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Population ecology of *Sorex* shrews in North-East Siberia

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The ecology of *Sorex* shrews was studied in two localities of North-East Siberia with continental and maritime climates (Kolyma river and the coast of the Sea of Okhotsk). During 1972–1988, 4608 shrews of 8 species were caught. *Sorex caecutiens* was the dominant species, accounting for 79% of all individuals. The dominant and sub-dominant species tended to be spatially segregated. An important feature of food selection is frequent consumption of larch seeds (when the harvest is abundant). The litter size of *S. caecutiens* was 8.6±0.3 in the Kolyma river basin and 7.5±0.3 on the north coast of the Sea of Okhotsk. Females may give birth to up to four litters during the breeding season. In the years of low spring density, young females of the first litters take part in reproduction, greatly contributing to the rapid recovery of populations after low density. Winter mortality was generally higher in the continental than in the maritime region, but between-year variation in winter mortality mostly depends on food availability.

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1. Introduction

In North-East Siberia, environmental conditions are extreme and pose particular problems for shrews. The winter temperatures are extremely low and the deep snow cover lasts for a long period. The breeding period for shrews is short, and the areas with suitable habitat are limited. The food supply is generally poor for insectivorous mammals. Nonetheless, in spite of the rigorous climate there are nine species of *Sorex* shrews in North-East Siberia: *Sorex caecutiens, S. daphaenodon, S. isodon, S. tundrensis, S. roboratus, S. minutissimus, S. gracillimus, S. camtschatica* and *S. jacksoni* (= *S. portenkoi*). In some habitats shrews actually numerically dominate the assemblages of small mammals. Shrews exhibit many ecological adaptations permittingthem to exist in the severe environment and to attain, occasionally, high population densities. In this paper I describe such adaptations and the characteristics of shrew populations in North-East Siberia more generally.

2. Study area and methods

Studies have been carried out in two localities in the Magadan district (Fig. 1). The first study area is located in the valley of the Omolon river (right tributary of the Kolyma river; 66°N), while the second one lies in the valley of the Chelomdzha river, on the north coast of the Sea of Okhotsk (60°N). Fig. 2 describes the climates of the two localities. The climatic conditions are especially severe in the more continental district of Omolon, where snow cover lasts for 7.5 months and frosts reach –67°C in winter. Frost and snow may appear during any month of the year. The Chelomdzha site is characterized by a milder climate during the winter months and by higher temperatures in August–September (Fig. 2). Both localities have montane taiga landscapes, typical to most of North-East Siberia. The dominant forest type is *Larix dahurica* forest. The larch found here is particularly resistant to the severe climate.

Shrews were trapped at Omolon during 1972–1981, while the studies in Chelomdzha were started in 1979 and are still going on. Shrews have been mostly trapped with metal cones, but snap-traps baited with oil-wetted bread have also been used. At Omolon, 1774 shrews of five species were caught, and in Chelomdzha 2834 individuals of six species have been trapped so far. In both localities, *S. caecutiens* is the dominant species,

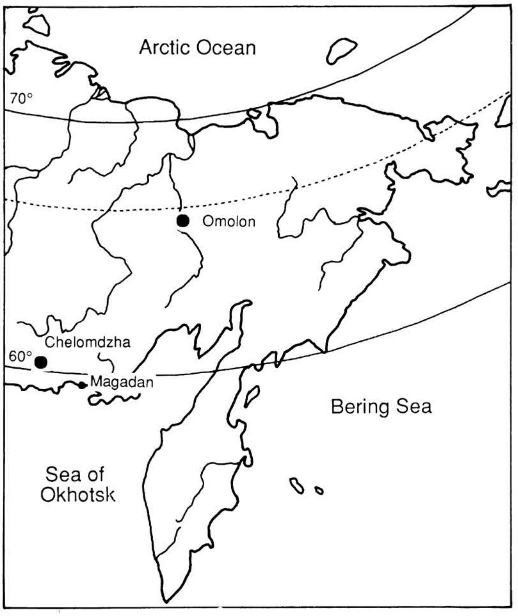

Fig. 1. Location of the study areas Omolon and Chelomdzha.

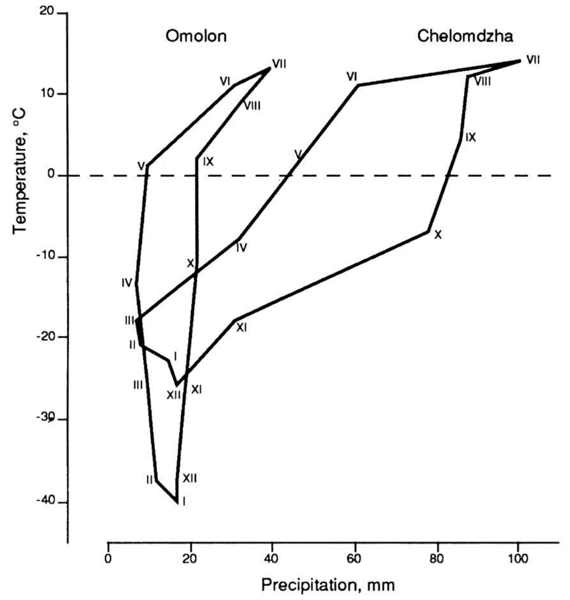

Fig. 2. Climatographs for the Omolon and the Chelomdzha study areas.

accounting for 84% of all shrews in Omolon and 76% in Chelomdzha. The basin of the Omolon river and the north coast of the Sea of Okhotsk (Chelomdzha) are inhabited by different subspecies of the masked shrew, *S. caecutiens koreni* and *S. caecutiens macropygmaeus*, respectively. The second most numerous species are *S. daphaenodon* in Omolon and *S. isodon* in Chelomdzha. All other species are rare. The methods of collecting and processing shrews are described in detail in Dokuchaev (1979, 1981).

3. Results and discussion

3.1. Habitat selection

Shrews have been trapped in three main habitats: riparian larch forest (Fig. 3), sparse larch forest on mountain slopes (Fig. 4) and poplar-tchosenia-willow (*Populus-Chosenia-Salix*) forest on islands. The highest and most constant numbers of shrews have been found in the riparian larch forest (Table 1), which is more favourable for shrews than the other habitats in terms of microclimate, food availability and shelter. In general, the most abundant species tend to be spatially segregated. Thus *S. caecutiens* dwells mainly in larch forests, and it is the only species which can reach high densities in the sparse larch forest on mountain slopes. *Sorex daphaenodon* is found mostly in the riparian larch forests, where it may compete with *S. caecutiens*, especially in winter. In the winter months *S. daphaenodon* was mostly trapped in hollows while *S. caecutiens* was distributed more evenly in this habitat. *Sorex isodon* is most abundant in poplar-tchosenia willow forests on islands. The fact that the shrew assemblages tended to be dominated by a single species may reflect severe interspecific competition.

3.2. Food selection

A characteristic feature of food selection by shrews in North-East Siberia is frequent consumption of larch seeds. Data on stomach contents of shrews from the basin of the Omolon river reveals the importance of larch seeds, especially in winter (Table 2). Data from Chelomdzha demonstrate that larch seeds are also consumed in large quantities in summer, provided that there has been a rich harvest of seeds in the previous year (Table 2: there was a rich harvest in Chelomdzha in 1984 and 1987). When the harvest is low shrews do not consume larch seeds at all.

Fig. 3. Riparian larch forest in the Chelomdzha river basin.

Fig. 4. Sparse larch forest in the Omolon river valley.

Shrews had more brown adipose tissue (BAT) in their body in September in the years with a large crop of larch seeds than in the years with a small crop. For example, in 1981 the harvest of larch seeds was abundant while in 1982 there was no harvest at all. The BAT contents in young *S. caecutiens* in September 1981 and 1982 were 131±6 mg (n=39) and 107±5 mg (n=11), respectively. The respective proportions of body weight were 29.2±0.96‰ and 23.3±1.07‰. The difference is highly significant (P<0.001).

I have tested the consumption of larch seeds by three species of shrew, *S. caecutiens*, *S. daphaenodon* and *S. tundrensis*, in captivity. All species used larch seeds even if they had animal food available as well. The same was found to be true by Tupikova (1949), Zablotskaja (1957) and Lukjanova (1974) for several species of shrew, including *Neomys fodiens*. Frequent use of seeds in northern coniferous forests may be due to relatively low abundance of invertebrates in comparison with more southern localities. Increasing percentage of plant material in the diet of shrews with increasing latitude has been reported by Rudge (1968) and Ivanter (1975).

The most notable feature in the animal diet of shrews is the frequent consumption of Myriapoda (Chilopoda), which were found 6 to 12 times more frequently in the stomachs of *S. caecutiens* in the Omolon valley than in Central Yakutia (Volpert & Averenskii 1983), West Siberia (Judin 1962) and Karelia (Ivanter 1975). This difference probably reflects high abundance of Chilopoda in North-East Siberia (Berman & Bukhkalo 1985).

Table 1. Numbers of the most abundant shrew species in the three main forest habitats in the Omolon and Chelomdzha valleys (individuals per 100 trap-nights, trappings conducted in August).

	Omolon (1977)			Chelomdzha (1987)		
	Riparian larch	Sparse larch	Poplar-tchosenia	Riparian larch	Sparse larch	Poplar-tchosenia
S. caecutiens	51.1	7.1	–	90.4	6.1	3.6
S. daphaenodon	21.5	2.9	3.3	6.7	0.9	–
S. isodon		absent		8.7	–	18.2
Trap–nights	135	70	30	104	114	55

Table 2. Percentage of *S. caecutiens* individuals with larch seeds in their stomach (number of stomachs in brackets).

Locality	Febr.-May	June	July	Aug.	Sept.
Omolon (1974–1977)	74 (46)	33 (12)	18 (71)	32 (202)	65 (34)
Chelomdzha (1985)	–	100 (10)	97 (105)	88 (142)	–
Chelomdzha (1988)	–	98 (45)	80 (140)	51 (65)	–

3.3. Reproduction

Male reproductive activity

In the Omolon population the testes of *S. caecutiens* males begin to grow in March. In the second half of March some males had mature spermatozoa, and in April 92% of males had spermatozoa in the cauda epididymidis, and the size and weight of their testes were almost the same as in the summer months (April: size 6.4±4.2, weight 118±4; June–August: size 6.4±4.5, weight 121±3; mean±*SE*). In September the spermatogenesis diminishes, the testes become decrepit and decrease in size (size 5.3±4.5, weight 55). In some males signs of slowing down of spermatogenesis have been observed as early as in late July. The old males practically disappear in the Omolon valley by September. For instance, of the 14 old individuals caught in September only two were males.

In contrast to the pattern of male reproductive activity in the Omolon population, in Chelomdzha males mature later and their reproductive organs do not show any degradation by September. In this population males apparently live longer than in the Omolon population, and the sex ratio is about 1:1 in September.

Female reproductive activity

In Omolon, overwintered females mature one month later than males, and they begin to mate in late April–May. Signs of copulation were observed in 90% of individuals during the first ten days of May. Most females give birth at the end of May, and the first young shrews have been caught on June 11 to 18. Exceptionally, in 1976 the first young shrews were caught on July 4. Overwintered females may have three or even four litters during the breeding season. The young from the latest litters start to live independently at the end of September, when environmental conditions are already fairly severe. During the seven years of study in the Omolon valley, some females had four litters in 1974, 1975 and 1977.

In the Chelomdzha valley the breeding season of *S. caecutiens* extends from the end of April until the end of September, and it is about two weeks longer than in the Omolon valley due to a relatively warm autumn (Fig. 2). In Chelomdzha, only a few females start to breed in late April-beginning of May, and females with their first pregnancy can be found from late April until June 20. However, because of the relatively warm autumn, many overwintered females have still time to give birth to four litters (observed in five out of ten years, with the proportion of females with four litters reaching 67%, a higher figure than in the Omolon population, 21 to 33%).

The breeding season of *S. caecutiens* begins at roughly the same time in Omolon, in Chelomdzha and in the Amur region, at the end of April. In the Amur region the beginning of reproduction coincides

Table 3. Litter size (mean±*SE*, number of females) of overwintered *S. caecutiens* in Omolon and Chelomdzha valleys.

	Omolon		Chelomdzha	
Months				
May	9.2 ± 0.42	20	8.0 ± 1.00	2
June	10.2 ± 0.37	12	9.8 ± 0.58	5
July	7.7 ± 0.59	11	7.9 ± 0.40	16
August	6.5 ± 0.62	11	6.5 ± 0.45	17
September	– –	–	6.8 ± 0.25	4
Pregnancies				
First	9.3 ± 0.40	22	8.0 ± 1.00	2
Second	10.3 ± 0.43	11	8.9 ± 1.47	10
Third	7.3 ± 0.37	15	7.5 ± 0.37	20
Fourth	5.7 ± 1.09	6	6.2 ± 0.47	12
Total	8.6 ± 0.30	54	7.5 ± 0.28	44

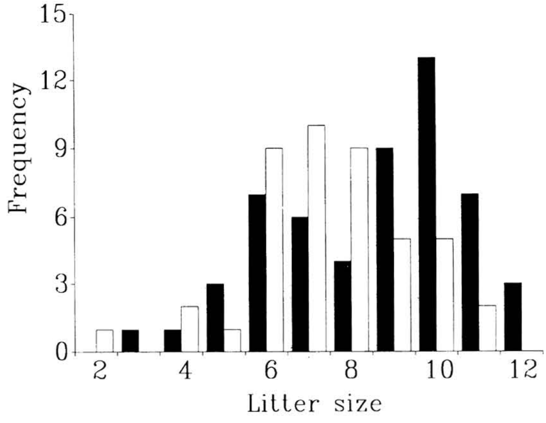

Fig. 5. Frequency distributions of litter sizes in overwintered *Sorex caecutiens* in Omolon (black, *n*=54) and in Chelomdzha (white, *n*=44).

with the time of snow-melting (Bromlei et al. 1984), while in Chelomdzha and, in particular, in the Omolon valley, the first pregnancy and lactation take place under snow cover. Deep snow cover protects the breeding females against low temperatures, which are still common at this time of the year. For instance, in the Omolon valley the average minimum temperature in May is –5.8°C and frosts can reach –35°C.

Litter size

The litter size of overwintered *S. caecutiens* varied from 3 to 12, averaging 8.6 in the Omolon valley and 7.5 in the Chelomdzha valley (Table 3). It appears that the litter size is higher in North-East Siberia than in any other part of the geographical range of *S. caecutiens*. Only in Karelia (Ivanter 1975) does the average litter size equal that observed in the Chelomdzha valley (7.5). An analysis of litter size in *S. caecutiens* suggests that it is highest near the boundaries of its geographical range and especially in the northern localities (Dokuchaev, unpubl.). Litter size varies during the breeding season, with the largest litters observed in the second pregnancies (Table 3). The fourth litters were 30–45% smaller than the second ones (Table 3). The second litters are produced during the most favourable season in July, when the temperature is highest and food availability is also most favourable for shrews.

Sorex isodon starts to breed in May, much later than *S. caecutiens*. Consequently, the second pregnancies of *S. caecutiens* coincide with the first pregnancies of *S. isodon*. In the latter species the largest litters occur in the first pregnancy, supporting the suggestion that the largest litters occur at the time of year when conditions are most favourable for young shrews after weaning.

In the Omolon population, females had more frequently litters of 6 or 10 than the average litter size, 7 or 8, while in the Chelomdzha population the most frequent litter size (7) was close to the average, 7.5 (Fig. 5). The asymmetry and excess coefficients of the distribution for Omolon are A=–0.49 and E=–0.63, and for Chelomdzha A=–0.35 and E=0.41, respectively (A and E are defined in Plokhinskii 1970). The frequency distributions of the litter size are significantly different between the two localities (λ=1.58; $\lambda(0.05)$=1.36; Fig. 5). The difference is apparently due to the substantial reduction in litter size from the second to the third litters in the Omolon population (Table 3).

Studies on *S. araneus* have shown that litter size is related to population density (Snigirevskaja 1947, Popov 1960, Novikov et al. 1970, Ivanter 1975 and others): in years of low population density, females give birth to larger litters than in years of peak numbers (but see Sheftel 1989). My data for *S. caecutiens* from the Omolon valley indicate that in years of low spring density litter size was higher than in years of high spring density. For instance, in 1975 (high spring density) the average litter size was 8.0±0.7 (n=15), while in 1976 and 1977 (low spring density) the average litter sizes were 9.3±0.9 (n=3) and 8.9±0.8 (n=10), respectively. These differences are not significant but the trend is suggestive. However, in the Chelomdzha population no such dependence of litter size on spring density has been detected.

Reproduction of young shrews

Several studies have demonstrated that young females, particularly the ones from early litters, take part in reproduction (Snigirevskaja 1947, Karaseva & Ilenko 1960, Popov 1960, Shvarts 1962, Lapin 1963, Reimers 1966, Dolgov et al. 1968, Novikov et al. 1970, Sheftel 1989). Stein (1961) was the first to pay attention to a negative relationship between the numbers of females maturing in their year of birth and general population density. In the Omolon valley, only females from the first litter matured in their year of birth, and only in the years when the spring density was low. Maximally less than 11% of all young females matured in their year of birth. The young females produced only one litter, but their litter size was only slightly lower than in overwintered females (young females: from 5 to 10 embryos, average 8.1±0.4; old females 8.6±0.3).

In the Chelomdzha population some young *S. caecutiens* females matured almost every year, and there was only a weak dependence between the numbers of young females maturing and spring population density (no females matured in the years of exceptionally high spring density, in 1985 and 1988). In Chelomdzha some young females managed to produce two litters. The litter size varied from 5 to 10, with an average of 7.6, which is the same as in overwintered females.

In the Omolon population young males mature only seldom in the summer of their birth. In Chelomdzha young males were observed to breed in four out of ten years, when the spring density was low, with the proportion of mature juvenile males varying from 5 to 10%.

3.4. Age and sex structure of populations

Young *S. caecutiens* appear mostly during the second ten days of June. In the Omolon valley, their proportion in samples varied from 0 to 55% in different years, with an average of 37%. In the Chelomdzha population juveniles already predominate in June with the average of 61% of all individuals. The difference in the proportion of juveniles in the Omolon and Chelomdzha populations in June and July is significant (P<0.01). Since the breeding season in the two populations starts at the same time, the above result is likely to be due to a difference in postnatal mortality, which appears to be higher in the Omolon population.

The sex-ratio of overwintered shrews varied according to spring density in the Omolon population. In the years with low spring density, for instance in 1976 and 1977, males clearly predominated, and their proportion amongst overwintered shrews increased from 50% to nearly 90% in July–August. In the years of high spring density, for instance in 1974 and 1975, the proportion of males was less than 40% (average 28%).

3.5. Population dynamics

Numbers of small mammals in natural populations change due to a variety of factors, often divided into external and internal factors. Data on the numbers of shrews in the Omolon and Chelomdzha populations are given in Figs. 6 and 7. In this paper I focus on the dominant species, *S. caecutiens*.

Many authors have stressed the importance of high mortality of shrews in winter (Formozov 1948, Popov 1960, Skaren 1972, Ivanter 1975 and others). In North-East Siberia, the most important factors affecting the survival of shrews are severe climate and food availability.

I have compared the level of winter mortality in *S. caecutiens* in severe and mild winters. In the winter of 1974–75, the depth of snow was less than 20 cm in the Omolon valley in the middle of January, and the average monthly temperatures were less than –41°C in December and January. Climatic conditions were exceptionally severe in this winter, but nonetheless the density of *S. caecutiens* was relatively high in the following spring. The survival of shrews in the winter of 1974–75 was apparently improved by an abundant supply of larch seeds. In contrast, in the snowy and warmer winter of 1975–76, when the average temperatures in December and January were –36.2 and –34.4°C, respectively, the numbers of shrews declined markedly.

These results point to a tentative conclusion about the lack of any direct connection between climate and winter mortality in shrews (see also Sheftel 1989). However, a comparison of the spring and autumn densities in the Omolon and Chelomdzha populations shows that winter mortality is generally much higher in the continental region (Omolon) than on the coast

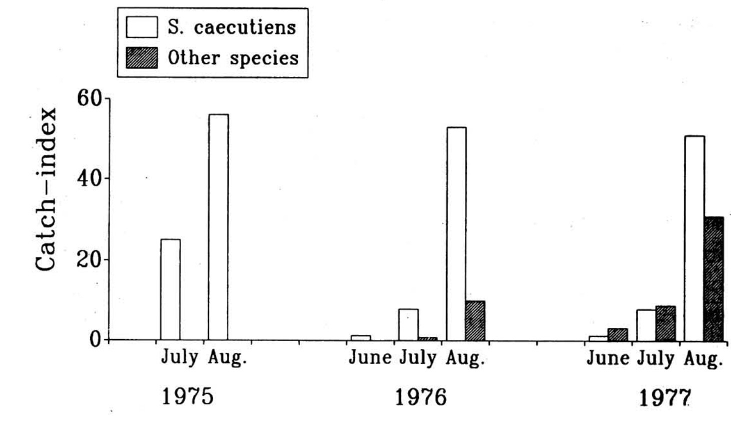

Fig. 6. Abundances of shrews in the Omolon valley in 1975–1977. *Sorex caecutiens* and the pooled numbers of all other shrew species. The vertical axis gives the numbers of individuals caught per 100 trap-nights (cone traps).

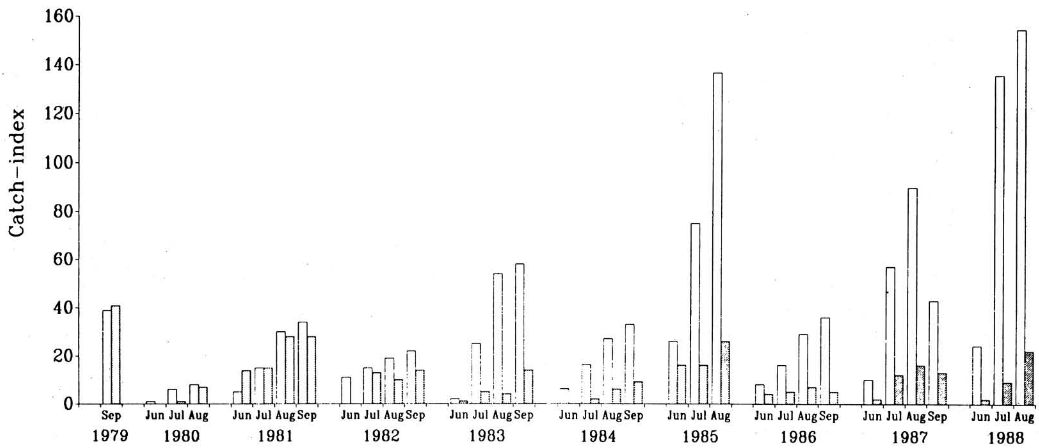

Fig. 7. Abundances of shrews in the Chelomdzha valley in 1979–1988. *Sorex caecutiens* (white columns) and the pooled values of all other shrew species (hatched columns). The vertical axis gives the numbers of individuals caught per 100 trap-nights (cone traps).

of the Sea of Okhotsk (Chelomdzha). Considering all the data available, I suggest that climate must also be taken into account as one of the factors affecting shrew numbers in North-East Siberia. In the continental parts of this region the climate is so severe that even "mild" winters are very difficult for shrews and winter mortality is always high.

Studies conducted in the Omolon and Tchelomndza valleys have convincingly shown that winter mortality of shrews is directly dependent on the larch seed harvest. I have compared winter mortality in the Chelomdzha population in years of good and poor harvest. The lowest spring densities of *S. caecutiens* were observed in 1980 and 1983 (Fig. 7), when in previous autumns the larch did not fruit at all. In contrast, after abundant harvests in 1981, 1984 and 1987 the numbers of shrews were exceptionally high in the June of the following year (Fig. 7). In years of good harvest the population lost from 5 to 15% of individuals per month, while in years of no harvestthe corresponding rate was from 30 to 35%. The correlation between the level of harvest in the previous autumn and the density of shrews in June is significant ($r=0.82$; $P<0.01$).

The seeds of *Larix dahurica* (the eastern race) drop in the autumn before the first snow-fall. In average years the harvest is 30 to 40 kg of seeds per hectare (Posdnjakov 1975), while in good years it is two to three times greater. One may estimate that a good harvest may satisfy up to 50% of the shrews' food requirements in winter, given a high autumn density of 250 individuals per hectare.

According to most authors, annual differences in the breeding intensity of shrews can be explained by intrapopulation regulation. As I have described above, in the Omolon population the fecundity of *S. caecutiens* was clearly density-dependent, while in the Chelomdzha population density-dependence was not clearly detected. A special feature of the Chelomdzha population is the maturation of young shrews of the first litters in almost every summer.

4. Conclusions

The assemblages of shrews in North-East Siberia are characterized by spatial segregation between the dominant and sub-dominant species. The by far most abundant species is *Sorex caecutiens.*

The breeding of shrews in North-East Siberia is characterized by an early beginning under a continuous cover of snow, enabling females to produce up to four litters per year. High fecundity and breeding by young shrews in years of low spring density enhance rapid recovery from low population density. In the continental locality of Omolon, both fecundity and breeding by young females of *S. caecutiens* were density-dependent, while in the maritime locality of Chelomdzha a high population growth rate was especially due to frequent breeding by young females. Winter mortality was higher in the more continental locality, apparently because of its exceptionally severe climate, but in both localities between-year variation in winter mortality depends primarily on the supply of larch seeds.

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