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Antipredatory behaviour of bank voles and prey choice of weasels — enclosure experiments

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The antipredatory behaviour of bank voles *Clethrionomys glareolus* and prey choice of weasels *Mustela nivalis* were investigated in a seminatural enclosure. Bank voles were observed for three consecutive days. During the second day a weasel was present in the enclosure. The daily activity rhythm of voles without predation risk was characterized by inactivity at nights with pronounced peaks at dawn. When the weasel was present in the pen, vole activity occurred throughout the day. When endangered by a predator, bank voles dramatically increased their above-ground mobility. At the same time, intraspecific aggressiveness decreased. Adult voles were less vulnerable than young ones to weasel predation. In three hunting sessions with different enclosed populations of bank voles, weasels primarily killed young voles.

1. Introduction

Microtine rodents are important prey for many predators in temperate areas. Field studies have provided extensive data on the impact of mammalian predators and raptors on rodent populations (e.g. Goszczyński 1977, Erlinge et al. 1983, Pearson 1985). However, the small size, shyness, and crepuscular/nocturnal activity of rodents have made it difficult for ecologists to gain an insight into rodent-predator relationships beyond the trophic impact. Recently it has been recognized that rodents, being simple laboratory animals, offer a fine opportunity to perform enclosure experiments on vital aspects of predation. Experiments have revealed that rodents have specific antipredatory defences (Sullivan et al. 1988), and that predation risk alters foraging, microhabitat choice, breeding behaviour, activity, and space use by rodents (e.g. Brown et al. 1988, Ylönen 1989, Jędrzejewski & Jędrzejewska 1990).

This paper reports enclosure experiments on bank voles *Clethrionomys glareolus* and weasels *Mustela nivalis vulgaris*. We set out to discover

1) the antipredatory behaviour of bank voles,
2) how this behaviour is related to specific searching tactics in weasels, and
3) whether the weasels selectively remove the voles.

2. Material and methods

2.1. Enclosure

We performed experiments in an outdoor enclosure in Białowieża, eastern Poland. The enclosure consisted of three adjacent parallel pens (a total of 144 m^2, each pen 4×12 m) surrounded by vole-proof walls 1.2 m high. The floor was natural rich soil supporting a diversity of vegetation (mainly *Aegopodium podagraria*, *Urtica dioica*, *Symphytum officinale* and grasses) which was mown to a height of 0.1 m prior to the experiment. Twenty-two 1-m long logs in each pen provided shelter and nests for voles. The pens were connected with passages to enable voles to move freely between them. The entire enclosure was covered with string netting for the exclusion of birds of prey.

Bank voles used in experiments were caught in the nearby Białowieża Forest. They were weighed, sexed, and individually marked by toe-clipping and ear-tags. Weasels were live-trapped two years before the experiments and kept in large cages under a natural photoperiod and fed live rodents (mainly laboratory mice).

2.2. Experiments on weasels' selectiveness in killing voles

We conducted three experiments: in the summer of 1987 (July–August), in the autumn of 1987 (September), and in the spring of 1988 (May–June). In each experiment a new set of 45 bank voles was used. The initial numbers of voles slightly changed in the course of the experiments due to mortality and reproduction. To reflect the age structure of natural bank vole populations, the composition of the 3 'populations' was the same as that of the total sample of voles we had captured in the forest during those three seasons. Voles that were used in spring had overwintered; all of them were reproductively active and females had litters in the enclosure. The summer 'population' consisted of both overwintered voles in reproductive condition and maturing juveniles (subadults) born in spring. All voles ceased reproducing towards the end of the experiment. Among bank voles used in the autumn experiment reproductively nonactive subadults predominated, although some overwintered voles still persisted. No reproduction was observed during the experiment. The sex ratio of voles in all experiments approached 1:1, which is typical for this species (Bujalska 1986).

In each experiment voles were allowed to space out for at least 7 days over the entire enclosure. We then checked the spatial distribution of voles throughout the three pens by live-trapping continuously for 22–33 days. We introduced a weasel(s) into one or two peripheral pens, twice during each experiment, at 11-day intervals. Weasels were allowed to penetrate the pen for 2 hrs, except for the first introduction in the summer experiment, when the weasel was present in the pen for 24 hrs. This 24-hr trial was used for detailed observations of vole behaviour (see below).

Each weasel was placed in a pen with its wooden nestbox and after the trial the weasel and its nestbox were removed from the pen. We observed the hunting efforts of the weasels during their presence in the pens. After removing the weasel we located and identified all prey captured by it during the trial. The weasels most often carried the voles to the nestbox after they had killed them.

The numbers and weight composition of voles available to a predator in a given pen were established from live-trapping. The number of nestlings was calculated on the basis of the reproductive histories of females and the numbers of young born in the pens when they first entered traps. The mean number of young per pregnant female calculated in this way was 4–5. This corresponds well with the data for the natural population of bank voles from Białowieża Forest at that time (M. Sikorski & A. Wójcik, pers. comm.).

2.3. Observations of voles' antipredatory behaviour

In the summer experiment, we carried out three-day observations on the behaviour of voles and a weasel. We observed two peripheral pens (1 and 3) concurrently. The first day (from 0600 hrs on 16 July to 0500 hrs on 17 July) was the control day. At 0600 hrs on the second day all passages between pens were closed and a weasel (a male) was introduced into pen 1 for 24 hrs. Pen 3 was not altered. After the weasel was removed (at 0500 hrs on the third day) the passages were opened and observations were continued for the third day.

Observations were made every second hour and lasted for 60 min. Each pen was observed for a total of 36 hrs within the 72-hr experiment. Observers sat about 2 m above the ground in order to have the whole pen in view. Two observers worked concurrently for 1 hr each. In all, eight trained persons participated in making observations. At night hanging electric 150 Watt lamps were used.

The following activities of the animals were recorded:

1) Above-ground mobility of bank voles. Two perpendicular lines made of white plastic, 3 cm wide, were placed on the ground in both pens (total length 4 m + 12 m). The numbers of voles crossing these lines, within each hour of observation, was noted.
2) Aggressive encounters between bank voles. We counted the number of fights and pursuits, accompanied by squeaks.
3) 'Arboreal' escape from weasel. Over twenty leafless branches, 1-m high, were placed vertically in each pen. Voles escaping from weasel attacks climbed these twigs and remained on them from several minutes to more than two hours. The voles sitting on twigs were counted at the end of each 5-minute observation bout.
4) Weasel's activity. The weasel was described as active (when it was penetrating the pen, hunting, chasing voles) or non-active (weasel in its nestbox).

The numbers of bank voles present in each pen during the three days of observation were taken from live-trapping performed just before the start of the observations (the numbers were the same for the first and the second days because the passages between the pens were closed) and soon after the end of the observations (numbers for the third day).

Long-term changes in space use by voles due to weasel penetration were described by Jędrzejewski & Jędrzejewska (1990).

3. Results

3.1. Mobility, intraspecific aggressiveness, and 'arboreal' escape in bank voles

During the first day of observations (without the presence of a weasel) and the second day (with a weasel present in one pen) 13, 10, and 11 bank voles were estimated to live in pens 1, 2, and 3. After the presence of a weasel in pen 1 most bank voles moved to pens 2 and 3 as soon as we opened the passages. There were then 3 voles in pen 1, 13 voles in pen 2, and 15 in pen 3.

The above-ground mobility was similar in both pens during the day preceding the weasel's presence (Fig. 1A). An average bank vole crossed the white line 5.8 times per hour (*SD* 4.84, range 0.09–12.45) in pen 3, and 6.01 (*SD* 5.08, range 0–19.38) in pen 1 ($U_s = 95$, $df = 6,12$, $P > 0.05$, Wilcoxon two-sample test). During the 2nd day (with a weasel present in pen 1) voles were more active in both pens. The slight increase in the index of aboveground mobility in pen 3 (no weasel) was probably caused by restriction of their trips to the other pens (passages closed) and was not significantly higher than during the 1st day ($U_s = 73$, $df = 6,12$, $P > 0.05$) (Fig. 1A). A dramatic increase in mobility in pen 1 (to an average of 14.49), caused by the weasel's presence, was significantly different from the values for the preceding day in the same pen 1 ($U_s = 130$, $df = 6,12$, $P < 0.05$) and in pen 3 ($U_s = 136$, $df = 6,12$, $P < 0.05$), as well as from the mobility index for the 2nd day in pen 3 ($U_s = 123$, $df = 6,12$, $P < 0.05$) (Fig. 1A).

On the 3rd day after removing the weasel from pen 1 and opening all the passages, the mobility of the few voles that remained in pen 1 dropped to an average of 11.25 crossings per vole per hour. Meanwhile an influx of intruders into pen 3 (voles which deserted pen 1 in response to a predator's presence) resulted in an increased mobility of voles in this pen also (Fig. 1A). The indices for the 3rd day were intermediate and not significantly different from days 1 and 2.

Aggressive encounters between voles were common in densely populated pens. On the first day we recorded an average of 0.85 (*SD* 0.97, range 0–2.7) fights per hour per individual in pen 1, and 0.58 (*SD* 0.52, range 0–1.82) fights in pen

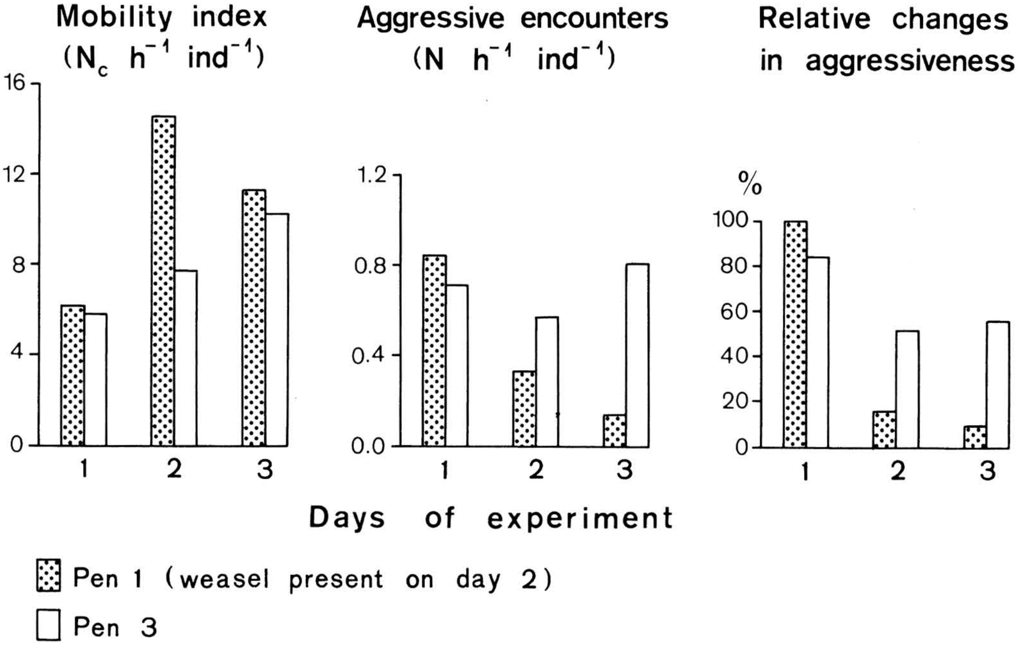

Fig. 1. Changes in the behaviour of bank voles due to the risk from the weasel introduced into the enclosure. The weasel was released into pen 1 on day 2. Pen 3 was a control. Mobility index = above ground mobility of voles expressed as the mean number of crossings per hour per individual of perpendicular lines placed on the floor. Aggressive encounters = mean numbers of fights per hour per individual. Relative changes in aggressiveness = number of aggressive encounters weighted by above-ground mobility index, the value for day 1 in pen 1 taken as 100%.

3 (Fig. 1B). In contrast, bank voles appeared to be very mild while the weasel was in pen 1 (mean = 0.37, *SD* 0.25, range 0.08–0.77) and still less aggressive on the days following the removal of a predator (mean = 0.14, *SD* 0.39, range 0–1.33) but the latter was apparently an effect of a sudden decrease in vole numbers. None of these indices, however, differed significantly.

The intraspecific aggressiveness may be a function of mobility. Increased mobility may be conducive to frequent contacts with conspecifics. We therefore calculated the corrected index of aggressiveness: the ratio of the mean number of aggressive encounters to the mean mobility index for each day, and we took the value for the first day in pen 1 as 100%. This enabled us to show the relative changes in aggression that occurred in the course of the experiment (Fig. 1C). Though highly mobile, the voles paid particularly little attention to intraspecific contests during the weasel's presence in pen 1. The level of aggressiveness differed significantly between the two pens on the 2nd day ($G = 19.92$, $df = 1$, $P < 0.001$, G-test for goodness of fit to the expected ratio 1:1), and on the 3rd day ($G = 38.09$, $df = 1$, $P < 0.001$).

On the first day (before a weasel's presence) bank voles did not climb twigs in either pen. When a weasel was penetrating pen 1 (the second day) and hunting for prey, the voles often used arboreal runways. An average of 2.95 voles were tallied on twigs at the end of each 5-minute observation period in pen 1. No voles were recorded on twigs in pen 3 that day. The fear persisted longer than the presence of a weasel. On the third day, in both pens, voles sporadically climbed

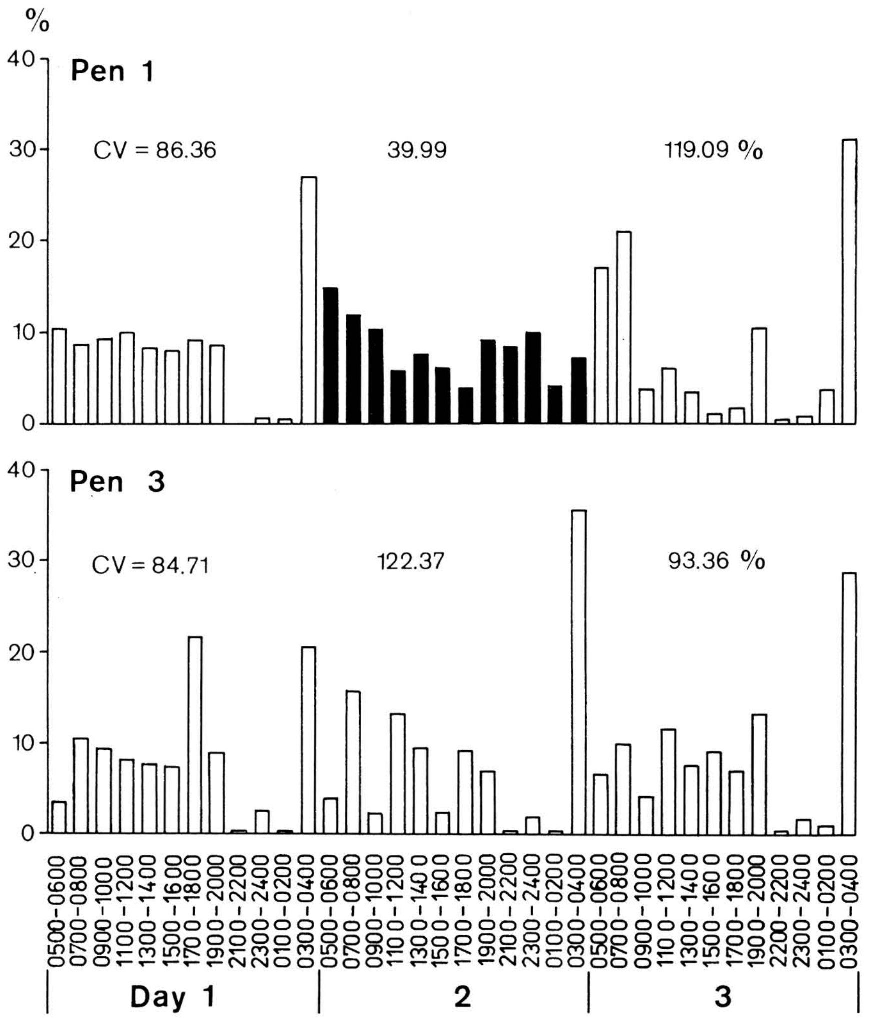

Fig. 2. Diel activity rhythms of bank voles in pen 1 (a weasel present on day 2) and pen 3 (control). Data calculated for above ground mobility to show percentages of total daily activity during each hour of observation. CV = coefficient of variation.

twigs in response to an atypical noise or the running of a conspecific (mean = 0.93 voles on twigs in pen 1 and 0.04 in pen 3 at the end of each 5-minute observation period).

3.2. Diel activity rhythm of bank voles

The temporal distribution of the voles' above-ground activity is shown in Fig. 2. In both pens during all days, except for a day with a weasel in pen 1, the diel activity rhythm was characterized by distinct peaks at dawn and almost complete inactivity during the nights (Fig. 2). The presence of a weasel in pen 1 on the second day made the bank voles active throughout the day with little differences between hourly observation periods (coefficient of variation 39.99 in contrast to 84.71–122.37 on the other days, Fig. 2). To test whether the presence of a weasel significantly differentiated the timing of the voles' activity across the six periods of 24 h, the data were ranked in increasing order of the per cent activity for each day and all possible combinations of pairs were compared. For days with no weasel, all but one combination (day 1 in pen 3 with day 3 in pen 1, $P > 0.05$) were significantly correlated (Spearman rank r_s 0.59–0.86, $df = 10$, $0.01 > P < 0.05$). The day with the weasel present (day 2 in pen 1) was not correlated with any other day (Spearman rank r_s –0.05–0.28, $df = 10$, $P > 0.05$).

When the weasel was inactive and stayed within its nest box (for a total of 13.5 hrs) the voles ran, foraged, and drank on the ground. When the weasel resumed hunting and chasing voles, the latter stopped foraging and hid under the ground, but very soon after the weasel had started to penetrate the burrows and tunnels, the voles escaped to the ground surface or climbed the twigs. The voles adjusted their activity (stopped foraging and panicked) to the activity of a weasel within one 5-minute observation period after the weasel had emerged from its box.

3.3. Selectiveness in weasels' predation on bank voles

Although weasels were introduced to three different enclosed populations of bank voles six times, the weasels killed voles during only three sessions. Most often the youngest voles fell prey to the weasels (Table 1). Out of ten voles removed, seven were unmarked nestlings born in the enclosure. Weasel selectiveness was clear. The weight distribution of voles killed differed significantly from that of voles which survived (pooled data, $G = 18.69$, $df = 3$, $P < 0.001$, G-test for independence).

Table 1. Selective removal of bank voles (ind.) by weasels in seminatural enclosure. See Sect. 2 for the experimental procedure.

	Body mass (g)				
	0–7	7.5–14	14.5–21	>21.5	Total
Experiment I					
Present	8	10	2	6	26
Killed	4	0	0	0	4
Experiment II					
Present	3	1	8	6	18
Killed	3	0	0	0	3
Experiment III					
Present	–	2	3	4	9
Killed	–	2	1	0	3
Total					
Present	11	13	13	16	53
Killed	7	2	1	0	10

4. Discussion

Edmunds (1974:232) suggested: "Prey species that are subject to serious losses due to specialist predators may themselves evolve defences directed at just one or a few species of predators". Further on, however, he stated (p. 283) that few predator specific defences had been described from vertebrates. The antipredatory behavioural defence of bank voles observed in this experiment is clearly a specific response to mustelids hunting both on and under the ground, day and night, killing both young and adult voles. Bank voles recognize a weasel's odour and avoid entering areas recently visited by a weasel (Jędrzejewski & Jędrzejewska 1990). Voles changed their diel activity, suppressed the intraspecific aggressiveness (or at least its noisy form), and used different methods of escape in response to weasel presence. Such plasticity has been documented for bank voles' activity patterns, which varied with season, food supply, age of voles, and population density (Saint Girons 1960, 1961, Greenwood 1978, Wójcik & Wołk 1985, Ylönen 1988).

In this study, adult bank voles had better chances than young ones to avoid weasel attacks. This clearly reflects the development of escape abilities as voles age (Table 2). Reproduction seems to be the period of high vulnerability to mustelid predation in bank voles, much the same as was documented in large herbivores preyed upon by canids (see review in Curio 1976). In rodents, however, not only are the nestlings most susceptible to weasels but the breeding activities of females are also in conflict with their antipredatory behaviour. Weasels recognize and prefer the odour of oestrous mice (Cushing 1985). In the laboratory experiment by Ylönen (1989) pairs of bank voles living in cages adjacent to a weasel's cage did not reproduce. In our enclosure experiments (Jędrzejewski & Jędrzejewska 1990) reproducing females and juvenile bank voles did

Table 2. Antipredatory behaviour of bank voles of different ages as a factor affecting their vulnerability to predation by weasels.

Response to risk	Nestlings	Juveniles	Subadults	Adults
Increased above ground mobility	–	+	+	+
Climbing twigs	–	?	+	+
Plasticity in diel rhythm of above ground activity	–	?	+	+
Microhabitat shift after weasel's presence[a]	–	–	+	♀ –, ♂ +
Probability of survival[b]	0.36	0.85	0.92	1.00

[a] after Jędrzejewski & Jędrzejewska (1990)

[b] calculated from Table 1 as proportion of bank voles which survived in a given age class.

not abandon their sites after the weasel had visited the area. Outside the reproduction period the more subtle behavioural traits, e.g. residency vs. transiency (Jędrzejewska 1989) may differentiate voles' susceptibility to weasel predation.

One should, however, keep in mind that the particular quantitative results obtained in these experiments cannot be simply applied to natural conditions because of the unnaturally high densities of prey and predator in our enclosure. Nonetheless, the general characteristics of the behaviour of bank voles and weasels described are most probably relevant to the free-living populations as well.

The antipredatory defences by bank voles against weasels are such that the voles escaping weasel attacks become more exposed to hunting raptors or ground searching mammalian predators. Charnov et al. (1976) supposed that "If the activities of one predator actually enhance encounters with prey for another predator, it may be advantageous for the second predator to forage near the first. The ideal individual to follow would be one that disturbed a large number of prey but pursued and/or captured few of them". McLee (1986) has observed a kestrel exploiting the hunting activity of weasels. The kestrel easily caught rodents that tried to escape weasels. Sludsky (1964) reported several observations on co-operation between the marbled polecat *Vormela peregusna* and the red fox *Vulpes vulpes* hunting great gerbils *Rhombomys opimus*. Paxton (1988) described pale chanting goshawks *Melierax canorus* and a black-backed jackal *Canis mesomelas*, which successfully attacked rodents fleeing from foraging honey badgers *Mellivora capensis*. In weasels, however, such foraging associations probably pose a risk to the weasel, which may fall victim to the other predator (Powell 1973, Korpimäki & Norrdahl 1989).

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