

# Small mammal dynamics in adjacent landscapes with varying predator communities

Berit Martinsson, Lennart Hansson & Per Angelstam

*Martinsson, B., Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Grimsö Wildlife Research Station, S-730 91 Riddarhyttan, Sweden*

*Hansson, L., Department of Wildlife Ecology, Swedish University of Agricultural Sciences, PO Box 7002, S-750 07 Uppsala, Sweden*

*Angelstam, P., Department of Wildlife Ecology, Swedish University of Agricultural Sciences, Grimsö Wildlife Research Station, S-730 91 Riddarhyttan, Sweden*

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Small mammal dynamics vary geographically, with differences in annual variations of total numbers, species composition, body weight and reproduction. Such differences have previously been related to large-scale variations in predator numbers and species composition as dependent on landscape composition. Landscape effects on locally equivalent habitat types were examined in this study for a distance as short as 50 km. Different landscape types were compared — first, taiga and agricultural landscapes and second, agricultural landscapes with different predation pressures. Taiga landscapes supported typically cyclic small mammal populations, agricultural landscapes more non-cyclic populations and a predator-free area unusually large small mammal populations. Differences in the relative numbers of small mammal species, seasonal dynamics and demography were consistent with predictions of varying predator impacts. Our study demonstrated that even short-distance differences in dynamics can be distinguished and interpreted in terms of community interactions.

## 1. Introduction

Recent country-wide surveys have demonstrated large geographical differences in small mammal population dynamics, which may be related to differences in landscape composition and the abundance and composition of predators (Hansson & Henttonen 1985). The geographical differences occur on both community and popula-

tion levels (Hansson & Henttonen 1988). More detailed studies in south-central Sweden have, furthermore, revealed changes in these dynamic patterns over distances of only about 50 km across a gradient of landscapes dominated by agriculture at one end and coniferous forests at the other (Hansson 1988, Angelstam et al. unpubl.). The mainly seasonal density fluctuations in the agricultural environment have been ascribed to den-

sity-dependent predation by generalist predators that rely on a broad food spectrum on fields and around human habitation during low rodent availability (Erlinge et al. 1983, Angelstam et al. 1984, Andrén et al. 1985, Erlinge 1987). The cyclic pattern in boreal forest areas, by contrast, has been ascribed to generally low predation rates, with delayed effects from specialist rodent predators (e.g. weasels) during and after rodent peaks (Hansson 1979, Henttonen et al. 1987, Hanski et al. 1991, Hörnfeldt 1991).

Ideally, critical tests of the idea that landscape composition affects predator species composition, and that this in turn affects the dynamics of prey populations, should be performed as replicated experiments with accurate controls. However, it is impossible to perform controlled experiments on this broad scale, both for logistic reasons, and because of intercorrelations among variables (Wiens 1989a). Moreover the testability of causal hypothesis decreases with increasing scale (see Wiens 1989b). Therefore, when the scale of the process to be studied is very large, we argue that it is necessary to replace controlled experiments with comparative studies.

The possible spatial scales on which studies of ecological patterns and processes can be performed form a continuum. This continuum may be partitioned into several sections (Wiens et al. 1986):

- 1) the space occupied by an individual,
- 2) a patch of a given habitat occupied by many individuals of several species,
- 3) a region that contains patches of many types of biotopes, and
- 4) a biogeographic scale that is large enough to encompass different climates, as well as different assemblages of plants and animals.

The ecological patterns and processes that can be studied differ among these scales. Population parameters must be measured on the scale of an area that is sufficiently large to contain a certain number of individuals, and the effects of habitat patch dynamics or landscape composition on populations must be studied in a regional context. The scale in this study is set by the predators who search for prey among patches of different biotopes, i.e. on the landscape scale. If, as in this study, the process studied occurs on a level en-

compassing both small mammals and their predators, having very different area requirements, i.e. about 1 hectare for small mammals (see Wolton & Flowerdew 1985) vs. the 100–1000 hectare home ranges of feral cats, foxes and common buzzard (see Liberg 1980, Lindström 1982, Sylvén 1982), the scale must be set by the group with the largest demands.

The aim of this paper is to test the idea that interactions between prey and predator populations in local habitat types depend on differences in the composition of the landscapes of which they are a part. Thus, we change the scale from country-wide to regional. To increase the generality of the study, we analyse population parameters of small mammal species that are ecologically different. We tentatively assume that lack of predators will give similar rodent dynamics as predator communities with few generalistic predator species but we recognize that inclusion of specialist predators may affect such dynamics profoundly.

Cyclic dynamics is observed in most or all small mammals in northern Swedish areas (Hansson & Henttonen 1988). However, the density variations are most pronounced in the most folivorous species such as *Microtus* and *Clethrionomys* voles. *Apodemus* mice and *Sorex* shrews also vary but with small amplitudes (Hansson 1987).

The cyclic variations in density are paralleled by variations in individual quality. Females breed longer and more intensively in years of increase and body sizes are largest in early peak phases (Krebs & Myers 1974, Hansson 1984). We thus hypothesize that both density dynamics and variations in individual quality differ between landscapes with many and few generalist predators.

On the basis of this hypothesis and in view of the predator community differences, we anticipate:

- 1) Cyclic population dynamics in the taiga landscape and in predator-free areas but not in agricultural landscapes, because of differences in the predator species between the two landscape types.
- 2) A higher proportion of *Microtus* and *Clethrionomys* voles in the increase and early peak phases in the taiga and in the predator-free

area, but a disproportionately greater decrease of these species, and especially of *Microtus*, in the crash phase.

- 3) Larger between-year variations in the numbers of voles than in the number of mice or shrews in taiga and in the predator-free area.
- 4) Greater body size variations between years in the taiga and in the predator-free area than in the other localities, with maximum weight in the early peak phase. Taiga and predator-free area animals are expected to attain larger body sizes than animals from the other localities, at least temporarily.
- 5) Greater variations in reproductive output between years in the taiga and in the predator-free area, with the largest proportion of reproducing animals and of young in the increase phase.

## 2. Study areas and methods

### 2.1. Description of the macro- and micro-habitats

Based on geomorphology and topography, Sweden has been divided into several distinct landscape types (Anonymous 1984). In a broad sense, Fennoscandia today contains two main kinds of managed landscapes: managed forest, and agricultural land. Along river valleys, and coasts in the north and in the south, the forest gives way to agricultural land that becomes continuous in the far south. The distribution of agricultural land in Sweden is largely limited by soil conditions. On the whole, these areas are largely associated with post-glacial deposits when ice-lakes and the sea still covered the landscape (Angelstam 1992).

The study area is situated at the border between the boreo-nemoral and boreal vegetation zones (Ahti et al. 1968), i.e. on both sides of the "limes norrlandicus", between 59° and 61°. This is a distinct border in geomorphology (de Geer 1910, 1919), zoogeography (Ekman 1922) and phytogeography (Fransson 1965, Malmgren 1982). The "limes" is also a border between taiga and agricultural landscapes and is a transition zone of rodent cyclicity with less regular small rodent cycles to the south (Hansson 1988) (Fig. 1).

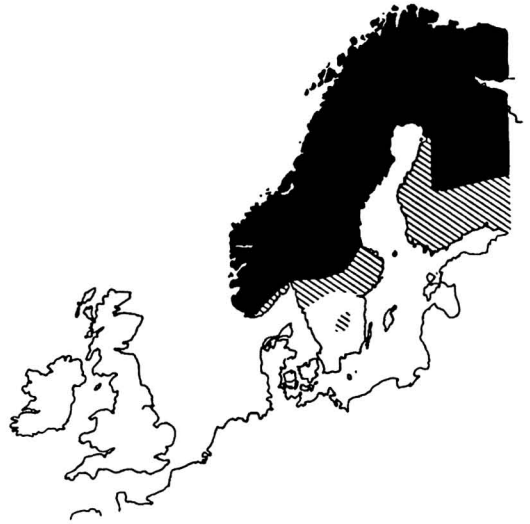


Fig. 1. Generalized and partly tentative picture of the distribution of strongly cyclic (dark), weakly cyclic "semicyclic" populations (hatched) and more or less non-cyclic (light area) microtine populations in north-western Europe. From Hansson and Henttonen (1988).

The localities were selected to represent landscape types with different proportions of forest and agricultural land, but with the same kind of microhabitat (Fig. 2). To check that our selection of study sites met these criteria we described the trap sites on a macro- and a microhabitat scale.

On the microhabitat scale, the vegetation was examined along the lines of forest edges where small mammals were trapped in the taiga and agricultural landscape type, respectively. The vegetation was sampled in a total of 50 circular 100 m<sup>2</sup> plots. We estimated vegetation type (field layer composition and moisture condition), number of plant species with large seeds and number of conifer trees and bushes. The macro-habitat (landscape) scale was described as the proportion of agricultural land in a 2.5 × 2.5 km square for each trapline.

At the microhabitat level there were no significant differences between the taiga and agricultural landscape types (unpaired *t*-test, Table 1) for number of conifer trees, number of conifer bushes, number of plant species with large seeds

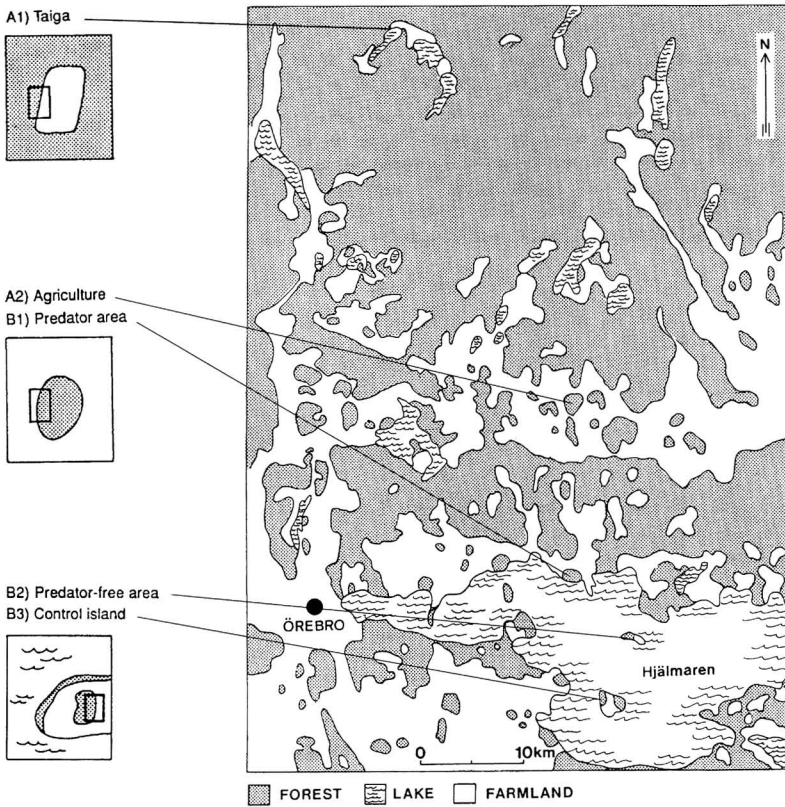


Fig. 2. Sampling sites in south-central Sweden.

and field layer composition and moisture condition, but the taiga and agricultural landscapes differed at the macrohabitat level (unpaired *t*-test, Table 1).

The design enabled the following two comparisons to be made:

A) Comparison between taiga and agricultural landscape types

A1) Taiga dominated by pine (*Pinus silvestris* L.) and spruce (*Picea abies* L.) forests on glacial till and granitic bedrock and with only about 10 % agricultural land on clay soils in concave parts of the landscape (Fig. 2).

A2) Agriculture with 50 % cropland on clay soil and 50 % taiga forest on glacial till and bedrock areas. The field layer vegetation in

Table 1. Description of the vegetation (mean ± SE) on microhabitat and macrohabitat levels in taiga and agricultural landscape types. *P* for *t*-test.

	Taiga	Agriculture	<i>P</i>
<b>Microhabitat</b>			
Conifer trees/100 m <sup>2</sup>	6.7 ± 1.9	5.8 ± 1.2	0.68
Conifer bushes/100 m <sup>2</sup>	1.1 ± 0.4	3.6 ± 2.4	0.34
Plants with large seeds/100 m <sup>2</sup>	3.6 ± 0.7	3.4 ± 0.4	0.80
Field layer composition and moisture condition	6.6 ± 0.6	5.1 ± 0.4	0.07
<b>Macrohabitat</b>			
Percent agricultural land	27.1 ± 2.1	49.0 ± 6.5	0.01

the forests of the taiga and agricultural landscapes was almost identical (Angelstam et al. 1987) (Fig. 2).

- B) Comparison within agricultural landscape types; landscapes with and without predators
- B1) Predator area on the mainland facing the predator-free island and with equal proportions of agricultural land and forest. Normal hunting occurred, without any special pressure on predators (Fig. 2).
- B2) Predator-free area, an island on the Large lake Hjälmaren, with approximately equal proportions of agricultural land and mixed coniferous-deciduous forest on clay soil types (Fig. 2). The size of the predator-free island is 120 ha. All middle-sized predators such as foxes (*Vulpes vulpes*, L.), badgers (*Meles meles* L.) and mink (*Mustela vison* Schr.) were continuously persecuted and kept extinct.
- B3) Control island on Lake Hjälmaren with similar landscape composition as the predator-free area but without any control of predators, serving as a partial control with respect to the predator-free island. The size of this island is 450 ha (Fig. 2).

## 2.2. Small mammal trapping

Small mammal trapping was performed during the years 1987–1989 in three periods: spring (May – early June), summer (July – August) and autumn (September – early October). Each trapline consisted of 50 snap traps within a distance of 100 m. The lines were run for three days on each trapping occasion. They were placed in forest 20 m from the border with agricultural land. In total there were 34 traplines. Five pairs of traplines were operated in the taiga and agricultural landscape, respectively. The mean distance between the five pairs was 6 km in the taiga and 5 km in the agricultural landscape. In the predator-free area and predator area there were seven single traplines, respectively, with a mean distance of 0.5 km. There were ten lines on the control island in the summer and autumn, 1989, with a mean distance of 1 km.

Trapped animals were weighed, and species, sex and age (juvenile, immature and adult) were determined from body and pelage characteristics (Hansson 1984). Due to the great variability in the weights of reproducing females and growing juveniles, weights were only compared between localities for adult males and autumn immatures. The number of embryos or placental scars were counted in adult females.

## 3. Results

Altogether 2424 small mammals were caught and examined. They belonged to six species, with the bank vole *Clethrionomys glareolus* (Schr.) as the most common species in the taiga, agricultural and predator area and the wood mouse *Apodemus sylvaticus* (L.) the second most common species at these three sites. The relations were reversed in the predator-free area for these two species. The other four species were considerably less numerous, with the field vole *Microtus agrestis* (L.) and the shrew *Sorex araneus* (L.) being intermediate, and *Apodemus flavicollis* (Melch.) (absent from predator-free area) and *Sorex minutus* (L.) only rarely caught. Therefore, these latter four species were ignored in the analyses of body weight and reproductive output.

### 3.1. Comparison between taiga and agricultural landscape types

#### *Total density*

Catches differed considerably between lines within localities. Therefore, analyses of covariance (ANCOVA) were performed with the maximum number of small mammals captured per line as covariate, considered to be a measure of the carrying capacity of each line. The mean maximum numbers did not differ significantly between localities. The ANCOVA disclosed, however, that seasonal capture rates per line differed significantly with respect to both localities and year. There were also significant interactions between localities and years in all three seasons, and therefore density changes had to be exam-

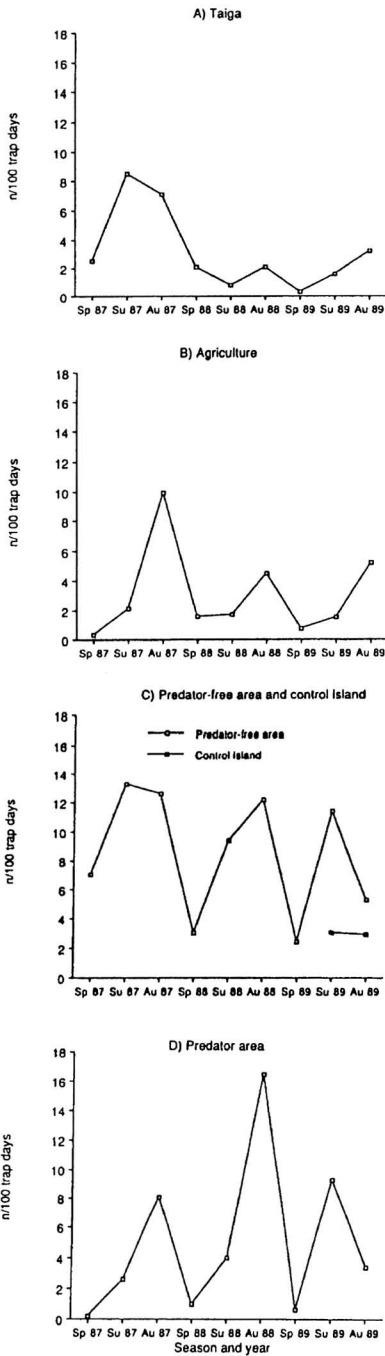


Fig. 3. Mean number of small mammals per trapline. A) Taiga, B) Agricultural land, C) Predator-free area and control island (filled and unfilled squares, respectively), D) Predator area.

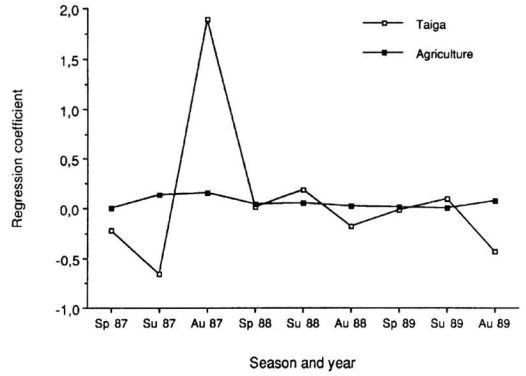


Fig. 4. Regression coefficients from analyses of covariance of differences in total small mammal numbers between taiga and agricultural landscapes, with % agricultural area as covariate.

ined more closely with regard to both local and temporal variation.

There were significant effects with regard to both locality and year in spring ( $F = 4.79, P < 0.05$  and  $F = 6.56, P < 0.01$ , respectively), summer ( $F = 6.92, P = 0.01$  and  $F = 15.62, P < 0.001$ , respectively) and autumn ( $F = 8.22, P < 0.01$  and  $F = 11.11, P < 0.001$ , respectively). In the taiga the small mammals exhibited cyclic population fluctuations with a peak in the summer of 1987, then a decline to low numbers in 1988 and no clear increase until the autumn of 1989 (Fig. 3A). The agriculture samples exhibited seasonal density peaks in autumn. Annual differences were small when the same seasons were compared (Fig. 3B).

These patterns were supported by an analysis of covariance of total small mammal catches in relation to the proportion of agricultural land in the various trapping localities in the two landscape types. The regression coefficients for the 9 trapping periods (spring 1987 to autumn 1989) varied little in the agricultural landscape but varied considerably in the taiga landscape (Fig. 4). Moreover, the differences in regression coefficients were significant during both the peak of the fluctuation (autumn 1987) and the low phase (autumn 1989). The taiga regression coefficient was negative at population increases, demonstrating higher survival in localities with little

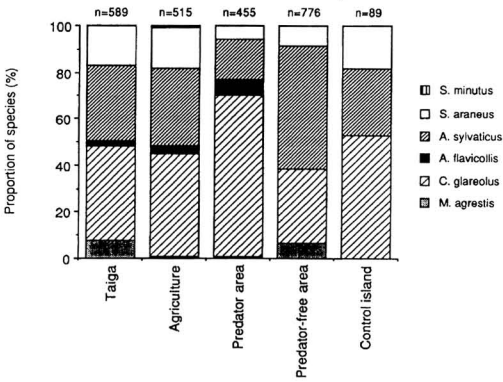


Fig. 5. Proportions of the various small mammal species in each locality.

agricultural land, and positive at peak-decline, demonstrating higher survival within agricultural area.

*Relative numbers of different small mammal species*

Species composition differed between taiga and agricultural land ( $\chi^2 = 36.09, P < 0.001$ ) as *M. agrestis* made up a relatively larger proportion of small mammals in the taiga than in the agricultural area (Fig. 5). The catches in taiga contained a high proportion of *Microtus* and *Clethrionomys*

voles at the peak in the summer of 1987 and then low proportions until the summer of 1989.

*Variation in abundance of species*

Coefficients of variation of the numbers of the various species were computed between years, and within seasons, so there were three estimates for each species and locality. Since these estimates were probably not normally distributed, a nonparametric test (Kruskal-Wallis) was used to evaluate differences in variability within any one species. When all species were included there was significant heterogeneity ( $H = 6.40, P < 0.05$ ). No significant difference ( $H = 0.28$ ) emerged when *M. agrestis* was excluded from the computations. *M. agrestis* thus exhibited considerably higher numerical variability than the other three common species.

*Body weight variations*

*C. glareolus* males from taiga were significantly heavier than males from agricultural land in both spring ( $t = 6.06, P < 0.001$ ) and summer ( $t = 6.12, P < 0.001$ ) but not in autumn (Table 2). Taiga animals were particularly large in the spring-summer in 1987.

The immature *C. glareolus* in taiga were significantly heavier ( $F = 36.35, P < 0.001$ ) than similar animals from agricultural land and par-

Table 2. Body weight variations ( $n$ , mean  $\pm$  SE) in adult males by season for the two most common small mammal species *Clethrionomys glareolus* and *Apodemus sylvaticus*.

Season and locality	<i>C. glareolus</i>	<i>A. sylvaticus</i>
<b>Spring</b>		
Taiga	24 28.3 $\pm$ 0.5	8 25.4 $\pm$ 1.3
Agriculture	12 23.5 $\pm$ 0.5	1 26.0 $\pm$ 0.0
Predator-free area	15 26.9 $\pm$ 0.6	42 27.1 $\pm$ 0.5
Predator area	6 23.3 $\pm$ 1.0	2 21.3 $\pm$ 0.3
<b>Summer</b>		
Taiga	17 25.6 $\pm$ 0.9	1 20.0 $\pm$ 0.0
Agriculture	24 19.3 $\pm$ 0.6	0
Predator-free area	22 24.0 $\pm$ 0.8	43 22.9 $\pm$ 0.8
Predator area	21 21.8 $\pm$ 0.7	5 16.0 $\pm$ 1.2
<b>Autumn</b>		
Taiga	11 24.6 $\pm$ 1.0	23 24.8 $\pm$ 0.6
Agriculture	12 21.7 $\pm$ 0.6	21 22.4 $\pm$ 0.7
Predator-free area	3 21.2 $\pm$ 0.2	13 24.9 $\pm$ 0.8
Predator area	4 21.9 $\pm$ 1.7	6 25.3 $\pm$ 1.1



ticularly so in 1987 and 1989 (Table 3). *A. sylvaticus* did not differ in weight between the two landscape types.

#### *Variation in reproduction*

Embryo and placental scar numbers could only be compared for *C. glareolus* and *A. sylvaticus* with regard to localities with one-way analysis of variance. However, neither embryos nor scars differed between localities for either of these species.

The distribution of age classes differed between years for *C. glareolus* in taiga (Fig. 6A–B) in summer ( $\chi^2 = 23.49$ ,  $P < 0.001$ ) and in autumn ( $\chi^2 = 10.94$ ,  $P < 0.05$ ). *C. glareolus* did not show any significant between-year difference in agricultural area. The annual variations in *C. glareolus* in taiga consisted of considerably more adults and juveniles in the low years 1988 and 1989 than in the peak year 1987. For *A. sylvaticus* there was no significant difference in age structure.

Age structure was most complex in summer and for *C. glareolus* it differed between taiga and the agricultural area ( $\chi^2 = 22.86$ ,  $P < 0.001$ ). Taiga had a much higher proportion of immatures in summer of the peak year 1987 than did the agricultural area.

### 3.2. Comparison within agricultural landscape types; landscapes with and without predators

#### *Total density*

The captures within the predator-free island differed from the predator area with regard to locality in spring ( $F = 16.90$ ,  $P < 0.001$ ) and summer ( $F = 15.32$ ,  $P < 0.001$ ) and with regard to year in autumn ( $F = 32.67$ ,  $P < 0.001$ ) (Fig. 3C and 3D).

The dynamics in the predator-free area showed two distinct characteristics: (i) peaks in density occurred usually in summer and (ii) spring densities were particularly high in the predator-free area (Fig. 3C). Densities in the predator area were higher in the autumn of 1988 than in the other two autumns (Fig. 3D).

Trapping in the predator-free area and control island was performed simultaneously only in the summer and autumn of 1989, but a two-way analysis of variance with regard to locality and season revealed significant differences between localities ( $F = 5.82$ ,  $P < 0.05$ ). The mean numbers in the predator-free area were considerably higher than on the control island (Fig. 3D), suggesting that the high numbers in the predator-free area were not simply an island effect.

Table 3. Body weight variations ( $n$ , mean  $\pm$  SE) in autumn immatures by locality in the two most common small mammal species *Clethrionomys glareolus* and *Apodemus sylvaticus*.

Year and locality	<i>C. glareolus</i>		<i>A. sylvaticus</i>	
1987				
Taiga	58	19.7 $\pm$ 0.2	66	17.4 $\pm$ 0.2
Agriculture	57	17.1 $\pm$ 0.3	58	17.2 $\pm$ 0.3
Predator-free area	17	18.7 $\pm$ 0.4	62	17.1 $\pm$ 0.3
Predator area	33	16.0 $\pm$ 0.2	1	17.0 $\pm$ 0.0
1988				
Taiga	21	15.7 $\pm$ 0.3	27	17.6 $\pm$ 0.6
Agriculture	39	15.3 $\pm$ 0.4	45	17.0 $\pm$ 0.4
Predator-free area	21	17.9 $\pm$ 0.4	62	17.8 $\pm$ 0.3
Predator area	102	18.6 $\pm$ 0.2	27	18.4 $\pm$ 0.4
1989				
Taiga	21	16.8 $\pm$ 0.5	4	15.0 $\pm$ 1.2
Agriculture	27	14.8 $\pm$ 0.3	17	14.7 $\pm$ 0.5
Predator-free area	3	15.7 $\pm$ 0.8	35	16.9 $\pm$ 0.3
Predator area	13	16.3 $\pm$ 0.3	14	14.8 $\pm$ 0.6



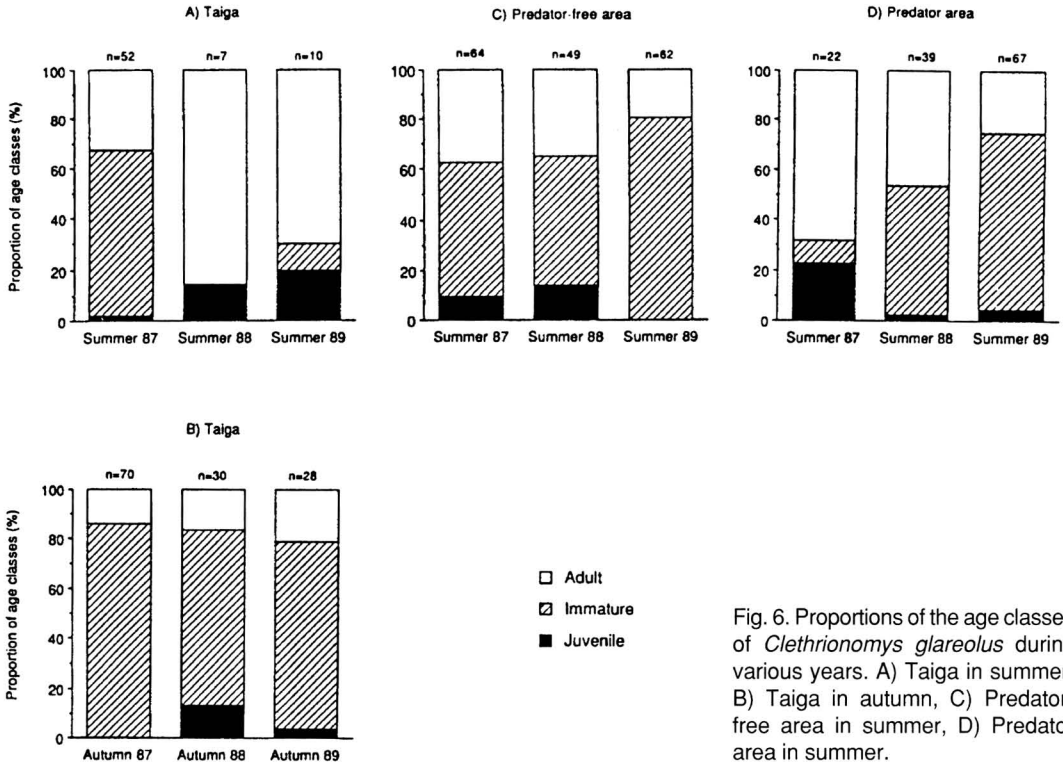


Fig. 6. Proportions of the age classes of *Clethrionomys glareolus* during various years. A) Taiga in summer, B) Taiga in autumn, C) Predator-free area in summer, D) Predator area in summer.

#### Relative numbers of different small mammal species

Species compositions from the predator-free island and the predator area differed clearly ( $\chi^2 = 255.16$ ,  $P < 0.001$ ). *C. glareolus* made up a relatively larger proportion in the predator area than in the predator-free area (Fig. 5). *A. sylvaticus* was the most abundant small mammal species in the predator-free area.

#### Variation in abundance of species

Coefficients of variation of the numbers of various species were computed between years and within seasons. The Kruskal-Wallis test showed a significant difference among all species ( $H = 6.41$ ,  $P < 0.05$ ). There was still a significant difference when *Microtus* was excluded ( $H = 4.82$ ,  $P < 0.05$ ).

#### Body weight variations

*C. glareolus* adults in the predator-free area were significantly heavier than the predator area

conspecifics in spring ( $t = 3.05$ ,  $P < 0.01$ ) and summer ( $t = 2.03$ ,  $P < 0.05$ ), but not in autumn (Table 2). *C. glareolus* immatures in the predator-free area and in the predator area differed only in weight with respect to year ( $F = 10.13$ ,  $P < 0.001$ ), with the smallest immatures in 1989 (Table 3).

#### Variation in reproduction

Neither the numbers of embryos nor scars in *A. sylvaticus* and *C. glareolus* exhibited any clear difference between localities.

The distribution of age classes differed among years for *C. glareolus* for the predator-free island in summer (Fig. 6C,  $\chi^2 = 17.11$ ,  $P < 0.01$ ). *C. glareolus* in the predator area differed in age distribution among summers (Fig. 6D,  $\chi^2 = 29.45$ ,  $P < 0.001$ ). For *A. sylvaticus*, there was one single significant annual difference in age structure, viz. for autumn animals in the predator area ( $\chi^2 = 13.94$ ,  $P < 0.01$ ).

The summer age-structures did not differ between the predator-free island and the predator

area ( $\chi^2 = 2.58$ ). Although the summer variations of *C. glareolus* in the predator-free area and in the predator area were consistent, with increasing proportions of immatures between 1987 and 1989, the proportions of immatures were still larger in the predator-free area (Fig. 6C and 6D).

## 4. Discussion

### 4.1. Differences between landscapes

As presumed, we observed strong differences in small mammal population dynamics between the different landscape types. In addition, the patterns of population fluctuations over years and seasons were similar to the north/south cyclic/non-cyclic trend established in previous long-term studies but on larger geographical scales (Hansson & Henttonen 1985, Hörnfeldt 1991).

Our detailed predictions were fulfilled in most respects. In the taiga, small mammal populations were cyclic whereas in the predator-free area they were characterized by higher densities than elsewhere. Both these habitats supported a high proportion of *M. agrestis*, which is the species with the most pronounced annual density variations of the small mammal species examined in this study. The taiga and predator-free island populations of *C. glareolus* consisted of animals of especially large body size, and this was particularly pronounced in the taiga population during the peak year. The taiga populations showed annual variations in reproduction, which was most intense during an increase year.

As expected, the taiga samples showed characteristics typical for cyclic small mammal population dynamics whereas the dynamics in the agricultural and the predator area were fairly non-cyclic. Typically cyclic features in the taiga population dynamics include a summer peak and a subsequent decline lasting almost two years (cf. e.g. Hansson & Henttonen 1985), relatively high numbers of *Microtus* voles and a constant number of shrews, high mean weights in one vole species, and an age structure dominated by reproductively active animals in the low years. However, the species composition was constrained by the habitat sampled; *M. agrestis* would

have made up a much larger proportion, and *C. glareolus* a smaller proportion, if the trapping had been performed in grasslands.

Small mammal populations in the predator-free area did not show cyclic dynamics but had some features that are typical of cyclic peak populations, i.e. generally high densities, relatively very high spring densities and peak numbers in summer. High and stable densities are characteristic features of confined populations, such as laboratory populations or populations on small islands (Gliwicz 1980). Furthermore, high spring densities and early peaks in mid summer, have been a consistent finding on one particularly well-studied small (4 ha) island, the Crab Apple Island in Poland (Petrušewicz et al. 1971, Bujalska 1985). However, these confined populations have also been exposed to few or no predators. The comparison between the predator-free area and control island suggested that dense populations may occur on a large island only when predators are absent or removed. There seemed to be no permanent populations of weasels in the predator-free area, and their absence may explain the lack of cyclic dynamics there.

The dynamics in the taiga and in the predator-free area were similar in some important respects; thus, peak years showed high spring densities and early peaks. This can be interpreted as a result of similar mechanisms; efficient predators are more or less absent during the prepeak winter, permitting high winter survival and a rapid population increase from an already high density level in early spring. In the taiga, lack of generalist predators and long-lasting snow inside the forest will prohibit efficient predation (Hansson 1979, Hansson & Henttonen 1985).

### 4.2. Interpreting studies on a landscape scale

This study attempts to test the idea that regional variation in landscape composition affects the local dynamics of small mammal populations. In the first part of the study, our n-number to test whether different estimates of parameters in small mammal populations are caused by differential effects of predation in two different landscape types (see also Andrén et al. 1985) is 5 pairs of

local populations. That these local sites are true replicates relative to predation levels is supported by the fact that they were situated on average 5–6 km apart, thus on a scale that ensures that the different local prey populations were affected by several different predator populations. In the second part of the study, population parameters on an island with very low predator densities were compared with mainland and island sites with normal predator densities. In this part of the study the *n*-number is 1, and the study obviously suffers greatly from pseudoreplication (Hurlbert 1984).

In the pseudoreplicative latter part of this study, our results were in agreement with the prediction. However, since we had only one predator-free island, we have merely demonstrated that the population parameters of small mammals on this island differed in the predicted direction, and we do not have a validated effect of the process (differential rates of predation).

If we claim to have observed an effect of the treatment, the latter part of this study is obviously impaired by the error of pseudoreplication. However, if one wants to study processes or patterns that occur on the regional or landscape scale, what are the alternatives? We are thus aware that it is difficult to evaluate studies of this kind. Nevertheless, we do consider such studies very important since it is the only way that large-scale patterns and processes can be studied (Karr & Freemark 1985). Naturally, statistical descriptions of differences should be interpreted with great caution. Furthermore, such studies should, if possible, be repeated in similar landscape types in different regions.

### 4.3. Conclusions

The results of our study strongly suggest that different patterns of dynamics for small mammal populations can be distinguished in different landscape types at short distances. There was thus a clear landscape effect as the trapping was performed in the same habitats in different landscapes. Furthermore, the differences in dynamics could fairly easily be related to proximate causes. There was thus no need to resort to predictions from chaos models (cf. Sandell et al. 1991) in order to explain local variability in dynamics.

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