

Effects of stoat's presence and auditory cues indicating its presence on tree seedling predation by meadow voles

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Predators may control the impact of herbivores on their plant resources by 1) decreasing herbivore numbers, 2) imposing predation risk affecting foraging behavior. The goal of the present study was to examine the effects of a predator and auditory cues indicating its presence on the rate of tree seedling (*Acer rubrum*, *Betula lenta*) consumption by meadow voles (*Microtus pennsylvanicus*). The first of our experiments involved introduction of a stoat (*Mustela erminea*) into an enclosed vole population and the second a playback of recordings of vole distress calls, movements of a stoat and its vocalizations. In both experiments we manipulated vegetation cover and the availability of food next to the experimental seedlings to assess the effects of microhabitat under the different risk situations. The results of the first unreplicated experiment suggested an increased rate of seedling predation in the presence of the stoat. Consistent with these results, the playback of predator sounds in the second replicated experiment caused an increased rate of seedling predation compared to control plots with no recordings. A mowed circle around a seedling station, representing increased risk of predation on the voles, decreased seedling consumption. This effect was modest in the playback treatment. We suggest the results to be due to displacement behavior by the voles exposed to prolonged risk and conflicting demands of foraging and avoiding predators. Alternatively, as suggested by the model of Lima and Bednekoff, prolonged risk of predation forced the voles to decrease their levels of vigilance during low-risk playback breaks. The modest inhibitory effect of cover removal on seedling predation in the playback treatment is consistent with this interpretation. The results confirm recent evidence for trophic cascades mediated by behavioral interactions between predator and prey. They are novel in suggesting that the presence of predation risk can increase the inhibitory effects of consumers on their resources.

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During the last decade the role of predation as a factor regulating populations and structuring communities has been emphasized. The top-down regulation idea states that the limitation of herbivores by their predators keeps herbivores from limiting their plant food resource (Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981, Power 1992). Most empirical evidence for the idea comes from aquatic ecosystems (e.g. Power 1990), but recent work has documented the existence of the trophic cascades also in terrestrial ecosystems (Atlegrim

1989, Spiller and Schoener 1990, 1994, McLaren and Peterson 1994, Chase 1996, 1998, Gutierrez et al. 1997, Moran and Hurd 1997, Dyer and Letourneau 1999, Pace et al. 1999). In addition to the impact of predators on herbivore population numbers, behavioral effects of predation risk on the rate and spatial distribution of consumption by herbivores have been proposed (Fryxell and Lundberg 1997, Brown et al. 1999).

Besides the growing empirical evidence of behaviorally mediated trophic cascades (Beckerman et al.

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1997, Schmitz et al. 1997, Peckarsky and McIntosh 1998, Post et al. 1999), there is a great body of evidence for effects of predation risk on behavior of herbivores. Many convincing studies have been conducted with small mammals. The effects of predation risk reported include reduced movements (e.g. Desy et al. 1990, Jedrzejewski and Jedrzejewska 1990, Jedrzejewski et al. 1993, Norrdahl and Korpimäki 1998; but see Lagos et al. 1995), reduced reproduction (Ylönen and Ronkainen 1994), reduced feeding activity (e.g. Brown et al. 1992, Kotler 1997), and selection of safe habitat (Merkens et al. 1991, Korpimäki et al. 1996, Parsons and Bondrup-Nielsen 1996, Kotler 1997, Lima 1998). All these behavioral responses have the potential to affect the amount and spatial distribution of plant consumption.

Of small mammalian herbivores, the voles and lemmings inhabiting northern latitudes seem to be most strongly regulated by their predators (Hanski et al. 1993, Reid et al. 1995, Korpimäki and Krebs 1996, Korpimäki and Norrdahl 1998). Specialist predators of voles, small mustelids, possess glands that they use for scent marking, and the behavioral responses by voles to olfactory cues left by small mustelids have provoked special attention. Under controlled laboratory conditions, voles respond to these olfactory cues (Ylönen and Ronkainen 1994, Koskela and Ylönen 1995, Parsons and Bondrup-Nielsen 1996), but in the field the responses have been equivocal or nonexistent (Parsons and Bondrup-Nielsen 1996, Wolff and Davis-Born 1997, Mappes et al. 1998).

The nonlethal effects of mammalian predators on their prey are rarely studied in field conditions (see however Dickman 1992). We do not know for sure what are the cues that reveal presence of these predators for their prey in the wild. It may be that predators avoid leaving cues like scent marks, which might potentially increase the alertness of their prey (Hillborn and Mangel 1997). It is still likely that a hunting predator at times produces some signals like rustling. Stoats have been observed to make noise also at will in a situation where the pursued prey has managed to escape into a refuge (Erlinge et al. 1974). In addition, the victims of predators may vocalize when attacked (Diamond 1997), a phenomenon also experienced by live-trappers when handling small rodents. Thus it may be that the cues indicating an acute risk of predation are often auditory. Rodents are known to react to voices of birds of prey (e.g. Hendrie et al. 1998), but the effects of auditory cues arising due to hunting activities of mammalian predators are unstudied.

Voles undergo pronounced fluctuations in numbers, and when abundant they may affect the distribution and abundance of the herbaceous plant species that they consume (e.g. Krebs et al. 1973, Ostfeld 1994). During high density periods, voles also attack tree seedlings (Ostfeld and Canham 1993), and they may

affect the establishment of woody plants in the later stages of old field succession (Ostfeld et al. 1997). The effect of voles on tree seedling establishment is best seen in areas with pronounced cyclic population fluctuations such as Fennoscandia, where forestry and agriculture suffer great losses when newly planted seedlings are destroyed in years of peak vole abundance (e.g. Hansson and Larsson 1980, Gill 1992). Besides vole density, the consumption of tree seedlings seems to be related to habitat features associated with predation risk and other costs of foraging, such as availability of cover and alternative food (Gill 1992, Ostfeld and Canham 1993). Preferences for patches providing safety (cover) and/or food should depend on information the forager has concerning the presence of its predators (Brown et al. 1999).

The goal of the present study was to examine the effects of a hunting predator and auditory cues indicating its presence, on the rate of tree seedling consumption by meadow voles (*Microtus pennsylvanicus*). We conducted two experiments the first of which involved an introduction of a stoat (*Mustela erminea*) into an enclosed vole population and the second of which involved playback of recordings of vole distress calls and rustling due to movements of a stoat and its vocalizations. In both experiments we manipulated vegetation cover and the availability of food next to the experimental seedlings to assess the effects of microhabitat under the different risk situations.

Material and methods

Study site

The experiments were carried out in six adjoining 40 m × 40 m enclosures in an old field on the property of Institute of Ecosystem Studies in southeastern New York State. Fences of the enclosures were made of galvanized hardware cloth with mesh size of 0.8 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.).

Experiment 1

To examine the responses by voles to the presence of a predator, we introduced a stoat into one of the enclosures and used another enclosure as a control. To keep the stoat inside the enclosure a 20-cm-wide sheet of aluminium flashing and double electric fence was installed on the top of the fence of the experimental enclosure. An electric fence was also installed in the control enclosure to exclude mammalian predators.

The stoat was caught on the IES property one month before the experiment and was housed in a 1 m × 1 m cage. In the beginning of the experiment the cage was installed in one corner of the enclosure and the door of the cage was removed to allow free exit and entrance. The stoat considered the cage as its resting place and returned there after hunting excursions, so we could confirm its presence in the enclosure by checking the cage. During one week the stoat was found in the cage three times, i.e. every second day. Thereafter it escaped and the experiment was terminated. The hunting activity of the stoat outside the cage was confirmed from demographic data of the vole population inhabiting the experimental enclosure and remains of a vole previously ear-tagged in the enclosure. The control enclosure was equipped with a wire cage of similar size to that in the experimental enclosure.

The meadow voles in the enclosures descended mostly from those naturally present within them before the enclosures were completed. We introduced some additional individuals to each enclosure six weeks before the experiment to ensure population densities (~180 individuals/ha) sufficient for at least moderate rate of tree seedling predation to occur (cf. Ostfeld and Canham 1993). The vole populations were censused two days before and immediately after the experiment. Both censuses were conducted by live-trapping during two successive nights. Each enclosure had 25 trap points arranged in a grid with 7.5-m intervals. We used Ugglan multiple capture traps baited with whole oats and a piece of potato to ensure water availability. All captured voles were ear-tagged during the first capture and subsequently checked for tag number, weight and sexual status. Population densities were estimated by using the Jackknife estimate of the CAPTURE program (Rexstad and Burnham 1998). Nine subadult individuals were removed from the control treatment before the experiment to equalize densities among the treatments. These individuals are excluded from the density estimate of the control enclosure.

In the beginning of the experiment, 14 July, we planted seedlings of red maple (*Acer rubrum*) in three 7.5 m × 7.5 m quadrats chosen randomly, but avoiding adjacent sites (Fig. 1A). Four seedling stations with 3-m intervals were established in each of the three quadrats. Seven ~10-cm-high seedlings were planted at 5-cm intervals in a 6 + 1 circle (Fig. 1A) into each seedling station. Vegetation cover around the station and food availability within the station were manipulated according to 2 × 2 factorial design within each quadrat. Each of the four seedling stations received at random one of the following microhabitat manipulations: intact vegetation, no extra food; intact vegetation, extra food; cover removal, no extra food; cover removal, extra food. The cover manipulation was conducted by mowing a 1-m-wide circle around the seedling station. The extra food was oats offered in 0.25-l glass bottles with

a 3.25-cm-diameter opening. The bottles were kept half full of oats. Seedlings were censused on days 2 and 7 after the beginning of the experiment. Those clipped at the base and killed were considered depredated. Prior research at these study sites indicate that voles are responsible for the vast majority of predation events on seedlings (Ostfeld and Canham 1993, Ostfeld et al. 1997).

Experiment 2

The design of the second experiment was identical to that of the first one with the exception that the predation risk manipulation was carried out by sound playback replicated in three experimental enclosures while the three remaining enclosures served as controls (Fig. 1B). Enclosures that received playbacks were randomly selected among those that were within reach of the 30-m-long speaker cables.

The recordings, used as a surrogate of predation risk, were composed of four different types of sounds: 1) distress calls of voles while handling during live-trapping, 2) distress calls of voles when introduced to the stoat cage within a small cage and approached by the stoat, 3) spontaneous vocalizations of the stoat, 4)

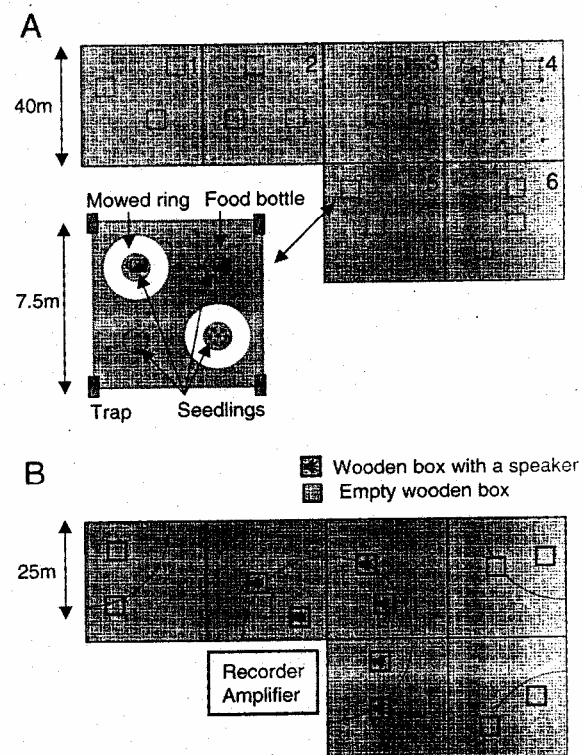


Fig. 1. Spacing of enclosures, vole traps, habitat manipulations (A), speakers and tree seedlings (B). Traps of only one enclosure and seedlings of only one seedling station are illustrated.

rustling produced by the stoat while moving in dry hay within a small terrarium. All recordings were made using a Sony Walkman TCD-D8 DAT recorder capable of recording sounds with frequencies between 20 and 22000 Hz. Compilations of these sounds were subsequently made using Canary 1.2 software (Charif et al. 1995). A typical compilation was made with the goal of imitating sounds arising when a stoat hunts a vole: The compilation started with some sounds of type 4 (see the list above) followed by sounds of type 1 or 2. Some of the compilations also included sounds of type 3. Potential auditory disturbance was removed using the software. Fourteen different compilations were made, almost all of them being composed of different segments of sounds. The distress calls of voles in each of the 14 compilations were emitted by different individuals. These 14 compilations together with three different individual segments of sounds (vole distress calls and stoat vocalizations) were recorded on a 2-h-long tape such that the 17 different compilations or sounds were each replicated 10 times in an order randomized for each replication and with the condition of no duplication. The duration of compilations and sounds varied between 3 and 12 s and the intervening breaks between 30 and 180 s.

The experiment started on 11 September when seedlings of red maple and black birch were planted into each enclosure according to the pattern described above such that each seedling station received four red maple (the central seedling and every second seedling in the circle, Fig. 1A) and three black birch seedlings. The produced tape was played back through three speakers (16.5 cm [height] × 10 cm [width] × 11 cm [depth]) in each experimental enclosure. The playback started simultaneously with the planting of the seedlings. The positions of the speakers were randomized among the trap stations within a sector illustrated in Fig. 1B. A buffer zone of at least 15 m was left between the speakers and the control enclosures to ensure that sounds did not penetrate to the controls. Speakers were not placed on neighboring trap stations and the position of the other of the speakers was always randomized among the trap stations next to the arch determined by the length of the speaker cable (Fig. 1B). Each speaker was placed 2 m away from a trap station within the vegetation. The speaker positions were changed every second day. Each speaker was sheltered by a wooden box (21.5 cm × 15 cm × 16 cm) open in the front. Speaker cables were raised at least 0.5 m from the ground by attaching them to two metal posts. Empty boxes and metal posts were positioned in the control enclosures according to the same rules and schedules used in the experimental enclosures. Thus the disturbance due to installation activities was similar among the treatments. The playback was mostly concentrated to the

hours when voles are most active, i.e. between dusk (19.00) and dawn (09.00). Between these hours playback was discontinued only for short breaks lasting between 3 to 15 min. There was also one playback period in the afternoon between 14.00 and 16.00. The volume level was adjusted by human ear such that the sounds could be heard up to 10 m from the speakers. The experiment lasted for two weeks during which the tree seedlings were censused every day during the first five days and every second day thereafter.

The vole populations were censused two weeks before and two weeks after the experiment. One density estimate was calculated for each enclosure using data from both two-day censuses and the Jackknife estimate of the CAPTURE program (Rexstad and Burnham 1998).

Experimental design and statistical analyses

Experiment 1 lacked true replication as the replicated seedling stations within the two enclosures can be interpreted as pseudoreplicates (Hurlbert 1984, Underwood 1997). Thus we performed no statistical tests on the results of this experiment. The dependent variable of experiment 2 was the proportion of tree seedlings depredated within the different predation risk treatments and manipulated microhabitats at the end of the experiment. The design involved replication at two levels of hierarchy: the playback treatment was assigned to enclosures each containing three quadrats from which the values of the dependent variables were measured. The design is thus nested, with the enclosures nested within the playback treatments and quadrats nested within the enclosures. This necessitates the inclusion of a term describing the variation among the enclosures within the treatments into the ANOVA model (e.g. Underwood 1997). This term takes into account, among other things, the vole density variation among the enclosures (Table 1). We consider the quadrats within enclosures as reasonably independent from each other due to small home ranges of voles (Ostfeld and Canham 1993, Pusenius pers. obs.). The microhabitat manipulation was conducted within the quadrats and included two fully crossed factors – cover and food – which are clearly interdependent. In addition the effect of tree species should be taken into account. Thus the appropriate model to analyze the data was a repeated measures analysis of variance (rmANOVA) with playback treatment and enclosure within treatment as between subject factors and cover, food and tree species as within-subject factors. The proportion of tree seedlings depredated was arcsine square-root transformed. Statistical analyses were performed using the statistical package SPSS for Windows 5.0 (SPSS Inc./Norusis 1992).

Table 1. Results of rmANOVA with playback treatment and enclosure within treatment as between-subject factors and food, cover and species as within-subject factors. All interactions where at least two of the within-subject factors were involved are dropped from the table ($P > 0.22$, in all these cases).

Source of variation	SS	DF	F	P
Playback (P)	6.37	1	7.83	0.016
Enclosure within Playback (EP)	16.56	4	5.08	0.012
Error	9.77	12		
Food (F)	0.75	1	7.27	0.019
P by F	0.22	1	2.15	0.168
EP by F	0.05	4	0.11	0.977
Error	1.24	12		
Ring (R)	4.42	1	15.74	0.002
P by R	2.45	1	8.71	0.012
EP by R	1.75	4	1.56	0.248
Error	3.37	12		
Species (S)	0.35	1	7.39	0.019
P by S	0.05	1	1.07	0.320
EP by S	0.23	4	1.21	0.356
Error	0.56	12		

Results

Experiment 1

Before the experiment, vole densities (individuals per enclosure \pm SE) were similar in both control (43 ± 4.4) and stoat (42 ± 4.3) enclosures. After the experiment the density was higher in the control enclosure (48 ± 4.5) than in the stoat enclosure (32 ± 3.5). Surprisingly, more tree seedlings were depredated in the enclosure with the stoat (21 out of 84) than in the control enclosure (8 out of 84). Presence of a mowed ring around a seedling station clearly inhibited tree seedling predation in both enclosures (Fig. 2).

Experiment 2

The proportion of tree seedlings depredated during experiment 2 was significantly greater in the enclosures with sound playback when compared to control (0.61 ± 0.19 [SE], $N = 3$, 0.90 ± 0.09 , $N = 3$, respectively; Table 1). The significant enclosure within playback treatment effect indicates differences between the enclosures. Vole densities varied considerably among the enclosures, but the different density levels were represented in both playback treatments (Table 2). When substituting the enclosure within treatment factor in the rmANOVA model with population densities of the different enclosures, density was a highly significant covariate in the model ($t = 3.56$, $P = 0.003$). Thus, the enclosure within treatment factor reflects mostly the effect of population density. Presence of extra food increased the consumption of tree seedlings, whereas the ring mowed around the seedling stations decreased it. The effect of the mowed ring was more pronounced in the control treatment, as indicated by the significant playback by ring interaction. Black birch was preferred

to red maple (Table 1). The trajectories of seedling predation in time differed somewhat among the playback treatments: in the enclosure with sound playback, most of the tree seedlings were depredated within one week, whereas a more gradual pattern seemed to occur in the control enclosures (Fig. 3).

Discussion

We found an increased rate of tree seedling predation by meadow voles in the presence of a stoat or auditory cues indicating its presence in relation to controls where these indicators of high predation risk were absent. Such results seem counterintuitive and inconsistent with the conventional view of the effects of predation risk on the behavior of prey animals. Prior studies have typically found a decrease in forager activity in the presence of predation risk (Koskela and Ylönen 1995, Norrdahl and Korpimäki 1998, Carlsen et al. 1999; see Lima 1998 for a review). The auditory cues used in our second

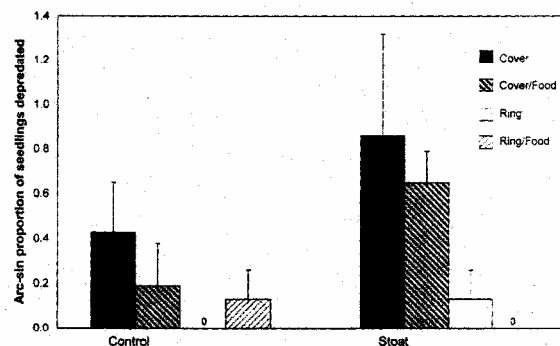


Fig. 2. Arc-sine proportion of tree seedlings depredated (\pm SE) in different microhabitat manipulation patches of control and stoat enclosures.

Table 2. Treatments and voles abundances in the different enclosures estimated (Jackknife, CAPTURE; Rexstad and Burnham 1998) from livetrapping censuses before and after Experiment 2.

Enclosure	Treatment	Number of voles
1	Control	126 ± 7.7
2	Playback	140 ± 7.8
3	Playback	100 ± 6.8
4	Control	98 ± 6.4
5	Playback	65 ± 5.4
6	Control	69 ± 5.6

experiment are novel in predation risk research but should not as such cause any unconventional responses. An important feature of the present study is the similarity of the patterns observed in both experiments, suggesting that the response due to sound playback corresponds with that caused by a real predator.

The possibility exists that the result of the unreplicated first experiment was due to some unmeasured differences between the compared enclosures and populations. Density differences between the stoat and control enclosures were minimal in the beginning of the experiment. During the experiment, the predator activity caused the vole density of the stoat enclosure to decrease in relation to that of the control enclosure. Thus, due to the well-demonstrated effects of vole density on tree seedling predation (Ostfeld and Canham 1993), we should have expected more seedling predation in the control than in the stoat enclosure, the opposite of what we observed. A difference in the inherent quality between these enclosures seems an unlikely explanation for the observed pattern. Other studies conducted in the same enclosure system (Ostfeld and Canham 1993, Pusenius et al. in press; Pusenius and Ostfeld unpubl.) gave no evidence for a spatial trend in the enclosure system that could account for the results of the playback experiment.

Interpreting the higher rate of tree seedling predation in the treatments with elevated predation risk necessi-

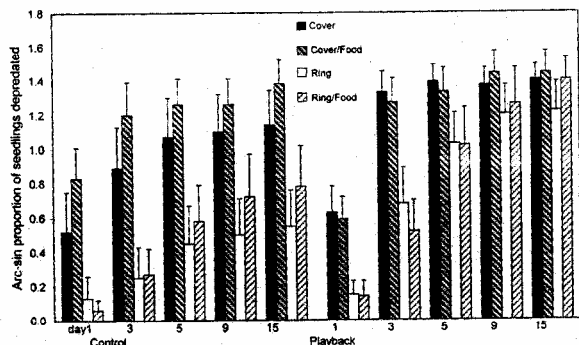


Fig. 3. Arc-sine proportion of tree seedlings depredated (+SE) in different microhabitat manipulation patches of sound playback and control treatments on days 1, 3, 5, 9 and 15.

tates a consideration of the nature of tree seedling predation. Finding tree seedling consumption by voles difficult to explain as a nutritional phenomenon, Batzli and Henttonen (1999) considered the possibility that tree seedling predation might represent a case of displacement behavior found in several animal species in situations with conflicting motivations or stress (e.g. Krebs and Davies 1993). The voles that continuously received signals indicating high predation risk probably faced a motivational conflict between the need to feed and the need to avoid being killed. The effect of playback did not appear immediately (Fig. 3), suggesting that the conflict became more acute with time and ultimately may have stimulated displacement behaviors like tree seedling predation.

The predation risk allocation hypothesis advanced by Lima and Bednekoff (1999) offers an alternative framework to interpret the results, especially those of the sound playback experiment. This model suggests that under conditions of varying predation risk, a prey animal should exhibit its greatest antipredator behavior during high-risk situations. If the high-risk situation becomes frequent or lengthy, the allocation to antipredator effort should decrease during the high-risk situation due to the need to feed. During intervening low-risk periods, prey animals may lose most of their vigilance and foraging efforts should be especially intense. Under these conditions, the net effect of predation risk on feeding, when compared to a system with low, constant risk, should be minimal or absent.

The prolonged exposure to risk, combined with the heterogeneity of habitat, may be the key to the observed pattern of more seedling predation by the voles exposed to perceived predation risk. As the playback of sounds covered more than half of each day, and as this situation continued for two weeks, the voles probably experienced a prolonged risk in the sense of Lima and Bednekoff (1999). According to the model, we should expect the voles to lose their vigilance during the playback breaks, especially later on during the experiment. The significant sound playback by ring interaction indicates that this happened. The voles exposed to the risk involved when crossing open areas, and they visited the stations surrounded by the mowed rings intensively especially in the latter part of the experiment. The reduction in the inhibitory effect of the rings seems to be responsible for much of the difference in seedling predation rates between sound playback and control (see Fig. 3).

Our experiments are among the few that have demonstrated a behavioral response of microtine rodents to the cues of presence of mammalian predators in field conditions. Most of the former studies have used urine or feces of predators as cues (e.g. Parsons and Bondrup-Nielsen 1996, Wolff and Davis-Born 1997, Mappes et al. 1998). Whether the presence of

urine and feces suggests past or current presence of predators compromises interpretations of these studies. In contrast, playbacks indicate an immediate risk that should continue at least as long as they are heard. Although tree seedlings are considered of only secondary importance as food for voles, the rate of their consumption correlates well with rates of consumption of more preferred food items (Puseenius and Schmidt unpubl.). However, whether generalization of the observed effects of predation risk on vole herbivory to the consumption of plants comprising the primary diet of voles is justified depends on the mechanism behind our finding. If the displacement behavior hypothesis is valid the generalization is not supported. If the mechanism is in accordance with the model of Lima and Bednekoff (1999) the generalization may be justified. In any case our results support recent claims (see Post et al. 1999) that behavior may be intimately involved in trophic cascades. However, whereas the study by Post et al. (1999) indicated that hunting behavior by the predator (wolves) affected the impact of prey (moose) on plants, our experiment indicates that behavior of prey (voles) in response to predators (stoats) may influence plant survival.

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