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An epizootic of sarcoptic mange among red foxes *Vulpes vulpes* reached central Norway in 1976, and by 1986 it had spread to the whole country, resulting in a severe decline in the red fox population. We analyse the change in the hunting bags of the predator species red fox and pine marten *Martes martes*, and the prey species capercaillie *Tetrao urogallus*, black grouse *Tetrao tetrix*, mountain hare *Lepus timidus* and willow grouse *Lagopus l. lagopus* from the period prior to and during the mange epizootic. The data are gathered from publications by Statistics Norway and are based on answers from more than 5,000 hunters yearly. On the national level, the hunting bags of capercaillie, black grouse, mountain hare and pine marten were significantly negatively correlated with that of the red fox. When the time series at the national level were detrended, there were positive correlations between the hunting bags of all species without time lag, except that of pine marten, which lagged one year behind the other species. At the local level there were negative correlations between the hunting bag of red fox and those of the small game species except for willow grouse. The study confirms that the red fox is a keystone predator in Scandinavia.

Key words: Martes martes, sarcoptic mange, small game, Vulpes vulpes

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In most studies of the effect of predator control on the population dynamics of birds (reviewed by Newton 1993) and mammals (Kinnear 1988, Marcström, Keith, Engren & Cary 1989, Pech, Sinclair, Newsome & Catling 1992) the reproductive success of prey has been found to improve. The increase in reproductive success has often been followed by higher postbreeding numbers (Beasom 1974, Trautman, Fredrickson & Carter 1974), sometimes by an increase in the number of breeding individuals (Blankenship 1966, Duebbert & Kantrud 1974, Duebbert & Lokemoen 1980, Slagsvold 1980), or in some cases by an increase in both (Marcström, Kenward & Engren 1988, Tapper, Potts & Brockless 1996). However, in other studies no effects of predator removal were found (e.g. Parker 1984), probably because of compensatory increases in other sources of mortality.

In the long term, predation will not be limiting if the number of breeding individuals, and thus the number entering the next generation, is unaffected by

predation, despite a reduction in the postbreeding number (Newton 1993). Especially where breeders form only part of the population, and most predation is caused by specialist predators, the number of breeding individuals will be little affected by predation (Newton 1993). In contrast high population levels of generalist predators, depending on more common and less vulnerable prey as their main food supply, are usually involved in the cases where the number of breeding individuals of a bird or mammal prey species is limited by predation (Andersson & Erlinge 1977, Erlinge, Göransson, Högstedt, Jansson, Liberg, Loman, Nilsson, Schantz & Sylvén 1984, Newton 1993).

In Fennoscandia, the populations of several small game species have declined during the last 50 years (Marcström 1979, Wegge 1979, Henttonen 1989); these declines were probably caused by increased predation by generalist predators (Henttonen 1989, Wegge, Rolstad & Gjerde 1992). A study of the effect of predation by red fox *Vulpes vulpes* and pine marten *Martes martes* on capercaillie *Tetrao urogallus*, black grouse *Tetrao tetrix* and mountain hare *Lepus timidus* actually showed an increase in reproduction and breeding density when the predators were culled, but was unable to show which of the predators was more important (Marcström et al. 1988, 1989, see also Lindström, Angelstam, Widén & Andrén 1987, Kurki, Helle, Lindén & Nikula 1997).

In other countries, the red fox has been found to be an important predator on different game species. Both in Denmark and Germany, populations of brown hare *Lepus europaeus* and grey partridge *Perdix perdix* increased when the shooting of red foxes was intensified in order to avoid the spread of rabies (Jensen 1970, Spittler 1972, Asferg 1983). Australian studies have highlighted the importance of red foxes as a control agent for some species (Newsome, Parer & Catling 1989, Newsome 1990) and as a threat to others (Kinnear 1988). In North America, the red fox has been found to be the most important predator on ducks' nests (Johnson, Sargeant & Greenwood 1989, see also Sovada, Sargeant & Grier 1995).

The outbreak of sarcoptic mange (*Sarcoptes scabei*) starting in the mid 1970s (Lindström & Mörner 1985), reduced the red fox population to less than half its former number in Sweden and Norway in general (Lindström 1989a), and locally even more, and provided an opportunity to study the effect of predator removal on a larger scale than otherwise possible. During this epizootic, temporal increases in small game populations, i.e. mountain hare, capercaillie, black grouse and hazel grouse *Bonasa bonasia*, as well as in populations of other predators, such as pine marten and goshawk *Accipiter gentilis*, have been reported (Danell & Hörnfeldt 1989, Lindström, Andrén, Angelstam, Cederlund, Hörnfeldt, Jäderberg, Lemnell, Martinsson, Sköld & Swenson 1994, Lindström, Brainerd, Helldin & Overskaug 1995, Selås 1998). The sarcoptic mange also reached Denmark, where the highest increases in the hunting yield of brown hare, grey partridge and pheasant *Phasianus colchicus* were observed in the regions where the hunting yield of red fox had decreased most (Asferg 1996).

In this paper, we present Norwegian data on the hunting bags of red fox and pine marten and some of their prey species from the period prior to and during the mange epizootic on three levels of scale: national, regional and local. The prey species, in the following termed small game, are the forest dwelling capercaillie, black grouse and mountain hare, and the willow grouse *Lagopus l. lagopus* inhabiting the lower alpine zone, which in Norway is regular red fox habitat. Our hypothesis is that red fox limits the populations of pine marten and small game. A prediction from this hypothesis is that the hunting yield of pine marten and small game will increase as the population of red foxes decreases due to sarcoptic mange.

Methods

Data on the national and regional levels presented in this study were extracted from the estimated yearly hunting statistics for Norway, which have been compiled during the past two decades on two levels of scale: for the whole country (Statistics Norway 1994) and for each of the 19 counties (Statistics Norway 1973-1994). Statistics Norway make the estimates from annual questionnaires sent to 4% of the currently 170,000 Norwegians who hunt yearly. An estimate is published only if the standard deviation is less than 20% of the estimate, judged by Statistics Norway. The estimates include pooled figures for willow grouse and ptarmigan *Lagopus mutus*, which mostly reflect the shooting of willow grouse, and therefore they are termed willow grouse in the following.

The figures for the nationwide shooting have been published as a yearly estimate for the period 1971-1993. On the county level, figures are published as the mean of the last five years from 1977-1993, for

the last four years in 1976 and for the last three years until 1975. Thus the value at the regional level for 1993 is the mean of the five years from 1989 to 1993. We have graphically presented 1993 as the value for 1991 in Figure 4, because these five-year means result in lags if there are decreasing or increasing trends. Our data on the county level are then presented graphically for the period 1972-1991. Statistics Norway present the county level data as five-year averages to reduce the uncertainty of the estimates. On the county level, data on capercaillie, black grouse, hare, willow grouse and red fox, but not pine marten, are available. Based on the following criteria, we selected three of the 19 Norwegian counties for analysis: data on the hunting bag should be available for all years, and the selected counties should not be adjacent. The latter criterion was set in order to ensure that the data from the counties would be as independent as possible; data from two adjacent counties would have come from the same region. The three counties chosen, which fulfilled our criteria, were, from north to south, Nord-Trøndelag (22,463 km^2), Hedmark (27,344 km^2) and Buskerud (14,965 km^2; Fig. 1).

At the local level, we succeeded in obtaining hunting statistics for the period 1978-1994 from a forested area covering 130 km^2 in the municipality of Elverum in the county of Hedmark (see Fig. 1), which is used by a local hunters' association. The data from this area consist of the number of small game reported shot by each hunter. Such reports are mandatory; no hunting licence will be issued for the following year if a report has not been delivered. At the county level, no data on red fox were available from 1984 in Nord-Trøndelag, from 1993 in Buskerud and from 1980 in Elverum, and at the national level, no data on pine marten were available from 1971. We did not extrapolate the missing data.

Following the first record of sarcoptic mange in Nord-Trøndelag in central Norway in January 1976, approximately 10 years passed before the parasite had spread to the whole country (Holt & Berg 1990). By 1977 it had spread to all of Nord-Trøndelag, by 1980 it had spread to most parts of Hedmark, and by 1982 most parts of Buskerud were affected (Loftsgaard 1979, Holt & Berg 1990).

To check if any changes in the hunting yield were due to corresponding changes in the hunting effort, we plotted the number of hunting licences sold on the national level in the years 1972-1992 (Fig. 2). In 1985, the number of hunting licences sold increased

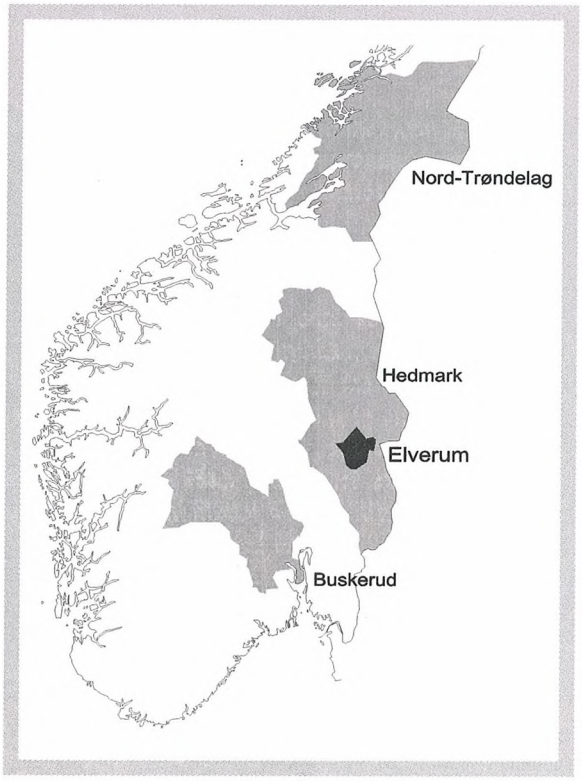

Figure 1. Location of the counties of Nord-Trøndelag, Hedmark and Buskerud and the municipality of Elverum which were selected for analyses of hunting bags.

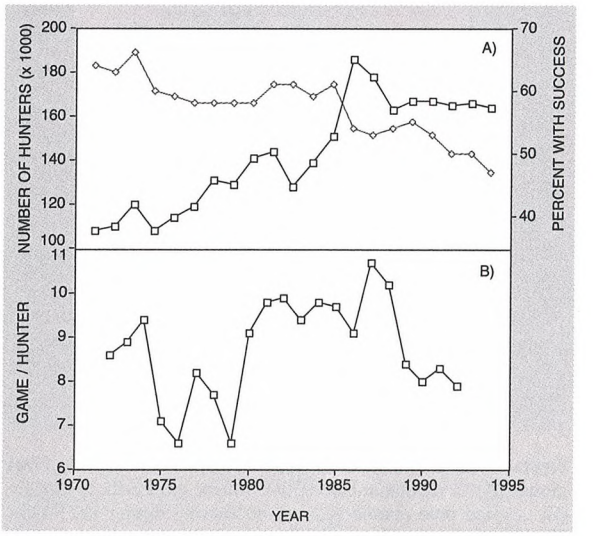

Figure 2. Number of Norwegian hunters taking out hunting licences (A;□) and the percentage of these hunters shooting one or more head of game each year (A;◊) and the number of individuals shot per hunter during 1972-1992 (B;□) in Norway.

suddenly because 1985 was the last year hunters could be registered without having attended a formal course. After the implementation of this hunter's course the number of hunting licences sold stabilised at a higher level than before 1985. However, hunting success, measured as the percentage of hunters obtaining at least one individual belonging to either of the small game species declined. Furthermore, we plotted the total number of game shot divided by the number of hunters with success, giving the number of game shot per successful hunter.

At the county level, for which data are based on five-year mean values, we present correlation values without levels of significance because the data are not independent between years. For cross correlation analysis, we square root transformed the data series in order to stabilise the variance (Minitab 1995).

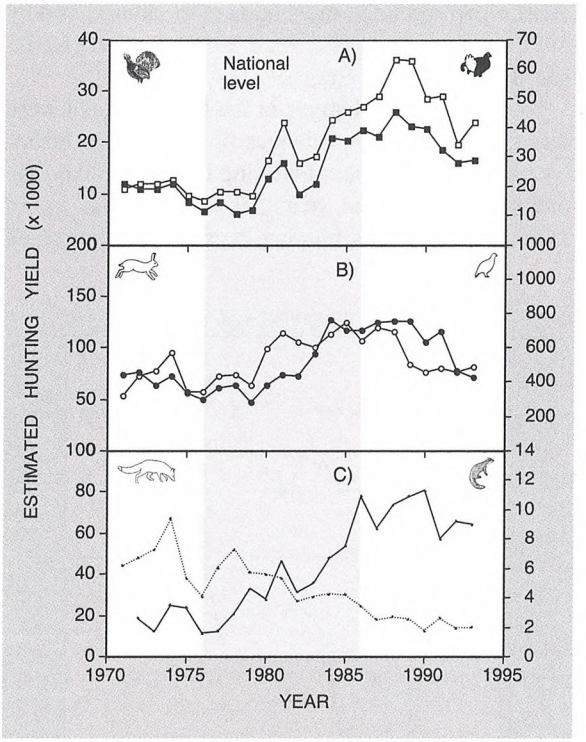

Figure 3. Estimated hunting yield of capercaillie (A;■), black grouse (A;□), mountain hare (B;●), willow grouse (B;○), red fox (C; ....) and pine marten (C;——) in Norway during 1971-1992. The shaded area indicates the period when the mange spread; it includes the years from the first record to the time when all counties were affected, after which the mange was present in all counties. The effect of the mange started to wear out in the counties where it first hit.

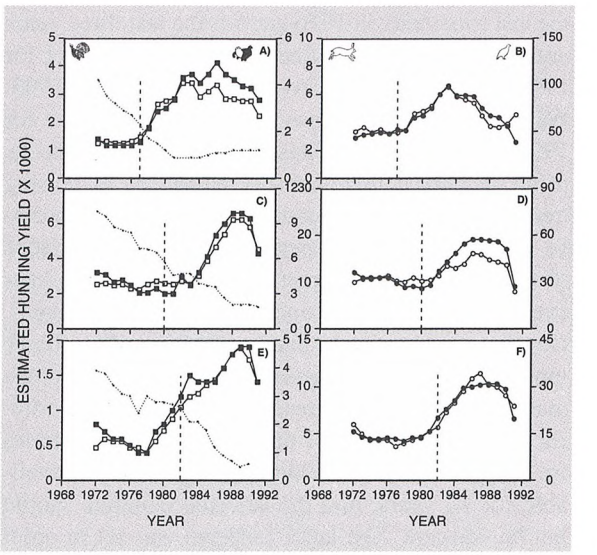

Figure 4. Estimated hunting yield of capercaillie (■), black grouse (□), mountain hare (●) and willow grouse (○) in Nord-Trøndelag (A-B), Hedmark (C-D) and Buskerud (E-F) during 1972-1991. Red fox hunting yields (·····) are indicated in A, C and E (the same axis as for black grouse). The vertical broken line in A-F indicates the time when the mange had reached most of the county, as reported by Holt & Berg (1990).

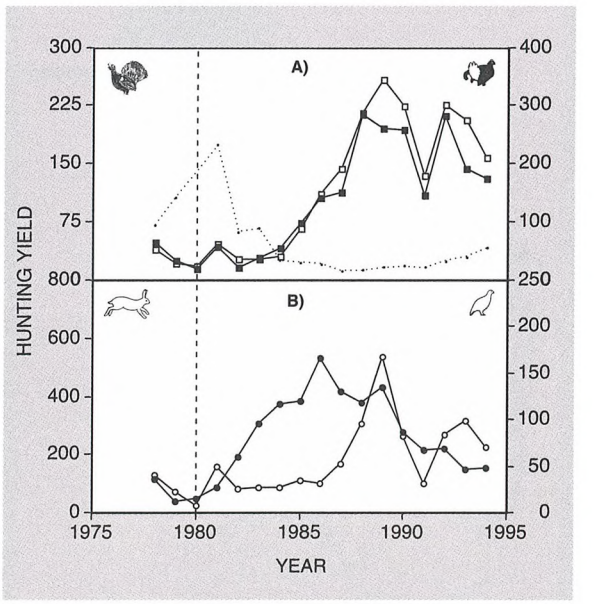

Figure 5. Hunting yield of capercaillie (A;■), black grouse (A;□), mountain hare (B;●) and willow grouse (B;○) in Elverum, Hedmark, during 1978-1994. Red fox hunting yield (.....) is indicated in A (the same axis as for the black grouse). The vertical broken line indicates the time when the mange reached the municipality.

Table 1. Correlation coefficients for the relationships between the estimated hunting bags of small game species at national (Norway), regional (N-Trøndelag, Hedmark, Buskerud) and local (Elverum) levels in Norway. Based on data from Figures 3, 4 and 5. For location of the regions see Figure 1. At the county level, for which data are based on five-year mean values, we present correlation values without levels of significance because the data are not independent between years. * $P < 0.05$, ** $P < 0.01$.

1st series	2nd series	Norway	N-Trøndelag	Hedmark	Buskerud	Elverum
Capercaillie	Black grouse	0.95**	0.96	0.98	0.98	0.98**
Capercaillie	Mountain hare	0.91**	0.80	0.84	0.94	0.32
Capercaillie	Willow grouse	0.63*	0.73	0.71	0.90	0.80**
Black grouse	Mountain hare	0.91**	0.85	0.78	0.97	0.28
Black grouse	Willow grouse	0.63*	0.81	0.66	0.93	0.86**
Mountain hare	Willow grouse	0.65**	0.87	0.94	0.98	0.19

Results

When the mange spread through the country during 1976-1986 the hunting bag of red fox decreased whereas the hunting bags of small game and pine marten increased (Fig. 3).

In all three counties investigated, as well as in the municipality of Elverum in the county of Hedmark, the hunting bag of mountain hare increased almost immediately when the mange hit (Figs. 4 and 5). This was also true for the grouse species in Nord-Trøndelag (see Fig. 4). In Hedmark and Elverum, however, the increase in the hunting bags of grouse was slow until three or four years after the mange first occurred (see Figs. 4 and 5), whereas in Buskerud, the increase in the hunting bags of capercaillie and black grouse started three or four years before the mange was first recorded (see Fig. 4).

The hunting bags of the different small game species were significantly positively correlated at the national level and highly correlated at the regional level (Table 1). At the local level, the correlations of capercaillie, black grouse and willow grouse were significant, whereas the correlations involving mountain hare were not (see Table 1). The time series of capercaillie and black grouse were highly correlated in all analyses (see Table 1); as black grouse are shot in higher numbers than capercaillie, we only used black grouse in the further analyses.

The hunting bags of the red fox and each of the other species investigated were significantly negatively correlated, at both the national and the local level for all species investigated except for willow grouse (Table 2). At the national level, a significant positive correlation between the hunting bag of pine marten and each of the small game species existed (see Table 2). For the detrended series at the national level, a positive correlation without timelag existed between the hunting bags of red fox and the small game species (Fig. 6). The hunting bag of pine marten, on the other hand, was positively correlated with the hunting bags of red fox and willow grouse with a time lag of minus one year (see Fig. 6).

The pattern of change in hunting bags observed (see Fig. 3) was not mainly due to an increase in the number of hunters (see Fig. 2). When correcting for the number of hunters, the hunting bag of red fox was still negatively correlated with those of the small game species except for willow grouse (Table 3). Hunting success was inversely correlated with the number of hunters ($r = -0.78$, $P < 0.001$) but was not correlated with the total head of game shot ($r = -0.14$, $P = 0.56$), or with game per hunter ($r = 0.13$, $P = 0.59$).

Table 2. Correlation coefficients for the relationships between the estimated hunting bags of two predator species (red fox and pine marten) and three game species (black grouse, mountain hare and willow grouse) at national (Norway), regional (N-Trøndelag, Hedmark, Buskerud) and local (Elverum) levels in Norway. Based on data from Figures 3, 4 and 5. For location of the regions see Fig. 1. At the county level, for which data are based on five-year mean values, we present correlation values without levels of significance because the data are not independent between years. * $P < 0.05$, ** $P < 0.01$.

1st series	2nd series	Norway	N-Trøndelag	Hedmark	Buskerud	Elverum
Red fox	Pine marten	-0.78**				
Red fox	Black grouse	-0.71**	-0.90	-0.79	-0.87	-0.59*
Red fox	Mountain hare	-0.61**	-0.70	-0.61	-0.90	-0.67**
Red fox	Willow grouse	-0.23	-0.70	-0.54	-0.85	-0.32
Pine marten	Black grouse	0.91**				
Pine marten	Mountain hare	0.81**				
Pine marten	Willow grouse	0.45*				

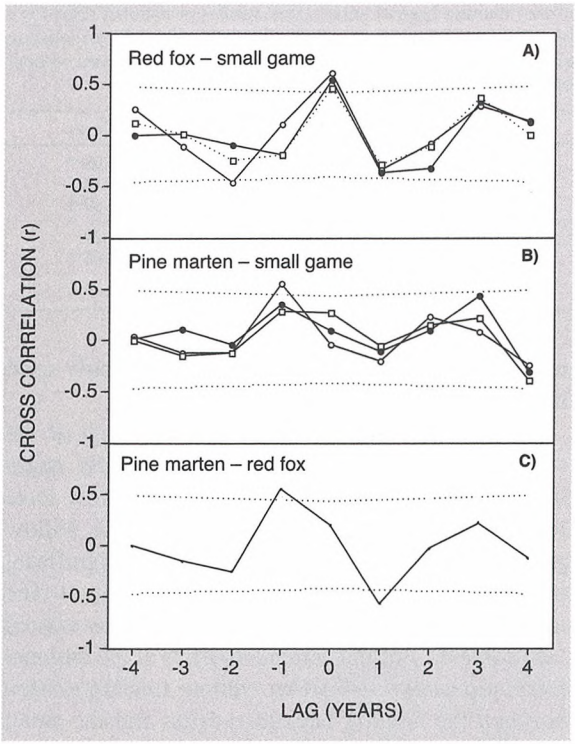

Figure 6. Cross correlation analyses of square root transformed and detrended (first difference) time series of the estimated hunting bag of red fox, pine marten and three small game species during 1971-1993 at the national level. The red fox (A) and the pine marten (B) were tested against black grouse (□), mountain hare (●), and willow grouse (○). In addition, pine marten was tested against red fox (C). The dashed horizontal lines correspond to the 95 % confidence limits. Based on data from Figure 3.

Discussion

The significant negative correlations between the hunting bags of capercaillie, black grouse and mountain hare on one hand, and the hunting bag of red fox on the other, offer support for the hypothesis that predation by red foxes was an important factor limiting the small game populations in the boreal forest of Norway prior to the mange period.

At the national level there was also a negative correlation between the hunting bags of red fox and pine marten (see Fig. 6c). The highly significant positive correlations between the pine marten and the forest grouse species suggest that pine marten is of minor importance to grouse compared to red fox. Possible reasons for the increase in pine marten populations when the red fox was hit by mange, may include reduced competition for food (Lindström 1989a, Storch, Lindström & Jounge 1990), as well as reduced predation by red foxes (Storch et al. 1990, Lindström et al. 1995). During the mange period, pine martens may have been able to utilise food resources, such as cervid carcasses in winter, which would otherwise have been unavailable because of high risk of predation by foxes.

Hunting statistics are of course not as objective as counts. One important point is that each hunter's effort, i.e. functional response, will vary according to the level of game population (Myrberget 1988). For grouse hunting, there will also be a numerical response of the hunters, because more hunters will go hunting in good than in poor years, and because a situation with increasing game trends and decreasing number of hunters is quite unlikely as long as hunters have ample opportunities to hunt. Therefore increasing trends in the game hunting bags, as in our case, will cause a high correlation with the number of hunters, also in situations where an increase in the number of hunters is not the cause of the increase in the hunting bag. However, for all species the trend in the hunting statistics should be in accordance with the actual trend in population fluctuations, given that any functional or numerical responses of the hunters are not seriously delayed (Myrberget 1988, Ellison 1991). The sudden increase in the number of hunting licences issued in the mid 1980s caused a drop in hunting success, indicating that the new hunters were not very dedicated, and the hunting success did not increase when more game was shot or when game per hunter increased (see Fig. 2). This means that rather than the small numerical response of the hunters, the functional response of a segment of the hunters based on a real population increase was responsible for the increase in hunting yield. A hunting licence also permits hunting of moose *Alces alces*, reindeer *Rangifer tarandus*, red deer *Cervus elaphus* and roe deer *Capreolus capreolus* for which the numbers bagged have more than doubled during our study

Table 3. Partial correlation between the hunting bags of small game and red fox after correcting for the number of hunters with game, and between the hunting bags of small game and the number of hunters with game after correcting for the hunting bag of red fox. Based on data from Figures 2 and 3.

	Red fox		Hunters with game	
Species	R	P	R	P
Capercaillie	-0.33	0.015	0.68	<0.0001
Black grouse	-0.43	0.0013	0.63	<0.0001
Willow grouse	0.20	0.15	0.94	<0.0001
Mountain hare	-0.30	0.036	0.69	<0.0001
Pine marten	-0.55	0.0002	0.50	0.0004

period (Smedshaug & Sonerud 1997). This might explain the increased number of hunters and the lower hunting success when considering the investigated species, as the hunting effort of hunters who primarily or exclusively hunt large game species do not influence the hunting success of the investigated species. Furthermore, the number of hunters increased after the initial increase in the hunting bags (see Figs. 2 and 3). Thus, for all small game species investigated, except for willow grouse, and for pine marten, the hunting bags confirm that increases did occur at least in the autumn or post-breeding populations during the mange period, and that they were not mainly caused by the increasing number of hunters.

If the reproduction of the investigated species for different reasons is usually higher in peak microtine years than in other years (e.g. Englund 1970, Myrberget 1974, Angelstam, Lindström & Widén 1984, Lindström 1989b, Wegge & Storaas 1990), a positive correlation without time lag should be expected for all cross correlations of detrended series. Only the pine marten deviated from this pattern, possibly because the reproduction of this K-selected species depends less on microtine peaks than that of the other species (Helldin 1998). The time lag of one year between the hunting bags of pine marten and two of the other species (willow grouse and red fox) may, however, have been caused by differences in the hunting methods used. In contrast to what is the case for the other species in our study, most martens are trapped and very few are shot. Juvenile martens are probably most easy to trap in winters with low microtine populations (Helldin 1998). Therefore, the effect of peak microtine years on pine marten may be increased juvenile survival due to favourable food conditions, and this will not be apparent in the hunting bags until the second winter after the summer with high microtine numbers, i.e. when the microtine populations have crashed.

At the regional and local levels, the hunting bag of mountain hare increased almost immediately when the mange occurred. The reason why this was not the case for grouse in all regions, may be that these species are more influenced by predation by other generalist predators (Lindström et al. 1994), or that they are more influenced by fluctuating levels of chemical defence compounds in food plants (Selås 1997). At the local level, the hunting bag of mountain hare was not correlated with those of the other small game species because it peaked before (see below). This is another indication that the mountain hare follows another pattern than the grouse, even though they are both limited by predation.

At the national and local levels, the hunting bag of willow grouse was not correlated with that of red fox, even though it increased during the mange. This might be due to the fact that the mountain ecosystem is somewhat different from the boreal forest ecosystem regarding the relative importance of different predator species.

In Hedmark and Elverum, the populations of *Clethrionomys*-voles, which feed on the same ericaceous dwarf shrubs as the grouse, were growing in 1980 when the mange arrived in the area and they peaked in 1980-1981, 1984-1985 and in 1988-1989 (G.A. Sonerud, unpubl. data). The peak in 1980-1981 came before the mange had reduced the red fox population and this may explain why capercaillie, black grouse and willow grouse did not peak until 1988-1989 in Elverum (see Figs. 4c, 4d and 5).

In Buskerud, capercaillie and black grouse, but not willow grouse and hare, started to increase several years before the mange was first observed (see Figs. 4e and 4f) . Also from an area located approximately 150 km farther south, in the county of Aust-Agder, some increase in the populations of forest grouse prior to the mange epizootic has been reported (Selås 1998). In this area grouse populations were particularly low in the mid 1970s, and the increase from the late 1970s onwards coincided with frequent years of high microtine populations (Selås 1998).

In Sweden, the period of low red fox populations during the mange epizootic generally lasted for 7-10 years in the various regions (Lindström et al. 1994). This agrees well with reports of increasing red fox populations from different parts of Norway in the last few years. The likely increase in red fox populations is, however, hard to detect in the hunting yield curves, probably because the fox hunting tradition was not upheld during the mange period (see also Selås 1998). In general, fox hunting is difficult and time consuming, and the slow recovery of the red fox hunting yield may be caused by a combination of reduced interest by hunters and loss of hunting skill and red fox hunting dogs. The difficulties associated with fox hunting mean that resumption of hunting efforts directed towards the red fox is not likely, because only a small number of hunters hunt the red fox intensively in winter, when small game hunting is no alternative. So, the decrease in the hunting yield of small game species and pine marten in the last years of our study period may have been caused by

an increasing red fox population. As could be expected, the decrease in the hunting yield of mountain hare and grouse first started in Nord-Trøndelag, the county where the red fox population was first reduced, and probably first recovered.

The red fox seems to have been a keystone predator in the boreal forest in Sweden and Norway in the 1970s and 1980s. We do not know for how long this has been the case, but the Norwegian red fox hunting bag increased profoundly from 1945 to the late 1960s (Smedshaug & Sonerud 1997). Before World War II and some hundred years back, the species was intensively persecuted by man in Fennoscandia. Hence, the red fox population may have been limited more by hunting than by food. However, unlike the pine marten and the larger carnivores, the red fox was never drawn close to extermination; the Norwegian red fox hunting yield fluctuates around the same middle value through the whole period from 1880 to 1930 (Statistics Norway 1978). The red fox may have been able to withstand the intensive human persecution throughout this period due to its high reproductive capacity (Lund 1963).

Another important factor associated with the increase in the red fox populations after World War II is increases in the populations of cervids like moose and roe deer. These increases have lead to higher availability of carcasses in harsh winters (see also Kjos-Hanssen 1962, Vainio, Marjakangas, Lindgren, Tornberg & Paaso 1997), and increases the opportunity to cache offal from the big game hunting in autumn (Smedshaug & Sonerud 1997). It may have been important for red foxes to be able to utilise this food resource with no risk of predation, because especially wolf *Canis lupus*, and in large areas also lynx *Lynx lynx*, have been rare after World War II (Lindström 1995). In addition to the increase in natural food resources, also the availability of organic refuse has increased. Lastly, modern forestry with clearcuts may have increased the populations of *Microtus*-voles (Christiansen 1979), which are important food for red foxes in summer. Overall, conditions have probably changed during the last 50 years to the advantage of the red fox and to the disadvantage of the small game species.

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