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Small carnivores and prey population dynamics in summer

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We studied interactions between small carnivore abundance in spring and prey population dynamics in the following summer in 10 agricultural areas during 1989–92 in western Finland. We estimated small carnivore and prey abundances on snow track lines in March and November and by snap-trapping small rodents in April and August. Only in least weasels (*Mustela n. nivalis*), we found a negative association of predator density with prey population dynamics. However, this relationship was only evident in large scale, probably because of high mobility of least weasels. This underlines the importance of proper spatial and temporal scale in small carnivore studies.

1. Introduction

The general picture of factors regulating animal populations is still incomplete: both predation and resource limitation regulate some groups, but there is a lack of supporting information from adequate predation studies, especially in birds and mammals (see Sinclair 1989, Crawley 1992 for reviews). Recently, more information has been published stressing the importance of predation by carnivores in mammals and some game birds. Predator-removal experiments on two islands indicated that carnivores had a limiting impact on mountain hares (*Lepus timidus*) and two woodland tetraonids (the capercaillie, *Tetrao urogallus* and the black grouse, *T. tetrix*; Marcström et al. 1988, 1989). Comparison of islands with and without red foxes (*Vulpes vulpes*) also suggested that foxes had a limiting impact on mountain hares (Angerbjorn 1989). In Australia, carnivores were probably regulating rabbits (*Oryctolagus cuniculus*) and house mice (*Mus domesticus*) when prey population densities were low, but not when densities exceeded a threshold value (Newsome et al. 1989, Sinclair et al. 1990, Pech et al. 1992). Also in Chile, predators significantly depressed prey (a caviomorph rodent, the degu, *Octodon degus*) densities when prey population densities were low but not when densities were high (Meserve et al. 1993). In southern Sweden, vole populations may be regulated by density-dependent predation in winter (Erlinge et al. 1984, 1988; but see Kidd & Lewis 1987). Our earlier studies in western Finland showed that vole mortality by breeding avian predators was directly density-dependent, whereas the number of voles killed by least weasels (*Mustela nivalis nivalis)* was delayedly density-dependent (Korpimäki & Norrdahl 1991a, Korpimäki 1993). Our results suggested that, in our study area, delayed density-dependent predation by small carnivores, especially by least weasels, may regulate vole populations (Korpimäki 1993; see also Hanski et al. 1993).

If carnivores are regulating or limiting prey populations, there should be a negative relationship between predation pressure and prey increase rate. In our study area, such relationship was found between voles and least weasels in winter: vole densities from autumn to spring decreased more in those winters when vole kill rate (predator density × proportion of prey in the diet) was high (Korpimäki et al. 1991). However, these results were based on a single study area and were restricted to winter period. Density declines continuing throughout summer despite continuous reproduction are a typical feature of cyclically fluctuating vole populations (e.g., Hansson & Henttonen 1985, 1988). Therefore, if small carnivores are a key factor in the regulation of cyclic vole populations, a negative relationship between small carnivore predation pressure and vole population dynamics should be evident in summer also.

In this paper, our aim is to study whether there is a relationship between small carnivore predation pressure (measured as small carnivore abundance) and prey population summer dynamics in several (8–10) study areas.

2. Material and methods

2.1. Study area

The study was carried out from 1989 to 1992 in western Finland (ca. 63°N, 23°E). In 1989, eight agricultural areas (each 3 km^2) were chosen for an avian predator removal experiment (the results of this removal experiment are presented elsewhere; breeding birds of prey did not seem to have long-term effects on small mammal dynamics). The proportion of agricultural fields in the study plots was 70–100% of the total area. In 1990, the number of areas was increased to ten. The distance from an area to its closest neighbour was 2.5–10 (mean 5.5) km (a river separated the closest areas). In half of the areas, we manipulated the numbers of breeding birds of prey by removing possible breeding sites of avian predators nesting in tree-holes and on stick-nests. In addition to natural stick-nests and tree-holes, the rest of the areas had several nest-boxes for Tengmalm's owls (*Aegolius funereus*) and kestrels (*Falco tinnunculus*) which, in addition to short-eared owls (*Asio flammeus*), were the most important birds of prey in the study plots. The least weasel, stoat (*Mustela erminea*) and the red fox were the most important mammalian predators.

Two voles (*Microtus epiroticus* and *M. agrestis*), were the main prey of vole-eating predators. The bank vole (*Clethrionomys glareolus*), common shrew (*Sorex araneus*) and water vole (*Arvicola terrestris*) were the most important alternative mammalian prey for these predators, followed by murids (harvest mouse, *Micromys minutus*, house mouse, *Mus musculus* and brown rat, *Rattus norvegicus*) (Korpimäki 1981, Korpimäki & Norrdahl 1991b, Korpimäki et al. 1991).

2.2. Predator densities

Density indices of mammalian predators (tracks km^{-1} day^{-1}) were obtained by snow-tracking in late November and early December (autumn abundances) soon after the first snowfall so that the tracks of only 1–2 nights were visible, and in late February and March (spring abundances) just before snowmelt using similar method. In each area, six track lines (length 915±190 m (mean ±*SD*)) were counted, and a manipulation-control area pair was counted on the same day. As both the density and activity of small carnivores affect our snow track indices, the snow track indices can be considered as a good index of small carnivore predation pressure (see Korpimäki et al. 1991 for further discussion on the reliability of snow tracking as an index of small mustelid density).

2.3. Estimation of prey densities

We monitored small mammal populations in the plots by using a "short line method", which was modified from the small quadrat method of Myllymäki et al. (1971) to suit the conditions of agricultural fields. Due to intensive cultivation, areas between ditches are unsuitable for voles most of the year so that voles have to occupy ditches and barns, especially in winter. The mean distance between ditches within study areas was 47–82 m. In each area, the ditches were numbered. Twelve forest sites (ca. 1 ha) were also numbered in areas including woodland. From these, a random subset was chosen for each trapping occasion (10 or 7 ditches + 3 forest sites in 1990, when vole densities were lowest, 8 or 6 ditches + 2 forest sites/trapping occasion in other years). In each selected ditch, ten mouse snap traps and one rat snap trap were set on a line with a distance of 10 m between traps for two nights and were checked once a day [a total of 220 (1990) or 176 (other years) trap nights per plot in each trapping session]. In forest sites, ten mouse snap traps were laid in two rows of five traps starting from the forest edge and extending straight in the forest, and the rat snap trap was set in a ditch close to the forest edge. The plots were trapped in April and August. Trapping was performed simultaneously in two areas (a manipulation-control -pair).

An independent index of pooled vole density in spring and autumn was obtained by counting the number of vole tracks in the track lines used to estimate small mustelid densities. We also calculated the tracks of hares (brown hares *Lepus europaeus* and mountain hares) and partridges (*Perdix perdix*) on the same lines.

2.4. Statistical analysis

In correlation analysis, we used Spearman rank correlation. Two-tailed statistics were used in all analysis.

The number of correlations calculated was 36 for pooled data, which means that ca. 2 significant relationships should have emerged by chance (we observed 6 of them). In the intra-annual analysis, the number of correlations was much higher (95), but we present the correlations as means with standard deviations. As the purpose of this paper is to study whether there is a relationship between small carnivore abundance and prey population dynamics in summer, type I errors are as harmful as type II errors (it would lead to a conclusion that predators do not have a strong impact on prey increase rate), and therefore we present the significance levels uncorrected despite a slightly higher type II error risk.

Table 1. Spearman rank correlation between small carnivore spring densities (tracks km^{-1} day^{-1}), and their spring and autumn densities during 1989–92. Number of areas was 10 (8 in 1989).

	L. weasel	Stoat	Red fox
# of years:	3	4	4
SPRING DENSITY:			
L. weasel			
– pooled[1]	—	–0.09	–0.18
– yearly[2]	–0.47 (.21)°	–0.02 (.27)	
Stoat			
– pooled	–	–	–0.12
– yearly	–0.10 (.44)		
AUTUMN DENSITY:			
L. weasel			
– pooled	0.36 *	0.21	0.09
– yearly	0.12 (.17)	0.04 (.57)	0.24 (.32)°
Stoat			
– pooled	0.10	0.26	0.21
– yearly	–0.44 (.42)°°	0.16 (.33)	0.25 (.17)
Red fox			
– pooled	–0.35 *	0.01	0.02
– yearly	–0.17 (.44)°	0.13 (.48)	–0.15 (.31)

1: N_{pooled}= areas * years = 38; * = $P < 0.05$.
2: Mean of yearly correlations (*S.D.*); each ° denotes one year with significant ($P < 0.05$) correlation.

3. Results

There was no obvious relationship between red fox and least weasel or stoat densities (Table 1). The spring densities of least weasels seemed to be negatively related to both spring and autumn densities of stoats when analysed on the yearly basis, but not in the pooled data. In the pooled data, the spring densities of least weasels positively correlated with the autumn densities of least weasels and negatively with autumn densities of red foxes (Table 1).

In the pooled data, the spring density of least weasels was negatively related to the density change of two *Microtus* voles and the bank vole from April to August, whereas no such relationship was found between stoat or red fox spring density and the density change of small mammals (Table 2). The same relationship was observed in the pooled snow track data: the change in the number of vole tracks from spring to autumn was negatively related to least weasel spring density (Table 3; Fig. 1). However, this negative relationship was mainly due to interannual dif-

Table 2. Spearman rank correlation between densities of small carnivores (spring density: tracks km^{-1} day^{-1}), and the change in the number of trapped small mammals from April to August during 1989–92.

	L. weasel	Stoat	Red fox
Water vole	–0.06	–0.04	0.25
Field vole	–0.39 *	–0.18	0.18
M. epiroticus	–0.40 *	–0.17	0.25
Bank vole	–0.51 **	–0.18	0.16
Common shrew	–0.27	–0.28 °	0.06

Pooled data, N = areas * years = 38; ° = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$.

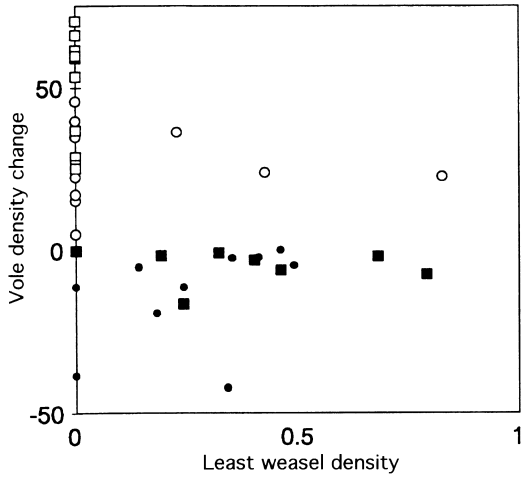

Fig. 1. The change in vole density from spring to autumn against the least weasel spring density in 1989 (black squares), 1990 (open squares), 1991 (circles) and 1992 (dots) in ten 3 km² study areas (8 in 1989). Density was measured as tracks km^{-1} day^{-1}.

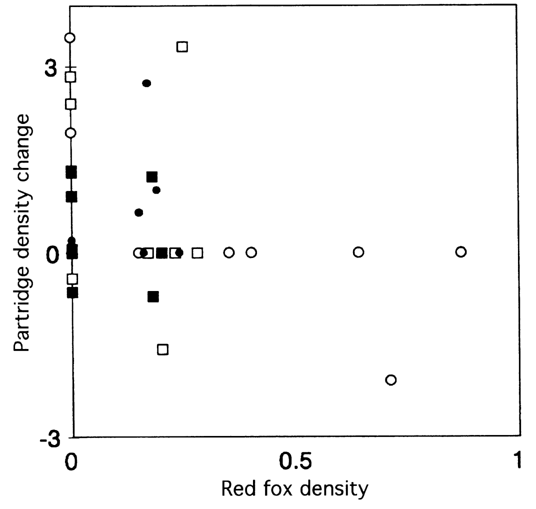

Fig. 2. The change in partridge density from spring to autumn against the red fox spring density in 1989 (black squares), 1990 (open squares), 1991 (circles) and 1992 (dots) in ten 3 km² study areas (8 in 1989). Density was measured as tracks km^{-1} day^{-1}.

ferences, as no such relationship was found in intra-annual comparisons (Table 4; Fig. 1).

There seemed to be a negative relationship between red fox spring density and the density change in partridges (Table 3; Fig. 2).

Table 3. Spearman rank correlation (*SD*) of small carnivore densities (spring density: tracks km^{-1} day^{-1}) with the change of prey densities from March to November during 1989–92. Number of areas 10 (8 in 1989).

	L. weasel	Stoat	Red fox
Voles:			
pooled[1]	–0.57 **	–0.28 °	0.13
yearly[2]	0.08 (0.58)$^{\square}$	–0.15 (.28)	0.02 (.31)
Hares:			
pooled	–0.06	0.03	–0.18
yearly	–0.02 (.51)	0.08 (.31)	–0.29 (.07)
Partridge:			
pooled	0.04	0.18	–0.29 °
yearly	0.30 (.08)	0.06 (.50)	–0.17 (.43)

1: N_{pooled} = areas * years = 38; ° = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$.
2: Mean of yearly correlations (*SD*); each $^{\square}$ denotes one year with significant ($P < 0.05$) correlation.

4. Discussion

4.1. Least weasel – small rodent interaction: scale matters

In accordance with the assumption that small carnivores regulate or limit small mammal populations, a negative relationship between least weasel spring densities and vole increase rate in the next summer was observed. However, this negative interaction was mainly caused by dif-

Table 4. Intra-annual Spearman rank correlation between least weasel spring densities (tracks km^{-1} day^{-1}), and the change in the number of trapped small mammals from April to August during 1989–92. Number of areas was 10 (8 in 1989).

	Least weasel density mean	*SD*
Change in density:		
Water vole	0.06	(0.32)
Field vole	0.17	(0.07)
M. epiroticus	0.12	(0.30)
Bank vole	–0.06	(0.24)
Common shrew	–0.05	(0.13)

ferences between years: the inverse relationship was only observed in the pooled data and disappeared when yearly data sets were analysed separately. There are at least two possible explanations for the observed pattern. First, the negative relationship in the pooled data may be caused by a strong one-way interaction: small rodent densities are regulated by some factor not studied, and least weasel densities reflect vole densities without having any strong impact on prey populations. Second, study areas (3 km^2) may have been too small in relation to the movements of least weasels. If this was true, the local spring density of least weasels was not a good index of predation pressure later in summer. The low correlation between least weasel spring and autumn densities in the intra-annual analysis suggest that this might have been true. In the pooled data, the correlation between least weasel spring and autumn densities was significant, and so was the correlation between spring densities of least weasels and prey increase rate. Recent results from Fennoscandia (Oksanen et al. 1992; K. Norrdahl and E. Korpimäki, unpublished data from live trapping and radio telemetry) suggest that movements of least weasels are extensive, especially when vole populations decline. Thus, it seems that, in a time-scale of several months, the predation impact of a least weasel is spread on a wide area (> 3 km^2), which means that pooled data probably gave a more reliable picture of the relationship between least weasels and their prey than the intra-annual analysis based on relationships within 3 km^2.

4.2. Stoats and red foxes: less important vole predators?

Stoats and red foxes are larger than least weasels, and their daily range of movement is probably larger than that of least weasels (e.g., Lockie 1966, Schantz 1981; but see Oksanen et al. 1992). Thus, if the 3 km^2 study areas were too small in the case of the least weasel, they may also have been so in the case of stoats and red foxes. This is also suggested by the lack of correlation between spring and autumn densities of stoats and red foxes in the intra-annual analysis. Yet, the lack of significant relationships between densities of stoats and red foxes, and small mammal density change in the pooled data implies that the impact of stoats and red foxes on prey populations was not as strong as the impact of least weasels. This result is consistent with previous studies indicating that the least weasel is the key predator eating voles in Fennoscandian areas with regularly oscillating vole populations (Henttonen et al. 1987, Korpimäki et al. 1991, Hanski et al. 1993, Korpimäki 1993, Norrdahl 1993).

4.3. Interactions within small carnivore guild

There were no relationship between red fox spring density and small mustelid densities in spring or autumn. This indicates that red foxes do not limit densities of small mustelids.

In the pooled data, there was no relationship between the densities of stoats and least weasels. In contrast, when the yearly data sets were analyzed separately, there was a weak negative interaction between the spring densities of stoats and least weasels (significant in one out of three years), and between the spring density of least weasels and the autumn density of stoats (significant in two out of three years). The former negative relationship probably reflects interspecific avoidance and/or food competition in small spatial scale, whereas the latter relationship may be explained by food competition: if least weasels markedly reduce local vole populations, stoats will shift to nearby areas with higher vole density. Thus, it seems that, in small spatial and temporal scale, there is a negative interaction between least weasels and stoats, whereas, in larger scale, the negative effects between these species are less clear or absent.

The negative relationship between the spring density of least weasels and the autumn density of red foxes may also be explained by the negative impact of least weasels on vole populations.

4.4. Small carnivores and game animals

Even though adult hares and partridges are very seldom killed by least weasels and stoats in our study area (Korpimäki et al. 1991), small mustelids may eat partridge eggs and chicks, and stoats may kill young hares. Yet, there were no relationship between small mustelid and hare or partridge density change in the course of summer. This indicates that small mustelids do not have a strong impact on hare or partridge populations.

The negative relationship between red fox density and partridge density change implies that red foxes may have a limiting impact on partridge populations in summer. Even though the spring density index may not accurately reflect local predation pressure in late summer, spring density may be a better index of predation pressure in early summer, when partridges are nesting. Predation on breeding partridges and their chicks in early summer may have a longer lasting effect on their population densities than in the case of small rodents, as small rodents continue to reproduce efficiently in late summer. Previous predator removal studies showed that the removal of small carnivores increased partridge nesting success, and that red fox was one of the main predators (Potts 1986). In these removal studies, several predators including stoats and carrion crows (*Corvus corone*) were removed and, thus, the relative importance of different predators remained unclear. Our study indicates that the stoat has a minor impact on partridge population dynamics, whereas predation by red foxes may be a limiting factor.

4.5. Scale of small carnivore studies

The question of scale seems to be central in studies on small carnivores. The negative interaction between least weasels and stoats seemed to operate on small spatial and temporal scale, whereas the negative relationship of least weasels to prey increase rate was evident only in comparisons on a larger scale. This is biologically relevant, if we assume that least weasels avoid patches with a resident stoat (Erlinge & Sandell 1988, Oksanen et al. 1992), and that least weasels live a nomadic-type life when vole populations decline staying in one patch only for few days or weeks before moving on. Then the negative relationship between stoats and least weasels would be clear only in small spatial and temporal scale, and the negative impact of least weasels on prey populations would be evident only if the study area is large enough to include a major part of the range of least weasel movements within the studied temporal scale. Little is known about the movement patterns of least weasels, especially when vole populations decline. Thus, at the moment it is unclear what would be a right size of study areas for least weasels. If predator densities are not monitored at few weeks intervals, 3 km^2 is probably too small.

4.5. Conclusions

Although our results are based on correlations, which do not reveal causes behind observed relationships, a few preliminary conclusions can be made. First, the least weasel seems to have a stronger impact on small rodent populations than the stoat or red fox have. This conclusion gives support to earlier papers stressing the importance of least weasels in regulating cyclically fluctuating vole populations (Henttonen et al. 1987, Korpimäki et al. 1991, Hanski et al. 1993, Korpimäki 1993, Norrdahl 1993). Second, the question of scale seems to be central in small carnivore studies. The spatial scale studied should be large enough in relation to the range of carnivore movements within the studied temporal scale. Third, small mustelids do not seem to have a strong impact on partridge or hare populations, whereas the red fox may have a limiting impact on partridge populations.

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