

## Mammalian predator scent, vegetation cover and tree seedling predation by meadow voles

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Herbivores are thought to respond to the increased risk of attack by predators during foraging activities by concentrating feeding in safe habitats and by reducing feeding in the presence of predators. We tested these hypotheses by comparing tree seedling predation by meadow voles within large outdoor enclosures treated either with scent of large mammalian predators (red fox, bobcat, coyote) or a control scent (vinegar). In addition, we compared the distribution of voles in relation to naturally occurring variation in vegetation cover and the tendency of voles to attack tree seedlings planted in small patches with cover manipulation (intact, reduced or removed cover). Predator scent did not affect the rate or spatial distribution of tree seedling predation by voles, nor did it affect giving up densities (a surrogate of patch quitting harvest rate), survival rates, body size or habitat distribution of voles. In both predator scent and vinegar treatments voles preferred abundant vegetation providing good cover, which was also the site of almost all tree seedling predation. We conclude that large mammalian predator scent does not influence the perception by voles of the general safety of habitat, which is more strongly affected by the presence of cover.

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Herbivores are capable of affecting the distribution and abundance of plants, at least during herbivore population outbreaks. Voles of genus *Microtus* are herbivorous small rodents famous for their population fluctuations. During high density years voles have a potential to affect the abundance of the herbaceous plant species that they consume (e.g. Krebs et al. 1973, Ostfeld 1994), but they may also affect the establishment of woody plants in successional habitats by depre-dating tree seedlings (Gill 1992, Ostfeld and Canham 1993, Bergeron 1996, Ostfeld et al. 1997, Pusenius et al. 2000).

In the long term voles are not likely to prevent reforestation in any community as population densities high enough to curtail establishment of tree seedlings do not usually persist more than one year (Manson et al. 2001). Predation seems to be an important factor affecting vole densities (e.g. Erlinge et al. 1983, Hanski

et al. 1993, Klemola et al. 1997, Korpimäki and Norrdahl 1998). In addition to direct mortality of voles, presence of predators seems to affect various aspects of vole behavior including the rate of resource use (e.g. Koskela and Ylönen 1995, Pusenius and Ostfeld 2000, Bolbroe et al. 2000). Prey animals like voles should respond to both direct cues indicating presence of predators in the immediate vicinity (e.g. sight, scents, vocalizations), and indirect cues or environmental features indicating the probability of being detected by an unnoticed predator (e.g. cover, illumination) (Thorson et al. 1998). The preference for high cover is most likely an adaptation for reducing predation risk imposed by birds of prey (e.g. Kotler and Blaustein 1995, Korpimäki et al. 1996, Koivunen et al. 1998). Several studies show that voles kill more seedlings within patches with protective vegetation cover when compared with patches having sparse cover (Gill and Marks 1991,

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Ostfeld and Canham 1993, Pusenius and Ostfeld 2000, Pusenius et al. 2000). However, direct cues indicating presence of predators that hunt efficiently within high vegetation (e.g. mammalian predators or snakes) may interact with habitat selection based on indirect cues (Merkens et al. 1991, Kotler et al. 1993, Bouskila 1995, Korpimäki et al. 1996, Herman and Valone 2000, Pusenius and Ostfeld 2000).

The objective of our study was to examine the effects of direct cues indicating presence of mammalian predators on the amount and spatial distribution of tree seedling predation by meadow voles. Our general approach was to manipulate predation risk to voles inside large outdoor enclosures and compare both the distribution of voles and the tendency of voles to attack tree seedlings. We applied scents from three common, local mammalian carnivores (coyote *Canis latrans*, bobcat *Felis rufus*, and red fox *Vulpes vulpes*) known to have a major impact on vole populations (Lin and Batzli 1995), and manipulated vegetative cover known to affect vole vulnerability to avian predators. To ensure that our design would measure differences due to perceived risk of predation and not neophobia due to the presence of unusual odors we applied a distinct but non-threatening odor, vinegar, in the control enclosures.

## Material and methods

### Study site

The study was carried out in six adjoining 40 × 40 m enclosures in an old field on the property of Institute of Ecosystem Studies in Millbrook, southeastern New York State. Fences of the enclosures were made of galvanized hardware cloth with mesh size of 1.0 cm and extending 1 m above and 0.5 m below ground. Vegetation in the enclosures was dominated by grasses (*Bromus inermis*, *Poa pratensis*, *Arrhenatherum elatius*, *Phleum pratense*) and forbs (*Galium mollugo*, *Solanum carolinense*, *Glechoma hederacea*, *Oxalis repens*, *Potentilla* spp., *Hieracium pratense*, and *Solidago* spp.).

### Vole populations

The meadow voles used in the experiment were animals naturally occurring in the enclosures. Each of the six enclosures had 25 Sherman traps arranged in a grid with 7.5 m intervals. The traps were baited with whole oats and supplied with cotton bedding. Captured voles were ear-tagged at first capture and subsequently checked for tag number, sex, body mass, and reproductive condition. We increased homogeneity of vole densities among the enclosures by intro-

ducing subadult voles from the enclosure with the highest population density to two enclosures with the lowest population density. This was done during a four night live-trapping period two weeks before the start of the experiment. During the experiment we conducted two live-trapping censuses: one and four weeks from the beginning of the experiment, 19 November 1997. Each census was conducted for three successive nights, during which traps were set just before sunset and checked in the morning. We computed Jolly-Seber estimates (Jolly 1965) for population densities and survival rates using software POPAN-5 (Arnason and Schwarz 1995). Data from a post experiment vole census in the end of January 1998 enabled us to compute these estimates.

### Tree seedlings

The tree species we used in the experiment was red maple *Acer rubrum*, which is common at successional sites throughout the eastern USA (Kricher and Morrison 1988). The seedlings were grown in a greenhouse from seeds purchased from Sheffield Seed Company, Locke, NY, and planted into field 19 November 1997, when they were, on average, 10 cm tall. Within each enclosure we randomly selected three, nonadjacent 7.5 × 7.5 m squares cornered by the trap stations of the trapping grid. We established three circular 1 m diameter plots in each square, with 1 m spacing between adjacent plots. We assigned a microhabitat treatment to each of the three adjacent plots: the middle plot was an unmanipulated control; one of the end plots was mowed; and the other end plot was mowed and provided with a cut grey dogwood *Cornus racemosa* shrub ca 0.5 m high for overhead cover. Grey dogwood is the dominant shrub in early successional old fields at IES (Glitzenstein et al. 1990). We call each set of three adjacent plots hereafter a seedling station.

We controlled for the patchiness of the old field vegetation by establishing each seedling station entirely within a patch-type covering most of the area in the given square. We classified the vegetation into three coarse classes according to overall cover. The first class was dominated by small annuals, which provided no cover after their death. The second class included small grasses that provided small patches of intermediate cover. The third class was dominated by large grasses, which offered substantial cover even during winter. The relative abundance of different cover types did not differ between predator scent treatment and control enclosures (Likelihood ratio  $\chi^2 = 4.08$ , DF = 2,  $p = 0.13$ ).

We planted nine red maple seedlings into each plot. Seedlings were planted in three rows of three

seedlings each, where the rows began at three different distances from the edge of the circle (5, 25, 45 cm). The distance between seedlings within a row was 10 cm. The experiment started when the tree seedlings were planted into the experimental enclosures (day 0). Thereafter the seedlings were censused on days 2, 5, 9, 14, 20 and 33. Seedlings that were missing, clipped at the base, or debarked by gnawing were classified as depredated by voles (see Ostfeld and Canham 1993). We wore latex gloves when planting seedlings and conducting censuses to prevent odor contamination.

### Giving-up densities

Tree seedlings are not a food item especially favored by meadow voles, and it is unclear whether they are consumed to obtain energy or for other non-nutritional reasons (Hansson 1990, Batzli and Henttonen 1999). Thus we added a measurement of patch quitting harvest rate that should reflect the decisions of a forager balancing its time between foraging under predation risk vs resting in a refuge. An optimal forager should depart from a resource patch when its harvest rate falls to the sum of predation (P), missed opportunity (MOC) and metabolic (C) foraging costs (Brown 1988, 1992). The rate of resource harvest at which this relationship holds and the forager ceases foraging is the patch quitting harvest rate.

We assessed quitting harvest rates by collecting giving-up densities from artificial food patches (Brown 1988) composed of plastic bowls (diameter 30 cm, depth 3 cm) containing 7 g oat seeds thoroughly mixed into 1.0 l of sifted sand. Voles foraging in the artificial food patches should experience diminishing returns as their harvest rate declines (i.e. resource depletion) with time spent in the patch. Given diminishing returns, a vole should exploit a patch until its harvest rate declines to the sum of its predation, energetic, and missing opportunity costs. The density at which this relationship is satisfied is the giving-up density (GUD) (Brown 1988, 1992). Predation cost of foraging is often large (Brown et al. 1994), and the method is suitable for detecting differences in perceived risk of predation while foraging. We collected GUDs between sunset and sunrise on the night of 20–21 December 1997. In each enclosure we placed two trays at five trap-stations randomized out of those visited by voles during the trapping sessions. We installed a wooden plate above one of the trays to provide cover, while the other was left uncovered. The distance between the two trays was ca 0.3 m. In the morning, we removed the trays, sieved the uneaten food and weighed the seeds to determine the GUD. In most cases, we confirmed vole activity in the patches based on the presence of feces and urine in the patch.

### Manipulation of predation risk

We randomized three out of the six enclosures to be treated with predator scent, and the remaining three served as controls. We used four different sources of scent; commercially available (LegUp Enterprises) urine of red fox, coyote, and bobcat, and fresh feces of captive bobcats (fed with rats and housed in Trevor Zoo in Millbrook, NY), as indicators of presence of these predators. Each of these different scent sources was applied sequentially to all three treatment enclosures.

Within the enclosures the spatial units receiving scent treatment were the  $7.5 \times 7.5$  m squares that were cornered by trap-stations of the live-trapping grid. We changed the scent source every second day. During each change we randomized six out of 13 squares (i.e. those without a seedling station) in each enclosure to be those receiving the treatment. We placed one source of odor in the midpoint of each of the five squares. We started to distribute the odors one week before the planting of the seedlings to ensure that voles perceived the cues before seedlings became available. We began the treatments by spraying the odors on the base of a pole that was installed in the midpoint of each treatment square. After two weeks we replaced the poles with dispensers, i.e.  $\sim 8$  cm long pieces of plastic tubing (diameter 0.6 cm) each containing three commercial cotton balls saturated with urine. The source for odor of bobcat feces was an uncovered petri dish (diameter 5 cm) each with a 5 cm long piece of the feces.

We subjected the three control enclosures to procedures similar to those applied in the predator scent treatments, but used vinegar as a substitute for urine and a piece of dirt as a substitute for feces. This allowed us to control both the effects of novel odor or objects in the neighborhood of voles as well as the disturbance associated with changing the odor sources.

On 14 December we reinforced the treatments by increasing the number of squares receiving the treatments in each enclosure to nine. In addition, on 20 December, when GUD measurements took place, we applied urine of all three predators simultaneously in the experimental enclosures such that all 13 squares without tree seedlings received randomly one of the treatments. During this experiment we deployed two to three dispensers per square and sprayed all the remaining (0.3 l) urine within vegetation of these squares. Again, all control enclosures were treated with vinegar according to the procedure applied in the experimental enclosures.

To improve the potential of our fences to prevent visits of mammalian predators, we installed an electric fence 5–10 cm above the upper edge of the fence of the control enclosures. According to our observations, visits of mammalian predators were rare within the enclo-

tures during the study. We know of one visit of a red fox and one visit of a feral cat *Felis catus* in the predator odor enclosures but are not aware of any predatory activity within the control enclosures.

### Statistical analyses

Our main goal was to study the effects of predator scent, cover manipulation, and their interaction on the amount of tree seedling predation by voles. We consider the seedling stations as independent replicates, while the three adjacent cover manipulation plots at each station are clearly interdependent alternative patches for voles visiting a given seedling station. Thus, we used a repeated measures ANOVA with a within-subject factor "cover manipulation" and between-subject factors "predator scent" and "enclosure nested within predator scent". We applied a similar model when testing effects of predator scent and cover on the GUDs. In the analyses where the dependent variables were based on counts (vole numbers per vegetation type, number of depredated seedlings per plot), we used log transformed data to improve compatibility with the assumptions of ANOVA. We performed statistical analyses with SPSS 10.1 software (SPSS/Norusis). We use univariate tests of rmANOVA whenever the criteria represented by Potvin et al. (1990) were met. The values of variables we will give in the results are means and standard errors throughout.

### Results

We began the analyses by comparing body weight and some basic demographic measures between the predator scent and control treatments. Mean body weights were  $29.28 \pm 1.83$  g and  $33.97 \pm 3.14$  g in November and  $26.19 \pm 2.03$  g and  $29.47 \pm 2.91$  g in December in control and predator scent treatments, respectively. rmANOVA revealed a significant time effect (Pillais' trace  $F_{1,4} = 24.14$ ,  $p = 0.008$ ), but no predator scent ( $p = 0.32$ ) or predator scent by time effects ( $p = 0.41$ ). Population densities (individuals per enclosure) and survival rates did not differ between the predator scent and control treatments (density:  $17.92 \pm 3.22$ ,  $16.48 \pm 5.01$ , respectively,  $t = -0.242$ ,  $DF = 4$ ,  $p = 0.821$ ; survival:  $0.92 \pm 0.08$ ,  $0.72 \pm 0.11$ , respectively,  $t = -1.438$ ,  $DF = 4$ ,  $p = 0.224$ ). Neither did the distribution of voles among different vegetation classes differ between the scent treatments (predator scent by cover,  $F_{2,12} = 0.23$ ,  $p = 0.80$ ). The type of vegetation, however, affected distribution of voles within the enclosures. The mean number of voles captured in the four traps surrounding each of the seedling stations was greater for the stations within at least moderate vegetation cover (classes 2 and 3:  $4.67 \pm 0.53$ ,  $N = 9$ ;  $4.50 \pm 0.96$ ,  $N = 4$ ;

respectively) compared with those within low cover (class 1:  $1.80 \pm 0.86$ ,  $N = 5$ ) ( $F_{2,12} = 5.60$ ,  $p = 0.019$ ).

The rate of tree seedling predation was low during the study. Only 14 out of the 486 experimental seedlings (2.9%) was attacked by voles. The mean number of tree seedlings depredated per seedling station did not differ between the predator scent treatment and control ( $0.78 \pm 0.78$ ;  $0.78 \pm 0.55$ ; respectively;  $F_{1,12} = 0.09$ ,  $p = 0.77$ ). Neither did we observe any effects due to the factors enclosure within predator scent treatment ( $F_{4,12} = 0.86$ ,  $p = 0.51$ ) nor cover manipulation (Pillais' trace  $F_{2,11} = 1.81$ ,  $p = 0.21$ ) or interactions between these two (Pillais' trace  $F_{8,24} = 0.93$ ,  $p = 0.51$ ) or between cover manipulation and predator scent treatment (Pillais' trace  $F_{2,11} = 1.11$ ,  $p = 0.36$ ).

Due to 1) the differences in vole densities among the different vegetation types and 2) relative low p-value when testing for the homogeneity of vegetation between the predator scent treatment (see Material and methods), we ran an additional rmANCOVA to test for the effects of predator scent, vegetation type, local vole density and all their interactions on the amount of tree seedling depredated in the manipulated patches of each station. The analysis (Table 1) revealed a significant vegetation type by local density by cover manipulation interaction. The interaction receives its interpretation from Fig. 1. Vegetation type around seedling stations affected the number of seedlings attacked: all except one of the attacks took place in the stations surrounded by vegetation class 3 (the exception occurred within one station of vegetation class 2, in a cover intact patch with a local vole density of 4 individuals per 16 trap-nights). Within these stations almost all seedlings were attacked in the cover intact patches and the local vole

Table 1. Results of repeated measures ANCOVA testing the effects of within subject factor cover manipulation and between subject factors predator scent, vegetation type, local vole density (covariate) and all their interactions to the rate of tree seedling predation (log transformed).

Source	DF	Mean square	F	p
Cover manipulation (C)	2	0.016	0.820	0.460
C × Predator scent (P)	2	0.004	0.196	0.824
C × Vegetation type (V)	4	0.036	1.870	0.172
C × Local density (L)	2	0.040	2.058	0.165
C × P × V	2	0.0004	0.196	0.824
C × P × L	2	0.0002	0.011	0.989
C × V × L	4	0.093	4.781	0.012
C × P × V × L	2	0.0002	0.011	0.989
Error	14	0.020		
P	1	0.004	0.165	0.697
V	2	0.097	4.167	0.064
L	1	0.113	4.873	0.063
P × V	1	0.004	0.165	0.697
P × L	1	0.0002	0.009	0.926
V × L	2	0.239	10.293	0.008
P × V × L	1	0.0002	0.009	0.926
Error	7	0.023		

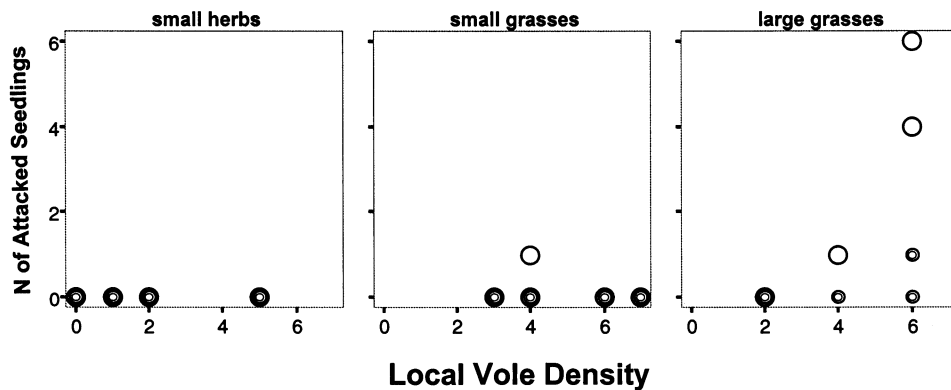


Fig. 1. Number of tree seedlings attacked as a function of local vole density in the different vegetation classes [small herbs (class 1), small grasses (class 2) and large grasses (class 3)] and cover manipulation patches. Large circles denote cover manipulation with cover intact, medium circles patches with dogwood cover and small circles mowed patches.

density correlated positively (Pearson's product moment correlation coefficient  $r_p = 0.92$ ,  $N = 4$ , 1-tailed  $p = 0.043$ ) with the number of seedlings attacked within that vegetation type, cover manipulation combination. Again neither predator scent nor any of the interactions it was involved with approached statistical significance (Table 1).

The results from the GUD trial are consistent with those from the seedling predation experiment. No effect of predator scent or scent by cover manipulation interaction was detected. However, voles ate more oats from the patches with artificial cover when compared to those without cover, leading to a lower GUD in the former ( $F_{1,18} = 12.48$ ,  $p = 0.002$ ).

## Discussion

Scents indicating presence of mammalian carnivores (bobcat, red fox, coyote) did not affect the amount or spatial distribution of tree seedling predation by voles, or any other behavioral or population feature that we measured during this study. Lack of any responses due to the presence of mammalian predator scent is consistent with the results from several recent field experiments where voles have been exposed to predator scents (e.g. Parsons and Bondrup-Nielsen 1996, Wolff and Davis-Born 1997, Mappes et al. 1998, Jonsson et al. 2000). However, these results disagree with those of many laboratory experiments that have demonstrated clear behavioral responses of voles to odors of mammalian predators (e.g. Jedrzejewski et al. 1993, Koskela and Ylönen 1995, Parsons and Bondrup-Nielsen 1996, Perrot-Sinal et al. 1999, Bolbroe et al. 2000). This discrepancy has usually been associated with the scale of the experiment (Wolff and Davis-Born 1997, Mappes et al. 1998, Jonsson et al. 2000). That is, the laboratory studies unnaturally restrict the prey within close proximity to powerful signals, whereas in field studies the

voles can leave the immediate vicinity of the odor source. We would like to raise a few additional points relevant to the outcome of predation risk experiments in mammals.

In a related experiment in the same enclosure system, we found that auditory cues indicating the presence of a stoat were strong enough to increase tree seedling predation, especially in open patches when compared to controls with no such cues (Pusenius and Ostfeld 2000). Although the direction of the effect was unexpected, the results clearly indicate that voles in their natural habitats do react to the perceived presence of mammalian predators. Differences between the results of studies using predator odors and those using predator sounds may arise from differences in the information provided to voles from the two sensory modalities. Scents indicate past presence of the predator but may not suggest imminent danger, especially if voles can assess the age of the scent deposit. In contrast, auditory cues indicate the current presence of the predator. The ability to separate between current and past presence of predation risk may be of great importance because in natural conditions predators come and go frequently. Lima and Bednekoff (1999) hypothesized that the strongest reaction to the cues indicating presence of predators should occur during brief periods of high risk. During prolonged periods of high predation risk, the prey may begin to ignore risks in order to avoid starving. Thus a long term study applying a constant level of risk may fail to find any effect also due to this phenomenon.

Our results demonstrated that patterns of vole foraging activity were associated with differences in habitat features. Voles preferred patches with protective cover and thus the highest potential for vole attacks against tree seedling occurred in these patches (vegetation classes 2 and 3). The most plausible explanation for this preference is avoidance of risk of avian predation (see also Korpimäki et al. 1996, Kotler 1997, Thorson et al. 1998). High vegetation provides voles a reasonable

protection against raptors like red-tailed hawk *Buteo jamaicensis*, which was a daily visitor in our study area. However, although presence of voles in moderately high densities seemed to be a necessary condition for tree seedling predation to occur, it was not a sufficient condition. The voles were equally abundant in the vegetation classes 2 and 3, but practically all tree seedling predation occurred within the class 3, i.e. the one with the most abundant cover. The low nutritional value (Batzli and Henttonen 1999) of tree seedlings may imply that these items are attacked only in conditions with especially low costs of foraging. These conditions most likely existed within the cover intact patches of the vegetation class 3, where the perceived risk of predation and the predation cost of foraging must have been the lowest among the available patches. The results of our GUD trial also indicate that cover was an important factor affecting costs of foraging in our study system.

Thus a kind of behavioral trophic cascade seems to affect the spatial pattern of tree seedling establishment in old fields: predation risk due to avian predators restricts habitat selection by voles, which in turn determines enemy-free space (e.g. Jeffries and Lawton 1984) for tree seedlings. This scenario is probably most pronounced during periods of low vole densities, such as the present study. The patchiness of vole impact on vegetation may disappear during high densities when all suitable habitat patches are inhabited and there are no gaps between vole home ranges (see Ostfeld and Canham 1993).

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