

Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia

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Summary. We tested the hypothesis that synchronous fluctuations in small game species in boreal Fennoscandia are caused by varying predation pressure. The main prey of predators are the cyclically superabundant voles. Small game species (alternative prey) are rare compared to voles. The following 4 predictions were checked: (1) Predators should shift their diet from main prey to alternative prey as main prey decline. – This was confirmed using data on red fox (*Vulpes vulpes* L.) diet.; (2) The mortality rate of alternative prey should be inversely correlated to the abundance of main prey. – This was true for mountain hare (*Lepus timidus* L.) mortality rates and the rate of nest predation on black grouse (*Tetrao tetrix* L.); (3) The total consumption of prey by all the predators should at least equal the critical losses in alternative prey during a decline year. – A tentative estimate of predator consumption amounted to 10 times the losses in grouse and hare.; and (4) The absence of synchrony between the species in the boreomoral region should be associated with a more diverse diet of predators. – This was the case for red fox diets throughout Sweden. Although all 4 predictions were confirmed, we could not necessarily exclude other hypotheses involving changes in quality or quantity of plant food.

Introduction

Within Fennoscandia populations of various species of small herbivores, as well as their predators, have been reported to fluctuate in synchrony (short-term population fluctuations or “the 3–4 year cycle”) (Siivonen 1948, Hagen 1952, Lack 1954).

Angelstam et al. (in press) examined the occurrence and distribution of synchronous short-term population fluctuations (referred to as cycles) within Fennoscandia and concluded that interspecific synchrony was confined to vertebrate communities in the northern parts of Fennoscandia, namely within the boreal and the alpine zones, each of which have at least partly separate sets of species. We concluded that a conceptual model describing the causal mechanisms behind the 3–4 year cycle has to explain: (i) the synchrony between the species, (ii) the time-lag of one year between spring densities of predators, grouse and hare versus voles, and (iii) the disappearance of synchrony towards southern Fennoscandia.

This paper examines an hypothesis put forward by several authors since Cabot (1912), but first presented in detail by Hagen (1952) and Lack (1954) and more recently revived by Keith (1974). The core idea of this hypothesis is that the interspecific synchrony is proximately brought about by varying predation pressure. The population dynamics of predators are largely determined by one particular prey type which at certain intervals becomes superabundant and then allows increasing predator densities. In Fennoscandia the main prey for a great many predators consists of vole species which fluctuate in 3 to 4 year cycles (Kalela 1949, Wildhagen 1952). At high main prey densities the predation pressure on other prey types with lower abundance or accessibility is relaxed, and these potential alternative prey species enjoy high survival rates and increase in numbers. As main prey populations decline, predators turn to the less abundant alternative prey types whose survival rates in turn are lowered. At the same time, the survival rate and reproduction of predators are reduced. A subsequent increase in main prey density then ignites a new cycle. As a shorthand we name this model of limitation of alternative prey density the *alternative prey hypothesis*.

In this paper we will examine the impact of predators on alternative prey within a set of species in the boreal coniferous forest. To avoid misunderstanding we wish to stress that we are not interested here in the possible impact of predators on the main prey, or in the reasons for the 3 to 4 year cycle in voles.

Predictions

We use our own data concerning a predator (red fox *Vulpes vulpes* L.) and two of its alternative prey species, viz. black grouse (*Tetrao tetrix* L.) and mountain hare (*Lepus timidus* L.), as well as data published by other workers, to investigate whether the following predictions from the alternative prey hypothesis are fulfilled. The first three predictions concern the occurrence of synchronized fluctuations. The last prediction concerns the geographical distribution of these fluctuations.

Prediction 1. Predators should shift their diet from voles to alternative prey when vole abundance declines and back to voles as soon as vole abundance increases.

Prediction 2. Most vole predators are small and relatively inefficient in capturing larger prey. Therefore these preda-

tors, when the main prey density declines, will primarily select alternative prey of about the same size and accessibility as voles. Thus, when shifting to tetraonids or mountain hare as alternative prey, vole based predators should take mainly eggs, chicks and juveniles. We therefore predict the mortality rates of eggs, chicks and juveniles, to be high during vole lows and low during vole highs.

Prediction 3. A shift in the predators' diet, i.e. functional response, is not enough to explain the differences in loss rates of alternative prey populations between vole highs and lows. The total consumption by the predators, the "predatory capacity" must also be sufficient. In our case, this means that it shall equal or exceed the observed losses in grouse and hares.

Prediction 4. An implicit assumption of the alternative prey hypothesis is that alternative prey are scarce or inaccessible compared to the main prey. If not, and particularly if the alternative prey comprises many different species or items, the effects of main prey fluctuations on the population dynamics of predators and thus also on alternative prey populations, will be swamped out. Thus, in areas where interspecies synchrony does not exist, the predators' diet should be more diverse compared to areas with synchronized population fluctuations. Since there is a decreasing trend of interspecific synchrony in Sweden from north to south (Angelstam et al. in press), there should also be an increasing trend in predator food diversity from north to south.

A fulfillment of these predictions, however, does not mean that other, possibly complementary, hypotheses inevitably must be rejected (see Angelstam et al. in press). However, if they are not fulfilled the alternative prey hypothesis must be rejected.

Study area

Our field studies were conducted within the Grimsö Wildlife Research Area in south-central Sweden (59°40'N, 15°25'E). The Grimsö area lies within the southern boreal zone (Sjörs 1965) and is totally dominated by forests of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) which cover about 70 percent of the total area. Only three percent of the area is used for agricultural purposes. The human population density is 1.5 per km² (1982). Forestry is commercially run. Small game species are hunted very little at Grimsö. For a detailed description of the study area see Angelstam et al. (in press).

Materials and methods

Predators' shift in diet

The occurrence of voles and mountain hares in the diet of foxes during the 4-year vole cycle from 1975 to 1979 was studied by Lindström (1982 and in prep.) using scat analysis. We have used those data to analyse the dietary shift in the predator.

Mortality rates of alternative prey

Using telemetry data, track counts, counts of mountain hares and mountain hare pellets, we estimated adult and

juvenile mortality rates during one vole cycle, viz. low phase to low phase 1975–79 (see Angelstam et al. in press for details). We analysed the population changes using K-factor analysis (Varley and Gradwell 1960). For black grouse the rate of nest predation was measured as the proportion of nests that were preyed upon out of 48 certain nesting attempts by radio-equipped hens which were caught before the start of egg-laying in 1978 to 1981 (Angelstam 1983) and in 1982 (Hoogeveen and van den Brink in prep.).

Consumption by the predator community

We tested prediction 3 by comparing losses of grouse and hares with estimated food requirements of predators in a year (1978) with maximal losses of grouse and hares. Note that the diet of predators also consists of several other species and items than grouse and hares.

Biomass of dead alternative prey. The number of hares dying during summer 1978 (from the first week of May to the last week of October) was estimated according to Angelstam et al. (in press). We approximated the weight of the hares that died to 3 and 1.5 kg for adults and juveniles. The number of black grouse, capercaillie (*Tetrao urogallus* L.) and hazel hen (*Bonasa bonasia* L.) that died was calculated from estimated spring density, clutch size, rate of egg loss and mortality rates of adult males, adult females and juveniles. We estimated the spring densities of all grouse from spring densities of black grouse (Angelstam 1983) and the relative abundance of adults of the 3 species during counts in August (approx. 3:2:1, black grouse, capercaillie and hazel hen, respectively, Angelstam unpubl.). Clutch size and loss rates were established for black grouse through counts in spring and in August as well as radio-tracking (Angelstam 1983). These rates were applied to all 3 species. We used the average weights of adult tetraonid males and females given by Haftorn (1971). An egg, a juvenile before 1 September and a juvenile after 1 September were estimated to weigh on the average 0.035, 0.3 and 1.0 kg, respectively.

Consumption by the predator community. We assumed that all adult predators survived the summer (defined as above). We estimated the daily food consumption of adult predators from the literature and from spring densities of predators based on our own experience from the Grimsö area (Table 1).

The total food requirements of the red fox population was derived from number of fox days per 10 km² (Lindström 1982), a daily food requirement of juveniles before 1 July of 0.24 kg (Sargent 1978) and the same food requirement of juveniles as for adults after 1 July. We had no figures on the reproductive success of the pine marten (*Martes martes* L.) and badger (*Meles meles* L.) but calculated the total food consumption of each population from the requirement of adults by assuming the same ratio between amount consumed by adults and amount consumed by juveniles as for the red fox. We have not included the consumption by stoats (*Mustela erminea* L.) and weasel (*Mustela nivalis* L.) since we have no data on their densities.

The food consumption of goshawk (*Accipiter gentilis* L.) was estimated from the spring density of adults and 2 young per pair. The food demand of one young until

Table 1. Spring densities and daily food requirements per adult of the predators within the Grimsö study area from 1 May to 31 October in 1978.

Species	Spring density		Food requirement	
	n/km^2	based on	kg/day	based on
Red fox	0.4	Lindström (1982); from den counts and breeding frequency	0.4	Lockie (1959), Goszczynski (1974), Sargeant (1978)
Pine marten	0.07	de Jounge (1981); from snow trackings	0.15	Schmidt (1943), Novikov (1956), Pulliainen (1981)
Badger	0.4	from distribution and abundance of badgers during den counts in June and from boxtrapping	0.5	Erlinge et al. (1983)
Goshawk	0.05	Widén (in prep.); from distribution of nests	0.15	Höglund (1964), Wikman (1977)
Common buzzard	0.2	from distribution of breeding territories	0.15	Erlinge et al. (1983)
Raven	0.06	from distribution of nests	0.18	} estimated from consumption of common buzzard and corrected for size using metabolic weight ($w^{0.72}$) (Lasiewski and Dawson (1967))
Hooded crow	0.2	from the distribution of nests and fledged broods	0.10	
Jay	4.0	Lundberg et al. (1980); from marked/unmarked ratio	0.04	

60 days of age (young still dependent on parents) was 10 kg according to Höglund (1964). We assumed that only one young was present per adult pair after 60 days of age due to mortality and emigration. The daily food demand of each of these young was assumed to be the same as for an adult hawk. We estimated the food consumption of common buzzards (*Buteo buteo* L.) from that of adults using the same ratio between consumption of adults to juveniles as for goshawks.

The food consumption of juvenile ravens (*Corvus corax* L.) and hooded crow (*Corvus corone* L.) was estimated to have been the same as for adults during the summer and the average ratio of adults to juveniles was estimated to 2/3 during the whole period (mean clutch size = 4–6 and 4–5, respectively (Haftorn 1971)). We obtained the average number of young jays (*Garrulus glandarius* L.) present throughout the summer from a mean clutch size of 6–7 (Haftorn 1971) and a juvenile frequency of 50% during November (Lundberg et al. 1980), assuming a constant instantaneous mortality rate. The ratio of food consumed by adults to food consumed by young during the first 40 days of the young (until independency) was assumed to equal the same ratio as for goshawks. During the rest of the period all jays irrespective of age were assumed to consume the same amount of food per day.

Latitudinal change in diversity of predators' diet

We calculated dominance diversity curves from Englund's (1965) data on the diet of foxes during winter 1959–60 in four areas in Sweden ranging from the southernmost Sweden to the far north. That winter Englund (1965) stated the supply of small rodents as "bad".

Results

Predators' dietary shift

The frequency of occurrence of mountain hares in red fox scats showed no consistent relationship to density of adult

and subadult mountain hares during spring and autumn (Fig. 1). However, the frequency was negatively correlated with the field vole index ($r = -0.68$, $P < 0.05$) (Fig. 2) and with the frequency of small rodents in the same scat samples ($r = -0.55$, $P < 0.05$) (Fig. 3).

Mortality rates of alternative prey

Mountain hare. Summer mortality of juveniles decreased as voles increased (1975 to 1977), then increased during the crash and low of the vole cycle (late winter 1978 – spring 1979) (Fig. 4). Total winter mortality rate followed the same pattern (Fig. 5). In each year the summer mortality contributed most to the total annual mortality (Fig. 5). However, it should be noted that "juvenile mortality" also included possible changes in reproductive rate since the calculations were based on the assumption that this parameter was constant (Angelstam et al. in press).

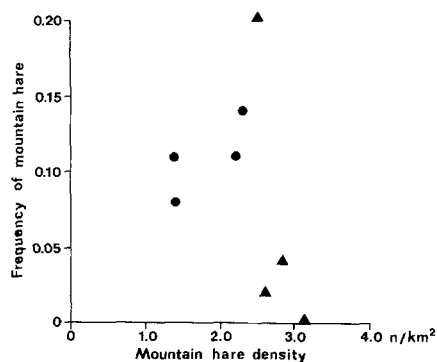


Fig. 1. Frequency of occurrence of mountain hare in the diet of red fox during spring (dots) and autumn (triangles) 1975 to 1979 (Lindström, in prep) in relation to mountain hare density (both sets of data from the Grimsö study area).

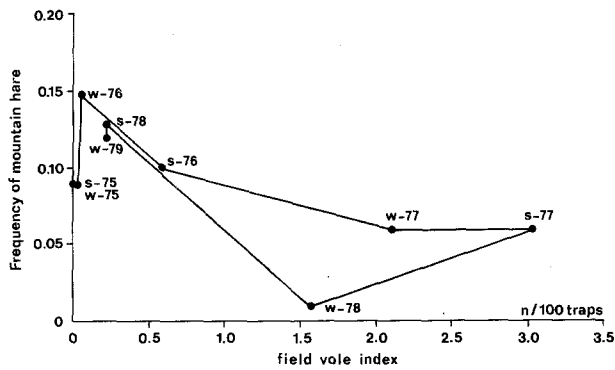


Fig. 2. Frequency of occurrence of mountain hare in the diet of red fox (Lindström, in prep) in relation to field vole (*Microtus agrestis* L) index (means of autumn year t and spring year $t+1$ as winter value, and means of spring year t and autumn year t as summer value) (Hörnfeldt pers comm). w denotes winter, s denotes summer and numbers denote year.

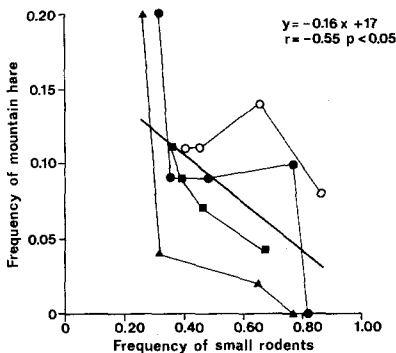


Fig. 3. Frequency of occurrence of mountain hare in red fox diet in relation to frequency of occurrence of small rodents (voles and mice) during spring (rings), summer (squares), autumn (triangles) and winter (dots) from 1975 to 1979 (Lindström in prep).

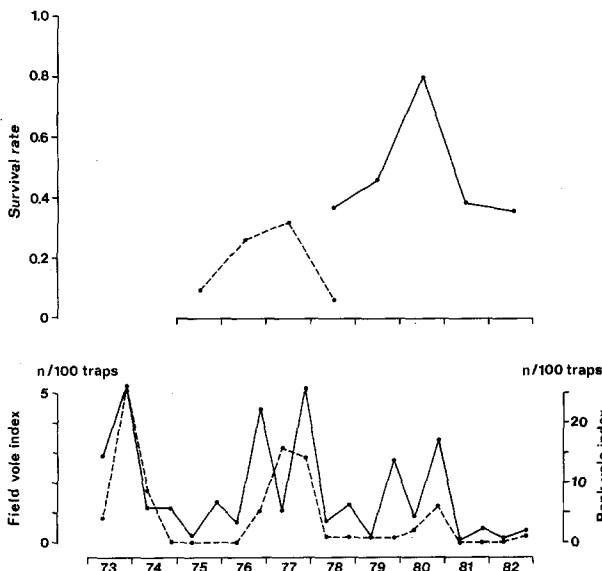


Fig. 4. Survival rate of juvenile mountain hare during May through October (top left), and the proportion of black grouse nests of radio-tagged hens that were not preyed upon (Angelstam 1983) (top right) in relation to field vole (broken line) and bank vole (*Clethrionomys glareolus* Schreb) (solid line) abundance (bottom) (Hörnfeldt pers comm).

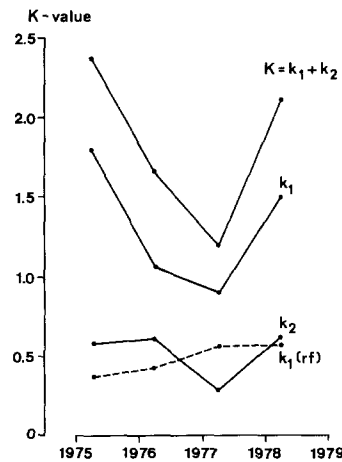


Fig. 5. K-factor analysis of mountain hare mortality within the Grimsö study area from spring 1975 to spring 1979 (calculated from data in Angelstam et al. in press). k_1 = adults and juveniles from 1 May to 31 October. k_2 = adults and subadults from 1 November to 30 April. (k -values were calculated from $\ln(\text{numbers})$). $k_{1(rf)}$ denotes losses during spring to autumn which could be covered by an estimate of red fox consumption.

Black grouse. As vole populations increased at Grimsö from 1979 to 1980 (Fig. 4), the proportion of black grouse nesting attempts that failed due to nest predation sank from 0.63 to 0.20. In late winter 1981 the vole populations crashed and in 1981 and 1982 vole densities were very low while the frequency of nest predation rose above 60%.

Consumption by the predator community

In the summer of 1978 the biomass of alternative prey species (grouse and mountain hare) that was lost comprised 20 kg per km² (Fig. 6). During the same period the total amount of food needed to satisfy the predator community in the corresponding area at Grimsö amounted to 190 kg per km² (Fig. 6).

For one predator, the red fox, we had quantitative data on the diet (Lindström in prep.) and could calculate the population's actual consumption rate of alternative prey (mountain hare) during a full vole cycle. During the summers 1975 to 1978 red fox consumption rate amounted to, on average, 41% of all mountain hare losses. However, the consumption rate by foxes did not parallel the total hare mortality pattern during summer, decreasing as vole density increased and vice versa (Fig. 5). Thus, our results for fox consumption on hares in summer did not conform to the alternative prey hypothesis.

We could not make an unbiased comparison between winter mortality of hares and consumption rate by foxes since the number of subadult and adult hares dying was calculated from those consumed by foxes. However, the K-factor analysis (Fig. 5) revealed that over-winter mortality contributed to the cyclic pattern of hare density. Thus, if our assumptions for calculating hare density and mortality, as well as Lindlöf and Lemnell's (1981) conclusion that foxes kill most of the hares that die during winter, held true, it follows that fox predation was important, at least as a proximate cause, in generating the mountain hare fluctuation pattern.

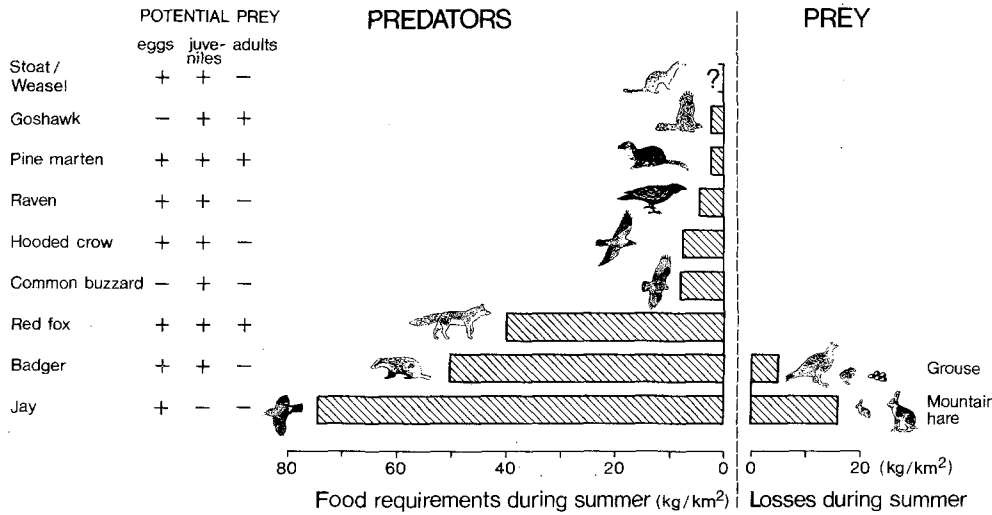


Fig. 6. Comparison between the biomass of mountain hare and grouse losses per km² (right) and the predators' estimated consumption per km² (left) within the vertebrate community at the Grimsö study area during the summer of 1978 when vole populations crashed.

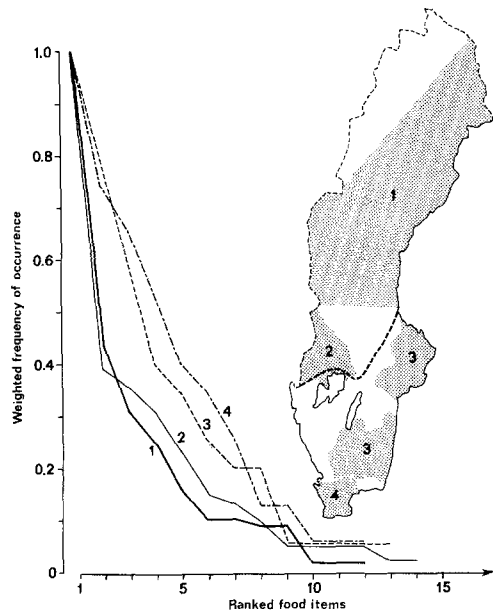


Fig. 7. Dominance-diversity curves of red fox diet in four areas in Sweden as shown on the map. Frequency of occurrence of food items in red fox stomachs during the winter 1959/60 were calculated from Englund (1965). x-axis denotes dominance rank, y-axis denotes frequency in relation to the most frequently occurring food item in each area, which was assigned a value of 1.00. Broken line on the map indicates the border between the boreal and the boreo-nemoral zones.

Latitudinal change in diversity of predator diet

Dominance-diversity curves of red fox diet during a vole low (Fig. 7) indicated that the diet was least diverse in the northern part of Sweden (area 1) and most diverse in the southernmost province of Sweden (area 4) (curve 1 runs below curve 4 and without overlap). The two areas (2 and 3) close to the border (Limes Norrlandicus, Sjörs 1965) between boreal forests with low human population density in the north, and mixed agricultural and forest areas with denser human population in the south, also fit the trend in diversity. The curve for area 2 runs below that of area

3 without overlap, indicating a less diverse diet of foxes north of the Limes Norrlandicus than south of it.

Discussion

Were the predictions from the alternative prey hypothesis fulfilled?

Prediction 1. We found that the red fox shifted its predation from voles to mountain hares as voles declined and vice versa. Also other predators occurring in this vertebrate community have been shown to shift their diet to alternative prey species in relation to vole abundance. Thus, Dunn (1977) and Tapper (1979) showed that weasel, and Moors (1982) that both weasel and stoat partly shifted from small rodents to birds when voles and house mouse (*Mus musculus* L.), respectively, were scarce. Goszczyński et al. (1976) showed that red fox increased the proportion of European hare (*Lepus europaeus* L.) in their diet when voles decreased. Soumos (1952) studied the diet of the common buzzard in a coniferous forest in Finland and recorded a dietary shift from vole to juvenile birds, among which chicks of capercaillie, black grouse and hazel hen formed a major part. Also badgers (Skoog 1970), jay and hooded crow (Haftorn 1971) are known to feed on voles when abundant but are very catholic in their diet and certainly also eat eggs of grouse. No doubt this applies also to the raven.

We therefore conclude that the predators in this vertebrate community potentially are able to shift their predation in relation to vole abundance.

Prediction 2. As predicted juvenile mortality rate of mountain hare and loss rate of black grouse nests were higher at low than at high vole densities. The same applied to over-winter mortality of adult and subadult mountain hares.

In an area in Norway very similar to our study area, Storaas et al. (1982) found that nest losses of capercaillie and black grouse were low (11%) in a small rodent peak year (1980) and high (78%) in a small rodent crash year (1981). Olstad (1932) and Myrberget (1970) observed an inverse relation between egg losses in willow grouse (*Lago-*

pus lagopus L.) and vole abundance in west and north Norway, respectively. Also losses of muskrat (*Ondatra zibethica* L.) nests (Danell 1978) in northern Sweden were negatively correlated with vole abundance. Moreover, duckling production of long-tailed duck (*Clangula hyemalis* L.) (Pehrson 1976) in the arctic mountain region in north Sweden was positively correlated with vole abundance.

Thus there is evidence of an inverse relation between loss rates in alternative prey populations and vole abundance.

Prediction 3. According to the alternative prey hypothesis the summer of vole decline should be particularly critical to the generation of the cycles due to shifting predation pressure. Our tentative comparison between the predators' estimated consumption and the biomass of dead grouse and hares during the summer of crash in vole density (1978) suggested that the estimated biomass of dead hares and grouse amounted to $\frac{20}{190} = 11\%$ of the predators' estimated requirements (Fig. 6). Thus, the predators may have accounted for all the losses in these prey populations if hares and grouse constituted 11% of their diet and if they killed all hares and grouse they ate. However, it should be noted that only foxes, martens and goshawks were capable of capturing adult hares and grouse and that the two species contributing most to the "predatory capacity", viz. jay and badger, presumably were only capable of robbing nests and killing small chicks and very young hares. In an experiment with dummy nests to reveal which predators may be responsible for nest predation on tetraonids, Angelstam (in prep.) found that most members of the predator community took part in the predation on the experimental nests but that predation from corvids dominated. We agree with Potts (1980) who pointed out the importance of including all potential predators when estimating the consumption of prey populations.

The nest losses of tetraonids (Olstad 1932; Myrberget 1970; Storaas et al. 1982) and muskrats (Danell 1978) which were inversely related to vole abundance were caused by predation. Also Pehrson (1976) argued in terms of different rates of predation in relation to vole abundance when explaining the connection between duckling production and fluctuations in vole density. Prediction 3 was not fully supported since fox predation rate on hares did not change in the predicted way in relation to the vole cycle during summer although it possibly did so during winter. During summer, however, many other predators in the vertebrate community according to our tentative calculation might have contributed to the losses of juvenile hares. We argue that there are enough predators within the boreal forest vertebrate community to account for all observed losses in alternative prey species populations.

The evidence presented in relation to predictions 1, 2 and 3 indicates that a shifting predatory pressure from generalist predators on adult and young hares, as well as on grouse eggs and chicks, may be an important force causing the cyclic fluctuations in grouse and hares.

All other limiting factors being constant we argue that it may be possible to predict the predation pressure (P) on alternative prey in relation to vole abundance. We assume that the rate of increase of voles, because of their much shorter generation time, is higher than that of predators and alternative prey. Thus the buffering effect of voles

would increase and the predation impact decrease, as the vole abundance increases from low phase to peak phase. Hence,

$$P_{\text{low phase}} > P_{\text{increase phase}} > P_{\text{peak}} \quad (1)$$

Owing to the longer time available for predator populations to build up their density during a 4-year cycle than during a 3-year cycle we hypothesize that a crash (C) in the vole population after a 4-year cycle (C_4) will be more severe to alternative prey than a crash after a 3-year cycle (C_3), because more predators will be present.

Thus,

$$P_{C_4} > P_{C_3} \quad (2)$$

During the low phase of the vole cycle the predatory pressure probably is relaxed due to the scarcity of predators compared to the preceding crash year and

$$P_C > P_{\text{low phase}} \quad (3)$$

By combining (1), (2) and (3) we can tentatively rank the phases of the vole cycle according to the predation pressure on alternative prey.

$$P_{C_4} > P_{C_3} > P_{\text{low}} > P_{\text{increase}} > P_{\text{peak}}$$

Prediction 4. As predicted the diet of the red fox became more diverse from the north to the south of Sweden (Fig. 7). The most obvious reason for this change in the diet presumably is a corresponding change in diversity of available food. We have no direct measurement of food availability to foxes in different areas of Sweden. However, we argue that human population density and the proportion of land used for agriculture provide indices to the diversity of available food. An increase in these factors gives rise to greater amounts of garbage and agricultural spill as well as a more diversified landscape. (Note that Swedish agriculture generally is small scale as compared to agricultural "steppes" in many other parts of the world). Hence, a comparison between diversity of red fox diet and these indices of prey diversity supports the argument that the dietary differences between different parts of Sweden reflect a change in diversity of available food (Table 2).

Accordingly, we should also be able to establish a negative correlation between human population density and proportion of land used for agriculture on one hand and an index of interspecific synchrony among small game species on the other. Since human population density and proportion of land-area used for agricultural purposes in Swedish counties are strongly correlated ($r=0.73$, $n=23$, $P < 0.001$, material from Statistical Abstract of Sweden 1970, excluding towns and boroughs), we have only used the latter parameter in our comparison. As an index we have adopted the mean (\bar{r}) of the correlation coefficients obtained in paired correlations between bag records of mountain hare, black grouse and red fox (Angelstam et al. in press). An inverse relationship between these variables supports our argument (Fig. 8). In Finland areas with no, or very little, agricultural land are only found in the northern part whereas almost two thirds of Sweden has a very low fraction of farmland (Fig. 9). Lindén and Rajala's (1981) data of autumn densities of capercaillie and black grouse in Finland suggest that these species exhibit 3–4 year cycles only in the northern areas while in Sweden such cycles occur also much further to the south (Fig. 9). The confinement

Table 2. Percent of land area covered by arable land, cultivated natural pastures and other grassgrown land (Statistical Abstracts of Sweden 1971) and human population density in rural communes (Statistical Abstract of Sweden 1970) in four areas with increasing diversity (from area 1 to 4, see Fig. 7) in red fox diet. (n = number of counties in each area, mean \pm SD).

	Amount of agricultural land (% of land area)	Human population density (n/km^2)
Area 1 ($n=5$)	2.3 \pm 1.7	4.2 \pm 3.4
Area 2 ($n=1$)	7.8	7.7
Area 3 ($n=6$)	17.9 \pm 5.8	32.5 \pm 17.7
Area 4 ($n=2$)	52.1 \pm 20.8	40.9 \pm 6.71

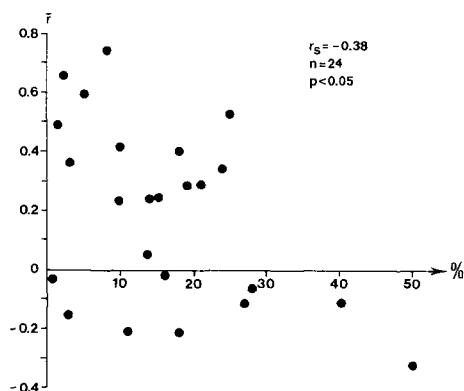


Fig. 8. Degree of synchrony between red fox, mountain hare and black grouse in relation to proportion of land area (%) used for agricultural purposes in 24 Swedish counties. The degree of co-fluctuation was calculated as the mean (\bar{r}) of correlation coefficients in paired correlations between bag records of the three species (Angelstam et al. in press).

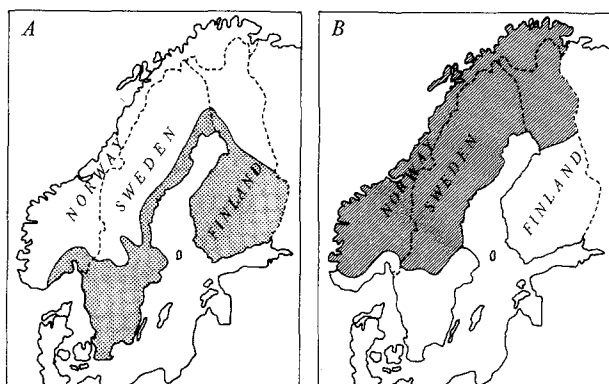


Fig. 9. A Areas with more than 3 percent of land area used for agricultural purposes within Fennoscandia (after Ahlmann 1976). B Tentative distribution map of the occurrence of short-term population fluctuations among some birds and mammals in Fennoscandia (from Angelstam et al. in press). Note that the scale of resolution is much higher in A (25 km^2) than in B (whole counties).

of 3–4 year cycles in capercaillie and black grouse to the northernmost part of Finland conforms to the prediction that the disappearance of 3–4 year cycles is associated with a more diverse food basis of the predatory community.

The confirmation of prediction 4 stresses the point that the dietary spectrum of predators must be limited in order for the alternative prey hypothesis to operate.

Some critiques of the alternative prey hypothesis

Two instances of direct or indirect criticism against the alternative prey hypothesis prompt some comments.

Siivonen (1954) criticized the alternative prey hypothesis on the ground that a decline in grouse (autumn) populations often coincided with high densities of the small rodents (season not specified). Siivonen's (1954, p. 4) data show that small rodents generally had two subsequent years with peak densities, the first of which coincided with the peak year of tetraonids and the second with the decline of tetraonids. According to the alternative prey hypotheses high small rodent densities should buffer predation on alternative prey such as tetraonids. Since a shift in the diet of predators can occur quite abruptly within a season, the timing and severity of the rodent decline are crucial to the resulting population trends in predators and alternative prey. For example, if the decline in rodents occurs in late spring or early summer, at least some predators may already have managed to raise their young prior to the most critical period. In this case predators would increase in numbers until next spring, whereas the alternative prey species would decline. Furthermore, if the first year after the small rodent peak is accompanied by a small to moderate decline in small rodents, then the reproduction and diet of predators and thus the survival rate of alternative prey might not be affected until the second year after the vole peak. Thus the timing of vole decline must be known in a more precise fashion than on a year to year basis in order to judge whether Siivonen's data reject the alternative prey hypothesis or not. Also, even if we always expect a crash year of small rodents to be a bad year for the alternative prey, a rodent peak year does not necessarily imply that the reproduction and survival rate of alternative prey must be good. Other limiting factors may affect the reproduction of alternative prey, such as extremely bad weather (Cartwright 1944; Semenow-Tian-Sjanskij 1960; McGowan 1969; Marcström and Höglund 1980). Thus, declines in the abundance of alternative prey species may also occur other years of the cycle than after the crash in rodents and may hence mask a basically cyclic pattern (cf. Angelstam et al. in press).

Pulliainen (1982) discarded predation as a driving force behind short-term fluctuations of mountain hare in northern Finland since no time lag between predator populations (red fox, pine marten, stoat and weasel) and mountain hare was observed. However, data for both predators and prey referred to autumn or winter populations in which, according to the alternative prey hypothesis, nor time lag is to be expected either between voles and alternative prey or between predators and alternative prey. Since predators do not affect their prey primarily by an increased numerical response as in classical predator prey oscillations (e.g. Shelford 1943), but instead depress the alternative prey by a strong functional response (dietary shift), predators will be affected by variations in the amount of main prey at the same time as they themselves influence the rate of mortality

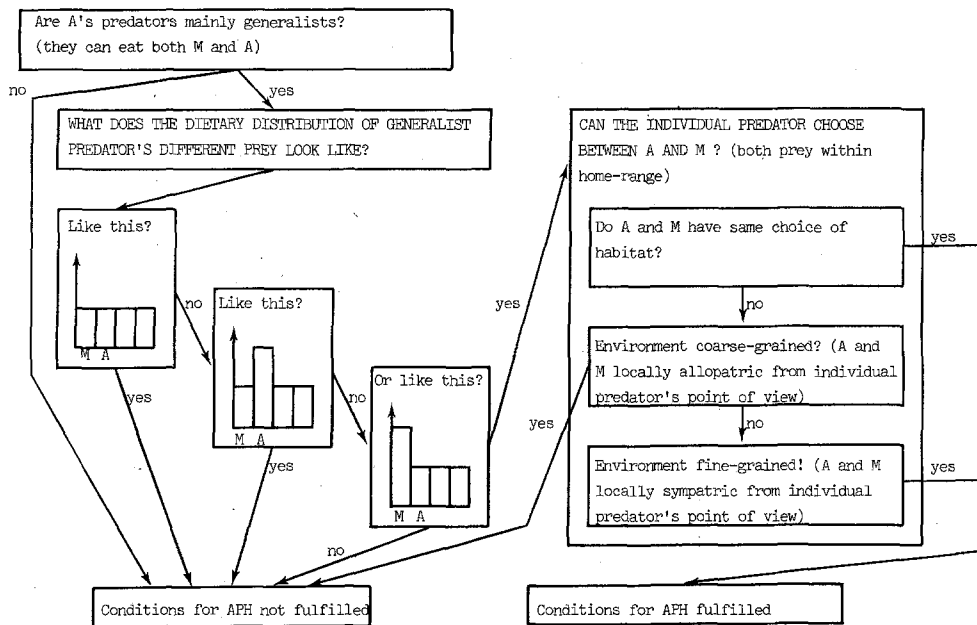


Fig. 10. Conditions to be fulfilled if the alternative prey hypothesis (APH) is to be valid for observed fluctuations in a prey *A* synchronized with another prey *M*.

in alternative prey. We therefore discard Pulliainens (1982) conclusion and suggest that the alternative prey hypothesis may explain his observations.

Other hypotheses

Our results on the whole confirm all four predictions of the alternative prey hypothesis. In spite of this we cannot exclude other mechanisms behind the short-term fluctuations in mountain hare and woodland grouse within the boreal coniferous forest (Angelstam et al. in press).

Since predation might only have been the proximate cause of death in hare and grouse, other factors might already have ultimately doomed them to become eaten by predators in the sense of Errington (1946) and Moss et al. (1982). Such factors may involve changes in the amount or quality of food of herbivores (Jenkins et al. 1963 and Siivonen 1957).

Changes in plant food can be caused by overgrazing (Harper 1977). We know of no reports of extensive overgrazing, such as reported by Wolff (1980) by hare or grouse in Fennoscandia except by mountain hare on small islands where predators are few or absent (Ottosson 1971; Angerbjörn 1981; Jokinen and Häkkinen 1982). Keith (1983) reviewed the role of food in hare cycles and concluded that a quantitative food limitation was unlikely to occur within the Fennoscandia 3–4 year cycle of the mountain hare. Circumstantial evidence suggested (Keith 1983) that the mountain hare might be food limited where it exhibits 10-year cycles in the eastern Soviet Union. In that area overgrazing by hares occurs at peak densities (Formozov 1935).

However, voles are known to graze heavily on field layer vegetation (e.g. *Vaccinium* species) during peak densities (Ericsson 1977). This vegetation is also an important food source for hares and grouse (e.g. Lindlöf et al. 1974; Kaasa 1959). Due to the greater biomass of voles (approximately 20 kg per km² during the spring of 1977 (Lindström et al. 1982) as compared to hares (4.2 kg per km²) and grouse

(all 3 species 5.5 kg per km² (Angelstam et al., in press)), as well as the faster metabolic and reproductive rates of voles, one might expect the voles to have the greatest impact on vegetation and thus to influence the grouse and hare populations much more strongly than the other way around.

Hansson (1979) found an association between quality and quantity of plants and vole cycles in the whole of Sweden. However, he found the same between year variation in plant species utilized and not utilized by voles. Therefore he concluded that voles were not responsible for the variations in plants. Neither did Myrberget's et al. (1981) results support the idea that rodents would affect grouse spring food. These authors were able to predict annual variations in the production of willow grouse from information about small rodent densities in nearby areas although voles were almost absent in the study area itself during the period.

However, changes in the quality and quantity of herbivory food may still be caused by an intrinsic plant cycle as the "mast year" phenomenon (Harper 1977), ultimately determining the fate of the individual hare or grouse by reduced viability of the individual itself, its offspring or both. If such plant cycles exist, we argue that the plant cycle and the alternative prey hypothesis are not mutually exclusive but rather complementary models (see also Haukioja et al. 1983 and Angelstam et al. in press).

Perspectives

As already mentioned, the four predictions tested in this paper were not exclusive to the alternative prey hypothesis. Thus, in order to distinguish between the alternative prey hypothesis and other plausible hypotheses for the synchronous fluctuations, we need more specific predictions.

In an attempt to formulate such predictions we started out with a more detailed analysis of the necessary conditions for the alternative prey hypothesis to be valid

(Fig. 10). Fundamentally, there are three questions that have to be answered: (1) Are there generalist predators present which can prey upon both the presupposed main and alternative prey? (2) Is the diet of these generalist predators asymmetric in such a way that we can use the terms "main prey" and "alternative prey" as presupposed? (3) Does this hold true not only for the population of predators, but also for the individual predator? I.e., does the individual predator have the possibility to shift between main and alternative prey? The answer to the last question will depend upon the habitat choice of the prey species and the structure of the environment as outlined in Fig. 10.

We have deduced three predictions, each bearing upon one of the questions above:

1. If the generalist predators were removed, the alternative prey species would not be affected by a decline in the main prey.
2. The same result would be obtained if the predators were provided extra food during a decline in the main prey.
3. If a fine-grained environment were turned into coarse-grained (see Fig. 10), we would also expect synchronous fluctuations to cease.

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