

Younger bank voles are more vulnerable to avian predation

Taru Meri, Matti Halonen, Tapio Mappes, and Jukka Suhonen

Abstract: The importance of predation on prey populations is mainly determined by the number of eaten prey. However, the total impact of predation might also be determined by the selection of certain prey individuals, e.g., different sexes or age categories. Here we tested selective predation by an avian predator, the pygmy owl (*Glaucidium passerinum* (L., 1758)), on bank voles (*Myodes (Clethrionomys) glareolus* (Schreber, 1780)). We compared the sex, age, and mass of hoarded prey with the animals snap-trapped from the field. There were no differences in the sex ratio between hoarded bank voles and those available in the field. However, hoarded voles were significantly younger than ones in the field sample. There was no statistically significant difference in mass between animals from larders and from the field. We suggest that the greater vulnerability of younger animals to predation might be due to their higher activity, or alternatively, they might be forced to forage in less safe habitats.

Résumé : L'importance de la prédation pour les populations de proies est surtout fonction du nombre de proies consommées. Cependant, l'impact global de la prédation peut aussi être déterminé par la sélection de certaines proies individuelles, par exemple de catégories différentes de sexe ou d'âge. Nous vérifions ici la prédation sélective chez un oiseau prédateur, la chevêchette d'Europe (*Glaucidium passerinum* (L., 1758)), sur les campagnols roussâtres (*Myodes (Clethrionomys) glareolus* (Schreber, 1780)). Nous avons comparé le sexe, l'âge et la masse chez les proies accumulées dans les nichoirs et chez les animaux capturés au piège à souris en nature. Il n'y a pas de différence entre les proportions des sexes chez les campagnols roussâtres accumulés et ceux qui sont disponibles en nature. Cependant, les campagnols roussâtres accumulés sont significativement plus jeunes que ceux de l'échantillon de terrain. Il n'y a aucune différence statistiquement significative entre les masses des animaux dans les garde-manger et en nature. Nous croyons que la plus grande vulnérabilité des animaux plus jeunes à la prédation peut s'expliquer par leur activité plus élevée; il se peut aussi qu'ils soient obligés de chercher leur nourriture dans des habitats moins sûrs.

[Traduit par la Rédaction]

Introduction

Predators usually take socially subordinate individuals, which are in poor condition and (or) young (Errington 1956; Hudson 1986; Temple 1987). For example, avian predators feeding on shrews and voles often catch smaller individuals and males (Lagerström and Häkkinen 1978; Korpimäki 1985; Halle 1988; Mappes et al. 1993; Koivunen et al. 1996a, 1996b; Christie et al. 2006). However, other studies have reported that young females have a higher probability of being preyed upon than smaller individuals or males (Longland and Jenkins 1987; Dickman et al. 1991). Smaller animals usually have lower social status than larger animals, which forces them to move and forage in less prof-

itable or safe habitats. Furthermore, the greater vulnerability of smaller animals might be related to age-specific behaviour. For example, young small-mammal males disperse more frequently (Ims 1989), which increases their risk of predation. However, accurate age determination is a problem with many small-mammal species, so the smaller prey are usually considered the younger ones in the previous studies.

We tested the hypothesis that sex, age, and mass of bank voles (*Myodes (Clethrionomys) glareolus* (Schreber, 1780)) affect their predation risk by the generalist avian predator pygmy owl (*Glaucidium passerinum* (L., 1758)) in late autumn and early winter. We expected that younger and lighter bank voles, especially the males, would be predated more often than expected according to their availability in the field.

Received 4 February 2008. Accepted 7 July 2008. Published on the NRC Research Press Web site at cjz.nrc.ca on 5 September 2008.

T. Meri,¹ M. Halonen, T. Mappes, and J. Suhonen.^{2,3} Department of Biological and Environmental Science, P.O. Box 35, University of Jyväskylä, FIN-40014 Jyväskylä, Finland.

¹Present address: Haartman Institute, Department of Bacteriology and Immunology, P.O. Box 21, University of Helsinki, FIN-00014 Helsinki, Finland.

²Corresponding author (e-mail: juksuh@utu.fi).

³Present address: Section of Ecology, Department of Biology, University of Turku, FIN-20014 Turku, Finland.

Materials and methods

Study species

The bank vole is a common mammal in coniferous forests of northern Europe (Stenseth 1985). The breeding period in central Finland lasts from May to September (Koivula et al. 2003). Pregnancy lasts between 19 and 20 days and pups are weaned until they are 3 weeks old (Mappes et al. 1995a). Reproducing female bank voles are territorial, whereas males and nonbreeding individuals are not since their home ranges overlap (Bondrup-Nielsen and Karlsson 1985; Mappes et al. 1995b; Koskela et al. 1997; Jonsson et al. 2002).

The pygmy owl is a generalist predator (Kellomäki 1977; Solheim 1984; Suhonen 1993; Halonen et al. 2007; Suhonen et al. 2007), because it exploits a wide range of food items. It also hoards food during late autumn and early winter, thereby improving its survival when food is more scarce, i.e., during mid-winter (Solheim 1984; Källander and Smith 1990; Suhonen 1993; Halonen et al. 2007; Suhonen et al. 2007).

Study site and procedure

The research was carried out in Konnevesi, central Finland (62°37'N, 26°20'E), during autumns and winters of 1990–1991 and 1991–1992. One hundred and five food-hoarding boxes (21 groups (or plots) of 5 boxes each) were placed in the winter territories of pygmy owls around Konnevesi. The distance between each plot varied from 5 to 7 km, which prevented the same owl from hoarding in two different plots simultaneously. In the plots, boxes were placed near each other so as to prevent the territorial owls from sharing caches with other owls. The entrance hole of each box was 45 mm in diameter, which is wide enough only for the pygmy owl (Solheim 1984; Halonen et al. 2007; Suhonen et al. 2007).

Hoarding boxes and their contents were checked at least twice a month from the beginning of October to the end of April each year. Bank voles hoarded by pygmy owls were exchanged with similar individuals that were toe-clipped to allow for the monitoring of consumption of stored prey (Halonen et al. 2007; Suhonen et al. 2007). We only considered the bank voles in detail, although birds and other species of mammals were found in the hoarding boxes as well.

The density of bank voles in the field was estimated each year in the beginning of October by snap-trap captures (see Halonen et al. 2007). To monitor the availability of prey reliably, trappings were done in three different habitats: abandoned field, spruce forest, and young deciduous tree forest. The total number of trap-nights was 900 and was the same every year. Abundance is given as the number of bank voles caught each autumn. Only the winters of 1990–1991 and 1991–1992 are used in the analysis, as there were sufficient numbers of bank voles both in the field and in hoarding boxes for data comparisons. Voles from hoarding boxes and snap traps were weighed with a Pesola® spring balance to the nearest 0.1 g. Autumn density of voles (*Myodes (Clethrionomys)* and *Microtus* Schrank, 1798 voles together) per 100 trap-nights was 9.3 in 1990 and 23.1 in 1991 (for more details about the voles killed by pygmy owls in our study area see Suhonen 1993 and Halonen et al. 2007).

Table 1. Sex of bank voles (*Myodes (Clethrionomys) glareolus*) in the field and in the hoarding boxes used by pygmy owls (*Glaucidium passerinum*) in the winters of 1990–1991 and 1991–1992.

	Field		Hoarded	
	<i>n</i>	Percentage	<i>n</i>	Percentage
Winter of 1990–1991				
No. of males	30	51.7	35	57.4
No. of females	28	48.3	26	42.6
Total	58		61	
Winter of 1991–1992				
No. of males	26	55.3	10	66.7
No. of females	21	44.7	5	33.3
Total	47		15	

Reasonably accurate age determination of small mammals has proven possible only in the case of *Myodes (Clethrionomys)* species, which can be determined from the teeth (Lowe 1971; Viro 1974; Mihok 1980; Gustafsson et al. 1982) because the roots continue growing throughout the life of the animal. Age determination is based on the first lower molar in the mandible or the second upper molar in the maxilla (Zejda 1977; Gustafsson et al. 1982). The proportion of the length of separate roots or the ratio of root length to length of the entire tooth have been used. To control the accuracy of measurements, staining solution injections were also used (Lowe 1971).

We used root measurements of the first lower molar tooth on the right and left mandibles to determine the age of the bank voles (for details see Gustafsson et al. 1982). The heads of individually marked bank voles were boiled to make the removal of teeth easier. The length of the tooth roots were measured under the microscope to the nearest micrometer (μm). The mean length of the tooth roots were highly correlated with age when 15 bank voles, whose exact ages were known, were tested with regression analysis. This regression ($\text{age} = 4.975 + 0.489 \times \text{length of tooth roots } (\mu\text{m}), r^2 = 0.81$) was then used to calculate the ages of all bank voles. Age-determined animals originated from the same population of bank voles as the hoarded and snap-trapped individuals; they also had similar developmental conditions in nature. We noted that the age of very young animals (<30 days) could not be measured from teeth because the neck structure of the tooth had not yet formed. In the snap-trapping sample, there were four voles that were younger than 30 days, as no neck structure was found in their teeth; thus, they were aged to be 25 days old.

Since the hoarded bank voles were found later than those snap-trapped in the field, the ages of hoarded voles were corrected to account for this time difference. Based on when the animal was found in the box and when the box was last checked, the age (based on tooth length) was reduced to be comparable with the age of the vole at the beginning of October when the snap-trapping was done. For example, the age of a bank vole collected from a hoarding box on 9 November was calculated to be 113 days. Boxes were checked on 2 November; the median day of two visits was considered to be the day of capture (in this case 6 No-

Table 2. Mean (SD) age and body mass of bank voles (*Myodes (Clethrionomys) glareolus*) in the field and in the hoarding boxes used by pygmy owls (*Glaucidium passerinum*) in the winters of 1990–1991 and 1991–1992.

	Field			Hoarded			Student's <i>t</i> test		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	<i>t</i>	df	<i>p</i>
Age of vole (days)									
Winter of 1990–1991	75	24	54	55	20	55	4.77	107	0.001
Winter of 1991–1992	81	23	43	48	20	15	4.17	56	0.001
Body mass (g)									
Winter of 1990–1991	17.7	2.6	58	17.5	2.7	61	0.35	117	0.73
Winter of 1991–1992	16.7	1.9	47	17.1	3.1	15	−0.46	60	0.65

Note: Age of hoarded bank voles was corrected by accounting for the differences between hoarding time and field snap-trapping days (for details see Materials and methods).

vember). The corrected age of 79 days, which is comparable with the age at the beginning of October when the snap-trapping was done, was obtained by subtracting 34 days from the estimated age of 113 days.

The body mass and corrected ages of bank voles from the field and hoarding boxes were compared using a Student's *t* test. Differences in sex ratio of bank voles between hoarded individuals and those snap-trapped in the field at the same time were tested using a log-likelihood test.

Results

There were no differences in the sex ratio of the bank voles trapped from the field and the larders of pygmy owls (winter 1990–1991: $G^2 = 0.38$, $df = 1$, $p = 0.54$; winter 1991–1992: $G^2 = 0.6$, $df = 1$, $p = 0.44$; Table 1). In both winters, there were no differences in body mass between snap-trapped bank voles from the field population and from the larders of pygmy owls (Table 2).

Bank voles from larders of pygmy owls were significantly younger than those trapped in the field (Table 1). During the winter of 1990–1991, the absolute ages of bank voles varied from 42 to 143 days. After correction (see Materials and methods), the oldest vole was 134 days and the youngest was −3 days. There was one individual, whose age estimate was below 0 day. It was taken from a hoarding box in January and its age was subtracted by 101 to match the date of snap-trapping in October. Its absolute age was 104 days, indicating that it had been born very late in autumn; this result is consistent with reports of late autumn or winter reproduction in bank voles (Larsson et al. 1973). During the winter of 1991–1992, absolute ages varied from 29 to 180 days. After correction, the maximum age was 180 days and the minimum was 27 days (Table 1).

Discussion

Although most early studies of small-mammal predation by birds of prey have shown that males are the more vulnerable prey sex (e.g., Southern and Lowe 1968; Lagerström and Häkkinen 1978; Korpimäki 1985; Halle 1988; Mappes et al. 1993; Koivunen et al. 1996a), we failed to find evidence for male-biased prey selection by pygmy owls. Only a few early studies have documented no sex preferences in predated voles by birds of prey (Boonstra and Krebs 1977; Koivunen et al. 1996b). A greater proportion of males dis-

persing to new, perhaps poorer, habitats is the reason for male dominance in the diet of avian predators (Korpimäki 1985), especially during the breeding season. Outside the breeding season, the proportion of males decrease, which may explain why there was as many male and female bank voles in the larders of pygmy owls. Also, several studies have shown that avian predators capture lighter voles compared with the ones available in the field (Mappes et al. 1993; Koivunen et al. 1996a, 1996b); we found no evidence to support this result. An explanation for this difference in results may be that the previous studies were done during the breeding season (i.e., late spring and early summer), while our study was done during late autumn and early winter.

Young bank voles seem to be more vulnerable to avian predation. Previous studies have shown that younger, small-mammal females are the most vulnerable to avian predators (Longland and Jenkins 1987; Dickman et al. 1991). Young individuals disperse more and are considered subordinates, which are often forced to forage in more open habitats (Dickman et al. 1991). There were no bank voles younger than 30 days in the caches, probably because there were only a few of them in our study area during our study period and because birds of prey were not able to find such young small mammals (Korpimäki and Norrdahl 1991). Behaviour of younger animals can be different from older animals and thus attract more attention. Juveniles may lack the experience and sensory skills to avoid predators.

The social structure of all *Myodes (Clethrionomys)* species involve exclusive female territoriality (Bujalska 1985). Mature females have territories without mature or immature males; dispersal in *Myodes (Clethrionomys)* species is highly male-biased and all mature males leave their natal range (Ims 1989). Some females stay and reproduce in the natal range, while others disperse and then avoid other females as much as possible (Ims 1989). Males have larger home ranges than females, which increases their mobility. The numbers of pygmy owls hoarding food and the amount of food items varied according to the density of bank voles. Density-dependent predation is thought to dampen population cycles (Murdoch and Oaten 1975).

A major assumption of our study is that the estimation of available prey (snap-trapped individuals) is randomly sampled from the prey population. If a different age class is more susceptible to snap-trapping, a pattern may result even

if the pygmy owls are randomly selecting from the prey population. Biased trappability is a general problem in field studies of small mammals. Individual differences in trappability can be estimated using long-term live-trappings, which could not be done in our case since our bank voles were snap-trapped. Future studies should focus more effectively on this possible artefact of the present study.

In conclusion, predation by the pygmy owl is strongly biased towards young bank voles. Young animals are subordinates, and in particular, females do not always breed. Since predation is not directed towards older and breeding females, the dampening effects of density-dependent predation might decrease. More research is needed to explain how predation towards different age classes affects population dynamics of prey.

Acknowledgements

We thank the staff of Konnevesi Research Station for assistance with the fieldwork, especially Antti Sirkka, who made the hoarding boxes. We thank Mikael Mökkönen for assistance with the English of the manuscript. This work was financially supported by the Emil Aaltonen Foundation to M. Halonen and J. Suhonen, Cultural Foundation of Central Finland and Jenni and Antti Wihuri Foundation to M. Halonen, Academy of Finland to J. Suhonen (no. 114841), Suomen Biologian Seura Vanamo to M. Halonen and T. Meri, and Societas Pro Flora et Fauna Fennica to T. Meri. This study was funded by the Academy of Finland, Finnish Centre of Excellence Programme (2000–2005) (J. Suhonen and T. Mappes), and the Academy of Finland (grant nos. 63789, 202166, and 206091 to T. Mappes).

References

- Bondrup-Nielsen, S., and Karlsson, F. 1985. Movements and spatial patterns in populations of *Clethrionomys* species: a review. *Ann. Zool. Fenn.* **22**: 385–392.
- Boonstra, R., and Krebs, C.J. 1977. A fencing experiment on a high-density population of *Microtus townsendii*. *Can. J. Zool.* **55**: 1166–1175.
- Bujalska, G. 1985. Regulation of female maturation in *Clethrionomys* species, with special reference to an island population of *C. glareolus*. *Ann. Zool. Fenn.* **22**: 331–342.
- Christe, P., Keller, L., and Roulin, A. 2006. The predation of cost of being a male: implications for sex-specific rates of ageing. *Oikos*, **114**: 381–384. doi:10.1111/j.2006.0030-1299.15130.x.
- Dickman, C.R., Predavec, M., and Lynam, A.J. 1991. Differential predation of size and sex classes of mice by the barn owl, *Tyto alba*. *Oikos*, **62**: 67–76. doi:10.2307/3545447.
- Errington, P.L. 1956. Factors limiting higher vertebrate populations. *Science* (Washington, D.C.), **124**: 304–307. doi:10.1126/science.124.3216.304. PMID:17807823.
- Gustafsson, T.O., Andersson, C.B., and Westlin, L.M. 1982. Determining the age of bank voles — a laboratory study. *Acta Theriol.* **27**: 275–282.
- Halle, S. 1988. Avian predation upon a mixed community of common voles (*Microtus arvalis*) and wood mice (*Apodemus sylvaticus*). *Oecologia* (Berl.), **75**: 451–455. doi:10.1007/BF00376950.
- Halonen, M., Mappes, T., Meri, T., and Suhonen, J. 2007. Influence of snow cover on food hoarding in Pygmy Owls *Glaucidium passerinum*. *Ornis Fenn.* **84**: 105–111.
- Hudson, P.J. 1986. The effect of a parasitic nematode on the breeding production of red grouse. *J. Anim. Ecol.* **55**: 85–92. doi:10.2307/4694.
- Ims, R.A. 1989. Kinship and origin effects on dispersal and space sharing in *Clethrionomys rufocanus*. *Ecology*, **70**: 607–616. doi:10.2307/1940212.
- Jonsson, P., Hartikainen, T., Koskela, E., and Mappes, T. 2002. Determinants of reproductive success in voles: space use in relation to food and litter size manipulation. *Evol. Ecol.* **16**: 455–467. doi:10.1023/A:1020854525220.
- Kellomäki, E. 1977. Food of the Pygmy Owl *Glaucidium passerinum* in the breeding season. *Ornis Fenn.* **54**: 1–29.
- Koivula, M., Koskela, E., Mappes, T., and Oksanen, T.A. 2003. Costs of reproduction in the wild: manipulation of reproductive effort in the bank vole. *Ecology*, **84**: 398–405. doi:10.1890/0012-9658(2003)084[0398:CORITW]2.0.CO;2.
- Koivunen, V., Korpimäki, E., and Hakkarainen, H. 1996a. Differential avian predation on sex and size classes of small mammals: doomed surplus or dominant individuals? *Ann. Zool. Fenn.* **33**: 293–301.
- Koivunen, V., Korpimäki, E., Hakkarainen, H., and Norrdahl, K. 1996b. Prey choice of Tengmalm's owls (*Aegolius funereus*): preference for substandard individuals? *Can. J. Zool.* **74**: 816–823. doi:10.1139/z96-094.
- Korpimäki, E. 1985. Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. *Ann. Zool. Fenn.* **22**: 91–104.
- Korpimäki, E., and Norrdahl, K. 1991. Do breeding nomadic avian predators dampen population fluctuations of small mammals. *Oikos*, **62**: 195–208. doi:10.2307/3545265.
- Koskela, E., Mappes, T., and Ylönen, H. 1997. Territorial behaviour and reproductive success of bank vole *Clethrionomys glareolus* females. *J. Anim. Ecol.* **66**: 341–349. doi:10.2307/5980.
- Källander, H., and Smith, H.G. 1990. Food storing in birds, an evolutionary perspective. *Curr. Ornithol.* **7**: 147–207.
- Lagerström, M., and Häkkinen, I. 1978. Uneven sex ratio of voles in the food of *Aegolius funereus* and *Strix aluco*. *Ornis Fenn.* **55**: 149–153.
- Larsson, T.-B., Hansson, L., and Nyholm, E. 1973. Winter reproduction of small rodents in Sweden. *Oikos*, **24**: 475–476. doi:10.2307/3543826.
- Longland, W.S., and Jenkins, S.H. 1987. Sex and age affect vulnerability of desert rodents to owl predation. *J. Mammal.* **68**: 746–754. doi:10.2307/1381551.
- Lowe, V.P.W. 1971. Root development of molar teeth in the bank vole (*Clethrionomys glareolus*). *J. Anim. Ecol.* **40**: 49–61. doi:10.2307/3329.
- Mappes, T., Halonen, M., Suhonen, J., and Ylönen, H. 1993. Selective avian predation of the field vole, *Microtus agrestis*: greater vulnerability of males and subordinates. *Ethol. Ecol. Evol.* **5**: 225–234.
- Mappes, T., Koskela, E., and Ylönen, H. 1995a. Reproductive costs and litter size in the bank vole. *Proc. R. Soc. Lond. B Biol. Sci.* **261**: 19–24. doi:10.1098/rspb.1995.0111.
- Mappes, T., Ylönen, H., and Viitala, J. 1995b. Higher reproductive success among kin groups of bank voles *Clethrionomys glareolus*. *Ecology*, **76**: 1276–1282. doi:10.2307/1940934.
- Mihok, S. 1980. Ageing young *Clethrionomys gapperi* with M² tooth characteristics. *Can. J. Zool.* **58**: 2280–2281. doi:10.1139/z80-310.
- Murdoch, W.W., and Oaten, A. 1975. Predation and population stability. *Adv. Ecol. Res.* **9**: 1–131. doi:10.1016/S0065-2504(08)60288-3.
- Solheim, R. 1984. Caching behaviour, prey choice and surplus kill-

- ing by Pygmy Owls *Glaucidium passerinum* during winter, a functional response of a generalist predator. *Ann. Zool. Fenn.* **21**: 301–308.
- Southern, H.N., and Lowe, V.P. 1968. The pattern of distribution of prey and predation in Tawny Owl territories. *J. Anim. Ecol.* **37**: 75–97. doi:10.2307/2712.
- Stenseth, N.C. 1985. Geographic distribution of *Clethrionomys* species. *Ann. Zool. Fenn.* **22**: 215–219.
- Suhonen, J. 1993. Predation risk influences the use of foraging sites by tits. *Ecology*, **74**: 1197–1203. doi:10.2307/1940490.
- Suhonen, J., Halonen, M., Mappes, T., and Korpimäki, E. 2007. Interspecific competition reduce the larders of Pygmy owls. *J. Avian Biol.* **38**: 630–634.
- Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations. *Ecology*, **68**: 669–674. doi:10.2307/1938472.
- Viro, P. 1974. Age determination in the bank vole, *Clethrionomys glareolus* Schreb. 1780, from the roots of the teeth. *Aquilo Ser. Zool.* **15**: 33–36.
- Zejda, J. 1977. A device serving to determine the birth date of *Clethrionomys glareolus* by the length of M1 roots. *Folia Zool.* **26**: 207–211.