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Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation?

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Summary. We studied responses of stoats and least weasels to fluctuating vole abundances during seven winters in western Finland. Density indices of mustelids were derived from snow-tracking, diet composition from scat samples, and vole abundances from snap-trapping. Predation rate was estimated by the ratio of voles to mustelids and by the vole kill rate by predators (density of predator × percentage of voles in the diet). We tested the following four predictions of the hypothesis that small mustelids cause the low phase of the microtine cycle. (1) The densities of predators should lag well behind the prey abundances, as time lags tend to have destabilizing effects. The densities of stoats fluctuated in accordance with the vole abundances, whereas the spring densities of least weasels tracked the vole abundances with a half-year lag and the autumn densities with a 1-year lag. (2) Predators should not shift to alternative prey with declining vole densities. The yearly proportion of *Microtus* voles (the staple prey) in the diet of stoats varied widely (range 16–82%) and was positively correlated with the winter abundance of these voles. In contrast, the same proportion in the food of least weasels was independent of the vole abundance. (3) The ratio of voles to small mustelids should be smallest in poor vole years and largest in good ones. This was also observed. (4) Vole densities from autumn to spring should decrease more in those winters when vole kill rates are high than when they are low. The data on least weasels agreed with this prediction. Our results from least weasels were consistent with the predictions of the hypothesis, but stoats behaved like "semi-generalist" predators. Accordingly, declines and lows in the microtine cycle may be due to least weasel predation, but other extrinsic factors may also contribute to crashes.

Key words: Stoat – Least weasel – Numerical and functional responses – Vole cycle – Time lag

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Cyclic fluctuations in abundance of small mammals are characteristic of many arctic and subarctic and some temperate areas. Recent developments in small mammal research show that there is a large regional variation in the occurrence of cyclic fluctuations: European microtine populations exhibit most regular multiannual cycles in northern Fennoscandia (above 65°N), whereas in southern Fennoscandia and in central and western Europe (below 60°N) they are mostly non-cyclic (Hansson and Henttonen 1985, 1988; Hanski et al. 1991). In the transition zone, as in western Finland, microtine cycles are less regular than in the north (Korpimäki 1986). Cyclic vole populations are very scarce in the low phase which lasts for 1–2 years in the north and 0.5–1 year in the transition zone, whereas non-cyclic vole populations show only seasonal changes with low densities in spring and high densities in autumn (Hansson and Henttonen 1985, 1988; Korpimäki 1986).

Among numerous hypotheses suggested to explain microtine cycles (for reviews, see e.g. Krebs and Myers 1974; Finerty 1980; Lidicker 1988), the key role of predation has been stressed by several researchers (e.g. Erlinge et al. 1983, 1984; Hansson 1984, 1987; Henttonen 1985; Korpimäki 1985, 1986; Erlinge 1987; Henttonen et al. 1987; Korpimäki and Norrdahl 1989a, b; Hanski et al. 1991). If predators drive vole cycles, they should affect both the amplitude (the difference between the peak and low density) and the length (the period between peaks) of the cycle.

Field data on predation impact suggest that predators either dampen or amplify microtine cycles (Korpimäki and Norrdahl 1989b with references). Resident generalist and nomadic specialist predators probably decrease the amplitude of the cycle by truncating the peaks. In addition, they do not prolong the cycle, as they shift to alternative prey and/or disperse from the area when microtines crash (Korpimäki 1981, 1985; Erlinge et al. 1983, 1984; Korpimäki and Sulkava 1987; Korpimäki and Norrdahl 1989a, 1991, in press). Resident specialists (e.g. small mustelids: the stoat *Mustela erminea*, the common weasel *M. nivalis vulgaris* and the least weasel *M. n. nivalis* may increase the amplitude and length of the cycle by deepening and prolonging the low phase (Maher 1967; MacLean et al. 1974; Fitzgerald 1977; Goszczynski 1977; Delattre 1984; Korpimäki and Norrdahl 1987). They may not be able to shift to alternative prey or disperse from the area during microtine crashes, because they are specialized on voles and are less mobile than avian predators. Therefore, Henttonen et al. (1987) suggested that the reasons for pronounced cyclicity of microtines in northern Fennoscandia might be spacing behaviour of voles slowing down the increase, and predation by small mustelids causing the decline. However, a theoretical study by Heske and Bondrup-Nielsen (1990) demonstrated that spacing behaviour does not stabilize cyclic vole populations. Accordingly, we intend to test the simple hypothesis that the decline and low phases of the microtine cycle are due to mustelid predation (hereafter called the "mustelid predation hypothesis", MPH).

Responses of predators to fluctuations in prey abundance are numerical (demographic) and/or functional (dietary) (Solomon 1949). Although the knowledge of responses is important in predicting effects of predators on prey populations, the responses of stoats, and especially of least weasels, to fluctuating small mammal abundances are not well known. Short-term data on numerical and functional responses exist in North America (MacLean et al. 1974; Fitzgerald 1977; Simms 1979) and long-term data on numerical responses in Finnish Lapland (e.g. Kaikusalo 1982) and in Siberia (e.g. Vershinin 1972). Most European studies on small mustelids have been performed in areas where only stoats and common weasels live and where vole populations are quite stable over different years (e.g. Erlinge 1974, 1975, 1981, 1983; Tapper 1979; King 1980; Debrot 1981; Delattre 1983, 1984).

In this paper, we present long-term data on the numerical and functional responses of coexisting stoats and least weasels to population fluctuations of voles. Considering factors that may destabilize predator-prey systems (e.g. Murdoch and Oaten 1975; Taylor 1984), we derived the following four predictions from MPH:

(1) Time lags tend to destabilize interactions between predators and prey (e.g. Murdoch and Oaten 1975; Taylor 1984). Accordingly, the densities of small mustelids should lag well behind the abundances of voles.
(2) Small mustelids should not be able to respond functionally to microtine crashes; in other words, they do not shift to alternative prey when vole densities decline.
(3) Changes in the ratio of voles to small mustelids throughout the cycle provide a crude estimate of predation impact (e.g. Fitzgerald 1977). This ratio should be smallest in poor vole years and largest in good vole years.
(4) "Kill" rate (density of predator × percentage of prey in the diet) also is an estimate of the predation impact of small mustelids on vole populations (Tapper 1979). Vole densities should decrease more in those winters when vole kill rates are high than when they are low.

Material and methods

Study area

The study was carried out at Alajoki farmland, in the province of South Ostrobothnia, western Finland (63°00′–63°05′N, 22°55′–23°00′N) in 1983–1990. The study area covers 28 km^2 where the proportions of different habitats are: cultivated field 73%, abandoned field 1%, pine forest 17%, spruce forest 7%, river 1% and inhabited area 1% (see Korpimäki 1984; Korpimäki and Norrdahl 1987, 1989c).

Abundances of small mustelids

Abundances of small mustelids were estimated by snow-tracking in late November and early December 1983–1989 soon after the first snowfall (autumn abundances) and in late February and March 1984–1990 just before snowmelt (spring abundances). Lines were skied after a snowfall so that the tracks of only 1–2 nights were visible. The total number of track-lines was 9 in autumn 1983, 13 in spring 1984 and 19–43 from autumn 1984 onwards (Table 1). Nearly all lines were on farmland, the main habitat of the study area, and the same lines were checked throughout the study. Tracks

Table 1. Density indices (the number of individuals crossing track-lines per km per day) of small mustelids and voles from autumn 1983 to spring 1990. *n* = number of track lines

Year	Season	Stoat			Least weasel			Vole		
		Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
1983	Autumn	1.2	1.8	9	0.6	1.0	9	3.5	4.3	9
1984	Spring	0.1	0.2	13	0.2	0.4	13	0.0	0.0	13
1984	Autumn	0.7	0.8	30	0.3	0.6	42	25.8	30.5	42
1985	Spring	0.5	1.0	26	0.2	0.3	38	3.7	6.3	38
1985	Autumn	1.3	0.8	24	0.4	0.6	38	33.6	34.0	38
1986	Spring	1.8	1.4	19	1.2	1.4	28	33.3	53.8	28
1986	Autumn	0.5	0.6	24	0.8	1.0	40	4.7	8.5	40
1987	Spring	0.2	0.5	24	0.3	0.5	41	0.3	0.8	41
1987	Autumn	0.3	0.3	25	0.1	0.2	43	2.4	3.4	43
1988	Spring	0.1	0.2	25	0.3	0.4	43	3.2	4.7	43
1988	Autumn	0.8	0.8	25	0.5	0.9	43	40.4	43.0	43
1989	Spring	0.5	0.6	22	0.9	0.8	34	28.5	25.2	34
1989	Autumn	0.3	0.4	26	0.6	0.6	42	0.5	0.9	42
1990	Spring	0.2	0.4	27	0.0	0.1	43	1.3	1.5	43

were identified according to Bang and Dahlström (1975) and Siivonen et al. (1982). Tracks of small mustelids were easily distinguished from those of other carnivores, which included mink *(Mustela vison)*, pine marten *(Martes martes)* and red fox *(Vulpes vulpes)*.

The minimum length and the distance between stoat track-lines were 500–550 m (the mean diameter of the home range of the stoat according to Nyholm 1959). The corresponding figure for least weasel track-lines was 50–60 m, which is the mean home range radius of the least weasel (Nyholm 1959). Smaller distances between least weasel lines than between stoat lines were used because female least weasels have small territories (e.g. Nyholm 1959; Erlinge 1974; King 1975) and mainly live below the snow cover in winter (Nyholm 1959; Simms 1979; Korpimäki and Norrdahl 1989c and unpubl.). Each carnivore track crossing the lines was measured to sex individuals and to ensure an individual was counted only once. Sexing of small mustelids was based on the track-dimensions of Nyholm (1959). The density index derived from the data was the number of individuals crossing the lines per kilometre per day.

To study the possibility that the mobility of small mustelids differs depending on food abundance (e.g. Nyholm 1959), trails of 120 stoats (84 males and 36 females) and 127 least weasels (110 males and 17 females) were mapped during the winters of 1983/84–1988/89 so that the tracks of only 1 day were visible. Mapping took place on days other than those on which track-lines were counted, and the number of track-lines crossed by each individual per day was calculated from the track-maps (Table 2).

Diet of small mustelids

Scats of small mustelids were collected during snow-tracking in winters 1983/84–1988/89 when recording daily trails and habitat utilization (see above). Scats of 1 day per individual were gathered in a plastic bag and regarded as one food sample. All scats of least weasels found at Alajoki were later analysed in the laboratory, whereas from each food sample of stoats one to three scats were randomly taken for identification. In addition, guts of a few small mustelids found dead in the study area were used for food analyses, but scat contents of these individuals were not identified. A total of 3 guts and 568 scats of stoats (643 prey items) and 7 guts and 143 scats of least weasels (158 prey items) were used to determine the among-winter variation in the diet composition. Scats collected from one daily trail were not entirely independent of each other, but using the daily trail as an observation unit does not alter the diet composition (Rinta-Jaskari 1990).

"Summer" scats of stoats (a total of 153 prey items) and least weasels (28) were gathered monthly from known "latrines" in April to November 1988–1989. These latrines were usually in the vicinity of barns containing hay or straw and were found during snow-tracking in the preceding winter. Summer scats were used to study seasonal variation in the diet composition.

Teeth, bone fragments, and hair and feather remains were used to identify vertebrate prey. To find remains of all prey items in each scat, the entire contents of the smallest scats were identified and hair and feather remains were taken from several parts of the larger scats. The scale patterns, cross-sections and medulla types of hair remains were examined and these were identified according to Day (1966), Debrot et al. (1982) and using the reference collection of small mammals of known species trapped at Alajoki. Feather remains were identified according to Day (1966) and reference material from the Zoological Museum, University of Oulu.

Each prey species found in the scat or gut was considered as one prey item killed and ingested, even if only a hair was detected. Diet composition was assessed as percentage of a prey type of the total prey number identified in a winter or season. Remains of more than one vertebrate prey were found in 15% (out of 528) winter scats and in 16% (97) summer scats of stoats. The corresponding figures were 12% (105) and 13% (24) for least weasels. There was no great among-winter variation in the proportion of the scats of the stoat including more than one vertebrate prey (range 10–21%) and this proportion was even smaller in the scats of the least weasel. Therefore, no correction factors (Erlinge 1981) were used when comparing the diet composition among winters and seasons.

Abundances of small mammals

Abundances of small mammals were estimated from least weasel track-lines. Because the identification of small mammal species was usually impossible, only two density indices were derived from the data. "Autumn vole index" is the number of small mammals crossing the least weasel lines per km per day in late November and early December and "spring vole index" is the corresponding number in late February and March.

Small mammals were trapped in May and in September. Two sizes of Finnish metal snap-traps were used each season: (1) "mouse" snap-traps and (2) "rat" snap-traps. (1) Four sample quadrats (a cultivated field, an abandoned field, a pine forest, and a spruce forest) were trapped each season and year. The number of trap nights totalled 22 564 during 1977–1990. At each quadrat, 50–100 "mouse" snap-traps were set 10 m apart in small mammal runs for four days and were checked once a day (see Korpimäki 1984, 1986 for further details). "Mouse" snap-traps were efficient in capturing common shrews *(Sorex araneus)*, bank voles *(Clethrionomys glareolus)*, field voles *(Microtus agrestis)* and common voles *(M. epiroticus)*, which are the most numerous small mammals at Alajoki (Korpimäki 1984, 1986; Korpimäki and Norrdahl 1987). (2) Abundances of water voles *(Arvicola terrestris)* were assessed by "rat" snap-traps from autumn 1981 onwards. The number of "rat"-trap nights totalled 3200 during 1981–1990. The distances between traps, trapping periods and time intervals between trap checkings equalled those in "mouse" snap-trappings.

The results from 4-night trapping periods were pooled. The three density indices used in the analyses were: (1) the number of animals caught per 100 trap nights in September (autumn trap index), (2) the number of animals caught per 100 trap nights in May (spring trap index), and (3) the mean number of animals caught per 100 trap nights in May and in the preceding autumn (winter trap index). Density indices of "mouse" snap-trappings were used for common shrews, bank voles and *Microtus* voles, and those of "rat" snap-trappings for water voles.

Results

Sex- and food-related differences in mobility

There were no marked intersexual differences in the number of track-lines crossed by small mustelids (Table 2; *t*-test, two-tailed, $t = 1.25$, NS for the stoat and $t = 1.94$, NS for the least weasel). The track-line interval of 500–550 m was quite suitable for both sexes of stoats, as they crossed on average one line per day. The track-line interval of 50–60 m seemed to be suitable for female least weasels, because they crossed on average one line per day, but this interval was obviously too short for males, because they crossed more than two lines per day. Therefore, density indices of least weasels derived from track-lines are not directly comparable with those of stoats, but they can be used when estimating among-winter density variations within species.

Erlinge (1983) checked the accuracy of density estimates of stoats based on live-trapping against records from snow-tracking in southern Sweden and found that the two estimates were in good agreement. Small mus-

Table 2. The number of track lines crossed by small mustelids per day in winters 1983/84–1988/89

Winter	Stoat						Least weasel					
	Males			Females			Males			Females		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
1983/84	1.0	0.0	2	–	–	–	–	–	–	–	–	–
1984/85	0.9	0.9	10	1.6	0.9	5	3.0	1.4	4	1.0	0.0	3
1985/86	1.3	0.6	24	1.1	0.7	16	3.5	1.4	12	1.0	0.0	1
1986/87	1.0	0.6	19	–	–	–	1.7	1.6	22	1.0	0.0	2
1987/88	0.7	0.5	28	0.4	0.6	14	2.4	2.2	21	1.5	0.7	2
1988/89	1.0	0.0	1	–	–	–	1.2	0.5	5	1.0	0.0	1

telids were live-trapped at Alajoki in April and October during 1984–1986. Because their trappability was much better in a poor vole year (1984) than in good ones (1985–86) (E. Korpimäki and K. Norrdahl unpubl. data), live-trapping did not seem to give reliable density estimates in our study area.

Significant among-winter differences were found in the daily number of track-lines crossed by male stoats (ANOVA, $F=2.89$, $P<0.05$), by female stoats ($F=7.30$, $P<0.01$) and by male least weasels ($F=2.66$, $P<0.05$), but the data from female least weasels were too scanty to study dissimilarities in the mobility (Table 2). There was no significant correlation between the autumn trap index of *Microtus* voles and the mean yearly number of track-lines crossed by stoats (Spearman rank correlation, $r_s=0.54$, $df=6$, NS for males and $r_s=0.60$, $df=4$, NS for females) and by male least weasels ($r_s=-0.30$, $df=5$, NS). Therefore, we did not correct the possible effects of food supply when analysing among-winter variation in density indices.

Density indices in relation to vole dynamics

Density indices of small mustelids showed marked year-to-year fluctuations (Table 1 and Fig. 1). These indices peaked in autumn 1983, and in winters 1985/86 and

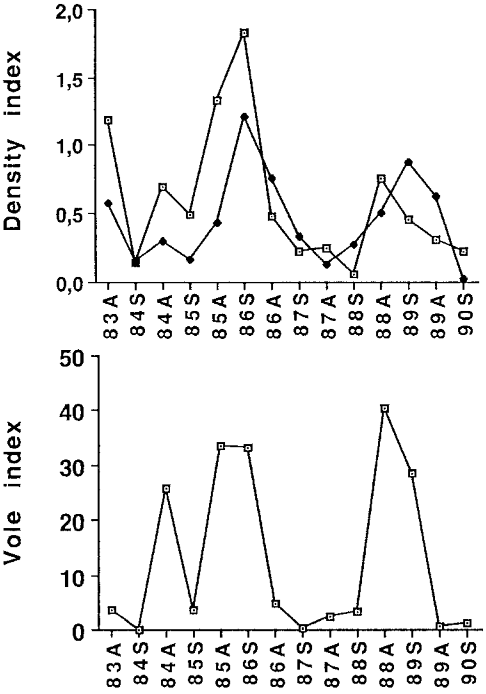

Fig. 1. *Above:* The variation in the density index (the number of individuals crossing the track-lines per km per day) of small mustelids from autumn (*A*) 1983 to spring (*S*) 1990. – ◻ – Stoat; – ◆ – Least weasel. *Below:* The same but for the density index of voles based on track-lines

Table 3. Above: Spearman rank correlations between the autumn (A) and spring (S) density indices of small mustelids and density indices of small mammals in the same season during 1983–90. Below: The same correlations but assuming that small mustelids tracked vole densities with a half-year (0.5-yr) to 1-year (1-yr) lag.

	Stoat		Least weasel	
	Autumn	Spring	Autumn	Spring
Vole track index A	0.68 NS		−0.18 NS	
Vole track index S		0.74*		0.68 NS
Trap index of				
– *Microtus* spp. A	0.40 NS		−0.13 NS	
– *Microtus* spp. S		0.20 NS		0.43 NS
– bank vole A	0.18 NS		−0.54 NS	
– bank vole S		−0.04 NS		0.14 NS
– water vole A	0.54 NS		−0.11 NS	
– water vole S		0.07 NS		−0.15 NS
– common shrew A	0.54 NS		−0.18 NS	
– common shrew S		−0.33 NS		−0.11 NS
Trap index of				
– *Microtus* spp. (0.5-yr)	0.22 NS	0.65 NS	0.24 NS	0.92*
– *Microtus* spp. (1-yr)	−0.39 NS	0.42 NS	0.71*	0.74*
– bank vole (0.5-yr)	0.29 NS	0.49 NS	0.50 NS	0.82*
– bank vole (1-yr)	0.00 NS	0.02 NS	0.86*	0.00 NS

Significance level (one-tailed): $*=P<0.05$

Table 4. The percentage of various prey types in the diet of stoats (A) and least weasels (B) during winters 1983/84–1988/90

Prey type	Winter						
	1983/84	1984/85	1985/86	1986/87	1987/88	1988/89	Total
Shrews A	1.9	–	–	3.3	–	0.8	0.6
B	–	–	–	4.0	4.3	–	1.3
Bank vole A	3.8	1.1	7.1	10.0	24.7	3.4	7.8
B	–	–	9.6	24.0	8.7	3.8	8.9
Water vole A	26.4	5.3	5.1	–	5.2	1.7	7.8
Microtus spp. A	17.9	15.8	63.3	23.3	39.2	82.4	46.8
B	66.7	78.6	55.8	56.0	78.3	92.3	68.3
Muskrat A	5.7	4.2	4.1	10.0	2.1	0.8	3.7
Red squirrel A	1.9	–	–	–	–	0.8	0.5
Hare A	0.9	–	–	3.3	1.0	–	0.5
Mouse A	19.8	66.3	11.2	–	17.5	10.1	21.0
B	11.1	14.3	21.2	12.0	8.7	3.8	13.3
Brown rat A	12.3	–	0.5	13.3	5.2	–	3.6
Mammals tot. A	90.6	92.7	91.3	63.2	94.9	100.0	92.2
B	77.8	92.9	86.6	96.0	100.0	100.0	91.2
Birds A	9.4	2.1	1.0	33.3	3.1	–	4.2
B	–	–	3.8	4.0	–	–	1.9
Common viper A	–	–	–	3.3	–	–	0.2
Others ([a]) A	–	5.3	7.7	–	2.1	–	3.4
B	22.2	7.1	9.6	–	–	–	6.3
No. of prey items A	106	95	196	30	97	119	643
B	18	14	52	25	23	26	158

([a]) Including insects, plants, etc.

1988/89. Small mustelids were scarce in spring 1984, in 1987, and in the springs of 1988 and 1990. The densities of stoats seemed to rise more rapidly than did those of least weasels in 1985 and 1988.

According to vole indices based on track-lines, microtines were scarce in autumn 1983, in spring 1984, in 1987 and in spring 1990 (Table 1 and Fig. 1). They increased rapidly in late summer 1984 and in the summers of 1985 and 1988. A steep crash happened in summers 1986 and 1989.

Vole indices based on the track-lines mostly reflected the abundances of *Microtus* voles, as autumn vole indices correlated significantly positively with the autumn trap indices of these voles during 1983–89 ($r_s = 0.90$, $P < 0.05$). A similar, but non-significant, relationship was also recorded for yearly spring vole indices and spring trap indices of *Microtus voles* ($r_s = 0.62$, NS). In addition, abundances of bank voles contributed somewhat to the among-year variation of vole indices ($r_s = 0.71$, $P < 0.05$ in autumn and $r_s = 0.57$, NS in spring). In contrast, among-year variation in vole indices was not associated with the trap indices of water voles and common shrews.

The spring densities of stoats were significantly positively correlated with the spring vole indices during 1984–1990, but this was not so for least weasels (Table 3: above). The autumn densities of small mustelids were not significantly related to the autumn vole indices. When the autumn and spring densities of small mustelids were plotted against the trap indices of *Microtus voles,* bank voles, water voles and common shrews in the same seasons, the correlations were non-significant (Table 3: above). Assuming a half- to 1-year time lag between

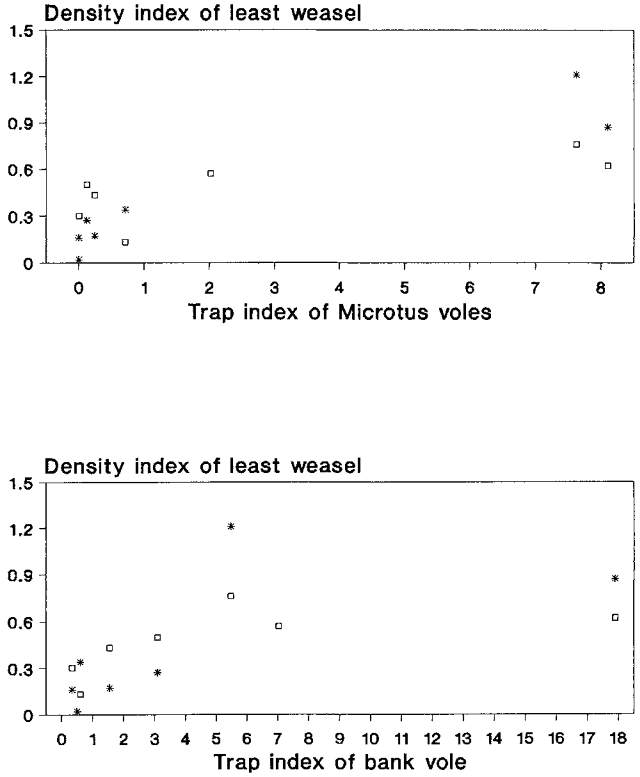

Fig. 2. *Above:* Density indices of least weasels during 1983–90 against trap indices of *Microtus* voles assuming that least weasels tracked vole densities with a half-year (spring) to 1-year (autumn) lag. Spearman rank correlation: $r_s = 0.92$, $P < 0.05$ for spring and $r_s = 0.71$, $P < 0.05$ for autumn. *Below:* The same but for the trap-indices of bank voles. $r_s = 0.82$, $P < 0.05$ for spring and $r_s = 0.86$, $P < 0.05$ for autumn ∗ Spring; □ Autumn

population fluctuations of small mustelids and *Microtus* and bank voles reveals that the spring densities of least weasels tracked abundances of these voles with a half-year lag and the autumn densities with a 1-year lag (Fig. 2 and Table 3: below). In contrast, time lags did not improve correlations between the densities of stoats and voles (Table 3: below).

Variation in the diet depending on the vole supply

Microtus voles were the staple prey of small mustelids at Alajoki constituting 47% of the pooled winter diet of stoats and 68% of that of least weasels (Table 4). Among the alternative prey, mice (the harvest mouse *Micromys minutus* and the house mouse *Mus musculus*) were most frequent in the food of the two carnivores, followed by the bank vole and water vole in the diet of stoats and by the bank vole in that of least weasels. Prey types other than rodents (shrews, birds, snakes and insects) were scarce in both predators' diet.

The proportion of *Microtus* voles in the diet of stoats varied widely between winters (range 16–82%; Table 4) and was significantly positively correlated with the winter trap index of these voles (Fig. 3). A curvilinear (concave) model ($y = 18.4 - 0.5x + 2.9x^2$, $r^2 = 0.92$) explained this relationship slightly better than did a linear one. The yearly proportions of alternative prey species (the water vole, bank vole and common shrew) were not significantly correlated with their trap indices ($r_s = 0.77$, NS for the water vole, $r_s = 0.03$, NS for the bank vole and $r_s = 0.01$, NS for the common shrew). Stoats took more small birds at low *Microtus* vole densities than at high ones ($r_s = -0.83$, $P < 0.05$).

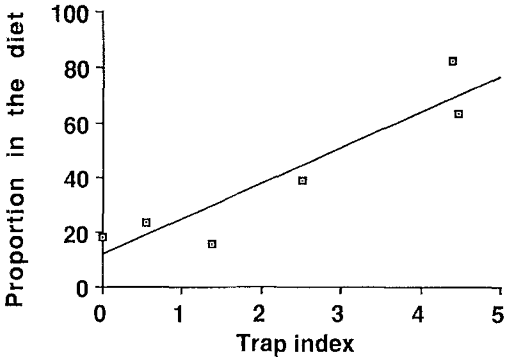

Fig. 3. Linear correlation between the proportion of *Microtus* voles in the diet of stoats (Table 4), and winter trap indices of these voles during winters 1983/84 – 1988/89. $y = 11.10 + 13.19x$, $r = 0.93$

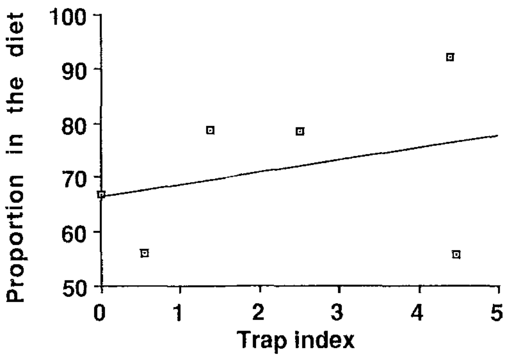

Fig. 4. Correlation between the proportion of *Microtus* voles in the diet of least weasels (Table 4) and winter trap indices of these voles during winters 1983/84 – 1988/89. $y = 66.14 + 2.32x$, $r = 0.32$

There was only a small among-winter variation in the proportion of *Microtus* voles in the food of least weasels (range 56–92%; Table 4), although vole abundances varied widely (Fig. 1). Thus, there was no correlation between the proportion of *Microtus* voles in the diet and the abundance of these voles in the field (Fig. 4). Similar results were also obtained for other small mammals ($r_s = 0.16$, NS for the bank vole and $r_s = -0.16$, NS for the common shrew).

Vole populations grew rapidly in 1988, but declined steeply in 1989 (see Korpimäki and Hakkarainen 1991:

Table 5. The percentage of various prey types in the food of stoats in different seasons from late 1987 to late 1989

Prey types	1987	1988						1989		
	Nov–Dec	Jan–Feb	Mar–Apr	May–June	Jul–Aug	Sep–Oct	Nov–Dec	Jan–Feb	May–June	Jul–Sep
Shrews	–	–	–	–	–	–	2.0	–	–	–
Bank vole	25.0	24.5	13.3	15.4	16.7	8.3	4.1	–	9.4	33.3
Water vole	–	6.1	6.7	7.7	–	–	4.1	–	12.5	4.8
Microtus spp.	55.0	32.7	71.1	69.2	66.7	91.7	71.4	93.3	65.6	23.8
Muskrat	5.0	2.0	–	–	–	–	2.0	–	–	–
Red squirrel	–	–	–	–	–	–	2.0	–	–	–
Hare	–	2.0	–	7.7	–	–	–	–	–	–
Mice	–	26.5	8.9	–	–	–	14.3	6.7	3.1	–
Brown rat	5.0	4.1	–	–	–	–	–	–	–	–
Mammals tot.	90.0	98.0	100.0	100.0	83.3	100.0	100.0	100.0	90.7	61.8
Birds	10.0	2.0	–	–	11.1	–	–	–	3.1	28.6
Bird eggs	–	–	–	–	–	–	–	–	3.1	4.8
Insects	–	–	–	–	–	–	–	–	–	4.8
Others	–	–	–	–	5.6	–	–	–	3.1	–
No. of prey items	20	49	45	13	18	24	49	30	32	21

Table 6. The percentage of various prey types in the diet of least weasels from late 1987 to late 1989

Prey types	1987/88 Dec–Mar	1988 Jun–Sep	1988/89 Dec–Mar	1989 Jun–Sep
Shrews	4.3	–	–	–
Bank vole	8.7	–	4.2	27.3
Microtus spp.	78.3	100.0	91.7	18.2
Mice	8.7	–	4.2	–
Mammals tot.	100.0	100.0	100.0	45.5
Birds	–	–	–	27.3
Bird eggs	–	–	–	9.1
Insects	–	–	–	18.2
No. of prey items	23	17	24	11

Fig. 1). These changes were reflected as increasing proportions of *Microtus* voles in the diet of stoats from January-February to September-October 1988 and as steeply decreasing proportions of these voles from January-February to July-September 1989 (Table 5). During the snowy period (in early 1988), mice and bank voles served as the most important alternative prey, whereas during the snow-free period (in summer 1989), bank voles, young birds and bird eggs were abundant in the diet.

The proportion of *Microtus* voles in the food of least weasels tended to increase from winter 1987/88 to autumn 1988, but in summer 1989 this proportion significantly decreased to as low as 18% (Table 6; Fisher test, $P < 0.001$). At that time, young birds, bird eggs and bank voles were the most important alternative prey.

Predation impact

The number of voles crossing the track lines gave a reliable estimate of the vole abundance (see above). The ratio of voles to small mustelids exhibited large changes in the course of the vole cycle (Fig. 5). In poor winters (1983/84, 1986/87 and 1989/90) there were < 10 vole tracks per 1 predator track but in good winters (1985/86 and 1988/89) this ratio increased to 20–90.

When vole kill rates were plotted against changes in trap indices of *Microtus* voles from autumn to spring in the same winter, the correlation was significantly negative for least weasels (Fig. 6). A similar but non-significant tendency was also seen in stoats. Vole densities remained stable or even increased in those winters when vole kill rates were low. In addition, vole abundances declined steeply in the course of the summers 1986 and 1989, and in these years both the spring and autumn densities of least weasels were also highest (Fig. 1).

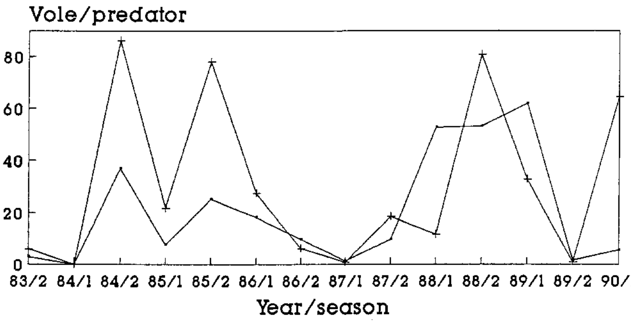

Fig. 5. The variation in the ratio of voles to stoats and least weasels from autumn (*2*) 1983 to spring (*1*) 1990. Data from Table 1. –•– Stoat; –+– Least weasel

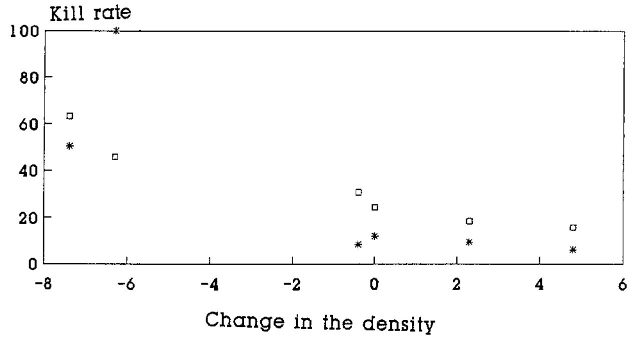

Fig. 6. Vole kill rates by stoats and least weasels (density of predator × percentage of *Microtus* voles in the predator's diet) plotted against the changes in trap indices of *Microtus* voles from autumn to spring in the same winters (1983/84–1988/89). Spearman rank correlation: $r_s = -0.77$, NS for the stoat (*) and $r_s = -1.00$, $P < 0.01$ for the least weasel (□)

Discussion

Densities of least weasels lag behind vole abundances

Densities of least weasels tracked half to 1 year behind vole abundances, consistent with prediction 1 of the mustelid predation hypothesis (MPH: see introduction). Similar results from common weasels have been obtained in England (Tapper 1979). There was no obvious time lag between the population fluctuations of stoats and voles, which was in disagreement with earlier studies reviewed by King (1989). For example, in Finnish Lapland the abundance of least weasels tracked vole densities with a shorter delay than did the abundance of stoats (Kaikusalo 1982). This difference is probably caused by stoats being better able to survive over vole lows in our study area, as they shift from farmland to woodland (E. Korpimäki and K. Norrdahl unpubl.) and/or to alternative prey (present study) when *Microtus* voles living mainly on farmland crash. When the abundances of these voles recover again, surviving stoats shift back to farmland. The spring densities of least weasels were highly dependent on vole abundances in the preceding autumn, indicating that they cannot survive in poor vole winters.

The numerical response of a predator is due to changes in natality, mortality, immigration and emigration (Andersson and Erlinge 1977). It is well known that least weasels and stoats cannot breed, or breed poorly, in low *Microtus* vole years (e.g. Erlinge 1974, 1983; Tapper 1979; King 1980, 1989). Decreases in the density indices of small mustelids from spring to autumn in 1986, 1987 and 1989 (Fig. 1: above) suggest poor reproductive success in these summers. Because stoats and, especially least weasels, need densities of *Microtus* voles over a threshold value to reproduce successfully (e.g. Erlinge 1974, 1983; King 1975, 1980; Tapper 1979; Henttonen 1987), they normally start to breed only in the increase phase of the vole cycle at Alajoki (Korpimäki and Norrdahl 1989c). This is probably the primary cause of the time lag between population fluctuations of voles and least weasels observed in this study.

The reproductive capacity of least weasels is large. There are records of breeding two times per summer in North America (Heidt 1970) and three times per year in captivity (Frank 1974), and even during winters of lemming peaks under the snow in Alaska (Fitzgerald 1981). However, more than one litter per summer and winter reproduction have not been recorded in Fennoscandia (Skarén 1983). As delayed implantation further slows down the natality of stoats (Sandell 1985), the reproductive capacity of least weasels is clearly higher than that of its larger relative, but, of course, the fecundity of both mustelids is much smaller than that of voles. On the other hand, stoats are longer-lived than least weasels (King 1983, 1989) and by shifting habitat they can respond more rapidly to an increase of voles in farmland. Better survival during vole scarcity obviously contributes more to a rapid numerical response than high natality at the time when voles are increasing.

The same is true in synchronous population fluctuations of breeding birds of prey and voles at Alajoki: emigration and immigration of adult predatory birds depending on the vole supply are important, while natality is not (Korpimäki and Norrdahl 1989a, 1991). Although larger carnivores perform nomadic movements (e.g. Ward and Krebs 1986), these movements are probably costly for less mobile mammals. The small size of stoats, and especially of least weasels, further reduces their ability to move. We suggest that the poor mobility of small mustelids is the most important factor causing their densities to lag behind the population fluctuations of voles. Other factors contributing to time lags are the low natality in the low phase of the vole cycle and the poor ability to shift among local habitats.

Stoats, but not least weasels, respond functionally to vole dynamics in winter

Stoats were able to shift to alternative prey at low vole densities, whereas least weasels continued to feed on *Microtus* voles in winter but partly shifted to birds in summer. The results from least weasels, especially in winter, supported prediction 2 of MPH (see introduction).

That common weasels eat many more *Microtus* voles than bank voles has been shown in many studies (e.g. Day 1968; Erlinge 1975; Tapper 1979; Delattre 1984; but see King 1980). Least weasels (mean body mass: males 48 g, females 35 g; Rinta-Jaskari 1990) in central and northern Finland are much smaller than common weasels in southern Sweden (100 and 40 g; Erlinge 1979) and in England (109 and 65 g; King 1980), but they are still highly dependent on larger *Microtus* spp., although the densities of smaller bank voles in fields are much higher than those of *Microtus* spp. in the low phase of the cycle (Korpimäki and Norrdahl 1987, 1991 and unpubl.). We suggest that least weasels are not only specialized on *Microtus* spp., but that they cannot catch bank voles as easily as *Microtus* spp. The behaviour of field and bank voles differed when they attempted to escape common weasels in an enclosure: field voles remained in their tunnels where they are accessible to small least weasels, whereas bank voles responded by climbing or by fleeing immediately (Erlinge 1975). In addition, field voles are clumsy (Hansson 1987) and their smell is stronger than that of bank voles (Henttonen 1987). Dissimilarities in habitat structure cannot explain differences in vulnerability to weasel predation, as bank voles also occupy fields especially in the low phase of the cycle (Korpimäki and Norrdahl 1987). Further evidence for our suggestion that least weasels experience difficulties in catching bank voles gives the result that least weasels were able to shift to flightless young birds and immobile bird eggs in summer (see also MacLean et al. 1974; Järvinen 1990).

Lindén and Wikman (1983) suggested that the shape of the functional response curve may be derived from plotting the proportion of the prey in the diet of the predator against the prey density. Using this method, the functional response curve of the stoat to changing abundance of *Microtus* voles was close to linear (type 1 according to Holling 1959) (Fig. 3). This indicates that stoats do not destabilize vole populations (see Murdoch and Oaten 1975; Taylor 1984), but additional data will be needed to test the validity of this conclusion.

Least weasels may increase the amplitude and length of the vole cycle

The ratio of voles to small mustelids was smallest in the low phase and largest in the peak phase of the vole cycle, in line with prediction 3 of MPH (see Introduction). There were only few voles available to a hunting predator in the low phase, suggesting that the predation risk by stoats and least weasels was high at that time (see also MacLean et al. 1974; Fitzgerald 1977). This risk may also alter the behaviour of voles. In an enclosure experiment, the breeding performance of voles was reduced in the presence of the least weasel (Ylönen 1989). If this also happens in the field, the mere presence of small mustelids or their smell may decrease the reproduction of voles and thus contribute to a crash.

Stoats at Alajoki shifted to alternative prey when voles crashed, but stoat densities were still high in the low phase of the cycle. Accordingly, they contributed to vole declines and deepened and extended low phases. Least weasels were probably the main predators causing declines and deepening and prolonging the low phases, as their densities were still high and they mostly ate *Microtus* voles in the crash phase. This destabilizing impact was probably largest in winter, as least weasels partly shifted to alternative prey in summer. Further evidence for this view is shown by a result that is compatible with prediction 4 of MPH (see Introduction): decreases in vole abundances in the course of the winter were larger when vole kill rates by least weasels were high than when they were low (Fig. 6). Other researchers (e.g. Maher 1967; MacLean et al. 1974; Fitzgerald 1977; Tapper 1979; Delattre 1983, 1984) also stressed the key role of small mustelids in increasing the amplitude and length of the vole cycle. Based on our earlier studies in the same study area (Korpimäki and Norrdahl 1989a, b, c, 1991, in press), avian predation impact acts in the opposite way; i.e. birds of prey dampen vole cycles by truncating population peaks, because they consume a larger share of the summer standing crop and production of vole populations in the peak phase than in the low phase.

Regional trends

The most important unsolved problems in studying vole cycles are which factor(s) cause the extremely low densities of the crash phase and the complicated regional trends of multiannual vole fluctuations recorded, for example, within Europe (see introduction). Multifactorial hypotheses that also include extrinsic factors other than predation (food, diseases and parasites) (e.g. Lidicker 1988; Desy and Batzli 1989; Heske et al. 1991) are difficult to test, and we therefore chose a one-factorial hypothesis, which was supported by our observational data on least weasels. As correlations do not differentiate between causes and consequences, we need to look at whether the removal of least weasels in the decline phase of the cycle slows down a decrease and shortens a low of vole populations. However, we do not claim that least weasel predation is the only factor driving vole cycles. Hanski et al. (1991) combined the impact of two kinds of predators in the same model and demonstrated theoretically that generalist predators stabilize the vole cycle driven by specialist predators.

MPH has potential to explain the regional trends in the multiannual fluctuations of voles recorded within Fennoscandia for the following reasons. (1) Stoats in our study area responded functionally to vole abundances and tracked vole densities without a delay. Accordingly, they behaved like "semi-generalist" predators. Stoats likely are not able to shift their diets and are therefore more attributable to vole crashes in northern Fennoscandia, where alternative prey types are scarce (Henttonen et al. 1987) and where possibilities to shift hunting habitat are limited. (2) Least weasels in our study area were able to take immobile nest contents of birds in summer, but in the north the breeding season of birds is short, which reduces the availability of the alternative food. Therefore, least weasels probably also deepen and prolong the low phase of the vole cycle in summer in northern Fennoscandia. (3) Densities of vole-eating birds of prey are high in our study area (Korpimäki and Norrdahl 1991) and decrease northwards in Fennoscandia (Hanski et al. 1991). These avian predators kill small mustelids, especially least weasels, in the crash phase of the vole cycle. This "secondary" predation may limit the densities of least weasels so that they are not able to cause vole crashes as deep and long as in the north (Korpimäki and Norrdahl 1989b, c).

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