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The interactions of predator and hare populations in Finland — a study based on wildlife monitoring counts

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Numerical relationships between predators (red fox *Vulpes vulpes*, pine marten *Martes martes*, lynx *Lynx lynx*) and mountain hare (*Lepus timidus*) were studied using the data from the Finnish wildlife monitoring scheme in 1989–2000. Line transect (wildlife triangle) data were used to obtain snow track indices of relative predator abundance. Finland was divided into 29 100 × 100 km squares, each including the mean of 348 km of transect line (total length > 10 000 km annually). The abundance of fox was related to the yearly growth rate of hare populations in 48% of the squares. The growth rates of fox and hare populations also correlated in 45% of the squares, indicating that there was a mutual relationship between hare and fox populations in about half of the squares. This relationship existed in areas with low/moderate hare and high fox numbers (a low hare/fox index) but was lacking in areas with a high hare/fox index, pointing to both functional and numerical response for foxes preying on hares. There was also a positive spatial correlation between hare and lynx numbers, but the correlation between hare and marten numbers was weak.

1. Introduction

The relationships between mammalian predators and their prey populations remain a central issue in boreal animal ecology (e.g. Angelstam *et al.* 1984, Erlinge *et al.* 1984, Hansson & Henttonen 1989, Lindström 1989, Marcström *et al.* 1989, Korpimäki 1993, and references therein). The problem is especially challenging because experimental research in this area is not easy.

Hearn *et al.* (1987) found that first-year survival rate of juvenile arctic hares (*Lepus arcticus*) in Newfoundland was only 0.15 and the main cause of natural mortality was predation by the red fox (*Vulpes vulpes*). They suggested that predation of juveniles by foxes is limiting the hare population. Hodges *et al.* (1999) found that > 75% of snowshoe hare (*Lepus americanus*) deaths resulted from predation even when predators were scarce, and mammalian predator reduction resulted in higher hare densities. The joint manipulation of food addition and predator control resulted in even higher hare densities (Krebs *et al.* 1995, Hodges *et al.* 1999). Francesco *et al.* (1996) found that fox predation was the main course of death of European hares (*Lepus europaeus*) in Italy.

Lynx (*Lynx canadensis*) numbers are known to peak one year after the peak in hare numbers (e.g. MacLulick 1937, O'Donoghue *et al.* 1997) and predators respond both numerically and functionally to hare abundance (Keith *et al.* 1977). Results of some studies suggest that lynx predation is partly or totally responsible for hare cycles in North America (Keith & Windberg 1978, Keith *et al.* 1984, Krebs *et al.* 1986, Sinclair *et al.* 1988, Keith 1990, O'Donoghue *et al.* 1997) and hence, there is a mutual relationship between hares and their predators.

In Sweden, mountain hare (*Lepus timidus*) densities increased when foxes and martens (*Martes martes*) were efficiently controlled from two islands (Marcström *et al.* 1989). When sarcoptic mange killed many foxes in Sweden during the late 1970s and 1980s, mountain hare populations increased and lost their cyclicity, but decreased again when foxes recovered from the disease (Danell & Hörnfeldt 1987, Lindström *et al.* 1994). When the mange spread through Norway during 1976–1986, hunting bag of fox decreased and that of hare increased (Smedshaug *et al.* 1999). These studies point to the conclusion that mammalian predators can limit/regulate hare populations also in Scandinavia.

The interactions between carnivores and mountain hare and game bird populations were also studied experimentally in Finland by removing predators from some areas and protecting them in others (Kauhala *et al.* 1999, 2000). According to the Finnish study, localized removal or protection of predators did not affect hare numbers; hence, these results are incompatible with those of the Scandinavian studies. Experimental removal studies in mainland circumstances are, however, difficult; the areas must be relatively small to have a considerable effect on predator density which inevitably means that they are small with respect to home range size of predators causing a continuous influx of individuals into the removal area. Therefore, a more generalized study of the relationships between hares and their predators is needed.

In Finland, we have a unique wildlife monitoring system covering the whole country, the so-called wildlife triangles (Lindén *et al.* 1996). The snow tracks of mammals have been counted from > 10 000 km of transect line each winter since 1989. Using these data it is possible to analyze the relationships between different mammal species. We used the data to study the relationships between the mountain hare, red fox, pine marten and lynx (*Lynx lynx*).

We tested the following hypotheses (mainly based on the references above):

1. The growth rate of predator populations (especially that of the fox) correlates with that of hare populations.
2. Lynx numbers follow hare numbers with a time-lag of one year (as it does in North America).
3. The growth rate of hare population is affected by predator density.
4. The growth rate of hare population is also affected by hare density, i.e. hare populations are regulated in a density-dependent manner.

2. Material and methods

2.1. Study areas and monitoring populations

The data were collected using wildlife triangle counts (*see* Lindén *et al.* 1996). In Finland, there are about 1 200 wildlife triangles situated randomly in forested areas. The triangles are equilateral and each side is 4 km long; thus, the total length of each inventory route is 12 km. These routes are permanent from year to year. Voluntary assistants perform the counts each year.

We divided the country into 29 squares (100 km × 100 km; Fig. 1). The mean number of triangles per square was 29 equaling 348 km of transect line. Tracks crossing the transect line were counted from > 10 000 km each year from 15 January to 15 March. The tracks were counted 1–5 days after a snowfall. While calculating the track index, the time after the snow fall was taken into account: the track index for each species gives the number of crossings per 24 h per 10 km. Here, we used the track indices of red fox, pine marten, lynx and mountain hare from 1989 to 2000. We assumed that the relationship between the track index and population density is linear (*see also* Högmander & Penttinen 1996).

We also calculated the growth rate for each species:

$$\text{Growth rate} = \log a_{t+1} - \log a_t \qquad (1)$$

where a_{t+1} is the track index of a species in year $t + 1$ and a_t the track index in year t.

2.2. Statistical analyses

We tested the trends in population densities by regressing the track indices against time. We also used correlation and regression analyses to test the relationships between hares and their predators. We calculated the impact of predator and hare density on hare growth rate and the dependence of predators on hare numbers. The *fox impact* is the r^2-value when hare growth rate was regressed against log fox index in each square. The *index of dependence* is the r-value from the correlation between the hare growth rate and the fox growth rate.

3. Results

3.1. Spatial variation in hare and carnivore populations

The hare index was highest in central and SE Finland and lowest in Lapland (Fig. 1) and declined during the study in S Finland but increased in two squares further north. The fox index was highest in SW Finland and decreased towards the east and north. The fox index declined in a few squares, but did not increase in any area. The marten index was highest in E and S Finland, lowest in central and W Finland. It increased in E Finland but declined especially in SW Finland. The lynx index was highest in SE and E Finland and increased in two squares there.

The mean hare index correlated positively with the mean lynx index and the mean fox index (Table 1), but correlation with the mean marten index was weak. The correlation was strongest between the hare and lynx indices. The mean marten index also correlated positively with the fox and lynx indices.

3.2. Temporal variation in hare and predator populations

3.2.1. The correlation between hare and predator growth rates

The growth rate of hare populations and that of fox populations correlated positively in 93% (27/29) of the squares; the deviation from equal numbers of positive and negative correlations was significant (sign test: $p < 0.001$). Since 45% (13/29) of the correlations were positive and also statistically significant ($p < 0.05$), hypothesis one came partly true: fox numbers increased with increasing hare numbers and decreased with decreasing hare numbers (Fig. 2a and b). The index of dependence was highest in areas where the fox index was highest (Fig. 2b).

The growth rate of the marten population correlated positively with that of the hare population in 76% (22/29) of the squares (sign test: $p = 0.067$), but only one correlation was positive and significant, indicating that the relationship between marten and hare was rather week.

The hare and lynx indices correlated positively in 61.5% (18/29) of the squares (sign test: $p > 0.10$) and only one correlation was positive and significant. When a time lag of one year was taken into account, 55% of the correlations were positive and two were positive and significant, indicating a weak relationship between hare and lynx, and hypothesis two did not come true.

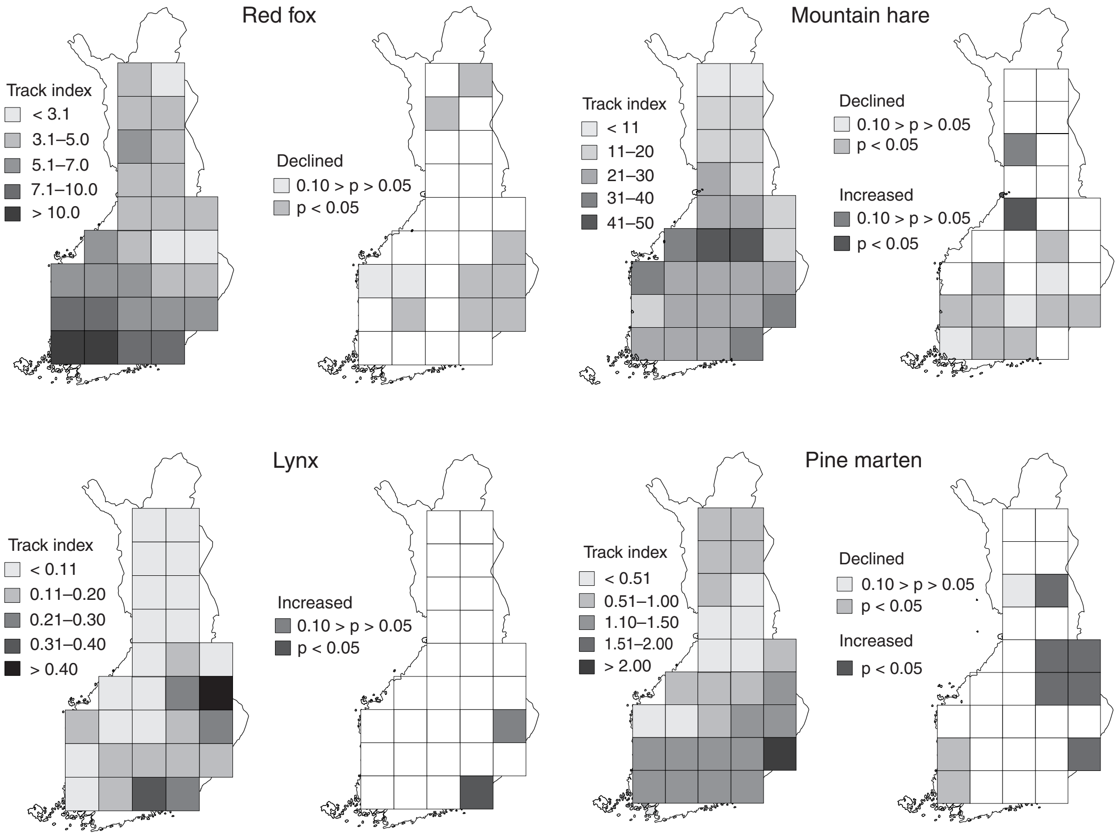

Fig. 1. Mean snow track indices, based on wildlife triangle counts, of the mountain hare and different predator species in each 100 × 100 km square during the study (from 1989 to 2000). The trends in track indices are also shown. Trends were tested by regressing the track index against time.

Table 1. Correlations between the mean log hare index and the mean log predator indices (1989–2000) in each square.

	Hare	Fox	Marten
r-values			
Fox	0.34		
Marten	0.23	0.39	
Lynx	0.48	–0.02	0.51
Probabilities			
Fox	0.069		
Marten	0.353	0.039	
Lynx	0.008	0.938	0.004

3.2.2. The effect of predator and hare density on hare populations

To reveal the possible negative effect of predators and/or hare density on the growth rate of hare populations, we regressed the growth rate of the hare population (from year t to year $t + 1$) against the predator and hare indices (year t) in each square (Table 2). The fox index was included in 14 models (48%), the hare index in 13 (45%), the marten index in 4 (14%) and the lynx index in 3 (19%) models. The fox abundance was thus the most important variable that possibly affected the growth rate of hare populations, and hypothesis

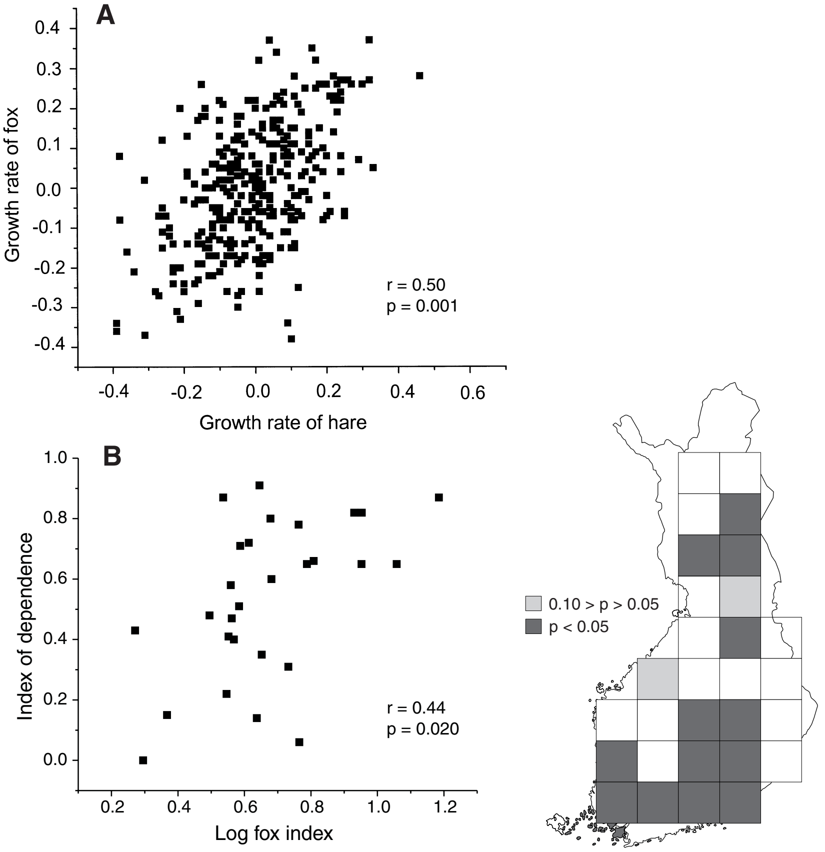

Fig. 2. — A: Correlation between the growth rate of hare and that of the fox population, data from all areas pooled. — B: Relationship between the index of dependence and mean log fox index in each square. Index of dependence is the *r*-value from the correlations between the hare growth rate and the fox growth rate. The map shows the squares with positive correlation and $p < 0.10$.

three came true. The fox impact (r^2-value from the regressions above) was strongest in areas where the hare index was lowest (Fig. 3). In some squares, fox had an impact on the hare growth rate, and the fox growth rate also correlated with that of hare, indicating a possible mutual relationship between hare and fox, but in other areas these two species seem to be independent of each other (Figs. 2–4).

4. Discussion

The spatial correlation between the hare and lynx indices suggests that the lynx numbers are high in areas of abundant hare populations and low in areas where hares are scarce. In North America, lynx even selected the habitats preferred by snowshoe hares (Murray *et al.* 1994). North American studies of lynx and snowshoe hare also showed that lynx numbers were associated to hare numbers (e.g. Elton & Nicholson 1942, Brand *et al.* 1976, Brand & Keith 1979). Hares are among the main prey species of the lynx in North America, and low hare densities have been connected with the increase of lynx mortality rate, increase of dispersal, decrease in recruitment and decline in lynx numbers (Brand & Keith 1979, Poole 1994, Mowat *et al.* 1996).

When we examined the temporal variation of hare and lynx numbers in Finland, the lynx numbers seemed to be independent of changes in the hare numbers. This may be due to the scarcity of lynx tracks; yearly the lynx indices were too small to permit reliable conclusions. But when the data from the whole study period (12 years) were pooled, the mean lynx index in each square was more reliable and revealed the positive spatial relationship between the hare and lynx numbers. Another explanation may be that European lynx is larger than the American lynx and preys more on larger species like the white-tailed deer (*Odocoileus virginianus*). European lynx may thus be less dependent on hare numbers than the American lynx.

There was a mutual relationship between fox and hare in some areas, but not in others. The relationship between hare and fox was strong in S Finland where the hare density was rather low/moderate and the fox density high. In these areas, the hare could not escape the control of foxes and the hare numbers remained rather low. When hare numbers are not very high, the functional response of foxes may also be important in limiting hare population growth (Angerbjörn 1989). It is, however, possible that the hare numbers were also limited by other factors, like disease, parasites or competition with the European hare. The positive correlation between the growth rate of hare and that of fox can also, at least partly, be a consequence of vole cycles; when voles are abundant, foxes prey mainly on them and less on hares, and hare numbers increase. Since also fox numbers increase after a vole peak, there may be a positive

Table 2. Results of stepwise (forward) regression analyses; the annual growth rate of the hare (from year t to year $t + 1$) was regressed against the log predator and hare indices (year t). All independent variables included in the model have a negative effect on hare growth rate. Variables were included when $p < 0.10$. Dependent variable: growth rate of hare.

Area	Model			Independent variables included in the model
	r^2	F	p	
1	0.37	5.20	0.049	hare index
2	0.45	7.36	0.024	fox index
3	0.41	6.11	0.035	hare index
4	0.78	13.83	0.003	hare index + lynx index
5	0.37	5.24	0.048	fox index
6	0.33	4.52	0.062	lynx index
7	0.29	3.74	0.085	fox index
8	0.33	4.34	0.067	fox index
9	0.57	5.27	0.035	hare index + marten index
10	0.32	4.23	0.070	fox index
11	0.61	6.12	0.024	hare index + marten index
12	0.78	14.05	0.002	fox index + marten index
13	0.42	6.50	0.031	hare index
14	0.66	17.35	0.002	hare index
15	0.72	23.61	0.001	hare index
16	0.32	4.30	0.068	hare index
17	0.29	3.60	0.090	hare index
18	–	–	–	–
19	0.63	6.93	0.018	hare index + fox index
20	0.87	26.14	< 0.001	marten index + lynx index
21	0.47	8.04	0.020	fox index
22	0.30	3.92	0.079	hare index
23	0.83	43.08	< 0.001	fox index
24	0.40	6.06	0.036	fox index
25	0.65	16.36	0.003	fox index
26	0.50	8.85	0.016	fox index
27	0.85	38.41	< 0.001	fox index
28	0.46	8.57	0.015	fox index
29	0.52	9.86	0.012	hare index

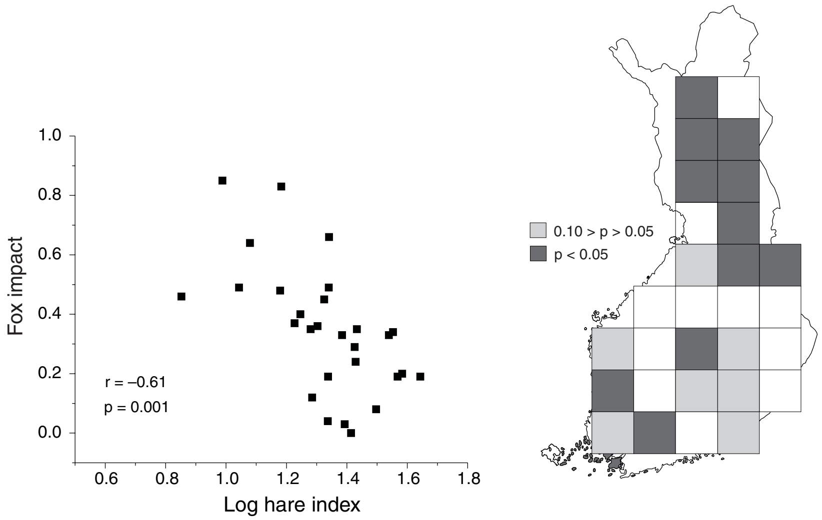

Fig. 3. Relationship between fox impact on hare growth rate and the mean hare index in each square. Fox impact is the r^2-value when hare growth rate was regressed against log fox index in each square. The map shows the squares where fox has an impact on hare growth rate and *p* < 0.10.

correlation between hare and fox numbers (Angelstam *et al.* 1984). Since in Finland vole numbers are not monitored well enough, we could not include them in the analyses.

In areas (e.g. E and Central Finland) with the high hare index and low fox index, hare populations have escaped the control of foxes and are density-dependent. This also explains why predator removal/protection did not affect the hare populations in E Finland (Kauhala et al. 1999). In areas with the high hare/fox index, other factors than hare numbers must have affected the fox density, i.e. fox numbers could not respond to the abundance of one of their main prey species. Especially in E Finland fox numbers are very low but the reason for this is not clear; disease and parasites (e.g. the mange) or hunting may be among the causes. In the predator removal experiment, we also found that in the predator removal areas the fox numbers did not follow the hare numbers because hunting kept the fox numbers at a low level (Kauhala *et al.* 1999). On the contrary, in the predator protection areas, where the system was not disturbed and fox numbers were higher, the fox numbers increased with the increasing hare numbers.

In northern Finland, there was also a mutual relationship between hare and fox. But unlike in S Finland where the hare numbers declined during the study, in Lapland the hare numbers probably show regular fluctuations (Fig. 4; Pulliainen & Tunkkari 1987). In Lapland, fox may have an effect on the hare population when hare numbers are low; if the prey species is cyclic, predation can deepen the low phase (e.g. Keith *et al.* 1977) but is unlikely to affect the prey population when prey numbers are increasing or high. In Lapland, the predator removal experiment was done between 1993 and 1997 when hare populations increased, which may explain, why the fox removal/protection did not affect the hare populations there, although it affected grouse reproductive success (Kauhala *et al.* 1999, 2000).

A predator removal experiment in Sweden showed that both the number of fox and marten in the study areas affected the numbers of mountain hare, and survival rates of hare were lowest when voles were scarce (Marcström *et al.* 1989). In the present study, the relationship between the marten and hare was, however, weak, although martens are known to prey on hares (Poole & Graf 1996).

The hare density also affected the growth rate of the hare population, indicating density-dependence in hare populations. When hare populations are abundant, scarcity of food, diseases and parasites tend to decrease hare numbers. When hare populations are moderate, also functional response of predators can affect hare populations (Angerbjörn 1989). Consequently, even when the hare density was the most important factor in the model affecting the hare growth rate, the effect of predators could not be excluded. Angerbjörn (1989) studied the functional response of predators and

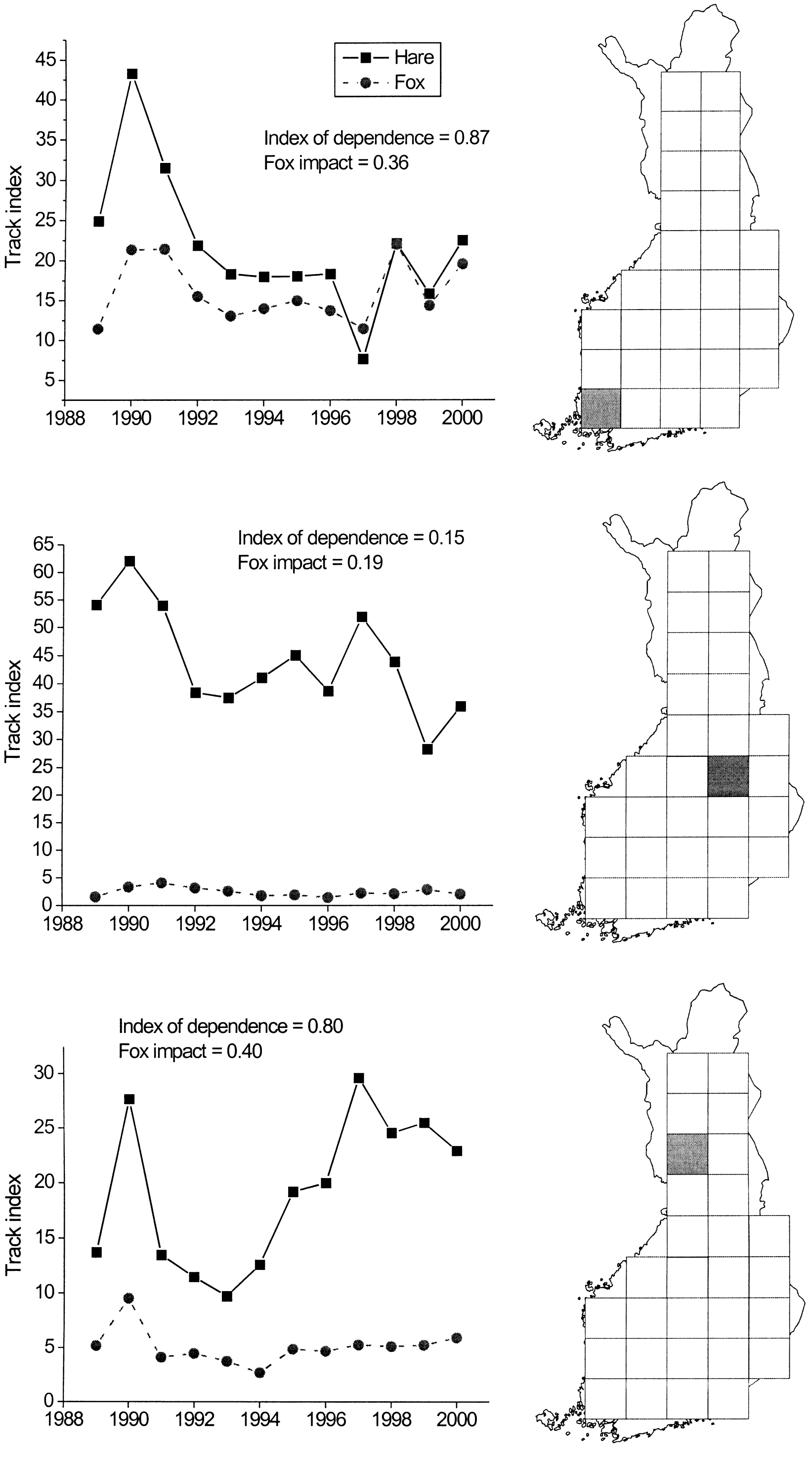

Fig. 4. Examples of three squares with low and high hare/fox ratio and consequently, strong and lacking mutual relationship between hare and fox populations. It should be noted here that the track indices are not equal to absolute population densities.

found that winter mortality of mountain hares was density-dependent during years of high predation pressure, but independent of density when predators were absent.

In conclusion, in Finland the relationship between fox and hare seems to be stronger than the relationship between hare and other predators. In areas (e.g. E Finland) where some factor limits fox numbers, the hare population is dense, density-dependent and has escaped the control of foxes. In areas (S Finland) with a dense fox population and low/moderate hare population, foxes may respond both numerically and functionally to the increase/decrease in hare numbers and can also limit the growth of the hare population. In areas, where hare populations are cyclic (N Finland), fox can affect hare population during the cyclic lows of hares. Lynx numbers are high in areas with a dense hare population, while marten numbers seem to be rather independent of hare numbers.

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