

Differential avian predation on sex and size classes of small mammals: doomed surplus or dominant individuals?

Vesa Koivunen, Erkki Korpimäki & Harri Hakkarainen

Koivunen, V., Korpimäki, E. & Hakkarainen, H., Laboratory of Ecological Zoology, Department of Biology, University of Turku, FIN-20014 Turku, Finland

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Predators of small mammals may selectively kill either large individuals, usually male or the old, or small individuals, often females and young. We studied the prey choice of breeding male Tengmalm's owls (*Aegolius funereus*) in western Finland. The owls fed mainly on sibling voles (*Microtus rossiaemeridionalis*), field voles (*M. agrestis*), bank voles (*Clethrionomys glareolus*) and common shrews (*Sorex araneus*). We identified, sexed and weighed prey items cached by the owls in their nest-boxes, and compared characteristics of these prey to small mammals trapped in the same study area during 1985–1992. For each of the three vole species, owls captured more males than females, but we did not find that owls preferred one sex of common shrews. Our long-term data indicated that male-bias of two *Microtus* species in the diet of owls was highest in the low phase of the vole cycle, and decreased through the increase and peak phases. This suggests that the two sexes of voles behave differently, but that these differences change over the course of the 3-yr cycle. The proportion of prey individuals with a small body mass was greater in owl caches compared to trapping censuses, irrespective of species or sex. Large dominant individuals may occupy safe habitats with dense vegetation cover, where avian predation risk is minimal.

1. Introduction

It is a traditional belief that predators kill mainly individuals of poor quality: the sick, injured, inexperienced, young or aged (Errington 1946, 1956). These members of a population may be more susceptible because dominant individuals force them into poor habitats where predation risk is high. If this is the cases, predators may scarcely affect prey densities in the most favoured habitats. Alternatively,

predators may selectively capture prey of a certain sex or age, and therefore cause marked changes in the structure and/or dynamics of prey populations. For example, the sex ratio of a prey population may change if predators preferentially take members of one sex; If females are preferred the intrinsic growth rate of the population could decline (Longland & Jenkins 1987).

Predators have been shown to select either large prey individuals, usually males or those of old age

classes (e.g. Morse 1980), or small prey individuals, often females or juveniles (e.g. Marti & Hogue 1979). Previous studies of avian predators which feed mainly on small rodents and shrews have generally shown that males are the most vulnerable prey type (e.g. Southern & Lowe 1968, Lagerström & Häkkinen 1978, Korpimäki 1981, 1985b, Halle 1988), but in other cases, young females are preferred (Longland & Jenkins 1987, Dickman *et al.* 1991). A few birds of prey appear not to discriminate between the sex or size of small mammals (e.g. Boonstra & Krebs 1977). The Tengmalm's owl (*Aegolius funereus*) is a small, nocturnal predatory bird, whose diet in our study area consist mainly of sibling voles *Microtus rossiaemeridionalis* (syn. *M. epiroticus*, see Wilson & Reeder 1993), field voles *M. agrestis*, bank voles *Clethrionomus glareolus* and common shrews *Sorex araneus* (see Korpimäki 1981, 1988). Densities of voles in the genera *Microtus* and *Clethrionomys* fluctuate in 3–5-year population cycles in central and northern Fennoscandia (Hansson & Henttonen 1985). When vole densities decline in the crash phase of the vole cycle, owls shift to prey on shrews and small birds (Sulkava & Sulkava 1971, Korpimäki 1981, 1988).

Tengmalm's owls usually store prey items in their nest-cavities during the egg-laying, incubation and early nestling periods in all the phases of the vole cycle (e.g. Korpimäki 1981, 1987a). In this long-term study, we compare prey animals cached by breeding male Tengmalm's owls with prey animals we trapped in the field to discover whether owls select individuals according to sex or body size, and whether this preference is consistent in different phases of the vole cycle.

2. Material and methods

The study was carried out during 1979–1992 in the Kauhava region of western Finland (ca. 63°N, 23°E), an area consisting mainly of pine and spruce forests (46%), but with high proportions of agricultural land (27%) and peatland bogs (23%) (see Korpimäki 1981, 1984, 1985a). The number of Tengmalm's owl nest-boxes was 355 in 1979, but later their number was gradually increased. From 1988 onwards, the study area covered 1 300 km² and contained 500 nest-boxes and 30 known natural cavities suitable for Tengmalm's owls (see Korpimäki 1987b, 1992a for further details).

Data on prey animals stored in nest-holes were collected during regular nest visits at the time of egg-laying, incubation and hatching. Prey animals were identified, sexed, and those

that were intact were weighed according to Siivonen (1974). The state of these prey items (whole/partly eaten) was also recorded in the early morning (6–9 am). To avoid repeated measurements, we cut of the tails of small mammals once we examined them. This technique could not be confused with the feeding behaviour of owls because Tengmalm's owls always begin to eat the head of their prey items first (Scherzinger 1971, Korpimäki 1981, 1987c).

To study the availability of voles in the field, snap-trap lines were set during May in 1985–1992 in four sample plots in both the central and western parts of the study area. Sample plots were placed in each of the four main habitat types (a cultivated field, an abandoned field, a spruce forest and a pine forest) in both parts of the area. In each plot, 50–100 Finnish metal snap-traps were placed at intervals of 10 m and were checked once a day for four days. Trap nights totalled 10 748 in the central part and 15 040 in the western part of the study area (see Korpimäki 1986, Norrdahl & Korpimäki 1993 for further details). Trapped small mammals were sexed and weighed.

All statistical tests are two-tailed.

3. Results

3.1. Sex of prey

There was a male-bias in both *M. agrestis* and *M. rossiaemeridionalis* voles cached by the owls during 1979–1992 (apart from *M. agrestis* in 1983; Fig. 1). The same trend was also evident in the two species of *Microtus* voles snap-trapped in the field during 1985–1992; however the surplus of males in these years was significantly or nearly significantly higher in caches than in the field (Wilcoxon matched-pairs signed rank test, $T = 2$, $n = 7$, $P = 0.04$ for *M. agrestis*; $T = 1$, $n = 7$, $P = 0.06$ for *M. rossiaemeridionalis*). In every year during 1985–92, males were recorded more often in caches than in the field (apart from *M. agrestis* in 1992 and *M. rossiaemeridionalis* in 1989 and 1990). The sex ratio (percentage of males) of bank voles and common shrews stored by the owls was also male-biased during 1979–1992 (Fig. 2). However, only in the bank vole was the sex ratio more male-biased among cached individuals than among individuals trapped in the field ($T = 3$, $n = 8$, $P = 0.04$ for bank voles and $T = 14$, $n = 8$, $P = 0.64$ for common shrews).

Our snap-trapping data showed that there was a three-year vole cycle consisting of successive low, increase and peak years in our study area during 1985–1992. In the low years (1987 and 1990), vole densities were low during the breeding period of owls (from

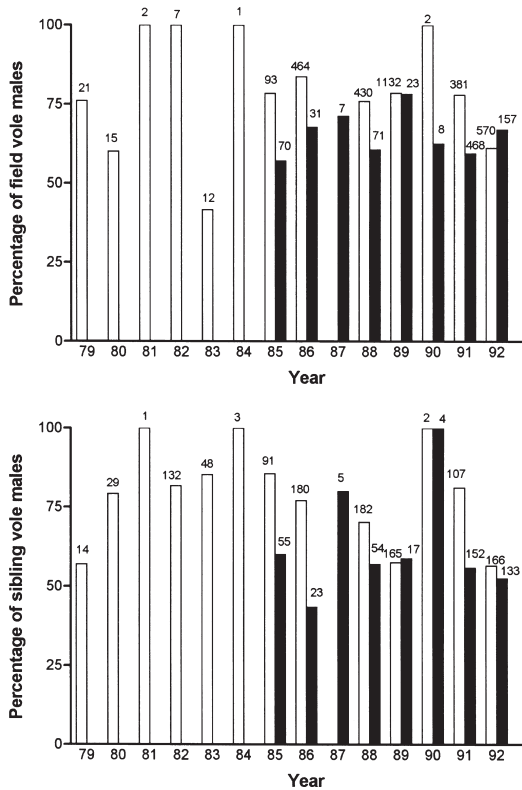


Fig. 1. Upper panel: Sex ratios (percentage of males) of *Microtus agrestis* voles captured by owls (open bars) from 1979 to 1992 and sex ratios from snap-trap censuses (filled bars) during 1985–1992. Total sample sizes are above the bars. Lower panel: the same but for *Microtus rossiaemerdionalis* voles.

March to June), but started to increase in late summer and autumn. In the increase years (1985, 1988 and 1991), vole numbers were intermediate in the early breeding stage of owls, but increased rapidly towards the end of the season and peaked in the following autumn. In the peak years (1986, 1989 and 1992), vole abundances were still high in the early breeding season of owls, but crashed rapidly to very low numbers in mid-summer (see fig. 1 in Korpimäki & Hakkarainen 1991 or in Korpimäki & Norrdahl 1991a for further details on the three-year vole cycle).

In the increase and peak phases of the vole cycle, the sex ratio of *M. rossiaemerdionalis*, *M. agrestis* and *C. glareolus* voles cached by the owls in their nest-boxes was significantly more male-biased than that of individuals snap-trapped in the field during the same periods (Table 1). However, the same difference was not evident for common shrews.

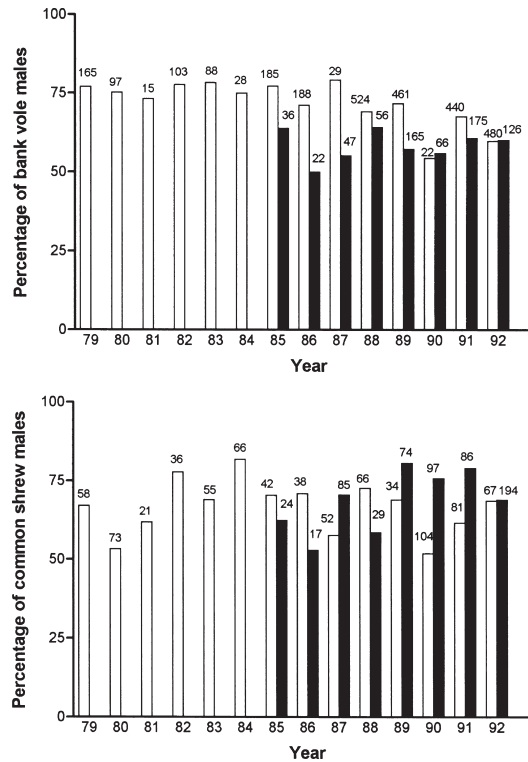


Fig. 2. Upper panel: the same as in Fig. 1 but for bank voles. Lower panel: the same as in Fig. 1 but for common shrews.

During the three-year vole cycle, the proportion of male *M. rossiaemerdionalis* voles appeared to decrease from the low through the increase to the peak phase for both those individuals captured by the owls and those trapped in the field, but these differences were not significant (Kruskal-Wallis test, $H = 4.0$, $P = 0.14$, and $H = 3.1$, $P = 0.2$, respectively; Fig. 3).

Among the voles we trapped, there was a trend for the male-biased sex ratio of *M. agrestis* to decrease from the peak phase through the low phase to the increase phase (Kruskal-Wallis test $H = 5.1$, $P = 0.07$, Fig. 3). Among the *M. agrestis* voles cached by the owls, the male bias tended to be higher in the low phase than in the increase and peak phases, but these differences were not significant (Kruskal-Wallis test, $H = 2.5$, $P = 0.2$).

Although male-biased, the sex ratio of bank voles did not change during the course of the vole cycle for both the individuals trapped in the field and those captured by the owls (Kruskal-Wallis test, $H = 4.5$, $P = 0.1$, and $H = 2.2$, $P = 0.3$, respectively; Fig. 4).

The sex ratio of common shrews was also stable during the vole cycle for both the individuals trapped in the field and those cached by the owls (Kruskal-Wallis test, $H = 0.2$, $P = 0.8$ and $H = 2.2$, $P = 0.3$, respectively; Fig. 4).

In the low phase of the vole cycle, the predominance of males among *Microtus* voles cached by the owls persisted throughout the breeding season, although the total number of prey items we sexed was low (Table 2). In the increase phase, the male-bias among *M. agrestis* voles in food caches decreased towards the end of the breeding season (Spearman correlation, $r_s = -0.83$, $P < 0.05$), whereas in the peak phase, the sex ratio showed only irregular variation during the breeding season. Within the breeding season of owls, the sex ratio of *M. rossiaemerdionalis* voles also declined in the increase phase, but not significantly (Spearman correlation, $r_s = -0.6$, $P > 0.1$). Among bank voles cached by the owls in the low phase, male predominance tended to decrease towards the end of the breeding season (Spearman correlation, $r_s = -0.87$, $P > 0.1$), but in

other phases there was no obvious trend (Table 2). In the peak phase, the percent of male of common shrews that were stored by owls decreased consistently towards the end of the breeding season (Spearman correlation, $r_s = -0.94$, $P < 0.02$), but in the other phases there was no such obvious trend (Table 2).

3.2. Body mass

The yearly mean body mass of voles and shrews stored by the owls was compared to the yearly mean body mass of small mammals we snap-trapped in the field during 1985–1992 (Figs. 5 and 6). These comparisons revealed that, for all 4 prey species, cached prey individuals of both sexes were significantly lighter than those trapped in the field (Figs. 5 and 6). This difference was consistent in every year with the exceptions of *M. rossiaemerdionalis* males in 1989, and common shrew males in 1987 and females in 1987 and 1990).

Table 1. Sex ratio (percent of males) of small mammals in caches of Tengmalm's owls and in the field during the low (1987 and 1990), increase (1985, 1988 and 1991) and peak (1986, 1989 and 1992) phases of the vole cycle. Total number of males and females within parentheses. Differences between samples from caches and the field have been tested by χ^2 -test or Fisher test (#). P -values are two-tailed.

Species	Low		Increase		Peak	
	male %	N	male %	N	male %	N
<i>M. agrestis</i>						
store	100.0	(2)	77.1	(904)	75.1	(2166)
field	66.6	(15)	60.3	(599)	68.2	(211)
χ^2			49.0		4.8	
P	0.56	(#)	0.0001		0.02	
<i>M. rossiaemerdionalis</i>						
store	100.0	(2)	77.0	(380)	64.2	(511)
field	88.8	(9)	57.1	(261)	50.2	(179)
χ^2			29.0		8.0	
P	1.0	(#)	0.0001		0.0004	
<i>C. glareolus</i>						
store	68.8	(51)	69.9	(1 149)	66.3	(1 129)
field	55.7	(113)	61.8	(267)	57.8	(313)
χ^2	2.4		6.6		7.6	
P	0.11		0.01		0.0005	
<i>S. araneus</i>						
store	53.8	(156)	66.1	(189)	69.3	(189)
field	73.0	(182)	71.9	(139)	70.8	(285)
χ^2	13.5		1.2		0.1	
P	0.0002		0.26		0.71	

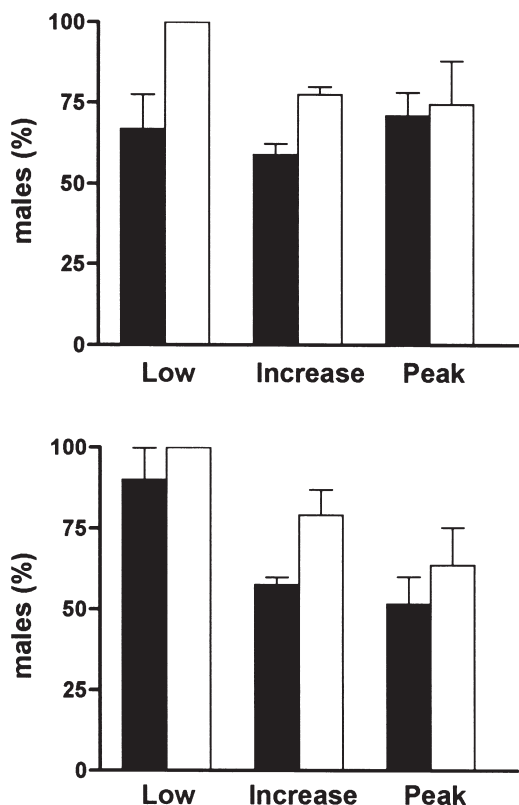


Fig. 3. Mean (95% confidence limit) sex ratio (percentage of males) of *Microtus agrestis* (upper panel) and *M. rossiaemeridionalis* (lower panel) voles captured by owls (white bars) and snap-trapped in the field (black bars). Stages of the vole cycle are separated into low (pooled data from 1987 and 1990), increase (1985, 1988 and 1991) and peak (1986, 1989 and 1992) phases.

4. Discussion

4.1. Trappability of small mammals

A certain type of trap may be selective in regard to the species, sex, age, or size of individuals it captures. However, earlier results suggest that our snap-traps do not select small mammals according to activity or species (Koivunen *et al.* 1996). The spring population of small mammals consisted entirely of animals which had overwintered, because we did not usually find juveniles in caches until early June. This means that the animals we trapped came from a relatively homogenous population until the end of May. The body mass of cached voles ranged between 5 and 50 g, and in the trapped individuals between 6

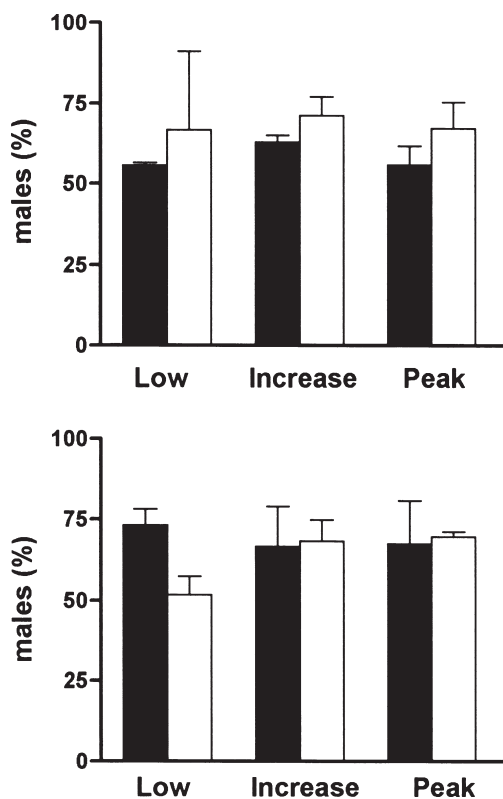


Fig. 4. The same as in Fig. 3 but for bank voles (upper panel) and common shrews (lower panel).

and 51 g, which is almost within the optimal weight range for the traps used (7–50 g, K. Norrdahl, unpublished). Therefore differences in body size of prey species should not have biased our results (see also Norman *et al.* 1993). Generally, a predominance of males is observed among trapped small mammals (e.g. Myllymäki *et al.* 1971, Korpimäki 1981, this paper). This male-bias is attributed to the larger home range of males compared to females (e.g. Bujalska 1989) and the fact that males may travel longer distances. It is possible that our trapping protocol also selected for males; however, as the predominance of males was even higher in caches, any such trapping bias only makes our comparisons between field and caches even more conservative.

4.2. Selectivity according to sex of prey

Our snap-trapping data showed that breeding Tengmalm's owls captured more male voles, but

not male shrews, than were predicted on the basis of availability in the field. These results suggest that male voles are more vulnerable to owl predation, perhaps because they are more active in spring compared to females. Many previous studies have also suggested that male-bias in the diet of avian predators is a result of the high activity of males looking for mature females (e.g. Korpimäki 1981, 1985b). Alternatively the higher vulnerability of male voles may be related to differences in microhabitat use between sexes. For example, juvenile female house mice *Mus musculus* that used open vegetation more than adults were most vulnerable to barn owl *Tyto alba* predation (Dickman *et al.* 1991).

A predominance of male voles in the diet has been shown in numerous other studies of avian predators (e.g. Korpimäki 1981, 1985b, Halle 1988, Mappes *et al.* 1993), others have failed to detect any sex ratio bias in the prey consumed (e.g. Boonstra & Krebs 1977).

The two *Microtus* voles, the main prey of Tengmalm's owls in our study area (Korpimäki 1981, 1988), were captured more frequently than expected based on their relative abundance in the field. Of the two species, *M. rossiaemerdionalis* was captured more frequently than *M. agrestis* (Korpimäki 1981, Koivunen *et al.* 1996). The male-bias of the pre-

ferred prey species (two *Microtus* voles) in the diet of Tengmalm's owls was high in the low phase of the vole cycle, and declined through the increase phase to the peak (crash) phase of the cycle. In addition, this predominance of males remained high during the breeding season of owls in the low phase of the cycle, but decreased continuously in the increase phase. This suggests that the magnitude of gender bias in the prey captured by Tengmalm's owls may vary according to the phase of the vole cycle. By contrast, such among-phase and within-season relationships were not found for the most important alternative prey species (the bank vole and the common shrew).

Perhaps the proportion of male *Microtus* voles caught by Tengmalm's owls decreases throughout the vole cycle because male-biased predation removes males faster than females. Other avian predators also capture proportionally more male than female voles; in our study area, this is true for breeding kestrels *Falco tinnunculus* (Korpimäki 1985b). In addition, *Microtus* voles are the main prey of many other predators, such as short-eared owls *Asio flammeus*, long-eared owls *A. otus* and small mustelids (Korpimäki & Norrdahl 1991b, Korpimäki *et al.* 1991, Korpimäki 1992b). Relatively fewer male voles may have been caught by Tengmalm's owls

Table 2. Sex ratio (percent of males) of small mammals cached by owls during the breeding season in the low (pooled data from 1981, 1984, 1987 and 1990), increase (1979, 1982, 1985, 1988 and 1991) and peak (1980, 1983, 1986, 1989 and 1992) phases of the vole cycle. Total sample sizes (male + female) is in parentheses. Significance level: $P < 0.05^*$.

	March	1–15 April	16–30 April	1–15 May	16–30 May	31 May– 30 June
Low phase						
<i>M. agrestis</i>	100.0 (1)	100.0 (1)	–	100.0 (1)	–	100.0 (2)
<i>M. rossiaem.</i>	100.0 (1)	100.0 (1)	100.0 (3)	–	–	100.0 (1)
<i>C. glareolus</i>	–	100.0 (2)	75.0 (36)	75.0 (20)	61.5 (13)	65.2 (23)
<i>S. araneus</i>	–	–	50.0 (28)	65.3 (55)	70.2 (36)	60.5 (124)
Increase phase						
<i>M. agrestis</i>	90.0 (30)	82.7 (231)	77.8 (166)	75.2 (274)	67.6 (105)	76.2 (126)*
<i>M. rossiaem.</i>	71.4 (21)	88.9 (117)	83.5 (121)	76.4 (199)	51.0 (53)	66.7 (15)
<i>C. glareolus</i>	64.5 (110)	72.0 (336)	76.2 (41)	72.0 (375)	65.9 (123)	68.4 (57)
<i>S. araneus</i>	71.4 (14)	57.4 (54)	69.3 (101)	80.0 (75)	76.7 (30)	22.2 (9)
Peak phase						
<i>M. agrestis</i>	70.4 (449)	80.1 (788)	74.5 (714)	66.8 (205)	70.4 (27)	70.0 (10)
<i>M. rossiaem.</i>	68.5 (184)	70.1 (211)	63.3 (147)	51.2 (41)	100.0 (3)	50.0 (2)
<i>C. glareolus</i>	68.9 (177)	67.0 (388)	68.6 (506)	64.6 (198)	81.5 (27)	66.7 (18)
<i>S. araneus</i>	100.0 (9)	75.0 (65)	65.1 (146)	65.2 (46)	60.5 (38)	46.1 (13)*

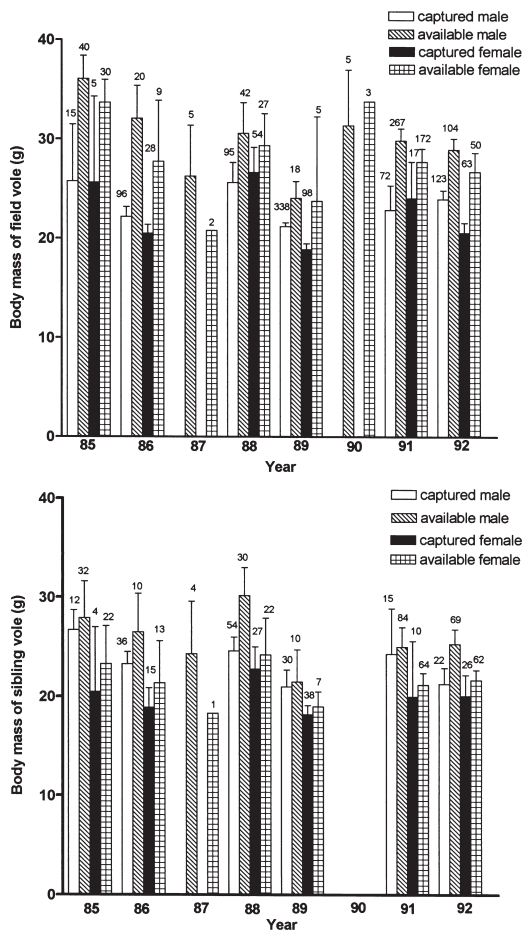


Fig. 5. Yearly mean (95% confidence limit) body mass (g) of *Microtus agrestis* (upper panel) and *M. rossiaemeridionalis* (lower panel) voles captured by owls compared to those censused by snap-trapping during 1985–1992. Total sample sizes are above the bars. Paired t -tests were used to compare the yearly mean body masses of males and females captured by the owls to those trapped in the field ($t = 5.5$, $df = 5$, $P = 0.003$ for male *M. agrestis*, and $t = 6.7$, $df = 5$, $P < 0.001$ for female *M. agrestis*, $t = 2.7$, $df = 5$, $P = 0.042$ for male *M. rossiaemeridionalis*, and $t = 4.9$, $df = 5$, $P = 0.004$ for female *M. rossiaemeridionalis*).

during the course of the 3-yr cycle perhaps because spacing behaviour of the male voles changed during this period. At low densities, males of both *Microtus* species have larger home ranges than at high densities (Norrdahl & Korpimäki 1993 and unpubl. data, Nelson 1994), which may explain why these males are so vulnerable in the low phase of the vole cycle.

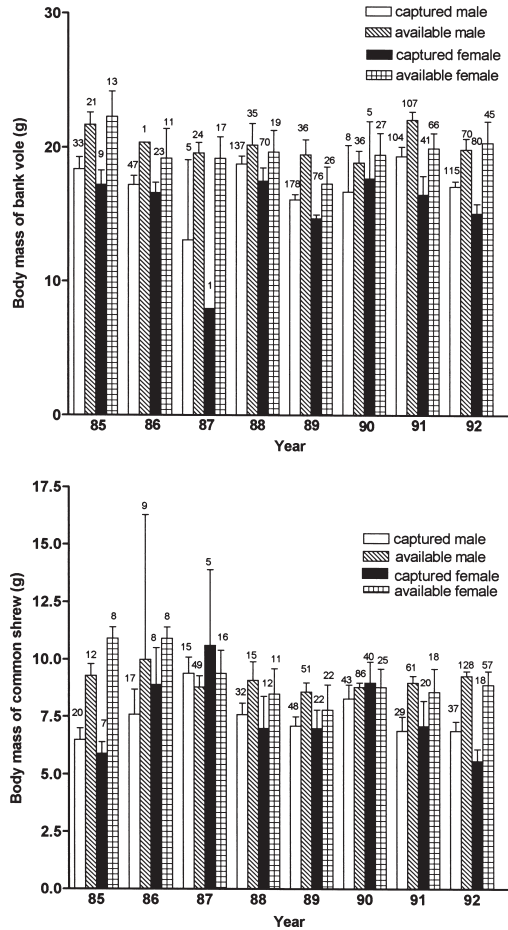


Fig. 6. Upper panel: the same as in Fig. 5. but for bank vole males and females ($t = 6.0$, $df = 7$, $P < 0.001$ and $t = 4.4$, $df = 7$, $P = 0.003$, respectively). Lower panel: the same as in Fig. 5 but for common shrew males and females ($t = 4.1$, $df = 8$, $P = 0.003$ and $t = 2.3$, $df = 8$, $P = 0.03$, respectively).

In general, there appears to be no consistent pattern to the sex ratio of wild vole populations, either cyclic or non-cyclic, as some census data are male biased (e.g. Heikura & Lindgren 1979, Halle & Lehmann 1987), some are female-biased (e.g. Bujalska 1986), and still others do not show any sex-related bias (e.g. Myllymäki 1977).

4.3. Doomed surplus individuals?

Our second main finding was that breeding Tengmalm's owls mostly selected light-weight voles and shrews more often than would be predicted from

availability in the field. This trend, evident in both sexes of voles and shrews, could not be explained by the fact that owls captured juveniles more often than adults, because all small mammals in food caches or caught by our traps until mid-May had overwintered. Therefore, owls were not eating juvenile small mammals that had left the nest but which did not enter our snap-traps.

Errington (1946, 1956) hypothesized that predators usually take socially subordinate individuals that are in poor physiological condition, because these prey are forced into suboptimal habitats with high predation risk. The predominance of light-weight voles and shrews in the diet of owls was consistent with this idea, but we can not be certain that the type of habitat occupied by small rodents in our study area depended upon social status. However, other recent studies have shown that social status affects the habitat occupancy of small rodents (e.g. Dickman *et al.* 1991). On the other hand, Koivunen *et al.* (1996) showed that smaller (as estimated by body length and mass) voles cached by Tengmalm's owls had more internal fat than larger ones available in the field. Thus, small individuals could be in even better physiological condition than large ones.

Another possibility is that voles with a small body mass are more vulnerable because they are less able to compete with con-specifics. Large dominant individuals may force light-weight and subdominant ones into poor habitats (Pusenius & Viitala 1993) where the risk of avian predation is high. This is plausible because low body mass evidently reflects lower social status of voles (Grant 1972).

In conclusion, male voles appear to be more susceptible than females to predation by Tengmalm's owls perhaps because males travel more frequently over open and risky habitats. A low body mass also seems to be associated with high predation risk in both sexes. Large individuals may force light ones to open habitats where the probability of being detected by an avian predator is high. Although it is clear that there are size and gender biases in the prey taken by Tengmalm's owls, we do not know the mechanisms responsible for this choice of prey. Further research on the microhabitat use and activity rhythms of small mammals according to their sex and size will help to determine why some individuals are more prone to predation than others.

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References

- Boonstra, R. & Krebs, C. J. 1977: A fencing experiment on a high-density population of *Microtus townsendii*. — *Can. J. Zool.* 55: 1166–1175.
- Bujalska, G. 1986: Sex ratio in an island population of *Clethrionomys glareolus* (Schreber, 1780). — *Acta Theriol.* 47: 805–816.
- 1989: Trap line and trap grid as Methods of Estimation of population Parameters in the Bank Vole Inhabiting Crabapple Island. — *Acta Theriol.* 34: 325–337.
- Collet, D. 1991: Modelling Binary Data. — Chapman and Hall, London. 369 pp.
- 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. 1946: Predation and vertebrate populations. — *Quart. Rev. Biol.* 21: 144–177.
- 1956: Factors limiting higher vertebrate populations. — *Science* 124: 304–307.
- Grant, P. R. 1972: Interspecific competition among rodents. — *Annu. Rev. Ecol. Syst.* 3: 79–106.
- Halle, S. 1988: Avian predation upon a mixed community of common voles (*Microtus arvalis*) and wood mice (*Apodemus sylvaticus*). — *Oecol. (Berl.)* 75: 451–455.
- Halle, S. & Lehmann, U. 1987: Population dynamics and individual features during the phase of decline in the Field vole. — *Acta Theriol.* 32: 21–29.
- Hansson, L. & Henttonen, H. 1985: Gradients in density variations of small rodents: the importance of latitude and snow cover. — *Oecol. (Berl.)* 67: 394–402.
- Heikura, K. & Lindgren, I. 1979: Reproduction in the field vole, *Microtus agrestis* L., in the vicinity of Oulu, Finland. — *Aquilo Ser. Zool.* 19: 33–43.
- Koivunen, V., Korpimäki, E., Hakkarainen, H. & Norrdahl, K. 1996: Prey choice of Tengmalm's owls (*Aegolius funereus funereus*): preference of substandard individuals? — *Can. J. Zool.* (In press.)
- Korpimäki, E. 1981: On the ecology and biology of Tengmalm's Owl (*Aegolius funereus*) in Southern Ostrobothnia and Suomenselkä western Finland. — *Acta Univ. Oul. Ser. A. Sci. Rer. Nat.* 118: 1–84.
- 1984: Clutch size and breeding success of Tengmalm's

- Owl *Aegolius funereus* in natural cavities and nest-boxes. — *Ornis Fenn.* 61: 80–83.
- 1985a: Clutch size and breeding success in relation to nest-box size in Tengmalm's Owl *Aegolius funereus*. — *Holarct. Ecol.* 8: 175–180.
- 1985b: Prey choice strategies of the Kestrel *Falco tinnunculus* in relation to available small mammals and other Finnish birds of prey. — *Ann. Zool. Fennici* 22: 91–104.
- 1985c: Rapid tracking of microtine populations by their avian predators: possible evidence for stabilizing predation. — *Oikos* 45: 281–284.
- 1986: Predation causing synchronous decline phases in microtine and shrew populations in western Finland. — *Oikos* 46: 124–127.
- 1987a: Prey caching of breeding Tengmalm's Owls *Aegolius funereus* as a buffer against temporary food shortage. — *Ibis* 129: 499–510.
- 1987b: Selection for nest-hole shift and tactics of breeding dispersal in Tengmalm's owl *Aegolius funereus*. — *J. Anim. Ecol.* 56: 185–196.
- 1987c: Timing of breeding of Tengmalm's Owl *Aegolius funereus* in relation to vole dynamics in western Finland. — *Ibis* 129: 58–68.
- 1988: Diet of breeding Tengmalm's Owls *Aegolius funereus*: long-term changes and year-to-year variation under cyclic food conditions. — *Ornis Fenn.* 65: 21–30.
- 1992a: Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's owls. — *J. Anim. Ecol.* 61: 103–111.
- 1992b: Diet composition, prey choice and breeding success of Long-eared Owls: effects of multiannual fluctuations in food abundance. — *Can. J. Zool.* 70: 2373–2381.
- Korpimäki, E. & Hakkarainen, H. 1991: Fluctuating food supply affects the clutch size of Tengmalm's Owl independent of laying date. — *Oecologia* 85: 543–552.
- 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.
- 1991b: Do breeding nomadic avian predators dampen population fluctuations 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 Fenn.* 55: 149–153.
- Longland, W. S. & Jenkins, S. H. 1987: Sex and age affect vulnerability of desert rodents to owl predation. — *J. Mammal.* 68: 746–754.
- Mappes, T., Halonen, J., Suhonen, J. & Ylönen, H. 1993: Selective avian predation on a population of the field vole, *Microtus agrestis*: greater vulnerability of males and subordinates. — *Etology, Ecology and Evolution* 5: 519–527.
- Marti, C. D. & Hogue, J. C. 1979: Selection of prey size in screech owls. — *Auk* 96: 319–327.
- Morse, D. H. 1980: Behavioral mechanisms in ecology. — Harvard Univ. Press, Cambridge, MA.
- Myllymäki, A. 1977: Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. — *Oikos* 29: 468–493.
- Myllymäki, A., Paasikallio, A. & Häkkinen, U. 1971: Analysis of a 'standard trapping' of *Microtus agrestis* (L.) with triple isotope marking outside the quadrat. — *Ann. Zool. Fennici* 8: 22–34.
- Nelson, J. 1994: Determinants of spacing behaviour, reproductive success and mating system in male field voles *Microtus agrestis*. — Ph.D.-thesis, Department of Animal Ecology, University of Lund, Sweden.
- Normann, A., Eifler, M., Gruenhagen, N. & Davelos, A. 1993: Differential effectiveness of standard and long shermann livetraps in capturing small mammals. — *J. Mammal* 74: 151–161.
- Norrdahl, K. & Korpimäki, E. 1993: Predation and interspecific competition in two *Microtus* voles. — *Oikos* 67: 149–158.
- Pusenius, J. & Viitala, J. 1993: Demography, and regulation of breeding density in the vole *Microtus agrestis*. — *Ann. Zool. Fennici* 30: 133–142.
- Scherzinger, W. 1971: Beobachtungen zur Jugendentwicklung einigen Eulen (Strigidae). — *Z. Tierpsychol.* 28: 494–504.
- Siivonen, L. 1974: Pohjolan nisäkkäät. — Otava, Helsinki.
- Southern, H. N. & Lowe, V. P. 1968: The pattern of distribution of prey and predation in Tawny Owl territories. — *J. Anim. Ecol.* 37: 75–97.
- Sulkava, P. & Sulkava, S. 1971: Die nistzeitliche Nahrung des Raufusskauzes *Aegolius funereus* in Finnland 1958–67. — *Ornis Fenn.* 48: 117–124.
- Wilson, D. E. & Reeder, D. M. (eds.) 1993: Mammal species of the world. A taxonomic and geographic reference. 2nd ed. — Smithsonian Institution Press.