

## Selection by size of the yellow-necked mice (*Apodemus flavicollis*) by breeding Tawny Owl (*Strix aluco*)

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**Abstract.** We investigated whether Tawny Owls (*Strix aluco*) selectively predate yellow-necked mice (*Apodemus flavicollis*) with respect to body size. We calculated the body mass of predated individuals using regressions, prepared on basis of mandible measurements ( $n = 581$ ) from *A. flavicollis* trapped in the non-vegetation period. The distribution and age composition of predated mice was compared to the trapping results. We found that the percentage of adult mice preyed upon by breeding *S. aluco* was in accordance with their percentage in the wild population (38.04% and 41.36%, respectively). Juvenile mice were under-predated (20.45% and 4.13%,  $p < 0.001$ ), while subadult *A. flavicollis* individuals were over-predated, comprising 38.18% in the population, but 57.83% in the prey items ( $p < 0.001$ ). Selective predation on *A. flavicollis* in the non-vegetative period should be one of the factors regulating the population, though the impact on the reproductive investment of *A. flavicollis* is not critical as the removed individuals are yet to begin reproducing. Through their relative lack of predation of adult *A. flavicollis* in winter and spring, *S. aluco* could be determinants of the population structure before the start of reproduction in spring. Removing subadult mice just before onset of spring reproduction delays population growth and postpones the maximum population size to the autumn season.

**Key words:** *Strix aluco*, owl diet composition, prey selection, *Apodemus flavicollis*, mice population structure.

### Introduction

The Tawny Owl (*Strix aluco*) is a generalist nocturnal raptor (Cramp 1998). The proportion of yellow-necked mice (*Apodemus flavicollis*) in the diet of *S. aluco* varies considerably in different countries, figures including 0.03% in Norway, 1.68% in the Near East, 39.45% in the Crimea, 27.06% in the Mediterranean region, 22.58% in Romania, 28.5% in Germany, 4.22–56.59% in Slovakia depending on habitat (Obuch 2011), and 0.56–26% in Poland depending on habitat and winter severity (Zawadska & Zawadski 2007, Wiącek et al. 2009, Romanowski & Żmihorski 2009, Obuch 2011), and generally account for less than 20% of the diet in terms of individuals caught in Lithuania (Balčiauskienė et al. 2005, 2006). However, in the central part of Lithuania, this proportion reaches even 30–45% in some years in the diet of breeding *S. aluco* (Balčiauskienė & Naruševičius 2006). In most of these countries, *A. flavicollis* is the subdominant species in the *S. aluco* diet and, as such, can be an interesting object for investigating predator-prey relationships.

*A. flavicollis* is also an important prey item for Tengmalm's Owls *Aegolius funereus*, Long-eared Owls *Asio otus* and Barn Owls *Tyto alba* (Love et al. 2000, Duma et al. 2009, Zárybnická et al. 2013).

Quite different patterns of prey selection have already been presented for different birds of prey and for the differing prey species. Non-random removal of prey may be conditioned by physical, physiological and behavioural characteristics of both the predators and their prey (Zalewski 1996, Bueno & Motta-Junior 2008, Sunde et al. 2012, Romanowski et al. 2013). Individuals selectively preyed upon may be males (Halle 1988, Taylor 2009, Sunde et al. 2012), young or smaller individuals (Fulk 1976, Lagerström & Häkkinen 1978, Korpimäki 1985, Birrer 2009, Graham 2012), subadult individuals (Halle 1988, Dickman et al. 1991), or large or adult ones (Karell et al. 2010, Rocha et al. 2011, Balčiauskas & Balčiauskienė in press). Differences have also been found when comparing rodent species within the diet of an individual owl species: bank vole (*Clethrionomys glareolus*) vs. field vole (*Microtus agrestis*) in the prey of Ural Owl *Strix uralensis* (Karell et al. 2010) and *C. glareolus* vs. *A. flavicollis* in the prey of *S. aluco* (Sunde et al. 2012). Selection of prey by body mass has also been found in owls (Zalewski 1996, Karell et al. 2010, Sunde et al. 2012, Balčiauskas & Balčiauskienė 2014).

In this study, we aimed to evaluate the prey size preferences of *S. aluco* with regard to *A. flavicollis* preyed upon in the breeding period, as

measured from prey remains in nestboxes. We calculated the body mass of predated individuals using regressions, prepared on basis of mandible measurements. To provide workable regression equations was also among our aims. The distribution of body mass and proportions of different age categories of predated individuals were compared with those in the population, as sampled from material collected in the non-vegetative period, representative of the stunted growth and body mass of *A. flavicollis*. We tested the hypothesis that the distribution of the body size of the prey is in concordance with the wild population.

### Materials and methods

Material for the *S. aluco* prey was collected from 1996–2005 in Lithuania, from nestboxes of Tawny Owls after the breeding season. In total, 581 mandibles of *A. flavicollis* were retrieved in Central Lithuania (87.2% of all retrieved mandibles), with fewer in the northern (6.2%), north-western (1.4%) and southern (5.2%) parts of the country.

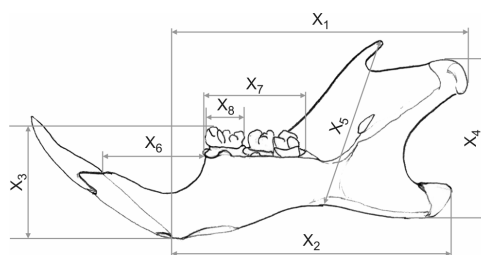
#### Cranial measurements used

Eight mandibular characters (Fig. 1) were measured under binoculars with an accuracy to 0.1 mm:  $X_1$  – 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 row;  $X_8$  – length of lower molar  $M_1$  (Balčiauskas & Balčiauskienė 2011). The same measurements were taken from the trapped individuals and from the mandibles of prey remains. If the bone was broken and an exact measurement of the character was not possible, the character was treated as “missing” and not used in later analysis. Measurements were taken from the right mandible.

To assess the age and body mass distribution of *A. flavicollis* in the wild, we used 220 *A. flavicollis* individuals, snap-trapped in October to April 2005–2009 in north-east Lithuania (Balčiauskienė et al. 2009). Mice were weighed to an accuracy of 0.1 g, then dissected and divided into three age categories: juveniles, sub-adults and adults, categorized according to the status of sex organs and atrophy of thymus, the latter decreasing in size with animal age (Balčiauskas et al. 2012). Skulls were cleaned by *Dermestes* beetles before measuring.

#### Body mass estimation

From the trapped *A. flavicollis*, 30 individuals were selected for control of regression suitability. We used a procedure of random subset sampling, as defined in Statistica for Windows ver. 6.0 software (StatSoft 2004). From the 190 remaining individuals, based on GLM method, the relationship between the dependent variable (body



**Figure 1.** Mandible measurements taken from *A. flavicollis*, trapped or retrieved from the prey remains; picture of mandible from Barčiová and Macholán (2009), measurements according Balčiauskas and Balčiauskienė (2011).

mass) and independent predictors (skull characters  $X_1$ – $X_8$ ) was explored. Using Statistica for Windows (StatSoft Inc. 2010), single predictor based best linear models were chosen, and linear regressions  $Q = A + Bx$  prepared for all mandible characters. We did not apply multiple regressions, as mandible characters in the prey remains were preserved unequally, limiting possibility to use several of them simultaneously for prey body mass estimation.

Additionally, factor analysis and PCA (principal component analysis) were applied to examine, which skull characters best determine body mass and how much of variability of the latter these factors explain. Age group was used as grouping variable. We accepted factors with eigenvalue > 1 (Norman et al. 1994). In PCA the two factors having the highest impact on body mass variation between age groups were defined (Quinn & Keough 2002).

We tested the applicability of obtained regressions by calculating the differences between the estimates (observed and expected weights of 30 control individuals). The differences were expressed as the ratio to the measured body mass of control individuals and tested using Student's *t* for independent variables (Balčiauskas & Balčiauskienė 2011).

#### Prey selectivity

The preferences of breeding *S. aluco* for certain *A. flavicollis* size groups were assessed by comparing the distribution of the calculated (predicted) body mass of the prey items with that of trapped individuals in the non-vegetative period. From the trapped individuals, the body mass of adult, subadult and juvenile mice was expressed by median and 25 percentile. For this comparison, chi-square statistic was used applying Bonferroni correction (Zar 1999).

### Results

#### Body mass and cranial measurements

##### of snap-trapped *A. flavicollis*

The distribution of body mass of the 220 *A. flavicollis* individuals trapped in the non-vegetative season was in perfect agreement with a normal

distribution (Kolmogorov-Smirnov's  $d = 0.06$ ,  $p > 0.20$ ). The average body mass for all trapped individuals was  $33.59 \pm 0.53$  (range 15.5–55.5) g. The average body mass of adult mice was  $39.25 \pm 0.67$  ( $n = 101$ , range 26.5–55.5) g, subadult mice  $30.29 \pm 0.46$  ( $n = 87$ , 16.5–42.00) g, and that of juvenile mice was  $24.69 \pm 0.63$  ( $n = 32$ , range 15.5–34.5) g. The differences among groups were highly significant (ANOVA,  $F_{2,217} = 112.54$ ,  $p < 0.0001$ ). We checked whether it was possible to attribute *A. flavicollis* age from the value of body mass and found that Q25–Q75 percentiles are non-overlapping: 50% of mice in the body mass range 22.9–26.2 g could be attributed to juveniles, 27.1–34.9 g to subadult mice and 35.0–42.5 g to adults.

Statistics of the measurements of the mandibular characters of snap-trapped *A. flavicollis* are presented in the Table 1. Characters  $X_1$ ,  $X_2$  and  $X_4$  were in accordance with normal distribution (Kolmogorov-Smirnov's  $d \leq 0.09$ ,  $p < 0.10$ ), while in  $X_3$ ,  $X_5$ ,  $X_6$ ,  $X_7$  and  $X_8$  the distribution of measurements differed from the normal. The overlap of the mandibular character measurements between

*A. flavicollis* age groups was significant (Table 1). Therefore, for the prey analysis, we relied on the body mass of predated individuals, recalculated on the basis of regressions (Table 2).

We revealed two factors, explaining 76.0% of body mass variation. PC1, with eigenvalue 5.20, explained 57.2% of body mass variation, while PC2 had an eigenvalue 1.64 and explained 18.2% of variation. PC1 included characters  $X_1$ – $X_6$ , PC2 included characters  $X_7$ – $X_8$ .

We found that correlations with body mass in trapped mice did not exist for all measured mandibular characters, thus yielding regression equations with various degrees of predictability (Table 2). Regression based on  $X_6$  yielded low predictability, while regressions based on  $X_7$  and  $X_8$  were not suitable.

The average measured body mass of the subsample of trapped *A. flavicollis* individuals used to check the suitability of regressions was  $32.44 \pm 1.36$  (range 22.0–52.0) g. The body mass recalculated according to regressions of these individuals is summarized in Table 2. On average, it was equal

**Table 1.** Mandibular measurements of snap-trapped *A. flavicollis* depending on age group.

	$X_1$ (mm)	$X_2$ (mm)	$X_3$ (mm)	$X_4$ (mm)	$X_5$ (mm)	$X_6$ (mm)	$X_7$ (mm)	$X_8$ (mm)
Adults								
n	91	91	97	90	92	97	97	97
Avg $\pm$ SE	13.18 $\pm$ 0.06	12.19 $\pm$ 0.06	4.50 $\pm$ 0.03	6.46 $\pm$ 0.04	7.00 $\pm$ 0.04	3.81 $\pm$ 0.02	3.70 $\pm$ 0.01	1.42 $\pm$ 0.01
Min-max	12.1–15.1	11.0–14.2	3.3–5.3	5.6–7.4	6.1–8.1	3.2–4.8	3.3–4.1	1.3–1.8
Subadults								
n	79	79	81	79	73	80	81	81
Avg $\pm$ SE	12.74 $\pm$ 0.05	11.68 $\pm$ 0.06	4.29 $\pm$ 0.02	6.15 $\pm$ 0.03	6.69 $\pm$ 0.03	3.72 $\pm$ 0.02	3.66 $\pm$ 0.01	1.42 $\pm$ 0.01
Min-max	11.7–13.8	10.7–13.1	3.7–4.8	5.5–6.7	5.6–7.3	3.4–4.0	3.3–4.0	1.3–1.6
Juveniles								
N	29	28	30	28	28	30	30	30
Avg $\pm$ SE	12.36 $\pm$ 0.10	11.33 $\pm$ 0.10	4.16 $\pm$ 0.04	5.90 $\pm$ 0.06	6.48 $\pm$ 0.05	3.61 $\pm$ 0.04	3.64 $\pm$ 0.05	1.42 $\pm$ 0.03
Min-max	11.4–13.7	10.5–12.9	3.8–4.7	5.3–6.6	6.1–7.1	3.1–4.1	3.4–4.6	1.3–2.2
Total								
N	199	198	208	197	193	207	208	208
Avg $\pm$ SE	12.89 $\pm$ 0.04	11.86 $\pm$ 0.04	4.37 $\pm$ 0.02	6.26 $\pm$ 0.03	6.81 $\pm$ 0.03	3.75 $\pm$ 0.01	3.68 $\pm$ 0.01	1.42 $\pm$ 0.01
Min-max	11.4–15.1	10.5–14.2	3.3–5.3	5.3–7.4	5.6–8.1	3.1–4.8	3.3–4.6	1.3–2.2

**Table 2.** Coefficients of linear regressions,  $Q = A + Bx$ , based on *A. flavicollis* individuals trapped in the non-vegetative period, and comparison of the regression-predicted body mass with actual body mass of sampled individuals (negative sign shows that the calculation underestimated body mass).

Character	Linear regression			Recalculated body mass and its difference from actual					
	A	B	$R^2$	n	$Q_{\text{rec}} \pm \text{SE}, \text{g}$	Min-max, g	$t$	$p$	% diff.
$X_1$	-79.62	8.79	0.41	28	32.31 $\pm$ 0.96	23.9–43.3	0.08	0.94	-0.41
$X_2$	-72.04	8.92	0.48	28	31.96 $\pm$ 0.86	24.8–40.3	0.30	0.77	-1.49
$X_3$	-42.74	17.51	0.38	29	32.08 $\pm$ 0.76	23.3–39.4	0.23	0.82	-1.12
$X_4$	-52.16	13.71	0.45	27	32.54 $\pm$ 0.98	21.0–42.4	-0.06	0.95	0.30
$X_5$	-55.57	13.13	0.41	28	32.00 $\pm$ 0.87	24.1–39.9	0.27	0.79	-1.36
$X_6$	-38.67	19.32	0.22	29	32.12 $\pm$ 0.61	27.1–39.5	0.21	0.83	-1.00

**Table 3.** Mandibular measurements of preyed *A. flavicollis* retrieved from the prey remains of *S. aluco* in the breeding period.

Character	X <sub>1</sub> (mm)	X <sub>2</sub> (mm)	X <sub>3</sub> (mm)	X <sub>4</sub> (mm)	X <sub>5</sub> (mm)	X <sub>6</sub> (mm)	X <sub>7</sub> (mm)	X <sub>8</sub> (mm)
n	311	168	279	323	330	268	568	271
Avg ± SE	12.70±0.05	11.57±0.07	4.58±0.02	6.52±0.02	6.75±0.02	3.84±0.01	3.71±0.01	1.48±0.01
Min-max	10.1–15.5	6.5–14.0	3.4–7.1	5.0–7.5	5.0–7.8	3.3–4.6	3.4–4.2	1.3–1.7
Preservation	53.5%	28.9%	48.0%	55.6%	56.8%	46.1%	97.8%	46.6%
Compared to trapped*	↑ <i>p</i> = 0.006	↑ <i>p</i> < 0.001	↓ <i>p</i> < 0.0001	↓ <i>p</i> < 0.0001	NS	↓ <i>p</i> < 0.0001	↓ <i>p</i> = 0.014	↓ <i>p</i> < 0.0001

\* - based on Student's *t* statistics; ↑ denotes measurements larger than obtained with trapped mice, ↓ denotes measurements smaller than in trapped mice

to 32.63 ± 0.53 g, and did not differ from measured mass (*t* = 0.13, *df* = 57, *p* = 0.90). Recalculated according to X<sub>1</sub>–X<sub>6</sub> characters, the mass of the individual on average differed from the recorded mass by about 1%, all differences being not significant. Regressions mainly underestimated the mass of the individual, with exception of X<sub>4</sub> which overestimated body mass by 0.3% (Table 2).

#### Cranial measurements and body mass of preyed *A. flavicollis*

Mandibular characters of the preyed *A. flavicollis* retrieved from prey remains were badly preserved, with exception of X<sub>7</sub>. Averages of the mandibular measurements X<sub>1</sub> and X<sub>2</sub> of preyed individuals were bigger than for trapped individuals, whilst X<sub>3</sub>, X<sub>4</sub>, X<sub>6</sub>, X<sub>7</sub> and X<sub>8</sub> were smaller; X<sub>5</sub> did not differ in size (Table 3). Characters X<sub>1</sub> and X<sub>2</sub> were in accordance with normal distribution (Kolmogorov-Smirnov's *d* ≤ 0.09, *p* < 0.15). For all other characters, the distribution was not normal.

The body mass of preyed *A. flavicollis* individuals, calculated from regressions, is tabulated in Table 4. ANOVA decomposition by year and character show that there was significant variation of calculated body mass depending on both parameters (year, *F* = 4.63, *p* < 0.0001; character, *F* = 47.11, *p* < 0.0001). To minimize body mass variation depending on character measured, we averaged the values obtained for every single mandible. The distribution of the obtained prey body mass is presented in Fig. 2.

#### Prey selectivity

On average, the body mass of preyed individuals was 34.04 ± 0.15 g, i.e. very close to that of trapped individuals (the difference not significant, *t* = 1.13, *df* = 799, *p* = 0.26). However, the distribution of body mass of trapped and preyed *A. flavicollis* individuals was not the same (Fig. 2).

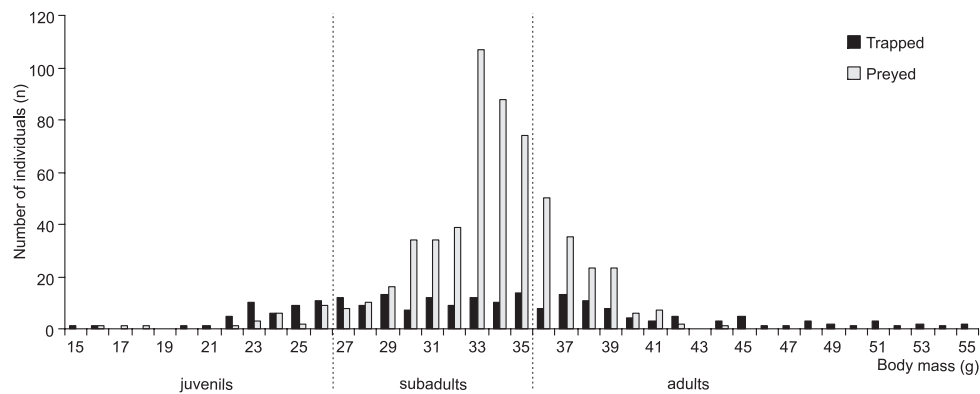
**Table 4.** Body mass of preyed *A. flavicollis* individuals based on mandibular measurements and regressions.

Character	Avg ± SE (g)	Min-max (g)
X <sub>1</sub>	32.1±0.42	9.4–56.3
X <sub>2</sub>	31.3±0.59	10.0–52.6
X <sub>3</sub>	37.3±0.36	16.9–65.2
X <sub>4</sub>	37.2±0.34	16.0–51.3
X <sub>5</sub>	33.0±0.32	9.7–47.1
X <sub>6</sub>	35.6±0.26	25.3–50.2

The proportion of juvenile mice with a body mass 14–26 g was 20.45% among trapped *A. flavicollis* individuals, but only 4.13% in the prey of *S. aluco* ( $\chi^2$  = 54.01, *df* = 1, *p* < 0.001), i.e. juvenile mice were under-predated. The over-predated group were subadult *A. flavicollis* individuals with a body mass of 27–34 g; these totaled 38.18% of the population in the wild, but 57.83% of the prey ( $\chi^2$  = 24.7, *df* = 1, *p* < 0.001). The predation of the adult *A. flavicollis* was in accordance to their proportion in the wild population. Such individuals, with body mass of 35 g and over, accounted for 41.36% in the population and 38.04% in the prey, the difference not significant ( $\chi^2$  = 0.74, *df* = 1, *p* = 0.39).

#### **Discussion**

Several authors have found that owls and other raptors prey on larger individuals among prey populations (Kirk 1992, Bellocq 1998, Karell et al. 2010, Sunde et al. 2012) than is the average available in the wild. In winter, Eurasian Kestrels (*Falco tinnunculus*) and Common Buzzards (*Buteo buteo*) preferred common voles *Microtus arvalis* with a body mass 15–23 g, whilst in the wild the most frequent individuals weighed only 10–14 g (Halle 1988). *T. alba* preyed upon on field voles *Microtus agrestis* with a body mass which was significantly bigger than that of the general wild population (Taylor 2009). In earlier studies, we also found that



**Figure 2.** Distribution of the body mass of *Apodemus flavicollis* individuals in Lithuania preyed upon by *Strix aluco* in breeding period 1996–2005 and trapped in the non-vegetative period of 2005–2009.

in winter and spring, both *S. aluco* and *A. otus* preferred larger than average *M. arvalis*, with most of the predated individuals being adults (Balčiauskas & Balčiauskienė 2014).

In studies of prey selectivity, where the availability of small mammals is assessed by results of live- or snap-trapping, the question whether trapping represents prey availability in the correct way is unavoidable (Petrovici et al. 2013). According to Sunde et al (2012), adults of *A. flavicollis* are more willing to enter traps than other individuals in the population. In our case, this might mean that the proportion of adult mice in the population was less than was actually obtained by snap-trapping.

According to Kirk (1992), breeding *S. aluco* change their diet in two ways: firstly, they prey on more birds and less small mammals, and secondly, switch from smaller prey (winter diet) to medium-sized prey (breeding season diet). This latter change was also stated by Yalden (1985). Switching to bigger prey while breeding is also characteristic of other owl species – Spotted Owl *S. occidentalis* (Barrows 1987), *A. otus* (Yalden 1985) and *T. alba* (Bellocq 1998).

The specific pressure of *S. aluco* on *A. flavicollis* in spring is little known. Individuals with body mass 23.5–34 g were found twice as frequently in pellets than in the wild (Vukićević-Radić et al. 2005). Depending on the season, these individuals should be subadults or adults. Subadults may be in a more vulnerable social position, as their home ranges are not established (Halle 1988). In Denmark, almost all predated individuals were sexually mature adults, predominantly males. Bearing in mind that *A. flavicollis* and *C. glareolus* together

accounted for more than 90% of all prey items (with a ratio 5.3 : 1), the impact of owls on spring populations is considerable (Sunde et al. 2012).

It is known that the breeding season of *A. flavicollis* starts early, typically in February or March (Adamczewska 1961, Bergstedt 1965, Flowerdew 1985, Horváth & Wagner 2003, Bujalska & Grum 2008). The reproduction of *A. flavicollis* decreases in winter and over-reproduction is avoided due to the dispersion of females and density-dependent reproduction (Horváth & Wagner 2003). In some years, winter breeding has been registered in Poland and Lithuania (Pucek et al. 1993, Balčiauskienė et al. 2009). Winter breeding is mainly observed in years with good mast crops (Gosálbez & Castién 1995).

However, the number of *A. flavicollis* individuals that survive winter is small. Winter mortality in NE Poland was estimated at 49–98% (Pucek et al. 1993, Bujalska & Grum 2006). In Lithuania, the average proportion of *A. flavicollis* in the total of small mammals trapped in the non-vegetation period is about 12%, but is less than 2% in April (Balčiauskienė et al. 2009). In the spring, the *A. flavicollis* population consists mainly of adult individuals (Pucek et al. 1993). In Romania, the subadult group was totally absent in the investigated population in spring 2001. It was however present in spring 2002 after a year of good forest crop (Benedek et al. 2002). In Lithuania, spring trapped juveniles of the species accounted for 5.6% of the population, while subadults for 8.3% of the population (Balčiauskienė et al. 2009). It is possible that selective predation of owls, i.e. only sparingly taking adults in winter and spring, could be determinants of the population structure

of *A. flavicollis* at the onset of reproduction in the spring.

Our data show that in Lithuania the proportion of adult *A. flavicollis* mice preyed upon by breeding *S. aluco* in spring was in accordance with their proportion in the population. However, if adult mice were relatively more likely to visit traps, then their proportion in the population was less than our estimate, thus the pressure of predation by owls could be greater than we had found. Juvenile mice were under-predated. The age group under the greatest pressure was subadult *A. flavicollis*, not participating in breeding at the time of being predated. Thus, the impact on the reproductive investment of *A. flavicollis* was less than in the case of *M. arvalis* in the same territory, as main predated group of *M. arvalis* was adult animals (Balčiauskas & Balčiauskienė in press).

*A. flavicollis* are sub-dominant in the prey of *S. aluco* and account for up to half of its diet in the breeding period (Balčiauskienė et al. 2006b, Obuch 2011, Romanowski & Žmihorski 2009, Sunde et al. 2012). Thus, selective predation of *A. flavicollis* in the non-vegetative period should be one of the regulatory factors for the population, working in combination with food supply and weather conditions. Through their relative lack of predation of adult *A. flavicollis* in winter and spring, *S. aluco* could be determinants of the population structure before the start of reproduction in spring. However, in removing subadult (and, possibly, adult) mice just before the onset of spring reproduction, the owls possibly delay *A. flavicollis* population growth and postpone the maximum population size to the autumn season. Predatory impact of the *S. aluco* on *A. flavicollis* population growth rate could be tested by experimental excluding of owls in part of the territory.

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