

1-1-2014

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BALCIAUSKAS, LINAS and BALCIAUSKIENE, LAIMA (2014) "Selective predation on common voles by Tawny Owls and Long-eared Owls in winter and spring," *Turkish Journal of Zoology*. Vol. 38: No. 2, Article 15. <https://doi.org/10.3906/zoo-1303-20>

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## Selective predation on common voles by Tawny Owls and Long-eared Owls in winter and spring

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Received: 14.03.2013 • Accepted: 08.12.2013 • Published Online: 17.01.2014 • Printed: 14.02.2014

**Abstract:** We studied size preferences of Tawny (*Strix aluco*) and Long-eared (*Asio otus*) Owls preying on common voles (*Microtus arvalis*) in the winter and spring seasons in Central Lithuania. Regression equations were used for body mass estimations. We found that both *A. otus* and *S. aluco* preferred larger *M. arvalis* than the average available in the population (the average body mass of predated individuals was  $21.45 \pm 0.12$  g compared to  $16.42 \pm 0.16$  g of snap-trapped individuals). Irrespective of the owl species, most of the predated *Microtus* voles were adults. In *S. aluco* prey, the winter proportion of young voles was significantly higher than in the prey of *A. otus*, 33.3% versus 5.2%. By contrast, the proportion of subadult and adult voles with a body mass in the range between 19 and 23 g was significantly higher in the prey of *A. otus*. Our results may indicate that the selection of the differently sized prey allows the 2 species of owls to coexist sympatrically.

**Key words:** Owl diet, prey size, diet selectivity, body mass prediction

### 1. Introduction

The process of nonrandom removal of rodents by predators depends on many physical and behavioural characteristics of both the predators and their prey (Zalewski, 1996; Bueno and Motta-Junior, 2008). Preferences for different sizes of prey are well known among raptorial birds. Age, sex, and body mass compositions of the different prey species may differ (Karell et al., 2010). Within a single prey taxon preference may be shown towards young or smaller individuals (Birrer, 2009), large or adult ones (Rocha et al., 2011), or to either of the sexes (Dickman et al., 1991; Taylor, 2009). Selection of “nonaverage” individuals depends on the predator and the prey: their behaviour, habitat selection, prey vigilance, prey condition, different probabilities of predator-prey encounter, season, etc. (Caro, 2005; Sunde et al., 2012).

Predicting body mass of small mammals preyed upon from the measurements of cranial or mandibular dimensions, some authors put emphasis on regressions based on mandibular characters while others showed the usefulness of the cranial characters (Pagels and Blem, 1984; Blem et al., 1993; Balčiauskienė, 2007).

The aim of this research was to evaluate the prey size preferences displayed by Tawny (*Strix aluco*) and Long-eared (*Asio otus*) Owls in regard to common vole (*Microtus arvalis* sensu lato) in the winter and spring periods. We

tested the hypothesis that predation is selective, i.e. that the size distribution of the prey differs from that in the population, and examined whether prey size depends on the predator species (generalist/specialist).

### 2. Materials and methods

The age and body mass distribution of common voles (*Microtus arvalis* sensu lato) was assessed from 573 individuals, snap-trapped in North-East Lithuania in the nonvegetative period (October to April) in 2005–2009. Snap trap lines (1–2 lines of 25 traps) were set to 3 days, baited with bread and oil (Balčiauskienė et al., 2009). Voles were weighed (with an accuracy of 0.1 g), then divided into 3 age categories: juveniles, subadults, 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).

Seventeen skull (8 mandibular and 9 cranial) characters were measured with an accuracy of 0.1 mm, under binoculars or with a digital calliper. According to Balčiauskas and Balčiauskienė (2011), these characters were:  $X_1$  – total length of mandibula at *processus articularis*, excluding incisors;  $X_2$  – length of mandibula, excluding incisors;  $X_3$  – height of mandibula, 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

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row;  $X_8$  – length of lower molar  $M_1$ ;  $X^9$  – length of *nasalia*;  $X^{10}$  – breadth of braincase, measured at the widest part;  $X^{11}$  – zygomatic skull width;  $X^{12}$  – length of cranial (upper) diastema;  $X^{13}$  – zygomatic arc length;  $X^{14}$  – length of *foramen incisivum*;  $X^{15}$  – length of maxillary toothrow;  $X^{16}$  – length of upper molar  $M^1$ ;  $X^{17}$  – incisor width across both upper incisors.

Regression coefficients were calculated from *M. arvalis* specimens trapped in 2005 and 2007–2009 ( $n = 477$ ), and their applicability was tested on the measurements of specimens trapped in 2006, selected on random basis ( $n = 93$ ). Using the generalised linear model (GLM) method, we explored relationships between body mass (dependent variable) and skull characters  $X_1$ – $X^{17}$  (independent predictors). Using Statistica for Windows (StatSoft, 2010), single predictor-based best linear models were chosen, and linear regressions  $Q = A + Bx$  were prepared for all characters. Multiple regression was not applied, as skull characters were preserved unequally in the prey remains, thus limiting the possibility to use several simultaneously for prey body mass estimation.

With respect to winter growth depression in *M. arvalis* (Balčiauskienė et al., 2009), regressions were prepared on the basis of individuals trapped in the nonvegetative period. According to Balčiauskas and Balčiauskienė (2011), the differences between estimates (measured and calculated weights) were expressed as the ratio to the measured body mass of control individuals and were tested using Student's t-test for independent variables.

Prey remains of voles (skulls and mandibles) were collected in 2004–2005 in the Kėdainiai and Jonava districts of Central Lithuania from pellets found in roosting sites and pellets/prey remains in nest locations. Feeding territories of both species, characterised by high numbers, inevitably overlapped. Samples were divided into 3 groups on the basis of the species of owl and the time of material collection. The first group represented winter and spring material relating to *A. otus* (Table 1). The second group represented *S. aluco* winter prey and the third group consisted of prey material recovered from both breeding and nonbreeding Tawny Owls in spring.

The prey preferences were estimated by comparing the distribution of the calculated (predicted) body mass of the prey items with that of trapped individuals in the

nonvegetative period. The body mass of each predated individual was calculated according to linear regressions based on all available characters for recovered crania and mandibles, and then the calculated results were averaged.

If the bone was broken and an exact measurement of the character was not possible, the character was treated as “missing” and was not used in later analysis. Measurements were taken from the right side of the skull. Individuals recovered from disintegrated pellets were also used for further calculations. It was not possible to pair maxillae and mandibles in prey remains collected from nest-boxes after the breeding season, as was the case also in broken pellets and in examples where the pellet contained more than one individual. For this reason, we separately calculated prey body mass from both crania and mandibles and tested if it differed significantly.

Influence of predator species (*A. otus*, *S. aluco*, or snap-traps) and season on the body mass of *M. arvalis* was tested using factorial ANOVA under the GLM in Statistica for Windows.

### 3. Results

#### 3.1. Regressions based on trapped *M. arvalis*

We found that in trapped voles all measured cranial characters significantly correlated with the body mass, yielding regression equations with various predictability (Table 2).

In general, the average of the measured body mass of trapped *M. arvalis* was  $17.73 \pm 0.49$  g (10.5–32.0 g in 2005 and 2007–2009; 7.8–33.5 g in 2006), while the average of the calculated body mass was  $17.14 \pm 0.14$  (14.6–22.1) g. The difference is not statistically significant, with an error of 3.3%; thus, regressions accurately predict body mass.

We calculated differences between measured and calculated body mass and expressed it as the ratio to the average body mass of the trapped individuals. Comparing single characters, just one regression (based on  $X^{17}$ ) showed a statistically significant difference between the measured body mass and that obtained from regression. The calculated body mass was underestimated in most regressions by 0.9%–6.0%, with the exception of the regression based on  $X_2$ , which yielded a 0.7% overestimation (Table 3).

**Table 1.** Sample data on recovered *M. arvalis*, preyed upon by *Strix aluco* and *Asio otus* in Central Lithuania, 2004–2005.

Owl species	Season represented	Collection time	Source	Measured crania	Measured mandibles
<i>A. otus</i>	Winter-spring	Spring	Pellets	419	443
<i>S. aluco</i>	Winter	Winter	Pellets	31	36
<i>S. aluco</i>	Spring	Spring	Prey remains and pellets	16	18

**Table 2.** Correlations of skull characters with body mass of *Microtus arvalis* individuals trapped in the nonvegetative period, coefficients of linear regressions  $Q = A + Bx$ , and character preservation rates. All presented correlations are significant at  $P < 0.001$ .

Character	N	Pearson's r	Regression			Preservation %
			A	B	R <sup>2</sup>	
X <sub>1</sub>	456	0.66	-45.11	5.24	0.44	90.4
X <sub>2</sub>	394	0.69	-48.65	5.75	0.48	57.4
X <sub>3</sub>	543	0.63	-25.60	8.82	0.40	97.8
X <sub>4</sub>	406	0.54	-31.13	7.88	0.30	73.4
X <sub>5</sub>	411	0.61	-38.18	8.43	0.37	56.6
X <sub>6</sub>	544	0.39	-11.88	9.01	0.15	98.0
X <sub>7</sub>	553	0.41	-20.02	7.57	0.17	90.0
X <sub>8</sub>	553	0.30	-12.74	11.66	0.09	99.0
X <sup>9</sup>	509	0.55	-19.07	6.38	0.30	32.5
X <sup>10</sup>	243	0.34	-36.47	5.53	0.12	11.5
X <sup>11</sup>	363	0.81	-57.99	6.13	0.66	81.1
X <sup>12</sup>	506	0.67	-31.88	7.52	0.45	87.2
X <sup>13</sup>	333	0.47	-19.63	4.98	0.22	27.3
X <sup>14</sup>	508	0.57	-16.17	8.45	0.33	89.3
X <sup>15</sup>	532	0.34	-16.81	6.03	0.12	91.5
X <sup>16</sup>	550	0.25	-4.66	11.27	0.06	98.9
X <sup>17</sup>	549	0.44	-24.99	17.43	0.20	77.0

**Table 3.** Regression-predicted body mass of *Microtus arvalis* and its comparison with actual body mass of sampled individuals (negative sign shows that the calculation underestimated body mass, NS: difference from body mass of trapped individuals not significant, \*:  $P < 0.05$ ).

Body mass calculated from mandibles (g)					Body mass calculated from cranium (g)				
Char.	N	Avg. ± SE	Min-max	Diff., %	Char.	N	Avg. ± SE	Min-max	Diff., %
X <sub>1</sub>	74	17.49 ± 0.30	12.7-24.8	-1.3 <sup>NS</sup>	X <sup>9</sup>	84	17.39 ± 0.23	13.2-22.0	-1.9 <sup>NS</sup>
X <sub>2</sub>	59	17.85 ± 0.34	12.7-25.4	0.7 <sup>NS</sup>	X <sup>10</sup>	30	17.11 ± 0.28	13.4-20.5	-3.5 <sup>NS</sup>
X <sub>3</sub>	90	17.28 ± 0.27	12.5-24.7	-2.5 <sup>NS</sup>	X <sup>11</sup>	51	17.48 ± 0.49	9.7-26.6	-1.4 <sup>NS</sup>
X <sub>4</sub>	67	17.32 ± 0.26	12.4-25.4	-2.3 <sup>NS</sup>	X <sup>12</sup>	87	17.42 ± 0.25	13.1-24.1	-1.7 <sup>NS</sup>
X <sub>5</sub>	65	17.56 ± 0.31	12.2-27.8	-0.9 <sup>NS</sup>	X <sup>13</sup>	53	17.20 ± 0.24	12.4-21.6	-3.0 <sup>NS</sup>
X <sub>6</sub>	91	16.79 ± 0.18	13.8-25.4	-5.3 <sup>NS</sup>	X <sup>14</sup>	86	16.82 ± 0.23	12.6-21.9	-5.1 <sup>NS</sup>
X <sub>7</sub>	91	16.83 ± 0.15	14.1-20.4	-5.1 <sup>NS</sup>	X <sup>15</sup>	89	16.79 ± 0.18	5.4-19.8	-5.3 <sup>NS</sup>
X <sub>8</sub>	91	17.01 ± 0.12	15.1-19.4	-4.1 <sup>NS</sup>	X <sup>16</sup>	93	16.85 ± 0.11	15.0-19.2	-5.0 <sup>NS</sup>
					X <sup>17</sup>	89	16.66 ± 0.15	13.5-21.5	-6.0 <sup>*</sup>

### 3.2. Body mass of trapped and predated *M. arvalis*

Factorial ANOVA showed that the effect of the sampling type (trapping, preying of *S. aluco*, and preying of *A. otus*) on the body mass of *M. arvalis* is significant ( $F_{1,1321} = 186.26$ ,  $P < 0.0001$ ), while effect of the season is not. Interaction of both factors is significant ( $F_{1,1321} = 7.36$ ,  $P < 0.01$ ); thus, the effect of sampling type in winter and spring is not the same. Furthermore, we analysed these differences in detail.

From trapped *M. arvalis* voles, it was found that the average body mass of juveniles was  $14.53 \pm 0.07$  g (7.8–22.3 g,  $n = 378$ ), of subadults was  $18.07 \pm 0.27$  g (13.0–25.1 g,  $n = 81$ ), and of adults was  $22.5 \pm 0.37$  g (13.3–33.5 g,  $n = 100$ ), with an average irrespective of age equal to  $16.42 \pm 0.16$  (7.8–33.5) g. Clearly, the distribution is biased towards individuals with small body mass (i.e. young individuals), prevalent in the population in most of the nonvegetative period. The body mass distribution of trapped *M. arvalis* individuals is shown in the Figure 1 (recalculated from Balčiauskienė et al., 2009).

The average body mass of *M. arvalis* preyed upon both by *S. aluco* and *A. otus* was  $21.72 \pm 0.12$  (14.3–29.3) g when estimated from crania ( $n = 366$ ) and  $21.45 \pm 0.12$  (9.2–30.4) g when estimated from mandibles ( $n = 497$ ); the difference is not significant. Having in mind better preservation of mandible characters and larger number of recovered mandibles (Table 2), absence of body mass difference made it possible to rely on results calculated from mandibles. Through comparison with the trapped individuals in the nonvegetative period, such an average body mass of predated individuals indicates that adult voles are being predated (Figure 1).

Comparison of the average body masses of the trapped and predated *M. arvalis* shows that predated individuals were significantly heavier by over 30% of body mass than trapped individuals. Predated *M. arvalis* were 5.03 g heavier; the difference is highly significant ( $t = 25.87$ ,  $df =$

1064,  $P < 0.001$ ). The underestimation of the body mass by most regressions (see Table 3) makes this difference even greater.

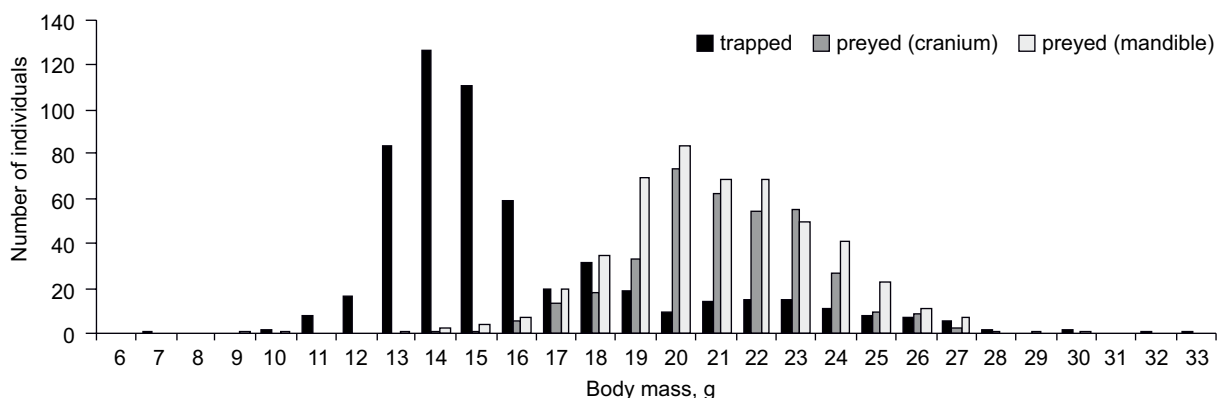
### 3.3. Prey preferences

Owl-predated voles were not only the heaviest individuals in the population (Figure 1); body mass also reflects different exploitations of the population of *M. arvalis*. In terms of age structure, juveniles (up to 16 g) were highly under-predated; they accounted for 71.8% of the population but only 3.4% in the prey items (the difference highly significant,  $\chi^2_1 = 516.9$ ,  $P < 0.001$ ). The proportion of subadult voles (body mass 17–19 g) in the tested population was 12.3%, while in the prey it was 25.2% ( $\chi^2_1 = 29.5$ ,  $P < 0.001$ ). Adult voles were highly over-predated; while they accounted only for 16.0% of the sampled population in the nonvegetative period, they made up 71.4% of the prey ( $\chi^2_1 = 335.73$ ,  $P < 0.001$ ).

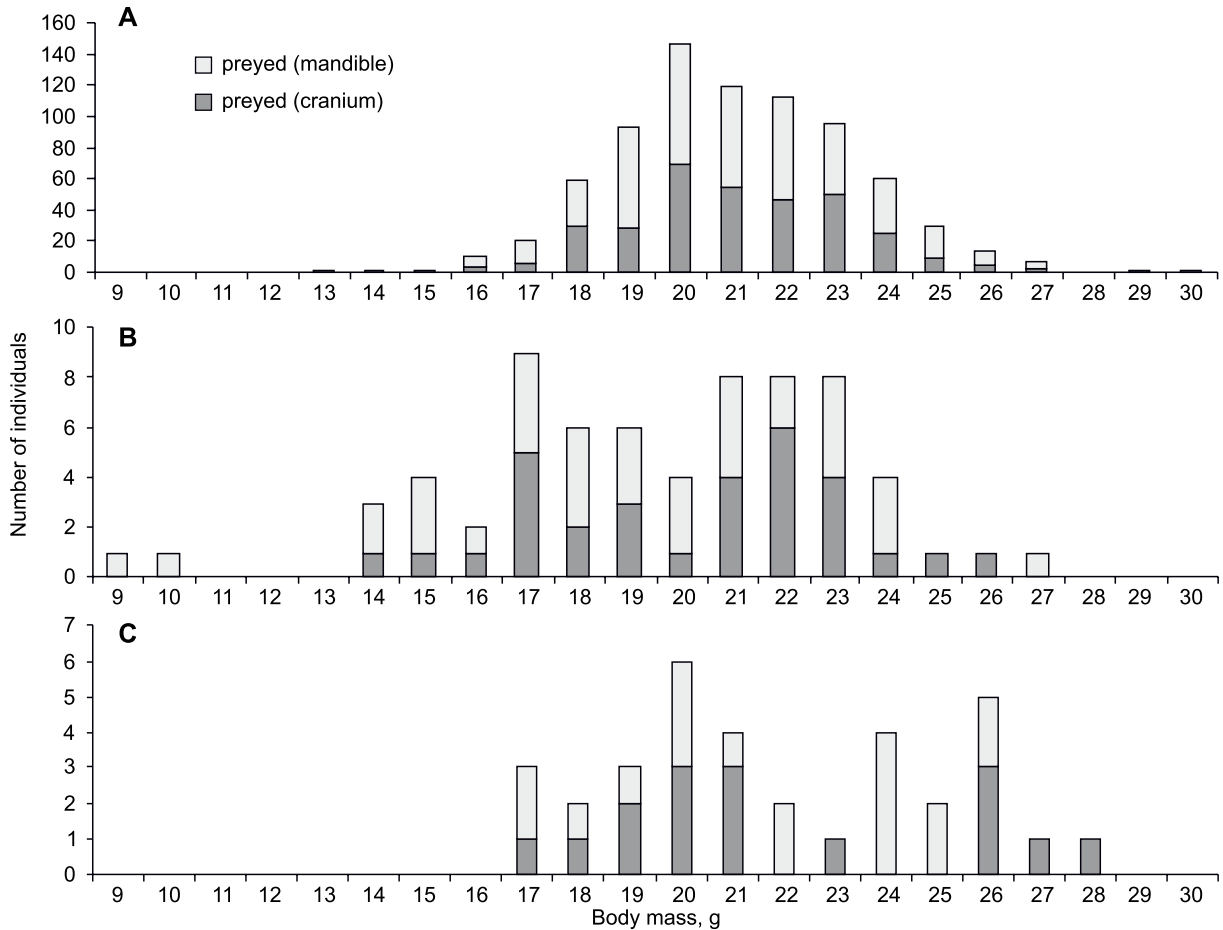
We found that the differences between the average body masses of the prey in the winter-spring diet of *A. otus*, the winter diet of *S. aluco*, and the spring diet of *S. aluco* were all significant ( $F_{2,494} = 6.42$ ,  $P < 0.001$ ). Within each of these groups, the difference of predated *M. arvalis* body mass calculated from crania and mandibles was not significant (Wilks' lambda = 0.97,  $F_{4,724} = 2.33$ , NS).

In winter and spring, *A. otus* preferred larger individuals of *M. arvalis* (average body mass  $21.56 \pm 0.11$  g) than *S. aluco* did in winter ( $19.59 \pm 0.66$  g); the difference is significant ( $t = 4.51$ ,  $df = 477$ ,  $P < 0.001$ ). However, the largest voles were preyed upon by *S. aluco* in spring (average body mass  $22.39 \pm 0.70$  g); i.e. the *S. aluco* prey was bigger in spring than in winter ( $t = 2.63$ ,  $P = 0.01$ ). Within this spring group, breeding *S. aluco* preyed upon larger voles than nonbreeding ones ( $21.80 \pm 1.08$  g).

The body mass distribution of *M. arvalis* preyed upon in winter by *S. aluco* and winter-spring by *A. otus* was significantly different (Figures 2A and 2B). In *S. aluco* prey, the proportion of young voles was significantly higher than



**Figure 1.** Distribution of the body mass of *Microtus arvalis* individuals, trapped in October–April and preyed upon by both *Strix aluco* and *Asio otus* in winter and spring, as estimated from mandibles.



**Figure 2.** Distribution of the body mass of *Microtus arvalis* individuals, preyed upon by *Strix aluco* and *Asio otus* in winter and spring 2004–2005, as estimated from mandibles: A) in the winter-spring diet of *Asio otus*; B) in the winter diet of *Strix aluco*; C) in the spring diet of *Strix aluco*.

in the prey of *A. otus*: respectively, 33.3% versus 5.2% ( $\chi^2_1 = 31.47$ ,  $P < 0.001$ ). By contrast, the proportion of subadult and adult voles with a body mass in the range between 19 and 23 g was significantly higher in the prey of *A. otus*, respectively, at 72.9% versus 55.6% ( $\chi^2_1 = 5.95$ ,  $P = 0.014$ ).

The distribution of the body mass of *M. arvalis* preyed upon by *S. aluco* in spring (Figure 2C) was biased towards the heaviest individuals in the population, i.e. adults. Individuals with a body mass of over 24 g accounted for 44.4% of the predated voles. This is significantly more than the proportion of the heaviest individuals in the winter-spring prey of *A. otus* (12.9%,  $\chi^2_1 = 5.64$ ,  $P < 0.02$ ) and in the winter prey of *S. aluco* itself (16.0%,  $\chi^2_1 = 7.71$ ,  $P < 0.01$ ). In addition, the proportion of heaviest individuals in the spring prey of nonbreeding *S. aluco* (4 out of 9 individuals) was also higher than that in the winter-spring prey of *A. otus* ( $\chi^2_1 = 5.15$ ,  $P = 0.02$ ) and in the winter prey of *S. aluco* ( $\chi^2_1 = 5.47$ ,  $P < 0.02$ ).

#### 4. Discussion

*S. aluco* is a generalist nocturnal raptor, while *A. otus* has been shown to be a vole specialist, preying mainly on *M. arvalis* in Central Europe (Cramp, 1998). However, further to the south in Europe (e.g., Italy, Greece), *A. otus* is not a specialised vole eater (Bertolino et al., 2001; Birrer, 2009). According to Goszczyński (1981), the diets of both species are most similar in autumn and winter, when *S. aluco* start eating more voles than birds.

In Lithuania, Balčiauskienė et al. (2006) showed that *M. arvalis* constituted 70.8% of *A. otus* prey items and 64.3% of biomass consumed. For *S. aluco*, the proportion of *M. arvalis* in the diet was less, being 27.9% by numbers and 25.0% by biomass. In neighbouring Poland, *M. arvalis* constituted from 1.35% to 16.06% of *S. aluco* prey items depending on the habitat and severity of winter (Romanowski and Żmihorski, 2009).

#### 4.1. Estimation of the prey biomass

Attempting to assess the biomass eaten, average prey size from the literature or trapping data has been used in the investigations of avian feeding ecology (Wijnands, 1984; Jędrzejewski and Jędrzejewska, 1993; Zawadzka and Zawadzki, 2007; Gliwicz, 2008; Zub et al., 2010). When raptors select prey of a particular species in a nonrandom manner, the use of average body masses for dietary calculations will lead to biased results (Marti et al., 2007).

Therefore, rather than using an average body mass, studies have been conducted to estimate the actual body mass of each of the individual small mammal prey items caught. The prey composition and selectivity of predators for certain age/sex/size classes have been evaluated using bones from pellets (Bueno and Motta-Junior, 2008), analysis of tooth wear in remains (Granjon and Traoré, 2007), prey cache examination in nests (Meri et al., 2008; Taylor, 2009; Karell et al., 2010), prey measures in camera monitors and later regression analysis (Steen et al., 2010), and equipping voles with transmitters and subsequent observation (Norrdahl and Korpimäki, 2002). Body mass of prey has also been obtained by direct weighing (Wijnandts, 1984).

#### 4.2. Methodological aspects of regression use in prey assessment

How accurate and useful are regressions in the analysis of predator diet in reconstructing the body mass of predated victims? For *M. arvalis*, the error in the used linear regressions was on average 3.3% (0.9%–6.0%, depending on the skull character used), while for another species of vole, *M. oeconomus*, the error of body mass recalculation was higher, 5.5%–15.0% (Balčiauskas and Balčiauskienė, 2011). Wijnandts (1984) obtained weights of prey items of *A. otus* by placing nests with nestlings on platforms equipped with electronic balances; the error of estimation was about 10%, i.e. about 3 times greater than in our case using regressions for *M. arvalis*. It should be noted, however, that regressions for body mass from measurable bone remains might yield significant errors if they are not tested on additional material (Balčiauskas and Balčiauskienė, 2011).

For *M. arvalis* it was shown that many skull characters have no statistically significant differences between males and females (Markov et al., 2012). In our sample of trapped voles, males were significantly heavier than females and had significantly larger skull measurements (excluding just  $X_8$  and  $X^{13}$ ). Nevertheless, the data of trapped male and female individuals were pooled when preparing regressions as the preyed individuals were not differentiated into sexes.

To maximise the accuracy of body mass assessment of prey, we used regressions prepared from *M. arvalis* trapped in the winter and spring, the same period for

which the analysis of owl predation was conducted. This is necessary as winter growth depression of *M. arvalis* has been reported in Lithuania (Balčiauskienė et al., 2009). Based on such a presumption, regressions prepared from individuals trapped in summer should not be accurate in winter. For the same reason, we tested what the differences would be if regressions were prepared from summer and autumn trapped individuals. Estimated from mandibles, the average body mass did not differ ( $21.45 \pm 0.12$  g for winter regressions,  $21.3 \pm 0.20$  g for summer regressions, difference not significant). However, when estimated from crania, the body masses differed significantly (respectively,  $21.72 \pm 0.12$  g and  $23.3 \pm 0.2$  g,  $t = 9.00$ ,  $P < 0.001$ ), and this difference influences the estimated average body mass of predated *M. arvalis* ( $21.56 \pm 0.08$  g and  $22.16 \pm 0.02$  g,  $t = 12.6$ ,  $P < 0.001$ ). Thus, regressions made from inappropriate trapping data may yield a significant bias in results.

As for crania/mandible-related differences, it is known that growth rates of various skull characters are not equal (Balčiauskienė, 2007). Various characters are of different value as predictors of body mass for the individual. For *M. arvalis*, we found that the best-working mandible character was  $X_1$  (total length of mandibula at *processus articularis*, excluding incisors), with a preservation rate of 90.4% and error of body mass prediction of 1.3%. From cranial characters, the best-working characters were zygomatic skull width ( $X^{11}$ ) and length of cranial diastema ( $X^{12}$ ), with preservation rates of over 80% and errors of body mass prediction of less than 2%. The best-preserved skull characters, such as length of upper molar  $M^1$  ( $X^{16}$ ), length of mandibular diastema ( $X_6$ ), and length of lower molar  $M_1$  ( $X_8$ ), have less prediction power ( $R^2 = 0.06$ – $0.40$ , error of body mass prediction is over 5%).

#### 4.3. Selectivity of trapping

The question as to whether snap-trapping accurately represents the availability of small mammal as prey items is unavoidable in investigations regarding prey selectivity (Petrovici et al., 2013). With factorial ANOVA, we found that the effects of both the animal age and sex on the body mass of *M. arvalis* in our sample were significant (respectively,  $F_{2, 550} = 459.37$  and  $F_{1, 550} = 77.07$ , both  $P < 0.0001$ ), while the effect of the year of trapping was not ( $F_{4, 550} = 1.34$ ,  $P = 0.26$ ). In the absence of body mass variations for *M. oeconomus* in the samples across the whole country (Balčiauskienė and Balčiauskas, 2011), we can also presume the same for *M. arvalis*. Both the trapping and the pellet collection were conducted in fragmented habitats with forest patches, meadows, and agricultural land. Thus, in a small territory such as Lithuania, the body mass of trapped voles can be considered similar in respect to year and site when the same habitats are involved.



Considering trapped *M. arvalis* in the nonvegetative period, a bias towards young individuals was noted, corresponding to existing knowledge of species biology. However, long-term trapping results (Balčiauskienė et al., 2009) noted that the proportions of juvenile voles ranged from 3.6% to 87.3% in different years, with subadults varying from 7.1% to 36.5% and that of adults from 1.8% to 89.3%. Likewise, in different months, the proportions of juveniles ranged from 27.9% to 94.8%, subadults from 2.1% to 24.3%, and adults from 0% to 47.9%. These differences cannot be explained by snap-trap selectivity, and we thereby conclude that the trapping results do reflect the availability of prey in nature.

#### 4.4. Selectivity of prey

Published data show contradictory vulnerabilities of owl prey. Some authors (Fulk, 1976; Lagerström and Häkkinen, 1978; Korpimäki, 1985; Halle, 1988) found that owls catch young rodents and male shrews. Others (Longland and Jenkins, 1987; Dickman et al., 1991) wrote that young females were more vulnerable in populations of many rodent species. According to Marti and Hogue (1979), *A. otus* selected small laboratory mice in preference to large ones, although owls do not hunt voles weighing up to 5 g (Goszczyński, 1977). Our data clearly support selectivity of larger prey, shown also by some other authors (Bellocq, 1998; Karell et al., 2010).

Preying upon on larger *M. arvalis* individuals than average in the wild has been reported not only in owls. Halle (1988) found that despite specimens of 10–14 g constituting the most frequent weight-class in the wild, the heaviest *M. arvalis* with body masses of 15–23 g were

preferred by Eurasian Kestrels (*Falco tinnunculus*) and Common Buzzards (*Buteo buteo*) in winter. According to Halle (1988), the higher proportion of subadult voles (body mass 17–19 g for *M. arvalis*) in the prey than in the population could be explained by their more vulnerable social position, as home ranges are not established. However, Halle's idea that the larger body mass of predated individuals may be related to predation in optimal habitats, which could support higher body masses among wintering voles, is not supported by our data on winter trapping (Balčiauskienė et al., 2009). Size distribution of trapped *M. arvalis* in the nonvegetative period was shifted towards young individuals. This corresponds to all knowledge of species biology, excluding possible trapping bias, shown by Sunde et al. (2012) for other rodent species.

The fact that breeding owls prey on larger prey items is known for *S. aluco* (Kirk, 1992). Our data on *S. aluco* and one prey species, *M. arvalis*, show significant differences between the sizes of selected prey items of breeding and nonbreeding owls; breeding *S. aluco* preyed upon larger voles than nonbreeding ones.

By preying on differently sized prey, *T. alba* was shown to coexist with Burrowing Owl (*Athene cunicularia*) (Bueno and Motta-Junior, 2008), the same mechanism involved in the coexistence of *A. otus* and *T. alba* (Marks and Marti, 1984) and with Little Owl (*Athene noctua*) (Zhao et al., 2011). Our results may possibly be taken as an indication of selection of differing sizes of the same prey species, which allows the coexistence of 2 species of owls sympatrically in the fragmented landscape of Central Lithuania.

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