Long-term population dynamics of the common shrew *Sorex araneus* in Finland

Heikki Henttonen, Voitto Haukisalmi, Asko Kaikusalo, Erkki Korpimäki, Kai Norrdahl & Uolevi A. P. Skarén

We have analyzed the regularity, regional variation and density-dependence in the long-term dynamics of the common shrew *Sorex araneus* in six regions in Finland. The impact of some external factors on shrew dynamics is also examined. Autocorrelation analyses revealed no regular multiannual cycles; seasonal fluctuations and erratic long-term fluctuations prevailed. No synchrony in the long-term dynamics of shrews between the regions was found. In each region either summer growth rate or winter mortality rate were density-dependent. The climatic factors analyzed (snow depth and winter temperature) correlated rarely with winter mortality. The summer declines of shrews at low densities were often synchronous with microtine declines, especially in Lapland, where the cyclicity of microtine rodents is pronounced. Synchronous summer declines suggest a common factor affecting both shrew and microtine dynamics, which most probably is specialist predation by weasels. In western Finland, however, the reasons for slight summer declines in shrews at high densities could be interference by rodents or predation by nomadic avian predators.

Heikki Henttonen, Finnish Forest Research Institute, Department of Forest Protection, P. O. Box 18, SF-01301 Vantaa, Finland.
Voitto Haukisalmi, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.
Asko Kaikusalo, Finnish Forest Research Institute, Ojajoki Field Station, SF-12700 Loppi, Finland.
Erkki Korpimäki, kp. 4, SF-62200 Kauhava, Finland.
Kai Norrdahl, Penttiläntie 2, SF-62100 Lapua, Finland.
Uolevi A. P. Skarén, kp. 2/82, SF-74300 Sonkajärvi, Finland.

1. Introduction

Traditional explanations for shrew dynamics include weather, especially the severe winter conditions (e.g. Formozov 1948, Ivanter 1975, Pankakoski 1985), and food availability (Kaikusalo & Hanski 1985). Recently there has been increasing interest in predation, mainly because of the interspecific synchrony often found in the dynamics of the microtine rodents and shrews in Fennoscandia (Hansson 1984, Henttonen 1985, Korpimäki 1986, Sonerud 1988). Intrinsic population regulation as a cause of population decline has not often been invoked for shrews (but see Sheftel, 1989).

This paper presents up-to-date material on long-term dynamics of the common shrew *Sorex araneus* in Finland. Earlier studies of shrew dynamics in Fennoscandia include those by Skarén (1972), Ivanter (1975, 1976), Kaikusalo & Hanski (1985), Henttonen (1985), Korpimäki (1986) and Sonerud (1988). The Finnish data sets have been up-dated for this paper and some new data have been included. We analyze the regularity and regional variation of density fluctuations, as well as the role of density-dependent processes in the population dynamics of shrews. In addition we examine the impact of some climatic factors (temperature and snow cover) on the winter mortality rate of the common shrew.

2. Material, methods and study areas

The long-term data sets come from six different regions in Finland (data collectors in parentheses).

1. *Kilpisjärvi* (69°03′N, 20°49′E) in the subarctic (orohemiarctic) birch forest zone in north-westernmost Lapland (coll. Kaikusalo). Trappings in April and September in 1964–1983, except for January and September of 1980, and early June and September in 1984–1988. There was no trapping in the springs of 1976 and 1977. 100–500 trap-nights per season, bait bread. For other details see Kaikusalo and Hanski (1985).

2. *Pallasjärvi* (68°03′N, 24°09′E) in the northern taiga (old spruce *Picea abies*) forests in western Lapland (coll. Henttonen). The small quadrat method (SQM, Myllymäki et al. 1971) was used in trappings, conducted in early June and September. 30 permanent quadrats (720 trap-nights per season), bait bread. For details see Henttonen et al. (1987).

3. *Kuhmo* (64°02′N, 30°20′E), in the central taiga (old spruce *Picea abies*) forests in eastern Finland (coll. Skarén). Trappings in June and August, mostly with 300–350 trap-nights per season in free lines on permanent sites, bait cheese.

4. *Sotkamo* (63°54′N, 28°26′E) in the central taiga (old spruce *Picea abies*) forests in eastern Finland (coll. Kaikusalo). Trappings on permanent sites in free lines in late May and late September – early October, 200–500 (1000) trap-nights per season, bait bread. No trapping in autumn 1969.

5 and 6. Two areas in western Finland (coll. Korpimäki and Norrdahl):

5. *Plains of Southern Ostrobothnia* (63°N, 23°E), including the localities Jurva, Ilmajoki, Seinäjoki, Nurmo, Lapua and Kauhava. Trappings in May and September with SQM or using groups of 5 traps on permanent sites (0.5–1.0 ha). 200–400 trap-nights per season, bait bread.

6. *Southeastern part of Ostrobothnia* (62.5°N, 24°E), including the localities Kuortane, Soini, Karstula, Ähtäri and Keuruu. Trappings in May and September with SQM or using groups of 5 traps on permanent sites (0.5–1.0 ha). 200–400 trap-nights per season, bait bread. For details of methods in western Finland see Norrdahl (1985) and Korpimäki (1986).

All data reported here have been obtained using Finnish snap-traps. Because the snap-trapping method does not give reliable results for the smaller species of shrews, their long-term data are not presented here.

Table 1 gives the long-term averages for temperature and snow depth from December to March in each study locality, measured at the nearest meteorological station (source: Monthly Reports of the Finnish Meteorological Institute). The first four regions are characterized by long and predictable winters with thick snow cover from late October till May (7 months). Regions 5 and 6 have much less snow, and the snow cover is unpredictable. In southern Ostrobothnia the average maximum snow depth in March is 30–40 cm, but snow cover is usually shallow in the early winter and lasts for less than 5 months. In the south-eastern part the snow depth averages 50–55 cm and the mean duration of snow cover is about 5 months.

3. Results

The year-to-year fluctuations in spring and autumn densities of *Sorex araneus* in Finland are presented in Figs. 1 to 6. Autocorrelation analyses did

Table 1. Long-term average temperature (1931–1960) and snow depth (1911–1960) from December to March in each study locality, measured at the nearest meteorological station. The same meteorological data have been used for Kuhmo and Sotkamo. Source: The monthly report of the Finnish Meteorological Institute.

| | Temperature | | | | Snow cover | | | |
	Dec	Jan	Feb	Mar	Dec	Jan	Feb	Mar
Kilpisjärvi	−10.2	−12.6	−13.1	−10.1	26	40	54	64
Pallasjärvi	−9.8	−13.0	−12.5	−8.4	28	41	52	59
Sotkamo and Kuhmo	−7.0	−10.6	−10.6	−6.7	18	37	50	59
Plains	−4.9	−8.4	−8.4	−5.2	11	22	30	36
Eastern part	−5.3	−9.0	−9.0	−5.5	17	33	46	54

not reveal any significantly regular multi-annual population cycles (Figs. 1–6). However, in some data sets there is an indication of some regularity. These include autumn data from Kilpisjärvi, Kuhmo and south-eastern Ostrobothnia. The same trend is not present in the respective spring data.

In addition to the erratic long-term fluctuations, the shrew populations show clear seasonal dynamics, typically with an increase in summer and a decrease in winter. However, in all data sets there are also some summer declines. At Kilpisjärvi 1 out of 20 summers showed a decline, at Pallasjärvi 4 out of 17, at Kuhmo 2 out of 20, at Sotkamo 4 out of 21, on the plains of southern Ostrobothnia 2 out of 12 and in south-eastern Ostrobothnia 4 out of 10. There are thus no regional differences in the frequency of summer declines. However, in Lapland the summer declines of shrews tended to be associated with microtine declines, but in eastern and western Finland there was no such association. Below we describe the phase of microtine dynamics for each of the years when a summer decline of shrews was observed.

At Kilpisjärvi, 1967 was a year of extended microtine decline (Laine & Henttonen 1983). At Pallasjärvi, 1971, 1975 and 1979 were deep microtine crash years (Henttonen 1985), but in 1987 microtines were approaching their peak (Haukisalmi et al. 1988). Microtine data are not available for Kuhmo. At Sotkamo, 1965 was an increase phase for microtines (Henttonen et al. 1977), and shrew density declined only slightly during the summer, still remaining at a

Fig. 1. Spring (open symbols) and autumn (closed symbols) density (shrews per 100 trap-nights) of the common shrew *Sorex araneus* in 1964–1988 at Kilpisjärvi, north-western Lapland. Inserted figures show correlograms (autocorrelation) based on spring and autumn densities (dashed lines denote the 95% confidence limits). For the autocorrelation analysis, three missing spring density values were replaced with the median of spring densities.
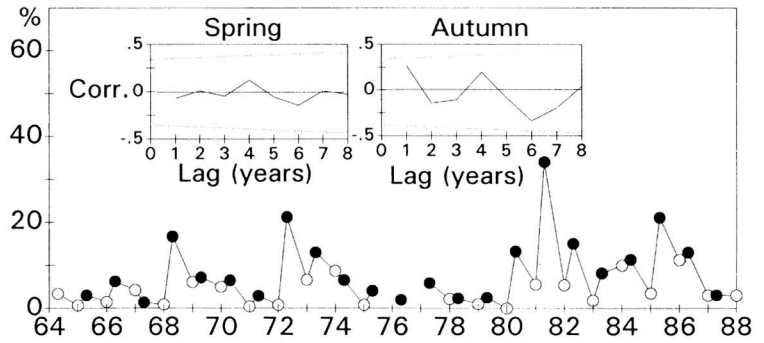

Fig. 2. Spring (open symbols) and autumn (closed symbols) density (shrews per 100 trap-nights) of the common shrew *Sorex araneus* in 1971–1989 at Pallasjärvi, western Lapland. Inserted figures show correlograms (autocorrelation) based on spring and autumn densities (dashed lines denote the 95% confidence limits).
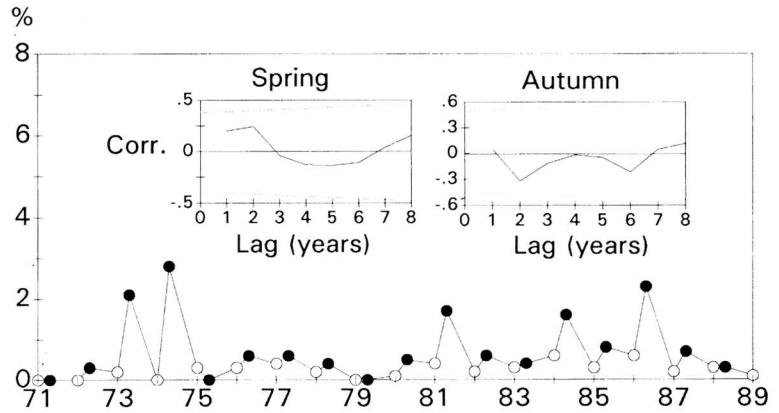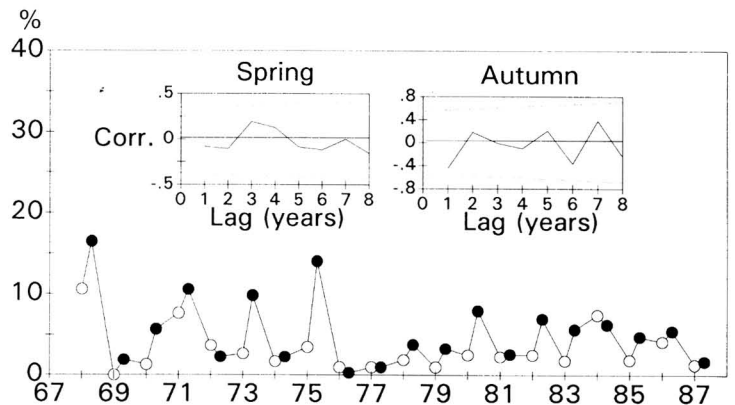

Fig. 3. Spring (open symbols) and autumn (closed symbols) density (shrews per 100 trap-nights) of the common shrew *Sorex araneus* in 1968–1987 at Kuhmo, eastern Finland. Inserted figures show correlograms (autocorrelation) based on spring and autumn densities (dashed lines denote the 95% confidence limits).

relatively high level. 1980 was a low phase for microtines, a year after the microtine crash, 1981 was a microtine increase phase, and 1985 was a decline year (Kaikusalo, unpubl.). On the plains of southern Ostrobothnia, a moderate shrew decline occurred at high densities in 1985, which was a microtine peak year
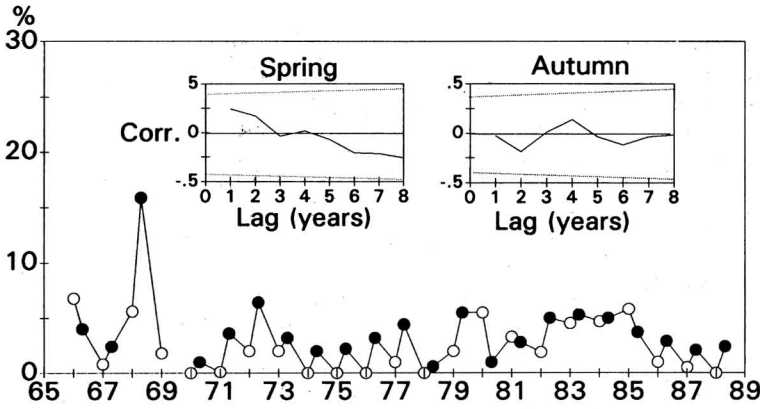
Fig. 4. Spring (open symbols) and autumn (closed symbols) density (shrews per 100 trap-nights) of the common shrew *Sorex araneus* in 1966–1988 at Sotkamo, eastern Finland. Inserted figures show correlograms (autocorrelation) based on spring and autumn densities (dashed lines denote the 95% confidence limits). For the autocorrelation analysis, one missing autumn density value was replaced with the median of autumn densities.
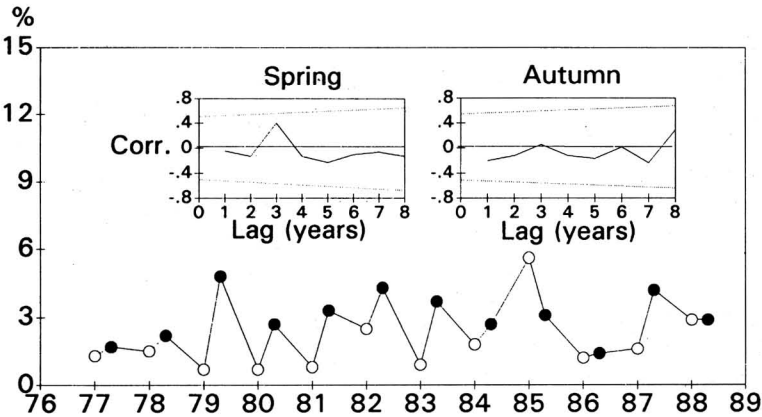

Fig. 5. Spring (open symbols) and autumn (closed symbols) density (shrews per 100 trap-nights) of the common shrew *Sorex araneus* in 1977–1988 on the plains of southern Ostrobothnia, western Finland. Inserted figures show correlograms (autocorrelation) based on spring and autumn densities (dashed lines denote the 95% confidence limits).
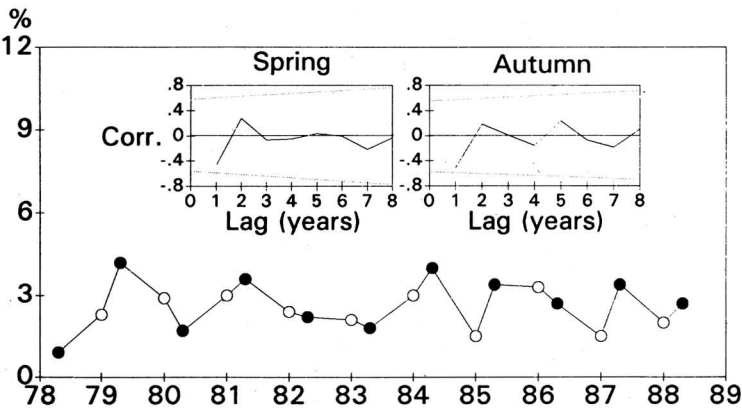

Fig. 6. Spring (open symbols) and autumn (closed symbols) density (shrews per 100 trap-nights) of the common shrew *Sorex araneus* in 1978–1988 in the southeastern part of Ostrobothnia, western Finland. Inserted figures show correlograms (autocorrelation) based on spring and autumn densities (dashed lines denote the 95% confidence limits).

(Korpimäki & Norrdahl 1989a). Shrews remained at high density as well in 1988, an exceptionally high peak year for microtines (Korpimäki & Norrdahl, unpubl.). In south-eastern Ostrobothnia, the slight decline of shrews in 1980 occurred when the microtines were in an increase phase (Norrdahl 1985). The rather stable dynamics of shrews in 1982–83 coincided with a moderate increase of microtine densities in both summers (Norrdahl 1985). In 1986 too microtines had a stable and moderate density through the summer (Norrdahl, unpubl.).

Regional synchrony in the spring and autumn densities of shrews between all pairs of localities was analyzed using Spearman's rank correlation. Most of the correlations, both within the main regions and between them, were far from significant (Table 2). Only two correlations in spring samples approached significance ($0.05 < P < 0.1$). There is thus no geographical synchrony in shrew dynamics.

We examined the effect of weather on winter mortality by using the monthly mean temperatures from December to March and the monthly mean snow depths as climatic variables (Table 3). Only two of the correlations were significant ($P < 0.05$), showing a negative relationship between winter mortality and mean snow depth in December at Kilpisjärvi, and a positive relationship between winter mortality and December temperature at Sotkamo.

To analyze density-dependence in the dynamics of the common shrew, the population growth rate during summer was compared with the logarithmic spring-early summer density, and the winter mortality rate was compared with the logarithmic autumn density (Table 4). The parameters used have been calcu-

lated according to Kaikusalo & Hanski (1985). The summer growth rate is defined as

$$N_a(n)/N_s(n),$$

and the winter mortality rate as

$$1-N_s(n+1)/N_a(n),$$

where $N_s(n)$ and $N_a(n)$ are the spring and autumn densities, respectively, in year n.

Table 2. Regional synchrony in the long-term dynamics of *Sorex araneus* in spring (above) and autumn (below) samples. The table gives the correlation coefficients (Spearman's r) and the degrees of freedom (in parentheses). Log($x+1$) transformation was performed on density values. All correlations were nonsignificant ($P > 0.05$). o, $P < 0.10$.

	Kilpis-järvi	Pallas-järvi	Sotkamo	Kuhmo	Plains	Eastern part
Kilpis-järvi	–	0.51° (13)	–0.01 (18)	–0.16 (16)	0.27 (8)	0.69 (7)
Pallas-järvi	0.39 (15)	–	0.14 (16)	0.06 (15)	0.23 (10)	0.47 (8)
Sotkamo	0.31 (19)	–0.21 (16)	–	0.27 (19)	–0.18 (10)	0.09 (8)
Kuhmo	0.26 (18)	–0.22 (15)	0.10 (17)	–	0.20 (9)	0.77° (7)
Plains	0.01 (9)	–0.32 (10)	0.42 (10)	0.01 (9)	–	–0.42 (8)
Eastern part	0.12 (8)	0.25 (9)	0.49 (9)	–0.42 (8)	0.38 (9)	–

Table 3. Partial correlation coefficients between winter mortality of *Sorex araneus* and some climatic variables in six regions in Finland. The coefficient shows the dependence between mortality and one of the climatic variables, temperature or snow depth, when the effect of the other variable is controlled. For definition and source of climatic variables, see Table 1. In all localities some climatic data for December were missing. Significant ($P < 0.05$) correlation coefficients marked with an asterisk.

	df	Temperature				Snow cover			
		Dec.	Jan.	Febr.	March	Dec.	Jan.	Febr.	March
Kilpisjärvi	17	0.24	0.26	–0.08	–0.02	–0.54*	–0.29	–0.21	–0.17
Pallasjärvi	11	–0.04	0.27	–0.19	0.33	0.00	–0.24	0.05	0.07
Sotkamo	17	0.46*	0.16	0.28	–0.05	–0.32	–0.28	–0.41	–0.05
Kuhmo	15	–0.23	–0.40	–0.12	–0.18	0.18	0.17	0.26	0.02
Plains	7	–0.20	0.54	0.40	0.01	–0.13	0.43	–0.15	0.18
Eastern part	6	–0.66	–0.26	0.16	0.03	0.61	–0.28	–0.34	–0.11

Table 4. The relationships between summer growth rate and spring density and between winter mortality rate and autumn density of *Sorex araneus* in six localities in Finland. *r* is Spearman's correlation. Logarithmic transformation was performed on spring and autumn densities. For the definitions of growth and mortality rates see the text. Zero observations were replaced with 0.1. The significance levels are: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.

Region	Summer growth rate r	df	Winter mortality rate r	df
Kilpisjärvi	-0.61*	18	0.11[NS]	20
Pallasjärvi	-0.11[NS]	16	0.78**	16
Sotkamo	-0.90***	20	-0.09[NS]	19
Kuhmo	-0.12[NS]	18	0.76***	17
Plains	-0.75*	10	0.59[NS]	9
Eastern part	-0.69[o]	8	0.74*	8

The summer growth rate was always negatively correlated with the spring density (Table 4), though only three of the six comparisons gave a significant result ($P < 0.05$) and a fourth one a nearly significant one ($P < 0.1$).

The winter mortality rate showed a significant ($P < 0.05$) positive relationship with autumn density in three of six comparisons and one positive relationship approaching significance. Both in Lapland and in eastern Finland the two study localities exhibited different relationships between winter mortality and autumn density, but western Finland showed a more uniform pattern. Notice that in each locality either summer growth rate or winter mortality rate was density-dependent.

4. Discussion

Our material supports the earlier observations from Fennoscandia (Skarén 1972, Ivanter 1975, 1976, Kaikusalo & Hanski 1985, Henttonen 1985 and Korpimäki 1986) and elsewhere (e.g. Formozov 1948, Mezhzherin 1960, Getz 1989) that regular population fluctuations (cycles) do not usually occur in shrews. In this respect, Sheftel's (1989) data from Central Siberia, showing clear cyclicity and interspecific synchrony among several sympatric shrew species, are exceptional.

In spite of the absence of clear regularity in shrew dynamics in Fennoscandia, some connections with microtine rodent cycles are apparent. In Lapland, where microtine cyclicity is clear (Hansson & Hent-

tonen 1985, Henttonen et al. 1985), most of the summer declines of shrews took place simultaneously with microtine crashes. Henttonen (1985), Hansson & Henttonen (1985) and Henttonen et al. (1987) have suggested that the summer declines of cyclic microtines could be caused by resident specialist predators (weasels). If the deep summer declines of shrews are synchronous with those of microtine rodents, the explanation could be the same for shrews and microtines and is most probably predation (Hansson 1984; see also Korpimäki & Norrdahl, 1989b).

The potential effect of predators on shrew dynamics is evidenced in several earlier long-term studies, including Hansson (1984), Henttonen (1985), Kaikusalo & Hanski (1985), Korpimäki (1986) and Sonerud (1988). Sonerud (1988) has shown that in Fennoscandia the shrew-microtine ratio mostly peaks two years after the microtine peak, which he suggested as being caused by selective predation. Kaikusalo & Hanski (1985) have shown that in Lapland the most rapid increases in shrew populations take place when predators are scarce, two or three years after the previous rodent peak. Sheftel (1989) states that shrew and microtine cycles in Central Siberia are synchronous, which could also mean a common regulating factor, although Sheftel is inclined towards intrinsic regulation in shrew dynamics.

In eastern and western Finland several slight summer declines at high shrew densities took place in microtine peak summers (see also Korpimäki 1986). Such declines can hardly be due to specialist predation; an alternative explanation is interference of shrews by voles. On the other hand, the differences in predator assemblages may contribute to these regional differences. Nomadic birds of prey are the most important predators in western Finland (Korpimäki & Norrdahl 1989a), whereas resident small mustelids seem to be the most important predators in Lapland (Henttonen et al. 1987).

In the present material it is hard to define the factors that bring about the observed density-dependent regulation of shrew populations. However, Kaikusalo & Hanski (1985) have shown that the food supply during summer, acting in a density dependent way, probably affects the population dynamics of *Sorex araneus* in northern Lapland (Kilpisjärvi). The commonness of density-dependent processes in the present analyses shows that food limitation may be a general regulatory factor for shrew populations.

Our analyses suggest that climatic factors do not play an important role in the regulation of shrew populations, contrasting, e.g. Ivanter (1975). First,

significant relationships between winter mortality rate and climatic factors (temperature and snow cover) were rare. Second, the dynamics of shrew populations in various regions were asynchronous; more synchronous dynamics at least within regions would be expected if weather conditions were an important regulatory factor.

Variation in the intensity of reproduction by young shrews is an additional factor potentially affecting the dynamics of shrew populations (Kaikusalo & Hanski 1985). Unfortunately, the reproduction by young shrews cannot be properly analyzed with the present data sets based on spring and autumn trappings. An example of the difficulties is provided by the situation at Pallasjärvi during summer 1986, a peak phase for shrews (Henttonen, unpubl.). In early July 9% (N=22) of the young females of Sorex araneus and 21% (N=28) of the young females of S. caecutiens were pregnant. However, in early September there were practically no reproducing shrews in the population and none of the young females of either species (S. araneus, N=60; S. caecutiens, N=29) showed signs of earlier reproduction. Thus, the autumn material does not give a true picture of the intensity of reproduction by young shrews earlier in the summer.

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