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How much do avian predators influence cyclic bank vole populations? An experiment during a peak year

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The influence of avian predators on bank vole (*Clethrionomys glareolus*) populations in four 0.5-ha enclosures was studied in central Finland in 1988. Two of the enclosures were covered with nets to keep out birds of prey, and two were left open to avian predation. A fence of metal sheet and continuous trapping kept out small mustelids during the breeding season. The only avian predators observed in the area throughout the year were the Ural owl (*Strix uralensis*) and the tawny owl (*Strix aluco*) and during summer the common buzzard (*Buteo buteo*). During autumn and winter pygmy owls (*Glaucidium passerinum*) was present in the study area. No Tengmalm's owls (*Aegolius funereus*) were observed around the area. During late winter and spring, the highest density of voles was observed in one of the open enclosures. No evidence of the influence of avian predators could be observed. During the summer the net covers had no effect on the survival of the voles; the highest density, with 100% survival of the young, was observed in an open enclosure. We suggest that avian predators have only a slight influence on breeding bank vole populations during a peak year in a patchy environment with boreal spruce forest. An explanation could be that bank voles are only an alternative prey for avian predators when field voles (*Microtus agrestis*) have high densities in more open habitats at the same time. The heterogeneity of the habitat and the dominance of the Ural owl in the owl community could also play a role.

1. Introduction

The impact of predators as a factor generating vole cycles has been the subject of several recent studies on both non-cyclic and cyclic populations

(e.g. Erlinge et al. 1984, Erlinge 1987, Korpimäki & Norrdahl 1989a, b). Support has been gained for the idea that generalist predators have a greater impact on non-cyclic populations, whereas specialist predators, especially small mustelids, are



Fig. 1. One of the two 0.5-ha enclosures with net covers.

more important in areas with cyclic populations (Henttonen et al. 1987). However, local or nomadic avian predators seem to be able to affect the geographical synchrony of microtine (and shrew) cycles (Korpimäki 1986a, b, Ydenberg 1987, Korpimäki & Norrdahl 1987). The importance of the habitat in determining the total impact of predation has been pointed out by Hansson (1989) and Korpimäki & Norrdahl (1989c).

We studied the impact of avian predators on enclosed bank vole (*Clethrionomys glareolus*) populations in a patchy central Finnish landscape consisting mainly of boreal forest interspersed with relatively small fields and meadows. We used four enclosures, two of which were covered with nets. We expected that if avian predators preyed on the vole populations, the winter survival of the voles in the covered enclosures would be better and population growth during the breeding season would be more rapid than in the open ones. We expected the greatest effect during the period after the snow melt, before the growth of

the vegetation, when the voles would be most exposed to predation (Taitt & Krebs 1983).

2. Material and methods

The study was carried out at Konnevesi (62°N), central Finland, which according to Hansson & Henttonen (1985) lies in the transition zone between the cyclic and non-cyclic populations. According to Korpimäki (1986b), however, the area with pronounced cyclicality extends further south in the boreal spruce forest zone of central and southern Finland. Ylönen (1989, 1990) has also observed a three-to-four-year cyclicality with typical summer declines in microtine densities in the Konnevesi area.

In autumn 1987 four 0.5-hectare enclosures were built on an abandoned field surrounded by spruce forest and patches of brushwood. The habitat of the old field was relatively homogeneous, with tall grasses, mainly *Elymus repens* and

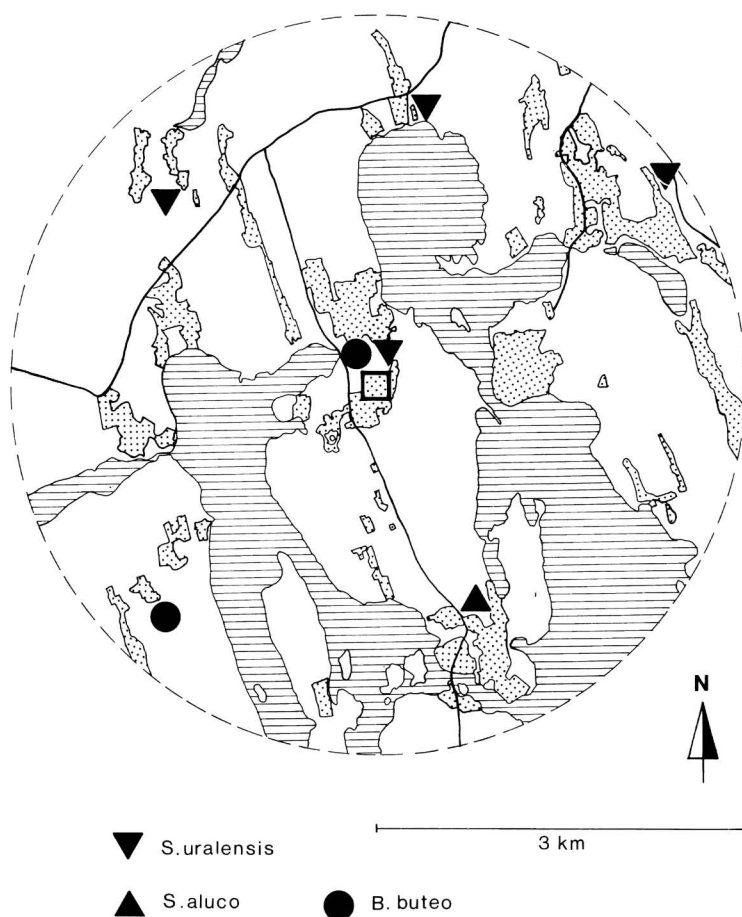


Fig. 2. The numbers and location of nest sites of owls and buzzards within a 3-km radius of the study site (marked with an open square). Of the land area, the fields and meadows are dotted and forests are white.

Phleum pratense together with *Filipendula ulmaria* and *Urtica dioica* and small bushy thickets with *Alnus incana* and *Rubus idaeus*. The fence of the enclosure consisted of a sheet of galvanized metal one metre high, with half a metre dug into the ground and half a metre rising above it. This fence together with continuous trapping of mustelids and water voles with Tomahawk traps presumably kept mustelid predators outside the enclosures (see Ford & Pitelka 1984), except in the winter when the snow cover was up to one metre deep. Foxes would have been able to enter the enclosures, but no signs of these (scent marking or tracks) were recorded during the study. At the beginning of March 1988, two of the enclosures were covered with a net (6 cm mesh), in order to keep out

avian predators (Fig. 1). The netting worked well for over eight months, but during wet weather and heavy snow in the late autumn of 1988, the net broke down and we had to finish the experiment. We had only two replicates of each experimental set (see Hurlbert 1984), because of the great difficulty of covering large areas with a net.

The enclosed vole populations were monitored by live-trapping, using Ugglan special traps. During a monthly trapping period, the traps were checked about 10 times a week. During the study the occurrence of owls and raptors was monitored around the enclosure area. The final estimate of the numbers of potential avian predators was based on the nest boxes used by owls and other known nest sites of owls and raptors within a radius of 3 km of the study site. As the area was

almost surrounded by water, we assumed that the study site would be included in the hunting area of the owls and raptors which nested on the same peninsula (Fig. 2). In late summer 1987 six nest boxes for Tengmalm's owls and three boxes for tawny owls were placed out in the immediate surroundings of the study area, but none of the boxes were occupied during the study. Within the 3-km radius, were several boxes for small and large owls. The owl density given in the Fig. 2 is based on checks of these boxes and known natural nest sites of Tengmalm's owls, Ural owls and tawny owls (A. Pirkkalainen, unpubl.).

3. Results and discussion

The years 1987 and 1988 were peak years of the local microtine populations (Ylönen 1989) and also of the owl community in general (Hakkarainen 1989). In summer 1988 the bank vole populations in the enclosures reached densities of 142 voles/ha and the densities of the surrounding field vole (*Microtus agrestis*) populations were about the same (Ylönen unpubl.). During the summer of 1988 the nest sites or territories of owls and raptors within a radius of 3 km amounted to seven: there were four Ural owls, two buzzards and one tawny owl (Fig. 2). One Ural owl and one common buzzard nested less than 0.5 km from the study area. The surprising absence — or very low density — of Tengmalm's owl from the area can be explained by the high number of Ural owls. In 1988 in the whole county of Konnevesi, with an area of 514 km, there were observed 18 breeding Ural owl pairs but no Tengmalm's owls (Hakkarainen 1989, A. Pirkkalainen, unpubl.).

During winter and spring 1988, avian predators had no visible impact on the density of the study populations (Fig. 3). The highest density during winter was observed in one of the open enclosures. Aggregation of voles seemed to attract maturing males moving on the snow surface. This caused an increase of the total density in an enclosure with a large winter aggregation (Fig. 3., Ylönen & Viitala 1991). Otherwise, the fluctuations of the densities in the different enclosures were similar until the beginning of June, when all the animals were removed (Fig. 3).

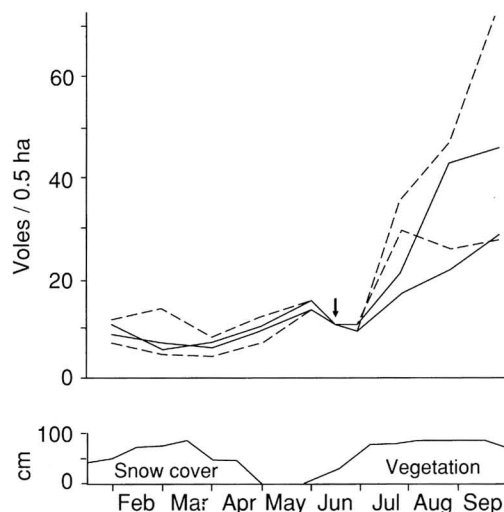


Fig. 3. The number of bank voles in the two open enclosures (broken lines) exposed to avian predation and in the two with net covers (solid lines). On 16 June the populations in the enclosures were adjusted to 10 individuals in each (see Ylönen et al. 1990), which is shown with an arrow. The heights of the snow cover and the vegetation in the enclosures are shown under the graph.

Immediately after the removal of the animals in June, 10 bank voles were introduced into each enclosure. During the following three months, one of the open enclosures reached a maximum density of 142 voles/ha (Fig. 3). The survival of the summer-born young in that enclosure was 100% (Ylönen et al. 1990). Thus avian predation did not affect the demography of the experimental populations during the breeding season. If there were any effects they were neutralized by the reproductive potential of the peak year breeding population.

Several studies have shown that predation can affect the growth and survival of experimental populations of rodents (Schnell 1968, Wiegert 1972, Beacham 1979, Taitt & Krebs 1983, Desy & Batzli 1989). In all of these studies the habitat has been relatively open and there has been a diverse spectrum of predators: foxes, cats, mustelids, many avian predators and snakes (see also Ford & Pitelka 1984). In the studies in western Finland (Korpimäki 1984, 1986a, b, Korpimäki & Norrdahl 1987, 1989a, b), carried out at

about the same latitude as the present study, the habitat was much more open, resembling that in the studies in southern Sweden (e.g. Erlinge 1987), and there were two *Microtus* species (*M. agrestis* and *M. epiroticus*), which have a high reproduction rate in grassy habitats. Both those regions have rich food resources for avian predators compared with the boreal forest zone, which largely represents a rather unproductive sub-optimal environment for *Microtus*, with only small patches of optimal habitats (e.g. old fields, meadows, forest edges and clearings). The boreal forest can hardly support as dense and diverse assemblages of owls and raptors as those found, for example, in Central Europe, southern Sweden and western Finland. A dense population of Ural owls in 1988 seemed insufficient to greatly reduce the peak vole populations. In addition, the presence of numerous Ural owls seems to restrict the occurrence of other owls in the area (Mikkola 1983).

We predicted that the best times to observe the impact of avian predators would be a relatively short period early in the spring, after the snow melt and before the growth of vegetation, and a period in the autumn after the withering of the vegetation and before the formation of the snow cover (see Taitt & Krebs 1983). During these periods the voles should be more exposed to predation than during winter and summer. However, the voles did not decline in spring in either the open or covered enclosures.

Nor could we observe any impact of avian predators during the autumn. This could be due to high field vole densities outside the fenced area. In a nest box 20 m away from the enclosure, which was used as a winter store by a pygmy owl *Glaucidium passerinum*, we did not find any marked individuals from the enclosures among the 29 food items (Mappes et al., unpubl.). During winter the snow cover of about 80 cm gives good protection against owls (Hansson 1987) and during summer the vegetation of tall grasses up to one metre high should protect the voles well (see Fig. 3). Korpimäki (1985, 1986) and Korpimäki & Norrdahl (1987, 1989a) have also shown that if there are both *Clethrionomys* and *Microtus* voles in a relatively open habitat, the numbers of *Microtus* taken by owls, raptors and possibly mustelids are greater than could be

expected from their abundance in the rodent community. Korpimäki (1985) has suggested that this could be due to energetic factors (smaller body size of bank voles), but is more probably due to the behaviour and mobility of bank voles, which make them more difficult to hunt (Korpimäki & Norrdahl 1989a).

As Hansson (1989) states, it is extremely difficult to evaluate the total impact of predation in a heterogeneous environment (see also Korpimäki & Norrdahl 1989a, b). Very large study areas should be used in estimating the true impact of different predators in different environments. Our enclosures of 0.5 ha are considerably larger than, for instance, those of Desy & Batzli (1989), which were 0.13 ha. In our study the unexpected dominance of the Ural owl, which has large territories (Mikkola 1983), could have decreased the total impact of predation. The environment presumably play an important role in determining the numbers and species of predators occurring in the area. The duration of the snow cover seems to be another important factor determining the hunting strategy and success of a predator (Hansson & Henttonen 1985, Sonerud 1986). It seems that in the boreal forest small mustelids have a greater impact on the vole populations during the peak and decline phases of the cycle than do avian predators. Mustelids are able to hunt inside the vegetation and under the snow, and are evidently able to find small "pockets of voles" in a patchy environment. According to Ylönen (1989), during one week mustelids were able to kill 30–100% of the local vole populations on an island or in enclosures.

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