

Impact of predator removal on predator and mountain hare populations in Finland

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The impact of predator removal on predator and mountain hare (*Lepus timidus*) populations was studied in southern, eastern and northern Finland in 1993–1998. In predator removal areas predators were intensively hunted, and in predator protection areas hunting was prohibited. Both predator (red fox *Vulpes vulpes*, pine marten *Martes martes*, stoat *Mustela erminea* and raccoon dog *Nyctereutes procyonoides*) and mountain hare populations were monitored in the study areas. Fox and marten populations were affected by predator removal/protection in eastern and northern Finland but the effect was not as evident in southern Finland. The stoat population was not affected by removal, but the raccoon dog population was to some extent. Trends in hare populations were similar in the removal and protection areas, indicating that localized control/protection of predators did not affect hare numbers. Hare population even increased in the protection area of northern Finland although predator numbers increased and vole numbers declined.

1. Introduction

The impact of predators on their prey animals varies with circumstances: in one community predators may affect considerably the prey populations, while in other areas only a slight effect or no effect at all is detected. The heterogeneity of the habitat and prey migrations may, for instance, affect the impact of predators on their prey populations (e.g., Sinclair & Norton-Griffits 1979). The

densities of both prey and predator populations affect the predation pressure (e.g., Angerbjörn 1989, Lindström *et al.* 1994). The nature of the predator (generalist *versus* specialist) is also important to predator–prey relationships; generalist predators may shift from their main prey (e.g., voles) to the alternative prey (e.g., hares) when vole populations crash (alternative prey hypothesis, Hagen 1952, Lack 1954, Angelstam *et al.* 1984).

Marcström *et al.* (1989) studied the effect of

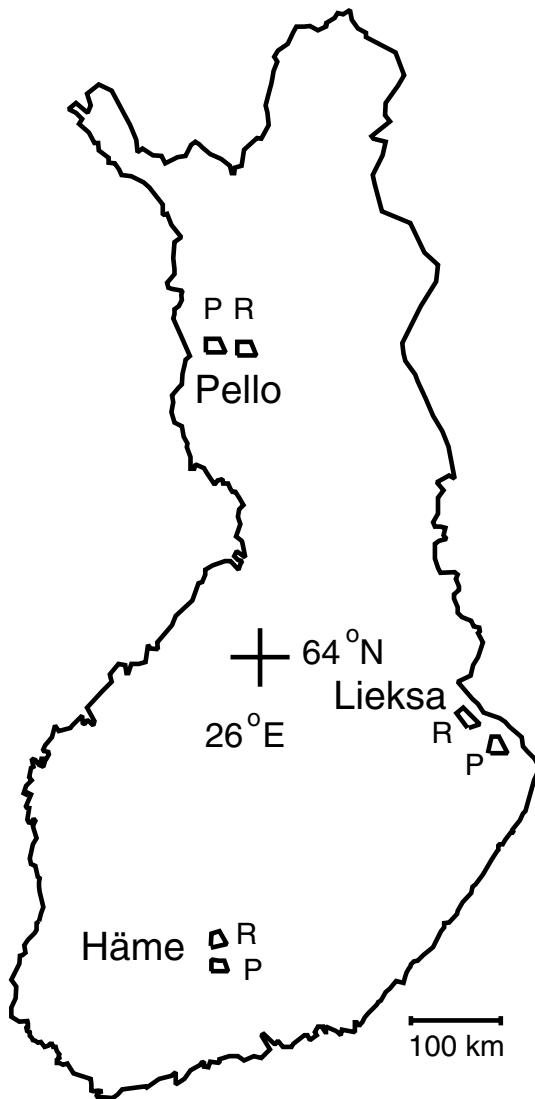


Fig. 1. The study areas in Finland. R = predator removal area, P = predator protection area.

experimental reductions of red foxes (*Vulpes vulpes*) and pine martens (*Martes martes*) on mountain hare (*Lepus timidus*) populations on two islands in Sweden. They found that hare densities increased when foxes and martens were efficiently controlled. This study was conducted in an island environment, however, and the results may not be valid in Finnish mainland habitats. In a closed system, such as an island, the impact of predators on their prey may differ from that in an open mainland system.

Foxes frequently prey on hares in Finland: al-

most 60% of red fox scats collected from fox dens in southern Finland during summer contained remains of hares (Kauhala et al. 1998), and 33% of fox stomachs contained hare remains in winter in NE Finland (Vainio et al. 1997). It remains uncertain, however, whether hare populations in Finland are limited by foxes or other predators; a high rate of consumption is by no means sufficient evidence for population limitation (Lindström et al. 1986). Frylestam (1979) found that population density correlated negatively with the reproductive rate of the European hare (*Lepus europaeus*) in Sweden. If a hare population suffers from a high predation rate, it may thus compensate for the high mortality rate by increasing its reproductive rate. As a result, even if predators kill a considerable proportion of hares, it does not necessarily mean that hare populations are limited by predators.

Experimental studies are needed to find out the relationship between the mountain hare and its mammalian predators in different environments. The aim of the present experimental study was to examine (1) whether red fox, pine marten, stoat (*Mustela erminea*) and raccoon dog (*Nyctereutes procyonoides*) populations can be controlled in Finland at a local scale using mainly normal hunting methods during hunting seasons, and (2) whether mountain hare populations benefit from the control, i.e. do predators limit mountain hare populations in Finland. If they do and if hares are alternative prey for, e.g., foxes, hare abundance should follow vole abundance in the predator protection areas, while if predator removal is effective there should not be a positive correlation between voles and hares in the predator removal areas. The experimental study thus makes it possible to address more theoretical aspects of prey-predator dynamics, including the alternative prey hypothesis and the time lag in this prey-predator system, and rate of immigration of individuals to areas made 'empty' by predator control, among others.

2. Material and methods

2.1. The study areas and experimental design

The study was performed between 1993 and 1997 in eastern and northern Finland (Lieksa and Pello) and between 1993 and 1998 in southern Finland (Häme; Fig. 1). Two study

areas were set up in each region: a removal (R) area where small and medium-sized carnivores were efficiently hunted and a protection (P) area where predator hunting was prohibited. The areas were as similar as possible in other respects. The carnivores removed were the red fox, the raccoon dog, the pine marten and the stoat. The raccoon dog was hunted only in Häme, because it is quite rare in Lieksa and Pello. The stoat was considered a relevant predator only in Häme and, thus, it was not hunted in Häme or Lieksa. In Häme, the R area was 55 km² and the P area 48 km². In Lieksa, the areas were 72 km² and 106 km², and in Pello 100 km² and 116 km², respectively. The distance between the R and P areas was at least 5 km.

Local hunters hunted the predator populations in the R areas using mainly legal hunting methods during the normal hunting season, because we wanted to test whether or not predators can be controlled effectively with legal methods. Predator removal/protection was initiated in August 1993. Other species were hunted normally in all areas during the experiment.

2.2. Monitoring populations

The mountain hare, red fox, pine marten and stoat populations were monitored each winter (15 January–15 March) in the study areas by snow track counting. We used the wildlife triangle method (Lindén *et al.* 1996), but the snow tracks were counted from straight transect lines rather than triangular routes. The lines crossed the areas from south to north at intervals of 1 km, except in southern Finland where they were set at intervals of 500 m. The tracks crossing the lines were counted 1–5 days after a snowfall. The abundance index for each species gives the number of crossings per 10 km per 24 hours. We used 3-year moving averages to smooth the data.

Since the snow track counts cannot be used for winter-dormant species, we used 'the scent station method' (*see* Linhart & Knowlton 1975) to monitor the raccoon dog population in Häme. Scent stations are patches of sand (radius about 1 m) with a stick in the middle which is dipped in gray fox gland lure (a commercial product distributed by J. R. and Sons, Monroeville, Ohio). The lure attracts animals, which come to sniff the stick, leaving their footprints in the sand. We checked the stations (50 per area) each morning and levelled the sand if tracks were observed. We gathered these data during a 5-day period in late May or early June in 1994–1998. The abundance index gives the percentage of scent stations visited by a raccoon dog during the 5-day period. The results show the relative density of adult raccoon dogs, because the pups are usually born in May and are too small to move around in early summer. We also calculated an abundance index for the red fox using this method.

We also monitored the abundance of small mammals by trapping in September (360 trap-nights each). In Häme, trapping was done in both areas (starting in area P in 1992 and in area R in autumn 1994), but in Lieksa and Pello

trapping was done in one place between the two study areas. The trap index gives the number of small mammals caught per 100 trap-nights. Small mammals were mainly voles (*Microtus* spp. and *Clethrionomys* spp.), but we also caught some shrews (*Sorex* spp.).

Since the experiment was very laborious and expensive, we had only one R and one P area in each region. This limited the possibilities to use statistical tests to analyse the data.

2.3. Wildlife triangles

We compared the results of the experimental study to those obtained from wildlife triangle scheme to find out possible long-term effects of foxes on hares (data from 1989–1998). The method used in this National monitoring program is otherwise the same as used in our predator removal/protection areas, but the transect lines are 12 km long and triangular in shape (*see* Lindén *et al.* 1996). Wildlife triangles situating within 50 km from the centre points of our three study areas were taken into account. The mean annual total lengths of transects for southern, eastern and northern Finnish study areas are 416, 501 and 431 km, respectively.

3. Results

3.1. Predator abundance

The numbers of predators removed are shown in Table 1. Estimated autumn densities of foxes are based on the winter density and the available data on the reproduction and mortality rate of red foxes: we estimated that 5 pups are born per pair of foxes and that 50% of pups die during the summer (e.g., Lloyd *et al.* 1976, Lindström 1988, Kauhala 1996). Winter densities of red fox, pine marten and stoat are derived from track densities using the method introduced by Formosov (1932) and Malyshev (1936). The data needed in the conversion — the mean daily cruising distance of the individuals of a species — for these species are adopted from Finland and Soviet Karelia (Helle 1990, Danilov *et al.* 1996). Estimated winter and autumn densities of raccoon dogs are based on available data on the home ranges, productivity and mortality rate of raccoon dogs: two home ranges per 10 km², the mean productivity 6.9 pups per a pair, but 50% of them dying during the summer (Helle & Kauhala 1993, 1995, Kauhala *et al.* 1993).

In Pello and Lieksa, fox and marten indices increased in the P areas but decreased in the R ar-

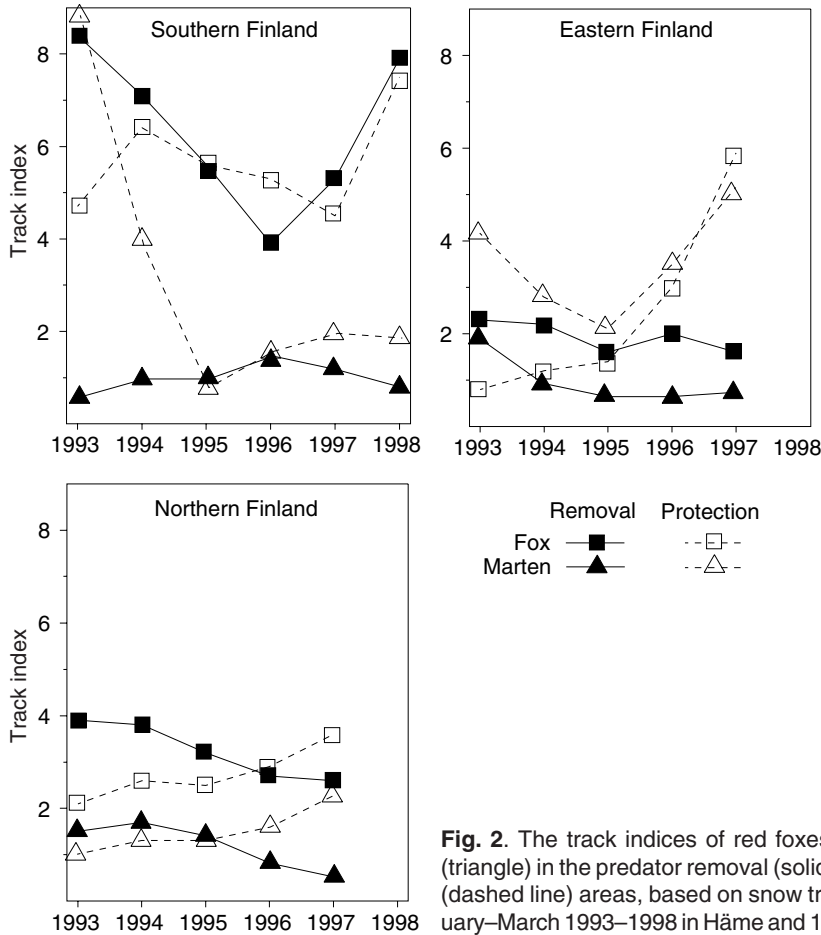


Fig. 2. The track indices of red foxes (square) and pine martens (triangle) in the predator removal (solid line) and predator protection (dashed line) areas, based on snow track counts performed in January–March 1993–1998 in Häme and 1993–1997 in Lieksa and Pello.

cas during the experiment (Fig. 2) suggesting that predator removal was effective. The mean annual

growth rate (N_{t+1}/N_t) of the fox population was 0.90 in Pello R and 1.15 in Pello P, while it was

Table 1. The estimated winter and autumn densities of predators and the number and percentage of predators removed from predator removal areas during the experiment.

Area/ Species	Winter density ind./10 km ²	Estimated autumn density ind./10 km ²	Number removed per 10 km ²	% of autumn population removed
Häme R:				
Raccoon dog	4.0	10.9	11.7	107.0
Red fox	2.0	4.5	1.8	40.0
Pine marten	0.5	–	1.5	–
Lieksa R:				
Red fox	0.6	1.4	2.0	143.0
Pine marten	0.3	–	1.4	–
Pello R:				
Red fox	1.1	2.5	1.8	72.0
Pine marten	0.4	–	0.7	–
Stoat	2.2	–	1.0	–

0.94 and 1.99 in Lieksa R and Lieksa P, respectively. The growth rate of the marten population was 0.79 in Pello R and 1.24 in Pello P, and 0.79 and 1.14 in Lieksa R and Lieksa P, respectively. The stoat index declined in both areas in Pello during the study (Table 2).

In Häme, the snow track index of fox was almost equal in both areas after the experiment. The results obtained using the scent station method, however, suggested that fox density declined and remained low during the latter half of the experiment in Häme R (Fig. 3).

The mean raccoon dog index during the study was 41.3 for Häme R and 36.8 for Häme P, respectively (Fig. 3). The index increased, however, in Häme P during the study and decreased in Häme R after 1996, indicating a possible effect of raccoon dog removal/protection on raccoon dog populations.

3.2. Hare abundance

In Lieksa and Pello, hare numbers increased in both areas and the population growth rate was even faster in the P areas than in the R areas in the latter half of the experiment (Fig. 4). The mean annual growth rate (N_{t+1}/N_t) of the hare population was 1.31 in Lieksa R and 1.18 in Pello R, while it was 1.82 and 1.29 in the P areas of Lieksa and Pello, respectively. In Häme, the hare index declined during the study in both areas excluding the last year when the index increased in the P area.

The annual change (%) in the hare index correlated positively with the annual change in the

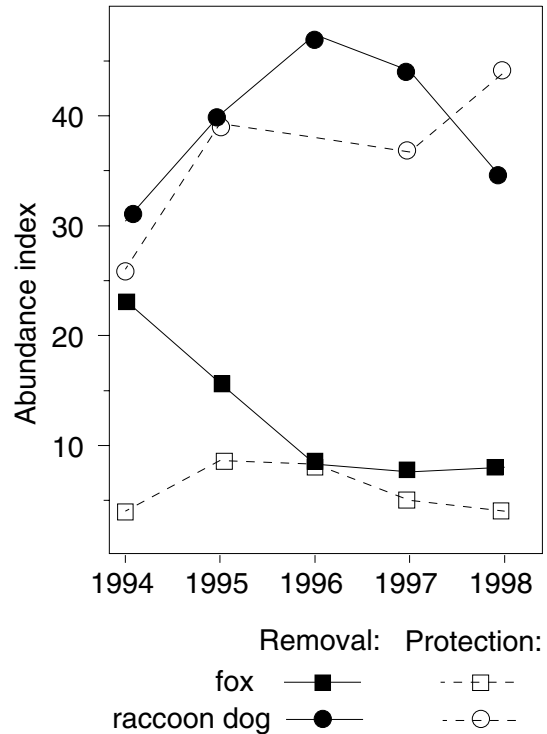


Fig. 3. The relative abundance of raccoon dogs (circle) and red foxes (square) in early summer 1994–1998 in the Häme study areas, based on the scent station method. Predator removal (solid line) or protection (dashed line) was initiated in August 1993.

fox and marten indices in the P areas (pooled data for 3 areas, fox: $r = 0.76$, $p = 0.003$, marten: $r = 0.56$, $p = 0.049$; Fig. 5), indicating that fox and marten numbers follow hare numbers when predators are not hunted. No such relationship existed in the R areas (fox: $r = 0.12$, $p = 0.703$, marten: $r = -0.45$, $p = 0.124$; Fig. 6).

Table 2. Trap-index of small mammals in the study areas. The trap-index gives the number of small mammals trapped per 100 trap-nights. The number of trap-nights was 360 per year and area. The snow track index of stoat (tracks per 10 km per day) in Pello is also given.

Area	1992	1993	1994	1995	1996	1997	1998
Voles:							
Häme R	–	–	23.0	5.3	0.8	2.8	3.9
Häme P	25.8	4.7	4.7	3.6	1.1	4.2	1.7
Lieksa	–	3.9	3.1	8.6	9.4	1.1	–
Pello	–	7.5	8.6	6.1	2.5	1.7	–
Stoat:							
Pello R	–	3.9	1.6	1.3	1.0	1.1	–
Pello P	–	18.4	4.4	5.3	3.5	3.8	–

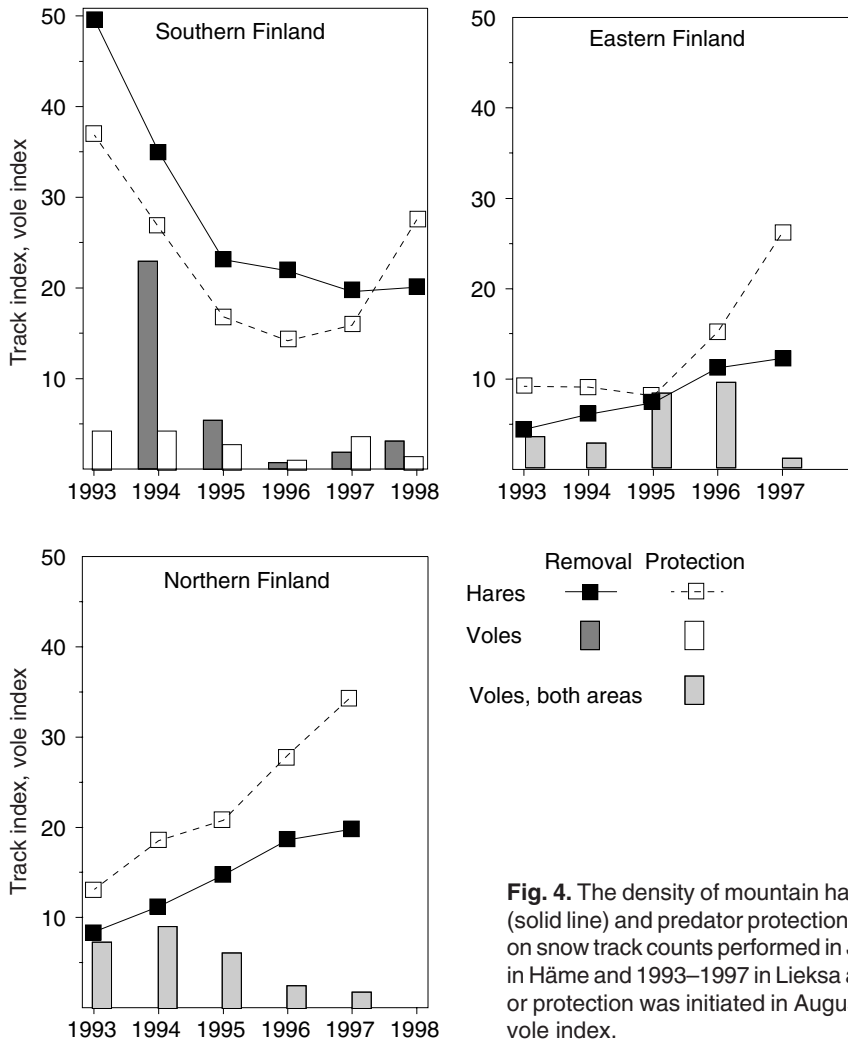


Fig. 4. The density of mountain hares in the predator removal (solid line) and predator protection (dashed line) areas, based on snow track counts performed in January–March 1993–1998 in Häme and 1993–1997 in Lieksa and Pello. Predator removal or protection was initiated in August 1993. The bars show the vole index.

We also calculated the correlations with a time lag of one year (fox: year t , hare: year $t + 1$). The results indicated that the fox had no effect on hare populations (R areas: $r = 0.00$, $p = 0.960$, P areas: $r = 0.13$, $p = 0.725$).

We also regressed the annual change in hare index (from year t to year $t + 1$) against the relative abundance of fox population in year t (the deviation from the mean track index). The results suggest that fox abundance did not affect hare populations (areas R: $t = 0.12$, $r^2 = 0.001$, $F = 0.01$, $df = 1, 11$, $p = 0.908$; areas P: $t = -0.915$, $r^2 = 0.071$, $F = 0.84$, $df = 1, 11$, $p = 0.380$).

3.3. Vole abundance

Vole numbers peaked in Häme P in 1992 and in Häme R in 1994 and declined thereafter (Table 2). Vole numbers were low or moderate during the study in Lieksa and Pello, and no vole peak was observed in these areas between 1993 and 1997. There were negative correlations between the abundance of hares and voles in Pello (area R: $r = -0.93$, $p = 0.022$, area P: $r = -0.92$, $p = 0.028$). The correlations were not significant in Lieksa (area R: $r = 0.05$, $p = 0.937$, area P: $r = -0.44$, $p = 0.457$), but there was a positive correlation in the

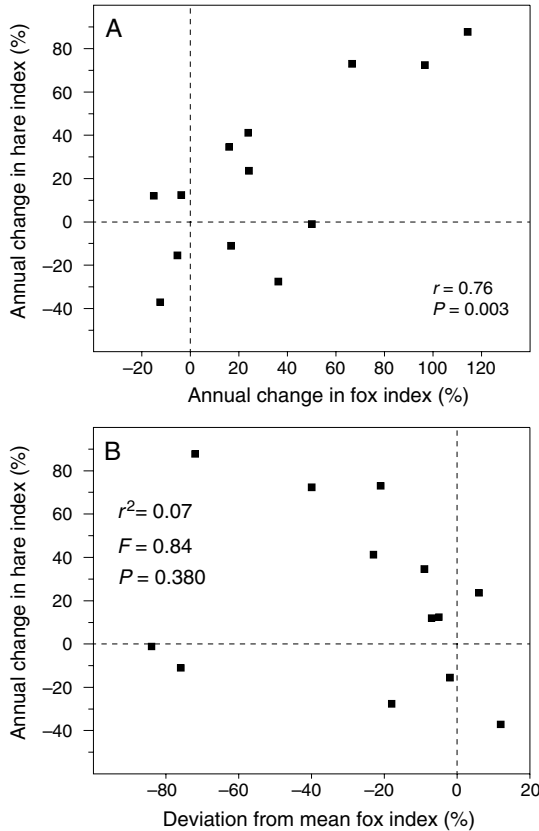


Fig. 5. Correlation between the annual change in fox and hare indices (A), and the annual change in hare index regressed against the relative fox abundance (B) in predator protection areas.

removal area of Häme (area R: $r = 0.97$, $p = 0.007$, area P: $r = 0.14$, $p = 0.818$).

3.4. Wildlife triangles

The change (%) in fox abundance (track index from wildlife triangles) correlated positively with the change (%) in hare abundance (pooled data from 3 areas), indicating that fox numbers follow hare numbers and not *vice versa* (Fig. 7).

We also calculated the correlation with a time lag of one year to find out the possible negative effect of the fox on the hare population. The change in fox abundance correlated negatively with the change in hare abundance but the result was not

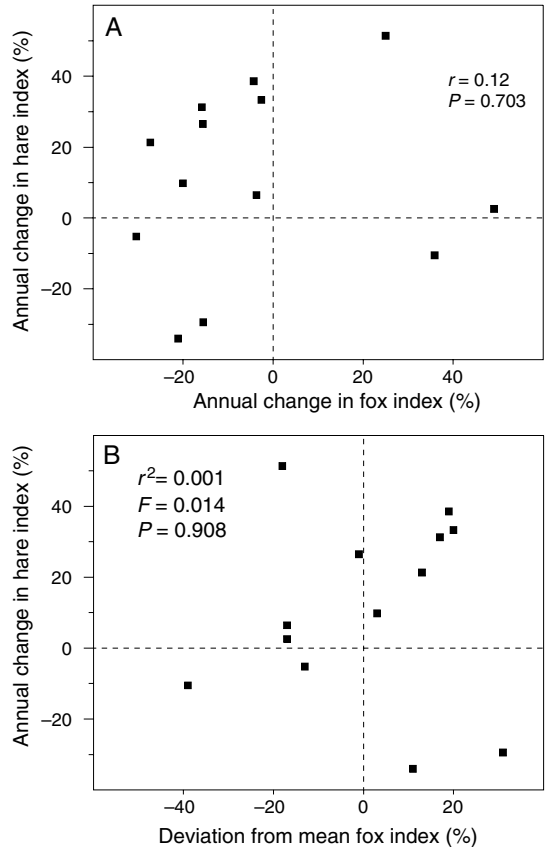


Fig. 6. Correlation between the annual change in fox and hare indices (A), and the annual change in hare index regressed against the relative fox abundance (B) in predator removal areas.

significant ($r = -0.33$, $p = 0.111$). The relative abundance of fox population (the deviation from the mean track index) in year t explained some of the annual change (from year t to year $t + 1$) in hare index ($t = -3.82$, $r^2 = 0.37$, $F = 14.6$, $df = 1, 25$, $p = 0.001$), indicating a negative effect of foxes on hare numbers.

4. Discussion

4.1. The impact of predator removal on predator populations

An annual average of about 72% of the autumn population of foxes was removed from Pello R

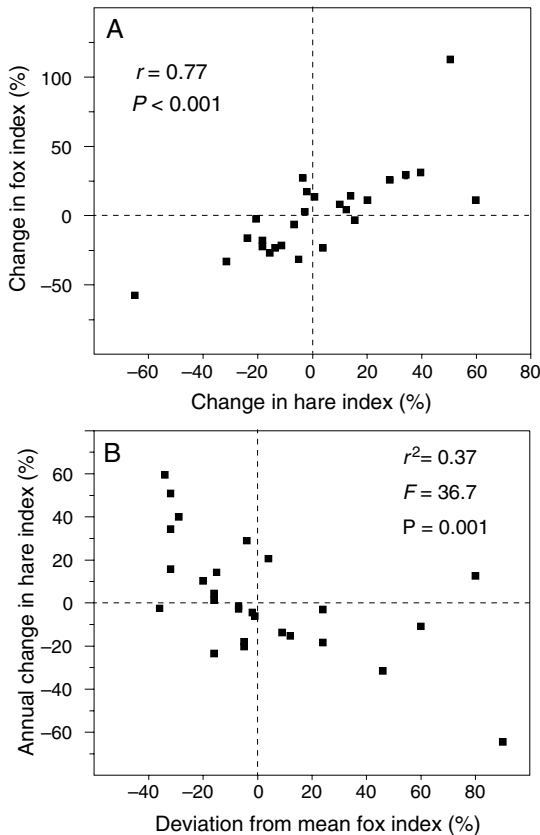


Fig. 7. Correlation between the annual change in fox and hare indices (A), and the annual change in hare index regressed against the relative fox abundance (B), based on the data from wildlife triangles.

resulting in a declining population. In Lieksa R, the number of foxes removed even exceeded the estimated size of the fox population in autumn, suggesting that foxes must have immigrated into the R areas. Reynolds *et al.* (1993) also found that when foxes were intensively controlled in a confined area, the area was repopulated within a few months by immigrants from surrounding areas.

In Häme R, about 40% of the autumn population was removed. The impact of fox removal was not as evident as in Pello or Lieksa; the population was probably harvested, but not controlled. The area was smaller and fox density higher than in Lieksa and Pello, which probably caused the difficulties of control in Häme: too many foxes immigrated from adjacent areas. Since snow conditions vary in Häme, the snow track index in Häme is not, however, as reliable as in Lieksa

and Pello where the snow cover is thick each year.

The results suggest that if fox populations are to be controlled, foxes have to be removed from a large area and hunting must be continuous, because foxes immigrate rapidly to an 'empty' area (see also Reynolds & Tapper 1996). The number of foxes removed must also exceed the annual recruitment. Marcström *et al.* (1989) controlled successfully fox populations in rather small areas in Sweden, but they operated in an island environment where immigration was not a problem.

The number of raccoon dogs removed from Häme R exceeded the size of the autumn population suggesting that also many raccoon dogs must have immigrated from adjacent areas to Häme R. Raccoon dog removal probably affected their numbers after 1996 when raccoon dogs were hunted intensively in late winter. In the beginning of the study, most raccoon dogs were removed during autumn and the bag consisted mainly of young individuals, most of which would have died anyway (Helle & Kauhala 1995).

4.2. The impact of predator removal on hare populations

In Lieksa and Pello, fox and marten numbers declined in the removal areas, while hare numbers increased. Hare numbers increased, however, also in the protection areas although fox and marten numbers increased, suggesting that these predators did not affect hare numbers during the experiment. Hare numbers increased in the protection area of Pello although vole numbers decreased, i.e. there was a negative, not positive correlation between hares and voles. According to the alternative prey hypothesis, predation on hares should have been heavy during a vole low. Angelstam *et al.* (1984, 1985) and Marcström *et al.* (1989) found that mortality rates of hares were inversely related to vole abundance. Siivonen (1948) and Lindström *et al.* (1983) found that the density of the mountain hare followed that of small rodents. Our results indicate that hare numbers did not follow vole numbers, but fox numbers followed hare numbers when foxes were not hunted. The results from wildlife triangles support this hypothesis. No interaction between foxes and hares was found in the removal areas, indicating

that removal of foxes had been effective; fox numbers did not follow hare numbers when the system was disturbed.

There was, however, a negative relationship between the relative fox abundance and the change in hare abundance, according to the data from wildlife triangles, suggesting that foxes may also affect hare populations. In the protection areas, fox index was below average during the study except for 2 years, which may have contributed to the increase in hare numbers in northern and eastern Finland. Probably fox and marten densities were too low in the study areas in northern and eastern Finland to affect hare density. We cannot thus exclude the possibility that a dense fox population might have some effect on hares.

In Sweden, hare populations benefited from predator control (Marcström *et al.* 1989), and hare harvests/populations also increased when sarcoptic mange killed many foxes (Danell & Hörnfeldt 1987, Lindström *et al.* 1994). When the fox population recovered from the mange, hare density once again decreased. Other factors than variation in predator numbers must, however, have affected the trends in hare populations in our study areas in Finland.

In conclusion, the present study does not give evidence to confirm the impact of localized control of small and medium-sized carnivores on mountain hare populations in Finnish mainland habitats. In southern Finland, the effect of control on predator numbers is not convincing, probably because the removal area was too small and immigration too intensive. In eastern and northern Finland, although predator control was effective, predator density during the experiment was so low that variation in predator numbers did not affect hare numbers. This study covered 5–6 years and it is well possible — taken into account the lifetime of individuals of predatory species in particular — that there might be some more long-term effects in hare–predator dynamics that were not found here.

Swedish studies (Danell & Hörnfeldt 1987, Angerbjörn 1989, Marcström *et al.* 1989, Lindström *et al.* 1994) indicate, however, that the fox especially can affect hare numbers and predator control can benefit hare populations, but only if predators are controlled in a very large area or in a closed system such as on an island.

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