# Indirect effects of least weasel presence on field vole behaviour and demography: a field experiment

Paavo Hellstedt<sup>1\*</sup>, Tiia Kalske<sup>2</sup> & Ilkka Hanski<sup>1</sup>

- <sup>1)</sup> Department of Ecology and Systematics, Division of Population Biology, P.O. Box 65, FIN-00014 University of Helsinki, Finland (\*e-mail: paavo. hellstedt@helsinki.fi)
- <sup>2)</sup> Department of Ecology and Systematics, Division for Instruction in Swedish, Zoological Laboratory, P.O. Box 65, FIN-00014 University of Helsinki, Finland

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Predation by small mustelids is widely considered to be the most likely mechanism to maintain multiannual fluctuations of vole populations in Fennoscandia. Apart from the direct effect of predation, small mustelids have been suggested to have indirect effects on vole population dynamics. We studied in a field experiment the indirect effects of the presence of the least weasel (*Mustela nivalis nivalis*) on behaviour and demography of field voles (*Microtus agrestis*). We constructed grids made of drainpipe with small holes and covering an area of 0.24 ha ( $4 \times 6$ -m grid, pipes with 10-m intervals). A least weasel moved in the experimental grid without having access to voles during the entire experiment, lasting for 11 weeks. We analysed the rate of maturation, breeding success, movements, and home range use of field voles in the experimental and control grids. The results indicate that weasel's presence had no or had only minor effects on voles.

# Introduction

Currently the most popular hypothesis to explain multiannual vole cycles in Fennoscandia is predation (Hanski *et al.* 2001). According to the predation hypothesis, specialist mammalian predators, especially the least weasel (*Mustela nivalis*) *nivalis* L.) and the stoat (*M. erminea* L.), maintain multiannual oscillations of vole populations because of the time delay in the numerical response of the predators to changing prey population size (Korpimäki *et al.* 1991, Korpimäki 1993, Oksanen & Henttonen 1996).

Predation has an obvious direct effect on

prey individuals and populations, but it has been suggested that indirect effects of predators might also be strong enough to influence prey population dynamics (Ylönen 1989, Lima & Dill 1990). Here indirect effects refer to those induced by the smell and other signs of the presence of the predator which may cause changes in behaviour, maturation and reproduction of the prey. Heikkilä *et al.* (1993) suggested that predators cause stress to vole individuals, which is reflected in the weight (and presumably function) of adrenals. Stress would cause avoidance of mating, lower breeding effort and delayed maturation.

The indirect effects of predators on voles have been studied using odours, auditory cues (Pusenius & Ostfeld 2000) and the presence of live predators. The results obtained so far are mixed and appear to depend on the species of the predator and of the prey used, as well as on the type of experiment conducted (*see* reviews in Norrdahl & Korpimäki 2000, Ylönen 2001).

Weasel odour and presence have been shown to influence the behaviour and physiology of the bank vole (Clethrionomys glareolus Schreber) (Jędrzejewski & Jędrzejewska 1989, Ylönen 1989, Ylönen et al. 1992, Jędrzejewski et al. 1993, Korpimäki et al. 1994, Koskela et al. 1996 but see also Lambin et al. 1995, and Mappes et al. 1998). It has been suggested that the presence of the weasel suppresses breeding of bank voles, which is called the breeding suppression hypothesis (BSH; Ylönen 1989, Koskela & Ylönen 1995). In contrast, studies on field voles (Microtus sp.) have yielded conflicting results. Field voles seem to avoid mustelid scent, leading to reduction in general activity (Gorman 1984). Like in the case of bank voles, the presence of the weasel has been found to suppress breeding in field voles (Koskela & Ylönen 1995). Likewise, Carlsen et al. (1999) showed a negative effect of predator presence on the weight of field voles. In contrast, Wolff & Davis-Born (1997) and Jonsson et al. (2000), using American mink (Mustela vison Schreber) odour to signal predator presence, did not find any significant behavioural responses in grey-tailed voles (Microtus canicaudus Miller). In the laboratory, mustelid odour affected Microtus sp. voles (weasel: Koskela & Ylönen 1995, Borowski

1998b, Bolbroe et al. 2000; stoat: Gorman 1984, Parson & Bondrup-Nielsen 1996, Borowski 1998a, Pusenius & Ostfeld 2000), but this has not been the case in several field experiments (weasel and American mink: Jonsson et al. 2000; weasel and stoat: Korpimäki et al. 1994; American mink: Wolff & Davis-Born 1997; and stoat: Parson & Bondrup-Nielsen 1996, but see also Gorman 1984, and Borowski 1998b). One factor that should be noted is that Wolff & Davis-Born (1997) made their study in an area where microtine populations are not cyclic (Oregon, USA), which might have relevance especially when considering the demographic and population-level consequences of indirect effects. According to Hansson (1990), the reproduction of voles from cyclic regions is more sensitive to disturbance than reproduction of voles from non-cyclic regions.

To summarise the previous research on Microtus voles, which are the main prey of the least weasel (Korpimäki et al. 1991, Korpimäki 1993, Oksanen & Henttonen 1996), most studies have been conducted in the laboratory and the few field studies suffer from various problems (Gorman 1984, Korpimäki et al. 1994, Norrdahl & Korpimäki 1995, Parson & Bondrup-Nielsen 1996, Wolff & Davis-Born 1997). In this paper, we report a field experiment in which a live weasel was present for a prolonged period of time within the area occupied by a vole population. The weasel was confined to an extensive grid made of drainpipe with small holes, making the presence and movements of the weasel evident across the experimental vole population. The aim of the experiment was to study whether the presence of the weasel had any effect on the behaviour and demography of the field vole (Microtus agrestis L.) in the seminatural conditions. We were also interested in finding out whether any population-level impact would occur, though such results would remain tentative, as we could not replicate the experiment at the population level.

# Material and methods

The study was conducted in an agricultural landscape near the Lammi biological station in

southern Finland (61°N, 25°E) about 100 km north of Helsinki. In the experiment we used two moist meadows (dominant plants: *Phleum pratense*, *Dactylis glomerata*, *Deschampsia cespitosa*, *Anthriscus sylvestris*, *Artemisia vulgaris* and *Taraxacum* spp.), which were situated at opposite sides of a small road. A narrow deciduous forest section also occurs between the two meadows (Fig. 1).

In March 1998, two  $40 \times 60$ -m drainpipe grids (2400 m<sup>2</sup>) were set up on top of the snow cover on the two meadows. Every parallel pipe line was at 10 m distance from each other, and hence, the total length of the pipe per grid was 560 m. The diameter of the plastic drainpipe (Veto PVC, Oy Uponor Ab, Nastola, Finland) was 80 mm. There were small holes in the drainpipe allowing the weasel's odour and sounds of movement to spread to the environment around the pipes. When the snow melted, the pipe grid descended to the ground with minimal disturbance. After the first live trapping period (26-30 April), we placed a male weasel inside the experimental pipe grid, the other similar grid remaining as a control. The weasel was able to move freely in the pipe grid. We set up a 1.5-m<sup>3</sup> cage in the nearby forest, about 50 m from the grid, with a cup for water and a wooden box as a den. The cage was connected to the experimental grid with a pipe. At the centre and in every corner of the grid we placed a pail for a water cup and for food. We placed one dead chicken (40-50 g) in a different pail every day of the week. The weasel had a radiotransmitter to facilitate observations of its location and movements in the grid.

The most numerous rodents in the study area are the field vole, the bank vole and the water vole (*Arvicola terrestris* L.). The common shrew (*Sorex araneus* L.) and the pygmy shrew (*S. minutus* L.) are also common. The male weasel was born in captivity at the Lammi biological station, and it was  $\sim$ 11–13 months old during the experiment.

We monitored vole individuals and populations using live trapping (CMR-method, capturemark-recapture, Myllymäki 1977). We placed one Ugglan special trap (Grahnab, Hillerstorp, Sweden) within every 100 m<sup>2</sup>, with the outermost traps laid 15 m outside the edge of the grid

**Fig. 1.** The design of the field experiment. The drainpipe grids were located on meadows (broken lines). The upper grid was the control area and the lower grid was the experimental area. Solid lines are the drainpipe grids. Dots are trap stations and stars are pails where the weasel obtained food. The weasel cage is shown by an arrow, and it was connected to the experimental grid. Dotted lines are roads and ditches. Dark rectangles are buildings.

(altogether 80 traps/area). Traps were located in the middle of each grid cell (Fig. 1). The size of each trapping area was 6300 m<sup>2</sup>. There were 9 live trapping periods between 26 April and 16 July, each of which lasted from 2 to 4 nights (Fig. 2). The trapping periods were 26–30 Apr., 5-8 May, 11-13 May, 19-21 May, 2-5 Jun., 9-11 Jun., 16-18 Jun., 30 Jun.-2 Jul. and 12-16 Jul., running up to 3595 trap nights. Traps were baited with oats, green grass was added on warm sunny days, and they were checked every 8 hours. Between the trapping sessions the traps were left open in their regular positions. We recorded the weight, sex, age, reproductive condition and trap location for each captured vole. Each Microtus and Clethrionomys vole was individually marked by toe clipping. Individuals of other species were released without marking.

Simultaneously with live trapping, we followed the movements and activity of mature female field voles by radio-tracking. We attached



radio-transmitters (TW-4, Biotrack, Dorset, UK) to mature females that weighed more than 23 g. We used receivers (Televilt RX-8910 He, Televilt international Ab, Lindesberg, Sweden and ATS, Advances Telemetry Systems Inc., Isanti, Mn, USA) with external antennae (Y-4FL 230-232 MHz, Televilt Int., Lindesberg, Sweden and AMA-2, A-M Luoma, Oulu, Finland). The transmitters' range varied in our study habitat from 20 to 100 m. We checked the location and activity of each vole with a radio-transmitter 2-4 times per day. Voles were observed at a distance of 5-20 m for a minimum of 15 min at each location. During every telemetry session we registered individual, time, action and location within 1 m<sup>2</sup>. We also recorded the prevailing weather conditions. All individuals included in the radio-tracking study (n = 10) were mature females, and some of them were pregnant from the beginning of the experiment (later on all were pregnant). The body weights of these voles varied from 23 to 49 g (mean 35.8 g, SD 9.1 g). Four of the tracked voles were overwintered individuals.

Home ranges of the radio-tracked voles were estimated by the harmonic mean (Dixon & Chapman 1980) and the core convex polygon methods (Mohr 1947, Mohr & Stumpf 1966). Both methods are non-parametric and are widely used in home range studies (Kenward 1987). The home ranges of mature male field voles were estimated based on live trapping data. The analysis includes individuals that were trapped four or more times in two different trapping periods and in at least three different traps (n = 11). We analysed the data by the 100% minimum convex polygon (MPC) and ellipse methods (Jennrich & Turner 1969), which are practical methods to analyse home range sizes when there are only a few observations per animal (Kenward & Hodder 1996).

Data were analysed using Systat<sup>®</sup> 7.0 for Windows. Home ranges of females were estimated with Ranges V program (Kenward & Hodder 1996).

## Results

## Activity of the weasel

The weasel was located by radio-tracking altogether 64 times and observed in every part of the grid during the study period. 35 times out of 64 the weasel was in the cage and 29 times in different parts of the grid. The recorded durations of the visits to the grid varied from 10 min to three hours.



During the study we did not see or catch any wild weasel in the study area. Least weasels are easily caught in Ugglan traps, especially when there is a vole inside (Hellstedt, pers. obs.). Based on lack of any direct observations and no signs of weasel predation in the study population, we conclude that there were no native weasels in the study area during this experiment.

### Space use and activity of voles

In the following sections, we will examine the influence of the presence of the weasel on the behaviour of voles, on the reproduction and maturation of young voles, and finally on the observed population growth rate. If any effects are present, we expected them to show up in this order.

Data on space use were collected by both radio-tracking and live trapping methods (Table 1).

Table 1. Statistics on live trapping results.

There was no difference in home range sizes of radio-tracked mature females between the experimental and control grids (Table 2). Likewise, the home ranges of mature male field voles were not significantly different between the experimental and control grids (Table 3). The average home range size was 3 to 4 times greater in the control grid, but this difference was largely caused by one individual.

The movement activity of females was estimated by the mean distance moved between two consecutive observations. This method is relatively crude but it does reflect the time that the vole spends outside its nest (Norrdahl & Korpimäki 1998). The mean movement distances were not significantly different between the control  $(5.04 \pm \text{SE } 0.56 \text{ m})$  and experimental areas  $(6.36 \pm 1.14 \text{ m})$  (mean/all obs. Mann-Whitney *U*-test, *P* = 0.28). There was no difference in the total activity of females between the experimental and control grids, (Table 4).

	Experimental grid	Control grid	$\chi^2$ statistic (df = 1)
Number of <i>Microtus</i> voles	57	72	
Males/females	35/22	37/35 <sup>1</sup>	1.29, <i>P</i> = 0.26
Mature males/females	20/16	16/24	0.47, <i>P</i> = 0.49
Immature males/females	15/6	21/9	
Gravid or lactating females	13	17	
% of all mature females	81%	71%	
Juveniles	47	62	0.02, <i>P</i> = 0.88
Mean no. of new juveniles/trapping period $\pm$ SD	7.8 ± 7.2	10.3 ± 8.1	
% of juveniles which were retrapped	36.0% (7/10)	34.4% (7/14)	
Mean number of captures/animal	4.1	3.9	
Voles that visited several traps, % of total	25 (12/13), 43.8% 39 (21/18) 68 4%	30 (13/17), 41.7%	0.00, <i>P</i> = 0.96
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<sup>1</sup> Maturity status of two females is missing.

<sup> $^{2}$ </sup> Resident vole = vole that visited traps two or more times during the same trapping period and in the same trapping area (Pusenius & Viitala 1993).

Table 2.	Mean	home	range	sizes	of fema	le fie	d voles	s in	the	experimenta	l and	control	grids	based	on	radio
tracking	and live	e trapp	oing da	ta.												

Grid	Home range (ha) $\pm$ SD	Mann-Whitney U-test
Experiment $(n = 3)$	$0.04 \pm 0.02$	<i>U</i> = 6.50, <i>P</i> = 0.35
Control $(n = 3)$	$0.02 \pm 0.01$	
Experiment $(n = 3)$	$0.02 \pm 0.02$	<i>U</i> = 2.50, <i>P</i> = 0.35
Control $(n = 3)$	$0.03 \pm 0.01$	
	Grid Experiment $(n = 3)$ Control $(n = 3)$ Experiment $(n = 3)$ Control $(n = 3)$	GridHome range $(ha) \pm SD$ Experiment $(n = 3)$ $0.04 \pm 0.02$ Control $(n = 3)$ $0.02 \pm 0.01$ Experiment $(n = 3)$ $0.02 \pm 0.02$ Control $(n = 3)$ $0.03 \pm 0.01$

# Reproduction and maturation of young voles

Breeding success was measured by counting the number of new young individuals per trapping period. There were no differences between the experimental and the control areas in this respect ( $\chi^2_3 = 1.62$ , P = 0.65). The numbers of juveniles occurred in proportion to the numbers of gravid or lactating females in the two grids. Similarly, there were no differences in sexual maturity neither in sex ratio between the experimental and the control areas (Table 1), nor in the weights of the different functional groups of voles (Fig. 2).

### Population growth rate

During the entire trapping period 129 field voles, 25 bank voles, 3 common/sibling voles (*M. arvalis* Pallas/*M. rossiaemeridionalis* Ognev) as well as a small number of water voles, common shrews and pygmy shrews were caught.

During the first three trapping periods all field voles were over-wintered mature individuals. In both trapping grids population density was 4.7 voles per hectare in the beginning of study. The initial population growth was somewhat higher in the control grid (Fig. 3A), but after some weeks, by the end of June, the two populations were equally large and overall there was no difference in population growth rate (Kolmogorov-Smirnov test for two samples, P = 0.97). Neither were there significant differences in the numbers of individuals in different functional groups (mature individuals P = 0.97) and immature individuals P = 0.97), in the numbers of mature females and males (Fig. 3B, P = 1.00 and P = 0.66), nor in the proportion of immature and mature voles (males,  $\chi^2_1 = 1.39$ , P = 0.24 and females  $\chi^2_1 = 0.00$ , P = 1.00) between the experimental and control grids.

## Discussion

The purpose of this study was to investigate whether the presence of a weasel within the home ranges of field voles has indirect effects on their behaviour, reproduction and population dynamics. The experimental design allowed the voles to live in their natural habitat during the entire experiment, while the weasel's presence was expected to become apparent due to diffusion of the predator's scent through the holes in the drainpipe, and through the noises of the weasel in the pipe. This design does not

 Table 3. Home range sizes of mature field vole males based on live trapping results.

Method	Grid (no. of individuals*)	Home range (ha) ± SD	Mann-Whitney U-test		
100% Minimum	Experiment $(n = 5)$	0.03 ± 0.01	<i>U</i> = 15		
convex polygon	Control $(n = 6)$	$0.09 \pm 0.12$	<i>P</i> = 0.93		
75% Ellipse analysis	Experiment $(n = 5)$	$0.06 \pm 0.03$	<i>U</i> = 9.00		
	Control $(n = 6)$	$0.23 \pm 0.35$	<i>P</i> = 0.27		

\* Number of individuals = voles for which a sufficient number of observations was accumulated to allow statistical analyses.

**Table 4.** Observations on the activity of female field voles. Active = individual moved outside the nest, Inactive = vole immobile. Active in the nest = vole moved inside the nest. Distribution of observations among the 3 classes in experiment and control areas were random ( $\chi^2_{\gamma}$  = 2.88, *P* = 0.24).

Grid	Observations	Active (%)	Inactive (%)	Active in the nest (%)
Experiment	148	53 (36)	71 (48)	24 (16)
Control	128	48 (38)	68 (53)	12 (9)



Fig. 3. Field vole population growth during the study period. -A: Different functional groups in the experimental and control areas. -B: Numbers of mature female and male voles in experimental and control areas.

correspond exactly to a freely-moving weasel roaming across voles' home ranges, but we consider that this design is far superior to most, if not all, alternative designs used in the previous laboratory studies. In any case, results from experiments with different designs should be used in the final assessment of the hypothesis that the indirect effects due to predation risk have significant influence on prey behaviour and demography.

Most of the previous studies that have found behavioural or physiological changes in voles in response to apparent risk of predation have been conducted in the laboratory. An inevitable problem with such studies is that laboratory conditions as such may have a substantial influence on the behaviour of voles. Laboratory stocks of voles have to survive in the new environment, hence they may be expected to go through artificial selection. Less than 50% of fieldborn voles breed in the laboratory (Hansson 1995). Laboratory conditions favour smaller voles (Hansson 1992), and food consumption differs between laboratory and fieldborn voles (Hansson 1999). Furthermore, voles may become more sensitive to stress in laboratory environments (Hansson 1995). Consequently, the indirect effects of mustelids on voles observed in the laboratory may be laboratory artefacts (Korpimäki & Krebs 1996, Mappes et al. 1998). An additional problem is that it is difficult to interpret the strength of the signal used in laboratory experiments with respect to natural populations.

Our results do not indicate that the presence of the weasel would have had any significant influence on voles under natural conditions and during a prolonged period of time. There were no significant differences in the weights of different functional groups, female movement activity nor in home range sizes between the control and experimental study grids. Home range sizes of mature males were somewhat smaller in the experimental than in the control area, but even this difference was not significant.

The vole populations did not exhibit any demographic differences between the experimental and control areas, but the vole numbers and population growth rates were similar in the two treatments (Fig. 3). There was a slight delay in the maturation of young voles in the experimental area as compared to the control area, but this difference and differences in the home range sizes of males cannot be confidently attributed to the experimental treatment, because the treatments were not replicated. In any case, the short time lag in the growth of the experimental population did not affect the final population size at the end of the experiment. There was no elevated emigration from the area where the weasel was present: 68% of voles in the treatment and 64% of voles in the control area were long-term residents.

The breeding suppression hypothesis (BSH;

Ylönen 1989, Koskela & Ylönen 1995, Mappes & Ylönen 1997) is based on presumed behavioural responses of voles to the presence of the predator, of which the primary response is delayed breeding by females. It has been suggested that there are differences in this respect between cyclic and non-cyclic bank and field vole populations (Ylönen et al. 1995). Norrdahl and Korpimäki (2000) have lately modified the BSH by suggesting that during the best breeding season predators have no indirect effects on vole reproduction but during spring and autumn voles may be better off by delaying breeding. On the other hand, Klemola et al. (1997) have observed that during the increase phase of the vole cycle, small mustelids may prefer to prey upon mature female voles, in which case preference and biased predation, rather than any breeding suppression caused by mustelids, might explain the higher proportions of males and nonbreeding females than mature females in trapping results during presumed intense risk of predation. Female bank voles exhibit delayed maturation in peak populations, but this is caused by intraspecific response to high population density (Prévot-Julliard et al. 1999) rather than by predation. Our results are consistent with these alternative explanations to the BSH.

The expected behavioural changes in voles in the presence of predators provide the rationale for using chemical repellents to prevent vole damage to tree saplings (Sullivan *et al.* 1990). There are several specific natural and synthetic odours that have been developed to avoid vole damage (e.g. Myllymäki 1987, Sullivan *et al.* 1988, Merkens *et al.* 1991). Based on the present results, we doubt whether odours of weasels could be effective repellents to decrease the damage by *Microtus* voles to tree saplings.

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