

The effects of weasel proximity on the foraging activity of voles

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The presence of a predator can cause changes in the feeding behaviour of prey. These changes may have consequences on ecological systems, i.e. behavioural trophic cascades. The proximity of the prey and predator is likely to vary in nature and the intensity of prey responses may vary accordingly. Therefore the occurrence of behavioural trophic cascades may partly depend on whether the prey changes its behaviour when not in immediate contact with the predator. We conducted a laboratory experiment where we measured the foraging activity of wild-caught and laboratory-born voles at different distances from a caged weasel. Both groups responded by reduced activity at the closest distance, 0.15 m. The feeding behaviour of neither group deviated from control (no weasel) when the distance to the weasel was 3.5 metres. At an intermediate distance, 1.5 metres, only the wild-caught voles responded. The response of voles to the presence of a weasel varies between laboratory-born and wild-caught voles and seems to be restricted only to the immediate surroundings of the weasel.

Introduction

The mere presence of a predator can affect the life and behaviour of its prey. Studies conducted with diverse taxa have shown that risk of predation influences foraging decisions, activity and reproduction of prey (for reviews, *see* Lima 1998a, 1998b). These changes in prey behaviour may have important consequences on ecological systems. For example risk-averse feeding of herbivores may have effects cascading to the distribution and abundance of plants (e.g. Beckerman *et al.* 1997, Puseenius & Ostfeld 2000).

A prey animal foraging under an elevated risk of predation should minimize its exposure

to risk while fulfilling its energy requirements (Sih 1993). Therefore foraging activity usually decreases with increasing risk of predation (Lima 1998b). Foragers may also favour safer food types rather than more risky ones, even if the former might have a lower energetic value; feeding decisions should be based on the ratio between net energy gain and total risk while handling (Sih 1993). There are not many studies on the effects of predation risk on diet choice. However there is evidence that inherently less preferred food is chosen instead of more preferred food, when the former occurs in a safer patch than the latter (Brown & Morgan 1995).

In natural conditions the movements of a predator, searching for a prey, likely cover only a portion of the area inhabited by a given prey population. The distance between the predator and each of the individuals of the prey population thus varies. The awareness of prey of the presence of a predator, likely decreases with increasing distance between the predator and the prey. However, the slower the decrease the higher the proportion of prey that perceive the increased risk of predation and the more pronounced are the predator's indirect effects on the prey population.

One of the most studied predator-prey relationships where the presence of a predator has been thought to have a high impact on prey behaviour is that between voles and their specialist mustelid predators, weasels (e.g. Gorman 1984, Koskela & Ylönen 1995, Norrdahl & Korpimäki 1998, Carlsen *et al.* 1999). Least weasels (*Mustela nivalis*) and many other members of the mustelid family have a large pair of anal glands, which contain species-specific strongly odorous substances used for scent marking (King 1989). This has raised a hypothesis suggesting that weasel odour may be a potential cue indicating elevated risk of predation for voles (Stoddart 1976). Besides olfactory cues, also other cues such as auditory ones indicating the presence of weasel are able to cause behavioural responses in voles (Pusenius & Ostfeld 2000). Furthermore, the effects of olfactory cues alone seem to be relatively mild in relation to effects caused by the presence of a living weasel (Koivisto & Pusenius 2003).

Demonstrated responses of voles to the presence of a weasel or the cues indicating its presence range from cessation of breeding to changes in feeding behaviour (Ylönen 1989, Parsons & Bondrup-Nielsen 1996, Bolbroe *et al.* 2000, Pusenius & Ostfeld 2000). Voles generally decrease their feeding activity due to an increased risk of predation (Koskela & Ylönen 1995, Koivisto & Pusenius 2003, but *see* Pusenius & Ostfeld 2000). They also choose safer feeding patches and food sources when exposed to elevated risk (e.g. Korpimäki *et al.* 1996). There is also experimental evidence of a behaviourally mediated trophic cascade in a system composed of voles, their food plants and mustelid predators (Pusenius & Ostfeld 2000).

The majority of positive responses of voles to increased risk of weasel predation have been observed in laboratory conditions. However, there have been several instances of disagreement between results of laboratory and field experiments: in the field no or only a very mild effect is detected (Wolff & Davis-Born 1997, for a review *see* Mappes *et al.* 1998, Jonsson *et al.* 2000, but *see* Fuelling & Halle 2003). The cause of this obvious discrepancy may lie in the different levels of intensity of contact between predator and prey; in laboratory experiments predator and prey are usually forced to be in close contact with each other, while in field experiments the contacts are likely to be more occasional (Mappes *et al.* 1998, Wolff 2003). Furthermore, weasels are efficient predators and thus close encounters between them and voles will most likely cause detection, attack and death of a vole. Especially field voles (*Microtus agrestis*), which are heavily built, clumsy rodents, may have very few chances of fleeing from a weasel once it has noticed the vole (Bolbroe *et al.* 2000). Therefore, the risk of weasel predation could be a potent factor changing foraging behaviour of field voles in natural conditions, if voles notice the weasel early enough to avoid being killed, but still become alerted and change their foraging activity accordingly. However, there are no studies on the effect of proximity between a vole and a weasel on the vole foraging activity.

Another problem in laboratory studies on rodents is the possible difference in behaviour between laboratory colonies and natural populations. It is likely that behaviour is modified by habituation to laboratory conditions. In addition, genetic variation may be lost in laboratory colonies as only a fraction of animals breed in the novel conditions. This could cause directional selection for traits like responsiveness to stress and threat (McPhee 2003, Wolff 2003). There are only a few studies on these effects. Recently, MCPhee (2003) showed that the response of old field mouse, *Peromyscus polionotus*, to a silhouette of a flying owl decreased with increasing generations in captivity.

The aim of this study was to examine (1) the effect of the distance from a weasel on the behaviour of voles, and (2) whether voles born in a laboratory colony respond differently to the

presence of a weasel at different distances from them as compared with voles newly caught from nature. Furthermore we examined (3) whether exposure to the presence of a weasel influenced the choice of voles between more and less preferred food items when the less preferred food items were situated in a safer neighbourhood than the more preferred ones. To achieve these goals we conducted a laboratory experiment where we measured the foraging activity of field voles in a feeding arena situated at different distances from a caged least weasel. To test whether the perceived risk of predation affects the choice between food items of different quality, the voles were offered a choice between birch seedlings (poor items, e.g. Harju & Tahvanainen 1997) available next to their nest box and oat seeds (high-quality items) situated at a greater distance from the nest box but closer to the weasel. The voles used in the experiment were either captive-born or wild-caught.

Material and methods

The least weasel used in the experiment, an old male, was trapped in the area of Lake Pielinen, eastern Finland, in 1998. The least weasel was housed in a cage in a different room than the voles and fed with cat food containing game meat. Altogether 32 voles were used in the experiment. Half of the voles were captive-born and the other half was caught from the wild using oat seeds as bait in Joensuu, eastern Finland in August 2003, two weeks before the beginning of the experiment. The weight of the voles varied from 17 to 50 g. The mean weight of voles did not differ among the treatment combinations (ANOVA: $F_{7,24} = 0.80$, $P = 0.59$). Prior to the experiment, voles were housed in standard laboratory cages, from one to three animals in each, and fed with oat seeds, carrots, potatoes, nuts and pellets designed for laboratory rodents. The animals were cared for in accordance with the principles and guidelines of the Finnish Council on Animal Care.

The experiment was conducted in a ca. 20 m² room at normal room temperature (20 °C) and lighting corresponding to dusk. Two 0.5 × 0.5 m arenas were connected with a 0.5-m-long (diam-

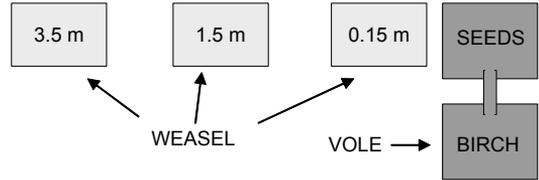


Fig. 1. Experimental system used in the study. The positions of the weasel cage at different distances to the feeding arena are illustrated.

eter 0.1 m) acrylic tube to give voles an opportunity to move freely from one arena to another (Fig. 1). The arenas were constructed of 0.8-m-high hardware cloth, with 0.2-m-wide metal sheets on the top of the fence to prevent voles from escaping. One arena contained a water bottle and a nest box with nesting material inside. The floors of both arenas were covered with a grid of Petri dishes (diameter ca. 3 cm) screwed to the floor in four rows of five dishes (20 in both arenas). All trials were conducted in September 2003.

We ran two trials per day, one from 08:00 to noon and the other from noon to 16:00. We ensured that morning and afternoon trials were evenly distributed among the applied treatments. All the trials with wild-caught voles were conducted before those with captive-born ones. Each trial consisted of a habituation period lasting two hours and an actual two-hour experimental period. During the habituation period the voles experienced no predation risk and they had an opportunity to familiarize with the quality and location of the food items offered. Altogether five sticks of silver birch (*Betula pendula*) seedlings (length ca. 3 cm, diameter ca. 2 mm) were put in the arena with the nest box, and five oat seeds into the second arena. The amount of food supplied was somewhat smaller than that needed by voles to subsist for a two-hour period (Ryszkowski *et al.* 1973). By offering an insufficient quantity of food we motivated the voles to forage during the actual experimental period. At the beginning of the experimental period we put one oat seed into each of the 20 dishes in the arena with no nest box and 20 birch sticks into the one with the nest box and removed any food remaining from the habituation period. Overdispersion of food in the arenas forced the voles to move around the arenas when foraging and

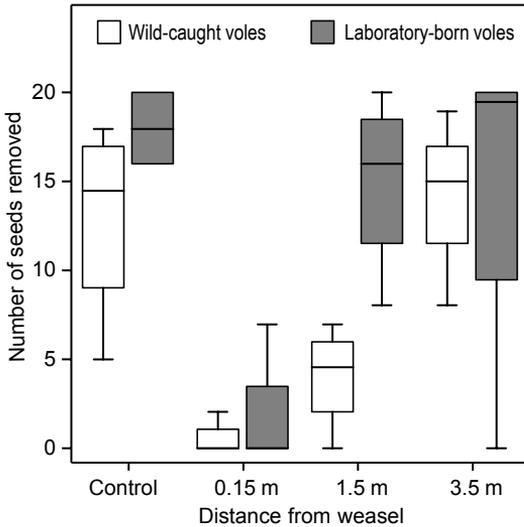


Fig. 2. Boxplots illustrating the median lines, upper and lower quartiles and extremes for the number of seeds removed by wild-caught and laboratory-born voles when exposed to the presence of a caged weasel situated at different distances from the feeding arena of voles.

thus expose themselves to potential predators. In addition, to get high quality food (seeds (Myllymäki 1977)) the voles were forced to go to the far end of the arena system without any protective cover. Both wild-caught and laboratory-born voles were familiar with oat seeds, and they also seemed to prefer them as food. At the end of the experiment all removed oat seeds were recorded, as well as removed or gnawed birch sticks with the exception of non-gnawed sticks found next to their Petri dishes. In these cases it was likely that the vole had displaced them accidentally while moving around the arena.

We manipulated the intensity of contact between vole and weasel by placing a cage (sides 1×0.55 m, height 0.5 m, bottom and three walls plastic, the front wall hardware cloth) with a weasel inside at one of three distances from the vole arena: 0.15, 1.5 and 3.5 metres (Fig. 1). In a control treatment there was only an empty clean cage next to the vole arena (distance 0.15 m). We chose not to use any harmless control animal, because previous experiments have shown that field voles clearly discriminate the odour of predators from those of non-predatory small mammals (e.g. Bolbroe *et al.* 2000). The voles must have been able to see, smell and hear the

weasel through the hardware cloth (mesh size 5 mm in the weasel cage and 9 mm in the vole arena). The weasel was supplied with water and a nest box. In addition, the cage contained a tree branch, tubes and dry hay to encourage movements of the weasel and to bring on rustling much similar to that created by a weasel when it moves and hunts in long grass. The vole arena with oat seeds was always closer to the weasel cage than the one with the nest box and birch sticks (Fig. 1).

We tested the effects of the distance between the vole arena and the weasel cage and the origin of animals (laboratory-born vs. wild-caught) and the interaction between these factors on the proportion of seeds removed by voles in the experimental period using standard two-way ANOVA. The proportion of seeds removed was arc-sine square-root transformed prior to the analysis. We used non-parametric two-way ANOVA (*see* Potvin *et al.* 1990) to analyse the effects of the aforementioned explanatory variables on the number of bitten seedlings. All statistical analyses were conducted using SPSS 11.5 software.

Results

The proportion of seeds removed by the voles increased with distance between the vole arena and the weasel cage (two-way ANOVA: $F_{3,24} = 12.21$, $P < 0.0001$) (Fig. 2). Also the origin of voles affected their feeding behaviour (ANOVA: $F_{1,24} = 5.58$, $P = 0.027$). The wild-caught voles removed fewer seeds than the laboratory-born ones (Fig. 2). There was no significant interaction between treatment and origin (ANOVA: $F_{3,24} = 1.25$, $P = 0.31$). We continued the analysis by assessing how the distance between the weasel and the vole arena affected seed removal in relation to control treatment. The results of the Dunnett test ($\alpha = 0.05$) ran separately for the wild-caught and laboratory-born voles indicated that as compared with the control, seed removal decreased at distances of 0.15 m and 1.5 m for the wild-caught voles, but only at a distance of 0.15 m for the laboratory-born ones (Fig. 2).

Birch sticks were bitten only in seven out of 32 experiments. The number of bitten seedlings did not depend on the distance between the vole

and the weasel (Kruskal-Wallis non-parametric ANOVA: $\chi^2 = 2.10$, $df = 3$, $P = 0.55$) or the origin of the voles (Mann-Whitney U -test: $U = 119.50$, $N = 16$, $P = 0.75$). Neither was there any interaction between these factors (Kruskal-Wallis test: $\chi^2 = 0.83$, $df = 3$, $P = 0.84$). Thus, voles did not switch to poorer food when predation risk increased.

Discussion

Both laboratory-born and wild-caught voles decreased their feeding activity in the presence of a caged weasel when it was very close to the vole arena (0.15 m), but only wild-caught animals showed a reaction when the weasel was at a distance of 1.5 m. Neither group showed any reaction when the distance to the weasel was 3.5 m. Still we consider it most likely that voles have heard and smelled the presence of a weasel in the calm laboratory also at that distance. Thus, our results suggest that voles do perceive signals originating from the activities of a weasel as a threat, serious enough to induce reduced feeding, only when these signals indicate that the potential enemy is in their immediate vicinity. This finding may explain some of the discrepancies between laboratory and field studies on the effects of risk of weasel predation on vole behaviour (Wolff 2003). In laboratory experiments, close contacts between voles and weasels or cues indicating the presence of weasels clearly modified vole behaviour (e.g. Ylönen 1989, Koskela & Ylönen 1995, Bolbroe *et al.* 2000). However, in field conditions where contacts between voles and weasels or the cues indicating the presence of weasels are more casual, the effects are seldom found (but *see* Fuelling & Halle 2003).

Voles have a high metabolic rate and thus can not interrupt their food intake for long periods (Gebczynska 1970, Borowski 1998). Hansson (1971) estimated that even in the presence of high quality food, field voles must feed at least 15 times per 24 hours to keep a favourable energy balance. However, due to a high energy content of oats the voles may have kept their energy balance by feeding only once during the experimental period. Still refraining from feeding should soon have caused their energy

balance to become negative. Voles are poorly adapted to fasting (Mosin 1982). According to P. Nieminen and A.-M. Mustonen (unpubl. data) plasma glucose level of field voles drops 40% during a four-hour fasting period. This may significantly impair the ability of voles to sense their environment and escape predators. Therefore the cues suggesting a presence of a predator somewhere in a neighbourhood could motivate the voles to feed at least enough to keep their ability to sense and escape in a top condition. On the contrary when a weasel is next to a vole any feeding activities of the vole would likely cause a detection and attack by the weasel.

Voles could have fulfilled at least some of their energy requirements by feeding on birch seedlings relatively safely next to their nest box. However, they did not use that option. In fact, voles seemed to remove seedlings mainly in control conditions and when the predator was at its farthest, 3.5 m away. Seedlings are not preferred food items for voles (e.g. Ostfeld & Canham 1993). They contain only low amounts of energy and nutrients, but high amounts of secondary compounds and fibre (e.g. Palo *et al.* 1992). Handling of seedlings probably takes more time and effort than handling of seeds. Consequently, resorting to eating seedlings would have resulted in a heightened exposure to predators, but had only marginally improved nutritional status.

One possible explanation for the lack of response in vole feeding activity to the weasel farther than 1.5 m away may simply be that the clarity of the predatory cues decreases with distance. False predator detection, resulting in cessation of foraging and escape to the shelter, would also incur a cost. This would decrease energy intake and increase energy expenditure due to travelling back and forth between the shelter and foraging grounds. Accordingly, voles may mostly react to cues that are clearly identifiable.

The ability of voles to identify mustelid odour and react to it is most likely innate. For example Bolbroe *et al.* (2000) showed that laboratory born field voles with no earlier experience of predators changed their behaviour under a simulated risk of least weasel predation, but did not react similarly to rabbit odour. Also Parsons and Bondrup-Nielsen (1996) found that voles

originating from an island with no terrestrial predators reacted similarly to the odour of short-tailed weasels than voles originating from the mainland population with previous experience of mustelid predators. Nonetheless, as our results suggest, habituation seems to somewhat modify the reactions of voles towards weasels. The laboratory-born voles were most likely accustomed to living with no predation risk at all and may therefore have been less alert than the wild-caught ones. Laboratory-born individuals had also been repeatedly exposed to signals indicating the presence of other animals, and also humans and thus might have been habituated to certain levels of disturbance in their environment. In any case, our results show that the former living conditions of animals used in experiments can have effects on the results obtained (see also McPhee 2003).

These results add to evidence that the mere presence of a predator can affect the feeding behaviour of prey animals and therefore also possibly affect survival and reproduction (e.g. Borowski 1998, Bolbroe *et al.* 2000, Pusenius & Ostfeld 2000). However, the effects of weasel presence do not seem to be spatially very far-reaching: only the nearby surroundings of a predator appear to be the area of actual impact on vole behaviour. Thus, if the density of the predator species in the area is low, and the predator is not very mobile, its indirect effects on the prey animals are likely to be modest. On the other hand, when abundant enough, a very mobile predator like the least weasel might be able to keep its prey animals vigilant and affect their feeding decisions markedly.

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