Influence of weasel (*Mustela nivalis* Linnaeus, 1766) odour on spatial behaviour of root voles (*Microtus oeconomus* Pallas, 1776)

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**Abstract:** Findings concerning the influence of the odour of the specialized predator *Mustela nivalis* Linnaeus, 1766, the weasel, on the behaviour of Arvicolidae (voles) suggested that there is an impact on voles' utilization of space. This question was addressed by studying the influence of weasels and their scent on the utilization of space by free-living root voles, *Microtus oeconomus* Pallas, 1776. Eleven captured voles (6 males and 5 females) were selected for telemetric monitoring over 10 days. After the first 5 days a weasel in a cage was exposed, along with samples of its odour in the form of urine and faeces, at the determined “centre of activity” within the home range of these voles. The sizes of home ranges were compared between experimental and control voles and the former were found to be smaller than the latter following introduction of the predator. However the centres of activity did not shift, and the probabilities of individuals being encountered at them before and after were the same. To try to account for these reactions, a series of laboratory experiments with the same vole species (*n* = 50) was carried out to study the influence of weasel odour on locomotory activity and on distances from, and numbers of contacts with, the source of the odour. Voles recognized the predator’s scent and responded with a level of locomotory activity that was lower, as well as by fewer contacts being made with the source, in the experimental group than in the control group. However, the distances kept from sources of predator odour were no greater than from control sources, and in fact, voles spent more time close to the source than at greater distances. The reaction of a root vole to the presence of a weasel in the home range is therefore not to escape from the range but to reduce the probability of an encounter with this predator by decreasing locomotory activity.

**Résumé :** Si l’odeur du prédateur spécialisé *Mustela nivalis*, Linnaeus, 1766, l’Hermine, influence le comportement des Arvicolidae (campagnols), il faut s’attendre à ce que cette odeur affecte aussi leur utilisation de l’espace. Nous avons donc étudié l’influence d’hermines et de leur odeur sur l’utilisation de l’espace chez des Campagnols nordiques (*Microtus oeconomus* Pallas, 1776) en nature. Onze campagnols capturés (6 mâles et 5 femelles) ont été choisis pour être suivis par télémétrie pendant plus de 10 jours. Après les 5 premiers jours, une hermine dans une cage a été déposée, de même que des échantillons de son odeur sous forme d’urine et de fèces, dans le « centre d’activité » au sein du domaine des campagnols. La taille des domaines vitaux a été comparée chez les campagnols expérimentaux et les campagnols témoins et les domaines des campagnols expérimentaux étaient plus petits après l’introduction du prédateur. Cependant, les centres d’activité sont restés les mêmes et les probabilités de rencontrer des campagnols à ces endroits sont restées les mêmes, avant et après l’introduction du prédateur. Pour tenter d’expliquer ces réactions, une série d’expériences de laboratoire sur la même espèce de campagnol (*n* = 50) a examiné l’influence de l’odeur d’hermine sur l’activité locomotrice et sur le nombre et la distance des contacts avec la source de l’odeur. Les campagnols se sont montrés capables de reconnaître l’odeur du prédateur et ils ont réagi en réduisant l’intensité de leur activité à un niveau inférieur à celui des témoins, et en réduisant le nombre de leurs contacts avec la source de l’odeur. Cependant, les distances maintenues avec l’odeur du prédateur n’étaient pas plus grandes que les distances maintenues avec une source témoïn et les campagnols ont en fait passé plus de temps près de la source qu’à des distances plus éloignées. La réaction du Campagnol norique à la présence d’une hermine dans son domaine n’est donc pas une réaction de fuite de son domaine, mais une réaction propre à réduire la probabilité d’une rencontre avec le prédateur par diminution de son activité locomotrice.

[Intaduit par la Rédaction]

**Introduction**

The risk of predation is a very important element of the environment that impacts upon the behaviour, reproduction, and distribution of animals. In the case of small rodents, it is also an important factor shaping both the dynamics of populations (Goszczyński 1977; Erlinge et al. 1983; Korpimäki et al. 1991) and the behaviour of individuals (Jędrzejewska and Jędrzejewska 1990).

Rodents of the family Arvicolidae (voles) are a basic component of the diet of various predators, including some small mustelids that specialize in predation on this group (Erlinge 1974; Pearson 1985). Voles are able to distinguish between the odours of different predatory mammals and...
to react appropriately to their different hunting tactics (Jędrzejewski et al. 1993). Results obtained under laboratory conditions show that microtine rodents assess weasel odour as a real threat (Heikkilä et al. 1993; Ylönen et al. 1992).

Similar results have been obtained in studies of the bank vole (Clethrionomys glareolus) in semi-natural conditions. This rodent was found to react to the presence of a real predator (the weasel, Mustela nivalis Linnaeus, 1766) or to its odour, avoiding places where they would be exposed to either one or the other (Jędrzejewski and Jędrzejewska 1990).

The majority of data on voles’ reactions to mustelid predators or their odours were obtained in controlled conditions, so it was possible that in the natural environment, with its many predators, such reactions might not occur at all, or only in a modified form. For example, the latest findings of Parson and Bondrup-Nielsen (1996) are that gray-tailed voles (Microtus canicaudus) avoid the odour of a stoat (Mustela erminea) in the laboratory but not in the field. Similarly, in their research involving exposure of meadow voles (Microtus pennsylvanicus) to the odour (faeces and urine) of an American mink (Mustela vison) in field conditions, Wolff and Davis-Born (1997) were unable to confirm an avoidance reaction of the voles in an environment with a higher risk of predation by mustelids (tail grass).

The recognition that there have been few studies of antipredator reactions among rodents in the natural environment, combined with the wide variety of results obtained in laboratory and field experimentation, convinced the authors that the impact of weasel odour on the use of space by root voles (Microtus oeconomus) should be studied. This species was chosen because it is dominant within the grouping of small mammal species present in the open sedgelands of Poland’s Biebrza National Park (Raczynski et al. 1984), as well being the basic component of the diet of weasels occurring there. The root vole is a hygrophilous species inhabiting river valleys, the banks and shores of watercourses and lakes, and peatlands. Within its range it shows considerable plasticity in its use of space. In Poland, it shows a system of space utilization in which females are territorial and males use overlapping home ranges (Gliwicz 1997). A further reason for selecting this particular species was the lack of previous research into its reaction to predation by mustelids.

The aim of the experiments presented here was thus to answer three questions: (1) Do root voles escape from places where they are exposed to weasel odour in natural conditions? (2) Does weasel odour influence root voles to change their home ranges or “centres of activity” in the natural environment, with its multitude of predators (including raptors, snakes, and other terrestrial predators)? (3) Do root voles react to weasel odour in both the laboratory and the field?

**Study area, materials, and methods**

**Field experiments**

Field experiments were conducted in September 1995 in a study area within Biebrzański National Park in northeast Poland. The vegetation consisted of the Caricetum appropinquae association, dominated by Carex paradoxa with a few grey willows, Salix cinerea, and thus represented the typical early successional stage of the Salicetum pentandro-cinereae community (Matuszkiewicz 1981). This is a typical habitat for root voles (Raczynski et al. 1984). The sedgeland was flooded from April to June, while water levels in summer and autumn depended on the amount of rainfall. The density of root voles in the studied area in September 1996 was estimated at 270/ha (Z. Borowski, unpublished data).

A grid of 5-m squares was laid out to allow determined telemetric positions to be checked. Intersections were marked with numbered tapes and positions were found to be accurate to 2.5 m. Eleven of the voles captured (6 males and 5 females) were fitted with telemetric transmitters and followed subsequently, 6 on the experimental plot and 5 on the control plot. All were adult (weighing over 30 g), sexually active, born in the same year, and had been captured at least 3 times previously on the plots. Weighing between 2 and 3 g, the AWI Instrument Co. (U.S.A.) transmitters represented no more than 8% of the mass of individuals located (Berteaux et al. 1994). A few hours after the transmitters were affixed, the animals were released at the place of capture.

So that the area of capture would not influence spatial behaviour, voles were located 48 h after the capture areas were closed (Babińska-Werka 1990). Positions were determined during two periods: the first 5 days, when there was no exposure to the predator or its odour, and the subsequent 5 days, when each vole tracked on the experimental plot was exposed to two male weasels placed at the centre of activity within its home range in plastic/metal cages in such a way that there was contact with the substratum and the possibility of scent being left on it. Exposure to the predator occurred for 30 min in the morning and evening each day. To enhance the scent signal, cotton wool saturated with weasel scent was placed daily near the cages (having been taken from the nests of weasels kept outside the experimental area in wooden cages).

The centre of activity within a vole’s home range was taken to be the point around which the most fixes were concentrated. The location of each individual was determined ca. 10 times a day, concentrating on two periods, from 6 a.m. to 10 a.m. and from 6 p.m. to 10 p.m., in line with peak activity of the species (Gliwicz 1997), with occasional monitoring at other times of the day. The location points for each vole were ultimately noted 50 times before the start of the period of exposure to the predator and 50 times after. The combined data for the experimental group (six voles) involved 300 pre-exposure locations over the first 5 days and 300 during the subsequent 5 days of exposure. In the control group (five voles), the corresponding figures for these periods, with no exposure, were 250 and 250.

Home-range sizes were estimated using Kernel’s method (Worton 1989) and version 1.1 of the TRACKER program.

**Laboratory experiments**

The series of laboratory experiments was run in December 1995 and March 1996 to test the direct impact of weasel odour on root vole locomotory activity, and on distances kept from, and the number of contacts with, the source of the odour. The 50 voles (29 females and 21 males) involved, which were not sexually active, were born in 1995 and had been captured in Biebrzański National Park in February and November 1996. Up to the time of the experiments, they had been kept in cages in groups of three (two males and one females) and given rabbit pellets and water ad libitum, as well as carrot and apple. The conditions under which the animals were kept did not differ from those during the experiments, with a temperature of 16°C and natural lighting.

Trials were done in 70 × 30 × 50 cm glass terraria, with the floors covered in cardboard prior to each experiment so that the necessary details could be drawn on it (see below). To measure locomotory activity, the cardboard was marked into 24 rectangles. Distances from each wall were marked, to allow the distance of voles from the source of the odour to be estimated. Each vole was tested only once and the terraria were washed with water and detergent between trials. Each test involved the introduction of only one vole to the terrarium. In the terrarium voles were provided with water and granular food ad libitum. Each vole was acclima-
significantly greater than those of the experimental, predator-differ significantly (Mann–Whitney two-sample test, and 1314.6 ± 575.3 m², the respective mean sizes did not
i.e., prior to exposure of the latter to weasels. At 1025.1 ± 312.8
for control and experimental individuals during the first 5 days,
first comparison involved the home-range sizes determined
natural environment was influenced by predator odour. The
Field experiment
Cavia porcellus
pig,
the same position. The variants referred to were as follows:
variants of the experiment, involving the same vole, was placed in
location of the vole at that time. The foam used in two subsequent
test was placed in the middle, 14 cm from the side wall, near the
originated from a single weasel. The piece of control foam in each
odour, which was left on polyurethane foam over a 2-h period of
locomotory activity (Gebczynska 1970). Five weasels caught in au-
turn and kept in laboratory conditions provided the predator
odour, was left on polyurethane foam over a 2-h period of
confinement in a 1.5-L glass container. The odour used in each test
arose from a single weasel. The piece of control foam in each
test was placed in the middle, 14 cm from the side wall, near the
location of the vole at that time. The foam used in two subsequent
variants of the experiment, involving the same vole, was placed in
the same position. The variants referred to as follows: (i) clean foam (control), (ii) foam bearing the scent of a guinea-
Cavia porcellus (nonpredator), and (iii) foam bearing the scent of a weasel (predator). The three variants followed one another
directly, in the order given. Each was divided into six consecutive
5-min periods, during which note was made of the following:

- the number of times a line was crossed; the
time (min) spent at distances of up to 14, 14–40, and over 40 cm
from the source of the scent; and the number of times contact was
made with the foam. The total observation time for each vole was
thus 90 min, and for all 50 individuals was 4500 min (75 h).

Results

Field experiment
The aim was to check if the voles’ use of space in their
natural environment was influenced by predator odour. The
first comparison involved the home-range sizes determined
for control and experimental individuals during the first 5 days,
i.e., prior to exposure of the latter to weasels. At 1025.1 ± 312.8
and 1314.6 ± 575.3 m², the respective mean sizes did not
differ significantly (Mann–Whitney two-sample test, U = 11,
 p = 0.5368; Table 1). Home-range sizes during the second
5-day period were then compared, and those of the control
group (mean 1183 ± 204.2 m², n = 5) were found to be
significantly greater than those of the experimental, predator-
exposed, group (mean 709.4 ± 260.2 m², n = 6) (Mann–
Whitney two-sample test, U = 2.0, p = 0.0173; Table 1).
Further comparisons were made of home-range sizes within
the control and experimental groups, before and after exposure
of the latter to predators. In the experimental group, the
mean size declined from 1314.6 to 709.4 m² following the
onset of exposure (Wilcoxon’s signed rank test, W = 21, p =
0.0313), while in the control group there was no significant
difference in home-range sizes in the 5 days before and
after this time (Wilcoxon’s signed rank test, W = –13, p =
0.125).
To test the effect of the presence of predators at the centre
of activity within a vole’s home range, the probability of
each individual being recorded in this part of its range be-
before and after the introduction of weasels was calculated.
Reference was made to the proportion of located positions
confirming an individual’s presence at the aforementioned
centre. Introduction of the predator did not reduce the proba-
ability of voles being encountered at their centre of activity,
the values before and after exposure being 0.48 ± 0.12 and
0.49 ± 0.2 (Wilcoxon’s range test, p > 0.05).

Laboratory experiment
The influence of predator odour on locomotory activity
was tested under laboratory conditions, by reference to the
mean number of times per 5 min that drawn lines were
crossed by voles in the course of the aforementioned “control,” “guinea-pig,” and “weasel” variants of the experiment.
The mean activity of the 50 voles during exposure to clean
foam was 9.2 ± 11.02 crossings, while the values with the
guinea-pig and weasel odours were 7.5 ± 6.98 and 2.2 ±
1.98 respectively. Subsequently, the mean activities of voles
exposed to different odours were compared. Locomotory
activity during the “guinea-pig” variant was not significantly
different from that with the control (ANOVA, F = 11.49,
p = 0.2672), but voles exposed to predator odour were significantly less active than during either of the above variants (ANOVA, F = 11.49, p < 0.0001 and p = 0.0008, respectively; Fig. 1).

The mean lengths of time spent by voles at distances up to 14 cm from the source of odour (during 5 min of observation) were 3.35 ± 1.9 min for the control and 3.97 ± 1.54 and 3.38 ± 1.83 min in the presence of guinea-pig and weasel odour, respectively. The mean periods spent 14–40 cm from the piece of foam were 0.46 ± 0.96, 0.3 ± 0.75, and 0.42 ± 1.1 min for the control, guinea-pig, and weasel variant, respectively, while the corresponding values for time spent more than 40 cm away were 0.67 ± 1.09, 0.59 ± 0.13, and 0.66 ± 1.5 min. The three variants did not differ significantly in the time spent by voles at the three different distances (ANOV A, F = 39.49, p > 0.05; Fig. 2), but the amount of time spent up to 14 cm from the foam in all three variants was significantly greater than that spent at other distances (ANOV A, F = 39.49, p < 0.0001). The amounts of

time voles spent 14–40 or more than 40 cm away did not differ significantly (ANOVA, F = 39.49, p > 0.05).

The measure of the frequency with which voles made contact with the foam was the mean number of sniffings per 5 min calculated for each of the 50 individuals in each of the three variants. The numbers of contacts with the clean, control foam (X = 0.84 ± 1.05) and guinea-pig-scented foam (X = 0.55 ± 0.54) did not differ significantly (paired t test, t = 2.00, p = 0.086), but, with a mean value of 0.32 ± 0.31, the weasel-scented foam was sniffed significantly less often than either (paired t tests, t = 2.88, p = 0.0069, and t = 2.21, p = 0.0363, respectively; Fig. 1).

**Discussion**

The results do not support those from previous work which suggest that voles will abandon an area with a known predator (Jędrzejewski and Jędrzejewska 1990). Instead, animals exposed to olfactory cues from a predator reduced their home ranges significantly. This probably reflected a decline in locomotory activity, and hence a lack of visits to more distant parts of the range.

Exposure to both the predator itself and its odour at the centre of activity did not cause this centre to be shifted to a “safer” location, as would have been implied by any retreat from the source. This lack of escape from places bearing weasel odour was confirmed in laboratory experiments. The only reaction observed besides reduced locomotory activity was a reduction in the number of contacts made by voles with the source of the odour.
The root voles’ lack of an escape from a place where a weasel had been present, which is similar to observations of another species, the bank vole, in semi-natural conditions, may above all reflect differences in the environments inhabited. The bank vole is a typical forest species, while the root vole inhabits open grassland areas and may thus be characterized by different antipredator strategies. For example, while exposed to weasel odour, the bank vole increases its ground mobility (Jędrzejewska and Jędrzejewski 1990; Ronkainen and Ylönen 1994) and climbs up herb vegetation (Erlinge et al. 1974; Jędrzejewski et al. 1993). In contrast, microtine voles (like the field vole, common vole, and root vole) react to the influence of stout or weasel odour in completely the opposite way, by reducing their activity (Gorman 1984; this paper). It would seem that the differences in antipredator behaviour shown by voles in the different groups result first and foremost from the higher risk of predation by birds that characterizes open grasslands as opposed to forest areas. In open areas, voles must avoid predation by both mammals and birds, but the risk posed by the latter is higher than that incurred by microtine voles from weasels (Korpinak et al. 1996). A good example has been provided by Cushing and Cawthorn (1996), who showed that females of two different rodent species, prairie voles (Microtus ochrogaster) and cotton rats (Sigmodon hispidus), did not increase their activity during the oestrus period in the way that the females of many other small mammal species (like rats, hamsters, and deer mice) do. This phenomenon was accounted for by reference to convergence in the same open environment, where the risk of predation by birds is high. Research done by Metzgar (1967), Cushing (1985), and Gerkema and Verhulst (1990) suggests that rodents reduce their locomotory activity in response to a high risk of predation by both weasels and raptors. It would thus seem that in open grassland, the basic mechanism of defence against predation by weasels is a reduction in locomotory activity, resulting in a lower probability of encountering this predator. Such a predator-avoidance mechanism is also known from many other groups of animals, including zooplankton and dragonfly larvae facing the risk of predation by fish (for a review see Lima and Dill 1990).

The decision by root voles to remain within their home range when the risk of predation is high is also justified from other points of view presented below. The territory-holding by females that occurs in this vole species, amongst others (Gliwicz 1997), ensures that they can provide food for their young (Ostfeld 1990) while guarding them from the aggressive behaviour of other females, and a suitable nest site (Wolff 1993). In the case of males, the size of the home range reflects their position in the social hierarchy, with dominants occupying as much as 2600 m² (Borowski 1993), thereby guaranteeing them access to a relatively large number of females. A male abandoning his home range not only faces the uncertain fate of the migrant, but also most likely a different social status. In addition, both males and females expose themselves to predation by both birds and mammals if they are unfamiliar with an area and must move constantly (Metzgar 1967; Ambrose 1972; Smirin 1975, cited in Jędrzejewska 1989).

It would thus seem that voles inhabiting an open grassland area in a multipredator environment must balance minimization of the risk of predation by terrestrial predators (e.g., weasels) versus avian predators (e.g., owls and kestrels). That is, the antipredator reactions of voles to one of these groups should not significantly increase the risk of predation by the other.

Future research should focus both on comparing the antipredator reactions of voles living in an open grassland area (Microtus sp.) and in a forest area (Clethrionomys sp.), and on comparing the impact of weasel odour on the behaviour of microtines of different age groups throughout the season (above all in spring). For young voles in the dispersal phase, the detection of weasel odour may bring forward their departure from the maternal home range. Equally, voles may react differently to the presence of a weasel in early spring, when predation pressure is intense and densities of voles are low enough to allow for movement across a wider area, and hence perhaps for a more complex antipredator response.

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