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Synchronous Population Fluctuations in Voles, Small Game, Owls, and Tularemia in Northern Sweden

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Summary. 1. The population fluctuations in time in northern Sweden are examined for the following species: voles, mountain hare, willow grouse, black grouse, capercaillie, hazel hen, red fox, long-eared owl, Tengmalm's owl, and tularemia. Necessary population data have been obtained from the period 1963–1975/76 as revealed by catches, literature survey, hunting statistics, bird ringing, and obligatory reporting of tularemia in man.

2. The populations of the species under consideration are found to fluctuate synchronously in time and show a 3- or 4-year cycle for the period 1963–1975. Population peaks have occurred in connection with the peak densities of voles in the winters 1963–1964, 1966–1967, 1969–1970 and 1973–1974.

3. Voles caused extensive forest damage (mainly bark-eating) in at least the latter three peak winters. From consideration of the available literature it is apparent that bark is a marginal food. Thus, increased bark-eating during peak densities of voles in winter should be interpreted as a shortage of preferred food.

4. The species studied appear to form a unit (subsystem) within the boreal forest ecosystem. This idea is supported by the connecting predator-prey relationships and the demonstrated synchronous population fluctuations. The subsystem contains herbivores, their food vegetation, and predators. Tularemia is regarded as only one among other predators on voles and mountain hares.

5. It is postulated that voles play a central role in causing the overall synchronism in the population fluctuations of the subsystem.

6. The synchronous population fluctuations described can be explained by the following model for their regulation:

a) An initial decline in vole numbers is brought about by food shortage at winter peak densities.

b) Predator populations (built up with the help of the rich supply of voles) cooperate with food shortage and at some critical point predators alone are able to fulfil the decrease in vole numbers.

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c) Because of the decrease in vole numbers the predators are forced into a decline themselves and must turn to alternative prey species. Mountain hare and gamebird populations represent a low biomass compared with vole populations and predation thus causes the decline in numbers of these small game.

d) Low numbers of predators and excessive food supply then allow voles, mountain hares, and gamebirds to increase again.

e) The building up of vole populations sets the stage for another increase in the number of predators and a new cycle is started.

1. Introduction

Microtines in arctic and subarctic areas show population peaks, generally every third or fourth year (see Krebs and Myers, 1974, for a recent review). In addition to this 3- or 4-year cycle in small rodents there is a "10-year" cycle in the snowshoe hare (*Lepus americanus* Erxleben) in North America (see Keith, 1963, for a review).

In many predators and gamebirds there are cycles corresponding to those of the rodents. Lack (1954, pp. 204–226) showed that the periodicity is 3 or 4 years, or 10 years, depending on whether the dominating herbivores are microtines or snowshoe hares. He suggested that the cycles are based on a predator-prey interaction between the dominating herbivore and its food vegetation. This would lead to a predator-prey oscillation between the dominating herbivore and its predators on one hand, and between the predators and their alternative (more scarce) prey species on the other hand.

Keith (1974) has made a comprehensive study on the "10-year" cycle in the snowshoe hare, gamebirds and predators. He presents a detailed model of the 10-year cycle which in principle is a further development of Lack's (1954) theories.

Concerning the different species involved in the 3- or 4-year cycle there is a lack of corresponding concentrated information. The data published refer to geographically scattered areas and/or often involve only a few species.

In Fennoscandia much of the basic knowledge of the 3- or 4-year cycle in small mammals was provided by Kalela (1949) and Wildhagen (1952). Some authors have also shown synchronous population fluctuations in different species in Fennoscandia. Kloster (1921) and Hagen (1952) reported coinciding peak densities in *Lagopus* sp. and small rodents in Norway. Myrberget (1974) again showed the synchronous population fluctuations in Norwegian willow grouse [*Lagopus lagopus* (L.)] and small rodents.

Siivonen (1948) published data from the Finnish game statistics. "Short-cyclic" (3- or 4-year) fluctuations occurred in willow grouse, black grouse [*Lyrurus tetrix* (L.)], capercaillie (*Tetrao urogallus* L.), mountain hare (*Lepus timidus* L.) and red fox [*Vulpes vulpes* (L.)]. The data on tetraonids (*Tetraonidae*) were further confirmed later (Siivonen 1952, 1954a, b, 1957) and this group, including the hazel hen [*Tetrastes bonasia* (L.)] was shown to fluctuate fairly synchronously in Finland. The synchronism in the 3- or 4-year fluctuation in numbers of tetraonids and small rodents was also stressed.

Englund (1970) concluded that the number of red fox in northern Sweden varies greatly. This is due to varying reproduction and survival which in turn is determined by the availability of rodents as food. Pearson (1975) showed a high correlation "between times of human epidemic tularemia *(Francisella tularensis)* and small mammal 'highs' in Sweden".

The number of breeding pairs of Tengmalm's owl [*Aegolius funereus* (L.)] varies synchronously with the field vole [*Microtus agrestis* (L.)] abundance according to Linkola and Myllymäki (1969). Linkola's and Myllymäki's (1969) data on the long-eared owl [*Asio otus* (L.)] showed similar but less clear trends than the data for Tengmalm's owl.

The first aim of this paper is to present data, from a defined area, on the population fluctuations in time among some species that take part in the 3- or 4-year microtine cycle in Sweden. For this purpose data were gathered from the period 1963–75/76 dealing with population fluctuations (as revealed by catches, literature survey, hunting statistics, bird ringing and obligatory reporting). The following species were studied: voles *(Cricetidae)*, mountain hare, willow grouse, black grouse, capercaillie, hazel hen, red fox, long-eared owl, Tengmalm's owl, and tularemia.

The second aim is to discuss the 3- or 4-year cycle in the light of prevailing predator-prey relationships between the species involved.

2. Material and Methods

The main study area consisted of "Västerbottens län" (the county of Västerbotten[1]) in Sweden (Fig. 1) which, according to Ahti et al. (1968), belongs to the middle and northern boreal zones.

The small mammal abundance has been surveyed yearly since 1971 within the BIG-project ("*B*as*I*nventering *G*nagare" or rodent survey), which will be presented in detail in another paper. A 100 × 100 km continuous area (Fig. 1), covering a wide range of habitats, is censused every spring and autumn. Catches are carried out, with the use of about 2800 snap traps for three consecutive nights, in 64 regularly distributed plots (Fig. 1). The catches of the dominating species, bank vole [*Clethrionomys glareolus* (Schreb.)], grey-sided vole [*C. rufocanus* (Sund.)] and field vole were pooled for each trapping period. These numbers were plotted as a 2-point moving average of trapped voles/100 traps. Additional information on vole peak years and on years with forest damage caused by voles was extracted from Hansson (1969) and Larsson (1973, 1976).

Game preservation organizations report annually the supply of game and the game shot to the Swedish Sportsmen's Association. With regard to the data on small game for Västerbotten, statistics are based on reports of small game shot from about 180 (80–85%) of the organizations in the area. The reports cover an area of approximately 800,000 ha, i.e. about one fifth of the total estimated hunting area. In order to calculate the total bag in Västerbotten the reported figures are multiplied to represent the whole hunting area (Hopfgarten, pers. comm.). It should be noted that this procedure magnifies eventual errors in the basic statistics.

Data were obtained from the Bird Ringing Office of the Swedish Museum of Natural History on the numbers of ringed specimens of long-eared owl and Tengmalm's owl. The figures are based on reports from authorized ringers and from bird stations. The number of ringers has been subject to small variations during the period 1963–1976, i.e. a gradual decline from 278 to 225 and because of restrictions little new recruiting. The number of bird stations during the period 1963–1976 varied between 7 and 8. The ringing refers to the whole country and comprises birds of all ages (S. Österlöf, pers. comm.).

Since 1931 all cases of tularemia in Sweden have had to be reported. Information on tularemia in Västerbotten was received from the County Public Health Office. The figures show the numbers of diagnosed cases of the disease in man.

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[1] Län is translated as county for simplicity's sake, but in the strict sense is an Administrative Province

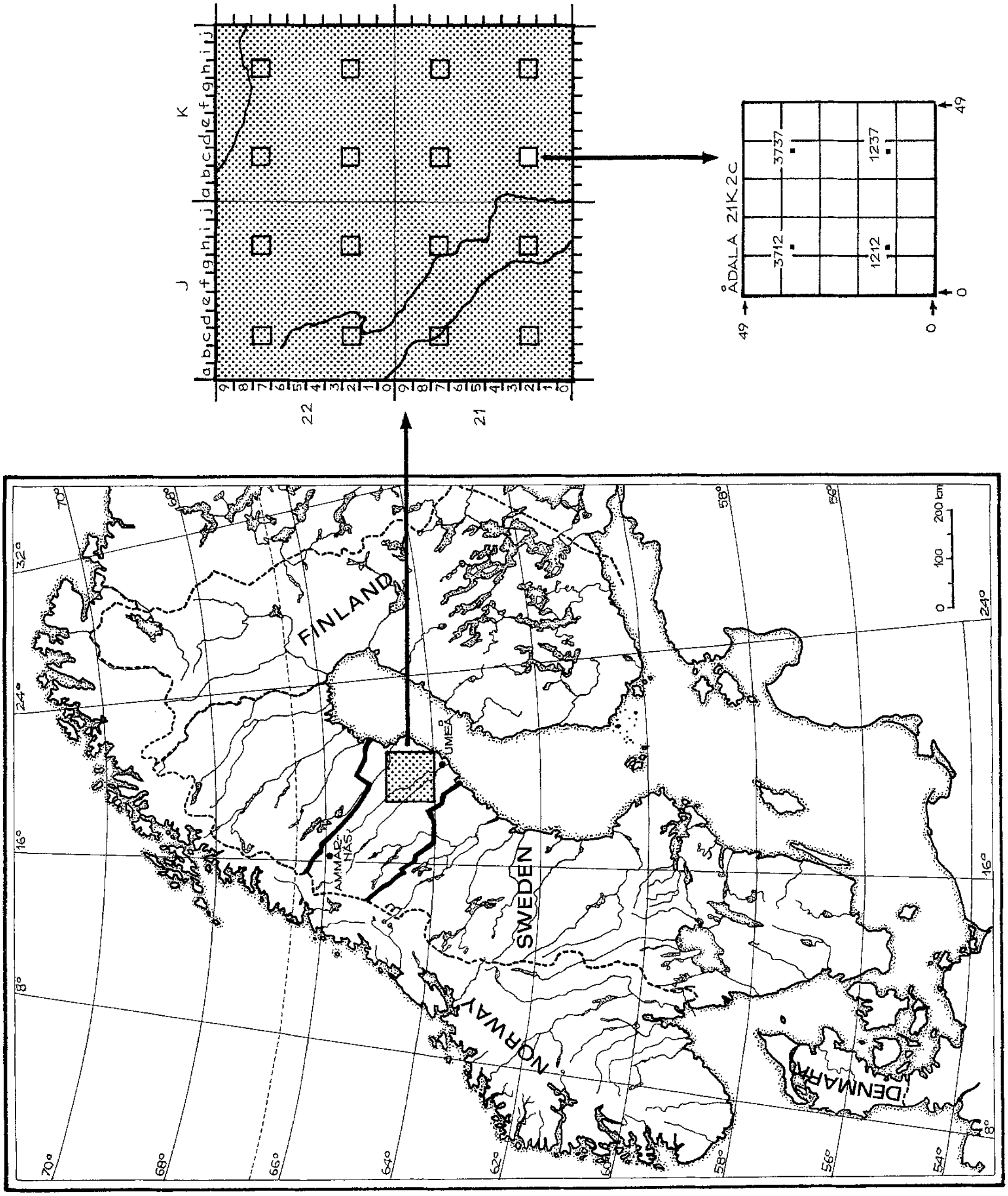
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Fig. 1.

The variations in catch effort are unknown concerning the hunting statistics and bird ringing. Similarly, the reporting effort in registration of cases of tularemia is unknown. Consequently it is not possible to make the corrections necessary for a statistical analysis of this material. In view of this, only the general trends should be observed (J. Nordlander, pers. comm.).

3. Results and Discussion

3.1. Synchronous Population Fluctuations in Northern Sweden

The results are shown in Figure 2. From the Ammarnäs area (Fig. 1) Hansson (1969) reported vole peak years in 1963 and 1966 with population crashes in the following springs and Larsson (1973) pointed to 1969–70 as the next "peak year". My own investigations show that vole numbers reached a new peak in 1973, but voles were almost as abundant in 1974. Voles caused extensive forest damage (mainly bark-eating) in the winters 1966–1967, 1969–1970 and 1973–74 in northern Sweden (Larsson, 1973, 1976). Whether this was the case in the winter of 1963–1964 is unclear (Larsson, 1973).

Mountain hare and gamebirds show population peaks for 1966, 1970 and 1974. The red fox numbers are high for the same years, however there is an uninterrupted high for 1964–1967. For Tengmalm's owl, short-eared owl, and tularemia, the peak years are 1967, 1970 and 1974. The short-eared owl shows an "extra" peak for 1969. The cycle which gave the winter vole population peak in 1963–1964 is incomplete. However, in 1963 there seem to have been large numbers of mountain hare, gamebirds, short-eared owl and Tengmalm's owl. The number of red fox is high for 1964. However, the number of cases of tularemia among the human population of Västerbotten does not show any comparable peak during this cycle.

The data used here do not refer to exactly the same area. Furthermore, all populations, with the exception of voles, are estimated only once a year. Thus, only rough comparisons are possible. Nevertheless it is quite obvious that the population fluctuations have been synchronous in time among voles, mountain hares, gamebirds, red fox, long-eared owl, Tengmalm's owl, and tularemia cases during the period 1963–1975. Population peaks have occurred in connection with the peak densities in voles in the winters 1963–1964, 1966–1967, 1969–1970 and 1973–1974. The only deviations from a strictly synchronous pattern are found in the number of tularemia cases and the red fox population. The absence of reported cases of human epidemic tularemia in Västerbotten, in connection with the cyclic high among voles in winter 1963–1964, does not prove that the disease was not involved in this cycle. In the adjacent county of Norrbotten there was an epidemic in 1964 (Berglund, 1965). The outbreak occurred within a restricted area in connection with an increase in the mountain hare population. The total vector situation for transmitting tularemia in Västerbotten may have been aberrant by that time. This may have kept the abundance

Fig. 1. Location of the main study area, the county of Västerbotten (bordermarking = ——) in Sweden. The rodent survey (= the BIG-project) is carried out within the dotted area. Within this area 16 squares (size = 5 by 5 km) are sampled and within each of these 4 hectare-squares. The sampling grid is according to The Sedish National Grid

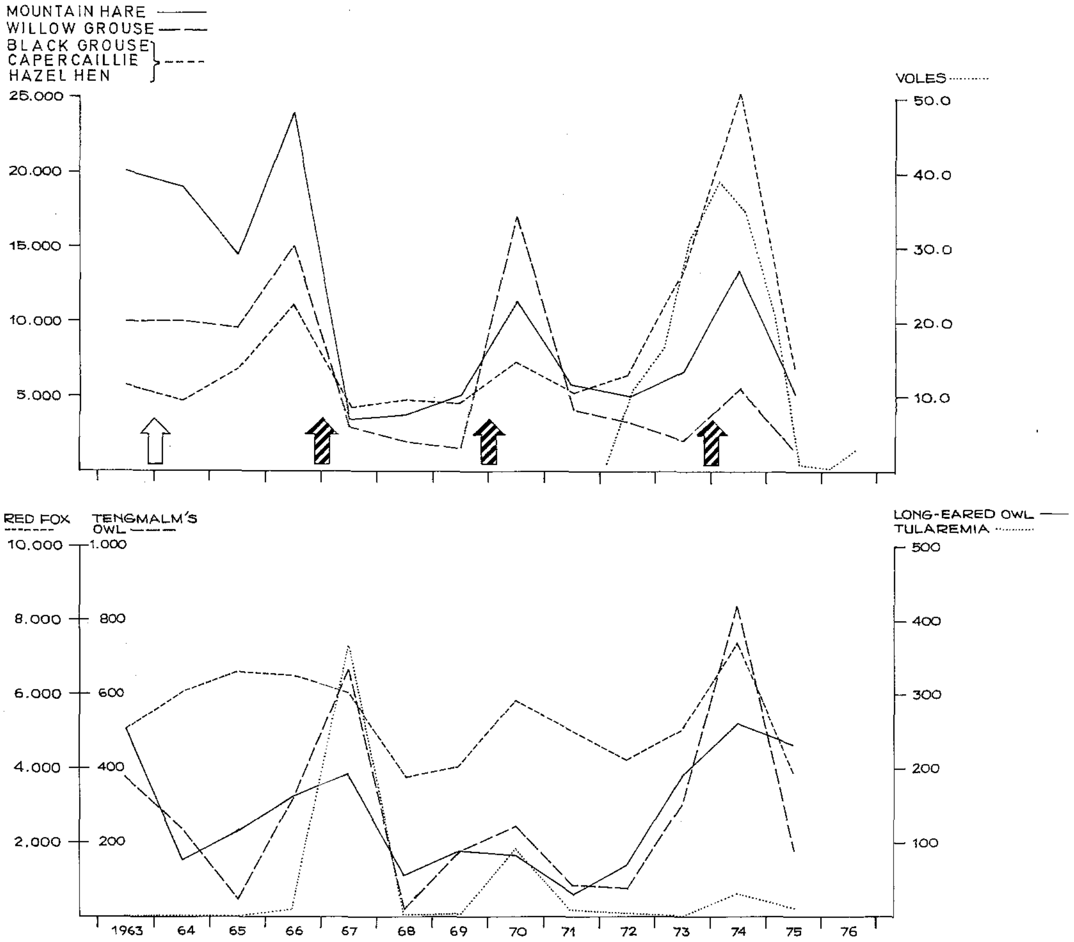

Fig. 2. Population fluctuations in voles (bank vole, grey-sided vole and field vole collectively), small game (mountain hare, willow grouse, black grouse, capercaillie, hazel hen and red fox), owls (Tengmalm's owl and long-eared owl) and tularemia as revealed by catches and literature survey, hunting statistics, bird ringing, and obligatory reporting of tularemia in man respectively. *Arrows* show winters with peak densities in voles whereas the hatched ones also indicate extensive forest damage (caused by voles) at the same time

of the bacteria at a low level, at least low enough not to be detectable through human cases.

If an orthodox synchronism is to be expected, there also ought to be a dip in the red fox curve between the two vole peak winters in 1963–1964 and 1966–1967. This is not the case and hunting statistics show a high fox density lasting for four consecutive years (from 1964 to 1967). Two expected peaks, however, might melt together. Suppose one microtine cycle ends with good conditions for fox reproduction and survival. Then the following hunting bag will be fairly good. When the first microtine cycle is then replaced by another starting with good conditions for fox recruitment, a high red fox population level may be maintained (as shown in the hunting statistics). Hansson's (1969) data from the Ammarnäs area of Västerbotten (Fig. 1) showed that rodent numbers were at a peak level in 1963, at an average in May 1964, at a low in June 1964 and at an average in June 1965. Thus, rodent numbers recovered very quickly, perhaps already by the summer of 1964. The food supply of the red fox might have been depleted for a short time only, which could explain why fox numbers were maintained at a high level during two microtine cycles.

3.2. Food Habits of the Species Studied

The staple diet of the bank vole (e.g. Holišová, 1966, 1971), the grey-sided vole (Kalela, 1957) and the field vole (Hansson, 1971) is vegetable. This also applies to the mountain hare (Siivonen, 1968), willow grouse, hazel hen, black grouse and capercaillie (Semenow-Tjan-Sanskij, 1960). Small mammals, mainly rodents, constitute more than 90% of the food of both the long-eared owl (Sulkava, 1965) and Tengmalm's owl (Sulkava and Sulkava, 1971). The main prey for the red fox in most parts of Sweden is rodents, mostly voles, but mountain hares and gamebirds are also eaten (Englund, 1965).

Both voles (Dahlstrand et al., 1971) and mountain hares (Borg et al., 1969) are susceptible to tularemia. The species discussed in this paper appear to form a unit (subsystem) within the boreal forest ecosystem. This is expressed both through the connecting predator-prey relationships and the demonstrated synchronous population fluctuations. The subsystem contains herbivores, their food vegetation, and predators. Even more species could probably be fused into it, e.g. several species of owls, birds of prey and some of the mustelids *(Mustelidae)*.

3.3. Predation on Voles and Small Game

At present it is not possible to explain the overall synchronism in the population fluctuations of the subsystem. I postulate, however, that voles play a central role in it.

Semenow-Tjan-Sanskij (1960) calculated the biomass of the most important animal prey species in the taiga biocoenose and found that small mammals, voles, and shrews *(Soricidae)*, on average may make up 3–4 times as much biomass as the gamebird species together. Although the biomass of mountain hare was not estimated, figures point to the proportionately high importance of voles as prey if the biomass is considered. Furthermore, the high total biomass represented by voles is made up of many individuals which increases the predator's chances of meeting and catching them.

During most of the cycle predators benefit from the abundant voles and build up their stocks. The influence of predators is normally not supposed to start a decrease in the vole populations (Pearson, 1966; Krebs and Myers, 1974). It is logical, however, to assume that once the decrease has started (and is in progress) the impact of the predators grows more and more effective (cf. Pearson, 1966; Keith, 1974). At some point the control by predators alone must be sufficient to maintain the decline.

Once voles have declined, the numbers of many predators are above the level of carrying capacity and they decline themselves. Their chance to survive may be improved by switching to other prey species. Some predators are opportunistic in their choice of prey. For example, when voles are abundant, red foxes prey intensively on them while predation on alternative prey species relaxes (Englund, 1965; Ryszkowski et al., 1973). The same thing probably applies to other generalists such as the corvids *(Corvidae)*. In a specialist such as the weasel *(Mustela nivalis* L.) males turned to lagomorphs as alternative prey when their main prey, small rodents, became scarce (Erlinge, 1975).

Thus, after the vole decline, it can be expected that the total impact from different predators will exert an immense predation pressure on gamebirds and mountain hares and cause their decline. Many smaller predators perhaps do not prey on adult small game. However, they have the physical capacity to prey on eggs and young. When predation is directed in that way young individuals ought to be subject to fluctuations. This is in agreement with Myrberget's (1972) findings in willow grouse, where the fluctuations between years were manifested mainly through changed production of young birds. This in turn was determined by egg predation, which was most severe after a small mammal decline. The stoat *(Mustela erminea* L.) was the most important predator.

3.4. The Role of Tularemia in the 3- or 4-Year Microtine Cycle

In Sweden tularemia has been isolated from mosquitoes (Olin, 1942), mountain hares (Borg et al., 1969) and voles (Dahlstrand et al., 1971). I find it natural to regard the bacteria only as one among other predators on voles and mountain hares. The additional influence of tularemia strengthens the total impact of predation. Tularemia, however, does not prey actively by itself but is likely to be influenced by all of its different vectors. The situation in tularemia-infected rodents is thus more complicated than in a pure predator-prey relationship. A high rodent abundance increases the chance of infection. The actual abundance of tularemia, however, can be expected to be heavily modified by the occurrence of other vectors like mosquitoes. Their populations do not necessarily fluctuate synchronously with the rodents. Weather conditions, such as temperature, have a major influence on the mosquito populations, both on their longevity and activity (Reeves, 1965). Thus, such random factors can be expected to cause the influence of tularemia to vary in magnitude from time to time. The varying number of cases of outbreaks in man may support this conclusion.

Tularemia probably always accounts for some of the mortality during rodent declines. Borg et al. (1969) showed that the tularemia outbreak of 1966–1967 was accompanied by severely diminished mountain hare numbers. This might have been the exception to the rule since similar strong influence has not been shown in connection with the other epidemics. Whether the average effect of tularemia on rodent mortality is more important than that from other predators cannot be evaluated at present. First it is necessary to quantify the impact of each predator at different times of the rodent cycles.

3.5. *The Food Available to Voles*

This discussion is focused on the position of voles in the synchronous population cycles described. Many theories have been put forward to explain the cause of vole population cycles and their decline, but none has become widely accepted (see Krebs and Myers, 1974, for a recent review).

From a nutritional point of view it seems reasonable to assume winter to be the most severe time of year for voles in northern Sweden. The vegetable production is minimal and the risk of occurrence of food shortage is greatest. Voles also cause conspicuous forest damage through bark-eating, in connection with peak densities in winter, during at least the latter three cycles. This may very well be a reflection of winter food shortage of some sort and is supported by several reports. The bank vole (Holišová, 1966, 1971; Larsson and Hansson, 1977), grey-sided vole (Kalela, 1957) and field vole (Hansson, 1971) have been shown to consume bark more often in winter than at other times of year. Holišová (1971) also showed that the part of bark in the total food volume was doubled in bank voles at high as compared with low densities. Field voles at peak densities (in Västerbotten) in October 1973 were found to consume more bark than the declining population in the autumn of 1974 (Larsson and Hansson, 1977). Myllymäki (1970) reported that voles prefer green vegetation (such as clover) to the bark of apple trees and Hansson (1971) found from feeding experiments with field voles that an unusual diet increased the interest in bark. In a field experiment Larsson and Hansson (1977) treated some areas with grass herbicides, the effect of which tended to increase the bark consumption in the field vole.

Thus, the facts presented suggest that bark is a marginal food and forest damage during high vole densities (in the winters 1966–1967, 1969–1970 and 1973–1974) should be interpreted as a shortage of preferred food. This food shortage might force the voles into the initial decline in a similar way as Keith (1974) suggested for the snowshoe hare.

4. Conclusions

The synchronous 3- or 4-year population fluctuations described can be explained by the following model for their regulation:

1) An initial decline in vole numbers is brought about by food shortage at winter peak densities.

2) Predator populations (built up with the help of the rich supply of voles) cooperate with food shortage and at some critical point predators alone are able to fulfil the decrease in vole numbers.

3) Because of the decrease in vole numbers the predators are forced into a decline themselves and must turn to alternative prey species. Mountain hare and gamebird populations represent a low biomass compared with vole populations and predation thus causes the decline in numbers of these small game.

4) Low numbers of predators and excessive food supply then allow voles, mountain hares, and gamebirds to increase again.

5) The building up of vole populations sets the stage for another increase in the number of predators and a new cycle is started.

When this model (cf. Lack, 1954; Keith, 1974) applies there should be a time lag in the population fluctuations among the species studied. A prerequisite for analyzing time lags is that continuous quantitative data are available for both voles, small game and tularemia. In Sweden this is only the case for the last 5 years (1971–1975). Further limitations are set by the fact that all but the vole populations have been estimated only once a year.

During the period 1971–1975 voles reached peak density in 1973. The population levelled off (and a decline was evidently initiated) in connection with the forest damage in the winter of 1973–1974. Mountain hare, gamebirds, red fox, long-eared owl, Tengmalm's owl and tularemia peaked one year later (in 1974) without any visible time lag between prey species and predators. This, however, should not be taken as evidence against the existence of a time lag. A time lag of almost one year may escape detection, depending on inaccuracy in the estimation of the time lapse for these population fluctuations.

In order to understand the mechanisms of population regulation for the species discussed here it may be fruitful to treat them as a unit. The model presented is built up from very fundamental predator-prey relationships and I think that much effort will be necessary if this model is to be replaced by others of essentially different construction.

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