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Behavioural response of field voles under mustelid predation risk in the laboratory: more than neophobia

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In the present study, we focus on the time budgets around feeding behaviour, by observing the behaviour of 24 field voles *Microtus agrestis* (Linnaeus, 1761) in the laboratory, exposed to no odour, faeces from a least weasel *Mustela nivalis* Linnaeus, 1766 and a domestic rabbit *Oryctolagus cuniculus* (Linnaeus, 1758). The voles did show a comprehensive response when exposed to weasel odour, while exposure to rabbit odour caused only a single minor effect. The difference in response to the two odours rules out neophobia as the underlying cause of the behavioural changes. Voles exposed to weasel odour were more inactive, ate less of a high preference food that was placed far from the nest-box, displayed a smaller variation of behaviour types and their activities were overall more interrupted. Our study confirmed that the mere risk of predation affects voles' feeding behaviour. This may explain indirect effects of predation risk on other processes like reproduction.

1. Introduction

There are few things in a lifetime where a proper reaction must not fail, one of them is meeting with a predator. Risks associated with predation will significantly influence animal behaviour, such as the decision between where, when and what to eat compared with the probability of being preyed upon (Lima & Dill 1990).

Field voles *Microtus agrestis* are heavily built, short-legged rodents, which may have few chances of evading predators once detected. Therefore,

their antipredatory strategies must rely on avoiding contact with predators. Mammalian predators often mark their territories with faeces, urine and secretions from their skin-glands (Gorman 1984). A by-effect of such scent marks is that they warn the prey animals (Calder & Gorman 1991). In response to this, prey animals can change behaviour and/or distribution.

Several experiments showed that voles have a behavioural response to odours from different carnivores: *Microtus agrestis* reduce their activity when exposed to stoat (*Mustela erminea*; Linnaeus, 1758) scent or avoid the area of scent marks (Gorman 1984); Orkney voles *Microtus arvalis* (Pallas, 1778) show avoidance to red fox *Vulpes vulpes* (Linnaeus, 1758) faecal odours both in the laboratory and in the wild (Calder & Gorman 1991). As compared with two other species *Apodemus sylvaticus* (Linnaeus, 1758) and *Clethrionomys glareolus* (Schreber, 1780), the field vole *Microtus agrestis* showed the least avoidance to traps with fox faeces (Dickman & Doncaster 1984).

Batzli and Lesieutre (1991) suggested that the availability of high quality food may be a major factor affecting patterns of distribution for microtine rodents. Desy *et al*. (1990) found that the home-range size was not affected by food availability, although exposure to predation did reduce the home-range size in prairie voles *Microtus ochrogaster* (Wagner, 1842). The choice between feeding on high or low preference food combined with the need to minimise the predation risk is a razor-sharp balance.

In the present study, we investigate the specific behavioural response of field voles *Microtus agrestis* to a predator odour (weasel) and a neutral odour (rabbit) in comparison with controls (no odour). We investigated the voles' use of two food sources of different quality and risk (a high preference food far from the nest-box and a low preference food close to the nest-box) under exposure to the different odours to see if there were any difference in response to these. The response to the two odours in relation to the control response may either be the same, suggesting neophobia, or different, suggesting a specific predator reaction.

2. Methods

For the experiments we used voles born in the laboratory from wild mothers trapped near Copenhagen, caged individually after weaning (at the age of three weeks). Once a week the cages were cleaned and the hay was replaced. The voles were fed on the standard laboratory pellets (Altromin nr. 1324, Chr. Petersen A/S, Ringsted, Denmark) and water *ad libitum*, and received fresh lettuce two or three times a week. The voles were between four and eight months old during the experiment (November 1997–March 1998), but in each replicate all voles had the same age. A total of 12 male and 12 female voles were used. Two female least weasels were caught in the same area as the voles.

At the start of the experiment (day zero), the voles were put in individual terraria (W × L × H: 30 × 60 × 40 cm) with a thin layer of sawdust and a nest-box (W × L × H: 8.5 × 14 × 7 cm) filled with hay. The terraria were kept in a photoregulated room L:D = 12:12, with a temperature of around 20 °C and relative humidity at 30%–65%. The terraria were divided into three zones (a, b and c, from right to left) with lines drawn on the front- and the rearglass (Fig. 1). The nest-box was situated in the hind-corner of zone "a" along with the water bottle and a cup with crushed wheat which were placed just outside the nest-box. Zone "b" was empty. In zone "c", there was a cup with small pieces of lettuce and, outside the observation periods, a cup with crushed altromin pellets. In a pilot study (unpublished data), lettuce was found to be highly attractive to the field voles while the crushed wheat was acceptable, but not preferred. Food was crushed or torn into small pieces to avoid hoarding. The cups were refilled daily.

On day five, after acclimation to the terraria, all food was removed and animals were not fed for 24 h to increase their feeding motivation on the next day (Table 1). The voles did not show any sign of discomfort from the lack of food. On day six, a cup with 30 g of crushed wheat was offered in zone "a" (near the nest-box) and a cup with 20 g of lettuce in zone "c" (far from the nest-box). In the central zone "b", an empty cup was

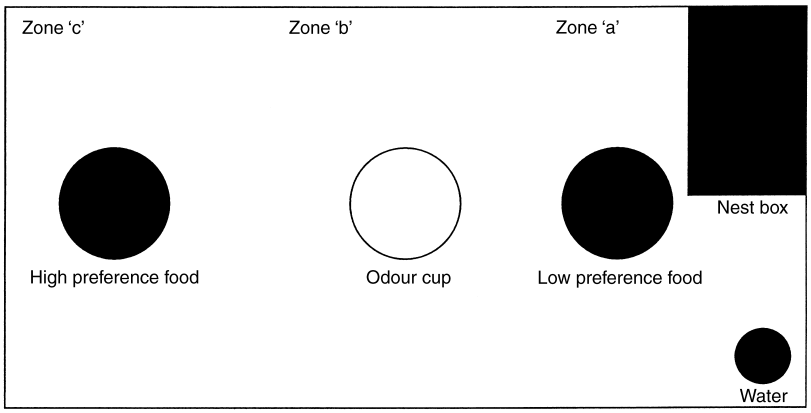

Fig. 1. Terrarium seen from the above during observation periods.

Table 1. Schematic representation of two simultaneous observation blocks with one day in between. In the control observations (a, b, c and A, B, C) the voles are exposed to an empty cup, serving as an odourless control. In the weasel and the rabbit observations the voles are respectively exposed to a cup with weasel and rabbit faeces.

Day	Test condition, group one	Test condition, group two
0	Vole placed into terraria (three replicates)	
1		Vole placed into terraria (three replicates)
2		
3		
4		
5	Food removed, 24 h starvation	
6	Food replaced + no odour; c1 obs.	Food removed, 24 h starvation
7	Food removed, 24 h starvation	Food replaced + no odour; c1 obs.
8	Food replaced + w/r odour; w/r obs.	Food removed, 24 h starvation
9	Food removed, 24 h starvation	Food replaced + r/w odour; r/w obs.
10	Food replaced + no odour; c2 obs.	Food removed, 24 h starvation
11	Food removed, 24 h starvation	Food replaced + no odour; c2 obs.
12	Food replaced + no odour; c3 obs. Terraria cleaned and then voles returned to their respective terraria	Food removed, 24 h starvation
13		Food replaced + no odour; c3 obs. Terraria cleaned and then voles returned to their respective terraria
14		
15		
16		
17	Food removed, 24 h starvation	
18	Food replaced + no odour; c4 obs.	Food removed, 24 h starvation
19	Food removed, 24 h starvation	Food replaced + no odour; c4 obs.
20	Food replaced + r/w odour; r/w obs.	Food removed, 24 h starvation
21	Food removed, 24 h starvation	Food replaced + w/r odour; w/r obs.
22	Food replaced + no odour; c5 obs.	Food removed, 24 h starvation
23	Food removed, 24 h starvation	Food replaced + no odour; c5 obs.
24	Food replaced + no odour; c6 obs. End of observation.	Food removed, 24 h starvation
25		Food replaced + no odour; c6 obs. End of observation.

placed, serving as an odourless control. Immediately after, the behavioural observation began and lasted for 60 minutes. Afterwards the food was weighed (the weight of the lettuce was corrected for evaporation, calculated from a control cup placed in the room) and returned to the terrarium, together with a cup of crushed Altromin pellets.

After 23 h (day seven) the food was removed again for 24 h. On day eight, a food cup with 30 g of wheat was again placed in zone "a", 20 g of lettuce in zone "c" and a cup in zone "b". However, this time the cup in zone "b" contained faeces either from an adult male rabbit (r) or alternatively from a wild caught adult female least weasel (w), fed on live voles and mice. After 60 minutes of observation, the food was weighed and returned together with a cup of crushed Altromin pellets and the odour cup with faeces was removed. On day ten and day 12, the observations were repeated with no odour. Both observations were again preceded by a starvation day as on day 6.

After day 12 the terraria were cleaned, the bedding was replaced and then the voles were returned to their respective terraria. The whole experiment, as described above, was then repeated, but those voles that were exposed to rabbit faeces in the first observation block, were now exposed to a cup with weasel faeces, and vice versa. After the second observation block, the experiment was concluded.

The experiment was carried out simultaneously with two groups of three voles, with one day between groups. Four series of six voles were run between November 1997 and March 1998.

Twelve of the voles (six males and six females) were exposed to the odours in the following order: [control 1, rabbit, control 2, control 3 — terraria cleaned — control 4, weasel, control 5, control 6], referred to as [rw]. The other twelve voles (again six males and six females) were offered odours in order: [control 1, weasel, control 2, control 3 — terraria cleaned — control 4, rabbit, control 5, control 6] referred to as [wr]. According to the 2 one-day staggered parallel observational sequences, there were as many voles which were offered rabbit odour first, as voles which were offered weasel odour first. The 24 voles were in the terrarium for 24 days and each were observed for eight hours during the whole experiment, which gives a total of 192 observation hours.

The observations were focal and included one class with 11 behavioural categories. Data were collected with a Psion Workabout and the program Observer (Noldus Information Technology, Wageningen, The Netherlands).

The 11 categories were named as follows: inactive, low preference foraging, high preference foraging, drink, move, escape, investigate, alert, grooming, eliminating, and other (Table 2). The category "inactive" was the default recording on the Workabout. The categories "drink", "escape", "alert", "grooming" and "eliminating" occurred very rarely (1.09% of total time) or were difficult to detect; therefore, they are not included in the following comparisons. For the other categories, we calculated the total amount of time spent by an animal on this activity during the observation period ("total duration"), the number of times the activity was observed ("frequencies") and the mean duration of each of these activity bouts ("mean time").

2.1. Data analysis

The complete data set was investigated in a repeated measurements MANOVA (STATISTICA). The analyses comprised all effects: block (the four observation rounds), sequence (whether the animal was first submitted to weasel and then to rabbit odour or the reverse), sex, order (control 1, odour, control 2 and control 3) and treatment (12 day period with weasel odour versus 12 day period with rabbit odour). The first analysis showed that there were no differences (MANOVA) between the two groups of "rabbit" treatments (control, rabbit, control, control) whether the voles were exposed to rabbit odour as the first treatment [rw] or as the second odour treatment [wr], the same was true for the "weasel" treatment (control, weasel, control, control). Therefore, the two groups of the "rabbit" treatments were pooled and the two groups of the "weasel" treatments were pooled and then named (control a, rabbit, control b and control c) and (control A, weasel, control B, control

C). One-way comparisons of total duration, frequency and mean time of occurrence for each of the behavioural elements during the different treatments were tested in a Friedman Repeated Measures (ANOVA).

3. Results

3.1. General patterns

Although the total amount of time spent eating was not equal between "blocks" (the periods in which each replicate was carried out), the "block" alone did not cause any significant differences as compared with the experimental set up.

The female voles spent more time eating than the male voles, but sex showed no interaction with the treatment effect. The "order" (whether an observation was made during one of the control treatments or odour treatment) had a clear effect, just like the interaction between the "order" and the "treatment" (weasel or rabbit odour; Fig. 2). Most activities decreased under weasel odour, while rabbit odour had very little effect. As mentioned above, it appears that the sequence has little effect.

3.2. Friedmann, sequences combined

The results for each behaviour are given in Table 3, summarised per observation session with all individuals pooled with regard to "sex", "sequence" and "block". "Total duration", "mean time" and "frequency" is shown for each observation phase.

There was a clear reaction on several behavioural measures of the voles when they were exposed to weasel odour. They were more "inactive", "moved" less around the terraria, spent less time on "high preference foraging" and foraged in shorter bouts. Even when they were "low preference foraging" just outside the nest-box, they foraged in significantly shorter bouts. They almost ceased all secondary behaviour (categorised as "other"). Looking at the "total duration" of "investigate", it occurs more often in the presence of

Table 2. Catalogue of recorded behavioural categories.

Name	Description
Inactive	The vole is inactive without sniffing or looking around. When the vole was in the nest-box without making any noise, the behaviour was also recorded as "inactive"
Low preference foraging	Time spent on eating from the cup with low preference food (crushed wheat in zone "a")
High preference foraging	Time spent on eating from the cup with high preference food (lettuce in zone "c")
Move	The individual is moving from one place to another, without sniffing or looking aroumd
Investigate	The individual is rearing, sniffing or looking around
Drink	The individual is drinking from the water bottle
Escape	The individual suddenly moves fast or jumps
Alert	The individual suddenly interrupts the ongoing behaviour and starts looking and/or sniffing around
Grooming	The individual is grooming
Eliminating	The individual is defecating or urinating
Other	A rest category with behavioural elements that cannot be placed in any other of the categories. These included digging, gnawing in the nest-box or collecting material for the nest-box. Often voles were very noisy doing these activities (about 90% of the time)

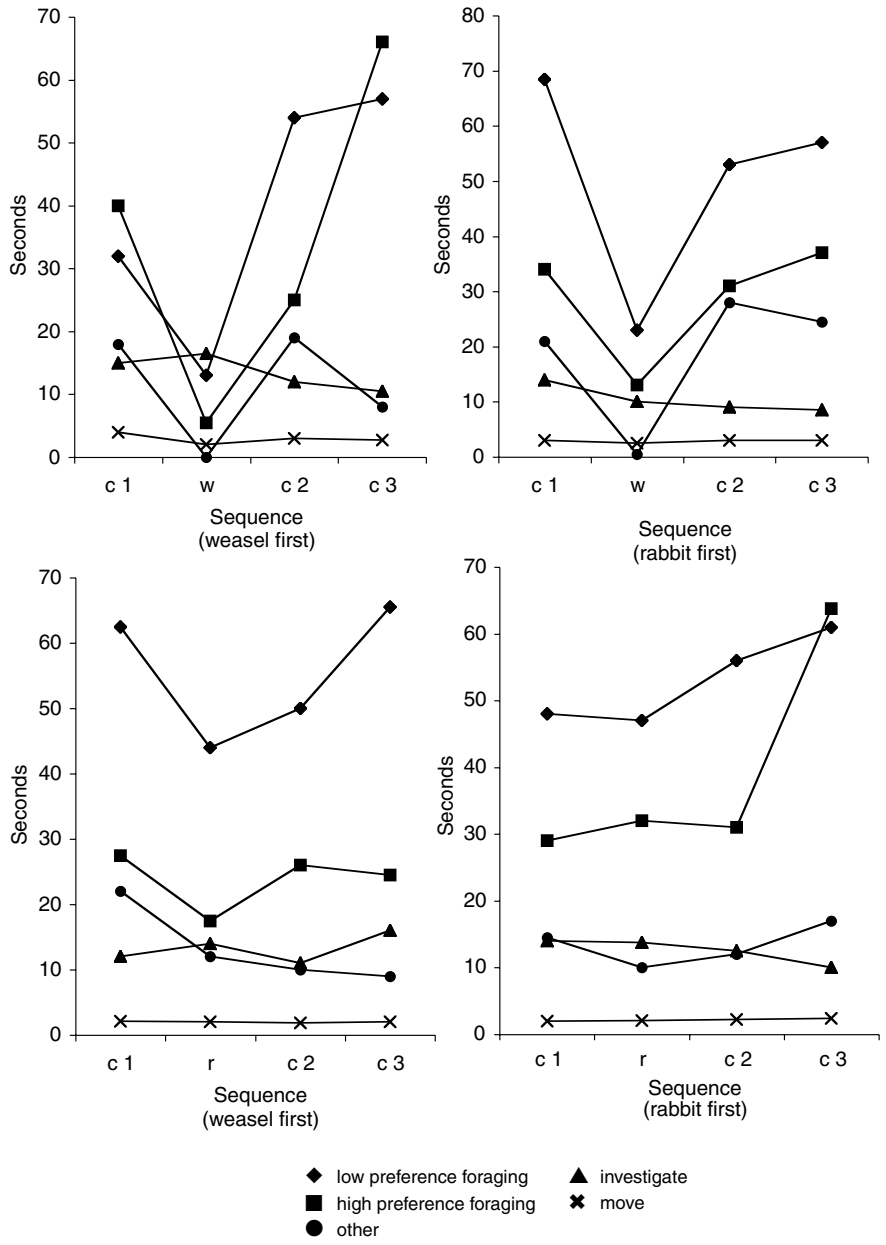

Fig. 2. Mean duration of activity bouts of five behavioural elements, specified in legends. Top: observation sequences with weasel odour. Bottom: observation sequences with rabbit odour.

weasel odour, although this difference was not significant at $p = 0.05$.

When exposed to rabbit odour the voles spent significantly more time on "investigate" in comparison with the controls, but there were no other clear differences.

These differences seen in the main behaviours are presented below in more detail.

3.2.1. Foraging

When exposed to weasel odour the "mean time" spent on each visit to the low preference food (crushed wheat, close to the nestbox) was significantly shorter ($p < 0.0001$) than the three controls (controls A, B and C). There was no difference in the number of times the voles were low prefer-

Table 3. Total duration of different behaviour types, average duration of the behaviour per instance and frequency with which the behaviour occurred during the different observation phases calculated on the average upon 24 animals. Differences between days were tested by Friedman Repeated Measures (ANOVA) on Ranks, when different at $p < 0.05$ Pairwise Multiple Comparison (Student-Newman-Keuls) was applied to find out which observations were different.

Observation phases	Total duration	Mean time	Frequency
Inactive			
Control a	2547.99	569.54	12.21
Rabbit	2336.89 $p = 0.27$	277.52 $p = 0.11$	13.08 $p = 0.24$
Control b	2414.58	445.72	11.83
Control c	2521.98	386.54	10.08
Control A	2438.51	370.42	13.42
Weasel	2781.91 $p = 0.003$	681.14 $p = 0.14$	12.17 $p = 0.05$
Control B	2335.33 w > A, B, C	238.33	14.58
Control C	2407.14	446.99	9.67
Low preference foraging			
Control a	382.32	47.67	8.13
Rabbit	373.15 $p = 0.08$	49.88 $p = 0.06$	8.58 $p < 0.05$
Control b	390.67	60.26	6.46
Control c	299.75	79.10	5.04 c < b, r, c
Control A	274.85	68.04	5.71
Weasel	241.02 $p = 0.06$	31.57 $p < 0.0001$	6.16 $p = 0.29$
Control B	373.38	70.22 w < A, B, C	7.92
Control C	319.14	69.30	5.92
High preference foraging			
Control a	136.99	23.72	3.75
Rabbit	211.73 $p = 0.06$	39.66 $p = 0.004$	6.16 $p = 0.35$
Control b	234.70	34.68	6.83
Control c	254.36	54.98 c > a, r, b	5.41
Control A	264.1	39.53	6.25
Weasel	78.55 $p < 0.0001$	12.92 $p < 0.0001$	5.37 $p = 0.15$
Control B	266.47 w < A, B, C	41.68 w < A, B, C	7.08
Control C	297.79	60.80 C > A, B	6.50
Move			
Control a	40.74	2.18	15.04
Rabbit	48.87 $p = 0.19$	2.45 $p = 0.19$	18.63 $p = 0.23$
Control b	39.83	2.26	15.63
Control c	48.67	2.67	17.63
Control A	50.91	3.11	17.33
Weasel	31.81 $p = 0.004$	1.92 $p = 0.007$	13.50 $p = 0.08$
Control B	56.21 w < A, B, C	2.66 w < A, B, C	21.17
Control C	49.37	2.64	17.42
Investigate			
Control a	349.77	13.61	26.13
Rabbit	482.85 $p = 0.002$	16.30 $p = 0.17$	34.08 $p = 0.02$
Control b	324.96 r > a, b, c	12.95	28.88 r > a, b, c
Control c	304.70	13.20	24.88
Control A	351.51	15.79	27.58
Weasel	431.15 $p = 0.16$	15.56 $p = 0.03$	29.33 $p = 0.37$
Control B	347.73	11.25	33.92
Control C	303.92	11.04	28.88
Other			
Control a	105.55	16.11	4.08
Rabbit	118.35 $p = 0.33$	11.04 $p = 0.96$	7.29 $p = 0.01$
Control b	154.40	12.86	7.21 r > a, b, c
Control c	119.98	14.01	5.75
Control A	192.17	17.61	7.50
Weasel	1.11 $p < 0.0001$	0.55 $p < 0.0001$	0.17 $p < 0.0001$
Control B	169.59 w < A, B, C	21.39 w < A, B, C	7.50 w < A, B, C
Control C	174.39	18.67	6.29

ence foraging. Despite the difference in "mean time" there was no difference in "total duration" spent on low preference foraging in the three odour treatments.

The voles spent significantly less ($p < 0.0001$) "total duration" on eating high preference food (lettuce, placed far from the nest-box) when exposed to weasel odour, while rabbit odour had no significant effect on "total duration". Also "mean time" spent on each visit was significantly shorter ($p < 0.0001$) when the voles were exposed to weasel odour as compared with the controls. Control c was significantly higher ($p < 0.004$) than the other observations in "mean time" spent on high preference foraging in the rabbit sequence. However, there was no differences in the frequencies.

The intake of low preference food showed no significant difference under exposure to either rabbit or weasel odour (Table 4). But when exposed to weasel odour the voles ate significantly less ($p < 0.0005$) of the high preference food than during the three controls (controls A, B and C). The voles ate less during the first control observation (control a) ($p = 0.003$) than when exposed to rabbit odour or the later controls (controls b and c).

3.2.2. Inactivity and other behaviours

When exposed to rabbit odour the voles showed no reaction in "total duration", "mean time" or "frequencies" of activity bouts when compared with the three controls. When exposed to weasel odour they were significantly more inactive in "total duration" ($p = 0.003$).

There was a significant decrease in moving around in both "total duration" ($p = 0.004$) and "mean time" ($p = 0.007$) when the voles were exposed to weasel odour.

The voles spent more time ($p = 0.002$) on "investigate" and did it more often ($p = 0.02$) when they were exposed to rabbit odour as compared with the three controls, but "mean time" remained the same. There was no such significant effect of weasel odour. The significant difference ($p = 0.03$) in "mean time" in the weasel sequence did not bring out any specifications.

When focusing on the total duration spent on "investigate" relative to the time the voles were actually active, significant results appeared (c^2-contingency table, $p < 0.0001$; all voles were pooled). In the weasel sequence the relative values were (52.53% ± 6.3%, mean ± S.E.) when weasel odour was present and during the three controls (respectively 36.33% ± 4.6%; 28.70% ± 2.6% and 24.21% ± 2.7%). In the rabbit sequence, the relative values were (39.64% ± 2.8%) when exposed to rabbit odour and (37.85% ± 5.5%; 30.43% ± 2.9% and 29.2% ± 2.8%) for the controls. "Other" behaviour occurred significantly less frequently and lasted shorter ($p < 0.0001$) when exposed to weasel odour. When exposed to rabbit odour there was a significant increase ($p = 0.01$) in the frequency as compared with the three controls (controls a, b and c).

Table 4. Intake of low and high preference food in grams during the different observation phases calculated on the average upon 24 animals. Differences between days were tested by Friedman Repeated Measures (ANOVA) on Ranks, when different at $p < 0.05$ Pairwise Multiple Comparison (Student-Newman-Keuls) was applied to find out which observations were different.

Observation phases	Low preference food intake (g)	High preference food intake (g)
Control a	0.41	1.30 a < r, b, c
Rabbit	0.45 $p = 0.71$	2.00 $p = 0.003$
Control b	0.40	2.01
Control c	0.38	2.4
Control A	0.38	2.82
Weasel	0.32 $p = 0.40$	0.99 $p < 0.0005$
Control B	0.46	2.33 w < A, B, C
Control C	0.42	2.68

4. Discussion

Our results indicate that laboratory born field voles with no earlier experience with predators do change their behaviour under a simulated risk of predation from a least weasel. When exposed to faeces from a weasel, the voles were more inactive, and, while they were active, they moved around less, ate less, spent a longer part of their active period on investigating the surroundings, and their behaviour was more frequently interrupted than when the voles were exposed to no odour or rabbit odour. When exposed to rabbit odour, the amount of "investigating" was different from the control situation, indicating that the voles did detect the rabbit odour and that the rabbit odour for that reason was a relevant control stimulus. No other behavioural measures were influenced by the rabbit odour. Sex, age, treatment block, treatment sequence, and order in which controls and odours were presented did not have any severe effects on the behavioural response of the voles compared with the experimental set up.

For approximately the last decade the hypothesis of breeding suppression by predation pressure has been developed (Ylönen 1989, Ylönen *et al*. 1992, Korpimäki *et al*. 1994, Ronkainen and Ylönen 1994, Ylönen and Ronkainen 1994, Ylönen *et al*. 1995 and Koskela *et al*. 1996). Mappes *et al*. (1998) questioned the validity of this hypothesis which was based on their field experiment. Moreover, these authors claimed that alleged breeding suppression in the earlier laboratory experiments is a methodological effect due to neophobia and lack of controls. However, our results show that there is a significant response from the voles when exposed to weasel odour, a response which is absent under exposure to rabbit odour. Thus, in our experiments, neophobia can be ruled out. Also rabbit scent did not change bank voles' distribution in a terrarium (Jedrzejewski *et al*. 1993). It is, however, interesting to observe that our voles "investigate" longer and more frequently when exposed to rabbit odour as compared with the controls. This suggests a curiosity to investigate a novel odour. With a predator odour, that curiosity may be overruled by increased fear and immediate appropriate behavioural changes.

Wolf and Davis-Born (1997) found that gray-tailed voles *Microtus canicaudus* Miller, 1897 do not respond to the odour of mink *Mustela vison* (Schreber, 1777) as compared with the voles exposed to rabbit *Oryctolagus cuniculus* odour or no odour. The predator odour that they used, however, came from farmed mink, which are commonly fed fish-based food. Nolte *et al*. (1994) found that the aversiveness of coyote *Canis latrans* Say, 1823 urine to herbivorous rodents varies with the change in the predator's diet. In our experiment, the weasels, whose faeces were used as predator odour, were fed voles and mice, so that any diet-related odour components in the faeces were relevant for our set-up with voles.

Earlier laboratory experiments by Batzli and Lesieutre (1991) showed that the availability of high quality food may play a major fole in the distribution of arctic microtine rodents. In our experiment, as soon as the voles were exposed to the weasel odour, they ate significantly less high preference food from the remote, more risky, food source. Moreover, although the voles were not eating less of the low preference food in total, they spent significantly less time on each visit to the cup with the low preference food. Cassini (1991) found that guinea pigs *Cavia aperea* Erxleben, 1777 try to reduce the predation risk by increasing scanning rates and by foraging first in near zones and returning to cover in a hurry. Holmes (1984 & 1990) showed that the feeding behaviour of Alaskan hoary marmots; *Marmota caligata* (Eschscholtz, 1829) and collared pikas *Ochotona collaris* (Nelson, 1893) was influenced by both the availability of forage and the risk of predation. Otter (1994) found that eastern chipmunks, *Tamias striatus* (Linnaeus, 1758) modified their foraging behaviour on the basis of the relative exposure of the patch. Barreto and MacDonald (1999) found that water voles (*Arvicola terrestris*) entered cages treated with mink odour significantly fewer times than they entered control cages (no odour). These earlier results, supported by ours, show that predation risk may be an important factor in foraging decisions.

In our study, the risk of predation leads to reduced food intake (both in quality and quantity) and more interruptions in activity, which would lead to a poorer condition of the voles. Carlsen *et*

al. (1999) showed that field voles exposed to predator faeces in a laboratory experiment lost more weight as compared to the control voles, despite equal intake of food in both groups of voles. Hik (1995) suggested that snowshoe hares *Lepus americanus* Erxleben, 1777 favour survival over condition, avoiding predators before eating. Our experiment indicates that voles exposed to predators odours strongly suppress activities which are not immediately vital (the "other" categories). Voles which are forced to suppress collecting nest-material, or other noisy hygienic activities which could draw predators' attention, may end up with poorer nests. This and the reduced food intake will lead to a poorer body condition, which can be the cause of a breeding suppression. Therefore, breeding suppression under predator pressure can, to a large extent, be explained by the indirect effect of a poorer physical state that the female voles are in, rather than a deliberate strategy. After all, such a strategy would seem extremely risky for short-lived rodents which cannot readily expect that the risk of predation will seriously decrease later in their life.

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