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# Influence of predation risk on early development and maturation in three species of *Clethrionomys* voles

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We studied in the laboratory the effect of the risk of predation by weasels (*Mustela nivalis*) and stoats (*M. erminea*) on early development and maturation of red voles *Clethrionomys rutilus*, grey-sided voles *C. rufocanus*, and cyclic and non-cyclic populations of bank voles *C. glareolus*. In red voles, predation risk lowered the weight of embryos, but had no effect on the weight of adult females. Predation risk had a marked effect on the growth of young voles and on the weights of their testes and ovaria, indicating a lowered rate of maturation when at high risk of predation. The weight of the adrenals was significantly lower in experimental than in control females but not in males. In cyclic bank voles, predation risk had a strong effect on the growth rate of young voles. There was a marked effect on the weight of testes but not on the weight of ovaria. In non-cyclic bank voles predation risk had no effect on females but a marked effect on the growth rate of males. The weight of the testes indicated only a marginal effect on maturation in non-cyclic voles. In grey-sided voles, there was no effect of predation risk on the growth or the weight of testes, ovaria and adrenals. These results 1) support the notion that young voles may delay reproduction under great risk of predation, 2) indicate that the response varies among different species living in the same area, and 3) show predictable differences between conspecific voles from cyclic and non-cyclic populations.

## 1. Introduction

The relationships between microtine rodents and their predators have been discussed in the literature for decades (Elton 1942, MacLean et al. 1974, Andersson & Erlinge 1977, Oksanen & Oksanen 1981, Henttonen 1987, Henttonen et al. 1987, Ims & Steen 1990, Newsome 1990, Oksanen 1990, Hanski et al. 1991, Korpimäki & Norrdahl 1991, Korpimäki et al. 1991 and references therein). Recently, population ecologists have focused on the idea that the relatively regular, multiannual cycle of microtine rodents in northern Fennoscandia (Hansson & Henttonen 1985) is due to predation by small mustelids (Henttonen et al. 1987, Hanski et al. 1991). Weasels (*Mustela nivalis*) and stoats (*M. erminea*) are specialist small mammal predators and well adapted to winter conditions (King 1989). Hanski et al. (1991) demonstrate theoretically how the interaction between predation by small mustelids and predation by generalist predators may explain the patterns of small mammal cyclicity observed in northern Europe.

Apart from the direct demographic effects of killing and surplus killing of rodents (Jędrejewska & Jędrejewski 1990, Oksanen et al. 1985), stoats and weasels can affect the dynamics of their prey populations indirectly by inducing changes in prey behaviour. In particular, predation risk could affect rodent dynamics by modifying the rate of reproduction, by suppressing reproduction in mature individuals or by blocking the sexual maturation of juveniles.

Behavioural changes, including various kinds of antipredatory behaviour, have been documented in rodents exposed to predators experimentally in small enclosures (Gerkema & Verhulst 1990, Jędrejewska & Jędrejewski 1990, Ylönen et al. 1992) and in larger enclosures in the field (Desy & Batzli 1989, Desy et al. 1990). But little attention has been paid to physiological responses, including the reproductive behaviour.

In field studies on small mammals, reliable assessment of the actual predation risk is very difficult. Some observations from fenced vole populations suggest that reproduction is delayed because of the presence of weasels (Ylönen 1989), but predation risk in this study was inferred from snow tracks and a few visual observations, whereas the frequency and duration of predators' visits to voles' home ranges remains unknown.

In this paper we report laboratory experiments involving a weasel or a stoat and unborn and juvenile red voles *Clethrionomys rutilus*, juvenile bank voles *C. glareolus* from two different origins, and juvenile grey-sided voles *C. rufocanus*. The experiments were conducted to find out whether predation risk affects the maturation of young voles and early development of embryos during the first days of development), and furthermore whether there are differences in the responses of voles originating from cyclic and from non-cyclic populations.

Because predation risk in northern Fennoscandia varies regularly from one year to another, due to the regular cycle of small mammals and their predators, and because estrous females (Cushing 1985, in mice) and young individuals (Jędrejewska & Jędrejewski 1990, in bank voles) are especially vulnerable to predation, it might be advantageous for young voles to delay the beginning of reproduction until the predation risk is low. In particular, we could expect young voles to delay maturation until the following spring if predation risk is high during the summer of their birth. A similar response might not be advantageous for older, over-wintered individuals, which would not, in any case, survive until the following summer. Therefore, we expect that the effects of predation risk on old voles would be less marked than the effects on juveniles. We could also expect that because of continous and heavy predation in southern Fennoscandia (Erlinge 1987, Erlinge et al. 1983), young voles from that non-cyclic area would react less markedly to predation risk than would young voles from northern cyclic populations.

## 2. Material and methods

This study is based on measurements of somatic growth of young voles and of growth of organs important to reproduction that is, testes, ovaria and adrenals. We examined the possible effects of predation risk on red vole embryos during the first seven days of development, and on sexual maturation of young voles from cyclic red (northern), and of bank and grey-sided vole populations, and of non-cyclic (southern) bank vole populations, studying all of these latter from the age of 20–22 days to the age of 41–43 days, the age at which they normally reach sexual maturity.

Voles in all experiments described below were kept individually in transparent plastic mouse cages (size 25×40×15 cm) and were housed under standard laboratory conditions. The red vole stock originated from the Kilpisjärvi Biological Station (69°03′N, 20°49′E) in the early 1970s. Grey-sided voles and cyclic bank voles originated from Pallasjärvi (68°03′N, 24°09′E), the former in the early 1980s and the latter in 1991. The non-cyclic bank vole stock originated from Stensåffa Biological Station (55°42′N, 13°28′E) in 1990. Some new individuals have been added at irregular intervals to the older stocks to prevent inbreeding depression. Animals were housed in a 16L:8D photoperiod (early spring) with food and water provided ad libidum. During all experiments, weasels and stoats, originating from the Helsinki zoo and from the wild, were fed on live laboratory mice and provided with water ad libidum. Surroundings were similar in the experimental and control rooms.

### *Experiment 1: Effects on early development*

This experiment is part of unpublished research material by the author Kaarsalo and Henrik Wallgren, concerning the effect of weasel presence on pregnancy block in red vole females. Here we restrict ourselves to data on female weight, litter size and litter weight. The complete results will be published later, together with results of other pregnancy block experiments.

A male weasel originating from the Helsinki zoo, was housed in the experimental room (size 2×4 m) in a metal wire-cage (size 60×80×80 cm). Experimental females ($n = 9$) were transferred to this room immediately after the vaginal plug was detected. The weasel cage was located among the vole cages (distances were from 10 to 20 cm from all vole cages) to allow visual contact. A stuffed weasel was placed in the same setting, in a cage, among the control voles ($n = 11$). New females were introduced in pairs to control and experimental groups whenever available, and females were removed from the experimental room after seven days of exposure. Neither the weasel nor the voles were moved during the exposure period; hence each pregnant female was exposed to the weasel for seven days continuously.

Voles were killed after eleven days had elapsed from the beginning of the experiment. Their weights were measured, and the number of embryos was counted and their total weight measured. Because females are sensitive to disturbance during the early days of pregnancy (Mallory & Brook 1980, Clulow et al. 1982, O'Keefe et al. 1985), and such prosedures as weighing them can affect the growth of their offspring (Myers & Master 1986), their initial weights were not measured before the experiment nor during the experiment.

### *Experiment 2: Effects on sexual maturation*

In these experiments, laboratory-reared juvenile red, bank and grey-sided voles were weaned at the age of 20 to 22 days and were then kept in individual cages. Experimental and control animals were selected randomly from the same litters as far as possible. We had to use both weasels and stoats as predators because of difficulties in getting live animals for the experiments. The similarity both of anal gland secretion of weasels and stoats (Brinck et al. 1983) and of antipredatory responses of bank voles to weasels and stoats (Ylönen et al. 1992), however, suggested that voles are likely to react similarly to these two predator species. In the experiments, juvenile voles were exposed to the presence of a male weasel from the zoo (red voles) or from the wild (grey-sided voles) or a male stoat from the wild (bank voles), first for 24 hours continuously and afterwards for one hour per day during the next three weeks. The daily exposure hour was randomly selected to fall between 7 am and 6 pm. The exposure was carried out in the same manner as was the first experiment, except that the predator was now moved daily to the room with the experimental voles. Control voles were housed in a separate room and were fed and handled at the same time and in the same way as the experimental animals. A stuffed weasel in an empty cage was used daily with control voles. Individual voles were weighed at the beginning of the experiment. Sample sizes (males/females) in the experimental groups were: 14/14 red voles, 14/13 northern bank voles, 11/14 southern bank voles and 10/10 grey-sided voles. In the control groups we had 12/14 red voles, 15/13 northern bank voles, 13/14 southern bank voles and 10/10 grey-sided voles.

Voles were killed after three weeks and their weights were measured. Testes, ovaria and adrenals were removed and weighed.

## 3. Results

### 3.1. Effects on early development

There was a significant difference in the weights of red vole females between the experimental

Table 1. Weight (g) of pregnant females, and size and weight of their litters, in experimental (*n* = 9) and control (*n* = 11) groups of *C. rutilus*; mean ± *SD*. Female net weight is the gross weight minus litter weight. *P* gives significance of *t*-test.

| | Experiment | Control | *P* |
|---|---|---|---|
| Female weight | 33.8 ± 3.4 | 37.4 ± 2.5 | 0.01 |
| Litter size | 7.2 ± 1.4 | 8.2 ± 1.3 | 0.12 |
| Litter weight | 6.1 ± 1.7 | 8.1 ± 2.3 | 0.04 |
| Female net weight | 27.7 ± 2.7 | 29.3 ± 1.9 | 0.15 |

Table 3. Effects of predation risk (treatment) and sex on growth of juvenile red voles *C. rutilus*, bank voles *C. glareolus* (c = cyclic and nc = non-cyclic) and grey-sided voles *C. rufocanus*, using starting weight as a covariate (ANCOVA).

| | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| *C. rutilus* | | | | |
| Treatment | 1 | 24.88 | 4.67 | 0.035 |
| Sex | 1 | 0.37 | 0.07 | 0.794 |
| Treatment × Sex | 1 | 12.24 | 2.30 | 0.136 |
| Starting weight | 1 | 35.30 | 6.63 | 0.013 |
| Error | 50 | 5.93 | | |
| *C. glareolus* (c) | | | | |
| Treatment | 1 | 67.71 | 29.13 | <0.001 |
| Sex | 1 | 18.56 | 7.98 | 0.007 |
| Treatment ×Sex | 1 | 0.78 | 0.34 | 0.565 |
| Starting weight | 1 | 5.38 | 2.32 | 0.134 |
| Error | 50 | 2.32 | | |
| *C. glareolus* (nc) | | | | |
| Treatment | 1 | 34.81 | 11.71 | 0.001 |
| Sex | 1 | 45.98 | 15.47 | <0.001 |
| Treatment × Sex | 1 | 3.92 | 1.32 | 0.256 |
| Starting weight | 1 | 33.86 | 11.39 | 0.001 |
| Error | 47 | 2.97 | | |
| *C. rufocanus* | | | | |
| Treatment | 1 | 5.64 | 1.32 | 0.259 |
| Sex | 1 | 66.31 | 15.51 | <0.001 |
| Treatment × Sex | 1 | 3.68 | 0.86 | 0.360 |
| Starting weight | 1 | 0.46 | 0.11 | 0.745 |
| Error | 35 | 4.28 | | |

and control groups (Table 1). However, much of this difference was due to a parallel difference in litter weight, and the difference in female net weight was not significant. There was no significant difference in litter size, which was however greater in the control group. The average size of embryos was smaller in the experimental group (0.85 mg) than in the control group (0.99 mg).

In summary, litter size and weight and female weight were all smaller in the experimental than in the control group. The reductions were greater for litter size (13%) and for total weight (25%) than for female net weight (5%). It is worth emphasizing that predation risk did not lead to abortion of entire litters.

### 3.2. Effects on sexual maturation

Weights at the beginning and growth during the three-week experiments are given in Table 2. There was a significant difference between the experimental and control individuals in growth, but no difference between the two sexes in red voles (Table 3). The treatment effect on growth rate was

Table 2. Weight (g, mean ± *SE*) at three weeks of age and growth during the following three weeks in male and female red voles, bank voles (c = cyclic and nc = non-cyclic origin) and grey-sided voles.

| | | Males | | | Females | | |
|---|---|---|---|---|---|---|---|
| | | Weight | Growth | *n* | Weight | Growth | *n* |
| *C. rutilus* | Experiment | 13.3 ± 0.43 | 7.2 ± 0.55 | 14 | 12.6 ± 0.52 | 8.3 ± 0.53 | 14 |
| | Control | 13.2 ± 0.43 | 9.5 ± 0.55 | 12 | 13.1 ± 0.46 | 8.4 ± 0.91 | 14 |
| *C. glareolus* (c) | Experiment | 11.8 ± 0.63 | 5.7 ± 0.48 | 14 | 10.9 ± 0.33 | 4.9 ± 0.32 | 13 |
| | Control | 11.7 ± 0.42 | 8.2 ± 0.47 | 15 | 10.8 ± 0.39 | 6.9 ± 0.32 | 13 |
| *C. glareolus* (nc) | Experiment | 9.1 ± 0.62 | 6.5 ± 0.51 | 11 | 9.3 ± 0.47 | 5.1 ± 0.59 | 14 |
| | Control | 8.8 ± 0.61 | 8.9 ± 0.54 | 13 | 9.0 ± 0.52 | 6.4 ± 0.44 | 14 |
| *C. rufocanus* | Experiment | 14.0 ± 0.57 | 8.8 ± 0.60 | 10 | 14.3 ± 0.50 | 5.6 ± 0.50 | 10 |
| | Control | 14.8 ± 0.58 | 8.9 ± 0.84 | 10 | 14.6 ± 0.49 | 7.0 ± 0.60 | 10 |

Table 4. Effects of locality (cyclic / non-cyclic) and sex on weight at three weeks of age (weight A) in control individuals of *C. glareolus* (ANOVA).

| | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Locality | 1 | 78.07 | 23.81 | <0.001 |
| Sex | 1 | 1.67 | 0.51 | 0.479 |
| Locality × Sex | 1 | 4.05 | 1.24 | 0.272 |
| Error | 51 | 3.28 | | |

Table 5. Effects of locality (cyclic / non-cyclic) and sex on growth from three weeks to sex weeks of age in *C. glareolus*, using starting weight as a covariate (ANCOVA).

| | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|
| Locality | 1 | 0.03 | 0.01 | 0.917 |
| Sex | 1 | 49.98 | 17.33 | <0.001 |
| Locality × Sex | 1 | 4.79 | 1.66 | 0.203 |
| Starting weight | 1 | 0.40 | 0.14 | 0.710 |
| Error | 50 | 2.88 | | |

highly significant in both cyclic and non-cyclic bank voles, and in both cases the effect of sex was significant. In grey-sided voles there was no difference in growth atributable to the treatment, but a significant difference appeared between sexes. There was a difference in weight at the beginning of the experiment between cyclic and non-cyclic bank voles of both sexes (Table 4), but no difference in the amount of growth during the three-week experimental period (Table 5).

Between the predator-exposed and control groups, weight of ovaria differed highly significantly in red voles but not in bank voles nor in grey-sided voles (Table 6). Weight of testes differed highly significantly in red voles and in cyclic bank voles but less significantly in non-cyclic bank voles. There was no difference between control and predator-exposed groups for grey-sided voles.

The average weight of the adrenals was significantly greater in the control than in the experimental groups of female red voles, but there was no difference in this regard for red vole males nor for other species. There was no correlation between body weight and adrenal weight for any species.

## 4. Discussion

Our results showed relatively small effect of predation risk on old red voles but a substantial and significant effect on the weight of their embryos and on the maturation of juvenile red voles. We also found a strong effect on maturation of cyclic male bank voles. Magnhagen (1990) showed with the marine fish *Gobius niger* that the trade-off between reproduction and predator avoidance, and the degree of risk-taking during reproduction are both related to the expected reproductive opportunities and therefore to the age of the individual. She found that older individuals (4–5 years) spawn, whereas younger (2–

Table 6. Ovaria and testes weights (mg, mean ± *SD*) in experimental and control groups of young females and males of *C. rutilus*, *C. glareolus* and *C. rufocanus* (c = cyclic and nc = non-cyclic origin). Individual values are means of the left and the right organs. *P* gives significance of *t*-test.

| | Experimental | *n* | Control | *n* | *P* |
|---|---|---|---|---|---|
| Ovaria | | | | | |
| *C. rutilus* (c) | 1.9 ± 0.5 | 12 | 3.1 ± 1.2 | 11 | 0.009 |
| *C. glareolus* (c) | 1.8 ± 0.5 | 13 | 2.0 ± 0.6 | 13 | 0.214 |
| *C. glareolus* (nc) | 1.9 ± 0.6 | 13 | 2.1 ± 0.6 | 14 | 0.477 |
| *C. rufocanus* (c) | 2.7 ± 0.5 | 10 | 2.6 ± 0.5 | 10 | 0.584 |
| Testes | | | | | |
| *C. rutilus* (c) | 59.6 ± 32.0 | 14 | 117.7 ± 39.4 | 12 | <0.001 |
| *C. glareolus* (c) | 61.2 ± 42.9 | 14 | 137.4 ± 59.1 | 15 | <0.001 |
| *C. glareolus* (nc) | 157.9 ± 54.5 | 11 | 217.5 ± 44.6 | 13 | 0.007 |
| *C. rufocanus* (c) | 159.2 ± 32.1 | 10 | 161.0 ± 38.6 | 10 | 0.910 |

3 years) individuals do not spawn in the presence of a predator. A related species, *Pomatoschistus minutus*, did not respond at all to the presence of the predator: *P. minutus* reproduces during only one season and hence gains nothing by delaying reproduction.

We found a significant and fairly large (25%) difference in litter weight between the experimental and control females, which is probably due to disturbance of feeding in the presence of a predator. Although lactation is the most critical period energetically from the mother's point of view, pregnancy also increases females' food requirements, and even small behavioural changes due, for instance, to predator avoidance can have a negative effect on weight gain by the offspring. The effect of handling of pregnant voles, which according to Myers & Master (1986) may affect the weight of the newborn young in *Peromyscus*, can be excluded here because we did not handle either control or experimental voles during the experiment.

It is known that *C. rutilus* females are sensitive during early pregnancy to disturbance by unknown males of the same species, and by males of the grey-sided vole *C. rufocanus*, but not by females of *C. rufocanus* (Kaarsalo & Wallgren 1991). It is believed that disturbance by conspecifics is caused by male pheromones (Bruce 1959, Dominic 1965, Marchlewska-Koj 1983). It is less clear whether the same applies to interspecific disturbance. However, if a general stress effect were caused by the presence of a dominant competitor (*C. rufocanus*), then heterospecific females should induce the same response. The results on predation risk are comparable with the effects of grey-sided vole females on red vole reproduction (Kaarsalo & Wallgren 1991). Ylönen (1989), however, found that the presence of a weasel suppressed reproduction (mating) in mature bank voles *C. glareolus*. It is possible that different species of *Clethrionomys* show different kinds of responses, but more likely the difference is due to the long exposure-time in Ylönen's (1989) experiment: 15 days in very close proximity to a predator.

Our results on juvenile red voles *C. rutilus* revealed a significant effect of predation risk on growth rate, and a very marked effect on the development of ovaria and testes. The less heavy organs in the experimental group in both sexes were undoubtedly functionally immature, though we have not verified this histologically. In males, 8 of the 14 individuals in the experimental group had a testes length between 5 and 7 mm (weight between 50 and 100 mg), whereas the rest had testes less than 5 mm. In the control group only one individual had a testes length less than 8 mm. According to Viitala and Henttonen (pers. comm.), testes length of around 7–8 mm generally indicates sexual maturity in *Clethrionomys* voles. On this basis, little more than half of our experimental red vole males were nearing maturity, and none of them had yet reached full maturity. In the control group, after three weeks all males except one were mature.

In bank voles *C. glareolus*, we found a marked effect of predation risk on the growth of young voles. There was also a difference in growth rate between the two sexes. Females from both cyclic and non-cyclic populations were least affected by predation risk (no difference in weight of ovaria between groups), whereas males from the cyclic population reacted similarily to red vole males. In the experimental group, the testes weights of cyclic males were at or below 100 mg, whereas the control males were at or above this limit. In non-cyclic males, all individuals had a testes weight above this limit, indicating maturity both in the experimental and control groups.

An additional observation was the difference in body weight at three weeks of age between cyclic and non-cyclic bank voles, and the greater growth rate in the non-cyclic males, compared to cyclic males. Increase in body weight with latitude has been observed in *C. glareolus* and *Microtus agrestis* in Sweden by Hansson (1985) and Hansson & Jaarola (1989). They found it difficult to explain these differences by ecogeographic rules, demographic characters or nutritive adaptations. We hypothesize that the differences observed in body weight and testes weight between cyclic and non-cyclic male bank voles may indicate an interaction between reproductive biology and life-history parameters. In the warmer climate and in the presence of continous predation in southern Fennoscandia (non-cyclic area), it would be advantageous for voles to start reproducing as early as possible, whereas under more extreme climatic conditions and under changing predation pressure in the north, young voles might improve their fitness by growing larger and maturing more slowly. According to Stearns (1992), maturity will be delayed if it improves the juvenile survival rate sufficiently.

In grey-sided voles *C. rufocanus*, we found no effect of predation risk on growth rate or in the weights of ovaria and testes. Both in the experimental and control groups testes weights were well above the 100 mg limit, indicating maturation in both experimental and control groups despite predator exposure.

Several previous studies have found differences between the sexes of voles in regard to adrenal weights during maturation. According to Selander (1967), reproductive state is the most important factor affecting adrenal size in rodents, especially in females. Chitty & Clarke (1963) found that in laboratory-reared field voles *M. agrestis*, adrenals of pregnant females were larger than those of nulliparous individuals, but that adrenals did not increase in weight with increase in body weight. Christian & Davis (1966) pointed out that adrenal weight of *M. pennsylvanicus* increased sharply at sexual maturation, but no further changes occurred relative to body size during further development. However, adrenals of field-caught male and pregnant female *M. agrestis* increased in weight with increasing body weight (Chitty & Clarke 1963). Pankakoski & Tähkä (1982) observed in field-caught material a difference between the sexes in adrenal weights in sexually mature *Sorex araneus*, *S. minutus*, *C. glareolus*, *Ondatra zibethica* and *M. agrestis*. The functional basis for the differences observed in adrenal weights between the sexes may be the greater capacity of female than male adrenals to convert precursors to corticosterone (Tähkä et al. 1985 for *C. glareolus*). We can compare our results with the adrenal weights of Pankakoski & Tähkä (1982) for *C. glareolus*, assuming that the weights are about the same in all *Clethrionomys* species. In our material, adrenal weights for all species and sexes were below the values for adult bank voles. In red and grey-sided voles the adrenal weights were between the values for immature and mature males, and in the bank vole below the values for immature individuals (Pankakoski & Tähkä 1982). These results suggest that the voles in our experiment were still in the process of maturation. Christian & Davis (1966) report that rapid growth of adrenals occurs suddenly in the course of maturation.

In both experiments one possible factor affecting the experimental voles is what is called neophobia. However, we doubt that neophobia could be an important factor affecting the maturation of young voles inparticular, for several reasons. First, the two rooms used in the experiments, including the fixtures in these rooms, were similar. Second, the control animals were exposed to a stuffed weasel. Third, all the animals in the experiments were from the laboratory stock, and were familiar with new objects and the daily activities of animal keepers. Fourth, the strength of the response differed among the three vole species and among bank voles from two localities.

## *Conclusions*

Our experiments with red voles *C. rutilus* demonstrate that predation risk can substantially affect reproduction in voles. The extent of the response appears to depend on the species, the origin and the age of individuals, young voles being most affected. Mature voles have a shorter expected life-time and are more resistant to disturbance than are young voles, which in turn can be more flexible in their reproductive behaviour.

The observed difference in average size of embryos between the experimental and control females can affect the fitness of the offspring, small individuals generally being more vulnerable to many other causes of mortality than are large ones. The smaller offspring born to predator-exposed females may be inferior in competition for territories, and may have a higher dispersal rate than the others, as suggested by Hanski et al. (1992) for the common shrew *S. araneus*. Prenatal stress may also disrupt reproductive behaviour and physiology in the offspring (Vandenbergh 1983, Herrenkohl 1986).

The advantage of delayed reproduction in young voles is based on temporally varying predation risk. In cyclic populations, represented by our red voles *C. rutilus*, northern bank voles *C. glareolus*, and grey-sided voles *C. rufocanus*, there is a regular between-year variation in predation risk, reflecting cyclic multiannual changes in numbers of voles and their predators. In non-cyclic vole populations, represented by our southern bank voles, predation risk remains more constant, and as could be expected, these voles showed weaker responses to predation risk than did conspecifics from a cyclic population.

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