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Antipredatory behaviour of *Clethrionomys* voles — 'David and Goliath' arms race

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The evolution of antipredatory behaviour in animals requires unsuccessful hunting by predators. Voles are relatively slowly moving rodents with little possibility to escape predators in direct confrontation. Therefore their antipredatory behaviour should be based on advanced recognition of risk, an adaptive 'cleverness' called the 'David and Goliath' arms race. In the case of mammalian predators, odours form the basis of this advanced recognition. Studies on *Clethrionomys glareolus* and *C. rutilus* under predation risk, manipulated in the laboratory and outdoor enclosures, and observed in the field in Fennoscandia and Poland are reviewed. The odours of mammalian predators, especially small mustelids immediately elicited short-term changes in the behaviour of voles, their spatial and vertical distribution, diurnal activity, mobility, and intraspecific aggressiveness. The presence of odour of the small mustelids also affected reproductive parameters of voles: sexual maturation of young voles was delayed and female breeding was suppressed. The consequences of breeding suppression may be severe. The advantage of the delay is discussed in terms of predictability of the environment. In Northern and Central Europe the most pronounced 'Goliaths' were not the largest but the smallest predators (weasel and stoat), highly specialized in hunting voles.

1. Introduction

During its life an animal faces various environmental situations to which it has to adapt its behaviour in order to survive or to promote the survival of its offspring. Sih et al. (1990) pointed out that the basic characteristics of individual life histories are feeding, mating, predator avoidance and their interactions. How these needs can be combined to maximize the life-time reproductive success of an individual depends basically on its lifespan expectation and the predictability of the environment. The effect of predation risk on animal performance has only recently been measured and quantified. Antipredatory adaptations were studied in invertebrates (Sih et al. 1988), fish (e.g. Milinski & Heller 1978), birds (e.g. Lima 1985, Lima et al. 1987), and mammals (e.g. Carl & Robbins 1988, Caine & Weldon 1989, Holmes 1991).

In small rodents, predation is an important factor both in shaping their population dynamics (Goszczyński 1977, Erlinge et al. 1983, Hanski et al. 1991, Korpimäki et al. 1991) and in the behaviour of individual voles (e.g. Ylönen 1989, Jędrzejewski & Jędrzejewska 1990).

Voles of the genus *Clethrionomys* are very suitable for research on antipredatory behaviour in mammals. The bank vole *C. glareolus* is a common boreal rodent inhabiting woodlands all over Europe. It exhibits various types of population fluctuations, from 3–4-year cycles in the North to non-cyclic dynamics with seasonal fluctuations in Central Europe (Hansson & Henttonen 1985). In the northernmost part of its range, the bank vole is accompanied by the red vole *C. rutilus* and the grey-sided vole *C. rufocanus*, both having the same kind of social behaviour as the bank vole (Viitala 1977, 1987). *Clethrionomys* voles form, together with grassland dwelling *Microtus*, the basic food resource for several predators in northern and Central Europe. In several studies the biology of *Clethrionomys* and *Microtus* has been compared (see e.g. Viitala & Hoffmeyer 1985 for review). In the present paper we exclude, however, studies on antipredatory adaptations in *Microtus* — but there already exists a good empirical basis for a suggestion that much of the behavioural trends described in the present paper are valid for *Microtus* behaviour as well (Ylönen & Koskela, unpubl.).

The predator guilds within the geographical range of the bank vole vary from a multi-species guild of generalist predators together with specialized small mustelids in Central Europe to a narrow guild of specialist mustelid predators, few generalists and some nomadic owls in northern Europe (Hanski et al. 1991, Jędrzejewski & Jędrzejewska, in press).

Bank vole antipredatory adaptation is a question of winning an evolutionary race against predators (c.f. Abrams 1986). The chances of an individual vole winning are like those of David in his fight with powerful, massive Goliath. The vole's armoury, like David's, is to anticipate the risk, to be smart and fast and to avoid direct physical encounters with its enemy.

The aim of this paper is to review our knowledge about antipredatory adaptations of the bank vole and the red vole. We discuss the recent experimental and field studies on the short-term effects of predation risk on an individual vole's behaviour, evaluate the possible physiological effects of predation risk on the maturation process of individuals and, finally, we discuss possible reproduction strategies of voles under different environmental conditions in the light of life history theory. The authors represent research groups working in Northern and Central Europe, which enables them to draw conclusions on evolutionary relationships between bank voles and their predators in various parts of the bank vole's geographical range.

2. *Clethrionomys* vole and a small mustelid, the experimenters' favourite duet

2.1. Space use, activity and escape tactics of bank voles under predation risk

The first indication that the use of space by voles may be altered by the presence of predators was the voles' avoidance of live traps tainted with odours of the weasel *Mustela nivalis*, stoat *M. erminea* and red fox *Vulpes vulpes* (Stoddart 1976, 1980, Dickman & Doncaster 1984, Gorman 1984). The ability of voles to recognize their enemy is based on olfactory cues and is most probably inherited.

In experiments in which the bank voles were given a choice of either remaining in the risky place or moving to a risk free place, they most often chose the latter. Their avoidance was equally strong and long-lasting after the place had been visited by a weasel or tainted with its scent only (Jędrzejewski & Jędrzejewska 1990). The avoidance, however, varied with the age and reproductive status of voles: nonreproducing subadults and adults of both sexes and reproductively active males shifted their positions in response to predation risk. Juveniles of both sexes and reproducing females remained in their ranges despite the perceived predation risk (Jędrzejewski & Jędrzejewska 1990).

Bank voles are relatively slow runners — compared e.g. with some desert rodents (H. Ylönen, pers. observ.) — and they can hardly rely on their escape by running away from a pursuing weasel or stoat. Instead, they often resort to 'arboreal' escape by climbing twigs and even herbaceous plant stems, or they stay immobile (Jędrzejewska & Jędrzejewski 1990, Jędrzejewski et al., unpubl.) when recognizing the presence or scent of weasel or stoat. In experiments conducted in outdoor seminatural enclosures, the 'arboreal' escape by voles was often successful, especially when bank voles climbed the twigs or shoots too thin to support the pursuing weasel (W. Jędrzejewski, pers. observ.).

The high and persistent risk of weasel predation disturbed the daily activity rhythm of bank voles. Without predation risk, the voles' activity was characterized by inactivity at nights and pronounced peaks at dawn and dusk. When the weasel was present in the experimental pen for the entire day, vole activity was more uniformly distributed throughout the day (Jędrzejewska & Jędrzejewski 1990).

There are obvious differences in the diel activity of the bank vole between seasons (Ylönen 1988) and probably also between populations in various geographical locations. The summer activity of the bank vole in Central Finland was characterized by a relatively uniform polyphasic pattern (Ylönen 1988). The presence of stoat scent in the experimental arenas decreased the total activity of the voles but did not change their diurnal pattern (Ronkainen & Ylönen, unpubl.).

2.2. Maturation of voles under predation risk

Red voles *C. rutilus* delayed their sexual maturation in response to the presence of a weasel (Heikkilä & Kaarsalo, unpubl.). After the young red voles from Kilpisjärvi, Finnish Lapland, had been exposed to the presence (the odour) of a weasel for one hour per day for 3 weeks, their gonads remained smaller than those of individuals in the control group (Table 1). In addition, the adrenal weight in females was smaller in individuals exposed to predation risk compared to

Table 1. Ovaria, testes, and adrenal weights (in mg), uterus width, and testis length (in mm) in groups of *Clethrionomys* voles experimentally exposed to the presence (perceived by sense of smell) of weasel *Mustela nivalis* in comparison to control groups. Mean values ± *SD* from 10–14 individuals in *C. rutilus* and 13–15 individuals in *C. glareolus*. Individual values were means of the left and right sides of the organs. Data from Heikkilä & Kaaresalo's and Heikkilä's unpubl. material. *** $P < 0.001$, ** $P < 0.01$; Student *t*-test.

Organ weight/length	Exposed to predation risk	Control	Significance of difference
Clethrionomys rutilus			
Ovaria weight	1.94 ± 0.47	3.13 ± 1.20	**
Testis weight	59.86 ± 32.01	117.70 ± 39.37	***
Adrenal weight, males	2.55 ± 0.49	2.78 ± 0.66	ns
Adrenal weight, females	2.53 ± 0.30	3.94 ± 0.14	**
Clethrionomys glareolus			
Ovaria weight	1.75 ± 4.83	2.04 ± 6.43	ns
Uterus width	0.79 ± 0.18	0.94 ± 0.28	ns
Testis weight	61.24 ± 42.89	137.40 ± 59.05	***
Testis length	6.00 ± 1.49	7.98 ± 1.68	**
Adrenal weight, males	1.69 ± 0.26	1.76 ± 0.26	ns
Adrenal weight, females	1.67 ± 0.20	1.87 ± 0.45	ns

the control animals. The presence of a weasel did not, however, affect the growth rate of young red voles of either sex.

In bank voles *C. glareolus* from Pallasjärvi, Finnish Lapland, only males exhibited delayed sexual maturation in response to the weasel's presence (Heikkilä, unpubl.). In an experiment similar to that with red voles, the weight and length of the testes were significantly smaller in experimental males than in control ones (Table 1). Females did not react to the odour of a predator; there was no difference in the ovaria and adrenal weight between control individuals and those exposed to predation risk (Table 1).

Therefore, besides the obvious benefits, the rapid sexual maturation of young voles must have costs of increased risk of predation. Cushing (1985) noted that oestrous deer mice *Peromyscus maniculatus* were more vulnerable to weasel predation than non-oestrus ones. Hence, for females it is beneficial to come to breeding condition after the predation risk has decreased. For a male, staying in a non-reproductive condition allows him to remain on a small home range and not run after reproducing females. Thus, mobility may be important for the susceptability to predation. Daly et al. (1990) reported that the mobile kangaroo rat *Dipodomys merriami* was most susceptible to predation. Roberts & Wolfe (1974) showed experimentally that a cat *Felis catus* (but not a red-tailed hawk *Buteo jamaicensis*) captured cotton rats *Sigmodon hispidus* in order of most to least dominant. The dominant rats are more mobile than subordinate ones (Summerlin & Wolfe 1971). By contrast, the experiments with reproductively nonactive bank voles showed that the susceptibility of males and females to weasel predation did not differ (Jędrzejewska 1989). However, there exist some indications that the different sexes could have almost opposite responses to predation risk due to their different contributions to breeding and care of the litter (Ylönen, unpubl.) and this field deserves a good deal of attention in future studies.

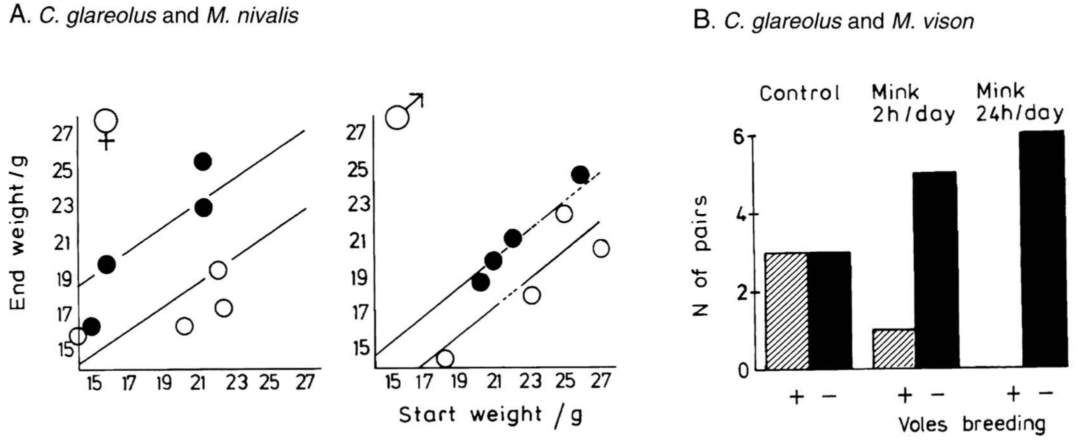
2.3. Predation risk and reproduction in Clethrionomys voles

The presence of odour of a small mustelid predator was shown to suppress reproduction in bank voles. In the experiment by Ylönen (1989) four pairs of mature voles were placed around the cage of a weasel for two weeks. This extremely harsh procedure affected both the breeding and physical condition of the voles (Fig. 1A). Not a single pair around the weasel cage bred while all four females from control pairs were gravid. The weight of voles of both sexes exposed to predator risk decreased and the testis weight of males was affected adversely, which indicated a very high level of stress for both females and males during the experiment.

In another experiment (Ylönen, unpubl.), pairs of bank voles were exposed to a mink *Mustela vison*. The exposure time varied: (1) mink present all the time, (2) mink present 2 h a day, and (3) mink not present (control). Six cages with male-female pairs in breeding condition were subject to each treatment under natural light conditions for ten days. During that time females had a chance to come into oestrus twice. As little as a 2-h presence of mink each day had a suppressive effect on the breeding of voles and none of the pairs exposed to mink continuously bred (Fig. 1B).

In a prolonged experiment with a stoat *Mustela erminea* as predator (Ylönen & Ronkainen, unpubl.), only an odour, supplied by an aqueous solution of stoat urine sprayed once a day on to the experimental cages of the voles, had a significant suppressive effect on the breeding of bank voles. Under experimental conditions it is, of course, difficult to adjust the treatment to as natural a level as possible. In this last experiment the behaviour and breeding of females only was affected, but not the behaviour and testis weight of males, which indicates a "relatively natural" odour treatment.

Heikkilä & Kaarsalo (unpubl.) showed that body weights of pregnant red voles exposed to the odour of a weasel for 5 days at the beginning of their pregnancy did not change in comparison to control individuals. The litter sizes of control and experimental females did not differ either. However, the total weight of foetuses of females exposed to predator odour was about 25% lighter than that of control female foetuses. This may indicate a disturbance in female feeding under predation risk, which in consequence may influence the survival of offspring.


A. *C. glareolus* and *M. nivalis*

B. *C. glareolus* and *M. vison*

Fig. 1. Effects of mustelid predator on reproduction of bank vole pairs held in cages in the vicinity of a predator. — A: experiments with *Mustela nivalis* (according to Ylönen 1989). Open circles = 4 vole pairs exposed to weasel presence (no breeding in females, weight loss observed in both sexes). Closed circles = 4 control vole pairs (all females bred, increase of weight observed). — B: experiments with *M. vison* (Ylönen, unpubl.). Pairs of bank voles were exposed to mink presence for whole days and 2 h a day and compared to control pairs (no mink). + = breeding observed, − = no breeding.

Some field observations indicated that mustelid presence may delay the onset of breeding in voles. In Central Finland, winter breeding is not very common in the bank vole, but during moderate density years with abundant food supply breeding started in February under the snow cover (Ylönen & Viitala 1985). In late January 1988, females in an overwintering expriment in eight large outdoor enclosures had open vaginae but the first litters were born about 10 weeks later, at the end of April (Ylönen & Viitala 1991). During that particular spring the enclosures were frequently visited by stoats and weasels, one of which was captured in a vole trap.

A remaining question, in the suppression of breeding in voles exposed to the mustelid predator, is the mechanism of the suppression. One possibility is an early abortion due to exposure to a predator's odour, similar to the Bruce effect, that is abortion caused by the odour of a strange male of the same species (Bruce 1959) or a dominant, sympatric species as was shown for *Clethrionomys rufocanus* and *C. rutilus* (Kaarsalo & Wallgren 1991). Another possibility is a behavioural mechanism based on altered mating behaviour of either of the sexes (Ylönen & Ronkainen, unpubl.).

The delayed beginning of reproduction in young voles as a consequence of predator-caused stress may be one of the factors that help individual voles to avoid predation. It may also slow the growth rate of vole numbers. One of the unanswered questions is whether voles of different ages respond differently to predation risk. Magnhagen (1990) showed that the trade-off between reproduction and predator avoidance in gobid fishes is related to the future reproductive opportunities, that is to the age of an individual. If the same applies to voles, one would expect older voles that have already reproduced to be more resistant to predation risk than just matured individuals. A decision to delay breeding should be more likely in individuals that have a life expectancy long enough to reach the next breeding possibility. In laboratory stocks, bank vole females can survive over two winters (Buchalczyk 1970) and during the long-term enclosure study in Central Finland (1982–1987) two females that produced litters in two summers (not including their birth summer) were recorded (Ylönen, unpubl.). In the field, however, this is relatively uncommon. Therefore, the delay of breeding, if it is adaptive, should be of the greatest advantage to young individuals.

3. What information on *Clethrionomys* antipredatory behaviour did we obtain from field studies?

Some field studies yielded information on behaviour of the bank vole that may be interpreted as antipredatory adaptation. In Wytham Wood (England), Southern and Lowe (1968) found that bank voles were most numerous in places with a dense cover of herbs and bushes and least numerous in places with bare ground, whereas tawny owls *Strix aluco* (the voles' prime enemy in this area) preferred to hunt over bare ground (c.f. Kotler et al. 1991). In the mature primeval forests of the Białowieża National Park, bank voles were most often trapped under fallen logs and uprooted trees (Olszewski 1968) obviously because in their movements voles chose the routes with overhead cover. Such spatial distribution and microhabitat selection may be an antipredatory behaviour against visually hunting raptors.

In winter, bank voles stay and forage in subnivean spaces. Due to this behaviour, snow cover significantly lowers the predation of tawny owl and pine marten *Martes martes* on bank voles (Jędrzejewski & Jędrzejewska, in press). This should be even more pronounced in northern Europe where the snow cover is deeper and lasts longer (Hansson & Henttonen 1985). In northern Europe most avian predators migrate to the south and the resident small mustelids, which can hunt in subnivean spaces as well, gain even more in importance as regards the winter survival of voles.

Increasing group size in the prey in response to predation risk is a commonly reported behaviour among birds and mammals (reviewed by Elgar 1989). Rodents, however, are generally much smaller than their predators, so the groups of voles might attract predators rather than distract them. The observed pattern of social overwintering in groups or larger aggregations (Ylönen & Viitala 1985, Ylönen 1990) can hardly be expected to improve antipredatory abilities of voles, especially in northern Europe against weasels and stoats. Staying aggregated seems risky and the choice of wintering strategy is thought to be determined by food availability and thermoregulative advantage (Madison 1984, Gæbczyński 1969). Karlsson (1988) found that solitary bank voles had significantly poorer survival rates over winter than the voles living in close proximity to each other and interpreted this by differences in quality of food patches occupied by solitary and grouped voles. He did not, however, report any occurrence of predators in or around his study area.

Radio-tracking of the least weasels conducted in the Białowieża National Park in the autumn of 1990 showed that at the high densities of rodents, the social huddling of few (2–4) bank voles in one nest much improved (in comparison to solitary voles) their chances of surviving weasel attacks (Jędrzejewski et al. 1992). Weasels were always able to take only one vole from a group and the other ones escaped successfully in various directions. When attacking the groups of bank voles a weasel was successful in 12% of all attacks, whereas as much as 27% attacks on solitary voles were successful. Only 5% of bank voles wintering in groups of 2–4 and attacked by weasels were captured in comparison to 27% of solitary voles. In a whole sample of observations, 23% of weasels' attacks on bank voles were successful. Thus to join a group could improve an individual vole's chances of not being attacked by a predator but with increasing group size increase the probability that a predator finds the group (c.f. Abrams 1986). However, in an outdoor enclosure with extremely high densities of bank voles, but with a natural microhabitat structure only about 30% of weasel attacks succeeded (Jędrzejewski et al. 1992). Also, in their choice of age classes out of an enclosed population of bank voles, weasels were able to kill only the youngest voles (mostly nestlings) with antipredatory abilities not yet physically developed (Jędrzejewska & Jędrzejewski 1990).

Unsuccessful predation is necessary for evolution of antipredatory behaviour, because, as Vermeij (1982) stated: "selection in favor of antipredatory traits can occur only when some members of a prey population survive to reproduce after being detected, pursued, or assaulted by a predator, that is, when predators are less than 100% efficient at [...] their interactions with prey".

4. *Clethrionomys glareolus* in a multi-species predator community

Over the geographical range of the bank vole, the community of its potential predators includes no fewer than five species of mammalian predators and five species of raptors in the Northern boreal forests, and eight species of mammalian predators and nine species of raptors in the temperate broadleaf forests of Central Europe (Henttonen et al. 1992, Jędrzejewski & Jędrzejewska, in press). It has been shown relatively unambiguously that the direct effect of predation has a different impact on the fluctuations of small rodent populations in northern and central Europe (e.g. Erlinge et al. 1983, Hanski et al. 1991). Little is known about the differences in the indirect effects of predators on the behaviour of prey individuals and possible further effects on their population dynamics, however (Ylönen & Ronkainen, unpubl.). The same is true for differences in the responses of prey individuals to different types of predators in a multi-predator environment (c.f. Lima 1992).

So far it has been proved that the bank vole recognizes the scent of six species of native mammalian predators and two non-native species. Dickman & Doncaster (1984) provided evidence that bank voles recognized the faecal scent of badgers *Meles meles* and avoided it. Ylönen (unpubl.) documented the voles' recognition of American mink odour. In the terrarium experiment (W. Jędrzejewski, B. Jędrzejewska & L. Rychlik, unpubl.), bank voles were able to distinguish Canidae from Mustelidae, and responded to all mustelid species by climbing twigs (as a substitute of arboreal escape). Among mustelids, bank voles were clearly able to recognize the least weasel, stoat and stone marten *Martes foina* from the polecat *Mustela putorius*. The scent of weasel, stoat and marten caused bank voles to run out of the tubes provided by the experimenters as substitutes for 'tunnels' and 'burrows'. The voles responded by immobility to red fox and weasel odours (Table 2). By contrast, bank voles did not react to the odour of the tawny owl, although it was perceivable to the experimenters. Aerial hunting by the tawny owl does not cause the dispensing of olfactory information to the ground.

Edmunds (1974) has pointed out that: "...there is tremendous selection pressure on prey animals to improve and perfect their anti-predatory defences. There will also be selection pressure favouring those predators that are best able to overcome the defences of prey, so there is a perpetual arms race between prey and predator...". We can expect, therefore, that the antipredatory behaviour of the bank vole will be more developed against those species of predators which are more specialized in taking bank voles. The results of experiments on the voles' response to the scent

Table 2. Antipredatory responses of bank voles to odours of seven species of predators inhabiting Central Europe (data from terrarium experiments, W. Jędrzejewski, B. Jędrzejewska & L. Rychlik): no = no response, + = observed response: avoidance of box 'visited' by a predator, climbing twigs, escape from 'burrows', or immobility.

Predator	Bank vole response to predation risk			
	Avoidance	Climbing	Escape	Immobility
Mustela nivalis	+	+	+	+
Mustela erminea	+	+	+	no
Martes foina	+	+	+	no
Mustela putorius	+	+	no	no
Vulpes vulpes	+	no	no	+
Nyctereutes procyonoides	+	no	no	no
Strix aluco	no	no	no	no
Control (rabbit)	no	no	no	no

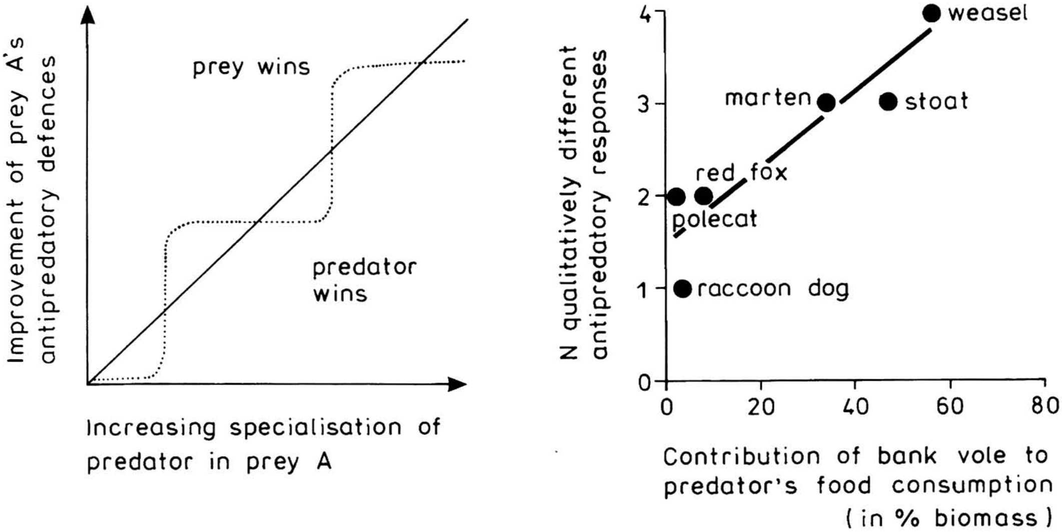


Fig. 2. Schematic model of predator-prey evolutionary arms race (left) and the contemporary relationships of the bank vole and 6 species of mammalian predators inhabiting forests in Central Europe (right). Data on food specialisation of predators from Białowieża Primeval Forest, eastern Poland (after Jędrzejewski & Jędrzejewska, in press). Data on antipredatory responses of bank voles from terrarium experiments conducted in Białowieża (see Table 2; data for marten regarding the diet composition of pine marten *Martes martes* and experiments with closely related stone marten *M. foina*). Regression line (right figure): $Y = 1.5 + 0.04\ X$, $df = 4$, $r = 0.92$, $P < 0.01$.

of 6 predatory mammals from the Central European community of predators were compared with the role the voles play in the diet of each of those predators. There is a significant positive correlation between the contribution of the bank vole to the diet of a predator and the number of different antipredatory defences that the voles showed in response to the odour of that predator (Fig. 2). The contemporary relationships of bank voles and its predators in Europe can thus be considered to be the result of an evolutionary arms race. Weasel — bank vole relationships are most advanced in this race.

5. Conclusions and prospects

The bank vole with its wide geographical range and its coexistence with many species of predators at various latitudes constitutes a good tool for studying antipredatory behaviour. In the present review based mostly on our experiments and field studies conducted in Fennoscandia and Poland we can draw conclusions about antipredatory behaviour and its consequences in *Clethrionomys* voles, as well as point out some questions worth further studies.

1. Short-term changes in the behaviour of voles (escape, avoiding places visited by a predator, changes in activity and intraspecific competition etc.) under predation risk should be the same in voles from different geographical locations. These responses to risky situations change as soon as the situation changes. High and prolonged risk causes a lot of disturbance to the normal population processes (abandoning of territories, disturbance to intrapopulation relationships, delay of maturing of young voles, delayed reproduction). The high and long-term risk of mustelid predation is likely to have consequences to population demography beyond the exploitation of prey by predators. These long-term changes, which involve a direct fitness component (reproductive behaviour, breeding), should be more sensitive to the predictability of environment. If an individual suppresses or delays breeding, the options for reproduction should be better during the next breeding opportunity, of-

ten after the bottle-neck of surviving the hard winter. These options should be better in the case of the cyclic populations of northern Fennoscandia than in the non-cyclic populations of Central Europe (Ylönen & Ronkainen, unpubl.).

2. The bank vole recognizes precisely (by olfactory cues) eight species of mammalian predators (weasel, stoat, marten, polecat, mink, fox, badger, raccoon dog), and it can relate at least some of them to species and react differently to their presence or odour. Antipredatory behaviour of bank voles against birds of prey (where recognition can hardly be based on olfactory cues) may include preference for places with dense overhead cover.

3. The contemporary relationships of the bank vole and its sympatric mammalian predators in Europe seem to be an effect of the evolutionary arms race between voles and their enemies; the most advanced and diverse anti-predatory defences by bank voles are against those species of predators which are most specialised in hunting bank voles, i.e. small mustelids.

4. The effectiveness of experimentally recognized antipredatory behaviour of bank voles against weasels was documented in radio-telemetry field studies, in which the hunting success of weasels was only about 30%.

5. Little is known about intersexual differences in antipredatory adaptations although one would expect that female bank voles, which have to maintain territories and respond to the increased energy demands during pregnancy and lactation, would be more vulnerable to predation than males. No data are available about annual changes in predation rate and predation risk in bank voles. During winter the goal of an individual is to survive, whilst during the breeding season the reproduction and survival of young also have to be taken into consideration. Carefully planned experiments supplemented by field studies with video recording of predators hunting bank voles would give a more comprehensive picture of the voles' defensive behaviour.

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