

## Selective avian predation on a population of the field vole, *Microtus agrestis*: greater vulnerability of males and subordinates

T. MAPPES, M. HALONEN, J. SUHONEN and H. YLÖNEN

*University of Jyväskylä, Department of Biology, Konnevesi Research Station, SF-44300  
Konnevesi, Finland*

Received 24 August 1992, accepted 25 March 1993

Selective predation on certain sex or age components within prey populations may greatly affect prey population dynamics. We studied predation by the pygmy owl *Glaucidium passerinum* on the different social groups of the field vole *Microtus agrestis* during the autumn after a peak year of cyclic microtine populations in central Finland. The availability of prey was monitored on a trapping grid consisting of field and forest habitats. The diet of the pygmy owl was studied in three separate areas with boxes available as food storage for the owls. Relatively more male field voles were taken than would be expected on the basis of their availability in the prey population. On average, males moved shorter distances than females during a trapping night, which indicates that the vulnerability of males is not due to their greater activity. Both the males and the females in the diet were lighter and obviously younger than the average of the prey populations. Lighter individuals in the population preferred the forest which is a suboptimal habitat for the field vole. Trappability, which measures social dominance, was lower among these lighter individuals. Subordinate individuals are obviously more exposed to predation by the pygmy owl in a forest habitat, which offers less shelter in late autumn. Due to the density-dependent mortality they cause, avian predators have been thought to dampen fluctuations in the vole population. We discuss how the distinct choice of certain class of prey affects the interaction between avian predators and small mammal prey.

KEY WORDS: *Glaucidium passerinum*, habitat use, *Microtus agrestis*, selective avian predation, social status, vulnerability.

---

Introduction . . . . .	520
Material and methods . . . . .	520
Results . . . . .	522
Discussion . . . . .	524
Acknowledgements . . . . .	526
References . . . . .	526

## INTRODUCTION

Predators often selectively catch certain sex or age types within prey populations. This is caused mainly by the interaction between the behaviour and the morphology of both predator and prey. The hunting efficiency of predators varies, especially in a heterogenous habitat, and so some individuals in the prey population may obtain absolute or partial refuge. For example, a cover of vegetation and snow affects selection of the feeding habitat and the catching efficiency of avian predators (KORPIMÄKI 1986, NYBO & SONERUD 1990, PRESTON 1990), whereas the spatial variation in predation risk and food acquisition together affect the microhabitat selection of the small mammal prey of these birds (SIMONETTI 1989, DICKMAN et al. 1991). Furthermore, the dominant individuals should occupy the most optimal microhabitats with regard to these two factors, and thus might, for example, force subordinates to choose areas that are less sheltered from avian predation (ERRINGTON 1956).

Birds of prey that feed on rodents and shrews in particular catch young males (PEARSON & PEARSON 1947; LOCKIE 1955; THOMSON 1955; FULK 1976; LAGERSTRÖM & HÄKKINEN 1978; BEACHAM 1979; KORPIMÄKI 1981, 1985; HALLE 1988). On the contrary, LONGLAND & JENKINS (1987) and DICKMAN et al. (1991) found that in populations of many rodent species young females were most vulnerable. However, some studies have reported no size or sex preference by avian predators (SOUTHERN & LOWE 1968, BÖNSTRA 1977). Male predominance in the prey may be due to the greater activity of male voles, especially during the breeding season. Indeed, later in the breeding season the proportion of males in the prey decreases (KORPIMÄKI 1981). Juvenile individuals are presumably more susceptible to predation due to their social position (ERRINGTON 1956). In fact, DICKMAN et al. (1991) showed that dominant adult mice forced subordinate juveniles to use a more open habitat, thus making them more vulnerable to predation by owls.

We studied predation on the field vole *Microtus agrestis* by the pygmy owl *Glaucidium passerinum* in central Finland during the autumn after a peak year for local microtine populations (YLÖNEN 1989a). In autumn the pygmy owl begins to hoard voles in suitable natural cavities or in nest boxes. The owls continue to hoard throughout the winter, but the intensity of hoarding varies (SOLHEIM 1984). In this study the diet of pygmy owls was monitored in three separate nest box areas. In addition, the dynamics and social system of potential prey populations of microtines was monitored in a long-term live trapping area.

The main questions we attempted to answer were: (i) is avian predation directed more towards the lower groups in the social hierarchy of the prey population? (ii) does habitat selection and/or use of space influence the vulnerability of individual voles?

## MATERIAL AND METHODS

This study was conducted at Konnevesi, central Finland (62°37'N, 26°20'E) during the autumn and winter of 1988-1989 after a peak summer for the local cyclic vole population (YLÖNEN 1989a). In our field area the densities of bank vole *Clethrionomys glareolus* had already declined during the summer of 1988, but the densities of field vole *Microtus agrestis* remained relatively high until mid-winter 1988-1989 (Fig. 1).

The diet of the pygmy owl was studied on 11 separate plots around Konnevesi Research Station from late October 1988 to late March 1989. On each plot five nest boxes were provided for the owls. The distances between the hoarding plots were 5-7 km. Around the three hoarding areas, where pygmy owls hoarded the voles, we determined the proportions and the structure of field and forest within a radius of 250 m: half of the areas consisted of spruce forest and the other half was abandoned field. The proportions of forest and field were the same as the live trapping area, where we studied the availability of voles (see below). The structure of forest and ground vegetation were very similar in hoarding areas and the trapping area. Moreover, one of the hoarding plots was in exactly the same area where the voles were trapped. The hoarding boxes had an entrance hole 45 mm in diameter, which is too small to be used by any owl other than the pygmy owl (SOLHEIM 1984). Prey items caught by pygmy owls and placed in nest boxes were checked and identified every week. The sex of each stored vole was identified and they were weighed with a Pesola-spring-balance to the nearest 1.0 g. All prey items were marked individually by toe clipping, and they were returned to the nest box after measurement.

In order to determine reliably the size classes of the prey items caught, we tested whether the weights became less with time. Freshly killed small mammals were placed into the nest box and changes in weight were determined 1 week later. The weights of stored prey items did not decline during the test. Instead, the weight of each prey item was significantly lower at the beginning ( $x = 13.1$  g,  $SD = 6.8$ ,  $n = 20$ ) than at the end of the week ( $x = 13.3$  g,  $SD = 6.9$ ,  $n = 20$ ) (paired t-test,  $t = -4.96$ ,  $df = 19$ ,  $P = 0.0001$ ). When measured separately, the weights of field voles were also significantly greater at the end of the test: in the beginning ( $x = 22.3$  g,  $SD = 4.0$ ,  $n = 4$ ) and in the end ( $x = 22.6$  g,  $SD = 4.1$ ,  $n = 4$ ) (paired t-test,  $t = -3.67$ ,  $df = 3$ ,  $P = 0.035$ ).

During the hunting period we studied the availability of mammalian prey for the pygmy owl on a trapping grid of 0.8 ha in the vicinity of the research station. Half of the trapping area consisted of spruce forest and the other half was abandoned field (see YLÖNEN et al. 1988). The ground cover of the forest consisted mainly of *Vaccinium myrtillus*, *V. viti-*

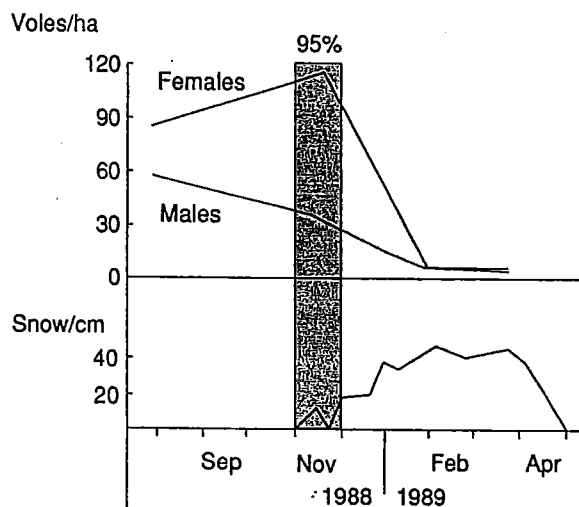


Fig. 1. — The number of *Microtus agrestis* in the 0.8 ha trapping area during the study period. The period in which 95 % of the voles were stored by the pygmy owl at Konnevesi is shown with a shaded bar. The depth of the snow cover in the abandoned field site of the trapping area is given under the graph.

*sidae*, *Equisetum sylvaticum* and mosses. However, the cover provided by this ground vegetation was highly reduced because most plant species had already dropped their leaves in November, when a dense dry grass still covered the ground on the abandoned field. The demography of the free-living population of the field vole *Microtus agrestis* was monitored by live trapping using 80 Ugglan Special traps. The trappings were carried out during August and November 1988 and in January, April and June 1989. During each trapping the traps were checked on average 10 times over 1 week, which ensured that all the vole individuals inside the grid were caught. Because weight may increase during the trapping period, the body weight of each vole was measured the first time the animal was trapped.

Based on data from the live trapping area we determined the density of the vole population, the sex ratio, weight distribution, habitat use, trappability and size of the home range for each individual of the population. Trappability, which measured the social position of the voles (VIITALA 1977), was determined as the captures of each individual as a percentage of the total number of possible captures. "Activity" of the voles was defined simply as the mean distance one individual moved during two trap checkings. Habitat use of the field vole was determined as the percentage of captures in the suboptimal forest habitat.

We used each individual vole as an independent observation for statistical testing. To test the sex differences in the diet of the pygmy owl and in the field, we used the log-likelihood test. To test differences in the weight distribution of individual field voles caught by pygmy owls compared to the voles in the field, we used the two-tailed Mann-Whitney U-test. The correlation of the weight of the individuals captured in the field against their trappability, habitat use and activity was tested with the Spearman rank correlation test.

## RESULTS

We found storages of the pygmy owls in seven nest box areas and three of these storage areas contained enough field vole *Microtus agrestis* for statistical analysis. The total number of prey items stored in these three areas between October and March was 113. Of the prey, 90.2% consisted of microtine rodents, field voles and bank voles *Clethrionomys glareolus*; 7 (6.2%) were harvest mice *Micromys minutus*, 2 (1.8%) were birds and 2 (1.8%) were shrews. Of the microtine rodents, 94 (92.2%) were field voles. Pygmy owls had taken only 8 (7.8%) bank voles, which was the same proportion as found in the field populations during that time (log-likelihood test,  $G^2 = 0.58$ ,  $df = 1$ ,  $P = 0.45$ ). The small number of bank voles forced us to restrict this study to the field vole.

During the second trapping in November the sex ratios and the weights of females and males did not differ between the storage plots (Tables 1 and 2), which

Table 1.

Sex ratio of the field voles in the control population and in the diet of the pygmy owl in November. The samples of the three different diet areas were pooled as the sex ratio did not differ between the areas ( $G^2 = 1.30$ ,  $df = 2$ ,  $P = 0.52$ ).

	Field	Diet
% females	72.9	55.8
% males	27.1	44.2
n	107	95

Difference between field and diet  $G^2 = 6.48$ ,  $df = 1$ ,  $P = 0.011$ .

Table 2.

The weight of the field voles in the control population and in the diet of pygmy owls in November. The samples of three different areas were pooled as the weights of females and males from different storage areas did not differ from each other (Kruskal-Wallis one way ANOVA, for males  $\chi^2 = 3.58$ ,  $P = 0.17$ , for females  $\chi^2 = 2.40$ ,  $P = 0.30$ ).

	Field			Diet			Mann-Whitney U-test	
	x	SD	n	x	SD	n	z	P
Females	25.8	4.1	65	24.0	3.3	53	-2.62	< 0.01
Males	27.4	4.0	29	23.0	2.8	41	-4.69	< 0.001
Total	26.2	4.2	94	23.5	3.1	94	-4.96	< 0.001

Table 3.

Spearman rank correlations for each sex of the field vole control population between the weight and three different variables; trappability, habitat use, and home range size.

	Total	Males	Females
Trappability × weight			
$r_s = 0.196$		$r_s = 0.270$	$r_s = 0.193$
$P = 0.030$ , n = 93		$P = 0.078$ , n = 29	$P = 0.063$ , n = 64
Habitat × weight			
$r_s = -0.205$		$r_s = -0.175$	$r_s = -0.177$
$P = 0.025$ , n = 92		$P = 0.181$ , n = 29	$P = 0.083$ , n = 63
Activity × weight			
$r_s = 0.116$		$r_s = 0.167$	$r_s = 0.218$
$P = 0.20$ , n = 55		$P = 0.261$ , n = 17	$P = 0.095$ , n = 38

minimizes the possibility that regional differences bias the results. Furthermore, the live trapping area and one of the storage plots were exactly in the same area, which also increases a reliance in the comparison between the composition of hoarded voles and the free-living population.

The density of field voles was high during late summer and autumn; in November there were still 133 voles/ha (Fig. 1). The density began to decline strongly after the formation of a permanent snow cover, and in February the density was 11 voles/ha. During the autumn period of high density, the sex ratio of the field population was strongly biased in favour of females (Table 1, Fig. 1) (chi-square test,  $\chi^2 = 30.96$ , df = 1,  $P < 0.001$ ), but evened out to nearly 1:1 by mid-winter. The last field voles disappeared before June 1989. Among all the field voles stored between October and March, 95.4% (n = 94) were stored in November (Fig. 1). In January only a single field vole was stored and after that none.

In the field population of *M. agrestis* the only variable that differed between sexes was activity, which was less for males: males moved an average of only 8 m/night (SD = 6), while females moved 15 m/night (SD = 14) (Mann-Whitney U-test,  $z = -2.03$ ,  $P = 0.04$ ). Females were encountered in the forest slightly more often (20%) than the males (10%) (Mann-Whitney U-test,  $z = -1.54$ ,  $P = 0.12$ ).

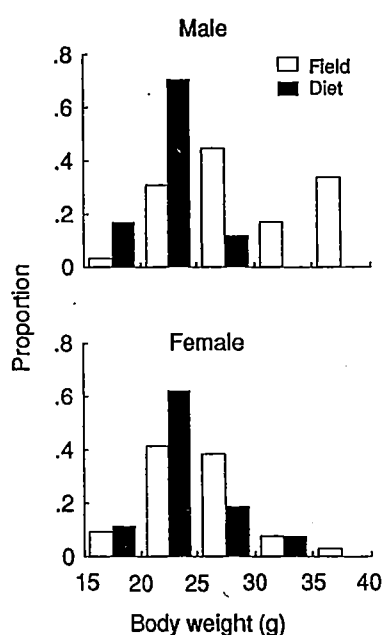


Fig. 2. — The body weights of *Microtus agrestis* in the field population compared with the body weights of voles in the diet of pygmy owls. Data are expressed as percentages within each field or diet sample (for statistics see Table 2).

Trappability of females was 24% compared with 19% for the males (Mann-Whitney U-test,  $z = -1.07$ ,  $P = 0.29$ ). Neither difference was statistically significant. The sex ratio in the field population of *Microtus* was female-biased (in the trapping area 73% of voles were females).

Pygmy owls took female field voles significantly less frequently than would be expected on the basis of their relative availability in the field (Table 1). The number of males and females caught were also significantly lighter than would be expected on the basis on their availability in the field (Fig. 2, Table 2).

When the weights of the field voles captured from the field population was ranked according to trappability, habitat use, and activity, a significant correlation was found between weight and trappability (Table 3), which indicates that lighter individuals occupied a lower social position (VIITALA 1977). There was also a significant negative correlation between weight and habitat use (Table 3), indicating that heavier individuals in the population made less frequent use of the suboptimal forest habitat. This habitat contains relatively poor ground vegetation of *Vaccinium* shrubs and mosses, compared to the abandoned field, which in autumn is covered with tall dense grass. The weight of the field voles did not correlate with their activity.

## DISCUSSION

In our study, outside the breeding season there were relatively more male field voles in the diet of the pygmy owl than in the vole population. Greater vulnerability of males to avian predation has also been shown in several other studies (THOMSON 1955; LAGERSTRÖM & HÄKKINEN 1978; BEACHAM 1979; KORPIMÄKI 1981, 1985; HALLE 1988). However, SOUTHERN & LOWE (1968) and BOONSTRA (1977) showed, that avian predators did not select either of sexes. Most researchers have suggested that male predominance is a consequence of their greater activity in seeking fertile females, especially during the breeding season. This picture is clarified by findings that male predominance decreases late in the breeding season (KORPIMÄKI 1981). According to our study, however, males also predominate in the prey after the breeding season. During the non-breeding season male field voles seemed to move less than females, which indicates that the vulnerability of males is not due to their greater activity. Nor did we find any significant differences

between males and females in habitat use or trappability. Possible explanations for the vulnerability of male voles might be differences between sexes in microhabitat use or diurnal activity. Sex differences in activity rhythms have, for example, recently been observed in the montane vole *Microtus montanus* (ROWSEMITT 1991).

The larger proportion of lighter field voles in the diet of pygmy owls might be a consequence of the social position of these individuals: intraspecific competition forces subordinate individuals to choose habitats that provide less protection against avian predation (ERRINGTON 1956). Indeed, we found that dominant individuals used the field habitat more than subordinate ones. Around the hoarding areas of pygmy owls, forest habitats were less covered than field habitats, especially in late autumn. The dense vegetation shelter and earlier snow cover, which determine the habitat selection of raptors (e.g. NYBO & SONERUD 1990, PRESTON 1990), probably offered better protection against avian predation in the field.

Further, the hunting behaviour of pygmy owls may have a great effect on our findings of selective predation. For example, a small raptor, like the pygmy owl (body mass 55-65 g), might actively select smaller prey individuals, and in that way reduce the cost of hunting, for instance the risk of injury. A further study on this subject has to be carried out before one can make a more reliable generalization about selective predation in larger species of raptors and owls.

In several species of small rodents the sex ratio changes with the season (see references KALELA 1971). Especially in the peak phase of microtine population cycles, the proportion of young male field voles decreases during the breeding season (MYLLYMÄKI 1977). In our field area the sex ratio of the field vole was also strongly female-biased during late autumn (Table 1, Fig. 1). The greater vulnerability of males in the present study may be one of the major reasons for this.

The density-dependent mortality of prey is thought to stabilize population fluctuations of prey (e.g. MURDOCH & OATEN 1975). KORPIMÄKI & NORRDAHL (1989, 1991a) presented evidence of density-dependent predation on a mixed microtine population by four avian predators and concluded that, as a result of their rapid numerical and functional response, nomadic predators have the potential to dampen the amplitude of microtine cycles. The rapid density-dependent predation of nomadic predators was also suggested to cause geographical synchrony in microtine population cycles (YDENBERG 1987, IMS & STEEN 1990). Predators may also affect the reproductive intensity of prey by affecting their behaviour (LIMA & DILL 1990), but these possible effects of avian predation on microtine populations have not yet been studied. The invulnerable class of prey should also stabilize the predator-prey relationship (MURDOCH & OATEN 1975). Theoretical analyses of this stabilizing effect are still rare, especially in those instances where the proportion of the invulnerable classes vary according to prey density. For example, the greater vulnerability of individuals of lower social cohorts when vole densities are high, as shown before, might reduce the stabilizing effect of predation. If, for example, density-dependent predation is only directed towards young field voles or males, the stabilizing effects on breeding females are decreased. This factor might thus abolish the dampening or synchronizing effects of avian predation on the population fluctuations of voles, especially if the predation rate is low.

During the present study a strong decline in vole populations was observed in the study area (Fig. 1). Predation by small mustelids has been suggested to have a stronger effect on population decline in cyclic microtines than do owls and raptors (HENTTONEN et al. 1987, HANSKI et al. 1991). We have no direct data on the occurrence of mustelids during the winter of 1988-1989, but they were abundant during

the previous winter (YLÖNEN 1989a, 1989b); and with the abundant food resources available during the summer of 1988, there should have been no cause for a decline in mustelids before our study period. There are also strong indications that diseases had an impact on this particular decline during the winter of 1988-1989: after the strong decline of *Microtus* during our study the remaining *Microtus* were inspected for possible diseases, as several field voles were found dead in traps in the spring of 1989. The cause of death of these voles was found to be infection by *Bordetella bronchispetica* bacterium, which causes lung fever (H. HENTTONEN pers. comm.).

In conclusion avian predators may have a strong dampening impact on their prey populations if the habitat is quite homogeneous (e.g. in large fields), and it does not give good protection for prey individuals during a large part of the year, and if the community of avian predators is diverse and dense (KORPIMÄKI & NORR-DAHL 1991b). In rather homogeneous habitats an especially high density of nomadic specialist predators may cause density-dependent predation in all age categories. Future work should evaluate how the distinct choice of certain classes of prey affects the vole populations, especially, if the more vulnerable voles are thought to have a lower reproductive value. Theoretical work should also pay more attention to how this selection affects the predator-prey interaction if the proportion of members of the invulnerable class varies with prey density.

#### ACKNOWLEDGEMENTS

We would like to thank R.V. Alatalo, E. Korpimäki, H. Pietiäinen and J. Viitala for valuable comments on the manuscript. Antti Sirkka and Jouni Berg for assistance in the field, and Joann v. Weissenberg for correcting our English. This study is supported by the University of Jyväskylä and Jenny and Antti Wihuri Foundation to T. Mappes, the Emil Aaltonen Foundation to M. Halonen and J. Suhonen, and the Academy of Finland to J. Suhonen.

#### REFERENCES

- BEACHAM T.D. 1979. Selectivity of avian predation in declining populations of the vole *Microtus townsendii*. *Canadian Journal of Zoology* 57: 1767-1772.
- BOONSTRA R. 1977. Predation on *Microtus townsendii* populations: impact and vulnerability. *Canadian Journal of Zoology* 55: 1631-1643.
- DICKMAN C.R., PREDAVEC M. & LYNAM A.J. 1991. Differential predation of size and sex classes of mice by the barn owl, *Tyto alba*. *Oikos* 62: 67-76.
- ERRINGTON P.L. 1956. Factors limiting higher vertebrate populations. *Science* 124: 304-307.
- FULK G.W. 1976. Owl predation and rodent mortality: a case study. *Mammalia* 40: 421-427.
- HALLE S. 1988. Avian predation upon a mixed community of common voles (*Microtus arvalis*) and wood mice (*Apodemus sylvaticus*). *Oecologia, Berlin* 75: 451-455.
- HANSKI I., HANSSON L. & HENTTONEN H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology* 60: 353-367.
- HENTTONEN H., OKSANEN T., JORTIKKA A. & HAUKISALMI V. 1987. How much do weasels shape the microtine cycles in the northern Fennoscandian taiga. *Oikos* 50: 353-365.
- IMS R.A. & STEEN H. 1990. Geographic synchrony in microtine population cycles: a theoretical evaluation of the role of nomadic avian predators. *Oikos* 57: 381-387.
- KALELA O. 1971. Seasonal trends in the sex ratio of grey-sided vole, *Clethrionomys rufocanus* (Sund.). *Annales Zoologici Fennici* 8: 452-455.



- KORPIMÄKI E. 1981. On the ecology and biology of Tengmalm's owl (*Aegolius funereus*) in Southern Ostrbothnia and Suomenselkä, western Finland. *Acta Universitatis Ouluensis (Series A, Scientiae Rerum Naturalium No. 118)*, *Biologica* 13: 1-84.
- KORPIMÄKI E. 1985. Prey choice strategies of the kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. *Annales Zoologici Fennici* 22: 91-104.
- KORPIMÄKI E. 1986. Diet variation, hunting habitat and reproductive output of the Kestrel *Falco tinnunculus* in the light of optimal diet theory. *Ornis Fennica* 63: 84-90.
- KORPIMÄKI E. & NORRDAHL K. 1989. Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuation of microtines. *Oikos* 54: 154-164.
- KORPIMÄKI E. & NORRDAHL K. 1991a. Numerical and functional responses of Kestrels, Short-eared Owls, and Long-eared Owls to vole densities. *Ecology* 72: 814-826.
- KORPIMÄKI E. & NORRDAHL K. 1991b. Do breeding nomadic avian predators dampen population fluctuation of small mammals? *Oikos* 62: 195-208.
- LAGERSTRÖM M. & HÄKKINEN I. 1978. Uneven sex ratio of voles in the food of *Aegolius funereus* and *Strix aluco*. *Ornis Fennica* 55: 149-153.
- LIMA S.L. & DILL L.M. 1990. Behavioural decision made under the risk of predation: review and prospectus. *Canadian Journal of Zoology* 68: 619-640.
- LOCKIE J.D. 1955. The breeding habits and food of Short-Eared Owls after a vole plague. *Bird Study* 2: 53-69.
- LONGLAND W.S. & JENKINS S.H. 1987. Sex and age affect vulnerability of desert rodents to owl predation. *Journal of Mammalogy* 68: 746-754.
- MURDOCH W.W. & OATEN A. 1975. Predation and population stability. *Advances in Ecological Research* 9: 1-131.
- MYLLYMÄKI A. 1977. Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. *Oikos* 29: 468-493.
- NYBO J.O. & SONERUD G.A. 1990. Seasonal changes in diet of Hawk Owls *Surnia ulula*: importance of snow cover. *Ornis Fennica* 67: 45-51.
- PEARSON O.P. & PEARSON A.K. 1947. Owl predation in Pennsylvania, with notes on the small mammals of Delaware County. *Journal of Mammalogy* 28: 137-147.
- PRESTON C.R. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor* 92: 107-112.
- ROWSEMITT C.N. 1991. Activity rhythms in female montane voles (*Microtus montanus*). *Canadian Journal of Zoology* 69: 1071-1075.
- SIMONETTI J.A. 1989. Microhabitat use by small mammals in central Chile. *Oikos* 56: 309-318.
- SOLHEIM R. 1984. Caching behaviour, prey choice and surplus killing by pygmy owls *Glaucidium passerinum* during winter, a functional response of a generalist predator. *Annales Zoologici Fennici* 21: 301-308.
- SOUTHERN H.N. & LOWE V.P.W. 1968. The pattern of distribution of prey and predation in Tawny Owl territories. *Journal of Animal Ecology* 37: 75-97.
- THOMSON D.Q. 1955. Ecology of lemmings. *Arctic Institute of North America, Final Report, Project no. ONR-133*.
- VIITALA J. 1977. Social organization in cyclic subarctic populations of the vole *Clethrionomys rufocanus* (Sund.) and *Microtus agrestis* (L.). *Annales Zoologici Fennici* 14: 53-93.
- YDENBERG R.C. 1987. Nomadic predators and geographical synchrony in microtine population cycles. *Oikos* 50: 270-272.
- YLÖNEN H. 1989a. Zum Einfluß der Musteliden *Mustela nivalis* und *M. erminea* auf zyklische Kleinnager am Beispiel von *Clethrionomys* populationen in Mittelfinnland. *Wissenschaftliche Beiträge Universität Halle* 1989/37: 553-562.
- YLÖNEN H. 1989b. Weasels *Mustela nivalis* suppress reproduction in cyclic bank voles *Clethrionomys glareolus*. *Oikos* 55: 138-140.
- YLÖNEN H., KOJOLA T. & VIITALA J. 1988. Changing female spacing behaviour and demography in an enclosed breeding population of *Clethrionomys glareolus*. *Holarctic Ecology* 11: 286-292.

