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Impacts of Climate Warming on Terrestrial Species in the Middle Yenisei Taiga

B. I. Sheftel[a], * **and V. D. Yakushov**[a]

[a] *Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia*

**e-mail: borissheftel@yahoo.com*

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Abstract—This paper examines the relationship between climate warming and processes occurring in communities and populations of terrestrial small mammals, reptiles, amphibians, and arthropods. The studies have been conducted at Mirnoe Yenisei Ecological Station, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences. The dynamics of climatic changes is determined based on meteorological data collected at seven weather stations located along an almost 1000-km stretch of the Yenisei River valley. The maximum increase in temperature over the period from 1972 to 2020 is registered in the spring months; the farther north the station is located, the stronger these changes are manifested. In the 21st century, the cyclic type of small mammal population dynamics previously observed in the study area is replaced by the fluctuating dynamics type. The abundance of small mammals in the 21st century is lower than it was in the 20th century. Statistically significant decreases in population are noted mostly for species of Siberian origin. New species have been registered in the vicinity of the Yenisei ecological station for the first time. The bank vole (*Clethrionomys glareolus*) and the taiga tick (*Ixodes persulcatus*) have appeared on the right bank of the Yenisei River; the common toad (*Bufo bufo*) has appeared on both river banks.

Keywords: climate warming, small mammals, population dynamics, taiga tick, amphibians, reptiles

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INTRODUCTION

Over the past 60–70 years, significant climate warming has been noted in most regions of our planet. However, it occurs unevenly: process intensity in different regions differs by seasons (Sherstyukov, 2012) and depends on the latitude, relief, and airflow parameters in each specific location.

The impact of global warming on biota can be divided into two components: (1) impact on the species diversity in a given region and (2) impact on the ecological characteristics of communities, populations, and individual species. In the first case, the impact is usually limited to invasions of some species from more southern regions; such species enter the existing communities and gradually increase their numbers. Normally, this happens due to an increase in the ecological volume (resources) caused by climate warming (Sheftel et al., 2020). However, such invasions can subsequently result in the displacement of native species and their replacement by southern or generalist species (Ehrlich et al., 2020).

Changes in the nature of population dynamics represent a widespread effect of climate warming on terrestrial communities. In many boreal communities of butterflies, partridges, and small mammals, cyclical changes in numbers have disappeared (Ims et al., 2008) and were replaced by fluctuating (i.e., having no definite periodicity) changes (Zakharov et al., 2011; Sheftel, 2010).

Changes in the nature of population and community dynamics cause significant transformations in the functioning of boreal ecosystems, which, in turn, can change traditional economic activities and adversely affect human safety.

In recent years, an increase in the maximum values of the Normalized Difference Vegetation Index (NDVI) reflecting the amount of photosynthetically active biomass has been registered in the tundra zone (Bhatt et al., 2010; Epstein et al., 2012). This phenomenon, dubbed “tundra greening,” can be clearly seen in aerial photographs (Tishkov et al., 2016). Unfortunately, no such clear environmental indicator exists for another boreal zone: the taiga zone. Therefore, many processes occurring in it can only be assessed based on indirect indicators, for instance, changes in the dynamics of mammal numbers (Berteaux et al., 2006; Bierman et al., 2006; Saitoh et al., 2006) or the appearance of new species (e.g., ixodid ticks) (Shadrina et al., 2011; Yamborko et al., 2015).

This paper analyzes indirect indicators reflecting, we assume, global warming and manifested in small mammals, reptiles, amphibians, and ixodid ticks inhabiting middle taiga in the Yenisei River valley.

MATERIALS AND METHODS

This study uses data collected at Mirnoe Yenisei Ecological Station, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, located in the middle reaches of the Yenisei River (62°17′ N, 89°02′ E), middle Yenisei taiga subzone, Turukhansk district, Krasnoyarsk krai.

Climatic changes were analyzed using data on average monthly surface air temperatures collected from 1972 to 2020 at seven meteorological stations located in the Yenisei River valley. The most southerly station is located ≈240 km south of the ecological station; the northernmost one is ≈600 km north of it. The closest weather station is located in the village of Bakhta, 20 km north of Mirnoe. The data were obtained from public online databases: www.pogodaiklimat.ru, rp5.ru, and aisori-m.meteo.ru/waisori. The interval from 1972 to 1990 was used as the reference period to compute climatological norms. Temperature anomalies were computed as the difference between the average annual air temperature in a certain year and the climatological norm for the selected reference period (*WMO*, 2017).

All calculations were performed in the PAST software (Hammer et al., 2001). To identify the presence of a trend, the nonparametric Mann–Kendall test for the trend was used (Gilbert, 1987). The linear trend coefficient determined using the least square method and reflecting the average rate of change in the climate variable corresponding to the trend was used as a climate change intensity measure (Glantz, 1998).

Small mammal censuses were performed using catching ditches. Catching ditches 20-m-long with two catching cylinders were used in accordance with the methodology proposed by A.P. Kuzyakin (1962). The cylinders were located 5 m from the ends of the ditches. The ditches covered most of the habitats within a 3-km radius of the biological station. Catching fences were used in waterlogged habitats instead of ditches (Okhotina and Kostenko, 1974; Sheftel, 2018). From 1973 to 1993, animals were caught nearly throughout the entire summer season; since 1994, they have been caught only for 10 days at the end of June and 10 days at the end of August. The studies were interrupted in 1995 and resumed in 2007. Long-time catches with ditches do not disturb the structure of the sedentary small mammal population, since they catch mostly migratory individuals (Bolshakov et al., 1973; Sheftel, 2018).

A comparative analysis of the state of the small mammal community and populations was performed on the basis of two parameters. First, changes in the nature of the population dynamics of red-toothed shrews were analyzed. The populations dynamics in the 20th century (1976–1984) was compared to that in the 21st century (2007–2020). Second, the abundance level computed for the entire small mammal community was compared with abundance levels of individual species constituting it.

The periodicity of changes in small mammal numbers was estimated using autocorrelation analysis, which determines the correlation degree between two series: (1) the studied time series and (2) the same series shifted by L time steps (L is the shift value called "lag"). The totality of correlation coefficients form a correlation function whose graph can be analyzed visually: peaks corresponding to a given lag indicate a greater or lesser closeness of agreement between the series and itself, the presence/absence of periodicity in changes in the studied values, and the repeatability of values at regular intervals (Korosov, 2007).

The abundance series produced for the entire small mammal community and for its individual species do not fully conform to the normal distribution; therefore, the Mann–Whitney nonparametric test was used to compare the levels of this parameter in the 20th and 21st centuries (Glantz, 1998).

No special herpetological studies were carried out at the Yenisei ecological station, and all information about the presence or absence of certain species is based on accidental encounters or their entrapments in catching cylinders intended for small mammals. In total, three amphibian species and one reptile species were registered in the vicinity of the station. In addition, this study analyzes the distribution of the common European viper (*Vipera berus* Linnaeus, 1758): this species has not yet been registered at the Yenisei ecological station; however, its expansion to the north within the middle taiga subzone was noted.

Many invertebrate species change their distribution ranges under the impact of global warming, but this paper only examines the situation with the taiga tick (*Ixodes persulcatus* Schulze, 1930), a species of great practical importance, since it contributes to the spread of such human diseases as tick-borne encephalitis and borreliosis. Data on the distribution of the taiga tick were collected on the basis of visual observations and interviews with the local population. We intend to conduct a detailed study of the taiga tick biotopic distribution and its preimagial phases in the near future.

RESULTS

An analysis of meteorological data collected at the selected stations made it possible to identify a statistically significant upward trend in average annual surface air temperature anomalies; this pattern is manifested especially clearly in spring and summer. With rare exceptions, no upward or downward temperature trends are observed in autumn and winter (Table 1). A temperature anomaly is the difference between the average annual air temperature in a given year and the

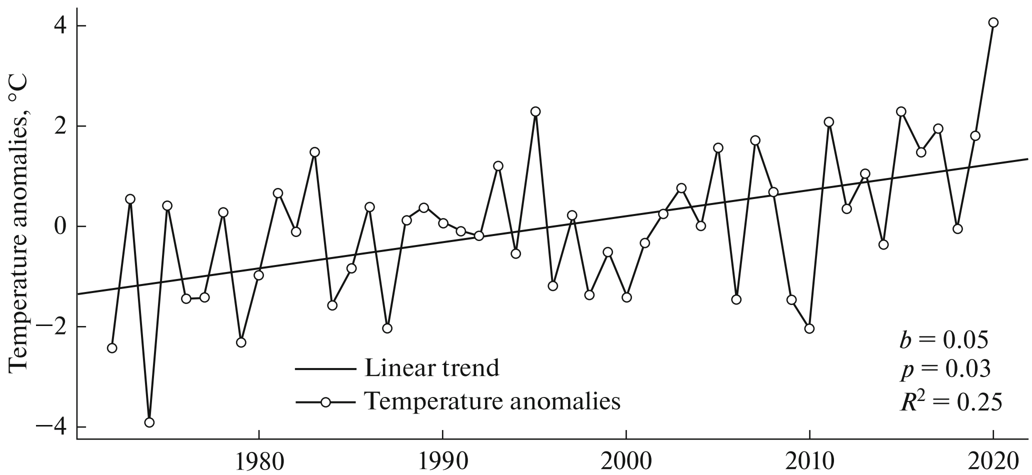

Fig. 1. Time series of spatially averaged average annual surface air temperature anomalies based on the data collected at seven Yenisei weather stations (from the village of Yartsevo in the south to the town of Igarka in the north) in 1972–2020. (*b*) Coefficient of the linear trend in temperature anomalies (°C/10 years); (*p*) upward trend significance level (Mann–Kendall test for trend).

climatological norm for a selected reference period (*WMO*, 2017).

For instance, the average rate of change in average annual temperature anomalies (the *b* coefficient) at the meteorological station located in the village of Bakhta (20 km north of the ecological station) was 0.05°C/10 years. In spring, this trend is manifested more strongly ($b = 0.1$°C/10 years). In the last decade (2010–2020), the average spring temperature is higher than that in the reference period ($\Delta = 3.6$°C). It is noteworthy that the farther north the meteorological station is located, the stronger the increase in temperatures is manifested (Table 1).

Average annual surface air temperature anomalies registered at all seven meteorological stations selected for analysis strongly correlate with each other (the correlation coefficient $r = 0.88$–0.99 at $p < 0.002$ taking into account the Bonferroni correction for multiple hypothesis testing). This makes it possible to estimate the general climatic trend in a given area using spatial averaging (Fig. 1 shows a graph of average temperature anomalies built for all weather stations selected for analysis). Overall, the average rate of temperature increase in a section of the Yenisei River valley stretching from the village of Yartsevo to the town of Igarka in 1972–2020 was 0.05°C/10 years; on average, the last decade is warmer than the reference period (1972–1990) by 1.8°C.

In total, 20 small mammal species were registered in the course of the censuses: 10 insectivores; 9 rodents; and 1 lagomorph species, Turuchan pika (*Ochotona turuchanensis* Naumov, 1934). The list provided in Table 2 consists of only 18 species since it does not include the rarest ones: the Turuchan pika and the harvest mouse (*Micromys minutus* Pallas, 1771).

Table 1. Estimates of the linear trend in average annual and seasonal surface air temperature anomalies for 1972–2020. The weather stations are arranged in order of descending latitude

Station	Year		Spring		Summer		Autumn		Winter	
	b	Δ	*b*	Δ	*b*	Δ	*b*	Δ	*b*	Δ
Igarka	**0.06**	2.1	**0.1**	4	**0.04**	1.2	0.04	1.2	0.05	1.2
Turukhansk	**0.06**	2.1	**0.1**	4.1	**0.04**	1.3	**0.04**	1.2	**0.05**	1.9
Verkhneimbatsk	**0.05**	1.9	**0.1**	3.7	**0.03**	1.1	0.03	0.8	0.05	1.9
Bakhta	**0.05**	1.8	**0.1**	3.6	**0.03**	1.2	0.01	0.4	**0.06**	2
Bor	**0.05**	1.8	**0.09**	3.3	**0.03**	1.1	0.02	0.7	0.06	1.9
Vorogovo	**0.05**	1.5	**0.09**	3.1	**0.03**	0.9	0.02	0.7	0.05	1.4
Yartsevo	**0.04**	1.4	**0.09**	3	**0.02**	0.8	0.02	0.5	0.05	1.4

b is the coefficient of the linear trend in temperature anomalies (°C/10 years) that reflects the average rate of change in the climate variable corresponding to the trend. Statistically significant ($p < 0.05$) trends are given in **bold**; Δ is the difference between the average temperature (°C) of the last decade (2010–2020) and the average temperature of the reference period.

Table 2. Comparison of small mammal numbers in the 20th and 21st centuries

Species	*Sorex araneus* Linnaues, 1758		***S. caecutiens* Laxmann, 1788**		*S. minutus* Linnaeus, 1766		*S. isodon* Turov, 1924		*S. roboratus* Holister, 1913	
Century	20th	21st	20th	21st	20th	21st	20th	21st	20th	21st
mean	47.4	35.8	**33.9**	**18.8**	5.4	5.5	10.2	8.4	1.9	2.2
sd	28.9	26.8	**19.7**	**16.4**	3.0	4.3	9.3	13.2	1.5	2.3
max	115.3	96.0	**64.5**	**69.8**	10.8	15.4	34.3	50.5	6.5	8.9
min	7.8	2.0	**5.2**	**4.3**	1.2	0.8	1.2	0.4	0.0	0.0
md	42.2	26.6	**33.8**	**11.6**	4.8	4.5	6.7	3.2	1.3	1.4
Species	***S. tundrensis* Merriam, 1900**		***S. minutissimus* Zimmermann, 1780**		***S. daphaenodon* Thomas, 1907**		*Neomys fodiens* Pennant, 1771		*Talpa altaica* Nikolsky, 1883	
Century	**20th**	**21st**	**20th**	**21st**	**20th**	**21st**	20th	21st	20th	21st
mean	**7.4**	**3.7**	**0.9**	**0.4**	**0.3**	**0.0**	0.7	0.3	1.1	1.4
sd	**4.4**	**5.8**	**0.6**	**0.2**	**0.3**	**0.1**	0.8	0.4	1.1	1.2
max	**16.7**	**19.0**	**2.2**	**0.9**	**1.2**	**0.3**	2.5	1.3	3.7	3.6
min	**1.3**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	0.0	0.0	0.0	0.0
md	**5.3**	**1.0**	**0.9**	**0.4**	**0.2**	**0.0**	0.4	0.1	0.8	0.9
Species	*Clethrionomys rutilus* Pallas, 1779		*C. glareolus* Schreber, 1780		***C. rufocanus* Sundevall, 1846**		*Microtus agrestis* Linnaeus, 1761		*M. oeconomus* Pallas, 1776	
Century	20th	21st	20th	21st	**20th**	**21st**	20th	21st	20th	21st
mean	18.2	13.6	0.3	0.2	**20.7**	**2.8**	3.7	1.5	9.1	8.5
sd	13.4	8.8	0.5	0.4	**21.6**	**1.9**	5.0	1.4	10.3	9.8
max	53.2	32.7	2.0	1.6	**81.0**	**8.2**	17.7	5.5	42.5	38.1
min	3.5	2.3	0.0	0.0	**2.7**	**0.4**	0.2	0.0	1.3	1.0
md	16.6	12.5	0.2	0.0	**10.4**	**2.3**	1.0	1.1	5.7	5.1
Species	*Myopus schisticolor* Lilljeborg, 1844		*Arvicola terrestris* Linnaeus, 1758		***Sicista betulina* Pallas, 1779**		**Total abundance**			
Century	20th	21st	20th	21st	**20th**	**21st**	**20th**		**21st**	
mean	5.9	1.6	0.3	0.0	**6.8**	**2.5**	**175.2**		**107.8**	
sd	10.3	2.0	0.3	0.1	**3.0**	**1.3**	**91.2**		**72.5**	
max	41.0	8.0	0.8	0.4	**12.7**	**4.8**	**376.2**		**280.1**	
min	0.0	0.0	0.0	0.0	**2.0**	**0.4**	**44.2**		**37.5**	
md	2.3	1.2	0.3	0.0	**6.1**	**2.7**	**150.6**		**86.6**	

Mean is the mean value; sd is the standard deviation. The abundance series produced for the entire small mammal community and for individual species do not fully conform to the normal distribution; therefore, the following indicators are more informative: max (the maximum value), min (the minimum value), and md (the median). Species featuring statistically significant decreases in population are given in **bold** (Mann–Whitney test; the p-level of significance is <0.05).

In the 20th century, the dynamics of small mammal numbers was clearly cyclical (Sheftel, 1989). There was a peak in numbers every 4 years, followed by a major depression in the next year. The depression was followed by a year of population growth. The next year was a prepeak one: the population is close to the peak value, but usually does not reach it. Over the years of research, 5 population abundance cycles were observed. It must be noted that a similar dynamics type was noted for most small mammal species, both insectivores and rodents, with medium or high abundance levels. In addition, this dynamics was synchronous on both banks of the Yenisei River. For most species with low abundance levels, it can only be said that

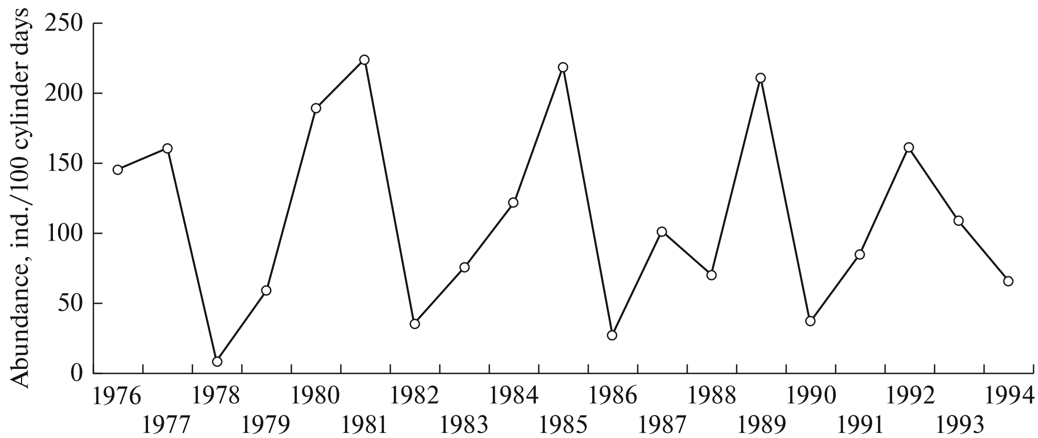

Fig. 2. Dynamics of small mammal numbers in the 20th century.

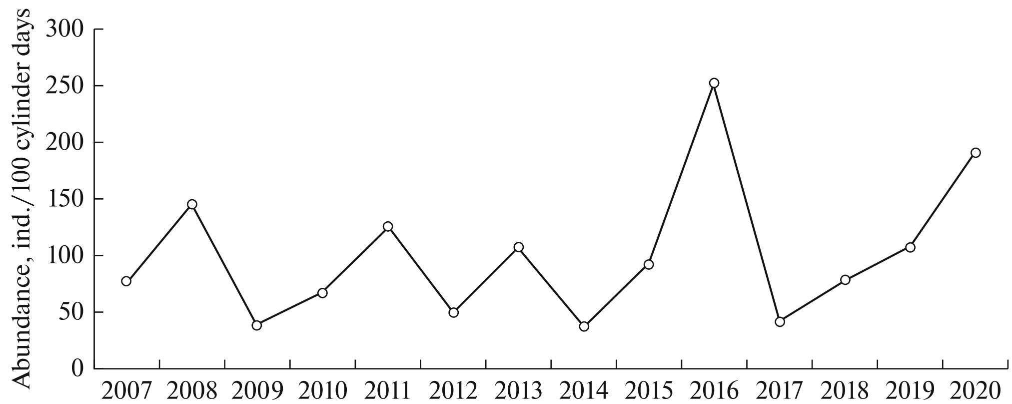

Fig. 3. Dynamics of small mammal numbers in the 21st century.

their dynamics demonstrate a similar trend. Figure 2 shows changes in the total numbers of all shrew species in the course of their cyclical fluctuations.

After the resumption of our studies in 2007, it turned out that the 4-year cycle no longer exists (Zakharov et al., 2011). The numbers change from year to year; sometimes it is possible to distinguish something reminiscent of 3-year cycles and sometimes the dynamics resembles a 'comb': increases in numbers alternate with decreases. Figure 3 shows changes in the population dynamics of the shrew community over the 13 years of research (from 2007 to 2019).

Autocorrelation analysis indicates the presence of a statistically significant 4-year period in the 20th century (correlation coefficient $r = 0.7$; p-level of significance = 0.0009) and the absence of a fluctuation periodicity in the 21st century (Figs. 4–5) (Yakushov and Sheftel, 2020).

A comparison of small mammal numbers in the 20th and 21st centuries shows a significant decrease in their abundance (Table 2).

The abundance of the following species has decreased statistically significantly: masked shrew (*S. caecutiens*), tundra shrew (*S. tundrensis*), Siberian large-toothed shrew (*S. daphaenodon*), Eurasian least shrew (*S. minutissimus*), grey red-backed vole (*Clethrionomys rufocanus = Myodes rufocanus*), and northern birch mouse (*Sicista betulina*).

The species composition of mammals has not undergone significant changes over the study period. The exception is the bank vole (*Clethrionomys glareolus = Myodes glareolus*): it was registered on the right bank of the Yenisei River for the first time. In 1976, this species was found on the left bank of the Yenisei River and has been encountered since then on a regular basis exclusively in the low willow–meadow floodplain (Shvarts et al., 1987). In 2017, the species was found for the first time on the right bank of the Yenisei River: one individual was caught in the low meadow floodplain. Another individual was registered in 2018 in an abandoned vegetable garden. In 2019, nine individuals were encountered on the right bank of the Yenisei River (one in the taiga, two in the low flood-

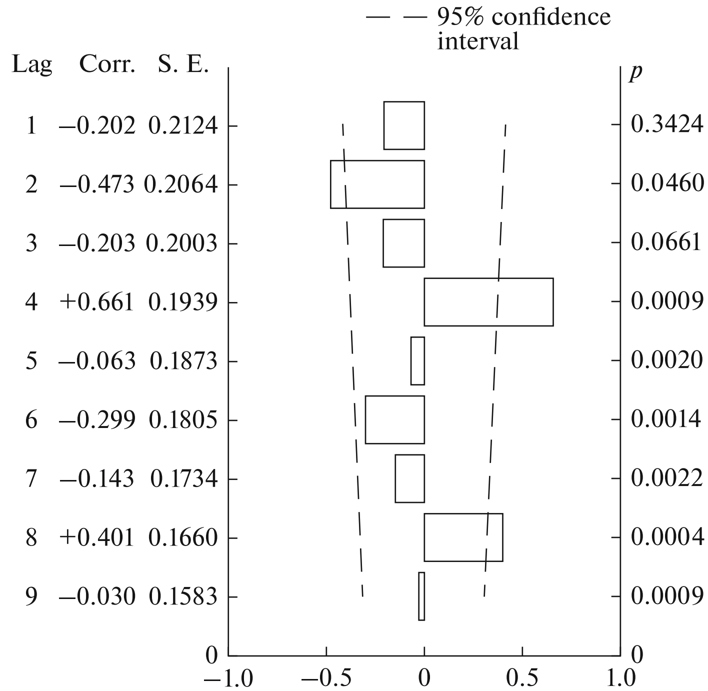

Fig. 4. Autocorrelogram of changes in small mammal community numbers in the 20th century. Lag is the value of the time series shift relative to itself, Corr. is the correlation coefficient, S.E. is the standard error of the correlation coefficient, and *p* is the significance level. A peak extension beyond the 95% confidence interval indicates a statistically significant period value.

plain, and six in abandoned vegetable gardens). In 2020, amid a high total abundance of small mammals, the bank vole expanded to residential buildings. That year, ten animals were caught in houses; all of them turned out to be bank voles and only three individuals were caught in natural biotopes.

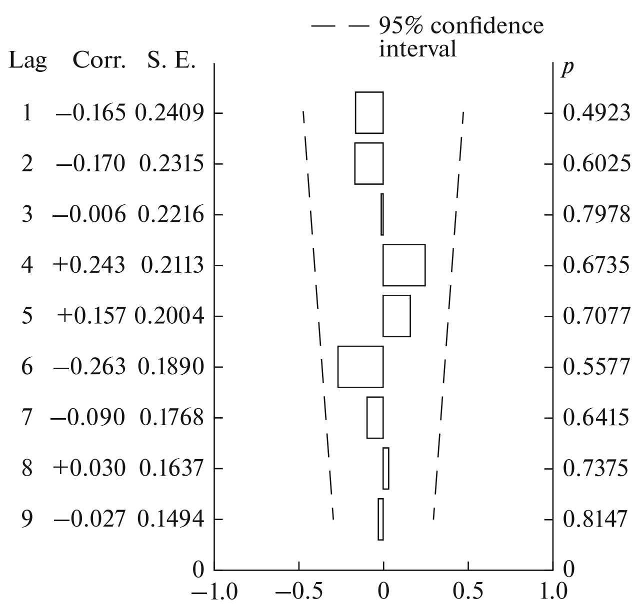

Fig. 5. Autocorrelogram of changes in small mammal community numbers in the 21st century. Lag is the value of the time series shift relative to itself, Corr. is the correlation coefficient, S.E. is the standard error of the correlation coefficient, and *p* is the significance level. Unlike the 20th century, no clear periodicity can be distinguished.

The common toad (*Bufo bufo* Linnaeus, 1758) was first discovered in Mirnoe in 2018. Two adults were caught in catching cylinders used for small mammal censuses; one of them was caught on the left bank of the Yenisei River in a spruce forest on the first terrace. The second one was caught on the right bank of the Yenisei River on the border between a hayfield upland anthropogenic meadow and taiga. In 1988, the common toad was abundant in Yeloguyskii Federal Game Reserve (61°52′ N, 86°02′ E) located some 150 km west of the Yenisei River.

The common European viper (*Vipera berus*) was never registered in the vicinity of the ecological station. However, in August 2017, two individuals of this species were found in willow stands on the right bank of the Yenisei River 200 m above the Podkamennaya Tunguska River mouth (61°35′ N, 90°08′ E). A very large individual with a typical color, apparently a female, and a small black individual, apparently a male, were lying together on a log and basking in the sun. According to our data, the place where these individuals were registered is also located northward of the border of their previously known distribution range. Similar to the common toad, the common European viper was encountered in 1988 in Yeloguyskii Federal Game Reserve (61°52′ N, 86°02′ E), some 150 km west of the Yenisei River.

The last of the species analyzed in this study, the taiga tick, has also significantly expanded its range. Back in the 1970s, the northern border of its distribution range was located 200 km south of Mirnoe Ecological Station, in the vicinity of the village of Vorogovo. In 2001, the first tick bite of a human was recorded at the ecological station. Currently, ticks are common mostly on the border of a hayfield upland anthropogenic meadow on the right bank of the Yenisei River. In June, after a 1-km walk across the hayfield meadow, a person is attacked by four or five taiga ticks. It is known that taiga ticks now attack humans in the township of Verkhneimbatsk, 120 km north of Mirnoe.

DISCUSSION

This study analyzes the general nature of climatic changes that occur on the Yenisei River on the basis of a single factor: surface air temperatures. Changes that have presumably occurred due to climate change at such levels as communities, populations, and individual terrestrial species are described.

We have shown that, according to the data collected at seven meteorological stations located in the Yenisei River valley, the maximum warming occurs in spring. This is consistent with data obtained by B.G. Sherstyukov (2012), who has shown that the maximum warming was recorded in Central Siberia specifically in spring; in other seasons, warming was either insignificant or cooling was even registered. According to our data, climate warming occurs in other seasons (e.g., in winter) as well, although not as much as in spring. The differences between the literature data and our data can be explained by the fact that the time series analyzed by B.G. Sherstyukov ends in 2011, while the most significant climatic changes were registered in the last 10 years.

It must be noted that a significant warming that occurs specifically in spring can extend the growing season; this is important both for communities and individual species, especially in northern conditions. The second important observation is that the warming rate is higher at higher latitudes (Table 1). This circumstance definitely contributes to the successful expansion of southern species to the north.

The disappearance of 4-year cyclical changes was registered in many boreal regions of Fennoscandia (Hörnfeldt et al., 2005), in Scotland (Lambin et al., 2006), in Greenland (Gilg et al., 2009), and in Japan on the Island of Hokkaido (Saitoh et al., 2006). The reasons behind this phenomenon are not fully understood; it is only certain that the observed increase in temperature or some side effects associated with this process disturb the cyclical changes in numbers at a global level (Oli, 2019). However, it must not be forgotten that cyclical fluctuations themselves remain the main environmental secret, the mystery of the last century (Myers, 2018). Generally speaking, we share the views of the above authors and will refrain from hypothesizing about factors causing cyclical changing and triggering their disappearance.

One interesting fact is that, in most of the above-mentioned regions, cyclical changes disappeared in the 1980s, while this happened later at the Mirnoe ecological station, presumably, on the cusp of the two centuries. The reason behind the later disappearance of cyclical fluctuations in Siberia in comparison with other regions is not yet clear. According to B.G. Sherstyukov (2012), climate warming in the studied region was not as intense as, for instance, in Fennoscandia; therefore, it can be assumed that this factor delayed the processes that have ultimately disrupted the cyclical changes in numbers.

The decline in the total abundance of small mammals and in numbers of individual species in the 21st century is of special interest. In theory, the increased duration of the growing season could enhance ecosystem productivity and, consequently, result in an increase in the numbers of small mammals. However, this did not happen. Presumably, the reason may be as follows: cyclical fluctuations are characterized by peaks in numbers registered on a regular basis; such peaks occur much less frequently if fluctuations are noncyclical; as a result, the overall abundance level in the course of a noncyclical dynamics is lower. On the other hand, the numbers of species inhabiting boreal forests or the Siberian region have statistically significantly decreased. These species include the masked, Eurasian least, tundra, and Siberian large-toothed shrews and the grey red-backed vole; the only species of European origin whose numbers have decreased is the northern birch mouse (Baskevich et al., 2020). However, there is still no definitive answer to the following question: what is the global warming effect on the small mammal community and individual species constituting it? Perhaps it will be resolved in subsequent studies.

At present, there is only one invasive species from the southern regions of Central Siberia who has entered the local mammal community. On the right bank of the Yenisei River, the bank vole was previously found in the vicinity of the village of Osinovo (61°26′ N, 89°56′ E) (Rossolimo and Syroechkovsky, 1961). An analysis of the species distribution in the northern part of its range shows its tendency to settlements (Shvarts et al., 1987). The penetration of the bank vole into residential premises of the Mirnoe ecological station is obviously associated with the absence of a typical synanthropic species, the house mouse (*Mus musculus*), there. It must not be forgotten though that the bank vole is the main circulator of the Puumala hantavirus, which causes one of the most dangerous variants of hemorrhagic fever with renal syndrome (HFRS) (Vapalahti et al., 2003). Therefore, the invasion of this species to the north, combined with its active penetration into residential buildings, can contribute to the formation of new disease foci and objectively threatens the health of the local population. The relatively small number of invasive species among small mammals can be explained by two reasons: the expansion of these species is limited by their relatively low movement speed in space and by the saturation of the existing small mammal community, which makes it difficult for competing species to penetrate into it.

Detailed descriptions of common toad distribution ranges are provided by S.L. Kuzmin in two editions of the atlas *Amphibians of the Former Soviet Union* (Kuzmin, 1999, 2012). In the first edition, the northern border of the common toad range on the Yenisei River passes in the vicinity of the village of Vorogovo (southern periphery of middle taiga); in the second edition, encounters with this species along the Yenisei River are noted throughout the entire middle taiga zone, and one species occurrence location is in the vicinity of the border between northern taiga and forest–tundra. This indicates that the common toad is intensively spreading to the north; it cannot be ruled out that the presence of the Yenisei River contributes to this. Nevertheless, first reliable encounters of the species in the vicinity of the Mirnoe ecological station were registered in 2018. Similar to the common toad, the northern border of the common European viper range passes in the vicinity of the village of Vorogovo (website of the Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences: www.sevin.ru/natreserves); therefore, the encounter of this species near the Podkamennaya Tunguska River mouth indicates its expansion to the north.

The expansion of the taiga tick to the north has previously been noted in many regions of Russia, including the Republic of Karelia (Bugmyrin et al., 2013), the Komi Republic (Glushakova et al., 2011), the Republic of Sakha (Yakutia) (Shadrina et al., 2011), and Arkhangelsk (Kotsov et al., 2010) and Magadan (Yamborko et al., 2015) oblasts. Extremely northern encounters of the taiga tick have been registered in Krasnoyarsk krai as well (for instance, in the vicinity of Turukhansk (66° N) and even in the Taymyr Peninsula (north of the 72nd parallel) (Khazova, 2007)). It must be noted though that single encounters of taiga ticks cannot indicate an expansion of the species distribution range, since many of them are results of accidental drifts (Korenberg, 2009). However, the fact that taiga ticks have been found in the same place on a regular basis for at least 15 years suggests the existence of a stable local population of this species in the vicinity of the Mirnoe ecological station. Unfortunately, no studies of the distribution of its larvae and nymphs have been conducted yet; such data are required to find out whether the local taiga tick population is stable or not. Most researchers agree that birds who spend a lot of time on the ground (e.g., blackbirds, pipits, and yellowhammers) contribute to the spread of ticks. Our data support this opinion. In the vicinity of Mirnoe, the main tick distribution focus is located on the right bank of the Yenisei River on small sites occupied by young forests that have been restored on the periphery of a hayfield meadow; no ticks have been found so far on the left bank. By contrast, in the vicinity of the nearby village of Bakhta located 20 km north of Mirnoe, ticks are present on the left bank of the Yenisei River in overgrown hayfield meadows. Such a territorial distribution cannot be explained by the terrestrial expansion of ticks; it implies the involvement of birds in this process. Birds have been flying south to north for a long time and could have transported ticks on themselves. Ticks found on birds usually are at preimagial development stages (mainly nymphs). Apparently, climate warming and earlier springs contribute to the successful molting of ticks from nymphs to imagoes, which has resulted in the formation of a local taiga tick population.

CONCLUSIONS

Significant climate warming is observed in Yenisei taiga. Based on the meteorological data collected at seven weather stations covering an almost 1000-km stretch of the Yenisei River valley, the most intense warming is registered in spring; the farther north the station is located, the higher the warming rate is. Similar to many other Holarctic regions, cyclical small mammal population waves have been replaced in Central Siberia by noncyclical fluctuations. In the 21st century, the abundance of small mammals has decreased in comparison with the 20th century; statistically significant decreases in population were noted mostly for species of Siberian origin. New species have been registered in the study area for the first time: the bank vole and the taiga tick appeared on the right bank of the Yenisei River, while the common toad appeared on both river banks.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflicts of interest.

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

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