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# Recent climate change has increased forest winter bird densities in East Europe

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**Abstract** Recent studies on climate change have reported serious impacts on winter forest birds in Western Europe. However, in areas where climate change has caused milder winters and more stable conditions in summer, one would expect resident bird populations to increase, rather than to decrease in winter. The aim of this study was to investigate the impact of climate change on the population dynamics of ten species of Passeriformes in the Tatarstan Republic, Russia. Ravkin's transect method was used to census fixed randomly selected plots spread over a large geographic area at least once every month for the past 26 years. Observers remained the same over the whole period. The abundance of nine species in the first half of the winter and four species in the second half of the winter showed significant increases during the study period. Unlike studies from countries in Western Europe, there were no significant decreases in these species. Significant changes in winter conditions, as well as during the breeding season, and an overall increase in annual temperatures are likely reasons for a significant increase in the number of birds in winter. Greater winter survival, an increase in the survival rate of fledglings and juveniles during the summer, and later onset of winter, are very important determinants of the winter population. Our findings show that numbers of birds in late winter are related to the severity of winter conditions. Our data do not support conclusions that the populations of forest bird species have decreased due to climate change.

**Keywords** Climate change · Winter bird monitoring · Long-term number dynamic · Tatarstan republic · Russia

## Introduction

The climate in Europe has undergone rapid change, with the large observed changes occurring during summer and winter (IPCC 2014). Significant climate changes in different seasons have been observed in the majority of Russian regions (Gruza et al. 2016). Since the 1960s, the climate in the Eastern edge of Europe has undergone rapid change. Annual summer and winter temperature trends remain strongly positive. In this part of Russia, climate change has been more rapid than in other parts of Europe, even in zones close to the Gulf Stream. Climate changes are known to have a serious impact on avian population parameters and in different seasons (Askeyev and Askeyev 2002; Visser et al. 2003, 2006; Both et al. 2009; Wesolowski and Cholewa 2009; Askeyev et al. 2010; Sokolov 2010; Saino et al. 2011; Thackeray et al. 2016; Källander et al. 2017).

Winter is the critical season in the life of most living organisms inhabiting temperate and boreal latitudes. An important demographic factor in the dynamics of bird populations in these latitudes is winter survival, which is influenced strongly by the prevailing temperature. By the end of the 20th century, traditional winters characterized by long periods of snow and temperatures well below zero were no longer prevalent in most countries in Europe. Even in Russia, winters have become markedly milder. However, in our view, the role played by increased winter temperature on the long-term changes in the dynamics of bird abundance is still poorly known. It is very important to know the combination of factors influencing long-term trends in the numbers of birds.

Only a study of the effects of changes in the temperature regime during the periods preceding winter can show a holistic picture of these influences on bird populations (Askeyev et al. 2017a). Many researchers are inclined to believe that global climate change has decreased the abundance of birds over the past few decades (Saino et al. 2011; Lehikoinen et al. 2014; Tayleur et al. 2016), while others are of the opinion that the general

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warming of the climate has contributed to an increase in the abundance of passerines (Sokolov 2010). Traditionally, it is believed that wintering species are well adapted to survive in severe winter conditions. But winter survival of different species varies greatly (Hilden 1982; Hildén and Väisänen 1991; Hogstad 1984, 2009, 2015) and this can lead to decreased or increased bird numbers in subsequent breeding seasons (Greenwood and Baillie 1991; Newton 1998). Climate change effects during the breeding season can lead to increased or decreased numbers of birds in autumn and the start of the winter period (Sokolov et al. 2000; Sokolov 2007). Furthermore, recent research suggests that gene flow in Great Tits *Parus major* may be regulated by environmental factors via movements related to the severity of the winter (Lemoine et al. 2016). However, long-term changes in bird numbers in the period after the breeding season have rarely been examined over large geographic areas.

It should be noted that many scientists attribute anthropogenically-related factors to changes in the number of birds in winter (Eglington and Pearce-Higgins 2012; Fraixedas et al. 2015). The range of different viewpoints raises difficult questions. Fortunately, long-term monitoring of winter bird populations over a large area can help to answer these questions, and such schemes have successfully operated for many years in Europe and North America. However, the study of population dynamics of birds during winter is often limited to a short period (e.g. Christmas counts). Furthermore, in studies conducted in Finland (Fraixedas et al. 2015; Lehikoinen et al. 2016), Sweden (Green et al. 2016), Denmark (Heldbjerg et al. 2013), Netherlands (Boele et al. 2008; Lehikoinen et al. 2016) and the USA (Prince and Zuckerberg 2015) data are collected by a large number of volunteers using standardised counting methods, which have some limitations. Most of the surveys are carried out in settlements and surrounding areas, in places of increased feeding of birds. Often without calculation the birds to the square that can be occupied by different habitats.

In this paper, we aim to investigate effects of climate on the long-term trends of wintering bird populations in the eastern edge of Europe (Tatarstan Republic). Our research is an analysis of the winter densities of 10 largely sedentary bird species. Unlike the studies mentioned above, we use data collected over the whole winter period.

Based on this background, we hypothesize that the population dynamics of the studied birds in winter depend largely on climatic factors. From this hypothesis, we make three predictions in relation to birds in East Europe: (i) that current climate change leads to growth rather than reductions of populations of winter birds, (ii) because winter bird abundance respond to temperature, we predict that in mild winters bird abundance in the second part of winter will be higher and (iii) that population trends in Eastern Europe, including Tatarstan, will differ from those in Western and Northern Europe.

## Methods

### Study area and environment

The Tatarstan Republic is located in the extreme East of Europe and lies within 53.58–56.40°N and 47.50–54.00°E. Traditionally, this area is considered to be in the historical–geographical provinces of European Russia—the Middle Volga and PreUral region. This region covers c. 68,000 km<sup>2</sup>, and includes two natural zones—forest and forest-steppe with various habitats (sub-taiga coniferous deciduous mixed forests, broad-leaved woodland, farmland, steppe landscapes, rivers, lakes, towns and villages). The southern borders of the distributions of Siberian spruce (*Picea obovata*) and Norway spruce (*Picea abies*) and the south-western border of the Siberian fir (*Abies sibirica*) distribution pass along this territory. In addition, the territory of the republic is close to the northern border of continuous forest with pedunculate oak (*Quercus robur*). The presence of these habitats and because the steppe zone is located immediately south of the republic, creates favorable conditions for winter occupancy by many forest bird species. Forest covers c.20% of the area and the relief is mostly flat or undulating lowland with hills (53–382 m a.s.l). The continental climate of the region is typical of Eastern Europe. The average annual temperature is c. 2 to 5 °C and monthly mean temperatures range from – 12 to – 14 °C in January to 19 to 21 °C in July. The lowest temperature recorded in the last 200 years was – 52 °C, and the maximum 40 °C. Average annual precipitation is c. 500–550 mm and snow cover (average to March 50–100 cm) lasts for 140–170 days. In each of the past 26 winters, there have been days with temperatures below – 25 °C. The maximum number of such days (20) was observed in the winter of 2005–2006. The minimum temperature noted during the study period was – 38.8 °C in winter 2002–2003.

### Bird numbers data

Twenty-six years of data on winter bird abundance (from 1 November to 5 March) were analysed. Fieldwork was carried out in the morning according to Y. S. Ravkin's transect methods (Ravkin 1967) without a fixed strip width with subsequent conversion to the area using group mean detection ranges. Counts were used to estimate numbers per km<sup>2</sup>, based on the mean detection distances, by the formula:

$$D = \sum \frac{40a + 10b + 3c}{Nkm}$$

where  $D$  = the number of individuals per km<sup>2</sup>,  $a$  = the number of individuals discovered at a short distance from the observer (up to 25 m),  $b$  = the number of individuals in the middle distance (25–100 m), and  $c$  = the number of individuals at a further distance

(100–300 m).

Censuses were carried out in woods and floodplain forests. Over all years only three observers (the authors) carried out the surveys on fixed randomly-selected plots, each year covering 30–40 plots with a total area of 1000–1200 km<sup>2</sup>. Over all years, the total length of routes that was covered on foot or by skiing was more than 40,000 km. On 60% of routes the bird counts were conducted monthly, and were done every two weeks on the remainder. In 80% of routes the bird census was conducted every year with equal intensity. On 95% of routes we did not observe any bird feeders that could have supplemented numbers of birds in our sites.

### Data analysis

Dynamics of numbers were studied for ten mainly sedentary Passeriformes species: Great Tit, Blue Tit (*Cyanistes caeruleus*), Willow Tit (*Poecile montanus*), Marsh Tit (*Poecile palustris*), Coal Tit (*Parus ater*), Crested Tit (*Lophophanes cristatus*), Long-tailed Tit (*Aegithalos caudatus*), Nuthatch (*Sitta europaea*), Tree-creeper (*Certhia familiaris*), and Goldcrest (*Regulus regulus*). All of these species regularly occur in mixed flocks during winter and hence good data was available for this species assemblage. Data was log-transformed prior to analysis. We divided winter into two periods centered around the winter solstice—the first half of the winter (day length decreasing), and the second half (daylength increasing) and calculated bird densities separately for each.

We used Principal Component Analysis (PCA) to determine the similarity of long-term population dynamics across species. We wanted to see if trends showed synchronous long-term variation. In the second step, we used Redundancy Analysis (RDA) to examine the climatic factors that determine densities in the first half of the winter. In this analysis, we examined the influence of annual and seasonal air temperature for winter (November–February), spring (before breeding period: March–April), summer (breeding season: May–July), autumn (autumn migration: August–October), date of the start of permanent snow cover, and annual precipitation. In the third step, we used multiple linear regression methods to determine the models that best describe bird densities in this period. Bird density was used as the response variable, while the predictors were: annual temperature, winter temperatures in previous year, summer temperature and date of the start of permanent snow cover. We checked predictor factors for multicollinearity using Variance Inflation Factor (VIF) and Tolerance value. The best model was selected on the basis of its Akaike Information Criterion (AIC), where the model with the lowest AIC is the one that best fits the data. In the fourth step, we used regression methods to identify the climate factors that determine bird densities in the second half of winter. For this, we used: average minimum temperature of winter period and winter severity, defined as the number of days

with minimum temperature below  $-25^{\circ}\text{C}$ . The climate data were obtained from five meteorological stations in Tatarstan, separated by 50–70 km distances each other. We use averaged climate data for these stations. All statistical analyses were done in R version 3.2.2 (R Development Core Team 2015), XLSTAT 2017, MINITAB 14.

## Results

### Climate dynamic

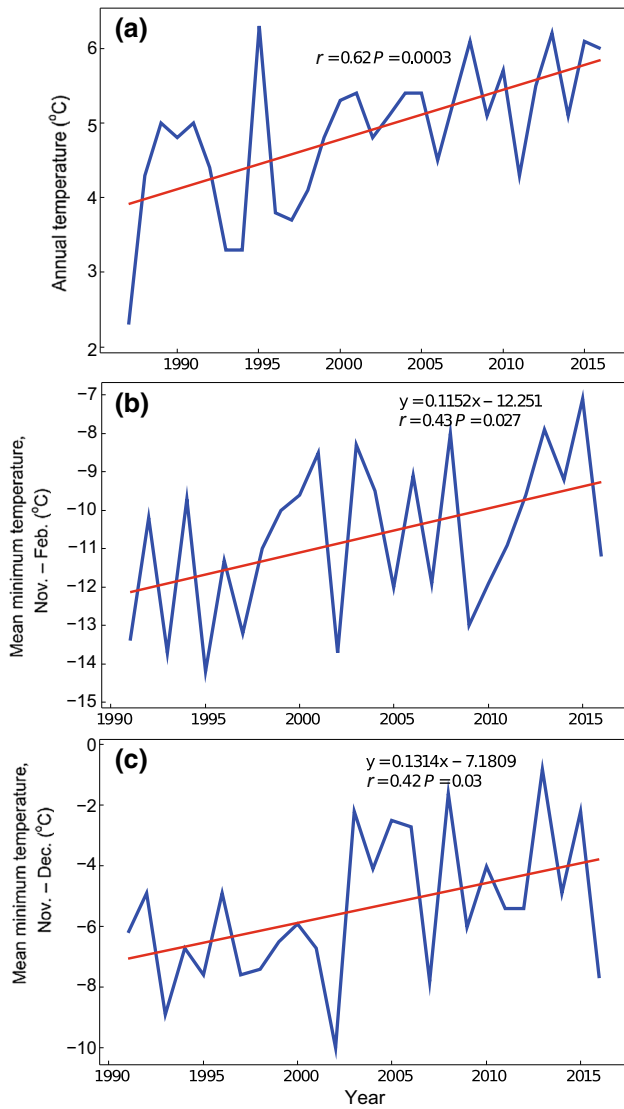
During the last 30 years, there has been a marked change in climate in the study area. Mean annual temperatures in the Kazan region of Tatarstan varied widely from 2.3 to 6.3 °C (Fig. 1a), with a significant increase (0.072 °C per year) equating to 2.16 °C over 30 years. During the study period, the most significant changes were warming in summer and autumn (Table 1). The warming in summer was particularly notable, equating to a temperature increase of 2.34 °C over 26 years. Mean winter temperature did not show significant change, but the average minimum temperature of the winter season increased significantly (Fig. 1b), by 3.00 °C over the whole period. Furthermore, temperatures in the first half of the winter (November–December) increased significantly (Fig. 1c), by 3.38 °C over 26 years. This, in combination with the late dates of onset of permanent snow cover in the region (Askeyev et al. 2017b), is a good illustration of the trend to a later start of winter.

### Bird number dynamics

Based on counts in the first half of the winter, there were large changes in bird densities over time (Fig. 2a) and nine species showed significant increases (Table 2a). Only the density of the Coal Tit did not change significantly. Bird densities in the second half of the winter also changed markedly over 26 years (Fig. 2b) and four species increasing significantly (Table 2b). There were no significant decreases in the numbers of any of the 10 species studied.

### Separation of “coniferous” and “mixed deciduous” birds

The first two components of the PCA analysis explained 66.9% of the total variance in numbers of the 10 species. All species were significantly and positively correlated with the primary axis, which explained 52.9% of the variation. The secondary axis explained 14% of the variation, and numbers of four species were significantly correlated with this. The sequence on the first axis shows that population dynamics have followed similar long-term positive trends. On the left we can see years with low winter densities and on the right side, years with high densities (Fig. 3a). The second axis appears to re-



**Fig. 1** The changes of **a** annual temperature, **b** average minimum temperature of the winter season (November–February), **c** mean temperature in first part of winter (November–December). Solid line represents the trend based on regression analysis. Equation, correlation coefficient and significant level represent in graphics

flect ecological differences in the population trends. Distinct positions on this axis are identified for “coniferous” species (Willow Tit, Coal Tit, Crested Tit,

Goldcrest) compared to “deciduous-mixed” (Great Tit, Blue Tit, Nuthatch, Treecreeper, Long-tailed Tit) (Fig. 3a). Marsh Tit was located between these two groups.

#### Effects of climatic factors on bird numbers

From the PCA, we can see there are some strong common factors that determine changes in the number of birds over time. Redundancy Analysis shows us these patterns. The first two components of the RDA analysis explained 84.7% of the total variance in the long-term dynamics of 10 bird species in the first part of winter (axis 1: 74%, axis 2: 10.7%; Fig. 3b).

Results obtained from the Monte Carlo test revealed that seven climatic parameters affect species dynamics (eigenvalue 5.32 for the first four canonical axes,  $P = 0.0001$ ). The first axis was strongly associated with annual temperature and temperature during the last winter, as well as date of the start of permanent snow cover. Temperatures in summer and snow data showed a high correlation with the first axis and second axis. Three other factors—spring and autumn temperatures and annual precipitation showed little correlations with these axes. RDA showed that abundance in the first half of winter was highly associated with particular climatic parameters for some species. For example, the abundance of Great Tit, Blue Tit, Nuthatch, Treecreeper, Long-tailed Tit and Marsh Tit were related to annual and winter temperatures in the previous year (Fig. 3b). Whereas densities of Goldcrest, Coal Tit, Crested Tit and Willow Tit were related to summer temperatures and to weather conditions at the start of winter (Fig. 3 b).

#### Factors explaining bird dynamics

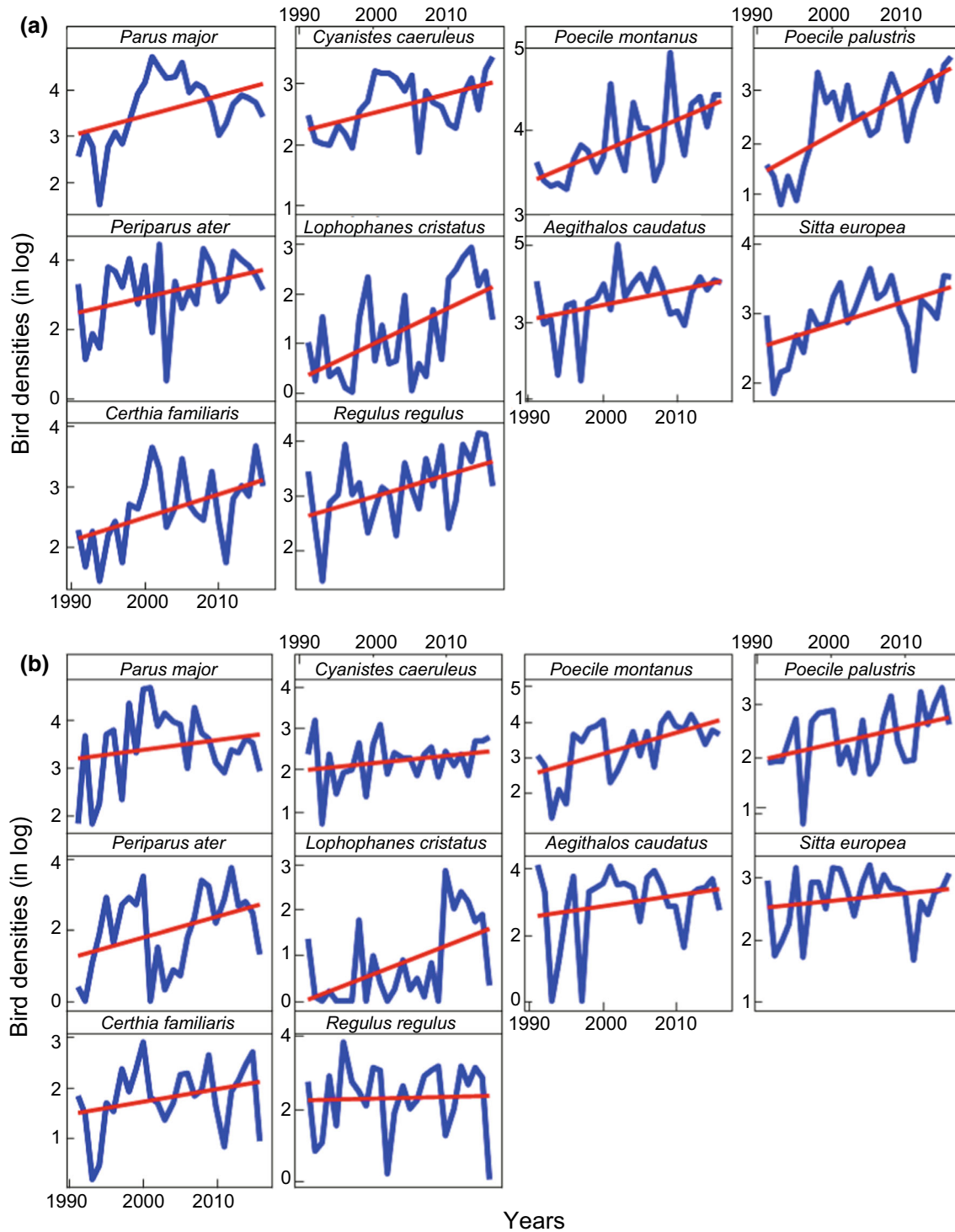
After RDA analysis we retained four factors for multiple regression analysis. Checking for multicollinearity revealed low values of VIF and Tolerance values, so all four variables were retained. Annual fluctuations in densities for all species showed statistically significant relationships with one or more of the remaining climatic variables (Table 3). All of the best explanatory models

**Table 1** Temperature changes in 1991–2016

Period	Mean temperature (°C)	Slope of regression	
		B	P
Winter (November–February)	$-8.3 \pm 1.78$	$0.054 \pm 0.046$	0.250
Spring (March–April)	$1.2 \pm 1.70$	$0.038 \pm 0.044$	0.403
Summer (May–July)	$17.7 \pm 1.42$	<b><math>0.090 \pm 0.030</math></b>	<b>0.012</b>
Autumn (August–October)	$11.9 \pm 1.0$	<b><math>0.084 \pm 0.021</math></b>	<b>0.0006</b>

Mean temperature  $\pm$  SD for seasonal periods are presented, Regression coefficients (B  $\pm$  SE) represent changes temperature (°C) per year. Statistically significant temperature increase marked in bold





**Fig. 2** Long-term dynamics of population densities of birds in first half of winter (November–December) **a** and in second half of winter (January–February) **b** in the Tatarstan Republic. Solid line represents trend-based regression analysis

selected on the basis of their AIC value were significant (Table 3). Climatic parameters explained from 25 to 50% variability ( $R^2$ ) of the changes in densities of different species (Table 3). For example, seven species were significantly related to temperature in the previous winter, 6 species to summer temperature and snow data

and 4 species to annual temperature. As an example, Fig. 4a shows the species trends of all ten species in relation to summer temperature.

The main factors explaining bird abundance in this period were climatic conditions in the previous winter and in the summer and variables indicative of the “start”

**Table 2** Changes in bird populations in the first half of winter (November–December) (a) (numbers per square km  $\pm$  SD) and second half of winter (January–February) (b) in Tatarstan, 1991–2017

(a)				
Species	Abbreviation	Mean density (km <sup>-2</sup> )	Slope of regression	
			B	P
Great Tit	GT	43.7 $\pm$ 28.0	<b>0.040 <math>\pm</math> 0.020</b>	<b>0.020</b>
Blue Tit	BT	14.5 $\pm$ 6.9	<b>0.031 <math>\pm</math> 0.010</b>	<b>0.008</b>
Willow Tit	PM	53.2 $\pm$ 27.3	<b>0.038 <math>\pm</math> 0.009</b>	< <b>0.001</b>
Marsh Tit	PP	14.2 $\pm$ 10.2	<b>0.080 <math>\pm</math> 0.014</b>	< <b>0.001</b>
Coal Tit	PA	31.1 $\pm$ 23.2	0.048 $\pm$ 0.025	0.070
Crested Tit	AC	4.4 $\pm$ 5.1	<b>0.071 <math>\pm</math> 0.020</b>	<b>0.002</b>
Long-tailed Tit	SE	44.0 $\pm$ 29.4	<b>0.039 <math>\pm</math> 0.019</b>	<b>0.050</b>
Nuthatch	CF	20.5 $\pm$ 9.0	<b>0.034 <math>\pm</math> 0.010</b>	<b>0.005</b>
Treecreeper	RR	15.5 $\pm$ 9.9	<b>0.039 <math>\pm</math> 0.014</b>	<b>0.010</b>
Goldcrest	LC	27.3 $\pm$ 16.9	<b>0.040 <math>\pm</math> 0.015</b>	<b>0.016</b>
(b)				
Great Tit		39.5 $\pm$ 27.1	0.020 $\pm$ 0.020	0.340
Blue Tit		9.6 $\pm$ 5.2	0.017 $\pm$ 0.014	0.233
Willow Tit		33.7 $\pm$ 19.5	<b>0.059 <math>\pm</math> 0.017</b>	<b>0.002</b>
Marsh Tit		11.7 $\pm$ 6.7	<b>0.030 <math>\pm</math> 0.010</b>	<b>0.045</b>
Coal Tit		11.3 $\pm$ 11.1	<b>0.056 <math>\pm</math> 0.028</b>	<b>0.050</b>
Crested Tit		2.6 $\pm$ 4.0	<b>0.060 <math>\pm</math> 0.020</b>	<b>0.006</b>
Long-tailed Tit		27.6 $\pm$ 17.1	0.033 $\pm$ 0.029	0.270
Nuthatch		14.7 $\pm$ 5.8	0.012 $\pm$ 0.012	0.325
Treecreeper		6.4 $\pm$ 4.3	0.024 $\pm$ 0.017	0.170
Goldcrest		13.5 $\pm$ 10.5	0.006 $\pm$ 0.026	0.824

In (a) and (b) regression coefficients (B  $\pm$  SE) represent changes in bird density per year. Data were log (x + 1) transformed prior to analysis. Statistically significant relationships marked in bold

of winter. Annual change in abundance of Willow Tit, Coal Tit, Treecreeper and Goldcrest depended on winter and summer temperatures, and climatic condition in early winter. Annual and previous winter temperatures affected Long-tailed Tit, Nuthatch and Marsh Tit. Blue Tit densities in the first half of winter depended on annual and summer temperatures and the date of start of snow cover. Great Tit densities in this period were significantly associated with conditions in the previous winter and the current winter. Only summer temperature had a direct effect on abundance of Crested Tit (Table 3, Fig. 4a).

#### Factors determining bird densities in second half winter

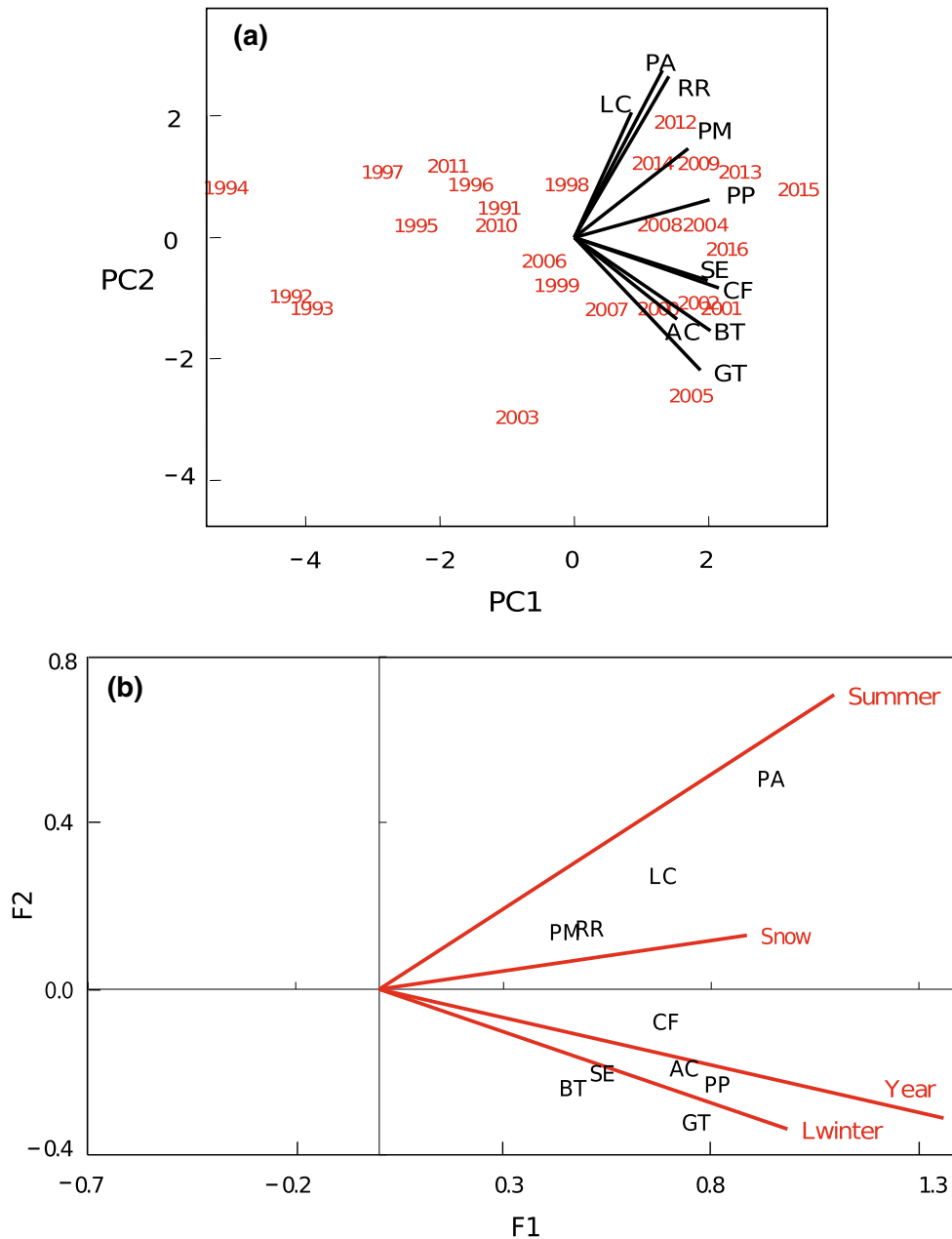
It was clear that for most species, abundance in the first half of winter depended on conditions in the previous winter, so the next step was to identify the factors that limit the number of birds over the winter period. We found highly significant positive correlations between densities in the first and second halves of the winter for nine species (Table 4a); the exception being Blue Tit. This shows that bird density in the second half of winter is primarily determined by the conditions during the seasons of the preceding year, and bird density in the first half of the respective winter. However, the severity of winter conditions appears to determine numbers of birds during this period. Densities of Blue Tit, Willow Tit, Long-tailed Tit, Goldcrest and Crested Tit in late

winter had highly significant relationships with average minimum winter temperature in that year (Table 4b). For two species, we also found a highly significant negative relationship between abundance in the second half of winter and winter severity (Fig. 4b). In general, in severe winters, lower densities of birds were observed in late winter.

The seasonal pattern of changes in the natural environment is the strongest factor affecting bird populations. For example, the dynamics of Treecreeper populations during the two winter periods, differing in climatic conditions (Fig. 5), are clearly influenced by the severity of conditions in the winter period. There are clearly pronounced seasonal differences and this should be taken into account.

## Discussion

The Earth's climate has continued to change in the 21st century, and there have been many studies on responses and changes in abundance and distributions of fauna and flora (e.g. Lehikoinen et al. 2013; Lehikoinen and Virkkala 2016; Tayleur et al. 2016; Thackeray et al. 2016). Many scientists attributed the cause of these changes to “global warming”. However, “global warming” is not the only term for describing recent climate changes affecting ecosystems. Even modern fauna have been subjected to significant influences of



**Fig. 3** Biplots of Principal component analysis (PCA) **a** performed on time series of the bird species abundance in first part winter (November–December). Species presented as vectors and abbreviation (see in Table 2) and **b** of first versus second axes of Redundancy Analysis (RDA), showing the relative influence on bird species abundance in first part winter of each climatic variable. Climatic variable represented as vectors and abbreviation: annual temperature (year), winter (November–February) temperatures in previous year (Lwinter), date of the start of permanent snow cover (snow), summer (May–July) temperature (summer). Only the main factors with high correlation levels with axes are shown. Species presented as abbreviation (see in Table 2)

both warming and cooling over time and organisms have developed exceptionally effective mechanisms of response to these changes. Therefore, we consider ‘recent climate change’ to be a more accurate term.

We found that over the past 26 years, winter abundance of 10 bird species have significantly changed in the Eastern edge of Europe. Our findings also show that a major factor associated with changes as well as annual fluctuations, is climate. The significant relationships between winter bird densities and temperature in sum-

mer and in winter confirmed our hypotheses about the existence of a “climatic” concept of regulation of number of birds. We have found increasing trends for most bird species. In the rest of Europe, most winter bird populations have also changed significantly during the last three decades. However, for most of the species of birds studied here, trends in other European countries differed significantly from those presented here. In Sweden in the middle of winter (Christmas’ census), numbers of Marsh Tit, Willow Tit, Crested Tit, Coal Tit,

**Table 3** The best explanatory models, which predicted different bird species densities in first half of winter

Species	Equation of the model	$R^2$	AIC	$P$
Great Tit	$Y = 3.733 + 0.17 \times \text{Lwinter} + 0.024 \times \text{Snow}$	0.33	- 23.20	0.004
Blue Tit	$Y = 2.151 + 0.502 \times \text{Year} - 0.089 \times \text{Summer} - 0.009 \times \text{Snow}$	0.56	- 53.73	0.0001
Willow Tit	$Y = 1.807 + 0.091 \times \text{Lwinter} + 0.133 \times \text{Summer} + 0.01 \times \text{Snow}$	0.42	- 49.25	0.006
Marsh Tit	$Y = 0.051 + 0.479 \times \text{Year} + 0.120 \times \text{Lwinter}$	0.26	- 15.05	0.008
Coal Tit	$Y = - 2.328 + 0.165 \times \text{Lwinter} + 0.313 \times \text{Summer} + 0.025 \times \text{Snow}$	0.42	- 6.09	0.007
Crested Tit	$Y = - 4.813 + 0.344 \times \text{Summer}$	0.27	- 8.65	0.006
Long-tailed Tit	$Y = 2.367 + 0.115 \times \text{Lwinter} + 0.433 \times \text{Year}$	0.43	- 23.42	0.002
Nuthatch	$Y = 1.105 + 0.373 \times \text{Year} + 0.059 \times \text{Lwinter}$	0.47	- 50.60	0.0001
Treecreeper	$Y = 1.265 + 0.181 \times \text{Lwinter} + 0.121 \times \text{Summer} + 0.014 \times \text{Snow}$	0.50	- 32.50	0.001
Goldcrest	$Y = 0.840 + 0.103 \times \text{Lwinter} + 0.133 \times \text{Summer} + 0.016 \times \text{Snow}$	0.30	- 24.72	0.044

Environmental factors which included in models represent as abbreviation: annual temperature (year), winter (November–February) temperatures in previous year (Lwinter), date of the start of permanent snow cover (Snow), summer (May–July) temperature (Summer)

Treecreeper and Goldcrest significantly decreased (Green et al. 2016; Lehtikoinen et al. 2016). In Finland, also in mid-winter, Willow Tit, Crested Tit and Goldcrest numbers decreased. In Denmark, Marsh Tit, Crested Tit, Goldcrest, Great Tit and Long-tailed Tit numbers significantly decreased (Lehtikoinen et al. 2016) and in the Netherlands, Coal Tit, Crested Tit, Willow Tit, Great Tit and Goldcrest numbers decreased (Lehtikoinen et al. 2016). Our results for these species differ markedly, with trends in the opposite direction. However, changes in numbers of Blue Tit and Great Tit (in Finland and Sweden) and Nuthatch (in Sweden, Denmark, and the Netherlands) were very similar.

Indeed, in comparing the population dynamics of birds in our region with data from other parts of Europe, we faced difficulties. Firstly, we could not find data on winter birds in European Russia comparable in coverage or seasonality of observations. Most of the data are from limited areas or collected in very limited periods. Secondly, we found that in practically all winter bird monitoring schemes in Europe, a range of counting methods were used, often from an extremely short time period (e.g. Christmas Counts) and often in very mild winter conditions. Thirdly, when we tried to compare abundances, we found significant discrepancies in the densities of many bird species in various European countries (Askeyev et al. 2017a). Above all, there are questions about the representativeness of the data. Indeed, as we can see in recent publications (e.g. Lehtikoinen et al. 2016) that in the boreal zone, where most of Finland and Sweden are located, the mean annual number, for example in Finland, for Great Tit at 6, 10 and even 30 times higher than that of Willow Tit, Goldcrest and Coal Tit, respectively, and in Sweden Blue Tit is one of the most numerous birds in the winter. Of course, all these numbers are caused by the fact that bird count is carried out mainly in settlements and in the southern regions of these countries (Fraixedas et al. 2015). Consequently extrapolations of these data for all boreal areas may not be valid.

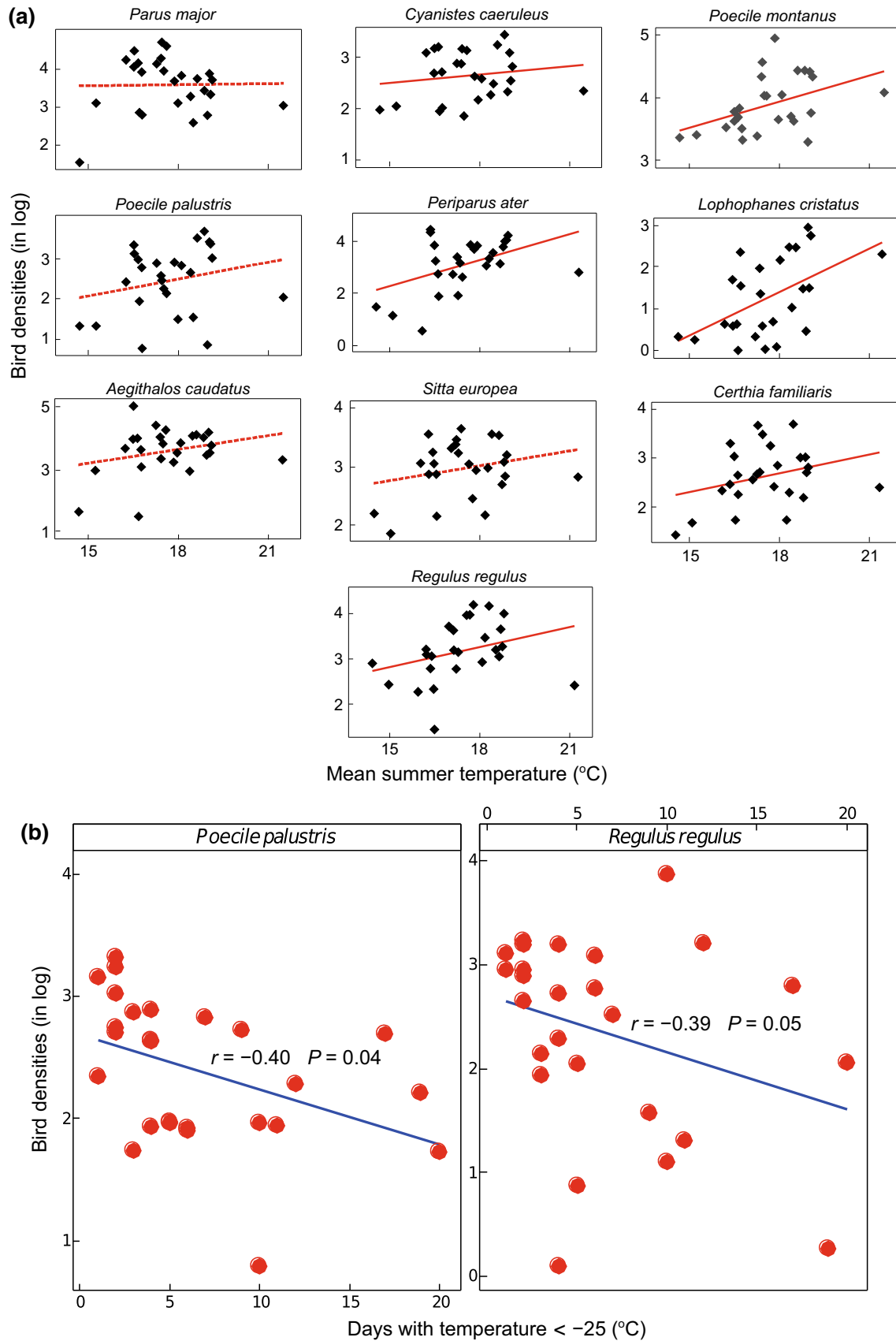
We found that among “coniferous” species (Willow Tit, Coal Tit, Crested Tit and Goldcrest) there were many similarities in the long-term dynamics. The same

phenomenon was also characteristic of the “deciduous-mixed” species. Hence, according to this ecological trait, there is a sufficiently clear differentiation in the abundance dynamics and with a high degree of probability, we can predict that in years of increased abundance of Willow Tit, there are likely to be increased abundance of Goldcrest and Coal Tit.

We found that “strong” factors influence variation in the densities of birds during this period. Indeed, the number of birds in the first half of the winter is determined by the climatic conditions observed before the beginning of winter. Unfortunately, we did not find any research on the impact of summer conditions on winter bird abundance over a large area. There are studies of the influence of climatic parameters in winter, spring and summer on numbers in autumn, but most of these were carried out over a very limited area such as bird ringing stations (Sokolov et al. 2001; Nilsson et al. 2006; Sokolov 2007). Certainly, it is very important to determine whether the densities of birds at the start of winter are correlated with abundance in the preceding autumn. Our past studies (Askeyev and Askeyev 2002) have shown a very strong relationship between these measures.

To test hypotheses about the effect of climatic parameters on the long-term dynamics of abundance, we analyzed the effect of fluctuations, and seasonal and annual temperature indices on populations in the first half of winter. Abundances of all species were found to be significantly related to temperature indices in the previous winter. Only the mutual influence of these climatic changes, could, in our opinion, cause the long-term increases in the species studied. An interesting point was that we did not find any correlation between the densities of birds with spring or autumn temperatures, or with precipitation. In contrast to the work of our colleagues (Sokolov 1999; Sokolov et al. 2000, 2001, 2002, 2007, 2017; Markovets and Sokolov 2002), where spring temperatures are recognized as the main factor influencing fluctuations in bird numbers in the autumn period, we believe that one period, even if very important (the beginning of reproduction), cannot be the whole explanation. Spring temperatures (in April) do not always play a significant role in survival, as they only



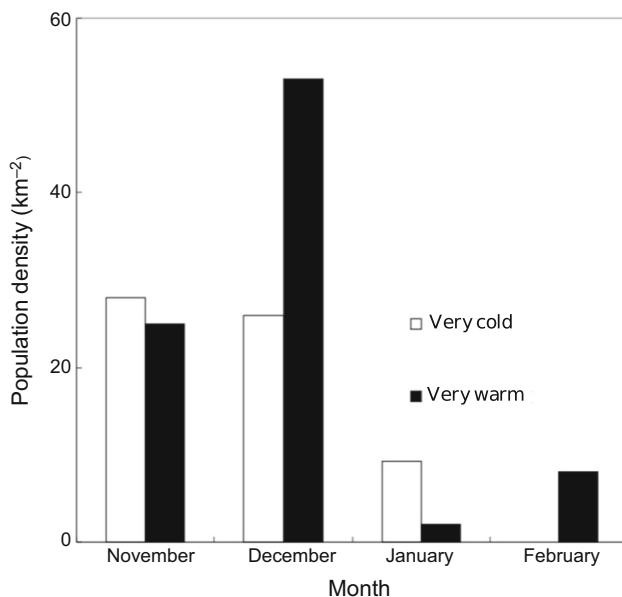


**Fig. 4** The relationships (a) between abundance of ten species in the first half of winter (November–December) and summer (May–July) temperature. Solid line represents significant relation and dashed lines non-significant relation and (b) between abundance of Marsh Tit and Goldcrest in the second half of winter (January–February) and numbers of days with temperature < -25 °C. Solid line represents relation between variables based on regression analysis

**Table 4** Spearman's rank correlations ( $r_s$ ) (a) between winter bird density in the first and second halves of winter and regression coefficients (b) (slope: Regression coefficients ( $B \pm SE$ ) represent changes between bird densities in the second half of winter and average minimum winter temperatures in the same year (effects of current temperature)

(a)		
Species	$r_s$	$P$
Great Tit	<b>0.69</b>	<b>0.00009</b>
Blue Tit	0.36	0.07
Willow Tit	<b>0.45</b>	<b>0.02</b>
Marsh Tit	<b>0.57</b>	<b>0.0024</b>
Coal Tit	<b>0.66</b>	<b>0.0003</b>
Crested Tit	<b>0.70</b>	<b>0.00006</b>
Long-tailed Tit	<b>0.52</b>	<b>0.006</b>
Nuthatch	<b>0.61</b>	<b>0.0009</b>
Treecreeper	<b>0.58</b>	<b>0.002</b>
Goldcrest	<b>0.63</b>	<b>0.0005</b>
(b)		
Species	Winter T	
	$B \pm SE$	$P$
Great Tit	0.13 $\pm$ 0.07	0.09
Blue Tit	<b>0.13 <math>\pm</math> 0.04</b>	<b>0.01</b>
Willow Tit	<b>0.15 <math>\pm</math> 0.07</b>	<b>0.048</b>
Marsh Tit	0.09 $\pm$ 0.06	0.15
Coal Tit	0.03 $\pm$ 0.11	0.79
Long-tailed Tit	<b>0.23 <math>\pm</math> 0.10</b>	<b>0.03</b>
Nuthatch	-0.02 $\pm$ 0.05	0.68
Treecreeper	0.08 $\pm$ 0.07	0.25
Goldcrest	<b>0.18 <math>\pm</math> 0.09</b>	<b>0.05</b>
Crested Tit	<b>0.16 <math>\pm</math> 0.08</b>	<b>0.05</b>

Statistically significant relationships marked in bold



**Fig. 5** The dynamics in monthly densities of Treecreeper in a cold winter (2002–03) and a warm winter (2001–02)

affect birds that have already survived the winter period. In early spring in Russia, there are still no nestlings. These will first appear in May and hence, conditions in early spring should have little effect. Furthermore, there are limitations to using the temperature regime of a single month as undertaken by some researchers (e.g. Nilsson et al. 2006; Sokolov 2007) to interpret its effect on bird populations.

In recognizing the importance of spring conditions for bird populations, it should be recognized that in our region, severe winters often occur and there are also more drastic changes compared to the western regions of Europe in summer temperatures. For sedentary bird populations, the climatic characteristics of the winter and summer periods are more important than those in spring. The warming of the winter period observed in recent years contributes to the greater survival of birds by the beginning of the breeding season. This is the first step, in our opinion, to an increase in abundance. The next important step affecting densities in the first half of winter is the increase in the survival rate of young individuals during the nestling, mass departure and dispersal periods. Changes in the temperature indices of these periods (May–July), which improve productivity, are the second step to increased bird abundance. The third step to increased abundance is the later onset of the winter season. Thus, we conclude that the dynamics of bird densities are primarily determined by climatic factors that have the greatest impact on the survival of adult birds in winter and the survival of young in the summer.

The influence of harsh winter conditions on the survival of birds in winter is well known (Hilden 1982; Newton 1998). Work carried out in parts of Europe where the winters are severe has a valuable role in understanding the impact of changing climatic conditions on the survival of birds. Our findings show that the abundance of birds in the first half of the winter influences numbers in the second half. However, we can see that abundance in late winter is determined to a greater degree by winter severity. We found that with increased average minimum winter temperatures, densities of most bird species increased in the late winter period. This is consistent with trends of greater survival by the end of the winter period.

Without taking into account seasonality or monthly changes in the natural environment, interpreting measures of bird abundance has limitations. Taking into account counts from only a short period, it is possible to obtain incorrect information about the actual number of birds. For example, if we used only data on Treecreepers in January, we might conclude that densities in the harsh winter were higher than in the mild winter. But using data also from the second half of the winter, the pattern is completely different. There are pronounced seasonal dynamics that can indicate significant spatial movements of winter bird populations during the winter.

In summary, the markedly different dynamics of winter bird numbers in different parts of Europe raises

the question as to what causes these differences? The likely reason for a higher survival rate of birds in our study area in winter and optimal breeding conditions in summer is the fact that the climate has changed rapidly, more rapidly than, for example, in Fennoscandinavia. In recent decades, the annual mean temperature at South Sweden (Falsterbo) increased by about 1.5 °C (Nilsson et al. 2006), but increased in our region by almost 1 °C more. Temperature in early winter (November–December) has increased significantly over the last 50 years in our region, but in Finland temperature changes were not significant (Fraixedas et al. 2015). Furthermore, annual mean temperatures in winter did not increase significantly during the study period in the Netherlands, Denmark, Sweden, or Finland (Lehikoinen et al. 2016) or in Tatarstan. Nevertheless, the average minimum temperature observed in winter in our region is increasing. In summer in Fennoscandinavia (Lehikoinen et al. 2014) temperature increase in the last 50 years was only 1 °C but in our region it was more than 2 °C. This is important for the interpretation of bird dynamics in different regions, especially for sedentary or short-distance migrants. Significant changes in winter conditions, as well as during the breeding season, and a general increase in annual temperatures were associated with a significant increase in the abundance of birds in winter. In our opinion, the combination of these changed climatic parameters caused increases in bird populations.

We consider that the dynamics of bird numbers are primarily determined by climatic factors, through their influence on survival rate of adult birds in winter and of juveniles in summer. However, we believe that methods of measuring the abundance of birds in the winter strongly affect the results. When studying the influence of climatic parameters (in particular temperature) on animal communities, the history of populations and the continuous natural cycle should be inextricably linked into a single chain, because in nature there is no separation of winter, spring, summer and autumn. Our data do not support conclusions that the abundance of boreal bird species have decreased.

We also wish to address some issues related to long-term field research. Our study is an example and a response to skeptics (Sokolov 2010) who find it difficult to imagine that the same researchers go to the same routes every year for several decades to count the birds. Our study is an attempt to encourage scientists in systematic and standardized field research. We agree with Tomasz Wesołowski (2012) that much field research is currently not being done in ways that produce reliable and valid data. Furthermore, research needs to be carried out taking into account seasonality and spatial heterogeneity in the distribution of animals. Indeed, it is impossible to pull a rabbit out of a hat with sophisticated mathematical methods without having it in the hat in the first place.

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