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Does risk of predation by mammalian predators affect the spacing behaviour of rodents? Two large-scale experiments

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Abstract Predator-prey interactions between small mammals and their avian and mammalian predators have attracted much attention. However, large-scale field experiments examining small-mammal antipredatory responses under the risk of predation by mammals are rare. As recently pointed out, the scale of experiments may cause misleading results in studies of decision-making under predation risk. We studied the effect of small mustelid predators on the spacing behaviour of the gray-tailed vole (*Microtus canicaudus*) and the bank vole (*Clethrionomys glareolus*) in two separate field enclosure experiments. The experiments were conducted during the breeding season in North America and northern Europe, where small mustelids have been suggested to be important mammalian predators of voles. As in most of the earlier laboratory studies, predation risk was simulated using fresh mustelid faeces and urine. This made it possible to compare the results from experiments at different spatial scales. We did not find any effect of increased predation risk on spacing behaviour (mean and/or maximum distance moved and home range size) or trappability in either vole species. Simulated predation risk did not affect the breeding of females in gray-tailed voles, as has previously been shown in bank voles. The results disagree with most of the studies conducted in laboratory conditions with small mammals. We discuss whether this discrepancy could be caused by differences in the scale of the experiments.

Key words Activity · Antipredatory behaviour · Breeding suppression · Mammalian versus avian predators · Small mammals

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Introduction

Antipredator decision-making has received much attention in ecology during the last decade. It has been shown that prey individuals often decrease their activity or use different spatial or temporal refuges to decrease their vulnerability to predators (see review by Lima 1998). However, prey have to trade off their antipredatory responses with other functions, such as foraging or mating (e.g. Gilliam and Fraser 1987). The antipredatory behaviour of prey may also vary with different types of predators. Therefore, the decision-making of prey under risk of predation by different predators should be known when hypotheses are being formed about the indirect effects of predators on reproductive success and survival of prey.

Rodents and other small mammals have two different types of predators, avian or mammalian, which cause spatially varying predation risk. There are already many studies indicating that small mammals have behavioural adaptations to avian predators. Individuals decrease their activity or use vegetation cover, which reduces their vulnerability to owls and kestrels (Brown et al. 1988; Longland and Price 1991; Korpimäki et al. 1996). Mammalian predators have also been found to cause changes in the spacing behaviour or decrease the general activity of small mammalian prey both in laboratory studies (Jedrzejewski et al. 1993; Ronkainen and Ylönen 1994; Parsons and Bondrup-Nielsen 1996) and small-scale outdoor experiments (Jedrzejewski and Jedrzejewska 1990). In a large-scale experiment on house mice (*Mus domesticus*), individuals selected denser vegetation when exposed to cat (*Felix catus*) faeces (Dickman 1992). In the other large-scale experiment *Microtus* voles increased their activity when the densities of natural avian and mammalian predators (small mustelids) were reduced (Norrdahl and Korpimäki 1998). As voles that were more mobile were more likely to be killed than voles that were less mobile, the authors concluded that vole individuals would react to their main predators, small mustelids, by decreasing their mobility. However, in that ex-

periment both avian and mammalian predators were removed at the same time and it is impossible to separate the responses of the prey to the different types of predators.

The aim of this study is to examine whether small mammals respond to the perceived presence of mammalian predators by changing their activity and/or spacing behaviour. Two large-scale enclosure experiments were conducted, one in North America and the other in northern Europe, with two common vole species, *Microtus canicaudus* and *Clethrionomys glareolus*, and their mammalian predators (mustelids). Predation risk was simulated by using fresh mustelid faeces and urine, which made it possible to compare our results with laboratory and small-scale experiments. Moreover, the study was designed to allow examination of the direct effect of predation risk without confounding changes in prey and predator population densities.

Materials and methods

Study sites and animals

Two separate studies were carried out; one at Hyslops Agronomy Farm in Oregon, North America, in May–September 1996 and another at Konnevesi Research Station, central Finland, in June–July 1994. Our study species were mature wild-caught gray-tailed voles (northern America) and bank voles (northern Europe). Both studies were conducted in outdoor enclosures during the breeding season. The enclosures at Konnevesi (each 0.25 ha) were large enough to allow the normal spacing behaviour (i.e. reproducing females have exclusive territories: Koskela et al. 1997) and breeding of bank voles compared to natural populations (Bondrup-Nielsen and Karlsson 1985; Mappes et al. 1998; P. Jonsson, E. Koskela and T. Mappes, unpublished work). Furthermore, the breeding and space use of gray-tailed vole had a similar pattern both in the enclosures and on open grids (Wolff et al. 1994).

To simulate a situation of increased predation risk, we used fresh faeces and urine from two mustelid predators: mink (*Mustela vison*) in northern America and least weasel (*M. nivalis nivalis*) in northern Europe. Even though we used odours from two different mustelid species, the anal sac secretion of these species is very similar (Brink et al. 1983). We are fully aware of the limitations of this kind of manipulation of predation risk, as it is impossible to perfectly mimic the natural scent marks left by mustelid predators. However, in a study by Jedrzejewski and Jedrzejewska (1990) there was no difference in the anti-predator responses of voles kept in pens visited by a weasel or in pens with only the scent of weasels. Furthermore, as individual voles estimate the predation risk by olfactory cues (Jedrzejewski et al. 1993), we suggest that our manipulation could have caused similar changes in the behaviour of voles as found in the small-scale studies. Avian predation was not controlled for in either the northern European or North American experiment.

North American study

The study was conducted in six 0.2-ha (45×45 m) enclosures planted with alfalfa (*Medicago sativa*) and a mixture of grasses. To monitor the individuals, we used 81 Sherman live-traps placed in a 9×9 array at 5-m intervals in each enclosure. Traps were baited with oats and sunflower seeds, set in the evening and checked early the following morning, and in between the trapping weeks the traps were left open. To simulate increased predation risk, mink faeces and urine were spread by hand in a regular pattern (about one tablespoon every 3 m on the ground and in the vegetation, but not on the traps) twice per week in three experimental enclosures. The predator odour mixture was collected from a local mink fur farm. As a non-predator scent (control) we used rabbit (*Oryctolagus cuniculus*) droppings and urine, spread in a similar way to the predator odour in three control enclosures.

In early April, we released six females (mature, non-pregnant) and five males, trapped from nearby forest during the winter, in each enclosure. The initial body mass of both sexes did not differ between the treatments or enclosures (one-way ANOVA: for all cases $P>0.17$). From May to August, individuals were monitored by 3 consecutive nights trapping at 2-week intervals. The gray-tailed voles were trapped twice before the start of the treatment (27 May–10 June: weeks 2–4), three times during the treatment with the two different odours (24 June–22 July: weeks 6–10) and twice after the treatment (5 August–19 August: weeks 12–14). We did one extra trapping for the reproductive data (26 August: week 15). For each capture we recorded sex, identity, body mass, reproductive condition and trap location. To avoid confounding effects due to increasing population density, the number of voles was allowed to increase to about 50 voles per enclosure;, we then selectively removed individuals, preferably old males, early pregnant females or juveniles (recaptured) from the enclosures.

Maximum distance moved and trappability were used as the variables representing the spacing behaviour and mobility of gray-tailed voles. The reproductive condition of the adults and the number of recruits were also determined. Females were considered as reproductively active if they were lactating, pregnant or had widely open pubic symphyses, while males were considered as adults if body mass was at least 30 g. Juvenile recruitment was estimated as the number of recruits (newly tagged voles) per number of adult females captured in the same enclosure 4 weeks (two trapping periods) earlier. The 4-week time lag allowed recruits to reach trappable size. Maximum distance moved was estimated as the longest straight-line distance moved within 1 trapping week (three trap checkings). Trappability was measured as the number of times the marked animals were captured by the end of each trapping week divided by total trap times. The program CAPTURE (Rexstad and Burnhamn 1992) was used to estimate population density of each enclosure for each trapping week. The estimates of population density were used to calculate the total number of females and number of recruits per week.

Northern European study

The design of the study in northern Europe was slightly different from the study in north America.

Twenty-five Ugglan Special multiple-capture live traps were distributed in each of eight 0.25-ha (50×50 m) enclosures in a 5×5 array with 10 m between the trap stations. A total of 40 overwintered female bank voles caught from nearby forests in the previous spring were used in the experiment. To obtain predator odour we had eight least weasels in separate cages. Every day the bedding (sawdust and hay), with faeces and urine of four least weasels, was collected and spread in four experimental enclosures as follows: half of the amount was distributed randomly in the enclosures and the other half was spread in places where voles frequently moved (trails and trap stations, not directly on traps). The other four enclosures served as controls and only clean bedding was distributed in the same way as in the four experimental enclosures.

To initiate the study (17 June: week 0), five females in similar reproductive condition (mature, non-pregnant but having reproduced once, earlier in the summer) and of similar body mass were distributed in each of the eight enclosures [mean body mass±SE: 23.3±0.6 g, no difference in body mass between the treatments (control odour vs. predator odour) or enclosures, one-way ANOVA, in both cases $P>0.4$]. Spreading of predator and control odour started after 10 days (week 2) and continued daily until the end of the study. On day 20 (6 July), three mature males were released in each enclosure. Before possible parturition, females were removed from the enclosures and housed in standard breeding cages in the laboratory until they gave birth (for breeding data see Mappes et al. 1998).

Home range size, trappability and maximum and mean distance moved between two successive trap checks were used as the

variables representing the spacing behaviour and mobility of bank voles. Individuals were monitored three times during the study: (1) before treatments and before releasing males in enclosures (22–26 June: week 1), (2) during treatment (control odour vs. predator odour) when females were most likely in the early stages of pregnancy (10–14 July: week 4) and (3) during treatment when females were in late pregnancy (19–23 July: week 5). The spacing behaviour of males was monitored only during manipulation (trapping weeks 4 and 5). During each trapping period traps were checked ten times, twice a day (morning and evening) for 5 days. Home range size was estimated using the 90% minimum convex polygon method (Kenward 1987). Home range size in both sexes was not correlated with the number of captures (Spearman rank correlation: for all cases $P>0.1$). The maximum distance moved was calculated as the longest straight-line distance moved between two successive captures during one trapping period, and the mean distance moved as the average distance moved between two successive captures during one trapping period. Trappability was measured as the number of captures per 10 trap checkings.

If an individual disappeared during the study (not caught during four subsequent trap checks) it was replaced from the laboratory stock with a new individual in the same reproductive condition. One male was lost from the control and two from the experimental group. Ten females were lost, one before and nine after the manipulation started. Of these nine females five were from control enclosures and four from experimental enclosures (Fisher's exact test, $P=1.00$). However, only the individuals that were present throughout the study were used in the analyses (30 females and 21 males).

Data analysis

The estimates of spacing behaviour differed between North American and northern European studies, as in the gray-tailed vole the number of captures does not allow the calculation of home range sizes. However, in the bank vole maximum distance moved was higly correlated with home range size (Pearson correlation coefficient for different trapping periods, in females: all $r>0.6$, in males: all $r>0.5$). Consequently, we suggest that maximum distance moved gives as reliable an estimate of the spacing behaviour of voles as home range size. The spacing behaviour and reproductive data of voles were analysed using repeated-measures MANOVA where treatment was used as a category variable (predation and control). In the north American study, the enclosure effect was excluded by using the mean values of each enclosure ($n=6$) for each dependent variable. In the European study the enclosure effect was controlled for by using it as a separate categorical variable in the analyses. To meet the assumptions of parametric tests, the trappabilities of both vole species and the proportion of reproductive gray-tailed vole females were arcsine square-root transformed before the analyses. All the tests were two-tailed. The data were analysed using SAS (SAS Institute 1990) and SPSS for Windows (Norusis 1992).

Results

North American study

There was no difference in maximum distance moved by the female gray tailed voles between the treatments ($F_{1,4}=0.41$, $P=0.557$; Fig. 1a) or treatment by trapping week interaction ($F_{6,24}=1.45$, $P=0.237$). Further, the maximum distance moved in males did not differ significantly between the treatments ($F_{1,4}=1.79$, $P=0.252$; Fig. 1b) and there was no treatment by trapping week interaction ($F_{6,24}=0.31$, $P=0.924$). Both female and male voles decreased their maximum distance moved during the season (females: $F_{6,24}=8.69$, $P=0.001$; males: $F_{6,24}=8.56$, $P=0.001$). The trappability of both sexes differed between trapping periods (females: $F_{6,24}=6.94$, $P=0.001$; males: $F_{6,24}=5.19$, $P=0.002$) but did not differ between treatments (females: $F_{1,4}=0.22$, $P=0.664$; males: $F_{1,4}=0.04$, $P=0.854$) or show interaction with treatment (female: $F_{6,24}=0.64$, $P=0.698$; male: $F_{6,24}=0.21$, $P=0.974$).

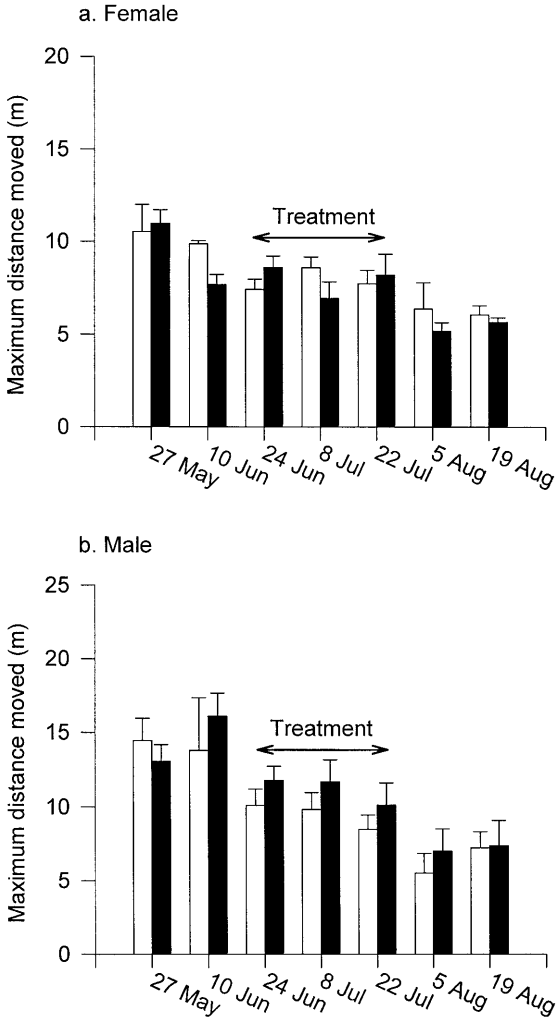

Fig. 1 The North American study: the maximum distance moved (mean±SE) by a adult female and b male gray-tailed voles, before, during and after the predation risk manipulation (open bars control scent from rabbit, filled bars mink scent)

Northern European study

There was no difference in the mobility of female bank voles between the two treatments measured either as maximum distance moved or mean distance moved between two consecutive captures (Fig. 2a, Table 1). Although mobility seemed to decrease during the study there was no interaction with treatment. The maximum distance moved by males did not change during the study ($F_{1,13}=1.87$, $P=0.195$) and did not differ by treatment (treatment: $F_{1,13}=0.23$, $P=0.637$; enclosure: $F_{6,13}=0.22$, $P=0.963$; Fig. 2b) or show a treatment by trapping week interaction ($F_{1,13}=0.7$, $P=0.389$). Howev-

Table 1 The effect of simulated predation risk on the mobility of female bank voles

Females	*df*	F^a	*P*
Maximum distance moved			
Treatment	1.22	1.97	0.174
Time	2.21	7.34	0.004
Treatment×Time	2.21	1.35	0.281
Enclosure	6.22	1.07	0.409
Mean distance moved			
Treatment	1.22	0.01	0.943
Time	2.21	2.65	0.094
Treatment×Time	2.21	1.95	0.167
Enclosure	6.22	1.54	0.212

[a]Repeated-measures MANOVA

Table 2 Home range size (mean±SE) of bank voles before and during the simulated predation risk treatment

	Week 1 No predation	Week 4 Predation	Week 5 Predation
Females			
Control	820±118	763±106	663±74
Predation	853±136	807±109	633±72
Males			
Control		1195±107	1445±106
Predation		1060±94	1335±95
Females	*df*	F^a	*P*
Treatment	1.22	2.64	0.118
Time	2.21	1.95	0.168
Treatment×Time	2.21	3.11	0.066
Enclosure	6.22	2.44	0.058
Males	*df*	F^a	*P*
Treatment	1.13	1.49	0.243
Time	1.13	11.88	0.004
Treatment×Time	1.13	0.43	0.525
Enclosure	6.13	1.03	0.447

[a]Repeated-measures MANOVA

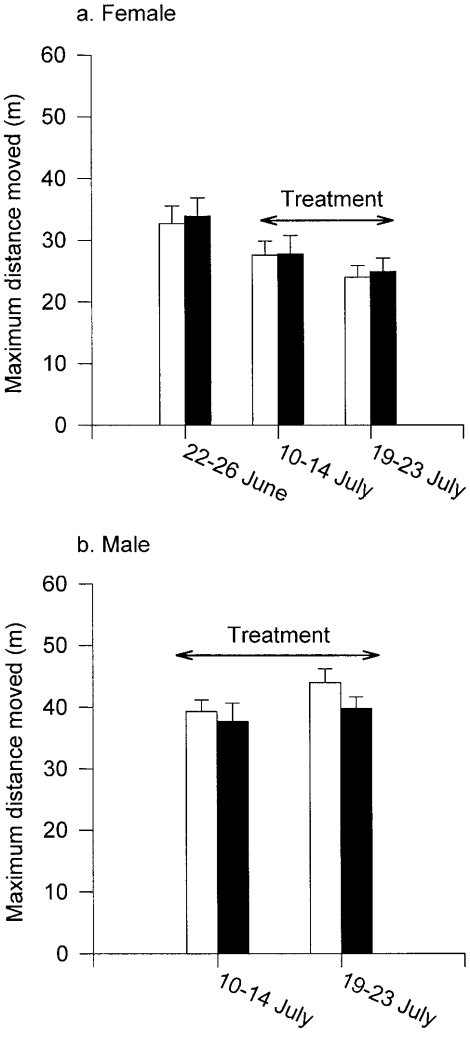

Fig. 2 The northern European study: the maximum distance moved (mean±SE) by **a** adult female and **b** male gray-tailed voles, before (females only) and during the manipulation of predation risk (*open bars* clean bedding, *filled bars* least weasel scent)

er, the mean distance moved by males increased during the study ($F_{1,13}$=5.50, P=0.036) but there was no difference between the treatments (treatment: $F_{1,13}$=0.32, P=0.583; enclosure: $F_{6,13}$=0.36, P=0.891, interaction: $F_{1,13}$=2.20, P=0.162).

The home range size of females tended to decrease during the study but there was no difference between the treatments (Table 2). In males the change in home range size during the study was significant, but again no differences between the treatments were found (Table 2). The trappability of females differed between trapping weeks ($F_{2,21}$=5.21, P=0.015), but did not differ between the treatments (treatment: $F_{1,22}$=3.04, P=0.095; enclosure: $F_{6,22}$=1.57, P=0.204) or show a treatment by trapping week interaction ($F_{2,21}$=1.10, P=0.351). Trappability of males did not change during the study ($F_{1,13}$=2.47, P=0.140) and there was no significant difference between treatment groups ($F_{1,13}$=0.47, P=0.507) or treatment by trapping week interaction ($F_{1,13}$=0.41, P=0.534).

Reproductive success in the gray-tailed vole

The proportion of adult females in reproductive condition decreased significantly over time from 80–90% (May) to 40–50% (August) ($F_{8,32}$=11.01, P=0.001), but did not differ among the treatments ($F_{1,4}$=0.01, P=0.993; Fig. 3a) or show a treatment by time interaction ($F_{8,32}$=1.90, P=0.094). The number of juvenile recruits per adults (total=1062) did not differ significantly between the trapping weeks ($F_{8,32}$=1.83, P=0.108) or between the treatment groups ($F_{1,4}$=0.07, P=0.799; Fig. 3b) or showed a treatment by week interaction ($F_{8,32}$=0.54, P=0.814).

Discussion

Predation risk has been suggested to be an important factor determining the activity and space use of the prey.

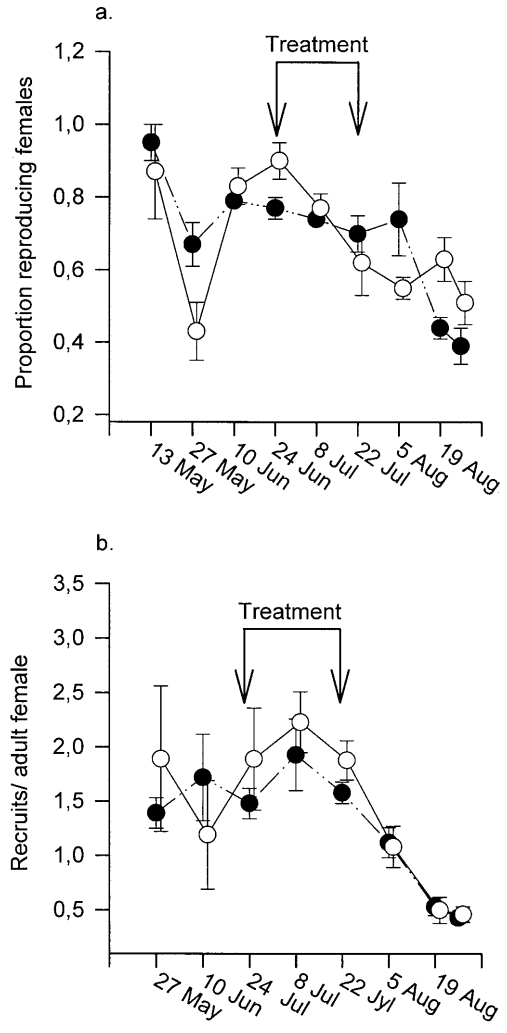

Fig. 3 **a** Proportion (mean±SE) of female gray-tailed voles in reproductive condition and **b** the number of recruits per adult female in different treatments during the study (*open symbols* control treatment, *filled symbols* predation treatment)

Both the benefits (decreased risk of death) and the costs of antipredator responses (e.g. decreased feeding and mating opportunities) modify the behavioural response of prey (Lima 1998). However, benefits from antipredatory behaviour can vary in relation to the spatial and temporal scale of predation risk. Here, we examined whether voles responded to mustelid predation risk by changing their spacing behaviour. Mustelids are small carnivores that have been considered to be the most important contributor to vole population cycles in northern Europe (e.g. Henttonen et al. 1987; Hanski et al. 1993; Korpimäki and Norrdahl 1998). Indeed, recent field experiments have shown that predation by small mustelids is the main mortality factor in voles (Norrdahl and Korpimäki 1995) at certain phases of the cycle. Consequently, voles might have evolved antipredatory tactics against mustelid predators. They could, for example, confine their movements or change the size of their home ranges, as they do under risk of avian predators (Longland and Price 1991; Kotler et al. 1992; Abramsky et al. 1996; Korpimäki et al. 1996). However, our results provide no evidence that voles do change their mobility under mammalian predation risk. This result is inconsistent with most of the experiments conducted in the laboratory (Jedrzejewski et al. 1993; Ronkainen and Ylönen 1994; Parsons and Bondrup-Nielsen 1996) or in small-scale enclosures (Jedrzejewska and Jedrzejewski 1990). However, one has to keep in mind that it is also possible that the contradiction between the present results and those obtained in small-scale enclosures could be caused by different ways of simulating of predation risk (presence of weasels vs. weasel scent only).

In the study of decision-making under predation risk the importance of scale has been stressed several times (e.g. Lima and Dill 1990; Korpimäki and Krebs 1996; Lima 1998). If a predator (or its scent) and prey are maintained in very close proximity the prey's response to predation risk may be so strong as to be potentially misleading. In a recent review, Lima (1998) lists some situations where the results obtained from microscale experiments have not been replicated under field conditions. Unfortunately, large-scale experiments examining spacing behaviour (activity/mobility, home range use) in small mammals under risk of predation by mammalian predators are scarce. In the first experiment conducted in large unfenced areas, Norrdahl and Korpimäki (1998) found that voles moved more when predation risk was lower. In their study the densities of both avian and mammalian predators were reduced, making it difficult to interpret the importance of different types of predator to the antipredator response of the prey. However, our results support the earlier work by Wolff and Davis-Born (1997). In their four-fold replicated experiment they found no difference in the activity of gray-tailed voles between control and predator-scented enclosures. Most of the earlier experimental work demonstrating antipredatory responses to mustelid predators has been conducted in Fennoscandia. Wolff and Davis-Born (1997) suggested that if mustelid predation had a significantly greater influence on vole life-histories in Fennoscandia than in North America, it could be one reason for disagreement between the results. However, as we did not find any behavioural response to simulated mustelid predation risk either in Fennoscandian or North American voles, this explanation is not supported by our study.

In the North American experiment we investigated whether voles suppressed their breeding under increased predation risk (breeding suppression hypothesis; for reviews of empirical and theoretical studies see Mappes et al. 1998; Kokko and Ruxton, in press). We found no decrease in reproductive success of gray-tailed voles (proportion of reproducing females and number of recruits) either during or after the odour treatment. These results support the hypothesis (Lambin et al. 1995; Mappes et al. 1998) that the earlier results showing breeding suppression under predation risk may be a laboratory or experimental artefact. As small-scale studies are especially prone to artefacts, laboratory experiments may sometimes produce results that are not found at a larger scale where the behaviour of individu-

als is more natural. Furthermore, even if the behaviour observed in the laboratory were "normal", the response may be too slight to have any measurable effect in the field (e.g. Parsons and Bondrup-Nielsen 1996).

Most studies that have demonstrated anti-predatory responses of rodents to mammalian predators (or their scent) have been performed in laboratory conditions. However, except for the study by Norrdahl and Korpimäki (1998) these results have not been replicated in large-scale experiments. Assuming that experiments conducted in more natural conditions should in general be more reliable, our study again emphasises the importance of scale in ecological experiments. The general knowledge of the antipredatory adaptations may also suffer from so-called "file drawer problem" (Rosenthal 1979; Csada et al. 1996): non-significant results are not being published but stored in file drawers by researchers. In his review Lima (1998) summarises 23 published studies of rodents examining the use of space under predation risk (mainly avian), and only 1 study reports a lack of response to predation risk.

As in our study individual voles do not seem to change their spacing behaviour or reproduction under predation risk, it may indicate that the possibilities of escaping their specialist mammalian predators are poor. The costs of avoidance behaviour may be too large in relation to the possible benefits for antipredatory behaviour to evolve in this predator-prey system.

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