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CRANIAL GROWTH OF CAPTIVE BRED BANK VOLES (*CLETHRIONOMYS GLAREOLUS*)

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Abstract. The cranial growth of *C. glareolus* was investigated using 444 captive bred individuals, aged from 5 to 680 days. Three growth patterns of skull characters were found: (1) rapid growth in the first decade of age, followed by a very slow change or stabilisation (width of molar M_1 and length of maxillary tooth row), (2) long period of flat growth (length of mandibular tooth row and length of mandibular diastema), and (3) long period of initial growth followed by the plateau phase (length of *nasalia* and length of *foramen incisivum*). The measurements of skull characters correlated best with body weight, whereas correlations with body length or individual age were less expressed. Out of 20 skull characters tested, the strongest correlation with animal age and body weight was observed in the length of cranial (upper) diastema. Other characters, which correlated with animal age, were the length of *nasalia* and the length of molar M_1. In captive bred individuals, fluctuations of body weight and skull measurements were quite variable, especially in older animals aged one year or more.
Key words: captive bred bank vole, growth, skull

Introduction

The bank vole (*Clethrionomys glareolus*) is among the main prey species of myophagous birds. For example, the food of the Tawny Owl (*Strix aluco*) in the breeding period in Lithuania comprises on average 25.2% of *C. glareolus* by numbers and 19.7% by biomass consumed (Balčiauskienė 2006). In different districts of Lithuania, these figures range from 12.1% to 29.8% by numbers and from 7.9% to 24.9% by biomass consumed (Balčiauskienė *et al*. 2000–2001, 2005; Balčiauskienė & Naruševičius 2006). From the content of *S. aluco* pellets, collected year-round in eight districts of Lithuania, we concluded that predation on the *C. glareolus* was even more expressed: 34.4% by numbers and 27.6% by biomass consumed (Balčiauskienė *et al*. 2006).

In the studies on the feeding ecology of myophagous birds, there were attempts to identify age groups or the size of individuals preyed on (Marti & Hogue 1979; Goszczynski 1977, 1981; Skierczyński 2003). Very few papers were devoted to investigations into small mammal species age/weight predictions from cranial measurements in prey remains (Pagels & Blem 1984; Dickman *et al*. 1991; Blem *et al*. 1993). Even the measurements of teeth may be sufficient for the identification of *C. glareolus* age group from remains of individuals preyed by the pine marten (*Martes martes*) and *S. aluco* (Zalewski 1996).

In Lithuania, age related studies on craniometry of *C. glareolus* are absent. The use of captive bred small mammals provides reference of their exact age (up to a day) and birth time. These data allowed to construct growth curves for all measured skull characters and also to define the limit for outsorting young animals from the whole set. In animals trapped from the wild we distinguished only three age categories. Therefore data from captive bred *C. glareolus* were the base for this analysis.

The aim of the present publication is to describe the growth dynamics of cranial characters, and correlations of cranial characters with body weight, length, and age in captive bred *C. glareolus*.

Material and methods

The cranial growth of *C. glareolus* was investigated using captive bred individuals. Voles were grown at the Institute of Ecology of Vilnius University (at that time, Institute of Zoology and Parasitology) in 1971–1974, under the supervision of Stasė Maldžiūnaitė. Four hundred forty four individuals aged from 5 to 680 days were kept in 60 × 120 cm therariums, with four 20 × 20 × 15 cm boxes, 2 motion wheels, and some refuges in each. Temperature was kept in the range of 10–26.5°C in summer and 9–20°C in winter. Food and water were provided *ad libitum* (Maldžiūnaitė 1976).

Skulls were prepared using the boiling procedure and mechanical hand cleaning. Unfortunately, no more information is available on this experiment.

Measurements of skull characters were taken under a binocular with a micrometric eyepiece with an accuracy of up to 0.1 mm. We measured the characters of the right set of skulls; the left set was measured only in a few cases, when skulls were damaged. The following skull characters (11 mandibular and 9 maxillary) of *C. glareolus* were used in our analysis (Fig. 1): X_1 – total length of mandibula at *processus articularis*, excluding incisors; X_2 – length of mandibula, excluding incisors; X_3 – height of mandibula at, and including, first molar; X_4 – maximum height of mandibula, excluding coronoid process; X_5 – coronoid height of mandibula; X_6 – length of mandibular diastema; X_7 – length of mandibular tooth row; X_8 – length of molar M_1 (Fig. 1F right); X_9 – length of molar M_2 (Fig. 1F right); X_{10} – length of molar M_3 (Fig. 1F right); X_{11} – width of molar M_1 (Fig. 1F right); X^{12} – length of *nasalia*; X^{13} – breadth of braincase, measured in the widest part; X^{14} – zygomatic skull width; X^{15} – length of cranial (upper) diastema; X^{16} – zygomatic arc length; X^{17} – length of *foramen incisivum*; X^{18} – length of maxillary toot row; X^{19} – length of molar M^1 (Fig. 1F left); X^{20} – incisor width across both upper incisors.

The length of mandibular and the length of maxillary tooth rows were measured as the distance from the anterior edge of the alveolus of the first molar to the posterior edge of the alveolus of the third molar.

A standard statistical approach (mean and standard error, range, and Student *t*-test for the comparison of means) was used. Box and whisker plots for all abovementioned variables were produced in Statistica for Windows ver. 6.0 (StatSoft 2004). Having realised that box and whisker plots were too crowded for easy understanding (see Fig. 6), smoothed line graphs were redrawn (Figs 2–5), using averaged character measurements for age groups arranged in decades (0–9, 10–19 days and so on).

Results

Due to unequal retention of cranial characters, 444 captive bred *C. glareolus* skulls yielded various numbers of measurements: from 248 for the coronoid height of mandibula (X_5) to 433 for the length of molar M_1 (X_8), – length of molar M_2 (X_9) – and width of molar M_1 (X_{11}). Average values of all measurements are given in Table 1. Most of the characters were sex-dependent (i.e., male-female differences were statistically significant).

Cranial characters quite strongly correlated with body weight and body length; but with age, to a lesser extent (Table 2). We found sex-related differences in correlation with skull characters, but the differences were not analysed in detail. Skull characters, the growth of which had the greatest correlation with animal age (length of *nasalia,* length of cranial (upper) diastema, length of molar M_1), were not all the same, which correlated best with body weight (zygomatic skull width, length of cranial (upper) diastema, and maximum height of mandibula, excluding coronoid process). Generally,

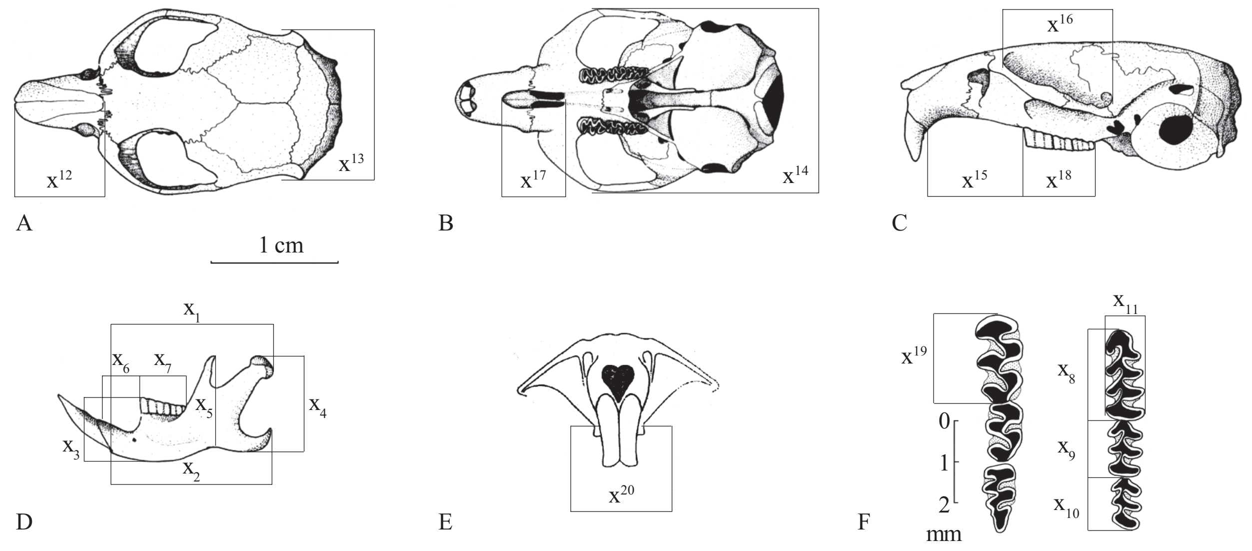

Figure 1. Skull measurements taken in rodents (*Clethrionomys glareolus* shown): A – dorsal view, B – ventral view, C – lateral view, D – mandible, E, F – tooth measurements (Lidicker & MacLean 1969; Niethammer & Krapp 1982).

Table 1. Average values (in mm) of mandibular and maxillary characters in captive bred *C. glareolus*, and significance of male-female differences (M–F).

	Total			Males		Females		M–F, *p*
	Avg ± SE	N	Min–max	Avg ± SE	Min–max	Avg ± SE	Min–max	
X_1	11.59 ± 0.03	423	8.9–13.3	11.73 ± 0.04	9.8–13.3	11.47 ± 0.05	8.9–13.2	<0.001
X_2	10.59 ± 0.03	402	8.4–12.0	10.68 ± 0.04	8.9–12.0	10.50 ± 0.05	8.4–12.0	<0.005
X_3	4.56 ± 0.01	430	2.8–5.7	4.60 ± 0.02	2.8–5.7	4.52 ± 0.02	3.2–5.2	<0.05
X_4	6.12 ± 0.03	405	4.0–7.3	6.22 ± 0.04	4.0–7.3	6.02 ± 0.04	4.0–7.3	<0.001
X_5	5.99 ± 0.03	248	3.9–7.0	6.07 ± 0.03	4.9–7.0	5.91 ± 0.04	3.9–6.8	<0.005
X_6	3.09 ± 0.01	427	2.8–3.4	3.11 ± 0.01	2.8–3.4	3.08 ± 0.01	2.8–3.4	<0.05
X_7	4.87 ± 0.01	429	4.3–5.3	4.89 ± 0.01	4.4–5.3	4.86 ± 0.01	4.3–5.3	NS
X_8	2.11 ± 0.01	433	1.7–2.4	2.12 ± 0.01	1.7–2.4	2.10 ± 0.01	1.7–2.4	NS
X_9	1.30 ± 0.003	433	1.0–1.5	1.30 ± 0.00	1.0–1.5	1.29 ± 0.00	1.1–1.5	NS
X_{10}	1.21 ± 0.004	428	1.0–1.5	1.22 ± 0.01	1.0–1.4	1.20 ± 0.01	1.0–1.5	<0.05
X_{11}	0.93 ± 0.003	433	0.6–1.1	0.94 ± 0.00	0.6–1.1	0.93 ± 0.00	0.8–1.1	NS
X^{12}	6.29 ± 0.02	368	4.0–7.6	6.35 ± 0.03	5.1–7.2	6.24 ± 0.03	4.0–7.6	<0.05
X^{13}	10.60 ± 0.02	404	9.6–12.5	10.62 ± 0.02	9.6–11.5	10.59 ± 0.02	9.8–12.5	NS
X^{14}	12.14 ± 0.05	350	9.5–14.5	12.30 ± 0.06	9.6–14.1	11.99 ± 0.07	9.5–14.5	<0.001
X^{15}	6.26 ± 0.03	424	4.0–7.4	6.37 ± 0.03	4.6–7.4	6.16 ± 0.04	4.0–7.4	<0.001
X^{16}	7.28 ± 0.02	396	5.9–8.3	7.35 ± 0.03	5.9–8.3	7.22 ± 0.03	6.3–8.3	<0.001
X^{17}	4.21 ± 0.02	354	2.7–5.2	4.28 ± 0.03	3.0–4.9	4.16 ± 0.03	2.7–5.2	<0.005
X^{18}	5.06 ± 0.01	426	4.1–5.5	5.08 ± 0.01	4.5–5.5	5.04 ± 0.01	4.1–5.5	<0.05
X^{19}	1.83 ± 0.004	429	1.6–2.1	1.84 ± 0.01	1.7–2.1	1.82 ± 0.01	1.6–2.0	<0.05
X^{20}	2.32 ± 0.01	417	1.8–2.9	2.35 ± 0.01	1.9–2.8	2.31 ± 0.01	1.8–2.9	<0.001

Table 2. Correlations of cranial characters with body weight, length, and age (in days) of captive bred *C. glareolus*; all coefficients are significant at $p < 0.001$.

	Body weight	Body length	Age
X_1	0.678 (N = 415)	0.641 (N = 117)	0.621 (N = 423)
X_2	0.681 (N = 395)	0.652 (N = 108)	0.571 (N = 402)
X_3	0.665 (N = 422)	0.578 (N = 117)	0.467 (N = 430)
X_4	0.739 (N = 398)	0.667 (N = 109)	0.646 (N = 405)
X_5	0.666 (N = 244)	0.576 (N = 61)	0.582 (N = 248)
X_6	0.489 (N = 419)	0.571 (N = 117)	0.450 (N = 427)
X_7	0.501 (N = 421)	0.429 (N = 117)	0.464 (N = 429)
X_8	0.640 (N = 425)	0.688 (N = 118)	0.736 (N = 433)
X_9	0.400 (N = 425)	0.444 (N = 118)	0.402 (N = 433)
X_{10}	0.398 (N = 420)	0.396 (N = 117)	0.404 (N = 428)
X_{11}	0.464 (N = 425)	0.590 (N = 118)	0.483 (N = 433)
X^{12}	0.698 (N = 364)	0.659 (N = 103)	0.772 (N = 368)
X^{13}	0.554 (N = 399)	0.477 (N = 113)	0.340 (N = 404)
X^{14}	0.817 (N = 345)	0.661 (N = 97)	0.714 (N = 350)
X^{15}	0.791 (N = 419)	0.722 (N = 113)	0.766 (N = 424)
X^{16}	0.640 (N = 391)	0.621 (N = 109)	0.564 (N = 396)
X^{17}	0.732 (N = 350)	0.673 (N = 100)	0.720 (N = 354)
X^{18}	0.504 (N = 421)	0.484 (N = 114)	0.426 (N = 426)
X^{19}	0.550 (N = 424)	0.351 (N = 114)	0.579 (N = 429)
X^{20}	0.593 (N = 412)	0.471 (N = 110)	0.591 (N = 417)

correlations of skull characters with body length were weaker than those with body weight (Table 2).

Intensive growth of body weight in captive bred *C. glareolus* occurred in the first 50 days of life, reaching ca. 18 g, then it stabilised until the age of about 4 months. Afterwards body weight increased again, and *C. glareolus* of 7–12 months age were weighing ca. 25–28 g. Body length grew up for about 2 months up to 90 mm, and since then fluctuated (Fig. 2).

We found different growth patterns in skull characters. The first pattern – rapid growth for a very short period (in the first decade of life only), followed by a very slow change or even stabilisation – was characteristic of the width of molar M_1 and the length of maxillary tooth row (Fig. 3). The stabilisation period took about one year or longer.

The second pattern is characterised by the opposite peculiarity – a long period of growth, which was of various rate in the beginning, but not very rapid in general. This growth pattern was inherent in several characters: length of mandibular tooth row, length of mandibular diastema, length of molars M_1 and M_3, and length of molar M^1 (Fig. 4).

The third pattern may be defined as intermediate between the first two: it was characterised by a long period of initial growth:

50–60 days for the height of mandibula at, and including, first molar,

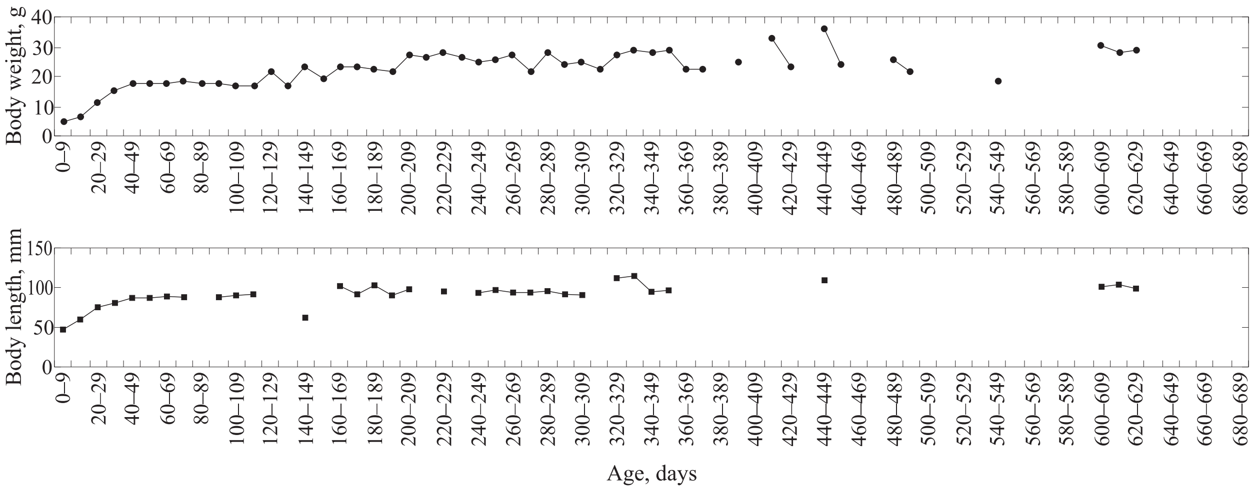

Figure 2. Dynamics of body weight and body length in captive bred *C. glareolus*.

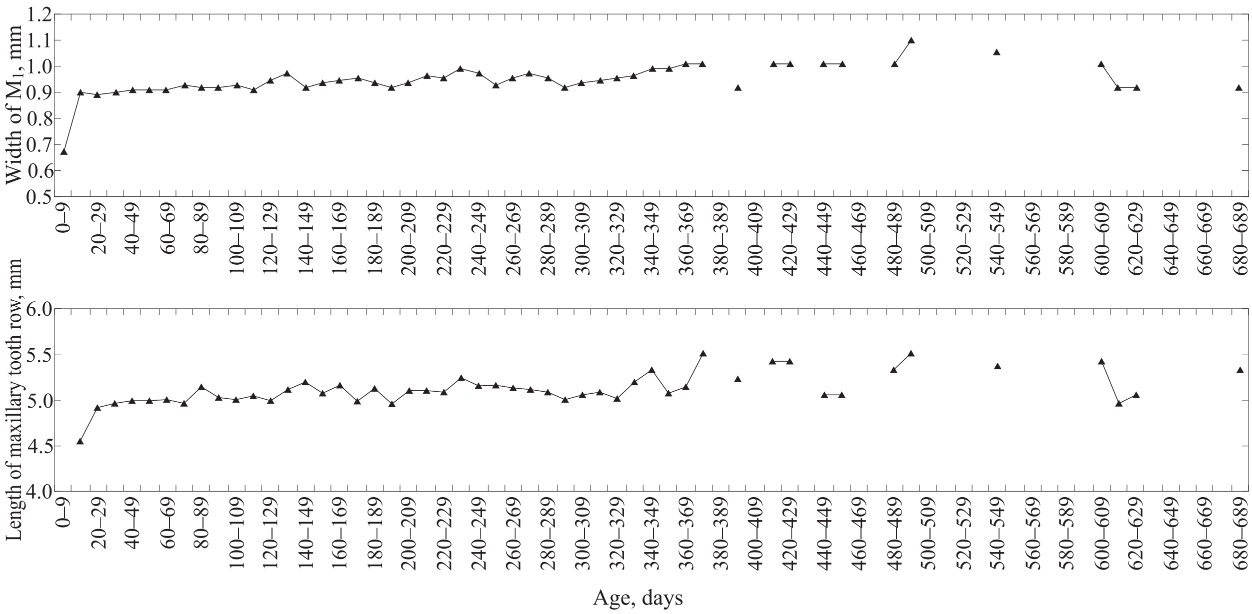

Figure 3. Dynamics of the width of molar M_1 and the length of maxillary tooth row in captive bred *C. glareolus*.

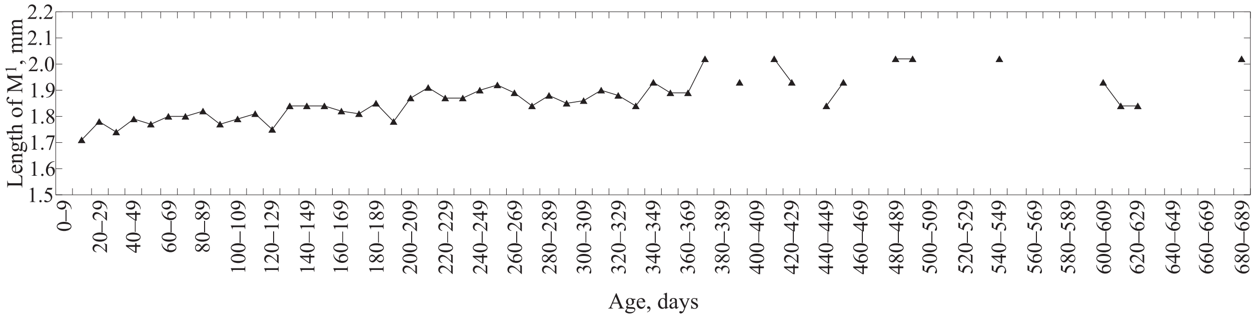

Figure 4. Dynamics of the length of molar M^1 in captive bred *C. glareolus*.

60–70 days for the total length of mandibula at *processus articularis*, excluding incisors, length of mandibula, excluding incisors, maximum height of mandibula, excluding coronoid process, coronoid height of mandibula,
70–80 days for the length of *nasalia*, breadth of braincase, measured in the widest part, length of cranial (upper) diastema,
80–90 days for zygomatic arc length,
90–100 days for the length of *foramen incisivum*.
After such initial period, a plateau phase occurred, taking the period up to 120–140 days of age (length of mandibula, excluding incisors, maximum height of mandibula, excluding coronoid process, or coronoid height of mandibula, Fig. 5) or up to one year of age (e.g., height of mandibula at, and including, first molar, breadth of braincase, measured in the widest part, total length of mandibula at *processus articularis*, excluding incisors), or the growth was very slow without a plateau (length of *nasalia*, Fig. 5, zygomatic arc length, length of *foramen incisivum*, or length of cranial (upper) diastema).

Discussion

Very high variability of body weight in *C. glareolus*, with amplitude of up to 240% in adult captive bred animals and up to 200% in animals living in the wild, has been found (Bashenina 1981). According to Bashenina (1981), a rapid growth of body weight slows down already at the age of one month, and such slow rate of growth continues up to the age of 5–6 months. She also stated that the growth dynamics of body weight was the same both in captive bred voles and in wild ones. Bashenina's (1981) data differ from the data of other authors. For example, Zejda (1971) states that various cohorts of *C. glareolus* exhibit different growth curves of body weight and body length, and that even minimum values of body length and body weight decrease during winter. Winter field samples of *C. glareolus*, starting from December, show that non-overcrowded populations have a much higher variation of body weight than overcrowded populations (Zejda 1964).

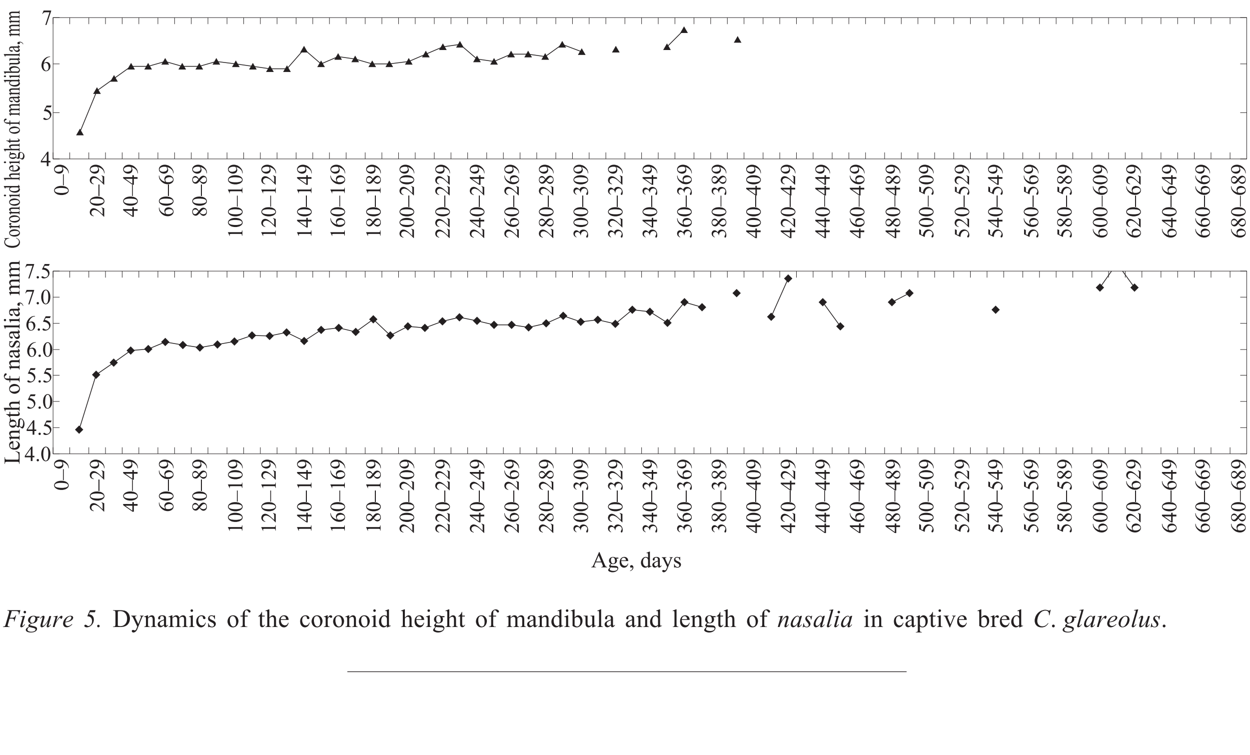

Figure 5. Dynamics of the coronoid height of mandibula and length of *nasalia* in captive bred *C. glareolus*.

Our data on the growth of body weight do not confirm Bashenina's (1981) statement either. A rapid growth of body weight was observed up to 1.5 months of age, reaching then ca. 17 g; and since then it stopped until ca. 4 months of age. The body length of these animals was reached up to 88–90 mm (Fig. 2). In older *C. glareolus*, fluctuations of body weight and length were observed.

Some of laboratory grown specimens that we used for analysis had measurements evidently smaller than the averages of the given age groups. It was because in some cases laboratory conditions had a strong inhibiting effect on the development and growth of animals. On the other hand, there were also animals, which exceeded their mates, especially in body weight (Fig. 6). Irregularities of growth, especially in captive grown animals, were discussed by different authors. For example, Gebczyńska (1964) found that some short-tailed vole (*Microtus agrestis*) specimens had considerably longer skulls – so great condylobasal lengths were not found in any other age group. The facts that *M. agrestis* kept in the laboratory are of larger measurements and live longer than those under field conditions are undoubtedly brought about by advantageous food conditions, being free from predators, etc. Larger measurements and faster development of angularity also indicate that the animal does not grow in the same manner in the laboratory as in the field.

We found that in captive bred individuals, fluctuations of body weight and skull measurements are quite variable, especially in older animals, aged one year or more. On the other hand, individuals of such old age are very rare among free living *C. glareolus*.

It is known that generally high growth rates are characteristic of spring-born cohorts of voles; this was also true for common voles (*Microtus arvalis*) grown in captivity in the same experiment as *C. glareolus* (Maldžiūnaitė 1976). In our study we were interested in the cranial growth of voles independently of their birth season, thus, sub-sampling procedure was not employed for the growth data.

As to *C. glareolus*, field trapped in Lithuania, the length of their tooth rows was significantly shorter in young animals, with no differences between adult and subadult voles. Distribution of the length of maxillary and mandibular tooth rows according to body weight and body length was without expressed regularities. Correlations of these characters with body weight and body

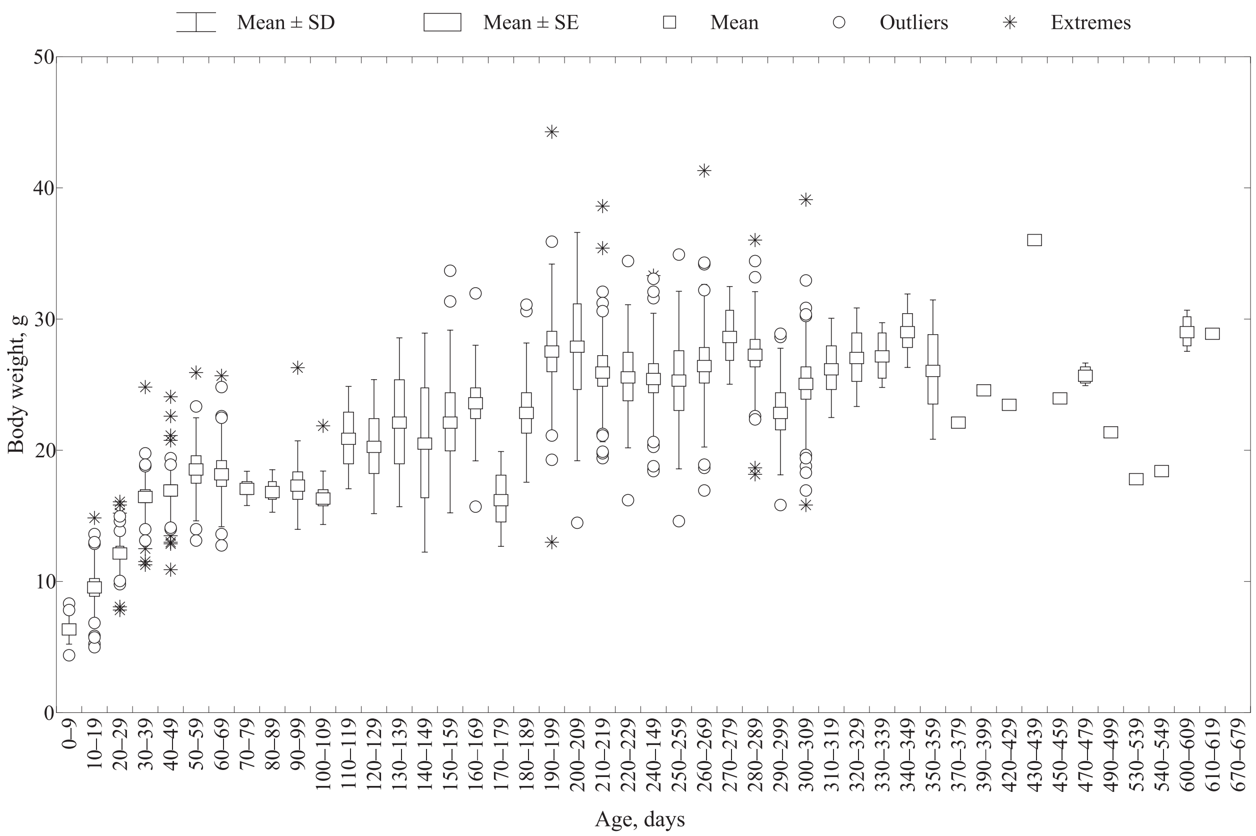

Figure 6. Dynamics of body weight in captive bred *C. glareolus*, showing that some specimens are characterised by much slower or faster growth (marked as extremes).

length were also weak (Balčiauskienė *et al*. 2004). In captive bred *C. glareolus*, correlation coefficients of the lengths of maxillary and mandibular tooth rows with animal age, body weight, and body length did not exceed r = 0.50 (Table 2), and thus, corresponded to what we observed in wild voles.

Conclusions

Three growth patterns of skull characters were found in captivity bred *C. glareolus*.

Measurements of skull characters correlated best with body weight; correlations with body length or individual age were less expressed.

The length of cranial (upper) diastema correlated best with age and body weight. Other characters, which correlated with animal age, were the length of *nasalia* and the length of molar M_1.

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NELAISVĖJE AUGINTŲ RUDŲJŲ PELĖNŲ (*CLETHRIONOMYS GLAREOLUS*) KAUKOLĖS AUGIMAS

L. Balčiauskienė

SANTRAUKA

Kraniometriniam rudųjų pelėnų (*Clethrionomys glareolus*) tyrimui panaudota 444 nelaisvėje užaugintų individų (5–680 dienų amžiaus) kaukolių kolekcija, kurią 1971–1974 metais surinko S. Maldžiūnaitė. Išaiškinti trejopi kaukolės augimo dėsningumai: (1) greitas augimas pirmąjį amžiaus dešimtadienį ir labai lėtas augimas arba jo vėlesnė stabilizacija (būdinga M_1 danties pločiui ir viršutinės dantų eilės ilgiui), (2) ilgas ir lėtas augimas (būdingas apatinio žandikaulio dantų eilės bei apatinės diastemos ilgiui) ir (3) ilgas pradinio augimo periodas, trunkantis 50–100 dienų, ir po jo sekanti plato fazė (pvz. nosikaulių arba kandžių angų ilgiai). Kaukolės matmenys labiau koreliavo su kūno svoriu, mažiau – su kūno ilgiu ir amžiumi. Su svoriu ir amžiumi geriausiai koreliavo viršutinės diastemos ilgis. Nelaisvėje laikytų rudųjų pelėnų augimo netolygumai labiausiai pasireiškė vyresniems nei vienerių metų amžiaus individams.

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