

Ural owl predation on field voles and bank voles by size, sex and reproductive state

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Predation on selected individuals from a population may have consequences for the prey population. We studied predation of breeding Ural owls (*Strix uralensis*) in southern Finland on their two main prey species, field voles (*Microtus agrestis*) and bank voles (*Myodes glareolus*), which fluctuate in abundance between years. We identified sex, body mass and reproductive state of the voles in Ural owl nests and of voles caught by snap-trapping in the study area. Our results showed that Ural owls preyed proportionally more upon reproductively active field voles than expected, whereas no such bias was found for predation on bank voles. There was no difference in sex ratio between preyed upon and trapped field voles or bank voles. Ural owls captured heavier individuals of both field voles and bank voles than expected, and in field voles, but not bank voles, reproductively active individuals were heavier than reproductively inactive individuals. We discuss how differences in social organisation, dispersal and reproductive behaviour may differently affect predation vulnerability of field voles and bank voles. In contrast to the pattern documented in other owl species, we find that Ural owls select larger and reproductively active voles, and may thereby exert a higher population-dynamical impact on vole populations than expected solely from the numbers of voles preyed upon.

Introduction

An individual's susceptibility to predation may depend on the selectivity of the predator or on the interactive behaviour of individuals in the prey population. Traditionally predators have been viewed to mainly prey upon poor quality individuals such as ill, injured, subdominant, inexperienced, juvenile or old (Errington 1946). Moreover, optimal foraging theory predicts that a predator should always attack the most profitable prey, e.g. the prey most easy to capture, or

the prey with the highest mass-specific energy content (Pyke *et al.* 1977). Such selective behaviour of the predator may have consequences for the evolutionary and population dynamics and the structure of the prey population. Differential predation on males and females may lead to skews in the population sex ratio, with potential consequences for evolutionary dynamics of sex-specific aging (Christe *et al.* 2006). Furthermore, predation on certain age classes may affect the demography of the population (Meri *et al.* 2008), and an enhanced predation risk of reproduc-

ing individuals may have a negative impact on population growth rate, and hence, on the population dynamics (Norrdahl 1995, Norrdahl & Korpimäki 1995).

Our knowledge of prey selection of predators on the basis of individual characteristics of the prey is to a large extent due to the numerous studies of birds of prey and their selection of mammalian prey individuals. Birds of prey, in particular owls, cache prey items in their nests, especially during the early nestling period (Lagerström & Häkkinen 1978, Korpimäki 1985, Koivunen *et al.* 1996). This peculiar behaviour of owls and the straightforward methods of trapping small mammals provide an ideal system to address questions about prey selection. Such studies of birds of prey feeding on small mammals have found considerable skews in the sex ratio of caught prey (reviewed in Christe *et al.* 2006). The vulnerability of a certain sex has generally been explained by the different behaviour of males and females. For example, male bias in vole prey of Tengmalm's owl *Aegolius funereus* during reproduction has been explained by the increased activity and movement of vole males in spring (Korpimäki 1981, Koivunen *et al.* 1996). On the other hand, a female bias in cached prey of owls has been proposed to be due to the higher activity of female voles during the night (Rowsemitt 1991). Dickman *et al.* (1991) proposed that female house mice were the preferred prey of barn owls (*Tyto alba*) because open spaces, the preferred hunting grounds for barn owls, were more often used by female than male mice.

In addition to sex, birds of prey have also been found to select their prey based on size. Both pygmy owls *Glaucidium passerinum* (Mappes *et al.* 1993) and Tengmalm's owls (Koivunen *et al.* 1996) capture smaller sized individuals than expected, whereas barn owls (Dickman *et al.* 1991) have been found to capture larger prey than expected. Less focus has been put on the reproductive state of the individuals that are being preyed upon by avian predators. Reproductively active individuals may be easier prey because of their behaviour (Magnhagen 1991) and they may also be valuable as their nutritional state may be higher in terms of hormones, antioxidants and other nutrients than

in reproductively inactive individuals. Prey individuals may differ also in more subtle ways, e.g., due to asymmetry or parasite load. Galeotti *et al.* (2005) found that tawny owls (*Strix aluco*) took more such wood mice (*Apodemus flavicollis* and *sylvaticus*) which had asymmetric leg bones. Parasites did not affect field vole vulnerability to Ural owl predation (Haukisalmi *et al.* 1994).

Despite the extensive literature on the predation by birds of prey on small mammals, little is known about species-specific differences in vulnerability to predation, which may arise from species-specific differences in social organisation and behaviour. Furthermore, reproductively active prey individuals are of great importance for population growth, but reproductive state has rarely been examined in studies of predation. Here we study Ural owl (*Strix uralensis*) predation on their main prey, field voles and bank voles in an increase (2002) and a decrease vole cycle phase (2003). Field voles and bank voles amount to 50%–55% of the total prey items during the nestling period during the increase and decrease phases (Blomqvist 2004). Surplus prey items can typically be found in the nest during the early nestling period (Pietiäinen & Kolunen 1993). By comparing sex, body mass and reproductive status of these cached voles found in Ural owl nest boxes during the nestling period with the voles caught in a simultaneously performed large scale snap trapping at 31 trapping sites in the study area, we were able to study the individual variation in susceptibility of voles to Ural owl predation. We predicted differences in vulnerability to predation between prey species because of their different social organisation and behaviour. We also predicted that reproducing individuals would be more prone to predation due to their behaviour. In this paper, we define 'prey selection' as a statistically significant difference between a pattern found in the snap trappings and the cached prey items in Ural owl nest boxes.

Material and methods

The study was carried out in 2002 and 2003 in an area covering ca. 1000 km² in Päijät-Häme, southern Finland, with ca. 120 nest boxes available for Ural owls. The nest boxes are situated in

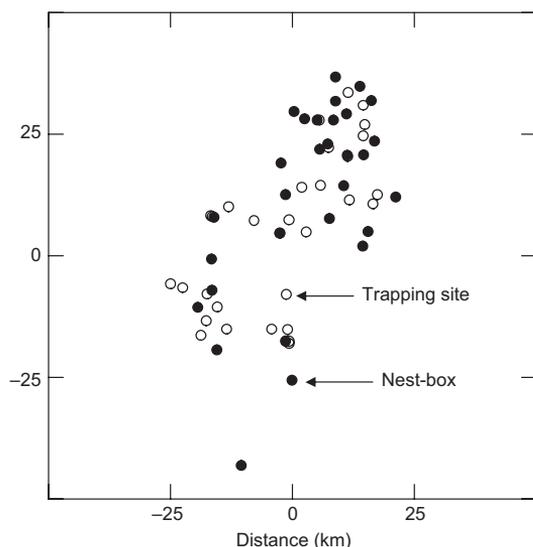


Fig. 1. Spatial distribution of Ural owl nests ($n = 30$, denoted by filled circles) and vole trapping sites ($n = 31$, denoted by open circles). The graph is oriented with north upwards. Axes denote the distance in kilometres from the centre of the study area. Vole trapping sites and nest boxes where cached prey items were recorded show clear spatial overlap.

coniferous and mixed forests, which generally are accompanied with clear-cuts, areas of young, often replanted forest of different ages, and fields and meadows. Based on the long-term trapping of voles in our study area, year 2002 was classified as an increase vole phase, whereas 2003 was a decrease vole phase of the vole cycle (Karell *et al.* 2009). For a more detailed description of the study area, see Pietiäinen (1989) and Brommer *et al.* (1998).

Cached prey in Ural owl nests

Cached prey items from Ural owl nest boxes were monitored during regular nest box visits in three-day intervals during the nestling period. On each visit we recorded prey species, their body mass, sex and reproductive state of all vole prey items found. The probability of measuring the same prey items during consecutive visits is unlikely. Observations during a supplementary feeding experiment revealed that an Ural owl family may consume as much as 300 g mouse prey per offspring within 24 h (authors' unpubl.

data). Cached prey was found in 25 Ural owl nests in 2002 and in 23 nests in 2003. Some nests were used both in 2002 and in 2003 and therefore, in total 30 different nests were used to observe cached prey in our study (Fig. 1). The complete prey items were weighed using a spring balance (Pesola) with 0.5 g accuracy. Sex was determined by external examination of the genitals. Females were categorized according to their reproductive state (reproductively active or not reproducing): gravid and lactating (oestrous) females had visible mammalian glands and/or were gravid, whereas non-reproducing females showed no such signs. Adult males were defined as reproductively active if they had clearly swollen testicles.

Prey availability in the field

We studied the availability of voles in the field by snap-trapping in the study area. Voles were trapped in April (14–24 April 2002 and 23–30 April 2003) some time before Ural owl offspring hatched (median hatch date 4 May in 2002 and 6 May in 2003). The voles were caught by snap trapping in 31 localities throughout the whole study area (Fig. 1). Snap traps were set in squares (15×15 m) with three traps in each corner as described in Myllymäki *et al.* (1971). Each trapping locality had three squares where one square was placed in an open habitat, one at the interface between open and forest, and one in the forest ($n = 36$ traps per locality). The trapping habitats correspond to Ural owl hunting grounds, since Ural owls are sit-and-wait predators that hunt by perching along the edges of forests (Nishimura & Abe 1988). All traps were set for two consecutive nights (1116 traps for 2 nights yielded 2232 trap nights in total per trapping). The trapped field voles and bank voles were weighed, sexed and their reproductive state was determined in the same manner as for cached prey.

Statistical analyses and model selection

We analysed if Ural owls selected their prey on the basis of prey body mass with linear mixed

models (LMM) in which we compared the body mass of voles in the prey caches (preyed upon) with that of voles trapped in the field ('capture'), while correcting for the other fixed effects 'year', 'sex', 'reproductive state', and the random effect 'sampling location'. We tested models separately for field voles and bank voles. The full models contained all the above-mentioned variables and their two-way interactions, and a stepwise backwards procedure fit by maximum likelihood was used to drop the non significant variables with likelihood ratio tests between models starting with the highest-level interactions until the minimal adequate model (MAM) was achieved (Crawley 2002).

Sex ratio and the proportion of reproductively active voles in prey caches and trapped in the field were analysed with Generalised Linear Mixed Models (GLMM) with binomial errors and sampling location (territory or trapping site) as random effect. In order to achieve the minimal adequate model (MAM) of the GLMMs by model simplification we used 'Laplace' approximation of likelihood implemented with the 'lmer' function (Matrix package, by D. Bates and M. Maehler), which allows a comparison of models with different fixed effects. For model selection we used likelihood ratio tests (LRT) to test between models retaining and excluding the variable. We additionally used AIC as a second model selection criterion and both AIC and LRT produced the same MAM for the data. We report χ^2 of the LRT between models in the results. For further details on the model selection procedure, see Karell *et al.* (2008). All analyses were carried out using R 2.8.1. (R Development core team 2008).

Results

During the nest box visits in spring 2002 and 2003 we found in total 124 field voles and 46 bank voles, most of which were from 2002 (2002: 59 field voles and 28 bank voles, 2003: 65 field voles and 18 bank voles). In 2002 cached prey was found in 25 nest boxes in the study area (mean 3.48 ± 0.86 (SE) prey per nest) and in 23 nest boxes in 2003 (mean 3.74 ± 0.96 (SE) prey per nest). At the same time, we trapped 129 field

voles and 59 bank voles in the study area (2002: 111 field voles and 44 bank voles, mean 5.00 ± 0.64 (SE) prey per trap site; 2003: 18 field voles and 15 bank voles, mean 1.06 ± 0.25 (SE) prey per trap site). The spatial distribution of the trapping sites and Ural owl nest boxes was similar (see Fig. 1).

Body mass of field voles and bank voles in prey caches and in the field

Field voles cached by Ural owls were heavier than the trapped field voles (Tables 1 and 2, "capture") although there was variation between years (Table 2, "year", "capture \times year"). Especially the difference in body mass of cached and trapped female field voles was pronounced (Table 2, "capture \times sex"). Reproductively active field voles were heavier than reproductively inactive ones (Table 2, "repr"). The mean body mass of the reproductively active field voles in the cached prey was clearly higher than the body mass of trapped reproductively active field voles (Table 2, "capture \times repr"). Furthermore, reproductively active field voles were heavier in 2002 (an increase vole phase) than in 2003 (a decrease vole phase) (Table 2, "year \times repr").

Bank voles trapped in the field weighed significantly less than the bank voles found among

Table 1. Field vole and bank vole mean body mass (\pm SE, n), sex ratio (proportion males), and proportion of reproductively active individuals in Ural owl nest boxes and trapped in the field. Sample size for prey items in the Ural owl nests varies, because some items were incomplete and thus could not be weighed (although they usually could be sexed and their reproductive state could often be determined as well). Data from both years are pooled.

	Ural owl nest	Field
Field voles		
Body mass	28.59 ± 1.06 (76)	26.44 ± 0.42 (129)
Sex ratio	63% (77/123)	52% (68/129)
Reproductively active	56% (65/115)	31% (40/129)
Bank voles		
Body mass	22.78 ± 0.81 (34)	18.75 ± 0.41 (59)
Sex ratio	54% (25/46)	52% (31/59)
Reproductively active	44% (20/46)	39% (23/59)

cached prey in the Ural owl nests (Tables 1 and 3, “capture”). Bank voles were heavier in 2002 than 2003 (Table 3, “year”). There was a significant interaction between capture and sex, in which the difference in weight between cached and trapped bank voles was more pronounced among females (Table 3, “capture × sex”).

The proportion of reproductively active individuals in cached prey and in the field

A GLMM revealed that Ural owls preyed especially upon reproductively active field voles as

their proportion in the cached prey was markedly higher than their proportion in the trapped voles (Table 1 and Fig. 2; capture: $\chi^2 = 17.0$, d.f. = 1, $p < 0.0001$). The proportion of reproductively active individuals differed between years (year: $\chi^2 = 17.24$, d.f. = 1, $p = 0.0002$). As shown in Fig. 2, the proportion of reproductively active male field voles was higher in cached than trapped individuals in both years (sex: $\chi^2 = 10.95$, d.f. = 1, $p = 0.004$). The difference in the proportion of reproductively active females in cached and trapped individuals was evident only in 2002 (year × sex: $\chi^2 = 6.07$, d.f. = 1, $p = 0.01$).

For bank voles, the proportion of reproductively active and inactive individuals in the

Table 2. Minimal adequate linear mixed effects model of the variation in body mass of field voles explained by ‘capture’ (1 = preyed upon by Ural owls, 2 = trapped), yearly variation, sex (0 = female, 1 = male), reproductive state (repr, 0 = inactive, 1 = active) and interactions. The random effect “sampling location” (territory or trapping site, $n = 49$) is included in the model to control for pseudoreplication (Variance = 5.38 (95% CI = 1.93–14.98), $\chi^2 = 10.81$, d.f. = 1, $p = 0.001$). The coefficients show the effect size and direction of the effect and their significance (t -test) are denoted by stars (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

Variable	Coefficient ± SE	<i>F</i>	d.f.	<i>p</i>
Constant	29.16 ± 1.75***			
Capture	−4.74 ± 1.87*	6.26	1,148	0.01
Year	−8.12 ± 1.88***	124.94	1,148	< 0.001
Sex	−0.67 ± 1.14	7.78	1,148	0.006
Repr	9.18 ± 1.79***	13.75	1,148	< 0.001
Capture × year		47.33	1,148	< 0.001
Trapped × 2003	5.97 ± 1.99**			
Capture × sex		6.39	1,148	0.01
Trapped × male	3.64 ± 1.37*			
Capture × repr		4.19	1,148	0.04
Trapped × active	−7.21 ± 1.88***			
Year × repr	−7.05 ± 1.90***	13.80	1,148	< 0.001

Table 3. Minimal adequate linear mixed effects model on the variation in body mass of bank voles explained by the fixed effects ‘capture’ (1 = preyed upon by Ural owls, 2 = trapped), yearly variation, sex (0 = female, 1 = male), and interactions. The random effect “sampling location” (territory or trapping site, $n = 42$) is non-significant, but included in the model to control for pseudoreplication (Variance = 1.4×10^{-7} (95% CI = 3.7×10^{-147} – 4.9×10^{132}), $\chi^2 = 0$, d.f. = 1, $p = 1$). Coefficients as in Table 1. The fixed effect ‘repr’ (reproductive state) was non-significant and dropped from the model.

Variable	Coefficient ± SE	<i>F</i>	d.f.	<i>p</i>
Constant	25.33 ± 0.84***			
Capture	−6.96 ± 1.05***	34.96	1,46	< 0.001
Year	−5.73 ± 1.13***	32.86	1,46	< 0.001
Sex	−0.72 ± 1.10	2.31	1,46	0.14
Capture × year		4.69	1,46	0.03
Trapped × 2003	2.82 ± 1.48			
Capture × sex		4.32	1,46	0.04
Trapped × male	2.86 ± 1.38*			

preyed upon and trapped voles did not differ (Table 1; GLMM, dropped variable: capture: $\chi^2 = 0.04$, d.f. = 1, $p = 0.84$). Only a high proportion of males among the reproductively active individuals (sex: $\chi^2 = 6.34$, d.f. = 1, $p = 0.01$) explained the variation in reproductive state.

Vole sex ratio in cached prey and in the field

The sex ratio of the preyed upon field voles was not statistically different from the sex ratio at the trapping sites (Table 1; GLMM, capture: $\chi^2 = 0.28$, d.f. = 1, $p = 0.60$). The sex ratio of both preyed upon and trapped field voles differed significantly between years (year: $\chi^2 = 6.82$, d.f. = 1, $p = 0.009$), and it was more male-biased among reproductively active individuals (repr: $\chi^2 = 5.65$, d.f. = 1, $p = 0.02$). No interactions were significant.

The sex ratio of bank voles did not differ between preyed upon and trapped individuals (Table 1; GLMM: capture, dropped variable: $\chi^2 = 0.004$, $p = 0.95$). The only variable accounting for variation in bank vole sex ratio was reproductive state, as the sex ratio was male biased in reproductively inactive individuals (repr: $\chi^2 = 6.05$, d.f. = 1, $p = 0.01$) in both cached and trapped bank voles.

Discussion

In this study, we investigated the selective nature of predation on field voles and bank voles by the Ural owl. In the northern hemisphere, avian predation is commonly thought to have only a stabilizing effect on the cyclic population dynamics of voles (reviewed by Sundell 2006). However, specific predation on selected individuals from a population may have consequences for life-history decisions of the prey, and hence, on the demography of the prey species. The two prey species studied here, field voles and bank voles, show marked differences in their social organisation. Field vole males are territorial whereas females have fixed home ranges that they do not defend (Myllymäki 1977). In contrast, bank vole females are territorial and dominant over males,

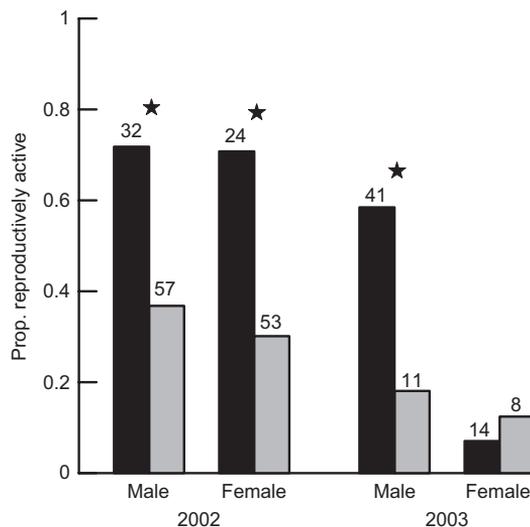


Fig. 2. Proportion of reproductively active male and female field voles preyed upon by Ural owls (black bars) and trapped in the field (grey bars). Total sample size is given above the bars and significant differences in a GLMM between preyed upon and trapped voles are indicated by stars above the bars.

and the males form groups in larger home ranges (Viitala and Hoffmeyer 1985). These major differences in the social structure inevitably predict differences between species in their vulnerability to predation, and that predation vulnerability would depend on an individual's life-history stage or reproductive state.

We found that Ural owls captured more reproductively active field voles than predicted from the trapping data. On the other hand, no selection for reproductively active individuals was found in Ural owl predation on bank voles. Mate searching strategies and pregnancy can increase the predation risk of small mammals (Magnhagen 1991, Koskela *et al.* 1996). Several studies have shown that least weasels (*Mustela nivalis*) prefer reproductively active voles and mice (Cushing 1984, 1985, Rozenfeld & Rasmont 1991, Ylönen *et al.* 2003, but *see* Sundell *et al.* 2003) and it has been suggested that this prey selection by mammalian predators is due to the intense odour of the reproductive (female) individuals (Sharpe & Millar 1990). However, in contrast to weasels and other mustelids, birds of prey do not use olfactory cues when hunting, but instead their vision (diurnal birds of prey, Viitala *et al.* 1995) or hearing (nocturnal birds of prey,

Bye *et al.* 1992, Koivula *et al.* 1997). Therefore, it is unlikely that Ural owls would selectively prey upon reproductively active vole individuals on the basis of olfactory cues. Instead, Ural owls may select reproductively active prey, simply because of their different and potentially more vulnerable behaviour (Magnhagen 1991). Indeed, the behaviour of reproductively active field voles is more exposing to predation than the behaviour of reproductively inactive ones. Reproductive voles conceivably need more energy and therefore would need to forage more often. In addition, reproductively active males rigorously defend their territories, and female field voles disperse frequently between weaning and giving birth to the next litter, which exposes them to predators (Myllymäki 1977, Viitala and Hoffmeyer 1985).

Field voles mainly disperse when in a reproductively active state, whereas bank voles disperse mainly at a younger age when they still are immature and not reproductively active (Viitala *et al.* 1994). This different dispersal pattern in field voles and bank voles could explain why Ural owls prey proportionally more upon reproductively active field voles but not on reproductively active bank voles. Different dispersal behaviour of field voles and bank voles could therefore affect the vulnerability of reproductively active individuals to predation by Ural owls.

Reproductively active field voles were heavier than reproductively inactive ones, whereas in bank voles there was no difference in body mass between reproductively active individuals and inactive ones. These results, in which Ural owls selected the heaviest and therefore also the most “valuable” individuals of both field voles and bank voles, are contrary to the findings in other studies on owl prey selection. Tengmalm’s owls (Koivunen *et al.* 1996), pygmy owls (Mappes *et al.* 1993), Magellanic horned owls (*Bubo magellanicus*, Longland and Jenkins 1987, Trejo and Guthmann 2003) and barn owls (Dickman *et al.* 1991) all prey on smaller prey individuals than expected from observations in the field. In contrast, our results suggest that Ural owls preyed upon the largest prey individuals, which most probably are the dominant individuals that inhabit the preferred habitats. It has been suggested that smaller prey individuals are

more vulnerable to predation, e.g. due to smaller (younger) individuals being inexperienced in predator avoidance (Longland and Jenkins 1987, Dickman *et al.* 1991) or because of their subordinate social status, which forces them to live in poorer and more open habitats (Halle 1988, Pusenius & Viitala 1993, Trejo and Guthmann 2003, Meri *et al.* 2008). A difference in selection of hunting habitat between these owl predators may explain the different pattern of prey selection based on size.

The proportion of reproductively active voles in a population differs between vole cycle phases (Norrdahl & Korpimäki 1995). We found that Ural owls cached proportionally more reproductively active than inactive field voles, which could be an effect of the vole cycle. However, we found similar results in both years (increase and decrease phase of the vole cycle) of the study. We only found that the difference in body mass between cached and trapped voles was more pronounced in the increase vole phase 2002 than in the decrease vole phase 2003. Moreover, a long-term study of Tengmalm’s owl predation on small mammals found no clear change in prey selection in the different phases of the vole cycle (Koivunen *et al.* 1996).

In our study, we assumed that our estimation of available vole prey by snap-trapping yields a random sample of the prey population. However, it is possible that there are individual differences in the probability of being caught in a snap-trap. Therefore, sex ratio, body mass and reproductive state of the individuals that were preyed upon may have differed from that of snap-trapped ones solely due to non-random probability of being caught in a snap-trap (or by an owl). For example, trap baits may attract field voles and bank voles differently depending on their state, size, or movements, and therefore snap-trapping may not mirror the real distribution. Another possible problem is that the cached prey items in the nest boxes are a non-random sample of the prey composition the Ural owl catches. Some of the prey items are consumed by the parent owl before they are delivered to the nest and these prey items may be of a certain sex, size or state. For example, the ‘load-size effect’ hypothesis predicts that small prey items are eaten more often at the capture site than large prey items

(Sonerud 1992). Future work should focus on relevance of these artefacts of possible over- or under-representation of a prey type in food caches as compared with trapped in studies of prey selection and vulnerability to predation. For example, any bias of snap-trapping can be evaluated by carrying out trapping in an enclosure with known composition of voles. Despite the issue of the extent of bias introduced by using data collected by snap-trapping as indicative of the abundance of voles in the field, our conclusions regarding the observed differences in prey selection by the Ural owl as compared with other owl species remains robust, since all these prey selection studies are based on a comparison of cached prey with snap-trapped prey.

We conclude that — in contrast to other owl species studied — Ural owls selected larger field voles and bank voles than expected from those trapped in the field. Our findings further imply that Ural owl predation is directed at reproducing individuals (especially in the field vole). By selecting the largest, reproducing individuals, Ural owls may have a larger impact on prey population dynamics than expected solely from the numbers of voles that they predate.

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