



Research article

## Effects of temporal variation in the risk of predation by least weasel (*Mustela nivalis*) on feeding behavior of field vole (*Microtus agrestis*)

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**Abstract.** Predation risk tends to vary in time. Thus prey animals face a problem of allocating feeding and antipredator effort across different risk situations. A recent model of Lima and Bednekoff (1999) predicts that a prey should allocate more feeding effort to low risk situations and more antipredator effort to high risk situations with increasing relative degree of risk in high risk situations (attack ratio). Furthermore when the proportion of time the prey spends in the high risk situation ( $p$ ) increases, the prey have to eventually feed also in the high risk situations. However the increase in feeding effort in low risk situations should clearly exceed that in high risk situations as  $p$  increases. To test these predictions we measured feeding effort of field voles (*Microtus agrestis*) exposed to varying presence of least weasel (*Mustela nivalis*) and its feces in laboratory conditions. We generated quantitative predictions by estimating attack ratios from results of a pilot experiment. The model explained 15% of the observed variation in feeding effort of voles. Further analyses indicated that feeding effort was lower in high risk situations than in low risk situations at high attack ratio, but not at a lower one. Voles exposed to a presence of a weasel for extended periods showed signs of nutritional stress. Still we did not find any increase in feeding effort with increasing  $p$ . This was obviously due to the relatively low maximal  $p$  we used as we included only conditions likely to occur in nature.

**Key words:** allocation, feeding, field vole, least weasel, predation risk

### Introduction

Actively hunting predators are usually very mobile. Thus the risk of predation perceived by their prey tends to vary in time. Due to the trade-off between antipredator behavior and other fundamental activities, like feeding and mating, a prey should greatly benefit from an ability to adjust its level of vigilance to the variation in the current level of risk. It seems that many animals possess this ability (Kats and Dill, 1998).

The predation risk allocation hypothesis by Lima and Bednekoff (1999) analyzes, how temporal variation in risk affects allocation of antipredator

behavior and foraging effort across different risk situations. The hypothesis states that an animal's response to predation risk at one time period should depend on the risk experienced at other times. In an environment with a variable risk of predation, the animal spends a certain part of its time in a high risk situation ( $p$ ), and the rest of it ( $1 - p$ ) in a less dangerous situation. In high risk situation the attacks of the predator occur at rate  $\alpha_H$  and in low risk situation at rate  $\alpha_L$ . The animal has to decide how much foraging effort (or vigilance) to allocate across the two risk states such that survival is maximized and the energy requirements are met.

According to the theoretical analysis of Lima and Bednekoff (1999) the attack ratio ( $\alpha_H/\alpha_L$ ) and the time spent in a high risk situation ( $p$ ) are the main factors affecting allocation decisions. In conditions with invariant risk ( $\alpha_H/\alpha_L = 1$ ) optimal foraging effort allows the animal to meet its energy requirements, but should not depend on the actual risk level (Houston *et al.*, 1993; Lima and Bednekoff, 1999). However when attack ratio increases ( $\alpha_H > \alpha_L$ ) a prey animal decreases its foraging effort in high risk situations and increases it in low risk situations. So the difference between levels of foraging effort in high and low risk situations should increase when  $\alpha_H/\alpha_L$  is increasing. The increase of  $p$  may force the animal to forage also during high risk situations, to meet its energy requirements. Of course in these conditions the animal tries to forage as efficiently as possible also during the short periods of lower risk intervening long periods of high risk. Thus foraging effort in both high and low risk situations should increase with an increase of  $p$ , but the increase should be even more pronounced in low risk situations than in high risk situations and especially when  $\alpha_H/\alpha_L$  is high. On the other hand the hypothesis predicts the animal to be most vigilant, and feed the least, during short periods of high risk when  $\alpha_H/\alpha_L$  is high (Fig. 1).

So far the predation risk allocation hypothesis has been tested in aquatic experimental systems. Each of the studies has observed some of the patterns predicted by the hypothesis but failed to observe some others (see Hamilton and Heithaus, 2001; Van Buskirk *et al.*, 2002; Sih and Mc Carthy, 2002). Thus it seems that the responses to temporal variation in predation risk vary among different systems. One relatively well studied predator-prey interaction is that between least weasels and voles. Predation by weasels seems to be capable to cause crashes in vole numbers (Korpimäki and Norrdahl, 1998), but the mere presence of weasels has been demonstrated to cause great changes in vole behavior (e.g. Gorman, 1984; Ylönen 1989; Koskela and Ylönen, 1995; Parsons and Bondrup-Nielsen, 1996; Borowski 1998a, b; Carlsen *et al.*, 1999; Bolbroe *et al.*, 2000; Pusenius and Ostfeld, 2000).

In the present study we assessed the effect of temporal variation in the risk of predation by least weasels (*Mustela nivalis*) on foraging behavior of field voles (*Microtus agrestis*). Least weasels are mobile predators with large home ranges

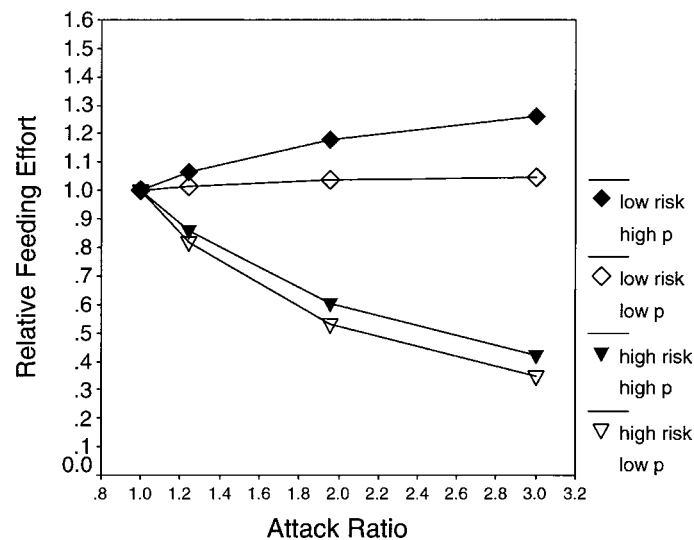


Figure 1. Relative feeding effort of prey as a function of attack ratio,  $\alpha_H/\alpha_L$  at different values of  $p$  (proportion of time spent in high risk situation) in low and high risk situations. The feeding effort values are calculated from the formulas: relative feeding effort<sub>low risk</sub> =  $1/[(1-p) + (\alpha_H/\alpha_L)p]$ ; relative feeding effort<sub>high risk</sub> =  $1/[(\alpha_H/\alpha_L)(1-p) + p]$ , given by Lima and Bednekoff (1999). The values of  $\alpha_H/\alpha_L$  used in the present study were 1.24 and 1.96 and those of  $p$  were 0.07 and 0.31.

in relation to those of their prey (e.g. Sundell *et al.*, 2000). They also have clear temporal activity patterns (Erlinge and Widen, 1975; Jedrzejewski *et al.*, 2000). Field voles feed on plant biomass with relatively low energetic value and thus they have to make several foraging excursions outside their nests each day (Hansson, 1971). Thus field voles in natural conditions most likely experience temporally varying risk to be killed by weasels. Moreover they should be able to refrain from foraging for short periods but during a more prolonged period of high risk they will probably soon get motivated to continue foraging.

We set up a laboratory experiment to simulate a scenario where field voles experience variable risk of predation by least weasels. We recorded the amount of seeds voles removed from an experimental grid in the presence of weasel or its feces (high risk situation) and in their absence (low risk situation). We chose the manipulation of attack ratio on the basis of the results from a pilot experiment where the presence of weasel had a stronger effect on vole foraging activity than the presence of weasel scent (see methods). Thus the procedures alternating presence and removal of a weasel vs. presence and removal of scent of a weasel should, relative to each other, represent conditions with high vs. low attack ratio, respectively. We based the manipulation of the proportion of time at high risk on the results from studies on activity patterns and space use of least weasels (Nyholm, 1959; Erlinge and Widen, 1975; Jedrzejewski *et al.*, 2000).

We estimated the values for  $\alpha_H/\alpha_L$  based on the results of our pilot study. Then we calculated relative predicted values for feeding efforts in low and high risk situations according to formulas of Lima and Bednekoff (1999) for different values of  $p$  and  $\alpha_H/\alpha_L$  and compared them with observed patterns of foraging activity. In addition we asked:

- 1) Is there a difference in seed removal between low and high risk situation and does it increase with increasing attack ratio?
- 2) Does the difference in seed removal between low and high risk situation increase with increasing proportion of time at high risk?

### **Material and methods**

The voles we used in the experiment were trapped from Joensuu, Eastern Finland, in autumn 1999 and Konnevesi, Central Finland, in autumn 2000. One of the least weasels, old male, was trapped from the area of Lake Pielinen, Eastern Finland, in year 1998 and the other, young female, from Mekrijärvi, Eastern Finland, in spring 2000. Voles were housed in standard laboratory cages, 1 or 2 animals in each, and fed with oat seeds, carrots, potatoes, nuts and pellets designed for laboratory rodents. Of the 63 voles used in the experiments, 35 were males (56%) and 28 females (44%). The least weasels were housed in cages in a different room than the voles, and were fed with cat food containing game meat and voles or mice once a week.

We conducted the experiment in two small  $2 \times 3$  m rooms with similar temperature (20 °C) and light regimes (corresponding dusk). Each of the rooms had one  $0.5 \times 0.5$  m arena fenced with 0.8 m high hardware cloth, with 0.2 m wide metal sheets on the top of the fence to prevent the voles to escape. We installed a water bottle and a nest box with cotton on one side of each arena and covered the arena floor with a grid of Petri-dishes (diameter ca. 3 cm) screwed to the floor in four rows of five dishes (Fig. 2).

Our experimental design included three fully crossed factors, risk-level, attack ratio and the proportion of time spent at high risk situation, each with two levels. In addition we had a control treatment with no exposure to weasel or its scent. We replicated all the treatments seven times. Each time we conducted trials we randomly chose the treatments and the experimental room for each treatment. Each trial lasted for 2 days and we ran one trial simultaneously in each of the two experimental rooms. We conducted the trials between March 2000 and June 2001.

Each trial consisted of a habituation period lasting from the beginning of the trial until noon of the second day, and an actual 2 h experimental period in the end of each trial. During the habituation period the vole was exposed to a combination of a given attack ratio and proportion of time at high risk (Ta-

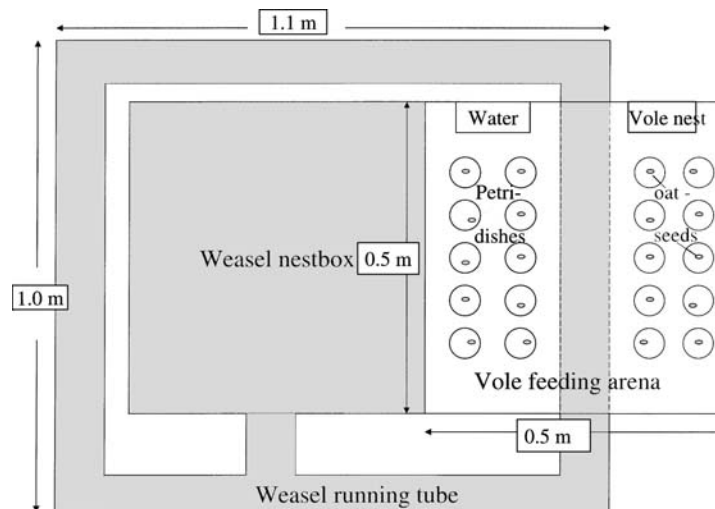


Figure 2. The experimental arena used in the present study.

ble 1). Thus during the experimental period we measured the combined effects of the preceding conditions as well as the prevailing level of risk. We supplied food for voles in five different occasions. At each occasion including the beginning of the experimental trial we put one oat seed into each of the 20 dishes. Thus when foraging the voles had to move around the arenas and expose themselves to potential predators. Besides oat seeds we also supplied some carrot ( $\sim 7.5$  g) to the voles during the habituation period. During the 27.5 h preceding the experimental period voles were given a chance to consume 62.5 kJ (four feeding occasions  $\times$  12.5 kJ/occasion from oat seeds plus altogether 12.5 kJ from carrot). This was slightly less than the calculated average energy requirement (64 kJ) of field voles used in the experiment (mean body mass  $26.75 \pm 5.35$  g) for that time period (see Hansson, 1971). Thus the voles were likely motivated to attack the seeds offered to them during the experimental period.

We simulated high risk situations ( $\alpha_H$ ) by exposing voles to the presence of a least weasel (treatments with a high attack ratio) or its fresh feces and some nesting material (treatments with a low attack ratio). During the low risk situations ( $\alpha_L$ ) no stimulus indicating risk of predation was present (Table 1). We assumed that the level of predation risk perceived by voles after the removal of either weasel or its feces is approximately similar. Therefore the procedures alternating presence and removal of a weasel vs. presence and removal of feces of a weasel should relative to each other represent conditions with high vs. low attack ratio, respectively. We chose the manipulation of attack ratio on the basis of a pilot experiment with a corresponding design used

Table 1. The levels of attack ratio ( $a$  = low,  $A$  = high), proportion of time at high risk ( $p$  = low,  $P$  = high), risk level ( $r$  = low,  $R$  = high), the corresponding treatments and their abbreviations used in text and the schedules applied during the trials of each treatment

Attack ratio	Proportion of time at high risk	Risk level	Treatment	Time							
				Day 1				Day 2			
				8.00	11.30	15.00	15.10	8.00	10.00	11.30	13.30
1	0	Low	Control	$V_{in}$							
Low	Low	Low	After short exposure to odor (apr)	$V_{in}$		$F_{in}$	$F_{out}$		$F_{in}$	$F_{out}$	$F_{out}$
Low	Low	High	During short exposure to odor (apR)	$V_{in}$		$F_{in}$	$F_{out}$		$F_{in}$	$F_{out}$	$F_{out}$
Low	High	Low	After long exposure to odor (aPr)	$V_{in}$	$F_{in}$	$F_{out}$		$F_{in}$			
Low	High	High	During long exposure to odor (aPR)	$V_{in}$	$F_{in}$	$F_{out}$		$F_{in}$			$F_{out}$
High	Low	Low	After short exposure to weasel (Apr)	$V_{in}$		$W_{in}$	$W_{out}$		$W_{in}$	$W_{out}$	$W_{out}$
High	Low	High	During short exposure to weasel (APR)	$V_{in}$		$W_{in}$	$W_{out}$		$W_{in}$	$W_{out}$	$W_{out}$
High	High	Low	After long exposure to weasel (APr)	$V_{in}$	$W_{in}$	$W_{out}$		$W_{in}$			
High	High	High	During long exposure to weasel (APR)	$V_{in}$	$W_{in}$	$W_{out}$		$W_{in}$			$W_{out}$

in the present study. During the 2 h experimental period voles removed less seeds in the presence of a least weasel than in the absence of any stimulus indicating increased predation risk (control) [ $10.70$  (out of  $30$ )  $\pm$   $6.14$  (SE),  $N = 5$ ; vs.  $20.97 \pm 5.39$ ,  $N = 4$ ; respectively;  $P = 0.04$ ]. However, voles removed only slightly less seeds in the presence of feces of least weasel ( $16.85 \pm 7.23$ ,  $N = 6$ ) than in the control ( $P = 0.34$ ). Based on previous experimental evidence (Bolbroe *et al.*, 2000) we, however, accepted weasel scent as a cue of risk of predation, but considered it to be a weaker such cue than the presence of a real weasel.

We manipulated the proportion of time at high risk by using high risk periods lasting from 10 min to 5.5 h (Table 1). In the treatments with low proportion of time at high risk, voles were exposed to least weasel or its feces for 10 min during the first day and for 2 h during the second day. In the treatments with high proportion of time at high risk, vole were exposed to weasel or feces for 3.5 h on the first day and 5.5 h on the second. Thus the values of  $p$  used in the experiment were 0.07 and 0.31 for low and high  $p$  treatments, respectively.

In the treatments where voles were exposed to the presence of the least weasel, we installed a nest box of the weasel (sides  $0.5 \times 0.5$  m, height 0.45 m) next to the feeding arena of voles. We supplied the nest box with water and nesting material. The weasel was able to exit the nest box and enter a plexi-tube (diameter 0.1 m), which passed through the feeding arena of voles and made a loop around the nest box of the weasel (Fig. 2). The part of the tube that went through the vole arena had holes (diameter 0.01 m) on both sides. These holes allowed weasel odor, rustling, sniffing and vocalizations to penetrate into the vole arena. In the treatments with weasel feces as a signal of elevated risk of predation a similar part of tube with fresh weasel feces inside crossed the vole arena. In the beginning of low risk situations we removed the weasel and its nest box or its feces from the experimental room. In control treatments we installed an empty tube within the vole arena.

Each of the trials began at 8 o'clock on day 1 when we randomly chose a vole, weighed and introduced it onto the experimental arena with 20 oat seeds. We supplied the voles with 20 seeds and counted seeds according to a same schedule in all treatments (day 1: 11.30, 15.00; day 2: 8.00, 11.30 and 13.30). During each seed count we recorded the number of seeds removed, replaced them, and removed all remains of food from the vole nest box. The measure of the amount of foraging activity during the experimental period (on day 2, between 11.30 and 13.30) was the number of seeds removed from the Petri-dishes.

To generate quantitative predictions, we estimated risk ratio values from the data of the pilot experiment (see above). According to Lima and Bednekoff (1999) the ratio of feeding efforts in low and high risk situations ( $f_L$ ,  $f_H$ ; re-

spectively) varies as an inverse of attack ratio ( $f_L/f_H = \alpha_H/\alpha_L$ ). Thus we used the quotients (number of seeds removed in control/number of seeds removed in the presence of weasel) and (number of seeds removed in control/number of seeds removed in the presence of scent) as the estimates of  $\alpha_H/\alpha_L$  for higher and lower risk-ratio treatments, i.e. 1.96 and 1.24, respectively. Using these values and the values of  $p$  above we calculated predicted values for feeding activity at different risk situations using the formulas from Lima and Bednekoff (1999):  $f_L = 1/[(1 - p) + (\alpha_H/\alpha_L)p]$ ;  $f_H = 1/[(\alpha_H/\alpha_L)(1 - p) + p]$ ; (Fig. 1).

We confronted the model of Lima and Bednekoff (1999) with our data by the means of regression analysis. We used the proportion of seeds removed as a dependent variable and the values predicted for each of the applied treatments including control as an independent variable. Besides model fitting we tested the effects of attack ratio, proportion of time spent in a high risk situation and the level of risk and all their interactions on the foraging activity of voles using ANCOVA. We adjusted the amount of seeds removed during the experimental period for individual variation in energy requirements by using vole body mass in the beginning of a trial as a covariate in the analysis. The data from control treatment was omitted from this analysis. Seed removal values were transformed to arc-sine square-root proportion of seeds removed prior to all analyses. All statistical analyses were conducted using SPSS-software.

## Results

The results of the regression analysis suggested only a moderate fit between the model and the data ( $R^2 = 0.15$ ,  $B = 1.03 \pm 0.32$ ,  $t = 3.24$ ,  $P = 0.002$ ). Foraging effort deviated from the predicted value especially in ApR- (lower than expected), apR- (higher than expected), aPr- (lower than expected) and APr- (lower than expected) treatments (Fig. 3).

The results of the ANCOVA indicated that rate of seed removal correlated positively with initial body mass of voles ( $B = 0.029 \pm 0.013$ ) and varied among treatments with different attack ratio (Table 2, Fig. 3). More importantly, the difference between foraging effort in high and low risk situations depended on attack rate as indicated by the observed attack ratio  $\times$  risk level interaction (Table 2). The foraging effort was lower in high risk situations than in low risk situations at the higher attack rate, while no difference between foraging efforts in high vs. low risk situations existed at the lower attack rate (Fig. 3). The proportion of time at high risk did not affect the difference in foraging effort between high and low risk situations (non-significant risk level  $\times$  proportion of time at high risk interaction, Table 2).

To identify the conditions where variation in the risk of predation altered the rate of seed removal compared with a situation with no variation in risk, we



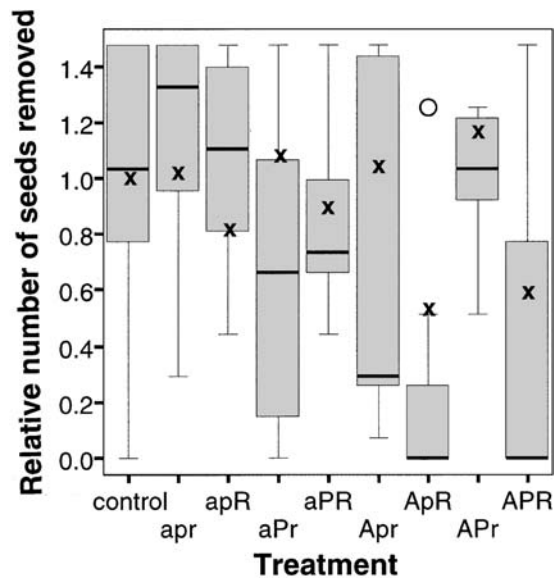


Figure 3. Boxplots illustrating medians, upper and lower quartiles and extremes (circle) of relative number of seeds removed by voles during the experimental period in the different treatments (for abbreviations see Table 1). Crosses denote the corresponding predicted values calculated according to the model of Lima and Bednekoff (1999) (see methods). The relative values were obtained by dividing each of the values by the mean observed in the control treatment.

contrasted each of the treatments with control. *A priori* simple contrasts (ANOVA, body mass as a covariate) indicated that only the rate of seed removal in ApR-treatment was significantly different (lower) from that observed in control (contrast estimate =  $-0.76$ ,  $df = 1$ ,  $P = 0.006$ ). The rate of seed removal in APR-treatment tended to be lower than that in control (contrast estimate =  $-0.53$ ,  $df = 1$ ,  $P = 0.054$ ).

Finally, we tested whether prolonged exposure to high risk affected nutritional state of voles as indicated by changes in their body mass during the trials. Body mass decreased significantly more in the treatments with high attack ratio and high proportion of time at high risk than in the other treatments (rmANOVA, body mass difference  $\times$  attack ratio  $\times$  proportion of time at high risk,  $F_{1,52} = 4.22$ ,  $P = 0.045$ ; Fig. 4).

## Discussion

The results of the present study demonstrated the importance of temporal variation in predation risk as a factor affecting foraging decisions of voles. Our results indicate that the feeding effort allocated to low vs. high risk situations

Table 2. The effects of the level of risk, attack ratio and proportion of time spent in high risk and their interaction to seed removal by voles

Source of variation	Sum of squares	df	<i>F</i>	Sig.
Body mass	1.14	1	5.09	0.029
Risk level ( <i>R</i> )	0.89	1	3.96	0.052
Proportion of time at high risk ( <i>P</i> )	0.06	1	0.28	0.60
Attack ratio ( <i>A</i> )	1.76	1	7.83	0.007
<i>R</i> × <i>P</i>	0.06	1	0.27	0.60
<i>R</i> × <i>A</i>	1.23	1	5.47	0.024
<i>P</i> × <i>A</i>	0.88	1	3.91	0.054
<i>R</i> × <i>P</i> × <i>A</i>	0.002	1	0.01	0.93
Error	10.56	47		

Seed removal during initial feeding period was used as a covariate.  $R^2 = 0.37$ .

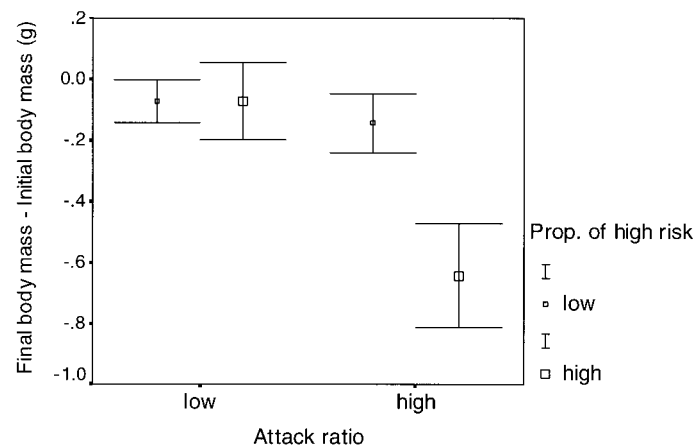


Figure 4. The change in body mass of voles ( $\pm$ SE) during the trials at different attack ratios and proportions of time at high risk.

depended on the relative degree of risk in high risk situations, i.e. attack ratio. It also seemed that voles exhibited their greatest antipredatory behavior during brief high risk situations. Thus our findings agree with some of the key predictions of the predation risk allocation hypothesis of Lima and Bednekoff (1999). However, we did not observe any clear evidence of changes in feeding effort related to variation in the proportion of time spent at high risk situations. In addition, the fit between the observed values of feeding effort and the values predicted from the model of Lima and Bednekoff (1999) was only moderate.

In the present study the increase of difference in foraging activity between low vs. high risk periods with increasing attack ratio was due to the decrease in foraging activity during high risk periods at high attack ratio. The actual presence of a weasel caused a clear decrease in foraging activity of voles, while

weasel scent caused only mild effects. It is obvious that auditory and visual signals indicating presence of a weasel size animal represent the greatest possible threat for voles. The presence of scent alone indicates that weasel has been around but the chance that it will come back may not be too great (see below). In fact the levels of feeding activity after the weasel visits corresponded with those measured in the presence of scent.

Although the greatest decrease in feeding effort occurred during a brief exposure to weasel, the feeding effort during the longer exposure to weasel was not much higher than during the shorter one. It could have been that the trials were too short to cause any changes in the nutritional condition of the voles. However, the decrease in body mass of voles during the trials with the highest  $p$  values and attack ratios (no decrease during the other trials), suggests that voles began to suffer from malnutrition in the prolonged presence of weasel. Thus, they should have been motivated to take risks in order to retain their energy balance. One reason that this did not happen maybe that the voles, housed in laboratory for an extended period, had initially a highly favorable energy balance.

Feeding activity seemed to restore rapidly after the encounters with weasels. However, it did not exceed the levels measured in low risk situations at the lower levels of attack ratio. In fact the relatively low attack ratios and  $p$  values used in the present study did not predict a particularly pronounced increase in feeding effort after an extended exposure to high predation risk. This feature was more pronounced in the pattern emerging from the simulation of Lima and Bednekoff (1999), which was based on a much wider range of parameter values than the present study. Still the observed feeding effort after an extended exposure to high risk did not increase even to those relatively low predicted levels (see Fig. 3).

The reason for choosing the values of  $p$  used in the present study was our aim to use parameter values taking into account behavioral traits of the studied animals. Least weasels have on the average 2 activity periods each lasting on the average 2 h (Erlinge and Widen, 1975; Jedrzejewski *et al.*, 2000; Sundell *et al.*, 2000). As weasels are very mobile and have large home ranges (Nyholm, 1959; Erlinge, 1974), it is quite unlikely that they would encounter a same field vole (average home range < 0.01 ha, Pusenius and Viitala, 1993; Sundell *et al.*, 2000) repeatedly during a given activity bout. Weasels also change their activity areas frequently and do not seem to stay within each of them more than few days (Nyholm, 1959). Thus, we believe that the higher proportion of time exposed to risk used in the present study (0.31) represents an upper estimate for a realistic exposure of field voles to least weasel predation risk at a time scale of few days. For any longer time period the value of  $p$  should be much lower. It is plausible to suggest that the encounters between weasels and voles are mostly brief and the lower  $p$  value used in the present study may represent a situation most likely to occur in nature.

Our results seem to be much similar with those of Van Buskirk *et al.* (2002). These authors exposed tadpoles of frogs to their dragonfly larvae predators, and found vigilance at high risk situations to increase with increasing attack ratio, but did not detect any effect due to variation in  $p$ . The results of Hamilton and Heithaus (2001) and Sih and McCarthy (2002) indicated an increased foraging activity of prey associated with high  $p$ . Both these studies exposed snails to crustacean predators. However, Hamilton and Heithaus (2001) detected the response at high risk periods, while Sih and McCarthy (2002) demonstrated a large increase in prey activity during a low risk period following an extended exposure to high risk. Based on the results of these studies and the present study it seems that the occurrence of the phenomena predicted by Lima and Bednekoff (1999) depends on the system studied. Van Buskirk *et al.* (2002) suggested that if the time available for the prey to collect the resources needed is short relative to the duration of high risk situations, then the value of  $p$  should have an effect on the allocation of feeding effort between high vs. low risk situations. We doubt whether voles could be exposed to such large proportion of time to increased risk of least weasel predation that this relationship would become favorable. Still voles may spend a considerable proportion of their time exposed to risk of predation due to multiple predator species hunting them (e.g. Lin and Batzli, 1995). Thus testing the hypothesis of Lima and Bednekoff (1999) with different samples of the predator guild hunting voles could give very different results (see e.g. Korpimäki *et al.*, 1996).

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