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Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange

K. Danell[1] **and B. Hörnfeldt**[2]

[1] Department of Wildlife Ecology, Swedish University of Agricultural Sciences, S-901 83 Umeå, Sweden
[2] Department of Animal Ecology, University of Umeå, S-901 87 Umeå, Sweden

Summary. During a severe outbreak of sarcoptic mange (*Sarcoptes scabiei vulpes*) starting among red foxes (*Vulpes vulpes*) in Sweden in the 1970s, we studied: 1) the establishment and spread of the disease in northernmost Sweden (by inquiries), and 2) the 1970–84 bag records for foxes and mountain hares (*Lepus timidus*) (an alternative prey to the fox's main prey, voles). Since the first case of sarcoptic mange in 1975 the disease spread rapidly, with >50% of the hunting organizations having reported the disease in 1981 and >75% in 1983. Also the disease became more abundant within the areas affected. In areas with a low mange infection rate (index) the number of foxes killed in the 1980s did not deviate markedly from the average level in the 1970s. However, there was a slight tendency towards a decline in areas with a medium index and numbers declined markedly where the index was high. Hare harvests initially were low (after a tularemia epidemic) in the 1970s. In that decade harvests increased dramatically and stabilized, increased gradually or changed little, respectively, where mange infection rates were low, medium or high in the early 1980s. In areas with a low mange index hare harvests remained cyclical and at the same level in the 1980s as in most of the 1970s. However, in areas with a medium index harvests increased and seemed to begin to lose their cyclicity, and where the index was high the low and relatively stable hare harvests increased annually. A predator-prey hypothesis, assuming predators to synchronize alternative prey declines to those of the cyclic main prey, predicts that a predator reduction would cause a gradual disappearance of the cyclicity and increasing numbers among alternative prey. Our hare data are partially consistent with this prediction.

Key words: Hunting statistics – Mountain hare – Red fox – Sarcoptic mange – Sweden

Sarcoptic mange has been found in foxes in Europe (e.g. M'Fadyean 1898; Schoop 1941; Henriksson 1971; Christensson 1972; Holt 1976), North America (e.g. Plummer 1936; Olive and Riley 1948; Trainer and Hale 1969) and the Soviet Union (Gerasimoff 1958). The disease is caused by a mite (*Sarcoptes scabiei vulpes*), which inhabits the upper layers of the skin.

In Sweden, an outbreak of sarcoptic mange started among red foxes (*Vulpes vulpes*) in 1972 and the general spread over the country has been documented by Borg et al. (1976), and Lindström and Mörner (1985). Today the disease is spread over almost the whole of Sweden.

Sarcoptic mange is commonly characterized by skin changes on the tarsal joints of the foxes, and after severe infestations hairless patches develop (Mörner 1984; Mörner and Christensson 1984). That the disease can have a considerable impact upon foxes is illustrated by an examination of 63 foxes with mange and who were found dead (Mörner 1984). The foxes were generally in a very poor condition and the majority of them had died of starvation.

As the host animal in this case is an important predator on e.g. mountain hare (*Lepus timidus*) (Englund 1965; Lindström 1982), it is possible that a reduction in the fox density due to the disease may increase the numbers of hares.

To study establishment and spread of sarcoptic mange among red foxes, and its effects upon the populations of the host itself and on mountain hare, we have studied the development of the disease in the northern part of Sweden between 1979 and 1983. We have also analyzed the hunting statistics for foxes and hares in the same area since 1970.

Study area and methods

We selected 93 local hunting organizations, which belonged to the Swedish Sportsmen's Association and were located between 63.5–67.5° N in the two northernmost provinces of Sweden: Norrbotten and Västerbotten.

A local hunting organization in this region often consists of 10–50 hunters, which on the average hunt on approximately 5000 ha. The organizations selected by us had been registered, and regularly reported the numbers of bagged small game animals, since 1970.

We collected the bag reports (numbers of killed foxes and hares) from each of the organizations over the period 1970–1984. By using the size of the hunting ground we later converted these data into numbers of animals reported per 1000 ha.

For the hunting years 1979–1980, 1980–1981, 1981–1982 and 1983–1984 we also collected additional data from the selected organizations. Inquiries were made about: (1) the year of the first case of mange on their land, and (2) number of foxes killed with typical signs of the disease.

The hunting organizations were later on divided into three groups according to the proportion of killed foxes with mange. If 0–5% of the foxes, during the hunting years 1980–1981 and 1981–1982, had mange this particular orga-

Offprint requests to: K. Danell

nization was given a low "sarcoptes" index. If 6–20 or 21–100% of the foxes were diseased medium and high sarcoptes indices were given, respectively. By this classification 23, 41 and 24 of the organizations were given low, medium and high indices, respectively. For the remaining five organizations, the total numbers of reported foxes were low (<10) and no index value could be given.

Results and discussion

Spread and infection rate of sarcoptic mange among foxes

The first case of sarcoptic mange occurred in 1975, and at the end of 1981 >50%, and in 1983 >75% of the organizations had found diseased foxes (Fig. 1). According to this measure the mange had spread very rapidly on a geographical scale, since it was first found in Västerbotten in 1975 (Borg et al. 1976) and in Norrbotten in 1976 (Rune Almqvist, pers. comm.).

The number of mange-infected foxes killed per 1000 ha (Fig. 2a) increased from 1979 to 1983 for the organizations with a medium sarcoptes index (Wilcoxon matched-pairs signed-ranks test; $P<0.001$). No statistically significant difference was found for the organizations with low and high indices ($P>0.05$), although there was an increasing trend.

Since there was no general increase in the numbers of foxes killed during the period 1979–1983 for any of the three groups (Fig. 2b), the finding of the increased number of mange-infected foxes in this period (Fig. 2a) suggests that there was a real increase in the infection rate in the population of bagged foxes. There was also a slight time-lag between areas given high, medium or low sarcoptes index; those with a high index being first (Fig. 2a). Thus, during the study period the disease both spread to new areas and became more abundant within the areas affected.

Hunting statistics for red fox

In areas with a high sarcoptes index the number of foxes killed fluctuated around an average level of 1.5 bagged foxes per 1000 ha in the 1970s (Fig. 2b). Thereafter a marked decline was noted. The number of foxes shot or trapped in 1984 was about one fourth of the highest figure recorded (in 1974) during the study period. The decline in the 1980s coincided well with the spread of sarcoptic mange.

In contrast, for areas with a low sarcoptes index, the fox statistics in the 1980s did not deviate markedly from the average level recorded in the 1970s. The mean level of foxes bagged by organizations with a medium sarcoptes index took an intermediate position with a slight tendency towards a decline in the 1980s.

In 1984 there were significantly fewer foxes killed per 1000 ha in areas with a high sarcoptes index than in areas with a low or medium index (Mann-Whitney U-test, $P<0.001$ and $P<0.05$, respectively). There was no statistically significant difference between areas with low and medium indices ($P>0.05$).

On basis of the increasing infection rate and the observed time-lag in the sarcoptes gradient, we expect the number of foxes bagged to decline further for the hunting organizations classified as highly infected, and the fox harvest in organizations with medium and low indices to decrease too, but later on.

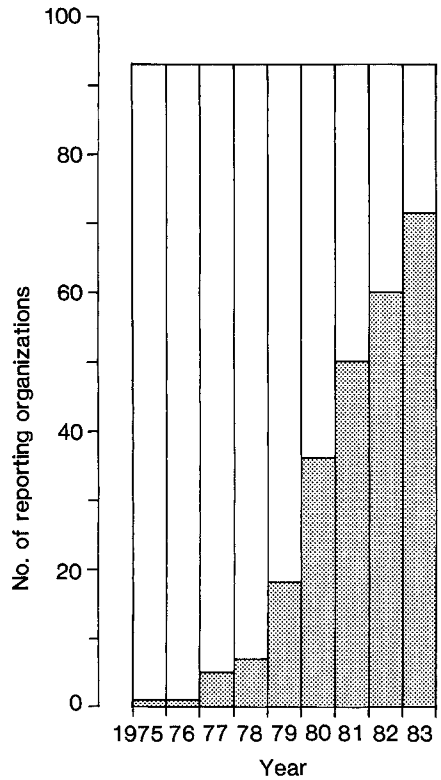

Fig. 1. The spread of sarcoptic mange in red foxes as reported by 93 hunting organizations in northern Sweden in 1975–1983. The organizations are for each year divided into those which have reported (the actual year or earlier) diseased foxes (hatched) and those which have not *open bars*

Hunting statistics for mountain hare

The low numbers of hares shot per 1000 ha in the whole study area in the early 1970s (Fig. 3) was probably due to the serious tularemia epidemic among hares in 1967 (Borg et al. 1969; Hörnfeldt 1978). After this period, the harvest of hares increased dramatically and then stabilized, fluctuating within a range of 13–24 hares per 1000 ha in areas with a low sarcoptes index.

In high infection areas the hare harvests remained at a low level in the late 1970s. In the 1980s, on the other hand, the numbers of hares shot have increased annually. This increase coincided with the spread of mange and the consequent decrease in the red fox population (Figs. 1, 2).

The number of hares shot in areas with a medium infection of mange was intermediate compared to hares shot in the high and low infection areas.

It is likely that the increase in the hare harvest after 1980 in areas with a high sarcoptes index was related to the decrease in the fox population and thereby relaxed predation. Perhaps even more interesting is the different development of the harvest patterns in the three groups in 1970–1980, when the impact of mange presumably was rather low. If we assume that the level of the hare harvest indicates the level of the hare population, there emerge at least two possible explanations for the different levels of hare populations. One is that areas with low hare populations and where the disease rapidly became established generally had lower quality of habitats, i.e. a lower carrying capacity. The other explanation is that the hare populations were depressed by a high predation pressure from foxes

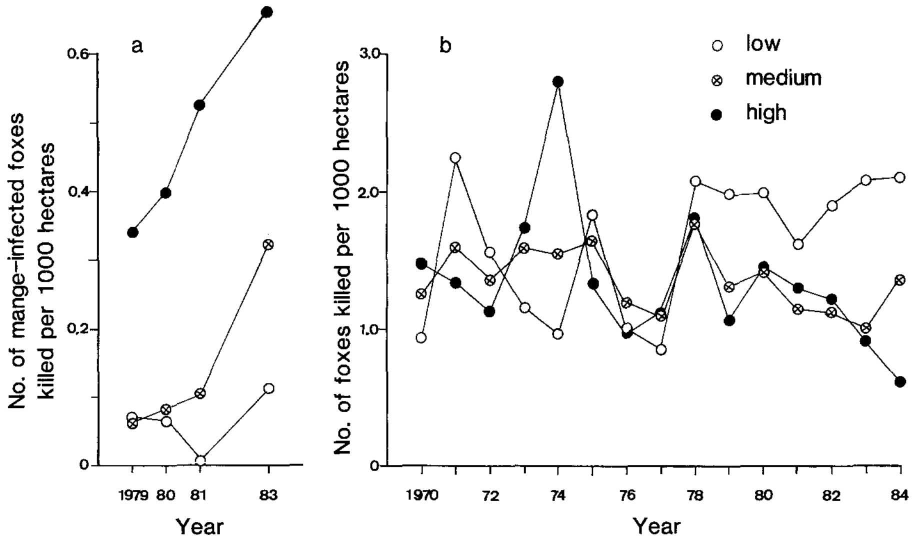

Fig. 2a, b. The mean number of shot or trapped foxes per 1000 ha for 88 hunting organizations in northern Sweden. The number of mange-infested foxes (**a**) and the total number of foxes (**b**) given for organizations classified according to the degree of infestation by sarcoptic mange

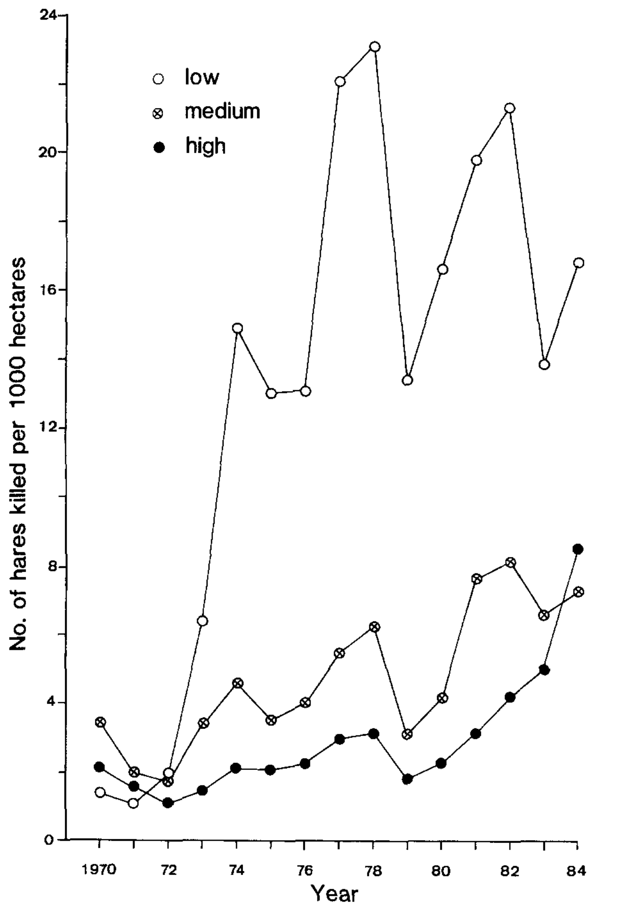

Fig. 3. The mean number of mountain hares shot per 1000 ha by 88 hunting organizations in northern Sweden. The organizations are classified according to the degree of infestation by sarcoptic mange

and other predators. However, the general pattern of the hunting statistics for foxes from the three groups of areas in the 1970s (Fig. 2b) does not immediately support the second explanation. The different levels attained for the harvests in the low vs high (and medium) infection areas may have been due to a differential predation pressure during a critical period only, as suggested by the fox hunting yields in 1973–1974. At present it is unclear as to whether the different hare patterns and numbers in the 1970s represent different degrees of predator regulation or differences in food limitation, or a combination of these. However, according to Keith (1983) it is unlikely that Fennoscandian mountain hares would be food limited.

Relation to a predator-prey hypothesis

In northern Fennoscandia there are regular 3- or 4-year fluctuations ("cycles") for voles (*Clethrionomys* and *Microtus* spp.) (e.g. Myllymäki et al. 1977; Hörnfeldt 1978; Hansson 1979; Hörnfeldt et al. 1986). The red fox is one important predator of the microtine rodents (Englund 1965; Lindström 1982) and foxes also display regular fluctuations (e.g. Hörnfeldt 1978; Lindström 1982; Hörnfeldt et al. 1986). Some of their alternative prey species fluctuate synchronously with the voles, but with a longer or shorter time-lag, within restricted areas of Fennoscandia. This pattern has been shown for muskrat (*Ondatra zibethicus*) (Danell 1978, 1985), mountain hare and black grouse (*Tetrao tetrix*) (Hörnfeldt 1978; Angelstam et al. 1985; Hörnfeldt et al. 1986) as well as for willow grouse (*Lagopus lagopus*), capercaillie (*Tetrao urogallus*) and hazel hen (*Bonasa bonasia*) (Hörnfeldt 1978; Hörnfeldt et al. 1986).

The impact by some important predators has been suggested to synchronize the fluctuations of the alternative prey species to the pattern of the dominant herbivore (staple food) during its decline phase, both for the 3- or 4-year "cycle" centering around voles (Hagen 1952; Lack 1954:204–206; Danell 1978; Hörnfeldt 1978; Angelstam et al. 1984; Hörnfeldt et al. 1986), and for the 10-year "cycle" centering around snowshoe hare (*Lepus americanus*) (Keith 1974). From this alternative-prey hypothesis it follows that a severe reduction in the numbers of predators (as with the red fox by mange) will influence the fluctuation patterns of the alternative prey species. A plausible outcome is that the "cyclicity" more or less disappears due to a weakened synchronization effect by predators during the decline phase of the dominant herbivore.

Our results on hare harvests are partly in accordance with this concept. In areas with a low infection rate, obviously with a low effect on the fox population, hare populations fluctuate around a high and fairly stable level. In medium infection areas with decreasing fox populations the hares seemed to begin to lose their cyclicity after the increase in the mange infection. Finally, in high infection areas with steadily decreasing fox populations the previously low and fairly stable hare populations have increased annually.

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