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Long-term and seasonal dynamics of shrews in Central Siberia

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The dynamics of shrew populations were studied over a period of 13 years in Central Siberia, in an area with nine coexisting species: *S. araneus*, *S. caecutiens*, *S. minutus*, *S. minutissimus*, *S. isodon*, *S. tundrensis*, *S. roboratus*, *S. daphaenodon* and *Neomys fodiens*. There is a highly regular four-year cycle involving both rodents and shrews. The minimum year of the cycle is the same for all species of shrew, but different species reach their peak density at different stages of the general four-year cycle. The species also differ in the seasonal changes of their numbers. There is a significant relationship between the seasonal and multi-annual cyclic abundance changes, with species of high fecundity having the earliest peaks both during each season and during the four-year cycle. The species with later peaks are suggested as being competitively superior to the earlier species, suppressing the abundance of the inferior species when they become abundant.

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1. Introduction

Population dynamics are affected by both external and internal factors. The commonly considered external factors include climate, food availability, predators and parasites. The internal factors are usually directly or indirectly related to population density, and they affect the rates of natality, mortality and dispersal, the physiological condition of individuals and the genetical structure of populations. Most studies on small mammals are focused on the dynamics of the dominant species only, but studies on the interactions of several coexisting, closely related species are also of great importance, as they may provide additional evidence for the factors that play the key roles in the dynamics of the species (Hanski 1987).

Seasonal changes in the population size of several coexisting shrew species are poorly documented. Such seasonal dynamics depend on e.g. precipitation (Popov 1960), reproduction (Dunaeva 1955) and interspecific interactions (Sheftel & Sapogov 1978). As both longterm and seasonal dynamics are often influenced by the same factors, I shall here compare changes in population size on these two time scales.

The aims of this paper are:

1) An analysis of long-term population dynamics of coexisting shrew populations in Central Siberia;
2) An analysis of the seasonal dynamics of these shrew populations; and
3) A comparison of the long-term and seasonal dynamics.

2. Study area and species

This study was carried out at the Northern Ecological Station Mirnoe of the A.N. Severtsov Institute of Evolutionary Morphology and Ecology of Animals, USSR Academy of Sciences, from 1971 to 1983. The station is located on the bank of the Yenisei (62°N, 89°E). The study area belongs to the well-drained region of the eastern part of the West Siberian plain, and has a typical mid-taiga landscape. The continental climate is characterized by cold winters (the mean January temperature varies from –18 to –23°C) and relatively warm summers (the mean June temperature is 14 to 17°C). Yearly precipitation varies from 400 to 500 mm. The snow cover lasts from early October until the end of April, with a mean depth of 80–110 cm. The vegetation period extends from 1 June to 25 August. The trees shed their leaves from 26 August to 20 September (Galakhov 1964).

The dominant tree species in the forest are *Pinus sibirica* and *Picea obovata*, while *Larix sibirica* and *Pinus silvestris* are less abundant, and *Abies sibirica* is rare. The most common deciduous trees are *Betula alba* and *Populus tremula*, both of which benefit from anthropogenic and pyrogenic influences. The common moss species in the taiga are *Pleurozium schreberi*, *Hylocomium splendens* and *Polytrichum commune*. The Yenisei poima (seasonally flooded area) is only partly wooded. The banks are covered with different species of willows, of which *Salix viminalis* is the dominant one. The central parts of the poima have spruce-fir forest with a dense understorey consisting of *Alnus fruticosa*, *Padus ovitum* and *Ribes nigrum*. At the periphery of the poima and extending to the first terassas of the taiga one finds tall spruce forest with a dense cover of mosses and grasses. This forest type has an aspect more typical to nemoralic forests.

The Mirnoe station is located on the eastern bank of the Yenisei, in a former village. The forest around the station has been affected by humans for a few centuries. The poima on the eastern bank consists of a grass meadow with a few bushes, and it is very narrow, from 70 to 100 m. The western bank has not been influenced by human activities, and the poima is more than one kilometre wide, with biotopes that are not found on the eastern bank. The minimum width of the river is more than 1700 m in the study area; hence the Yenisei comprises a significant dispersal barrier to many species of animals. The present study was conducted on both banks of the river.

Nine species of shrew occur in the study area, including eight species of *Sorex* and the water shrew *Neomys fodiens*. The large number of species is due to overlapping ranges of West and East Palearctic species in Central Siberia. The ranges of the European species *S. araneus* and *S. minutus* extend to the Baikal in the east, while *N. fodiens* occurs all the way from Europe to the Pacific Ocean. Three species are common throughout Siberia and northern Europe: *S. minutissimus*, *S. caecutiens* and *S. isodon*. *Sorex tundrensis* occurs from the extreme north-eastern part of Europe to the north-western part of Alaska, while two other species, *S. roboratus* and *S. daphaenodon*, are restricted to Siberia.

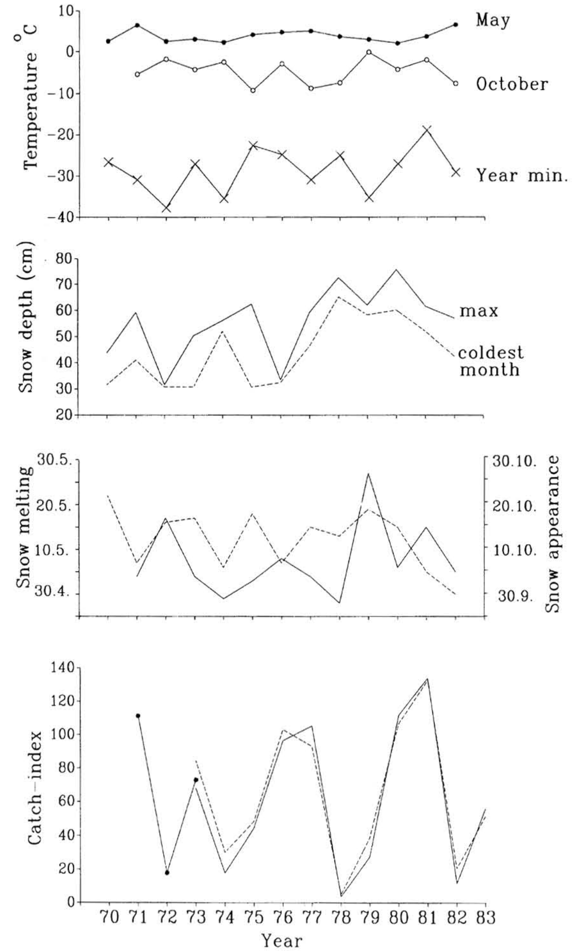

Fig. 1. Long-term changes in the pooled density of shrews on the eastern (continuous line) and western (broken line) bank of the Yenisei (lowest panel, the result for the years 1971 to 1973 is the average for the two banks). The catch index gives the numbers of individuals caught per 100 trap-nights. The upper panels give average temperatures in May and October, the yearly minimum temperature, snow depth and the dates of snow appearance (continuous line) and snow-melting (broken line).

3. Material and methods

This paper is based on trapping results from 1971 to 1983. In each year, trapping was continuous from 20 June to 3 September, with the exception of 1971, 1972 and 1975, when the trapping period was reduced to two 10-day periods at the beginning and at the end of the summer. Shrews have been trapped using 20 m long ditches of 15–20 cm depth and with two large pitfalls (diameter 20 cm, depth 50 cm) placed 5 m from the two ends of the ditch. In the habitats with a high level of ground water the ditches have been replaced by polythene fences of the same length with two pitfalls (Okhotina & Kostenko 1974). The pitfalls are provided with some water to kill the small mammals. The same permanent 30 ditches, located in several different types of habitats, have been used during the entire study period. The trapping results are expressed as the number of animals caught per 100 trap-nights.

The results of the trapping ditches are biased, to an unknown extent, towards dispersing individuals. Two different factors may thus contribute to large samples in the years of peak density: the numbers of individuals as such are high, and their mobility may be higher than in other years. It is probable that the ratio of maximum over minimum densities is higher in trapping ditch samples than it would be in samples consisting of resident individuals.

During the period from 1971 to 1983, 27 601 shrews were caught, consisting of 13 304 *S. araneus*, 9026 *S. caecutiens*, 1746 *S. minutus*, 216 *S. minutissimus*, 1198 *S. isodon*, 1402 *S. tundrensis*, 435 *S. roboratus*, 125 *S. daphaenodon* and 149 *N. fodiens*. The greater diversity of habitat types on the western compared to the eastern bank of the Yenisei is reflected in the

Table 1. Spring (S) and autumn (A) densities of shrew populations on the banks of the Yenisei (number of individuals per 100 trapnights). Spring density = mean value of the catch index for June 21 to July 5; autumn density = mean value of the catch index for August 20 to September 3.

	1976		1977		1978		1979		1980		1981		1982	
	S	A	S	A	S	A	S	A	S	A	S	A	S	A
Western bank														
S. araneus	11.6	35.6	21.5	24.1	–	–	2.7	15.2	8.5	39.4	41.9	34.1	1.5	10.0
S. caecutiens	10.2	42.6	19.2	72.2	0.4	5.2	3.3	10.8	8.9	53.3	22.6	57.0	0.7	11.1
S. minutus	–	1.8	–	–	–	2.6	3.8	9.3	1.2	5.3	2.2	2.2	3.0	7.8
S. minutissimus	–	0.7	–	0.4	–	1.1	1.0	0.4	0.4	1.6	–	0.4	–	0.4
S. isodon	0.8	27.4	0.6	25.6	–	–	0.4	2.6	0.4	18.9	1.8	10.7	–	3.3
S. tundrensis	4.1	16.6	5.1	12.2	–	2.2	2.3	10.8	5.9	31.5	15.2	15.5	2.6	9.2
S. roboratus	–	4.4	–	0.7	–	–	0.4	7.1	1.2	22.0	1.9	8.2	–	–
S. daphaenodon	0.4	5.9	1.2	2.2	–	–	–	0.4	–	2.6	–	0.4	–	0.7
Total	27.4	135.4	47.6	137.4	0.4	11.1	13.9	57.7	27.3	178.4	85.6	129.2	7.8	42.9
Eastern bank														
S. araneus	25.7	43.0	23.8	44.9	0.2	0.8	4.9	19.4	21.7	68.6	46.3	83.2	1.0	12.1
S. caecutiens	11.7	34.8	7.5	47.2	0.4	1.1	2.1	5.8	5.7	49.3	15.3	62.1	0.6	2.7
S. minutus	–	1.7	1.1	0.5	–	1.7	4.0	7.7	1.7	7.6	4.2	3.0	0.2	2.2
S. minutissimus	0.2	0.7	–	0.2	–	0.2	1.0	0.2	–	1.6	0.3	0.2	0.3	0.3
S. isodon	0.2	6.7	0.2	9.8	–	–	0.3	0.3	–	8.9	–	10.8	0.2	0.5
S. tundrensis	0.5	1.2	0.9	0.2	–	–	–	0.6	1.2	6.7	2.2	4.5	–	0.6
Total	38.5	88.4	33.5	102.8	0.6	3.8	12.3	33.8	30.3	142.7	68.3	163.8	2.3	18.4

higher diversity of shrews on the western bank. *Sorex daphaenodon* was found exclusively and *S. roboratus* was found mostly on the western bank (only three individuals of *S. roboratus* were caught on the eastern bank during the entire study period).

4. Results

4.1. Long-term population dynamics

The present investigation revealed a high-amplitude four-year cycle in the density of shrews (Fig. 1). In spite of the almost complete isolation of the populations on the two banks of the Yenisei, the long-term changes in abundance have been completely synchronized. To describe the different phases of the cycle I have used the terms introduced by Koshkina (1974): minimum year (the year of population depression), the year of population growth, the prepeak year and the peak year (maximum population density). During this study, two complete and well-defined cycles were observed, in 1974–1977 and 1978–1981. Table 1 gives the numbers of shrews caught in 15-day periods in June and in August in seven years. During the summer the numbers of each species usually increase.

Some authors (e.g. Formozov 1948) have suggested that mortality of shrews is greatly increased in severe and snowless winters. Fuller (1967) and others point out that the most critical periods are the beginning and the end of the winter. Fig. 1 shows that multiannual changes in population density are not related to general weather parameters (meteorological data are from Bakhta, located some 20 km north from Mirnoi). The crash of populations every fourth year is clearly not due to severe or snowless winters, and the winters preceeding the peak years have not been especially mild. Nonetheless, exceptional weather conditions can cause a shift in the phase of the cycle (Cherniavskii & Tkachev 1982: lemmings). A good example of such a shift occurred in 1974, when the numbers of shrews abruptly decreased instead of the expected increase (Fig. 1). In 1974 the snow melted very early (on 6 May) due to an exceptionally warm April. However, shortly afterwards the temperature again decreased to –15°C, and the mean May temperature was only 0.7°C, which is 2.2° lower than the long-term average. In other years with low temperatures in May (1970, 1972 and 1979) the snow melted later than in 1974, and not earlier than on May 15. Thus, in 1974 the combination of early melting of the snow and low May temperatures created a very unfavourable situation for small mammals, probably drastically decreasing food availability.

Comparing the dynamics of different species of shrew one finds differences in the timing of peak densities, though the minimum densities coincide in almost all species (in 1974, 1978 and 1982; Figs. 2 and 3). Some species have reached their maximum density by the third year after the minimum year, in agreement with the cycle of the pooled numbers of small mammals. In other species the maximum has been reached in the first or in the second year after the minimum year, and the abundances of these species have often slightly decreased before the general crash year. For instance, the peak density of *S. minutus* was always in the first year after the general minimum. In *S. tundrensis* and *S. daphaenodon*, the maximum abundances always occurred in the prepeak year. Finally, all peak densities of *S. caecutiens*, three peaks of *S. isodon*, and two peaks of *S. araneus* were recorded in the final year of the cycle. In the less abundant species, *S. minutissimus* and *Neomys fodiens*, year-to-year population fluctuations are not so pronounced, but even these species tended to increase in the years of general increase (Figs. 2 and 3).

Table 2 summarizes the occurrences of the peak years in different species during two four-year cycles on the two banks of the Yenisei (there are thus observations for four cycles). The number of peaks in the three years following the general minimum year were multiplied by the rank of the year (from 1 to 3), yielding a measure of the "earliness" of the occurrence of the species during the four-year cycle (sum of ranks in Table 2). *Sorex minutus* has the earliest occurrence, on average, while *S. caecutiens* has the latest mean occurrence (Table 2).

4.2. Changes in the age and sex structure of populations

As an example of the changes in the age and sex structure of shrew populations in the different phases of the cycle I analyse changes taking place in *S. caecutiens*, one of the dominant species in the present shrew community. *Sorex caecutiens* is the only species in which the multi-annual changes in abundance perfectly coincide with the respective changes in the entire community of shrews (Table 2). In *S. caecutiens*, the sex-ratio amongst juveniles became more female biased in the prepeak and especially in peak years, while in the years of lower numbers the sex-ratio was more male biased (Fig. 4). The same tendency can be seen in adult individuals. Similar changes in the sex-ratio with changing density have been observed in *Clethrionomys rutilus* in the Salair mountains (Koshkina & Korotkov 1975), in *Microtus agrestis* in northern Europe (Myllymäki 1977), and in *Dicrostonix torquatus* in Vrangel Island (Cherniavskii & Tkachev 1982). The increased number of females in the prepeak and peak years may be due to changes in the sex-ratio in the prenatal period (pri-

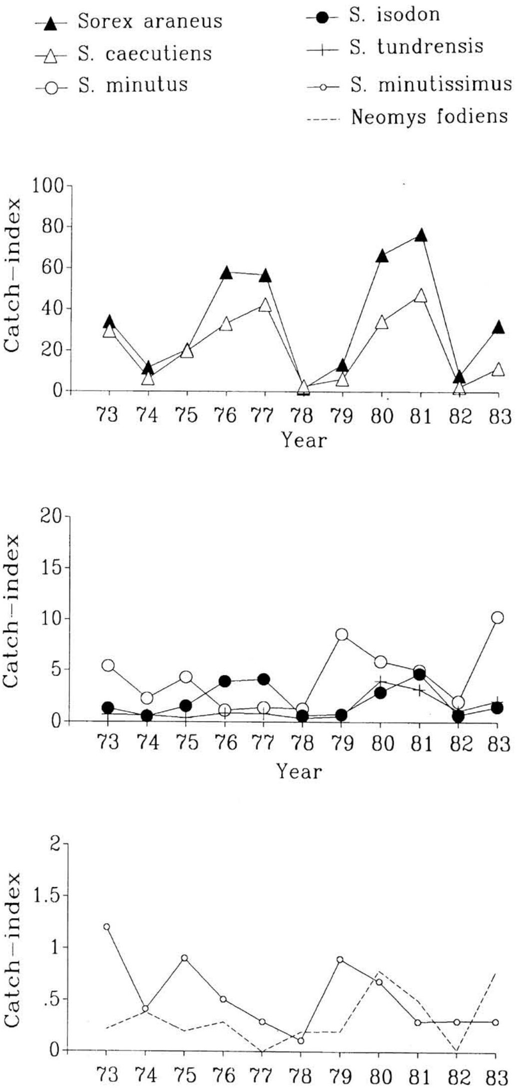

Fig. 2. Long-term abundance changes in seven species of shrew on the eastern bank of the Yenisei. The catch index gives the numbers of individuals caught per 100 trap-nights.

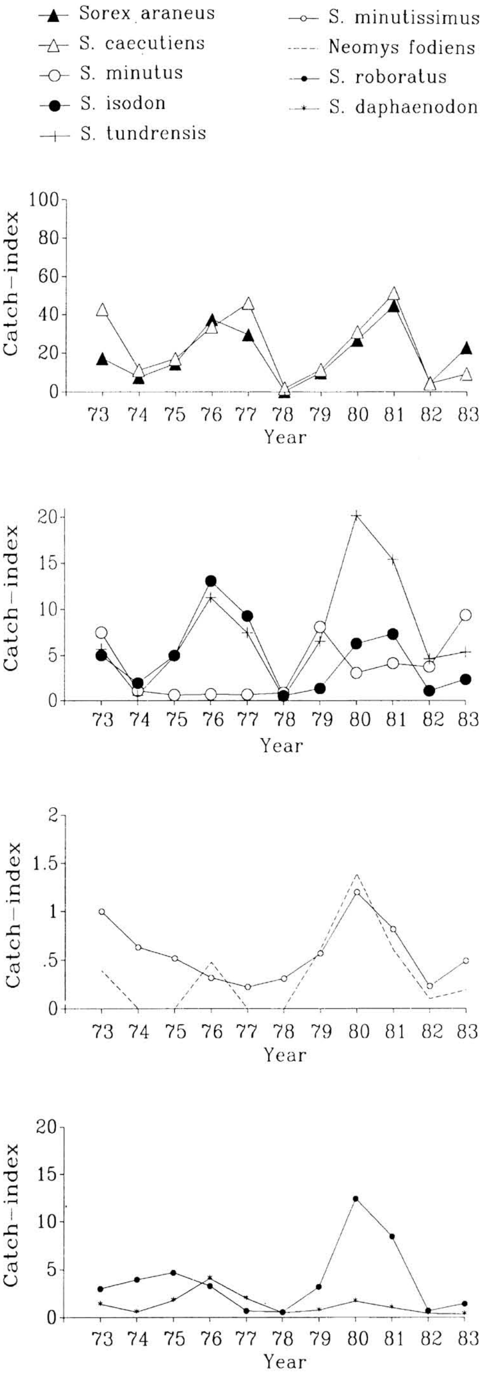

Fig. 3. Long-term abundance changes in nine species of shrew on the western bank of the Yenisei. The catch index gives the numbers of individuals caught per 100 trap-nights.

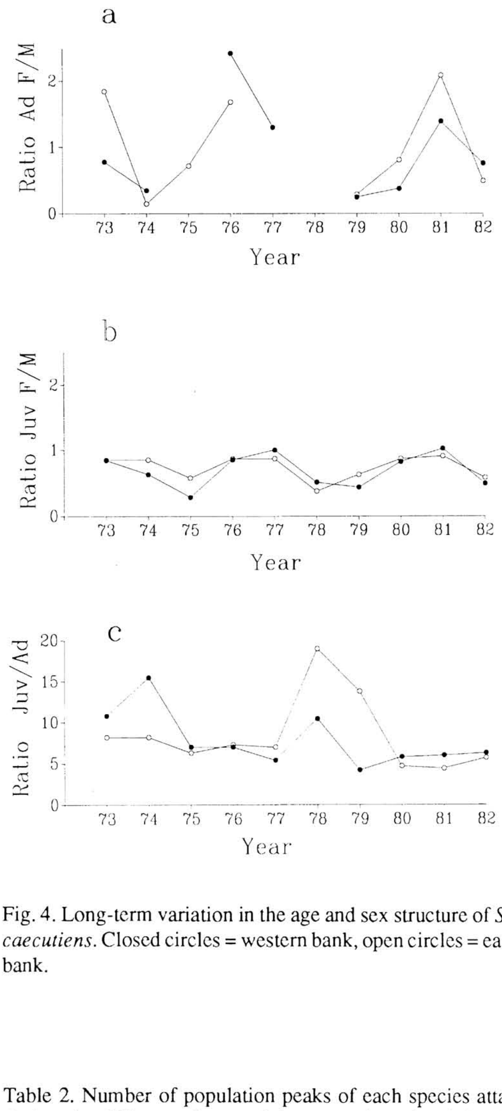

Fig. 4. Long-term variation in the age and sex structure of *Sorex caecutiens*. Closed circles = western bank, open circles = eastern bank.

Table 2. Number of population peaks of each species attained during the different phases of the general cycle of the shrew community (data for two four-year cycles on the two banks of the Yenisei). Sum of ranks = the number of peaks multiplied by the rank of the phase. *R* = rank order of the species.

Species	Increase rank 1	Prepeak rank 2	Peak rank 3	Sum of ranks	*R*
S. araneus	–	2	2	10	4
S. caecutiens	–	–	4	12	6
S. minutus	4	–	–	4	1
S. minutissimus	3	1	–	5	2
S. isodon	–	1	3	11	5
S. tundrensis	–	4	–	8	3

Table 3. Proportion of mature individuals amongst the juveniles (N) in nine years. The peak years are 1977 and 1981.

	1973		1974		1976		1977		1978		1979		1980		1981		1982	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
S. araneus	1203	0.3	231	2.2	2200	0.4	2007	0.3	31	22.6[1]	550	1.6	2361	0.1	3036	0.1	284	4.2
S. caecutiens	1076	–	149	–	1434	0.1	1766	–	43	4.7	270	0.7	1439	0.1	2162	–	95	2.1
S. minutus	222	–	50	–	36	–	46	–	53	1.9	372	0.3	214	–	212	–	114	–
S. minutissimus	45	–	12	–	18	–	10	–	8	12.5	36	2.8	37	–	19	–	10	–
S. isodon	65	–	31	0.7	287	–	233	0.4	9	11.1	27	–	171	0.6	253	–	34	–
S. tundrensis	47	2.1	15	–	176	1.1	114	–	9	11.1	103	1.0	421	1.0	306	1.6	81	4.9
S. roboratus	20	–	25	–	43	–	4	–	1	–	37	5.4	165	–	116	–	1	–
S. daphaenodon	5	–	5	60.0	53	–	23	–	–	–	5	–	17	–	9	–	5	20.0
N. fodiens	10	10.0	8	12.5	15	6.7	1	–	5	40.0	15	20.0	42	11.9	24	8.3	2	50.0

[1] Two mature juvenile males were trapped in 1978. In the other years the mature juveniles were females. The sex ratio was roughly the same in each year (see Fig. 4).

mary and secondary sex-ratios) and to an increase in the number of non-breeding and hence probably more mobile females in these years (tertiary sex-ratio).

The proportion of juveniles increased in the years of minimum numbers (Fig. 4). In these years the numbers of adult shrews in spring are low due to heavy mortality in the previous winter, but their breeding success may be very good (see Kaikusalo & Hanski 1985).

An important element in the regulation of population density in small rodents is the proportion of juveniles that breed in their first year. In some species of small mammals, all or nearly all individuals of the first and second litters reproduce in their first year of life (Koshkina & Korotkov 1975, Olenev et al. 1980, Kuprijanova & Naumov 1983). In shrews, young individuals do not generally reproduce. Some authors have even suggested that reproduction by young shrews is not possible because the pelvic bones of juvenile shrews are not adjusted for pregnancy (Dolgov 1961). Nonetheless, our results indicate that a small proportion of young females reproduce in their first summer (Table 3). The incidence of reproduction among young shrews reaches a maximum in the years of lowest density, as has been previously found by Pucek (1960), Stein (1961), Judin (1962), Jurlov et al. (1965), Kaikusalo & Hanski (1985) and others.

To analyse the intensity of reproduction in the different phases of the population cycle, I examined the numbers of embryos and the proportion of pregnant and lactating individuals amongst adult females. There does not seem to exist a general pattern in the changes of these parameters with population density in different species of small mammals (Semenov-Tian-Shanskii 1970, Krebs & Meyers 1974). For instance, *Dicrostonyx torguatus* and *Lemmus obensis* have the largest litters in the increase and peak years (in Vrangel Island; Cherniavskii & Tkachov 1982), but in *Clethrionomys rutilus* the largest litters were observed in the years of minimum density (in Salair Mountains; Koshkina & Korotkov 1975).

The present analysis is hampered by the small numbers of pregnant females caught in the years of lowest density. Comparisons of the litter size were possible only for the prepeak and peak years, and for the two most abundant species, *S. araneus* and *S. caecutiens*. In these species the numbers of embryos were slightly greater in the peak years (Table 4), but the proportions of pregnant and lactating females, averaged over the entire season, were higher in the prepeak year. In the peak year the breeding period is significantly shorter than in the prepeak year. The first litters (June and July) are generally larger than the litters produced in August, a result consistent with many previous observations (Brambell 1935, Crowcroft 1957, Tarkowski 1957, Cherniavskii & Tkachor 1982, Koshkina & Korotkov 1975, Dokuchaev 1989), which may explain the slightly higher number of embryos per pregnant female in the peak than in the prepeak year.

4.3. Seasonal population dynamics

The most significant seasonal changes in the catch index were detected in the populations on the western bank of the Yenisei (Fig. 5). On the eastern bank, where the dominance of *S. araneus* and *S. caecutiens* is much greater than on the western bank, such fluctuations were not so prominent (Fig. 6).

Table 4. Breeding performance of female shrews in different phases of the population cycle. Number of breeding females (N), percent age of individuals pregnant, lactating and those having finished lactation among breeding females. The table also gives the mean number of embryos and resorbed embryos per pregnant female.

Year and phase:	1976: prepeak	77: peak	78: low	79: increase	80: prepeak	81: peak	82: low
S. araneus							
N	146	136	3	33	113	306	20
% pregnant	38	47	33	42	42	43	45
% lactating	18	13	33	24	21	8	30
% finished lactation	38	31	33	30	34	35	20
embryos	6.7	7.4	11.0	6.5	6.7	6.7	7.2
resorbed embryos	0.7	0.2	–	0.5	0.7	0.6	0.3
S. caecutiens							
N	115	170	–	8	94	237	6
% pregnant	19	18	–	50	28	20	33
% lactating	20	8	–	13	13	4	–
% finished lactation	61	68	–	38	60	76	33
embryos	4.7	5.4	–	6.3	5.2	6.1	–
resorbed embryos	1.0	0.2	–	0.8	1.3	0.7	–
S. minutus							
N	4	1	1	11	7	14	4
% pregnant	50	–	100	64	57	57	75
% lactating	–	–	–	–	14	–	25
% finished lactation	50	–	–	36	29	43	–
embryos	6.8	–	–	6.6	7.0	7.0	8.3
resorbed embryos	–	–	–	0.1	–	0.3	–
S. minutissimus							
N	3	–	–	2	3	2	1
% pregnant	–	–	–	–	–	–	–
% lactating	–	–	–	–	33	–	–
% finished lactation	100	–	–	100	67	100	100
embryos	–	–	–	–	–	–	–
resorbed embryos	–	–	–	–	–	–	–
S. isodon							
N	19	33	–	2	13	37	6
% pregnant	16	27	–	50	46	30	33
% lactating	–	3	–	–	15	–	17
% finished lactation	84	70	–	50	38	70	50
embryos	5.3	5.1	–	7.0	3.5	6.1	5.0
resorbed embryos	–	0.3	–	–	2.1	0.6	0.5
S. tundrensis							
N	14	4	–	4	31	26	6
% pregnant	50	25	–	–	42	15	50
% lactating	–	25	–	50	10	12	–
% finished lactation	50	50	–	50	42	69	50
embryos	7.0	5.0	–	–	7.8	8.0	7.7
resorbed embryos	0.9	–	–	–	–	–	–
S. roboratus							
N	5	–	–	10	14	8	–
% pregnant	20	–	–	10	29	88	–
% lactating	20	–	–	–	–	–	–
% finished lactation	60	–	–	90	71	13	–
embryos	6.0	–	–	4.0	7.0	7.9	–
resorbed embryos	–	–	–	2.0	1.0	0.7	–
S. daphaenodon							
N	6	5	–	–	1	–	1
% pregnant	33	40	–	–	–	–	100
% lactating	–	–	–	–	–	–	–
% finished lactation	67	60	–	–	100	–	–
embryos	5.0	7.5	–	–	–	–	–
resorbed embryos	0.5	0.4	–	–	–	–	–
N. fodiens							
N	2	–	–	4	8	2	–
% pregnant	–	–	–	25	13	50	–
% lactating	–	–	–	25	25	–	–
% finished lactation	100	–	–	50	36	50	–
embryos	–	–	–	9.0	12.0	9.0	–
resorbed embryos	–	–	–	4.0	–	–	–

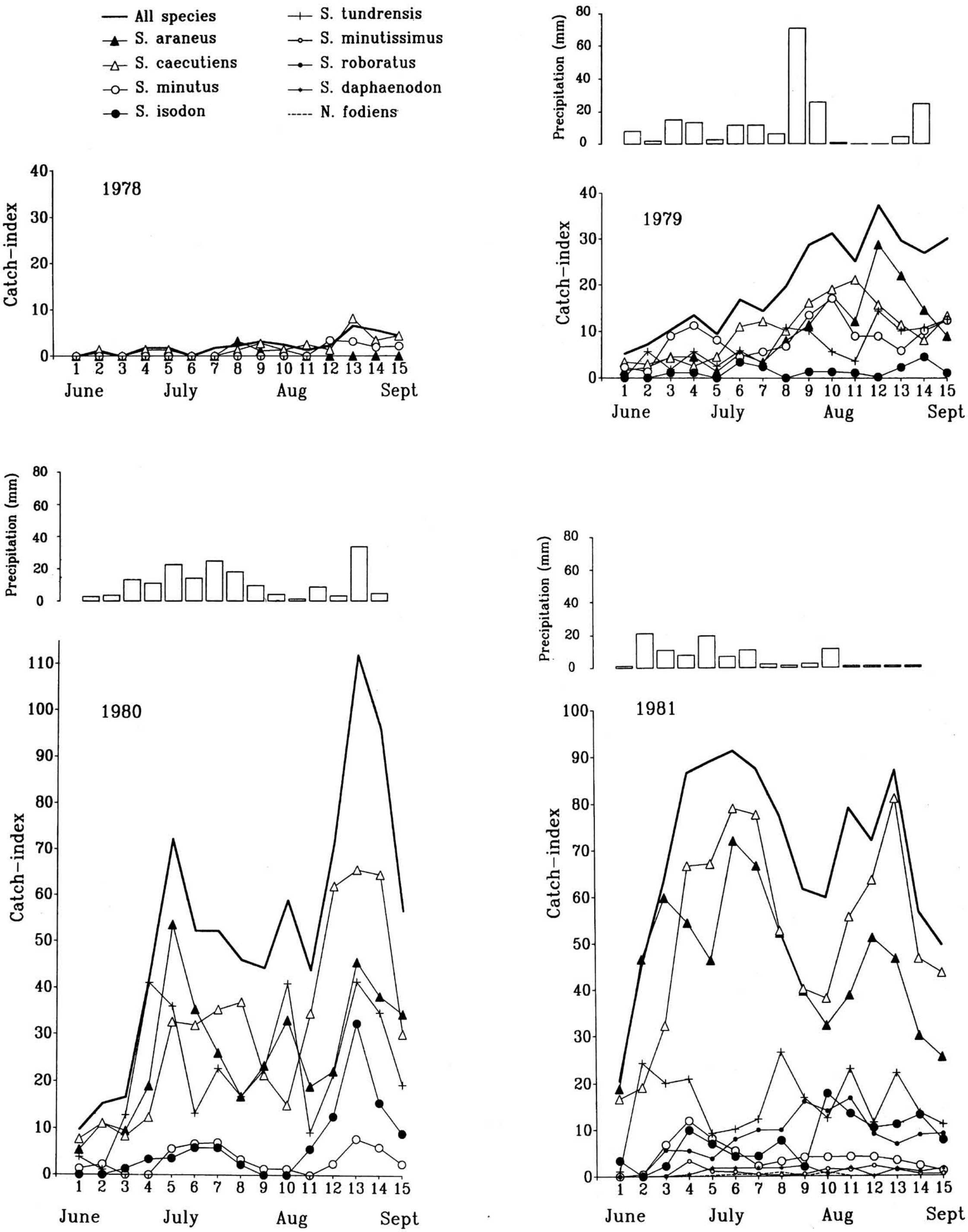

Fig. 5. Seasonal changes in the numbers of nine species of shrew and in their pooled numbers on the western bank of the Yenisei in the years 1978 to 1981 (one complete population cycle). The catch index gives the numbers of individuals caught per 100 trap-nights during 5-day trapping periods (the index value for all shrews has been multiplied by 0.5 to make it comparable to the individual species). The upper panels give seasonal changes in precipitation.

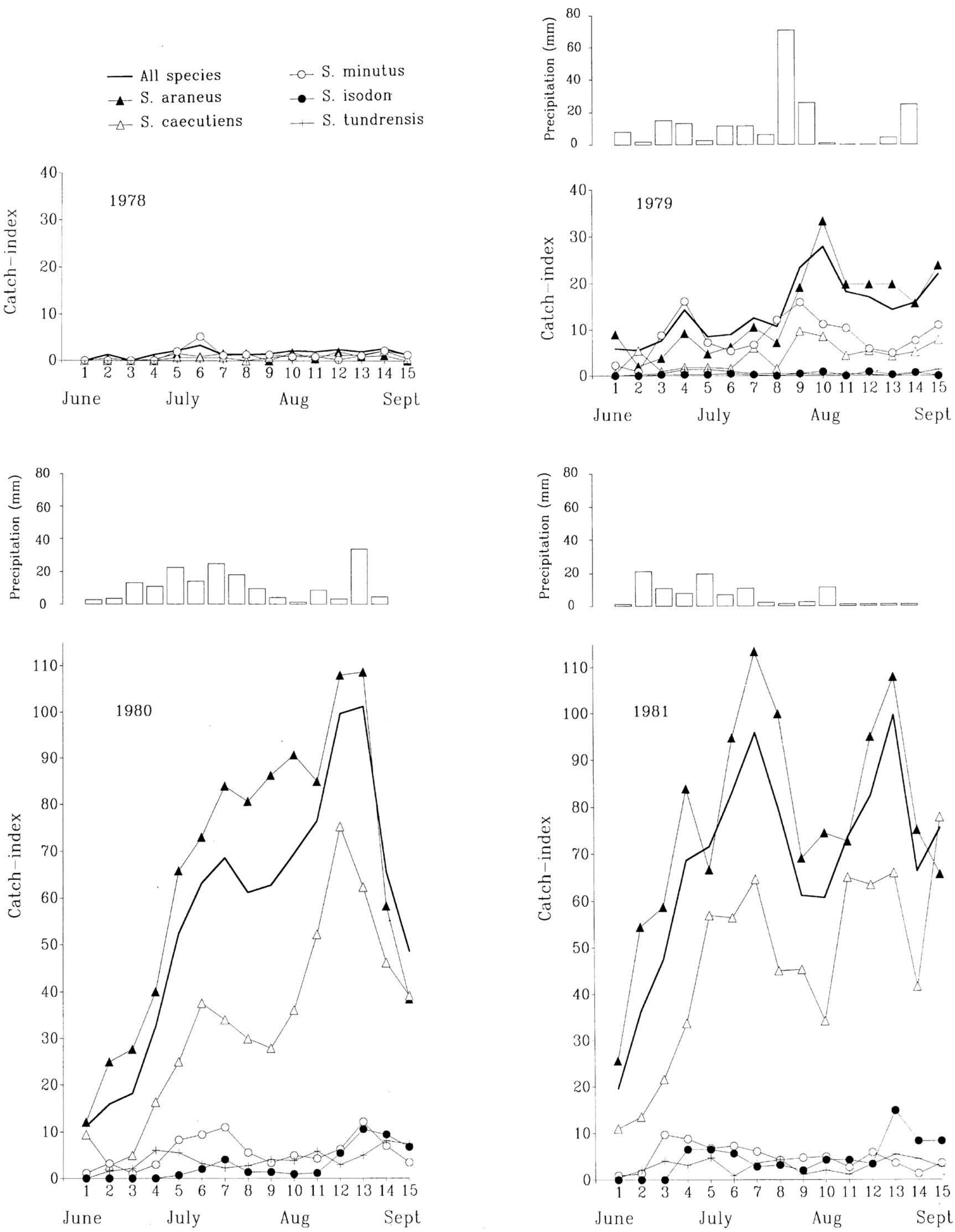

Fig. 6. Seasonal changes in the numbers of five species of shrew and in their pooled numbers on the eastern bank of the Yenisei in the years 1978 to 1981 (one complete population cycle). The catch index gives the numbers of individuals caught per 100 trap-nights during 5-day trapping periods (the index value for all shrews has been multiplied by 0.5 to make it comparable to the individual species). The upper panels give seasonal changes in precipitation.

Table 5. The number of the 5-day trapping period (from 1 to 15, see Figs. 5 and 6) corresponding to the median value of the catch index. Correlation between the western and eastern banks is significant (r=0.94, P=0.005). R = rank order of the species.

Species bank	Western bank	Eastern banks	Both	R
S. araneus	9.64	9.48	9.56	3
S. caecutiens	9.99	10.38	10.19	5
S. minutus	8.64	9.67	9.16	1
S. minutissimus	9.17	9.17	9.17	2
S. isodon	12.13	12.65	12.39	6
S. tundrensis	9.82	10.30	10.06	4

I examined possible correlations between the values of catch index averaged over 5-day periods and the amount of precipitation for the same period (Figs. 5 and 6). The strongest correlations were observed in the years of rapid population growth, while in the prepeak and peak years the correlations were weaker. In the years of rapid population increase interspecific and intraspecific interactions are probably less intensive than in the prepeak and peak years, which may explain this result. The correlations are stronger on the eastern bank, possibly because interspecific interactions may generally play a greater role in the more species-rich community on the western bank of the river.

The numbers of *S. minutus*, *S. tundrensis* and probably *S. minutissimus* (small sample size) peak relatively early in the course of the season, while the peak numbers of *S. caecutiens* and *S. isodon* usually occur at the end of the season; *Sorex araneus* is intermediate in this respect. The pattern is most evident in the average data for the seasonal dynamics during an entire population cycle (1978–1981).

To characterize the seasonal dynamics in each species, I calculated the number of the 5-day period corresponding to the median value of the catch index, separately for the two banks of the Yenisei. The results for the two banks are highly correlated (Table 5), hence the average for the two banks will be used below.

5. Discussion

This study revealed a highly regular multi-annual cycle in the numbers of shrews. The only deviation from the regular cycle was caused by anomalous weather conditions in the spring of 1974. Apart from this single event, analyses of temporal changes in weather conditions and in the numbers of shrews indicated that the two are largely independent of each other. In agreement with Cherniavskii & Tkachov (1982), I have shown that varying weather conditions do not create cyclic fluctuations in population density, but that anomalous weather conditions can be an important factor in syncronizing the population cycles on the two sides of the Yenisei, which forms an effective dispersal barrier to shrews.

The dynamics of shrew populations have been little studied, and the duration of observations has rarely exceeded 5 years (Formozov 1948, Mežhzherin 1960, Viktorov 1967, Dolgov et al. 1968, Ivanter 1976, Dokuchaev 1983, Gaisler 1983, Kaikusalo & Hanski 1985). Most of these studies did not record cyclic changes in population density. The exception is the work of Dolgov (1968) in the Perm region, where from 1958 to 1963 a well-defined cycle was observed. Many authors have suggested that unfavourable conditions in winter largely explain the fluctuations in density of shrews (snowless and severe winters: Formozov 1948, Dolgov et al. 1968, Ivanter 1976, Gaisler 1983).

The study region in Central Siberia is characterized by a deep and stable snow cover, decreasing the probability that the animals are exposed to severe frosts. Under such stable conditions, populations may reach a critical density, after which they crash. One possible reason for the crash is stress due to overpopulation (Christian 1950, 1955). The physiological condition of stressed animals deteriorates, possibly leading to mass mortality in winter. One indication of poor physiological condition of breeding females in the peak year is an increase in the level of fluctuating asymmetry of some skeletal characters in their offspring (Zakharov et al. 1984, unpubl.). However, the synchronous crash in many species of shrews and rodents (Sheftel unpublished) can also be due to other factors, such as predation or disease.

The role of interspecific interactions in the dynamics of many coexisting shrew species is not well understood, as only the dynamics of the dominant species are usually studied. Some authors have suggested that there are no important interspecific interactions at all (Bashenina 1977). Other ecologists working on small mammals have pointed out that the population cycles of closely related species are often not synchronized (Koshkina 1957, Kuprijanova 1978, Ivanter 1976). Such asynchrony has been explained by differences in the resource requirements of different species (Koshkina 1957, but see Koshkina 1964, 1971). Koshkina found that following the crash of the dominant species in the community the numbers of subordinate species increased. This could be explained by assuming that the subordinate species often have high reproductive capacity, which can be realised when the population density of the dominant species is low. In the Kola peninsula, where population lows are very deep, the subordinate species *Clethrionomys glareolus* can even dominate in numbers in some years. In the Salair mountains, where the population lows are not so deep, the subordinate species can only slightly increase when the density of the dominant species is lowest. The same phenomenon was observed by Gaiduk (1982) in southern Belorussia, where he studied the interactions between *Lepus timidus* and *Lepus europaeus*. In shrews, the effect of the dominant species upon the subordinate ones has been discussed by Ivanter (1976) and Dokuchaev (1983).

Different authors have no common opinion about the reasons for the seasonal fluctuations of shrews. Dunaeva (1955) explained such variation with varying level of dispersal in different cohorts of young shrews. Popov (1960) thought that seasonal variation in the catch index is related to increased mobility at times of flooding of previous shelters. Vickery & Bider (1978), working in Canada, showed for *S. cinereus* that morning rain depresses activity while evening or night rain increases it, and such varying responses were explained by the effects of rain on the prey populations.

The present study deals with several coexisting species and demonstrates that the seasonal changes in numbers are different for different species of shrew (Sheftel & Sapogov 1978). An interesting point is that the sequence of species is much the same in both long-term (cyclic) and seasonal changes of numbers (*R* from Tables 2 and 5, Spearman's rank correlation, $r=0.89$, $P<0.05$).

Why should the multi-annual and seasonal dynamics be correlated? Table 6 presents data on fecundity for the different shrew species. These data indicate that those species which have their maximum abundance at the end of the season and at the end of the general population cycle have a lower rate of potential reproduction than species with early seasonal and cyclic occurrence. Species with a high rate of reproduction can increase in abundance rapidly, but when the density of species with a lower rate of reproduction has sufficiently increased the former species may be even excluded from some habitats. This scenario assumes that the late species are competitively superior to the early ones. Such a process of competitive exclusion was demonstrated in a long-term study of the dynamics of shrew populations by Moraleva (1986, *S. caecutiens* excluded *S. tundrensis*).

Table 6. Numbers of embryos per pregnant female (Mean ± *SE* and *N*) in nine species of shrew. Pooled data for 1971–1983.

Species	Mean ± *SE*	*N*
S. araneus	7.14 ± 0.21	331
S. caecutiens	5.90 ± 0.17	137
S. minutus	7.03 ± 0.32	37
S. minutissimus	9	1
S. isodon	5.35 ± 0.31	34
S. tundrensis	7.50 ± 0.39	32
S. roboratus	7.55 ± 0.92	11
S. daphaenodon	5.70 ± 0.77	7
N. fodiens	9.25 ± 0.90	4

6. Conclusions

1. The shrew community in Central Siberia shows a regular four-year cycle in density. The regularity of the cycle is probably largely due to a predictable, continental climate, which decreases the role of abiotic factors and increases the role of intraspecific and interspecific competition in the population dynamics. The role of predation is unknown.
2. Seasonal changes in the trapping index of shrews depend mostly on precipitation in the years of low abundance, while interspecific interactions probably become increasingly important in the years with higher population densities.
3. Different species peak at different phases of the general four-year cycle and at different times of the season. The results indicate that competitively inferior species have a higher potential rate of reproduction than competitively superior species, and may hence increase in abundance in the years and in seasons when the latter are less numerous.

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