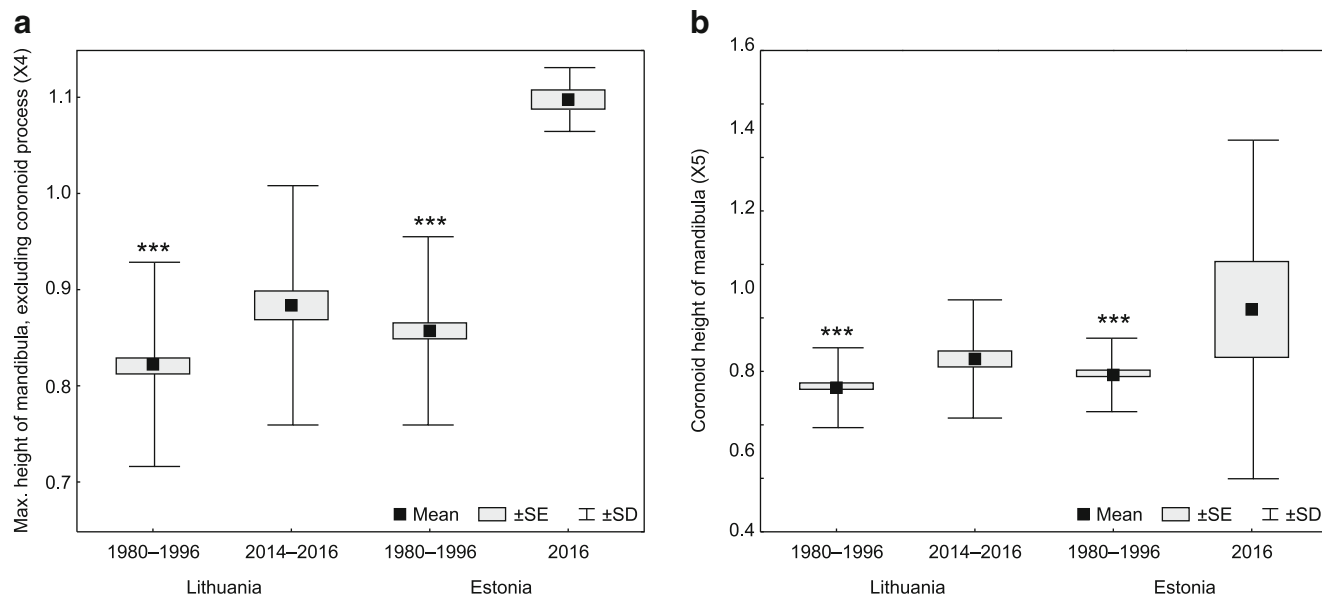
Fig. 5 Increase in adjusted skull measurements of *M. agrestis* in Lithuania and Estonia between the periods 1980–1996 and 2014–2016: a – maximum height of mandibula, excluding coronoid process, b – coronoid height of mandibula. Significance of difference in means between periods in the country: *** – $p < 0.001$, ** – $p < 0.01$

process, and coronoid height of mandibula increased in Lithuanian individuals by 8.4% and 7.0% respectively. Thus, changes were heterogeneous – alongside a reduction of skull length and braincase measurements, an increase in the facial part occurred, especially in mandibular measurements. The body condition factor of Lithuanian *M. agrestis* significantly increased by 6%.

Concluding, voles in Estonia became significantly smaller in body and skull size, while observed changes in Lithuania included decreasing body length (subsequently increasing body condition) and changing skull shape. According to Pergams and Lawler (2009), these changes do not all corroborate or contradict Allen's rule, nor do they correspond to Bergmann's rule.

In some investigations, changes of character size were also found in small rodents. Rapid morphological changes were found in rodents in 20 museum series collected on four continents – trends included both increases and decreases in the 15 investigated morphological traits, with size increases documented slightly more frequently (Pergams and Lawler 2009). For example, 9 of 15 compared measurements significantly differed between samples of white-footed mice (*Peromyscus leucopus* (Rafinesque, 1818)) from 1903 to 1976 and 2001–2003: mice became longer in total length, with broader, longer noses, and longer but shallower skulls (Pergams and Lacy 2008). During the twentieth century, the greatest length of skull and zygomatic breadth increased in Japanese field mouse (*Apodemus speciosus* (Temminck, 1844)), while the interorbital region and the length of the upper cheek teeth row slightly increased in Pratt's vole (*Eothenomys smithii* (Thomas, 1905)) (Yom-Tov and Yom-Tov 2004). Rapid

changes in skull morphometry also occurred in yellow-necked mice (*Apodemus flavicollis* (Melchior, 1834)) and bank voles (*Myodes glareolus* (Schreber, 1780)) inhabiting a colony of the great cormorants (*Phalacrocorax carbo* (Linnaeus, 1758)) in west Lithuania. Skulls in both species generally became longer, with the change taking just 25 years from the establishment of the colony in 1989. We hypothesized that altered skull morphometric features enhanced the ability of the species to survive in the specific conditions (Balčiauskienė et al. 2015).

Though it has been stated that variations in body size may evolve within a few years (Lomolino and Perault 2007; Yom-Tov and Geffen 2011), only a few recorded rates of changes have been so fast – increases in ear length in the northwestern San Diego pocket mouse (*Chaetodipus fallax fallax* (Merriam, 1889)) reached 0.63%/year, while the increase of zygomatic breadth in *P. leucopus* 0.58%/year. The greatest recorded negative changes reported are in black-footed brown lemming (*Lemmus trimucronatus* (Kerr, 1792)) from Alaska – 0.56%/year in tail length and 0.35%/year in hind foot length (Pergams and Lawler 2009). We recorded similar maximum increase and decrease rates for *M. agrestis* in Estonia, while the rates of changes in Lithuania were much lower.

There maybe many factors influencing body and skull size, these working simultaneously or independently, including changes of genotype (Bonnet et al. 2017; Kruuk 2017), migrations and environmental changes (Caumul and Polly 2005; Pergams and Lawler 2009), local environment (Millien et al. 2006) and habitat fragmentation (Schmidt and Jensen 2003; Lomolino and Perault 2007) and agricultural activities (Jánová et al. 2008). Changes in temperature, simultaneously

Table 2 Adjusted body and skull measurements of *M. agrestis* from Lithuania and Estonia, and their changes between the periods of 1980–1996 and 2014–2016

Character (mm) [a]	Estonia			Lithuania		
	Mean 1980–1996	Mean 2014–2016	Change, %[b]	Mean 1980–1996	Mean 2014–2016	Change, %
L	3.65	3.63	−0.69	3.59	3.39	−6.10
C	1.04	1.07	2.94	1.04	1.06	1.62
P	0.64	0.60	−6.00	0.61	0.65	6.05
A	0.42	0.43	3.70	0.43	0.43	−0.73
X1	2.24	1.95	−14.89	2.15	2.23	3.47
X2	2.19	1.94	−12.81	2.14	2.19	2.27
X3	0.93	0.79	−18.08	0.89	0.92	2.99
X4	0.86	1.10	21.90	0.82	0.88	7.02
X5	0.79	0.95	16.87	0.76	0.82	8.40
X6	0.61	0.50	−20.16	0.59	0.58	−0.88
X7	0.93	0.78	−18.03	0.88	0.92	4.39
X8	0.48	0.40	−19.26	0.46	0.47	3.47
X9	1.03	0.88	−16.62	1.04	1.04	0.54
X10	1.77	1.58	−12.53	1.74	1.68	−3.85
X11	2.32	2.08	−11.57	2.24	2.25	0.32
X12	1.17	1.04	−12.47	1.17	1.15	−1.76
X13	1.43	1.30	−10.34	1.38	1.38	0.40
X14	0.75	0.67	−12.25	0.74	0.75	0.59
X15	1.06	0.90	−17.84	1.02	1.05	3.26
X16	0.35	0.31	−11.88	0.35	0.36	3.79
X17	0.46	0.41	−9.81	0.45	0.45	1.05
X18	4.06	3.86	−5.15	4.06	3.94	−2.92
X19	2.48	2.18	−13.93	2.43	2.45	0.78
X20	1.59	1.50	−5.63	1.59	1.42	−11.59
X21	0.78	0.68	−13.77	0.76	0.78	2.50
X22	0.58	0.48	−21.87	0.56	0.58	3.40
X23	1.52	1.43	−6.55	1.56	1.53	−2.19

[a] abbreviations for characters are explained in Material and methods section

[b] in percentage, decrease shown as a negative number, increase as a positive number

affecting the food basis, is frequently reported as the main factor, relating it to global climate change (Van Buskirk et al. 2010; Yom-Tov and Geffen 2011 and references therein). The decline in size in recent decades is frequently linked to Bergmann's rule and climate warming. However, according McNab (2010), "the tendency of mammals to increase or decrease body size geographically and temporally depends on the abundance, availability and size of resources" and this is the so-called "resource rule". It was shown that diet can affect skull and dental form in mammals (Myers et al. 1996; Caumul and Polly 2005).

With regard to the complex relationships between the factors responsible for body/skull size changes in mammals, we cannot so far fully explain the driving forces of the observed changes in *M. agrestis* size. However, in analogy with another species of the same genus, root vole (*Microtus oeconomus* (Pallas, 1776)), changes in the habitat structure in the post-Soviet countries, coupled with climate warming (Balčiauskas et al. 2010), may not be excluded. Despite this limitation, we demonstrated rapid size change in the more northern population of *M. agrestis,* occurring simultaneously with decreased body condition. In the more southern population, body condition increased, confirming better adaptation to the changing environment and, consequently, feeding conditions. In both countries, changes of dental, toothrow length and height of mandible prove changes of food resources.

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