Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-voles relationships

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Predation risk is an important element of the environment influencing animal behaviour, reproduction and distribution. During the last decade, the literature abounded with reports on experiments with invertebrates, fish, birds, and mammals exposed to predation risk (review in Lima and Dill 1990). Studies on mammals showed that the recognition of mammalian predators by their mammalian prey could be based on olfactory cues: prey 'decided' the carnivore scents used for territory marking, individual and intersexual recognition. Most numerous studies on mammals as potential prey were those on small rodents. They showed that microtine voles responded to odour of weasels Mustela nivalis, stoat Mustela erminea, red fox Vulpes vulpes, and badger Meles meles (Stoddart 1976, Dickman and Dunstone 1984, Gorman 1984, Sullivan et al. 1988, Jędrzejewski and Jędrzejewska 1990).

The bank vole Clethrionomys glaevulatus, a common subject of those studies, is an important prey to many species of predators. It coexists with four species of

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mammalian predators and five species of raptors in Scandinavian boreal forests (Hamsh et al. 1991), and eight species of mammalian predators and nine species of raptors in temperate broadleaf forests of Central Europe (Jędrzejewski and Jędrzejewka 1993). The coexistence of bank voles with so many predators elicited a question of whether the voles distinguishes the odour of various predators and assesses the risk of their predation. Muller-Schwarze (1972) showed that black-tailed deer Odocoileus hemionus fawns are deterred from food mixed with odours of predators, and their response was stronger to the odours of sympatric predators (cytope Canis lupus and mountain lion Felis concolor) than to those of allopatric ones (lion Panthera leo, tiger P. tigris, and snow leopard P. uncia). The odours of wolf Canis lupus, fox, weasels and lynx Lynx canadensis, and bobcat L. rufus suppressed feeding in black-tailed deer (Sullivan et al. 1965b). The deer reacted least adversely to bobcat and Canadian lynx odours, the two species that rarely prey on deer (Sullivan et al. 1965b). Came and Wellden (1969) exposed red-bellied tamarins Saguinus fuscicollis to the odours of sympatric predators, the jaguar Panthera onca, the margay Felinus wiedii, and the jaguarundi Herpailurus yagouaroundi. The fecal extract of these predators elicited tammarins' avoidance of branches tainted with the scent and higher voles of their visual scanning than the odours of non-predatory mammals. The aim of our work was to study the response of bank voles to the odours of seven species of its sympatric predators from woodlands of Central and Eastern Europe. The experiments were supposed to supplement the long-term field research on prey-predator relationships in the pristine forests of the Białowieża National Park, eastern Poland (e.g. Jędrzejewski et al. 1989). Jędrzejewski and Jędrzejewka (1993). Two main questions were asked: (1) what are the anti-predatory defenses and behaviour of bank voles exposed to the odour of seven species of predators? and (2) how do these defenses relate to the role the bank vole plays in the food of these predators in the natural forests of Białowieża National Park?

Material and methods

Totally, 660 bank voles (including 360 voles livetrapped in nearby Białowieża Forest and 300 voles bred and raised at the Mammal Research Institute) were used in the study. Before the trials, the captured voles were kept in groups of 4 or 5 individuals in metal cages (0.25 x 0.42 x 0.15 m) in the laboratory, or in groups of 20 to 40 voles in large (4 x 12 m) outdoor enclosures under seminatural conditions (description of enclosures in Jędrzejewski and Jędrzejewka 1990). Of the total number of voles, 600 were used only once, and the other 60 voles were used in two trials but only once with the same species of predator.

The predators used in the experiment were: the weasel Mustela nivalis, the stone marten Martes foina, the red fox, the raccoon dog Nyctereutes procyonoides, and the tawny owl Strix aluco. Domestic rabbit Oryctolagus cuniculus was used as a control animal. The predator species, except for the stone marten, were chosen as being the most important predators of bank voles is Białowieża National Park (Jędrzejewski and Jędrzejewka 1993). Stone marten was used instead of the closely related pine marten M. martes, which was not available to us during the course of the experiment. Racoon dog is not native to Europe. It was deliberately introduced into the European part of the Soviet Union and it was first recorded in Białowieża Forest in 1955. Two weasels and one individual of all other species were used in the experiment. Before and during the trials predators were kept in outdoor cages (4.5 x 2 x 2.5 m).

Experiments were conducted indoors, in a glass terrarium, divided into three parallel pens (Fig. 1). The floor was made of sheet metal. Two small passages were at the bottom of each inside wall to allow the rodents to move freely between the three pens. Each passage had a metal door opening (closed or open) from the outside of the terrarium. During each trial, the floor was covered with a clean, white sheet of paper with a dark line drawn across the middle of each pen (to facilitate the count of rodent movements). Four plastic tubes (40 mm diameter, 120 mm long), four subcubes tubes (30 mm diameter, 200 mm long), four vertical twigs, one tray with oats, and one tray with water ad lib. were placed in each pen. The tubes simulate rodents' underground tunnels. Twigs allowed 'forb' escape by voles. After each trial the whole terrarium was carefully washed with

252
hot water and detergent. New sheets of paper, clean tubes, fresh twigs, oats and water were then provided. The terrarium was placed indoors, in a room 3 x 4 m at the Mammal Research Institute, Blaokwalsa.

We conducted a total of 48 one-day trials from July 1988 to December 1989. Six trials (replicates) were done with each species of predator (7 species) and 6 with a rabbit. For each trial, 15 bank voles were released into the terrarium in the evening preceding a trial. During the nights, the passages between the pens were open, so the voles could space themselves in the terrarium. Observations of behaviour (10 min), followed by counting the voles in each pen, began the next morning at 0730 hours. Until 1015 the observations were made each half an hour. At 1015, all rodents were removed from the terrarium (voles from each pen were put into a separate bucket) and a predator or rabbit was put into one peripheral pen for 5 min to dispense its odour. While in the pen, the predators usually sat quietly on floor, except for the weasel and the stoat, which moved around it. Weasels (but not stoats) were able to pass through the tubes and were seen doing that. Fezes, sporadically dropped by predators, were immediately removed from a pen. All mammalian predators and a rabbit occasionally left droplets of urine. Although in most trials no visible carrier of scent was deposited in a pen by predators, the odour of each animal (tawny owl and rabbit included) was strong and easily perceived by humans. After the predator had been removed, all rodents were released back to their pens. From 1030 until 1130, the observations were carried out every 15 min and from 1130 until 1430 - every half an hour. The last four observations were done at 1530, 1730, 1930, and 2130.

In the statistical analysis, 3 periods were distinguished: (I) before the introduction of a predator (0730 to 1030), six 10-min observations in each trial, (II) shortly after the introduction of a predator (1030 to 1530, twelve observations), and (III) later after the introduction of a predator (1730 to 2130, three observations).

During each 10-min observation, the number of crossings of the central ditch line by voles in each pen and the number of vole movements from one pen to another were noted (as a measure of motility). This was done to one (occasionally two) persons sitting outside the terrarium and watching all pens through the glass walls. After 10 min of observations, the passages between pens were closed and the voles on twigs and all other voles staying out of tubes were counted in each pen. Then all tubes were checked by lifting them with a hooked poked and voles hidden in the tubes were counted in each pen. After counting was finished, the passages between pens were opened again.

The following behavioral variables were measured here:

1. Mean number of voles present in the pen into which a predator was introduced in periods I, II and III of the trial (see above). For each predator and a rabbit, data from 6 replicates were averaged.
2. Mean number of bank voles on twigs in the whole terrarium (data absorbed except for periods I and II).
3. Mean number of bank voles staying out of the tubes in the whole terrarium calculated for periods I and II of the trial.
4. Mobility index of voles staying out of the tubes, calculated for periods I and II as a total number of crossings of central lines and movements between pens divided by the number of voles staying out of the tubes. This variable included both reduced movement activity and immobility (freezing).

Behavioural variables (points 2, 3, and 4) were not analysed in period III because the evening peak of daily activity of voles (variable not controlled in our experiment) made the voles excessively mobile at that time in all trials.

Results

Since the total number of voles released into the terrarium during each trial was 15, the expected distribution of voles in three pens in period I (before a predator’s visit) was 5:5:5. The observed mean numbers of voles in each of the 3 pens did not deviate significantly from the expected one in all trials (G-test, G = 0.06 to 0.38, df
Discussion

Bank voles' response to red fox, stoat, and weasel was consistent with the earlier findings (Stokkert 1970, Dickman and Domnster 1984, Gorman 1984, Ylönen 1989, Jędrzejewska and Jędrzejewski 1990). Thus, bank voles' recognition of mammalian predators in a widespread evolutionary adaptation of the species. The model information from our experiments was that the
<table>
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<th>Predators</th>
<th>Bank-vole response to predator odour</th>
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<tr>
<td></td>
<td>Avoidance of pen ('avoided') by bank-vole</td>
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<tr>
<td>Wiesel</td>
<td>+</td>
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<tr>
<td>Stoat</td>
<td>+</td>
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<td>Stone martens</td>
<td>+</td>
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<td>Polecat</td>
<td>+</td>
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<td>Red fox</td>
<td>+</td>
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<td>Bearded vulture</td>
<td>+</td>
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<td>Tawny owl</td>
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<td>European rabbit</td>
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<td>Control (rabbits)</td>
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Different antipredatory behaviours of bank-voles to various predation risks seemed to be adaptations against their modes of hunting. Weasels and stoats pursue rodents both on the ground and in their underground tunnels and burrows (King 1989). The most common behaviour of rodents staying in a burrow, that is being penetrated by a small mustelid predator, is an escape out of it (Slasky 1984, for the marbled polecat *Vormela peregous*; Erlinge et al. 1974, Jędrzejewski et al. 1992, for the weasel). Immobility in response to a predator is a way of staying silent which helps if the predator hunts by hearing and/or sight. Hunting by using sense of hearing was documented for red fox and weasel (Ostertom 1964, Erlinge et al. 1974, Jędrzejewski et al. 1992). Clamping ('arboreal' escape) was observed in experiments with bank vole and weasels in an enclosure (Erlinge et al. 1974, Jędrzejewski and Jędrzejewska 1986) and in the forest of Białowieża National Park by observing observations of weasels hunting for bank vole and yellow-necked mice *Apodemus flavicollis* (Jędrzejewski and Jędrzejewska 1992). 'Arboreal' escape was very often successful because the weasel quickly lost the target rodent from the field of vision.

To check whether the set of antipredatory behaviours of bank-voles against the tested species of mammalian predators was related to the degree of specialisation of these predators in hunting for bank-voles, we compared the numbers of various behaviours shown by the voles (see Table 1) with the contribution of the bank-vole to the biomass consumed by a given predator in the natural forests of Białowieża National Park (after Jędrzejewski and Jędrzejewska 1993). According to the arms race hypothesis (see Edmonds 1974), the antipredatory behaviour of the bank-vole should be more developed against those species of predators which were more specialised in taking bank-voles. We used data on autumn-winter food composition of predators because the mortality of voles (nearly exclusively caused by predation, Jędrzejewski and Jędrzejewska 1993) is very high at that time of the year. There was a significant positive correlation between the antipredatory abilities of voles and the degree of mammalian predators' specialisation.
Fig. 6. Number of qualitatively different antipredatory behaviours of bank voles to ten species of mammalian predators (as listed in Table 1) in relation to the role of bank vole in autumn-winter food of these predators in Białowieża National Park. To exclude the bias of between-pest variation, data on food composition were averaged for 3 or 4 yr (1995–1996; 1999–2000; from Jędrzejewski and Jędrzejewska 1995). The data for marten regard the voles' antipredatory behaviours against the stone marten Mustela nivalis and the food of closely related pine marten M. martes (see explanation in Material and Methods). Regression equation: \[ Y = 1.5 + 0.04X, \ \text{df} = 4, \ F = 21.657, r = 0.91, p = 0.000. \]

cialisation in that species (Fig. 6). This could be interpreted as an outcome of an evolutionary arms race between the bank vole and its mammalian predators that is still operating.

No response of bank voles to tawny owl odour in our experiments does not mean that bank voles lack antipredatory behaviour against this raptor. In Wytham Wood (England), Southern and Lowe (1966) found that bank voles predominantly occurred in places with dense shrub cover, whereas the tawny owls preferred to hunt in bare ground places. In the mature forests of Białowieża National Park, bank voles choose the routes with overhead cover (under fallen logs and uprooted trees) (Olejarski 1988; Mazurkewicz 1991) found that in forests with shrubs, the bank vole distribution was clumped in places with shrubs. Also, the density of voles in various plots correlated with undergrowth cover. Such spatial distribution and microhabitat selection may be an antipredatory behaviour against visually hunting raptors.

To avoid the risk of owl predation and the risk of mammalian predator may be two conflicting demands. Merkusz et al. (1991) exposed Townsend's voles Microtus townsendii to risk of predation marked by both the odour of mammalian predator (synthesised thiochrome and dihydroane) and the lack of cover, or by one of these factors. In the absence of cover, voles preferred to feed in the area free of predator odour. When cover was present, voles preferred to feed under cover, regardless of whether or not the odor was dispersed there. It indicates that microtus may perceive the risk of owl predation more 'serious' than that of mammalian predators. It is probably because rodents lack the efficient direct recognition of risk of owl predation and rely on indirect cues such as light intensity and the presence of overhead cover (Price et al. 1984, Brown et al. 1986, Harestad 1991).

In the pristine forests of Białowieża National Park, the bank voles made use, on average, 27% of biomass consumed by the tawny owl (Jędrzejewski and Jędrzejewska 1995). It places this predator behind weasel, stout and pine marten in its specialisation for bank voles (see Fig. 6). However, the density of tawny owl in Białowieża Nat. Park was 2-3 times higher than that of marten and weasel. (Comparison with stout is not adequate here, as the stout's optimal habitats are marshes and meadow.) In winter, an average 1 km² of the forest supported 2.5 kg of tawny owls (4.3–5.7 ind), 0.7 kg of martens (0.5–0.8 ind) and 0.16 kg of weasels (1.7–2.7 ind). Tawny owls were the most efficient predators of bank voles. They contributed on average 60% to the total winter predation on voles, where weasels – 17%, and pine martens – 14% (Jędrzejewski and Jędrzejewska 1993). We think that an important mechanism of this was that the voles' recognition and avoidance of tawny owl has not been as efficient as that of mammalian predators.

Tests by Daboux (1987) proposed a mathematical model exploring the effects of antipredatory behaviours of prey on the population dynamics of prey and predator. The model predicted that the higher the efficiency of antipredatory behaviour in prey, the density of the prey population always increases (or the predator density decreases) and the ratio of predator-to-prey density always decreases. The results of the model may explain the difference between the tawny owl-bank vole and the mammalian predator-bank vole relationships. As shown by this experiment and by the field studies (Jędrzejewski and Jędrzejewska 1995), the ratio of predator-to-bank vole densities are much lower in mammalian predators than in the tawny owl, against which the voles' antipredatory behaviour is not that efficient. A question that remains unanswered is how the hunting success of each predator species (in terms of captured prey per attempt) is related to the bank vole's antipredatory behaviour. Unsuccessful predation is a necessary condition for the evolution of antipredatory characteristics in prey (Verner 1982). So far, we have gathered data on weasels hunting bank voles in natural conditions of the forests of Białowieża National Park (Jędrzejewski et al. 1992). In autumn and winter, when