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Applicability of cranial features for the calculation of vole body mass

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While the non-random capture of prey by predators is well-known, few studies have investigated or compared the individual characteristics of prey selected by predators. This is due to the difficulty in assessing prey features based on the remains from pellets or faeces. This article shows relationships between craniometric features and body mass of the root vole (*Microtus oeconomus*). The comparisons involved 10 skull parameters: mandible length excluding incisors (ML), rostrum breadth (RB), mandibular tooth-row length (MT), *foramina incisiva* length (FI), upper- and lower-incisor lengths (UIL, LIL), upper- and lower-incisor breadths (UIB, LIB), upper- and lower-incisor weights (UIW, LIW). From cranial parameters listed above, only UIL was correlated with body mass with high accurancy. In this reason we highly recommended this parameter as a good indicator for calculating vole body mass.

Introduction

Predator–prey relationship is one of the central issues in ecology (e.g. Schoener 1971, Korpimäki & Norrdahl 1991, Sih *et al*. 1998). Accurate estimates of predator diets are required to understand e.g. food web structures and the role of predation in prey population dynamics. Predator diets can be estimated directly and indirectly. Direct methods are limited to occasions when direct observations of feeding by predators are possible and, consequently, can only be used for selected carnivorous species (e.g. lions, wolves). Indirect methods, based on the recovery of non-digested prey structures, are used most often in the reconstruction of predator diets (e.g. Goszczyński 1977, Pearson 1985, Longland & Jenkins 1987, Jędrzejewska & Jędrzejewski 1998).

The impact of predators on prey populations is usually estimated by comparing the number of predators in the area with the number of individuals from the prey population consumed within a given period. Usually, when calculating the share of biomass that a particular prey species accounts for in a predator's diet, mean prey body mass is used in the calculation (e.g. Andersson & Erlinge 1977, Jędrzejewska & Jędrzejewski 1998). However, predators do not kill prey with a mean body mass only. On the one hand, according to the assumptions of optimal foraging theory, predators should maximize net energy intake by capturing larger rather than smaller individuals (Krebs 1978). On the other hand, many studies have shown that small prey individuals are more vulnerable to predation than larger ones (e.g. Halle 1988, Blem *et al*. 1993, Mappes *et al*. 1993, Koivunen *et al*. 1998, Trejo & Guthman 2003). It seems that prey selection by predators is primarily limited by the probability of encounter between predator and prey (Temple 1987, Juanes 1994).

The non-random selection of prey by small rodent-eating predators is a result of the following factors: hunting habitat selection, differences in hunting strategies, prey status, habitat familiarity by prey and behavioural differences between prey individuals (Dickman *et al*. 1991, Metzgar 1967, Koivunen *et al*. 1998, Ims & Andreassen 2000, Trejo & Guthmann 2003). Predators selectively kill individuals in relation to their sex, body mass/age, activity, condition (nutritional status) and microhabitat use (Longland & Jenkins 1987, Dickman *et al*. 1991, Dickman 1992, Mappes *et al*. 1993, Murray 2002, Zalewski 1996, Ims & Andreassen 2000, Trejo & Guthmann 2003). Therefore, predator diet analyses should focus not only on recognized prey species but also on the differences among individuals within a prey species.

This paper describes a model relating selected craniometric features of skulls (possible to measure from prey remains) and the body mass of individuals of the root vole (*Microtus oeconomus*) — a prey often consumed by different predator species (Romanowski 1988, Jędrzejewska & Jędrzejewski 1998, Balčiauskienė *et al*. 2004).

Materials and methods

The research entailed measurements of 150 root voles caught in open marches near Barwik, in the lower basin of the River Biebrza, Biebrza National Park (ca. 53°N, 23°E). Animals were obtained from snap-traps, or found dead in live traps, in the summers (June–August) of 1996 and 1997, the autumns (October–November) of 1996, 1997 and 2002, and the winters (February) of 1996 and 1997. A total of 77 females and 73 males were captured (Table 1), weighed and sexed. In the laboratory, dead voles were decapitated, and their heads boiled before skin and muscle were removed. After several days of soaking in water the incisors were separable from the mandible and upper jaw. The skulls were then air-dried and characterized as described by Goszczyński (1977), Pagels and Blem (1984) and Canova *et al*. (1999), i.e. mandible length excluding incisors (ML), rostral breadth (RB), mandibular-toothrow length (MT), and the *foramina incisiva* length (FI) were measured. Six additional features were measured — i.e. upper-incisor length (UIL), lower-incisor length (LIL), upper-incisor breadth (UIB), lower-incisor breadth (LIB), lower-incisor weight (LIM), and upper-incisor weight (UIM) (Fig. 1).

Length measurements to the nearest 0.1 mm were made using an electronic slide calliper. Weights of teeth were determined on a laboratory balance to the nearest 0.1 g. In cases, when any bones were damaged during cleaning, we excluded these individuals from analysis. In case of the incisor length, mandible length, and toothrow length, the results are averages of measurements from the left- and right-hand sides.

We analyzed each cranial parameter using General Linear Models (GLM) with logarithmic link function and Gaussian error distribution specifications for the response variable; body mass. To find the best fitted relationship between craniometric features and body mass we used Akaike's Information Criterion (AIC) and then, for model evaluation, we used model's weight

Table. 1. Body mass (mean ± SD) of the root voles (*Microtus oeconomus*) caught in Biebrza National Park, Poland. n = sample size.

	Summer	Autumn	Winter
Male	35.0 ± 12.6 (n = 40)	29.2 ± 10.8 (n = 22)	26.8 ± 8.8 (n = 11)
Female	27.9 ± 9.57 (n = 42)	25.6 ± 5.1 (n = 21)	18.9 ± 4.9 (n = 14)
All voles	31.8 ± 11.8 (n = 82)	27.6 ± 9.0 (n = 43)	22.5 ± 7.8 (n = 25)

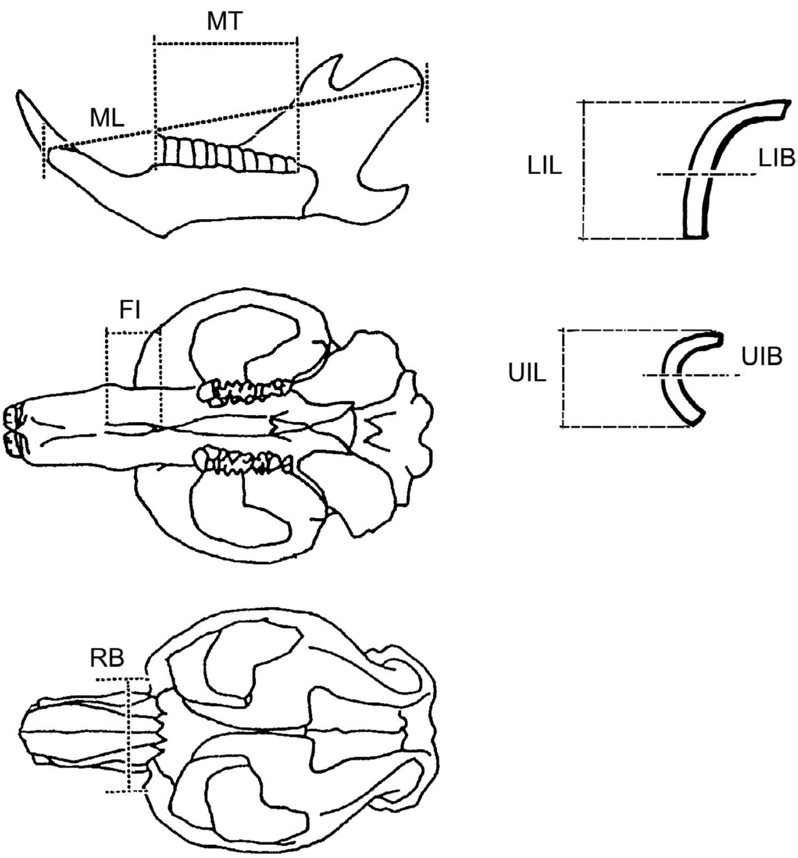

Fig. 1. Cranial measurements of *Microtus oeconomus* from Biebrza National Park, Poland. ML = mandible length excluding incrisors, MT = mandibular-toothrow length, FI = *foramina incisiva* length, RB = rostral breath, LIL = lower-incisor length, UIL = upper-incisor length, LIB = lower-incisor breadth, UIB = upper-incisor breadth.

(Burnham & Anderson 2002). The best models had the lowest AIC values and the highest weight (Johnson & Omland 2004). Relationships between body mass and cranial measurements are described with the models. All statistical analyses were carried out using the R statistical software (R Development Core Team 2005).

Results

From all 10 cranial parameters tested in this study, we evaluated four with the lowest AIC values (Table 2). Moreover, the results make it clear that these parameters vary non-linearly (exponential function) with body mass, hence may successfully be employed in estimating root vole's body mass. Comparing given features and body mass, it would appear that the most accurate estimate of body mass may arise from measurements of the upper-incisor length (UIL), AIC = 973.2, which precision (weight) is very high 0.99. Contrary to the UIL, the following three evaluated cranial parameters with the lowest AIC value (rostrum breadth (RB), AIC = 992.1, mandible length excluding incisors (ML), AIC = 996.9, and upper-incisor breadth (UIB), AIC = 1018.2) give us much lower accuracy in vole body mass prediction (Fig. 2). The distance between the best model (UIL) and subsequent model (RB) with the next lowest AIC value (ΔAIC) is relatively big and amounts to 18.89 (Table 2). This indicates, that the accuracy of vole body mass prediction based on UIL parameter is very high and amounts to 0.99 (Table 2).

Discussion

Our results clearly demonstrate, that from all 10 tested craniometric features the upper-incisor length (UIL) correlates best with the root vole body mass. This strong relationship between upper-incisor length and body mass of voles is explained by the fact, that rodents have teeth that never stop growing and heavier (older) voles should have proportionally longer incisors. In relation to our results UIL should be used for calculation of the root vole body mass from remains and for determination of prey selection by different predators. Usefulness of this parameter is particularly well visible, when we compare an accuracy of body mass prediction based on UIL with other craniometric parameters characterised with low AIC value, such as: rostrum breadth (RB), mandible length excluding incisors (ML) and upper-incisor breadth (UIB) (Table 2).

However, other studies showed a wide range of craniometric features highly correlated with small mammals body mass (e.g. Goszczyński 1977, Pagels & Blem 1984, Dickman *et al*. 1991, Blem *et al*. 1993, Canova *et al*. 1999, Trejo & Guthmann 2003, Balčiauskienė *et al*. 2004). In our opinion, differences in results between our study and studies described above, may result from differences in species and habitats (Sikorski 1982, Balčiauskienė *et al*. 2004). Moreover, the authors of cited studies did not calculate the relationship between UIL and body mass of small mammals. We have to be conscious that the applicability of craniometric features is strictly related to their presence in predators pellets and/or faces. Lack of information about UIL in earlier studies may suggest that this incisor preserved worse than other craniometric features. However, results obtained by Pokrzywka (2003) show, that UIL and ML were two best preserved root vole remains in long-eared owl pellets. Similarly, also study conducted by Zalewski (1996) show that UIL preserve well in the fox scats.

The limitation of the usage of craniometric features for calculation of body mass of prey eaten by predators is the fact that, the accuracy of this method strictly depends on the level of preservation of skull fragments. Our calculations presented here are based on complete prey remains (without any broken elements) and are very precise. Prey body mass estimates based on prey remains from predator faeces, stomach contents and spewings is less accurate. In some cases, when we are unable to calculate body mass based on UIL, we can use less precise parameter such as: mandible length (ML) as this is the most

Table 2. Summary of generalized linear models (GLM) of the relationship between cranial measurements and body mass of the root vole (*Microtus oeconomus*). Models with each one examined parameter are included in the set. The GLM used was with Gaussian error distribution and logarithmic link function. The models were ranked by Akaike's Information Criterion (AIC), cranial parameters with the lowest AIC value the best predict the body mass. Since number of parameters in the same in each model ranking by AIC is equivalent to that by residual deviance.

Cranial variables	Model	Deviance	AIC	ΔAIC	Weight	*F*
Upper-incisor length (UIL)	$y = \exp(0.34x + 0.0005)$	5744.5	973.2	0.00	9.99×10^{-1}	289.484
Rostral breadth (RB)	$y = \exp(-1.53x + 0.3)$	6521.1	992.1	18.89	7.89×10^{-5}	227.65
Mandible length excluding incisors (ML)	$y = \exp(0.25x + 0.51)$	6736.0	996.9	23.72	7.05×10^{-6}	225.64
Upper-incisor breadth(UIB)	$y = \exp(-0.15x + 0.76)$	7771.9	1018.2	45.04	1.66×10^{-10}	189.424
Lower-incisor weight (LIW)	$y = \exp(2.35x + 0.24)$	8469.3	1031.0	57.84	2.75×10^{-13}	141.391
Upper-incisorweight(UIW)	$y = \exp(3.31x + 0.19)$	9270.4	1044.5	71.31	3.28×10^{-16}	130.07
Lower-incisor length(LIL)	$y = \exp(3.24x + 0.31)$	9372.5	1046.1	72.94	1.45×10^{-16}	131.009
Lower-incisor breadth (LIB)	$y = \exp(3.32x + 0.15)$	11925.6	1082.0	108.84	2.32×10^{-24}	65.676
Mandibular-toothrow length (MT)	$y = \exp(-0.34x + 0.24)$	12384.5	1087.6	114.46	1.40×10^{-25}	58.304
Foramina incisiva lenght (FI)	$y = \exp(0.14x + 0.37)$	16265.7	1128.2	155.08	2.11×10^{-34}	10.319

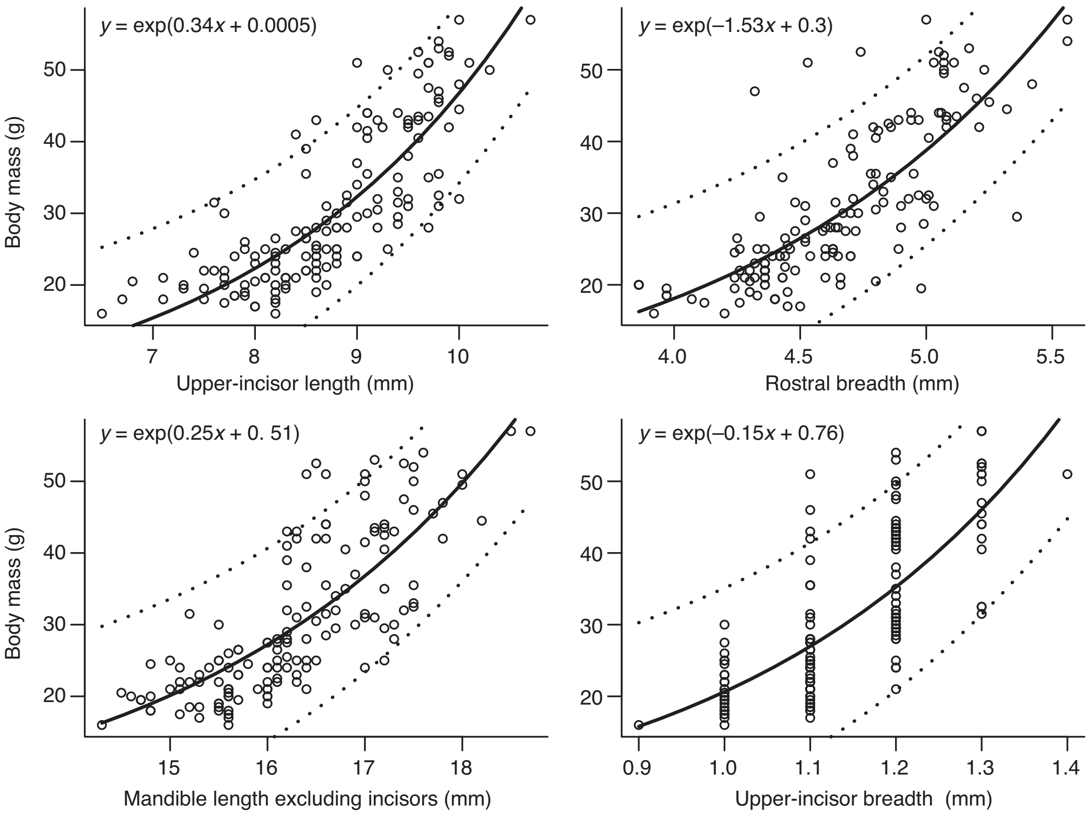

Fig. 2. Relationship between body mass and four cranial features that are, according to AIC, the best predictors of body mass. Dashed lines show 95% prediction intervals.

digestion-resistant part of prey (e.g. Raczynski & Ruprecht 1974, Goszczyński 1977, Blem *et al.* 1993, Zalewski 1996, Pokrzywka 2003).

Those planning to use the model presented here to assess the body mass of voles eaten by predators must be aware that such comparisons have limitations and are usually accompanied by a certain amount of error. It results from the fact that body mass of small mammals changes with social and environmental factors, whereas skull parameters do not change in a directional manner (Churchfield 1990, Canova *et al*. 1999). Furthermore, craniometric features may differ between individuals of a given species living in the same area but in different habitats (Sikorski 1982, Balčiauskienė *et al*. 2004). Notwithstanding these reservations, the comparisons made by Canova *et al*. (1999) show that the error reflecting the above factors is much smaller than that resulting from determinations of body mass on the basis of means taken from the literature. Despite the fact that the process of prey removal by predators is not random, usage of average or maximum adult body mass of prey from the literature is still a common method for the estimation of predator feeding habits (e.g. Marti 1976, Anderson & Erlinge 1977, Morris & Burgiss 1988, Yalden & Morris 1990, Jędrzejewska & Jędrzejewski 1998). Canova *et al*. 1999 showed that measured prey body mass and prey body mass taken from the literature may differ by more than 50%, which is why predator trophic niche overlap calculated using literature data may be overestimated (e.g. Jędrzejewska & Jędrzejewski 1998, Zalewski *et al*. 1995, Zalewski 1996).

Results from this study indicate that two tested cranial parameters (UIL and ML) are good and usefully indicators of body mass. Based on the formulas given here it is possible to calculate vole body mass even when only one tooth is available. Our study and data collected by other authors on different small mammal species

(Pucek & Zejda 1968, Janes & Barss 1985, Halle 1988, Dickman *et al*. 1991 and Canova *et al*. 1999) suggest that the relationship between cranial measurements and body mass is a common phenomenon among small mammals.

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