

Risk of predation and foraging activity in shrews

Jarmo Saarikko

Saarikko, J., Lammi Biological Station, University of Helsinki, SF-16900 Lammi, Finland. — Present address: Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland

Received 27 July 1992, accepted 8 October 1992

The responses of foraging common shrews *Sorex araneus* to the presence of a potential predator, the weasel *Mustela nivalis*, was studied on an experimental arena. The weasel was allowed to visit an enclosed part of the arena at will. A significant short-term (5 to 15 min) decrease of activity was observed after a visit by the weasel during both low and high level weasel activity. Individual variation in the shrews' responses was great. Some individuals decreased their foraging activity to a very low level following the weasel's visits while others did not show any change in activity at all. The magnitude of the shrew's response was positively correlated with its weight at the beginning of the experiment. The results demonstrate that, under risk of predation, large individuals could afford to decrease their foraging activity at the cost of weight loss but smaller individuals, with smaller body energy reserves, apparently could not do so.

1. Introduction

A potential prey individual may react to an increased risk of predation in several different ways. First, it may be indifferent, paying no attention to the potential risk of predation. Second, it may either increase or decrease its activity, or these changes may follow each other in a sequence. If the prey reacts when it encounters a predator it may either avoid (escape, freeze, hide) the predator or approach it (observe, inspect, attack), and the reaction may be followed by changes in general behaviour of the prey. The most common change is a reduction of activity due to an increased use of refuges (Lima & Dill 1990). Predator inspection is common in vertebrates and

may serve in predator recognition and in checking the state of the predator (Magurran & Girling 1986).

Predation risk may have long-term and short-term effects. For instance, it may affect habitat or microhabitat selection, the daily timing of foraging activity and patch residence times of prey (Brown et al. 1988, Stephens & Krebs 1986). Prey may use direct cues of the actual presence of a predator and/or indirect cues of an increased risk of predation, such as the light conditions in the environment (Brown et al. 1988). Many studies discuss the possible limiting effect of a predator on the foraging activity of the prey (Lima & Dill 1990), but there have been only a small number of experimental studies in this area

(Brown et al. 1988, Kotler 1984), and none on shrews. However, we do know that the presence of a potential competitor on an experimental arena does affect a shrews' foraging behaviour (Barnard et al. 1983).

There are two main causes of mortality in sorcid shrews: starvation and predation. Shrews have to spend most of their active time foraging because of their great food requirements and small body energy reserves (Genoud 1988, Hanski 1984, 1985, Saarikko 1989, Saarikko & Hanski 1990). The response of shrews to a decreased level of food availability and thus to a higher risk of starvation is usually increased activity. However, some individuals may also decrease their activity if they have, for example, previously hoarded food (Hanski 1989). This response may also be dependent on the size of the shrew and its body reserves, so that larger shrews may decrease and smaller ones increase their activity level during a temporary decrease in food availability (Hanski 1985). Consequently, one may predict that large shrews have more opportunities than small ones to temporally restrict their foraging activity and to suffer a weight loss in the case of a sudden and unpredicted increase in predation risk.

The most important predators of shrews are small avian predators such as the boreal owl *Aegolius funereus*, the barn owl *Tyto alba*, and the kestrel *Falco tinnunculus* (Korpimäki & Norrdahl 1989). During years of low vole density shrews may also act as an important alternative prey to several mammalian predators (Korpimäki & Norrdahl 1987). Small mustelids dislike the strong smell and taste of shrews (Erlinge 1981), and they usually avoid consuming shrews when other prey is available (Erlinge et al. 1974, Erlinge 1975). Nonetheless, weasels are potential predators of shrews, well capable of catching and killing them (Hamilton 1928, Korpimäki & Norrdahl 1987).

To test how the presence of a mammalian predator affects the foraging behaviour of shrews I conducted an experiment with a least weasel, *Mustela nivalis*, which was allowed to enter an enclosure on an arena in which shrews obtained their food. In particular, I recorded the effect of the predator's visits on the foraging activity of individual common shrews, *Sorex araneus*.

2. Material and methods

2.1. The experimental animals

Twenty-four common shrews were captured in the nearby forests at the Lammi biological station (one individual was born in the laboratory). During the experiments, all shrews, except one, were 9 to 15 months old. Nine of the shrews had been in captivity for 3 to 12 months before the experiment and the other fifteen were tested after 1 to 13 weeks in captivity. While not in the experiment, the shrews were kept in a separate animal room and housed individually in plastic containers (40×60×40 cm³). The shrews were fed once a day with raw fish (mainly roach or perch). Blowfly pupae and flaked oats were provided occasionally.

An immature female weasel was caught at Ojajoki, southern Finland, in October 1989. The weasel was kept out of doors in a terrarium (110×50×50 cm³), which was connected to the experimental arena by a tunnel through the wall. On the arena there was a fenced area which the weasel could visit at will during the experiments. At other times the 6-m long tunnel was closed at the wall. The weasel was usually fed live or freshly killed laboratory mice through the tunnel. The weasel entered the tunnel willingly and it would visit and search the arena several times per day, but usually only stayed for short periods on the arena at one time.

2.2. The experimental arena

The experimental arena was 2×2 m² in size and 6 cm high. The bottom was covered with plastic wall-paper and the whole arena was covered with a sheet of transparent Plexiglas. The inside of the arena was filled with plastic ropes and balls to create a more variable environment and to prevent wall-seeking behaviour in shrews. There were 8 feeders on the arena controlled by a computer. A separate nest-box for the shrew was connected with a tube to the arena. Drinking water was provided in the nest-box. The arena and the feeders have been described more thoroughly by Hanski (1989). The fenced-out area for the weasel was located on one side of the arena and was

about 60×80 cm² in size. The fence was made of aluminum mesh, through which the animals could see, hear and smell each other.

The visits to the feeders were registered by a computer. On each entry the shrew was rewarded with a certain probability (below) with one blowfly pupa. To receive a new reward the shrew had to exit and re-enter the feeder.

In treatments 1 to 3 (below) the reward probabilities were 0.4 in two of the feeders and 0.1 in the remaining feeders, thus giving an average reward probability of 0.19 for the whole arena. The location of the two good feeders among all the feeders was randomized at 6-hour intervals. In treatment 4 the arena was divided into two halves, with four feeders on each side. Both halves had an equal share of the length of the fence to the weasel enclosure. The reward probabilities were 0.25 in the four feeders in one half of the arena (constant schedule), and 0.55 in one and 0.15 in three feeders in the other half (variable ratio schedule), thus giving an average of 0.25 for these feeders, too. The location of the reward probabilities among the feeders of the variable half were randomized at 60-min intervals.

These experiments were part of a longer series of experiments studying the effects of variation in food availability on the foraging behaviour of shrews, which is the reason for the variation of reward rates among the feeders. This aspect of the experiment will not be analysed here. Between experiments, I washed the arena with a disinfectant and alcohol to remove possible scent-markings left by the weasel or the shrews.

2.3. The experimental treatments

At the beginning of an experiment a shrew was alone on the arena. When a weasel exposure was started, the weasel was allowed to enter at will the fenced-out area of the arena.

There were four treatments. The first treatment was a control with no weasel present. In the second, 6-hour treatment, the tunnel to the outside terrarium was closed after the weasel had entered the tunnel, and the tunnel was reopened for the exit of the weasel after 6 hours had passed. This treatment caused the weasel to visit the arena frequently (simulating a higher risk of predation).

The weasel was confined to the tunnel and arena during the first, third, sixth and eighth 6-hour block from the start of the weasel exposure. The purpose of this procedure was to disperse the weasel visits to the arena over both day and night hours. In the third, 48-hour treatment, the weasel was allowed to visit the arena from the terrarium for 48 consecutive hours at will. Treatments 1 to 3 were run from March till October 1991. In treatments 2 and 3, five weasel exposures were started on the second day of the experiment and five on the third day of the experiment. All experiments in treatments 1 to 3 were preceded by a training session of at least 20 hours with the reward probability set at 0.9 in all feeders.

In treatment 4 the weasel exposure was the same as in treatment 3, but always started after 48 hours from the beginning of the experiment. Treatment 4 was run with a different group of shrews from May till September 1990, one year earlier than the other treatments. Note that the foraging situation was somewhat different in treatment 4 than in the other treatments (previous section).

During the experiments the activity of shrews was monitored by registering their visits to the feeders (as in Saarikko & Hanski 1990). From these records I calculated inter-visit intervals. I divided the activity of the shrews into three categories according to the inter-visit intervals. "Foraging periods" are separated (by definition) by an inter-visit interval of 30 minutes or more, when the shrew was assumed to sleep. However, these "sleep" periods of no foraging include other activities outside the arena, for example, the maintenance of a nest. During one foraging period an inter-visit interval longer than 2 min but less than 30 min was defined as a "short rest bout". Consecutive inter-visit intervals less than 2 min in duration and which are separated by a sleep period or short rest bouts are "active foraging" periods. For details of and reasons for this classification see Saarikko & Hanski (1990).

The number of visits to feeders, the number of rewards earned and the pooled time of active foraging were calculated for each hour of the experiment. Also, I calculated the visit rate (visits per minute of active foraging) and the feeding rate (rewards earned per minute of active foraging).

ing) for each shrew. All visits to the arena by the weasel were registered by the computer, and the number of visits per hour was calculated.

3. Results

3.1. Short-term effects

I studied the short-term decrease in the shrew's activity following the weasel's appearance on the arena by comparing the number of visits to feeders before and after each time the weasel had entered the arena. Weasel visits that followed within 60 minutes of a previous visit were excluded from this analysis. I pooled the shrew visits into 5-min blocks. I conducted a repeated measures analysis of variance with the individual means of the number of shrew visits in 5-min blocks and the period of six 5-min blocks before and after predator appearance as the repeated dependent variables and the treatments (2–4) as the independent variable. The level of activity was significantly different between the treatments, and the differences among the 5-min blocks were significant (Table 1). The linear trend within the

5-min blocks was very significant ($df = 1$, $MS = 2.96$, $F = 46.84$, $P < 0.001$). Post hoc pairwise comparisons between the 5-min blocks revealed that the decrease of activity after the arrival of the predator was significant in all treatments, and the mean values of shrew activity reached the pre-predator level 20 to 30 minutes after the predator visit (Fig. 1). Between treatment post hoc pairwise comparisons of the shrew activity before the predator arrival showed that shrew activity was significantly higher in treatment 4 than in the other treatments (Fig. 1).

3.2. Long-term effects

To examine the general activity level of shrews and to find out about possible long-term changes in their behaviour in the presence of the predator a moving average of the number of visits per hour was calculated and drawn over the whole experiment for each individual. By long-term I mean a time-horizon of a few hours, because a common shrew is not able to refrain from foraging for longer than that. The individual behaviours were very variable. In a visual inspection, the most extreme cases were shrew no. 104, which reduced its foraging activity to a very low level after the appearance of the weasel, and shrew no. 119, which did not show any change at all in its behaviour in the presence of the predator. Some individuals changed their daily rhythm of activity by decreasing day-time activity and increasing night-time activity. This kind of behaviour is shown by shrew no. 142, and the effect is still visible two days after the last appearance of the weasel (Fig. 2).

The following auto-regressive model was used to test for the effects of the activity of the shrew itself and the weasel on the activity of the shrew during the next hour:

$$S_t = a + b S_{t-1} + c W_{t-1} \quad (1)$$

where S_t and W_t are the logarithms of the number of visits (plus 1) by the shrew and the weasel to the arena in hour t . The shrew's own effect on its activity in the following hour was negative in 15 out of 19 individuals, and it was negative in all the four individuals in which the effect was significant (Table 2). The negative effect obviously reflects the sleep-activity cycle, which has a total

Table 1. The results of univariate and multivariate repeated measures analysis of variance on the individual means of the number of visits to feeders in 5-min blocks. The two groups of six 5-min blocks before and after a predator visit are the second dependent variable ('predator'). The treatment (2–4) is the independent variable. The means were log-transformed before the analysis.

Source	SS	df	MS	F	P
Treatment (T)	10.80	2	5.40	7.06	0.006
Error	12.23	16	0.76		
Predator (P)	8.28	1	8.28	14.79	0.001
P × T	0.90	2	0.45	0.81	0.464
Error	8.96	16	0.56		
5-min-block (B)	6.23	5	1.25	17.78	0.000
B × T	0.63	10	0.06	0.89	0.543
Error	5.61	80	0.07		
P × B	2.92	5	0.58	5.70	0.000
P × B × T	0.63	10	0.06	0.61	0.798
Error	0.19	80	0.10		

Fig. 1. The individual means of the number of shrew visits before and after a predator visit to the arena in treatments 2, 3 and 4; *n* is the number of individuals in each treatment. The vertical lines at the top of the bars show the 95 per cent confidence interval of the mean. The stars under the bars show those groups which were significantly different in an a posteriori pairwise comparison (Dunnett two sided test) calculated separately for each treatment. The mean of the six 5-min blocks before the predator arrival was used as the control group against which the six 5-min blocks after predator arrival was compared. Only those predator visits are included which were not preceded by another predator visit within the previous 60 minutes (Table 1).

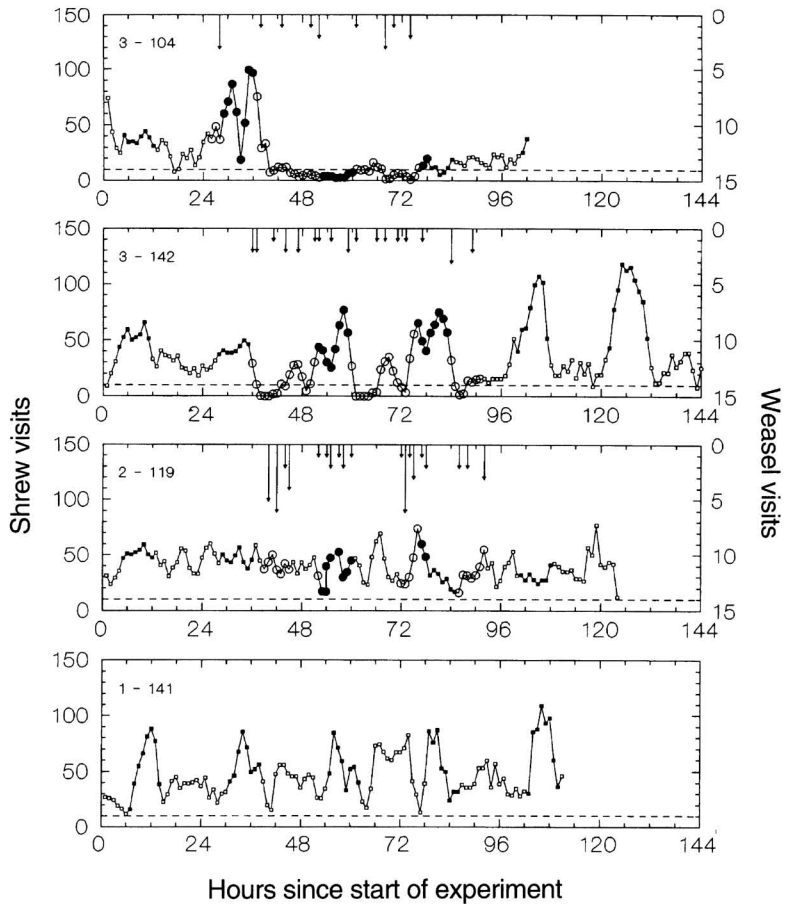
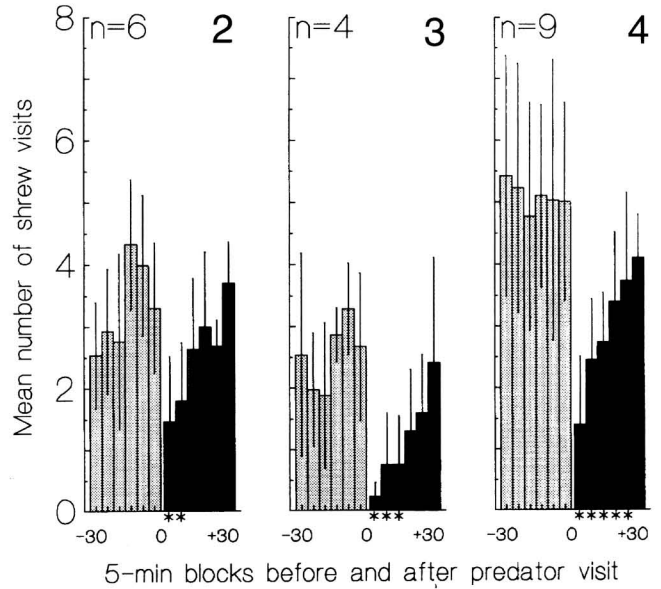


Fig. 2. The number of visits to feeders per hour shown as a moving average with a window of three consecutive hours. X-axis gives hours since the start of the experiment. The circles show the hours during which the weasel had access to the arena. Filled symbols are for night hours from 2300 to 0600. The vertical axis on the right and the inverted vertical arrows show the number of weasel visits to the arena per hour. Individuals no. 104 and 119 were in treatment 2, no. 142 was in treatment 3 and no. 141 in treatment 1.

length of 2.4 hours on average. The predator's effect is strikingly different among the treatments. In treatment 4 there were no significant negative coefficients at all, while in treatments 2 and 3 all 10 individuals had a negative coefficient and in 8 cases it was significant (Table 2).

The proportional weight loss in the experimental individuals was generally much greater in treatment 4 than in treatments 1 to 3 (Fig. 3). The larger individuals lost up to 30% of their initial weight during the 4 days of the experiment. An analysis of covariance of the proportional weight change during the experiment, with the initial weight as a covariate revealed a significant difference between treatment 4 and the three other treatments (Fig. 3). The effect of initial weight was also significant. The same result was reached with the final weight as the dependent variable. Thus the significantly greater weight loss in treatment 4 was greater irrespective of initial weight.

To correlate the weasel's effect on the activity of the shrews with their weight at the beginning of the experiment, I calculated an index of (low) activity with the equation

$$I = -\log(n+1),$$

where n was the number of hours in which the moving average of visits per hour decreased below the value of 10 in treatments 2 and 3 (the hatched line in Fig. 2). (Coefficient c in Equation (1) is not suitable for this purpose, because it is affected in a complex manner by the shrew's own activity.) In treatment 1 with no predator visits, the moving average never decreased below 10. The value of this activity index ranged from -3.5 to 0 in different individuals. The index value was significantly correlated with the initial weight of the shrew: large individuals decreased their activity more than small ones (Fig. 4).

Table 2. Coefficients, and their significance in the autoregressive model $S_t = a + bS_{t-1} + cW_{t-1}$, where S_t and W_t are the natural logarithms of the number of visits (plus 1) by the shrew and the weasel during hour t . Coefficient a was always significantly different from 0. MS is the mean square sum of the full model and P is the significance value of the F -test. The last column gives the number of hours included in the analysis for each individual. The three groups of individuals are for treatments 2, 3 and 4, respectively.

Ind	Coefficient					ANOVA model		n
	a	b	P	c	P	MS	P	
105	3.64	-0.16	0.05	-0.76	0.02	5.08	0.01	147
119	3.79	-0.11	0.22	-0.34	0.13	2.42	0.12	123
138	4.10	-0.09	0.30	-1.23	0.00	13.49	0.00	118
139	3.74	-0.25	0.01	-0.26	0.52	9.27	0.02	114
143	3.19	-0.11	0.25	-0.79	0.04	8.85	0.07	112
146	4.63	-0.22	0.01	-0.33	0.05	4.45	0.01	131
104	2.39	0.04	0.67	-1.43	0.00	8.40	0.01	101
140	3.74	-0.15	0.10	-1.45	0.01	12.15	0.00	113
142	2.00	0.35	0.00	-1.86	0.00	44.35	0.00	144
144	3.42	-0.00	0.98	-1.72	0.00	12.37	0.00	132
13	3.88	0.02	0.83	0.10	0.80	0.13	0.95	99
52	4.39	-0.20	0.09	0.04	0.91	3.21	0.15	98
57	3.30	-0.14	0.18	0.07	0.78	1.74	0.40	97
58	3.43	-0.20	0.05	0.48	0.05	4.34	0.02	96
60	3.78	-0.10	0.34	0.03	0.92	0.64	0.63	97
61	4.27	-0.27	0.01	-0.11	0.64	5.69	0.02	92
66	3.32	0.03	0.78	0.32	0.12	1.83	0.25	104
67	4.01	-0.23	0.02	-0.02	0.94	5.05	0.07	95
68	3.88	-0.01	0.91	0.38	0.08	1.55	0.21	95

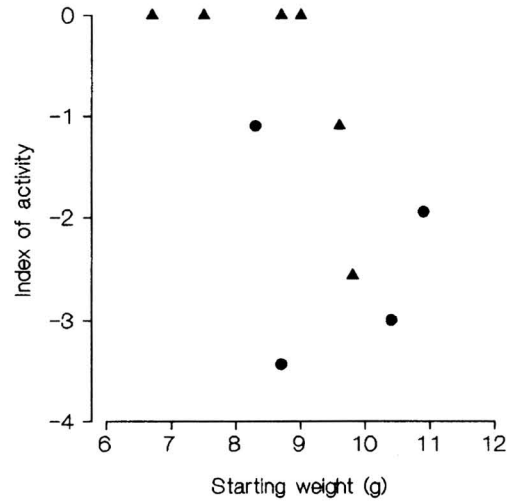
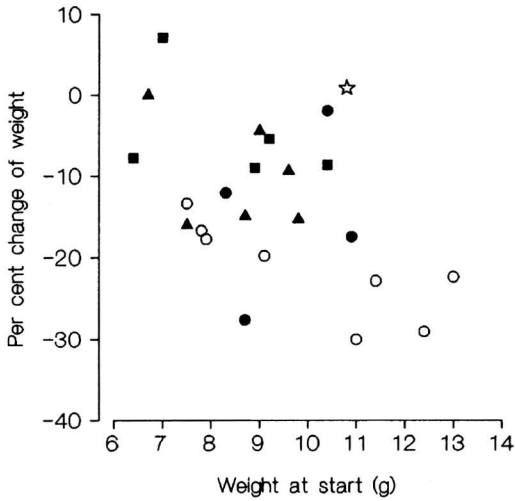


Fig. 3. The proportional change of weight against the weight at the start of the experiment. The filled squares are for treatment 1 (no predator), triangles for treatment 2, filled circles for treatment 3, and open circles for treatment 4. An analysis of covariance, with the starting weight as a covariate, revealed a significant difference between treatment 4 and treatments 1 to 3 ($n = 23$, $MS = 414$, $F = 8.49$, $df = 1$, $P = 0.009$; individual no. 61 in treatment 4 (marked with a star) was excluded from this analysis as a significant outlier). The effect of the starting weight was also significant ($MS = 235$, $df = 1$, $F = 4.81$, $P = 0.04$).

Fig. 4. The index of activity against the weight of the shrew at the start of the experiment. The Y-axis shows the natural logarithm of the activity index multiplied by -1 (hence activity increases upwards). The triangles are for treatment 2 and the filled circles for treatment 3. The correlation is significant ($n = 10$, $r_s = 0.583$, $t = 2.031$, $P < 0.05$).

4. Discussion

The most striking feature of these results is the great variability among individuals in their responses to the weasel's visits. In treatment 4, practically no shrews decreased or increased their rate of visiting the feeders following a visit by the predator, whereas in treatments 2 and 3 some individuals showed a pronounced decrease of activity, while others showed no decrease.

The results in Figs. 3 and 4 suggest an explanation for the observed variation among individuals. In treatment 4, the experimental individuals lost significantly more weight during the experiment than did the individuals in treatments 2 and 3. The average duration of a foraging period in all treatments (Table 3) was greater than 50 min, the average duration in our previous experiments on the same arena without a pred-

tor (Saarikko & Hanski 1990). In treatment 4 the foraging period was 64% longer (84 min; Table 3) than in our earlier experiments on the same arena. On the other hand, this average is almost exactly the same as measured in the field (86 min) by Karulin et al. (1974). These results suggest that especially in treatment 4 the experimental individuals were hard pressed to meet their food requirements. It is not clear why the shrews

Table 3. The means of individual averages over activity cycles in the four treatments. Treatment 0 is for the training sessions before treatments 1–3. Active foraging is the total foraging period minus short rest bouts within it. The durations are shown in minutes.

Treatment	Foraging active	Foraging total	Sleep	Number/cycle visits	Number/cycle rewards
0	14	43	75	22	19
1	42	75	65	106	21
2	41	70	71	107	21
3	35	69	76	94	18
4	49	84	65	123	29

in treatment 4 should have been so active and lost so much weight, with the nominal level of food availability higher than in treatments 2 and 3. It is possible that the food (blowfly pupae) used in treatment 4 was somehow defective. Nonetheless, long activity periods, which are generally associated with low food availability in shrews (Hanski 1985, Saarikko & Hanski 1990), and great weight loss in treatment 4 are associated with no response to the predator in the experiment. In other words, these shrews were apparently so hard-pressed to meet their food requirement that they could not afford decreasing foraging activity without seriously risking starvation.

In treatments 2 and 3, the great variability among individuals in their responses to the weasel may be explained by the same factor, because generally the larger individuals with larger body reserves decreased their activity more than did smaller individuals with smaller body reserves. Individuals with a larger body size may be more vulnerable to predation, because they have to spend more time foraging to fulfill their energetic needs while they are at the same time less agile than smaller individuals (McNamara 1990). By stochastic dynamic modelling McNamara (1990) showed that the mortality from starvation and predation are coupled and impossible to isolate from each other. An animal will take risks depending on its energetic state. Animals which have high energy reserves are able to respond to minute changes in predation risk while animals with low energy reserves are much more insensitive to predation risk (McNamara 1990). The present results agree very well with these theoretical predictions.

It is especially noteworthy that while there were no significant long-term effects in treatment 4, the short-term effects were significant in all treatments (Fig. 1). In other words, shrews in treatment 4 were "aware" of the predator.

Shrews may increase their activity level and spend less time resting in a dangerous area where the predator has been recently, but is absent at present. When a predator is actually observed shrews seem to decrease their activity and increase resting time. During the rest bouts, which are frequent when the predator is present, shrews stand still, and their muzzle constantly moves

from one side to the other, which may aid in predator recognition (Saarikko & Hanski 1990). In the present closed economy experimental setup, it was not possible for shrews to escape from the arena to the nest-box for an extended period of time, because the shrews cannot survive several hours without food. None of the shrews were seen to hoard food.

In treatment 4, the shrews appeared to respond to the absence of the weasel during the predator exposure period, exhibiting a significantly shorter duration of activity and higher rate of visiting during those activity periods when the predator did not appear on the arena. This further confirms that there was a response to the predator, though no decrease in the general level of activity. A similar difference was not observed in the other treatments, in which the shrews were less pressed to satisfy their food requirements. Barnard & Brown (1985) showed experimentally that in the absence of competition shrews increased risk-aversion with increasing food intake relative to the requirement. When a potential competitor was present, the shrews were risk indifferent regardless of their estimated requirement. If an animal is often interrupted by a conspecific or a potential predator it is important to consume food quickly (McNamara 1990). The present observation is in agreement with these results. In treatment 4, in the absence of the predator, shrews avoided risk by eating as fast as possible and leaving the arena sooner. After a visit by the predator, shrews were more indifferent, spent longer periods on the arena and foraged at a lower rate.

Acknowledgements. The arena was originally designed and constructed by Ilkka Hanski and Pertti Saaristo. Asko Kaikusalo provided me with the weasel, which was held captive under a licence issued to Jari Heikkilä by the Ministry of Agriculture and Forestry. Hannele Kettunen, Pia Palevuo, Maija-Liisa Prinkkilä, Pertti Saaristo, and Katrin Urban have helped in taking care of the animals. Lammi Biological Station provided good working facilities. The advice from Ilkka Hanski has been indispensable during the creation of several drafts of this paper. Burt Kotler, Esa Ranta and two anonymous referees made valuable comments. The experiments have been conducted with the permission of the Local Committee on Animal Experiments of the Faculty of Science, University of Helsinki. Financial support was given by the University of Helsinki through a research grant to Ilkka Hanski.

References

- Barnard, C. J. & Brown, C. A. J. 1985: Competition affects risk-sensitivity in foraging shrews. — *Behav. Ecol. Sociobiol.* 16:379–382.
- Barnard, C. J., Brown, C. A. J. & Gray-Wallis, J. 1983: Time and energy budgets and competition in the common shrew (*Sorex araneus* L.). — *Behav. Ecol. Sociobiol.* 13:13–18.
- Brown, J. S., Kotler, B. P., Smith, R. J. & Wirtz, W. O., II. 1988: The effects of owl predation on the foraging behavior of heteromyid rodents. — *Oecologia* 76:408–415.
- Erlinge, S. 1975: Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. — *Oikos* 26:378–384.
- 1981: Food preference, optimal diet and reproductive output in stoats *Mustela erminea* in Sweden. — *Oikos* 36:303–315.
- Erlinge, S., Jonsson, B. & Willstedt, H. 1974: Jaktbeteende och bytesval hos småvesslan. — *Fauna och Flora* (Stockholm) 69:95–101.
- Genoud, M. 1988: Energetic strategies of shrews: ecological constraints and evolutionary implications. — *Mammal Rev.* 18:173–193.
- Hamilton, W. J., Jr. 1928: Weasels eat shrews. — *J. Mammal.* 9:249–250.
- Hanski, I. 1984: Food consumption, assimilation and metabolic rate in six species of shrews (*Sorex* and *Neomys*). — *Ann. Zool. Fennici* 21:157–165.
- 1985: What does a shrew do in an energy crisis? — In: Sibly, R. M. & Smith, R. H. (eds.), *Behavioural ecology*: 247–252. Blackwell Scientific Publ., Oxford.
- 1989: Habitat selection in a patchy environment: individual differences in common shrews. — *Anim. Behav.* 38:414–422.
- Karulin, B. E., Khlyap, L. A., Nikitina, N. A., Kovalevskii, Yu. V., Teslenko, E. B. & Albov, S. A. (Карулин, Б. Е., Хляп, Л. А., Никитина, Н. А., Ковалевский, Ю. В., Тесленко, Е. Б. & Альбов, С. А.) 1974: Activity and use of refuges in the common shrew (from observations on animals labelled with radioactive cobalt) (in Russian). — *Bull. Moskv. Ob. Isp. Prirodi. Otd. Biol.* 79:65–72.
- Korpimäki, E. & Norrdahl, K. 1987: Low proportion of shrews in the diet of small mustelids in western Finland. — *Zeitschr. Säugetierk.* 52:257–260.
- 1989: Avian and mammalian predators of shrews in Europe: regional differences, between-year and seasonal variation, and mortality due to predation. — *Ann. Zool. Fennici* 26:389–400.
- Kotler, B. P. 1984: Risk of predation and the structure of desert rodent communities. — *Ecology* 65:689–701.
- Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. — *Can. J. Zool.* 68:619–640.
- Magurran, A. E. & Girling, S. L. 1986: Predator model recognition and response habituation in shoaling minnows. — *Anim. Behav.* 34:510–518.
- McNamara, J. M. 1990: The starvation-predation trade-off and some behavioural and ecological consequences. — In: Hughes, R. N. (ed.) *Behavioural mechanisms of food selection*. NATO ASI series, G 20:39–59. Springer-Verlag, Berlin Heidelberg.
- Saarikko, J. 1989: Foraging behaviour of shrews. — *Ann. Zool. Fennici.* 26:411–423.
- Saarikko, J. & Hanski, I. 1990: Timing of rest and sleep in foraging shrews. — *Anim. Behav.* 40:861–869.
- Stephens, D. W. & Krebs, J. R. 1986: *Foraging theory*. — Princeton University Press, Princeton. 248 pp.