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Periodic Changes in the Abundance of Laxmann's Shrew (*Sorex caecutiens*, Eulipotyphla) and Factors of Its Population Dynamics in the Foothill Taiga of the Northern Urals

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Abstract—Long-term data on fluctuations in the abundance of Laxmann's shrew (*Sorex caecutiens* Laxmann) in the foothill taiga of the Northern Urals (Pechora-Ilych State Biosphere Reserve) have been evaluated using spectral analysis of time series. Periodic components in the population dynamics of the species have been revealed, including a statistically significant component that had a period of 3 years but was not highly regular. Analysis of factors accounting for variation in abundance parameters has shown that the population dynamics of *S. caecutiens* are influenced by both weather conditions and mechanisms of density-dependent regulation.

Keywords: Sorex caecutiens, population cycles, climatic factors, density-dependent regulation, Middle Ural foothills

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Understanding the dynamics of abundance of small mammals is a central problem in population research [1]. In shrews, however, patterns of variation in abundance and factors responsible for this variation are relatively poorly known, and the majority of studies on their population dynamics have been performed on the common shrew. It has been found that the abundance of shrews is subject to both regular changes with a certain period (usually 3–4 years) [2–6] and irregular, aperiodic changes [7–9]. The former are often referred to as cyclic fluctuations, although their cyclicity is conditional.

Long-term changes in the abundance of small mammals, including shrews are contingent on a number of external factors and intrapopulation mechanisms [1, 10, 11]. An important role in the population dynamics of shrews is played by weather conditions [7, 12, 13], especially in the transitional seasons (early winter and spring) [3, 14, 15]. However, such dependence on the weather has not been observed in certain regions [16, 17], and some authors consider that density-dependent mechanisms are mainly responsible for periodic fluctuations in the abundance of shrews [5, 6, 18].

In this study, we analyzed the results of long-term studies on changes in the abundance of Laxmann's shrew in the foothill region of the Pechora-Ilych reserve in order to reveal periodicity in the population dynamics of the species and evaluate factors accounting for variation in its abundance. Since relevant publications on Laxmann's shrew are few in number, this study may contribute to insight into the problem at issue.

MATERIAL AND METHODS

The Laxmann's shrew (*Sorex caecutiens* Laxmann) is a widespread small mammal species in the foot hills of the Northern Urals, where it is second in abundance after the common shrew. Quantitative censuses of shrews were conducted in the Garevka ecosite located the upper reaches of the Pechora River (62°05′ N, 58°27′ E) in 1988 to 2018. The greater part of the study region (76%) is covered by polydominant dark taiga forests, which are characterized by well-developed moss layer due to sufficient moisture supply and proximity to mountain ridges of the Northern Urals. The connection of *S. caecutiens* with forest communities of taiga type is well known, and conditions in the study region are therefore favorable for this species.

Censuses of shrews were taken using trench traps and snap traps in the first half of August. Only the results of trapping in a green moss spruce forest (the most favorable habitat for the species) were included

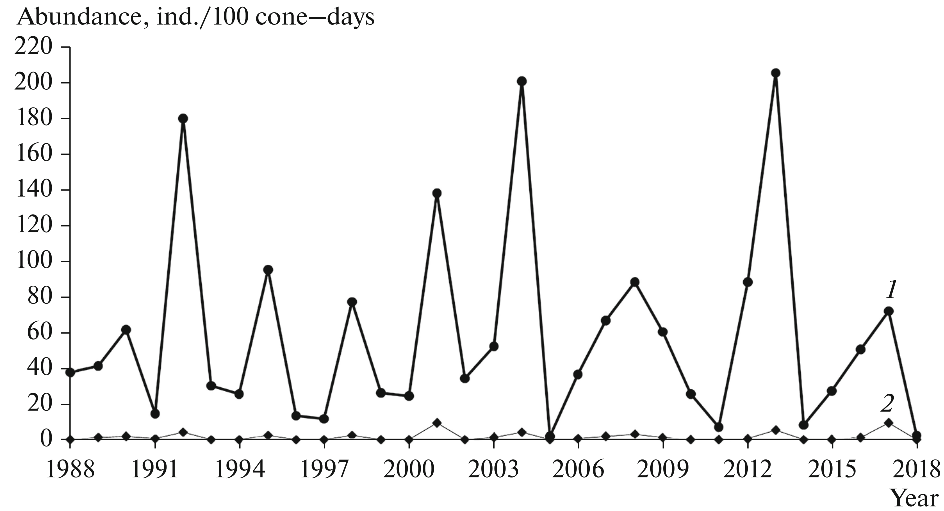

Fig. 1. Dynamics of *S. caecutiens* abundance in green moss spruce forest (the foothill region of Pechora-Ilych reserve) according to the results of catches with (*1*) trench traps and (*2*) snap traps.

in analysis, since data on animal abundance averaged over several different biotopes are usually an underestimate and provide a biased picture of species dynamics [19]. Trench traps 50 m long, with five cones in the bottom, were left open for 12–15 days; snap traps were set in lines at 5-m intervals (100 traps each) for 4 days; and the number of animals trapped per 100 cone–days or trap–days was calculated as a parameter of relative abundance. The total catch amounted to 1857 ind. over 3250 cone–days in trench traps and 163 ind. over 13 400 trap–days in snap traps, with the proportion of *S. caecutiens* among trapped small mammals being 25.7 and 8.2%, respectively.

To reveal and assess periodicity in the time series, the data on annual parameters of abundance were processed by the method of spectral analysis after preliminary conversion into logarithmic form, because the distribution of these parameters differed from normal (Kolmogorov–Smirnov test). The purpose was to resolve the time series into components (harmonics) with different amplitudes and frequencies. The most powerful of them, with distinct peaks at certain frequencies of the periodogram, were identified as periodic components. The dependence of animal abundance on different factors was estimated by Spearman's rank correlation test. Statistical data processing was performed using Statistica 6.0 for Windows.

RESULTS AND DISCUSSION

Chronographic Variability in the Abundance of S. caecutiens

During the observation period, the abundance of this species according to trench-trap censuses varied between years from 2.6 (2018) to 205.5 (2013) ind./100 cone–days; according to snap-trap censuses, from 0 to 9.3 ind./100 trap–days (2013). The shrews were often absent from snap-trap catches in years of population depression. The data on years with minimum and maximum abundance (population depression and peak) obtained by both methods generally coincided with each other (Fig. 1), especially in the case of maximum abundance. These population peaks were recorded in the second to fifth year after depression, most frequently on the third year.

Spectral analysis of trench-trap data revealed a statistically significant 3-year periodic component of variation in abundance, but this component proved to lack significance when snap-trap data were analyzed, since the recorded parameters of abundance were too low in this case (Fig. 2). However, the data obtained by both methods correlated with each other ($r = 0.82$, $p < 0.001$).

Periodic (cyclic) fluctuations with a 3-year period in the abundance of *S caecutiens* have been observed in the Upper Kolyma basin [5]. In Central Siberia, 4-year periodicity in the dynamics of many small mammal species changed in the late 1990s into chaotic fluctuations, which subsequently showed a tendency to occur with a 3-year period [4]. In the Pinega reserve (Arkhangelsk oblast), population peaks in shrews have been observed once in 3 years [20]. According to Erdakov et al. [6], the 3-year periodic component is well manifested in many populations of the common shrew, but its power is relatively low.

Effect of Weather Conditions and Other Factors on S. caecutiens Population Dynamics

Physiological features of shrews (small body size, high energy expenditures, etc.) make animals of this group highly dependent on weather conditions [21], which exert an effect on their life activities both directly (air temperature and precipitation) and indi-

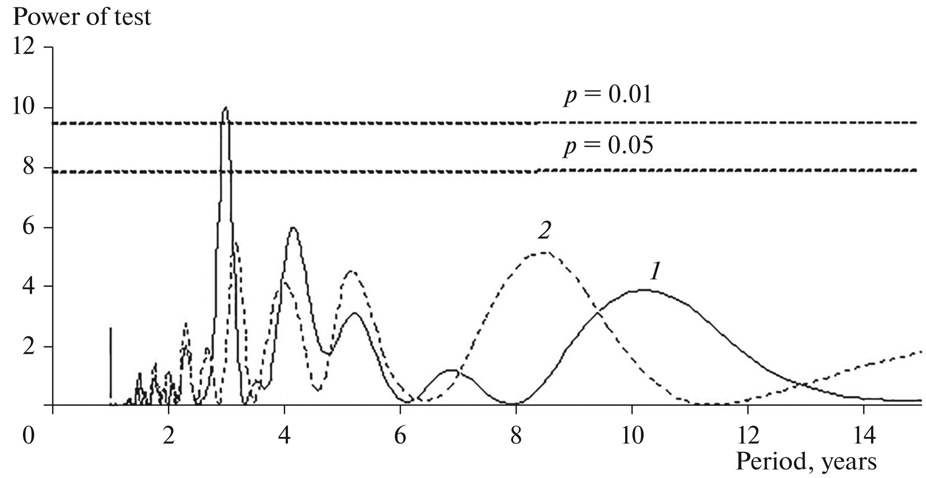

Fig. 2. Periodogram of variation in *S. caecutiens* abundance in the foothill region of Pechora-Ilych reserve according to the results of catches with (*1*) trench traps and (*2*) snap traps. Horizontal lines indicate significance levels.

rectly (through food availability). It is considered that this effect is more significant during the transition seasons of spring and autumn [3, 14, 15].

Therefore, the dependence of *S. caecutiens* on monthly average temperatures in spring and summer and on the amount of precipitation was analyzed in the first place. Corresponding correlation coefficient for the spring period proved to lack statistical significance (Table 1). The abundance of shrews showed a relatively weak but significant correlation only with air temperature in October of the previous year and in previous autumn as a whole: their survival at relatively high temperatures during these periods was higher than in other years. A positive correlation was also observed with precipitation in August of the current year, probably because food availability increases at higher moisture. The relationship between the abundance of shrews and the amount of precipitation has been noted in many regions [7, 18].

The number of climatic factors having a significant effect on the abundance of shrews may markedly vary between regions. As found for the common shrew [7, 22, 23], their number varied from 3 to 13 in different parts of the species range.

Winter conditions in the Pechora-Ilych reserve have no significant effect on shrews due to highly snowy winters in this region of European Russia. A deep snow cover (on average, 105 cm) is formed fairly early and prevents abrupt temperature shifts at the soil surface, which accounts for low winter morality of shrews. Therefore, their abundance in the Pechora-Ilych reserve is not correlated with snow depth (r = 0.18, p = 0.28), although such a correlation has been noted in other regions [15, 24].

Contradictory conclusions about the role of climatic factors may be drawn even for geographically close regions. Thus, according to Dokuchaev [12], winter conditions are the main factor regulating the abundance of *S. caecutiens* in northeastern Asia, while other authors consider that they have no significant effect on the population dynamics of this species in the region [5], and the same applies to the northern short-tailed shrew *Blarina brevicauda* in the northeast of North America, where climatic conditions are fairly severe [25].

However, climatic factors may have a differential effect on *S. caecutiens* populations at different phases of the cycle (Table 2): the number of such factors in the Pechora-Ilych reserve increases, and the values of correlation coefficients are high. Four factors have a statistically significant effect at the phase of population growth. The abundance of shrews is negatively correlated with air temperature in August of the previous year: the lower the temperature, the higher the abundance. Correlation with precipitation in July of the current year is also negative, with population

Table 1. Effects of different climatic factors on the abundance dynamics of *Sorex caecutiens*

Factor	Statistical parameters		
	r	*t*	*p*
Air temperature in April of current year	–0.04	0.21	>0.05
Air temperature in May of current year	–0.20	1.12	>0.05
Air temperature in October of previous year	+0.36	2.10	<0.05
Air temperature in previous autumn	+0.43	2.60	<0.01
Monthly precipitation in August of current year	+0.37	2.14	<0.05

Table 2. Effects of climatic factors on the abundance of *Sorex caecutiens* at different phases of population cycle

Factor	Statistical parameters		
	r	*t*	*p*
Depression phase			
Air temperature in October of previous year	–0.68	2.52	<0.05
Growth phase			
Air temperature in August of previous year	–0.70	2.59	<0.05
Monthly precipitation in July of current year	–0.75	3.00	<0.01
Monthly precipitation in November of previous year	+0.92	6.07	<0.01
Total precipitation in November and December of previous year	+0.73	2.95	<0.05
Decline phase			
Annual precipitation in current year	–0.80	2.82	<0.05

growth being retarded if precipitation is abundant. On the other hand, a large amount of precipitation (snow) in November and December of the previous year has a positive effect on population growth. The role of precipitation is also substantial at the phase of population decline.

Correlation with the onset of phenological stages is not manifested when the entire time series is analyzed, it is well detectable at different phases of the population cycle. At the peak phase, the date of snow cover melting in the forest has a significant effect: the earlier the date, the higher the abundance of shrews in the current year ($r = –0.66$; $p < 0.05$). The depth of population depression depends on the date of permanent snow cover formation in the previous year: the earlier this date, the higher the abundance parameters in the next year, with a delay in snow cover formation leading to deep population depression ($r = –0.60$; $p < 0.05$).

Interspecific interactions may also be a factor of species population dynamics. In eastern Fennoscandia, for example, the population size of *S. caecutiens* as a less competitive species increases only in the periods of low abundance of the common shrew [26]. The population dynamics of all common small mammal species in the Pechora-Ilych reserve are synchronous, and the coefficient of correlation between these closely related shrew species reaches 0.88 ($p < 0.001$). Therefore, interspecific competition has no significant effect on *S. caecutiens* population dynamics in the study region.

Role of Intrapopulation Factors in S. caecutiens Population Dynamics

Certain demographic parameters of *S. caecutiens* in the Northern Ural foothills show correlation with changes in population size. The proportion of overwintered shrews significantly increases during population depression and increases at the growth and peak phases ($r = –0.57$, $p < 0.001$). This is accompanied by considerable changes in the proportion of overwintered females, which is positively correlated with population size and increases when the abundance of shrews is high ($r = 0.51$; $p < 0.01$). Their proportion during depression varies from 0 to 50%, averaging 25.7 ± 6.2%, and that at the phase of population peak reaches 67.7 ± 6.7% (42.8–92.8%).

The average fecundity of overwintered females also varies depending on population size, with the embryonic litter size reaching 6.6 ± 0.3 embryos when the abundance of shrews and decreasing to 5.9 ± 0.3 embryos when their abundance is low.

A similar trend has been observed in our study on the common shrew in the foothill region of the Pechora-Ilych reserve [23]. Mechanisms of density-dependent regulation are the main factor responsible for periodic fluctuations in the abundance of shrews in the temperate zone of Russia [18]. They also play a certain role in the population dynamics of common and Laxmann's shrews in Tver oblast [14]. Significant differences in the average litter size depending on the level of animal abundance have been observed in several shrew species in the Baikal region [27]. It is considered that self-regulation mechanisms play the leading role in the population dynamics of Laxmann's shrew in the Upper Kolyma basin [5].

An effective mechanism of intrapopulation regulation is control over juvenile maturation rate and age at maturity. The involvement of young-of-the-year shrews in reproduction has been observed in certain regions [28], but its role in the north of European Russia is negligible [29]. Thus, the proportion of young of the year among reproductive *S. caecutiens* females in the Komi Republic varied between regions from 0.4 to 2% [23].

CONCLUSIONS

Analysis of fluctuations in the abundance of Laxmann's shrew in the Northern Ural foothills has revealed a statistically significant periodic (cyclic) component with a period of 3 years. In most cases, it is at such intervals that population peaks are observed in this species.

Weather conditions play a certain role in the population dynamics of Laxmann's shrew in the study region, with their effect being manifested more clearly in the periods of population growth, decline, and depression. The highest values are characteristic of correlation with the amount of precipitation in November and December of the previous year, which has an effect on the survival of shrews. Interspecific relationships do not affect the population dynamics of Laxmann's shrew: its abundance changes synchronously with that of other common species of shrews and voles.

A role in the population dynamics of the species is also observed for mechanisms of density-dependent regulation: the proportions of overwintered shrews and of adult females among them and also the average litter size vary depending on the level of animal abundance.

Thus, periodic fluctuations in the abundance of shrews in the Northern Ural foothills are a result of interaction between intrapopulation processes and variable environmental conditions.

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COMPLIANCE WITH ETHICAL STANDARDS

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest. The authors declare that they have no conflict of interest

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