

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

Włodzimierz Jędrzejewski, Leszek Rychlik and Bogumiła Jędrzejewska

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Bank voles *Clethrionomys glareolus* were exposed to odours of seven species of predators (weasel *Mustela nivalis*, stoat *M. erminea*, polecat *M. putorius*, stone marten *Martes foina*, red fox *Vulpes vulpes*, raccoon dog *Nyctereutes procyonoides*, and tawny owl *Strix aluco*) and a non-predatory animal (domestic rabbit) in a total of 48 one-day terrarium trials. In response to odours of each mammalian predator, dispensed in one of the 3 pens, the number of voles utilizing that pen decreased significantly (50–90% of initial numbers). Tawny owl and rabbit scents did not change voles' distribution in the terrarium. Bank voles climbed twigs ('arboreal' escape) in trials with mustelid (but not canid) predators. Odours of stoat, weasel and marten made the voles stay out of tubes simulating underground tunnels. Voles became significantly less mobile in response to fox and weasel odour. The numbers of qualitatively different antipredatory behaviours of voles against mammalian predators (from 1 in raccoon dog trials to 4 in weasel trials) correlated positively with the degree of specialisation of these predators in hunting for bank voles in natural habitats (Białowieża National Park, eastern Poland). No response of voles to tawny owl suggests that the lack of direct recognition of risk of owl predation by bank voles and their relying only on indirect cues (i.e. cover, light intensity) might be an important mechanism facilitating the owl's high contribution (60%) to the total predation on bank voles in autumn-winter seasons in Białowieża forest.

W. Jędrzejewski, L. Rychlik, B. Jędrzejewska, Mammal Research Institute, Polish Academy of Sciences, 17–230 Białowieża, Poland. (Present address of B. J.: Workshop for Ecology and Protection of the Natural Environment, 17–230 Białowieża, P. O. Box 23, Poland).

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 'decoded' the carnivore scents used for territory marking, individual and intersexual recogni-

tion. 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 *M. erminea*, red fox *Vulpes vulpes*, and badger *Meles meles* (Stoddart 1976, Dickman and Doncaster 1984, Gorman 1984, Sullivan et al. 1988, Jędrzejewski and Jędrzejewska 1990).

The bank vole *Clethrionomys glareolus*, 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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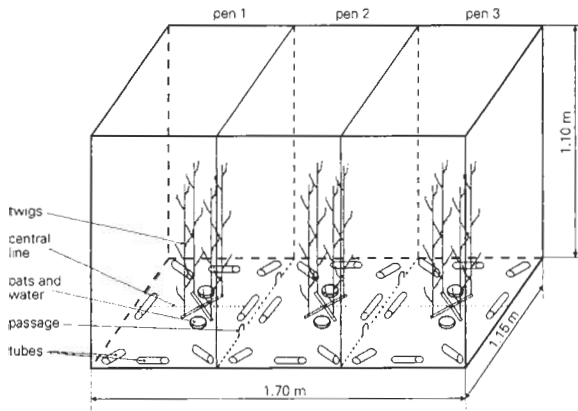


Fig. 1. The glass terrarium used for experiments with bank voles and predators. In each 1-day trial, 15 bank voles were used. Predator was introduced into one of the peripheral pens for 5 min.

mammalian predators and five species of raptors in Scandinavian boreal forests (Hanski et al. 1991), and eight species of mammalian predators and nine species of raptors in temperate broadleaf forests of Central Europe (Jędrzejewski and Jędrzejewska 1993). The coexistence of bank voles with so many predators elicits a question of whether the vole distinguishes the odours of various predators and assesses the risk of their predation.

Muller-Schwarze (1972) showed that black-tailed deer *Odocoileus hemionus* fawns were deterred from food mixed with odours of predators, and their response was stronger to the odours of sympatric predators (coyote *Canis latrans* 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, wolverine *Gulo gulo*, lynx *Lynx canadensis*, and bobcat *L. rufus* suppressed feeding in black-tailed deer (Sullivan et al. 1985b). The deer reacted least adversely to bobcat and Canadian lynx odours, the two species that rarely prey on deer (Sullivan et al. 1985b). Caine and Weldon (1989) exposed red-bellied tamarins *Sanguinus labiatus* to the odours of sympatric predators, the jaguar *Panthera onca*, the margay *Felis wiedii*, and the jaguarundi *Herpailurus yagouarundi*. The fecal extract of these predators elicited tamarins' avoidance of branches tainted with the scent and higher rates of their visual scanning than did 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 Jędrzejewska 1993). Two main questions were asked: (1) what are the antipredatory defences and behaviour of bank voles exposed to the odour of seven species of predators? and (2) how do these defences 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 630 voles livetrapped in nearby Białowieża Forest and 30 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 × 0.42 × 0.15 m) in the laboratory, or in groups of 30 to 40 voles in large (4 × 12 m) outdoor enclosures under seminatural conditions (description of enclosures in Jędrzejewski and Jędrzejewska 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, the stoat, the polecat *Mustela putorius*, 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 in Białowieża National Park (Jędrzejewski and Jędrzejewska 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. Raccoon 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 between the trials predators were kept in outdoor cages (4.5 × 2 × 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 operated (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 rubber 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 simulated rodents' underground tunnels. Twigs allowed 'arboreal' escape by voles. After each trial the whole terrarium was carefully washed with

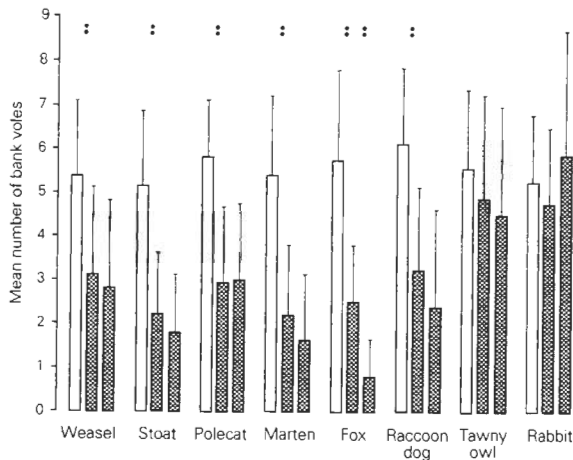


Fig. 2. Mean (\pm SD) numbers of bank voles in the pen to which a predator was introduced. White bars: period I (2.5–0 h before predator introduction), shaded bars: period II (0–5 h after a 5-min predator's visit) and period III (5–11 h after a predator's visit). Significant differences between two consecutive periods marked: ** $p < 0.01$. Test for Means with Unequal Variances (Sokal and Rohlf 1981).

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 3×4 m at the Mammal Research Institute, Białowieża.

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 night, 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 every 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 stoat) were able to pass through the tubes and were seen doing that. Feces, 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 1000, six 10-min observations in each trial), (II) shortly after the introduction of a predator (1030 to 1530, twelve observations), and (III) late after the introduction of a predator (1730 to 2130, three observations).

During each 10-min observation, the number of crossings of the central dark line by voles in each pen and the number of vole movements from one pen to another were noted (as a measure of mobility). This was done by one (occasionally two) person(s) 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 poker and voles hidden in the tubes were counted in each pen. After counting was finished, the passages between pens were opened again.

The following behavioural 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 ('arboreal' escape) calculated 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 from 0.06 to 0.38, df

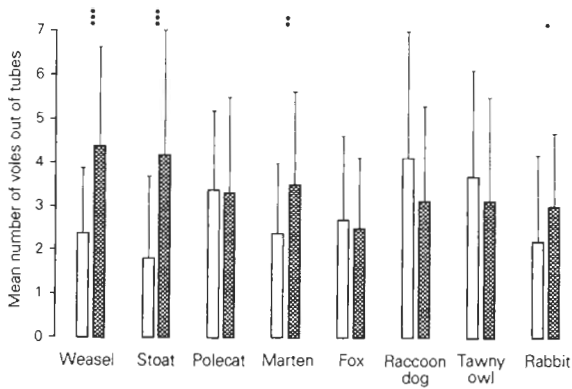


Fig. 3. Mean (\pm SD) numbers of voles staying out of rubber and plastic tubes in a whole terrarium. White bars – period I, shaded bars – period II (see Fig. 2). * $p < 0.05$. ** $p < 0.01$, *** $p < 0.001$ (test as in Fig. 2).

= 1, $p > 0.5$). After the 5-min visit of a predator to one of the peripheral pens, a strong avoidance of that pen by voles was observed in trials with all mammalian predators (Fig. 2). This strong avoidance lasted until the end of each trial. No such avoidance was observed in trials with tawny owl and rabbit (Fig. 2).

Although the distribution of voles in the terrarium was even and stable before a predator's visit, the number of voles staying out of tubes was very variable both between consecutive trials with the same predator and between various predators. Nonetheless, the reaction of bank voles to the odour of the smallest predators (weasel and stoat) was pronounced (Fig. 3). The bank voles stayed outside of tubes significantly more after the predator's visit than before it in stoat and weasel trials. Avoidance of tubes was also visible (though weaker) in marten trials. For all other predators and a rabbit, this change was much less pronounced.

The scent of four mammalian predators (weasel, stoat, marten and fox) caused a decrease in mobility of

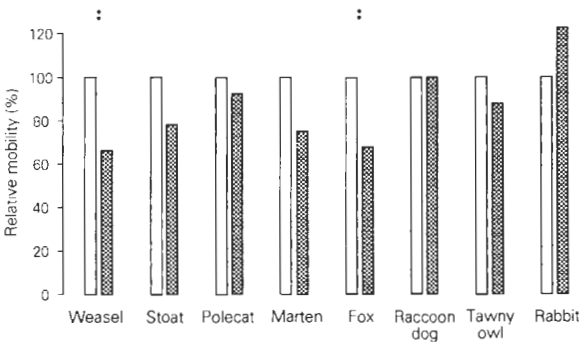


Fig. 4. Changes in movement activity of bank voles in a whole terrarium in response to predator odour. Mean mobility index during period I was taken as 100% in each predator series (white bars). Shaded bars – period II (see Fig. 2). ** $p < 0.01$, G-test for homogeneity of percentages.

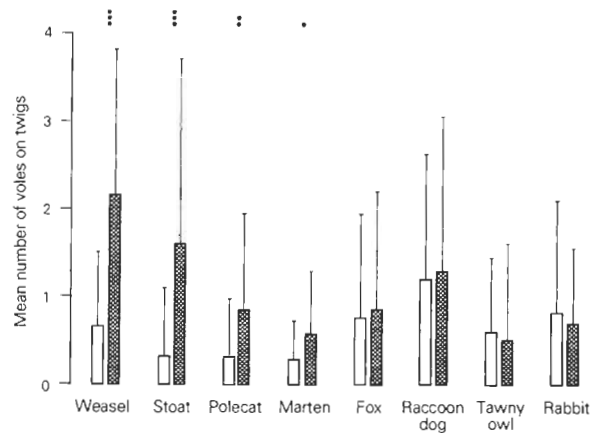


Fig. 5. Mean (\pm SD) numbers of voles on twigs in a whole terrarium. White bars – period I, shaded bars – period II (see Fig. 2). * $p < 0.05$. ** $p < 0.01$, *** $p < 0.001$ (test as in Fig. 2).

those voles which stayed out of tubes (Fig. 4). In response to weasel and fox odours, this reaction (including both reduced movement activity and immobility) was statistically significant.

The number of voles climbing twigs in period I (before a predator's visit) varied considerably (probably, due to individual variation in voles' behaviour) from an average of 0.3 in trials with marten to 1.2 in trials with raccoon dog. However, the voles showed a great tendency to climbing in response to the scent of all four mustelids, especially stoat and weasel (Fig. 5).

Bank voles reacted differently to odours of carnivores compared to odour of a raptor and a non-carnivorous mammal (rabbit) (Table 1). Also, the voles responded differently to various species of carnivores. The voles reacted by climbing twigs in response to mustelid odour but not to odour of fox and raccoon dog (Table 1). They became less mobile in response to fox odour but not to that of the raccoon dog. Among mustelids, three 'types' of predators were distinguished: a weasel, a pair stoat-marten (although in trials with marten, the voles' escape out of tubes was much weaker than against the stoat), and a polecat. The widest range of antipredatory behaviors by bank voles was observed in trials with the least weasel. No reaction was recorded in the trials with the rabbit and the tawny owl.

Discussion

Bank vole response to red fox, stoat, and weasel was consistent with the earlier findings (Stoddart 1976, Dickman and Doncaster 1984, Gorman 1984, Ylönen 1989, Jędrzejewska and Jędrzejewski 1990). Thus, bank voles' recognition of mammalian predators is a widespread evolutionary adaptation of the species. The novel information from our experiments was that the

Table 1. Antipredatory responses of bank voles to odours of seven species of predators inhabiting Central Europe – summary of experiments. no = no clear response, + = observed strong response.

Predator	Bank vole response to predator odour			
	Avoidance of pen 'visited' by a predator	Climbing twigs	Escape out of 'burrows'	Reduced mobility
Weasel	+	+	+	+
Stoat	+	+	+	no
Stone marten	+	+	+	no
Polecat	+	+	no	no
Red fox	+	no	no	+
Raccoon dog	+	no	no	no
Tawny owl	no	no	no	no
Control (rabbit)	no	no	no	no

bank vole exhibited such a diversified response to seven species of predators. Below, we discuss the adaptive significance of these behavioural patterns and examine how the currently observed differentiation relates to the specialisation of the predators in hunting for bank voles. Since the experimental set up was rather artificial for prey and predators, only the qualitative changes in voles' behaviour (and not particular quantitative results) are discussed.

The most pronounced difference was observed in the voles' responses to the mammalian predators and to the tawny owl and rabbit. Bank voles obviously perceived the odour of all mammalian predators as an advanced indication of risk. Canids and mustelids communicate with odours, which are produced and held in special sacs. Rabbits are similarly endowed, but no behavioural changes in voles occurred to the odour of this species. The odour of tawny owl, although easily perceived by the experimenters and most likely by the voles, too, did not seem to carry any information about risk. Aerial hunting by the tawny owl does not leave olfactory cues on the ground. Therefore, the olfactory recognition of owls by voles did not develop.

The antipredatory defences of voles might be based on recognition of both the family or genus-specific components of predator odour and the species-specific components of it. Chemical analysis of anal sac secretion of mustelids showed that they contained the genus-specific compounds (thietanes and dithiolanes in *Mustela*, benzaldehyde in *Martes*) as well as species-specific components (e.g. compounds differentiating *erminea*, *putorius*, and *nivalis* within the genus *Mustela*) (Brinck et al. 1983, Crump and Moors 1985). No such comparative studies on Canidae were known to us, but the analysis of red fox and wolf *Canis lupus* urine indicates that sulfides may be volatile constituents characteristic of canid predators (Wilson et al. 1978, Raymer et al. 1984). This variation of odours and the fairly long persistence of their chemical components once dispensed (up to few weeks, Sullivan et al. 1985a) make the olfactory cues an accurate indicator about risk of carnivore predation to the potential prey.

Different antipredatory behaviours of voles to various predatory mammals 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 (Sludsky 1964, for the marbled polecat *Vormela peregusna*; 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 (Osterholm 1964, Erlinge et al. 1974, Jędrzejewski et al. 1992). Climbing ('arboreal' escape) was observed in experiments with bank voles and weasels in an enclosure (Erlinge et al. 1974, Jędrzejewska and Jędrzejewski 1990) and in the forest of Białowieża National Park during observations of weasels hunting for bank voles and yellow-necked mice *Apodemus flavicollis* (Jędrzejewski et al. 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 showed 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 Edmunds 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' spe-

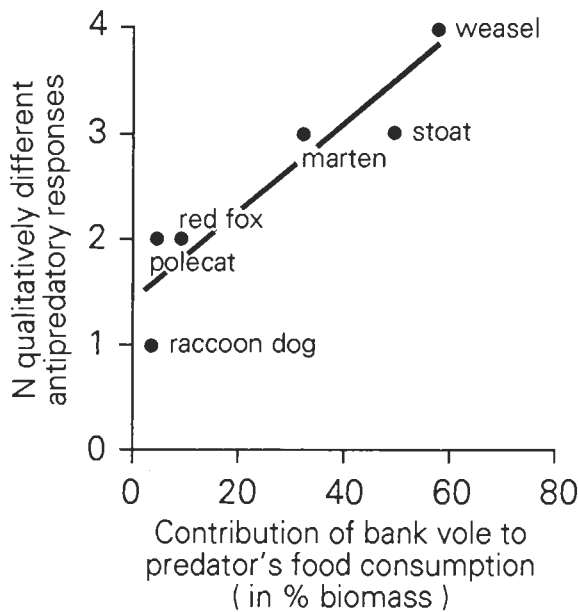


Fig. 6. Number of qualitatively different antipredatory behaviours of bank voles to six species of mammalian predators (as listed in Table 1) in relation to the role of bank vole in autumn-winter food of these predators in Białowieża National Park. To exclude the bias of between-year variation, data on food composition were averaged for 3 or 4 yr (1985/86–88/89; from Jędrzejewski and Jędrzejewska 1993). The data for marten regards the voles' antipredatory behaviours against the stone marten *Martes foina* and the food of closely related pine marten *M. martes* (see explanation in Material and methods). Regression equation: $Y = 1.5 + 0.04X$, $df = 4$, $F = 21.857$, $r = 0.92$, $p = 0.009$.

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 (1968) 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 chose the routes with overhead cover (under fallen logs and uprooted trees) (Olszewski 1968). Mazurkiewicz (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. Merckens et al. (1991) exposed Townsend's voles *Micro-*

tus townsendii to risk of predation marked by both the odour of mammalian predator (synthesised thietanes and dithiolanes) 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 odour was dispensed there. It indicates that microtines may perceive the risk of owl predation as 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. 1988, Harestad 1991).

In the pristine forests of Białowieża National Park, the bank voles made up, on average, 27% of biomass consumed by the tawny owl (Jędrzejewski and Jędrzejewska 1993). It places this predator behind weasel, stoat and pine marten in its specialisation for bank voles (see Fig. 6). However, the density of tawny owl in Białowieża Natl. Park was 2–3 times higher than those of marten and weasel. (Comparison with stoat is not adequate here, as the stoat's optimal habitats are marshes and meadows.) 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, whereas 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.

Ives and Dobson (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 with increasing 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 densities 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 1993), 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 (Vermeij 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

rodents were very abundant, the weasels' hunting success was about 27% only. Therefore, investigating the predation phenomenon as a story of failures seems as important for our understanding of predator and prey evolution as was acknowledging that "the commonest death for many animals is to be eaten by something else" (Elton 1927).

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