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The predation system seed – squirrel – marten under subarctic conditions

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Abstract

Seed yields of Scots pine *(Pinus sylvestris)* and Norway spruce *(Picea abies)* and populations of the red squirrel *(Sciurus vulgaris)* and pine marten *(Martes martes)* were studied under subarctic conditions in Finnish Forest Lapland in the winters of 1972/73–1980/81. Squirrels occurred in the area throughout, even though the quality and quantity of the seed yields of these conifers varied considerably from winter to winter, being especially poor in that of 1977/78. The "minimum maintenance diet" of the squirrel contained 10–12 % crude protein and 16–17 % crude fat. A good pine seed yield in the winter of 1972/73 and a very good spruce seed yield during the following summer and winter resulted in an increase in the squirrel population, which had then decreased by the next winter. This crash was not followed by any decrease in the local pine marten population, which was fairly stable throughout the period studied, being a generalist in its food intake. It is possible that the pine martens deepened the low in the squirrel population, but this is very difficult to show in figures. Only one kill of a squirrel per 670 km of pine marten track was recorded (over a total distance of 6700 km).

Introduction

The Scots pine *(Pinus sylvestris)* and Norway spruce *(Picea abies)* do not produce good seed yields near their northern limits every year (Numminen 1982; Pulliainen and Lajunen 1984), and this may be reflected in the state of the local red squirrel populations *(Sciurus vulgaris)*, since such seeds are known to constitute the chief food of these mammals (Rajala and Lampio 1963; Pulliainen 1973; Wiltafsky 1978). It has also been suggested that red squirrels may play an important, perhaps even decisive role in the nutrition of pine martens *(Martes martes)* (review in Danilov and Tumanov 1976).

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The present author has been studying the seed production of pine and spruce in relation to populations of the red squirrel and pine marten under subarctic conditions since late winter 1973. The purpose of this paper is to present the records obtained up to the winter of 1980/81.

Material and methods

The work was carried out in the Värriötunturi fell area of eastern Finnish Forest Lapland (67° 44′N, 29° 37′E). The area lies 266–475 m above sea level. The fell, with almost treeless summits and a mountain birch forest zone, is surrounded by old pine and spruce forests, mixed forests, mires, rather deep ravines and river valleys.

The numbers of squirrel and pine marten tracks crossing an observation line 5970 m long (running E-W) were recorded once a week during the snowy season of the year in the winters of 1972/73–1980/81. Indices representing the abundance of these populations were calculated per 24 observation times (per winter) and 100 m of observation line.

Fifty pines and fifty spruces were marked in a hilly terrain located about one km north of the eastern end of the observation line. All cones were collected from these each March before the spruce had dropped its seeds, and then stored in plastic bags at − 25 °C. Natural predation on these seeds is relatively low in this area, the squirrels, for instance, mainly occurring at lower altitudes (see Pulliainen 1973). The small amount of predation that does occur, however, introduces a minor source of error into the results obtained.

The seeds were extracted from these cones at + 45 °C under laboratory conditions. Each seed was individually cleaned of wings and other extraneous material. The number of seeds produced by each tree per year was counted. Chemical analyses were performed in the laboratories of Viljavuuspalvelu Oy and the Department of Chemistry of the University of Oulu (for methods, see Pulliainen and Lajunen 1984).

These data enabled the amount of crude (seed) protein and crude (seed) fat produced by the marked trees to be calculated. It should be noted in this connection that the crude fat component (ether extract) may contain the secondary compounds in addition to real fats, and is therefore used here as a rough indicator of energy investment in seeds.

Results

The main results obtained are as follows:

1. There were only an average of 18 seeds per spruce during the first winter (1972/73), but 792 seeds per pine. The protein and fat values were high for the latter species (Table). The number of squirrel tracks indicated a low population level for this species (Table).

Seed production was just the opposite during the second winter, there being an average of only 13 seeds per pine, but as many as 7658 seeds per spruce. There was thus a large

Numbers of squirrel and pine marten tracks observed crossing the 6-km observation line in the Värriötunturi fell area, E Finnish Forest Lapland, (calculated per 24 observation times per winter per 100 m of line), and the amounts of crude seed protein and crude seed fat (mg per tree, on average) produced by spruces and pines in the winters of 1972/73–1980/81

(for details, see text)

	Winters								
	1972/73	1973/74	1974/75	1975/76	1976/77	1977/78	1978/79	1979/80	1980/81
Squirrel tracks	21	580	121	33	1	8	18	41	63
Marten tracks	19	43	67	51	30	52	71	35	15
Spruce: seed protein	*	3037	0	0	29	59	25	8	245
seed fat	*	5780	0	0	28	82	28	8	396
Pine: seed protein	670	*	751	302	247	19	209	239	154
seed fat	661	*	958	203	225	12	129	230	157

* too little seed matter for analysis.

supply of spruce seed protein and fat available for the squirrels, and a clear peak for squirrel tracks was recorded on the observation line (Table).

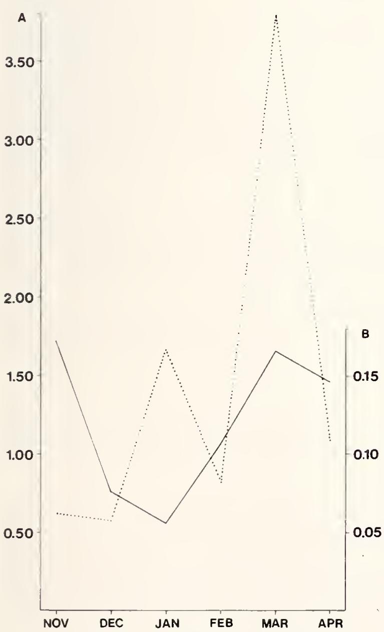
2. After this very good seed yield, the spruce did not produce any seeds during the following two years and only moderate or poor yields in the next four (238, 413, 165 and 91 seeds per tree on average respectively). The amounts of spruce seed protein and fat available were similarly low during this period (Table). The yield was better in late winter 1981 (916 seeds per tree on average).

The numbers of squirrel tracks recorded on the observation line indicate that the population crashed during and/or after the winter of 1973/74 and remained low to the end of the study period, although there was always a pine seed yield of varying proportions available (955, 989, 625, 81, 775, 442 and 233 seeds on average per tree in 1975–81; for quality variation, see Table).

The winter of 1977/78 is especially interesting from the standpoint of the squirrel population, since there was little seed protein available from either the pines or the spruces (Table), the spruce seed containing 11.6 % crude protein and 16.6 % crude fat.

3. The numbers of pine marten tracks on the observation line appeared to vary very little from winter to winter (Table). The crash in the local squirrel population did not lead to a crash or a disappearance of the local pine marten population. Trackings of pine martens (6700 km) carried out in the area in the winters of 1976/77–1980/81 revealed that only one kill of a squirrel per 670 km of pine marten track was recorded.

4. The smallest numbers of squirrel tracks are usually recorded in midwinter, which reflects a tendency to save energy and optimize heat economy (PULLIAINEN 1973). In the winter of 1973/74, when there were a large number of squirrels in the area, this activity pattern was not recorded (see Fig.).



The numbers of squirrel tracks recorded crossing 100 m of the observation line (4 recordings per month, solid line, scale B) in the winters of 1974/75–1981/82 and those recorded in the winter of 1973/74 (spotted line, scale A)

Discussion

Studies carried out in the present area (PULLIAINEN 1973, 1981a) have shown that both the red squirrel and the pine marten prefer spruce and spruce-dominated mixed forests as their habitats. Thus they are really sympatric. If there were a close predator-prey relationship between them, the populations of the former should follow those of the latter in abundance. The present data (Table) do not give any evidence of this. KEITH et al. (1977) show that in the lynx-hare relationship predation by the former may deepen the cyclic low of the latter (see also FINERTY 1980), and this may also be the case in the present marten-squirrel relationship, since the martens did sometimes kill squirrels even when the population of the latter was very sparse. It is very difficult to show this in figures, however.

The size of the local squirrel population depends on birth-rate and mortality together with the immigration and emigration rates. It is known that a female red squirrel may have two or three litters per year when food is plentiful (TITTENSOR 1975; for factors contributing to reproduction, see GILMORE and COOK 1981). On the other hand, winter mortality may be very high under adverse conditions (LAMPIO 1967). Squirrels may also migrate out of an area (LAMPIO 1957). The tendency shown by the northern squirrels to optimize their heat economy in midwinter (see PULLIAINEN 1973) indicates that wintertime may be critical in the life-cycle of this species under the hostile conditions prevailing in the north. Further evidence of this was obtained during the winter of 1973/74, when the squirrels were unable to employ their heat saving behaviour pattern because of the size of the population (Fig.). Another explanation may be that it was not necessary when plenty of food was available. At any rate, the population had diminished drastically by the following winter (Table).

It might be thought that an optimal situation for reproduction in the squirrel would involve an abundant conifer seed yield in winter (so that the squirrels are in good physical condition in the spring) followed by a good new yield of spruce seed in summer (on which to raise the new squirrel generation). In the winter of 1972/73 there was a high yield of good-quality pine seed available followed by an extremely plentiful good-quality yield of spruce seed the next summer (Table), a situation which did not occur again during the study period, and which offered chanches for good breeding results in summer 1973. The good yield of spruce seed enabled the population to survive during the following winter fairly well (Table), although exceptional behaviour from the standpoint of heat economy was recorded (Fig.), and it thus seems (Table) that an abundant yield of good-quality spruce seed in summer is a prerequisite for good breeding results in the red squirrel in the north. Pine seed alone is not enough (see Table).

One interesting point in the present data is that squirrels did occur in the area every winter, although in low numbers, even when the conifer seeds offered them a very poor nutritional base (Table). Conifer seeds may be replaced by the buds of these trees, and partly also by fungi, in the diet of red squirrels (see RAJALA and LAMPIO 1963). The "minimum maintenance diet" of squirrels seems to contain 10–12 % crude protein and 16–17 % crude fat (PULLIAINEN 1973; the present data). It is worth remembering here that Pine Grosbeaks *(Pinicola enucleator)* live in the present area for weeks in late winter solely on spruce buds, which contain 12 % crude protein and 11 % crude fat (PULLIAINEN 1974). The pine needle diet of the Capercaillie *(Tetrao urogallus)* contains only 7 % crude protein (PULLIAINEN 1970, 1979), presumably since a large-sized animal with a long caeca can probably better utilize plant matter.

The data published in the Table show that spruce seed and pine seed are similar in the amounts of crude protein and crude fat they offer to animals feeding on them (Table). This may be of importance for the nutrition received by these animals.

It is also possible that the few tracks of squirrels recorded on the observation line in the winters of 1976/77 and 1977/78 had been left by individuals which had migrated into the area from other districts (squirrels may cover long-distances during their wanderings, see LAMPIO 1957, VUOLANTO 1972). The seed yield of a particular conifer species is usually fairly consistent over a large area, however (see NUMMINEN 1982), so that the nutritional considerations mentioned here are still relevant even though the squirrels may have wandered hundreds of kilometres to reach the area.

The local pine marten population appeared to be rather stable during the period studied (Table). The trackings carried out here showed that the home ranges of two or more individuals may overlap and that their ranges can vary greatly (between 3 and 82 km^2 in the cases studied so far; PULLIAINEN 1981b, 1983a). Thus the variation recorded in the number of crossings of the observation line may be solely due to variations in the location of individual home ranges.

This kind of rather stable population may be possible for an animal species under unpredictable northerly conditions if it is a generalist in its food biology and if there are recources to replace the food items that are lacking. The pine marten is a generalist which eats small rodents if available, but will feed on a variety of items in their absence, ranging from berries and mushrooms to birds, mammals and various kinds of carcasses (PULLIAINEN 1981a, 1983b). Carcasses of semi-domestic reindeer *(Rangifer tarandus tarandus)* appear to be especially important in this respect.

ERLINGE et al. (1983) have recently shown in Southern Sweden that "a marked decrease in rodent numbers from autumn to spring equalled the numbers eaten by predators (mainly generalists) in the same period" and that "predation was the primary cause of non-cyclicity in the examined rodent populations", but this is evidently not the case in Northern Sweden, even though OKSANEN and OKSANEN (1981) and OKSANEN (1982) assume (on the basis of the observations which they record) that small mustelids (small rodent specialists) must have a strong impact upon small rodent populations in lush biotopes in northern Fennoscandia. The present data show that a medium-sized mustelid population in northern Fennoscandia, that of the pine marten, had no strong impact on the local squirrel population (Table). Other data suggest that local predator populations did not cause any appreciable decrease in the small rodent population during the course of the winter (PULLIAINEN 1983b).

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Zusammenfassung

Das Beutesystem Samen – Eichhörnchen – Marder unter subarktischen Verhältnissen

Die Samenerträge der Kiefer *(Pinus sylvestris)* und der Fichte *(Picea abies)* sowie die Bestände von Eichhörnchen *(Sciurus vulgaris)* und Marder *(Martes martes)* wurden im finnischen Wald-Lappland mit subarktischen Verhältnissen in den Wintern 1972/73–1980/81 untersucht. Eichhörnchen kamen in diesem Gebiet während des ganzen Untersuchungszeitraumes vor, obwohl die Quantität und Qualität der Samenerträge von Nadelbäumen je nach Winter stark variierten. Im Winter 1977/78 waren sie besonders schlecht. Die minimale lebenserhaltende Nahrung von Eichhörnchen enthielt 10–12 % Rohprotein und 16–17 % Rohfett. Der gute Samenertrag der Kiefer im Winter 1972/73 und der sehr gute Samenertrag der Fichte im nachfolgenden Sommer und Winter bewirkten einen starken Zuwachs im lokalen Eichhörnchenbestand, der sich mit dem nahenden Winter wiederum verminderte. Diesem Zusammenbruch des Eichhörnchenbestandes folgte keine Verkleinerung des lokalen Marderbestandes, der während des Untersuchungszeitraumes im großen und ganzen auf gleichem Niveau blieb, bedingt auch dadurch, daß der Marder in seinem Nahrungsanspruch ein sogenannter Allesfresser ist. Es ist möglich, daß die Marder den ohnehin kleinen Eichhörnchenbestand weiter verringerten, was aber zahlenmäßig schwer zu beweisen ist. Die Marder töteten im Schnitt ein Eichhörnchen auf 670 gewanderten Kilometern (untersucht wurden Fährten von insgesamt 6700 km Länge).

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BUCHBESPRECHUNGEN

Flury, B.; Riedwyl, H.: **Angewandte multivariate Statistik.** Computergestützte Analyse mehrdimensionaler Daten. Stuttgart, New York: Gustav Fischer 1983. 187 S., 91 Abb., 31 Tab. DM 39,–

Durch die Verfügbarkeit immer einfacher zu bedienender Programmpakete an Großrechenanlagen können komplexe statistische Methoden heute auch ohne umfassende mathematisch-statistische Kenntnisse benutzt werden. Diese durchaus positive Entwicklung birgt aber auch die Gefahr, daß Methoden wenig sinnvoll angewendet und Ergebnisse fehlerhaft interpretiert werden. Ziel der Autoren ist es, durch das vorliegende Buch dem empirisch arbeitenden Studenten, Wissenschaftler oder Qualitätsfachmann, der zur Lösung seiner fachspezifischen Fragestellung Methoden der multivariaten Statistik anwenden möchte, das jahrelange Erlernen der notwendigen mathematischen Grundlagen zu ersparen. An dem allgemein verständlichen Beispiel von Meßwerten einer Anzahl echter und falscher Banknoten werden zunächst die wichtigsten Begriffe der univariaten Statistik kurz rekapituliert. Durch Transformation der numerischen Werte in Chernoff-Gesichter wird dann eine Methode zur graphischen Darstellung mehrdimensionaler Daten erläutert. Es folgen Kapitel über mehrfach lineare Regression und Linearkombinationen, lineare Diskriminanzanalyse, Identifikationsanalyse,