European Journal of Ecology, 9.1, 2023, pp. 58-69

THE ROLE OF CLIMATE CHANGE AND FOOD SUPPLY ON WINTER POPULATIONS OF SEED-EATING BIRDS

Arthur O. Askeyev[1], Oleg V. Askeyev[1], Igor V. Askeyev[1], Tim H. Sparks [2,3,*]

[1]Biomonitoring Laboratory, Institute of Problems in Ecology and Mineral Wealth, Tatarstan Academy of Sciences, Daurskaya str. 28, Kazan 420087, Tatarstan Republic, Russia
[2]Department of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71c, 60-625 Poznań, Poland
[3]Museum of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK
Corresponding author: **e-mail: thsparks@btopenworld.com 68 Girton Road, Girton, Cambridge, CB3 0LN, UK. Tel +44 (0)1223 276726*

***ORCID:** Arthur Askeyev 0000-0002-1214-7355*
Oleg Askeyev 0000-0001-6589-0479
Igor Askeyev 0000-0002-5304-4985
Tim H. Sparks: 0000-0003-4382-7051

Abstract.

We studied the populations of four seed-eating bird species throughout the winter during a 30-year study in the forests of the Tatarstan Republic, Russia. Numbers of all species fluctuated from year-to-year by several orders of magnitude but with a significant underlying trend for increased numbers associated with rising temperatures and a greater food supply. We question whether the traditional view that such birds move further south only after exhausting the food supply is too simplistic. We believe that the severity of winter, or lack of it, is highly influential on the mortality and movements of these characteristic birds of the boreal forest zone.

Key words: long-term trends, winter bird monitoring, climate change, environmental factors, Republic of Tatarstan.

Introduction

Even with rapid climate change, there are still millions of birds that migrate in spring and autumn to seek more favourable environments (Piersma et al. 2005; Askeyev et al. 2009; Robinson et al. 2009; Haest et al. 2019). Birds making autumn migration from the northern boreal zone to more southerly regions of Eurasia are called “winter visitors” or “winter migrants” in those southern countries. They appear close to the beginning of winter, and are a characteristic feature of the forests of the middle latitudes of the Eurasian continent. The appearance of these species is apparently due to the presence of more favourable conditions (climate and food) in these host areas.

The Republic of Tatarstan is located in the middle latitudes of the extreme east of Europe. It has a diversity of landscapes, a wide variety of tree species, and a dramatic change of forest tree species from north to south. The latter aspect is of considerable interest for studying the distribution of typical forest bird species. In our earlier work (Askeyev et al. 2017a, b, 2018, 2020, 2022) we identified increases in abundance of insectivorous bird species and the significant role of climate in that process. However, there are other bird species whose winter densities fluctuate greatly from year to year, and which are typically seed and fruit eating birds (hereafter seed-eaters for brevity). They are highly dependent on tree species, whose seed production varies from year to year (Newton 1972, 1998). In many respects, the seed yield of trees also depends on climatic parameters. As a rule, they bear fruit in synchrony with each other, giving a huge abundance of seeds/fruit in some years and practically none in others, a phenomenon known as masting. Such synchrony can extend to vast areas, encapsulating an entire continent (Formozov 1960; Newton 1998, 2006). Seed-eating birds follow this pattern also; they concentrate where their food is abundant at this time, especially during autumn migration and in winter (Newton 1972; Haila et al. 1986; Koenig & Knops 2001). Accordingly, the population size of these species can differ from year to year by several orders of magnitude. In addition, there is a view (Meller et al. 2016) that a high abundance of seeds and fruit leads to a high proportion of resident individuals in the populations of seed eating birds. During the years of increasing numbers, these species are characterized by an explosive irruption in our region (Payevsky 2015). Mast years with a good harvest of Pine and Spruce seeds and some other tree species can be observed every two to four years (Formozov 1976; Koenig & Knops 2000). This is also controlled by climatic conditions, for example, good cone years for Spruce are preceded by a warm summer the previous year (Tishin 2006; Sjöberg et al. 2007; Askeyev et al. 2022). Climatic factors and the availability of food resources are the main drivers of changes in the abundance of birds. Wintering conditions are a major component of the biology of organisms living in temperate and boreal habitats. The most informative and clearly visible influence is the combined effect of the food supply and climatic factors on the dynamics of the number of birds during winter. Using winter visitors as indicators, we can trace these interactions in detail. However, the study of population dynamics of birds during winter has often been limited to a short time window (e.g. Christmas counts) and so globally there is still very little information published on changes of seed-eating winter visitors throughout the winter season. In addition, the relationship between habitat use and changing snow or temperature conditions, shifting ranges and migration during winter seasons is still only poorly understood (Deshpande et al. 2022).

The purpose of our study was to investigate: 1) the magnitude of interannual fluctuations in the number and synchrony of seed-eating birds in winter in this eastern part of Europe; 2) whether these species have pronounced differences between the first and second half of winter over a 30 year period; 3) what environmental factors (climate, feeding conditions) affect the long-term dynamics of the number of the studied species.

Material and Methods

Study area and bird counts

The Tatarstan Republic is located at the eastern edge of the European continent between 53°58′ and 56°40′ N, 47°15′ and 5415′ E. From west to east the Republic stretches for 460 km, and from north to south for 290 km, with a total area of 67,800 km^2. This location determines the severity and continentality of the climate. The maximum average monthly amplitude between the coldest month of the year (January) and the warmest (July) can reach 48 °C. Snow cover can lie for more than 150 days, while the greatest depth of snow cover in some years exceeds 1 m. The Republic includes two natural zones - forest and forest-steppe.

Thirty years of data (1991/2-2020/1) on winter bird densities (from 1 November to 5 March) were collected during fieldwork carried out according to Y.S. Ravkin's transect methods (Ravkin 1967) without a fixed strip width and with subsequent conversion to area densities using group mean detection ranges. Counts were used to estimate numbers per km^2, based on mean detection distances, by the formula:

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

where D = the number of individuals per km^2, 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. Only three observers (AO, OA, IA) carried out the surveys on fixed randomly-selected plots, each year covering 30-40 plots (Figure 1) with a total area of 1000-1200 km^2. Over all years, the total length of routes that was covered on foot or by skiing was more than 45,000 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.

In the current work, we focus on the dynamics of the densities of four species: Red Crossbill *Loxia curvirostra* (Linnaeus, 1758), Eurasian Siskin *Spinus spinus* (Linnaeus, 1758), Common Redpoll *Acanthis flammea* (Linnaeus, 1758), Bohemian Waxwing

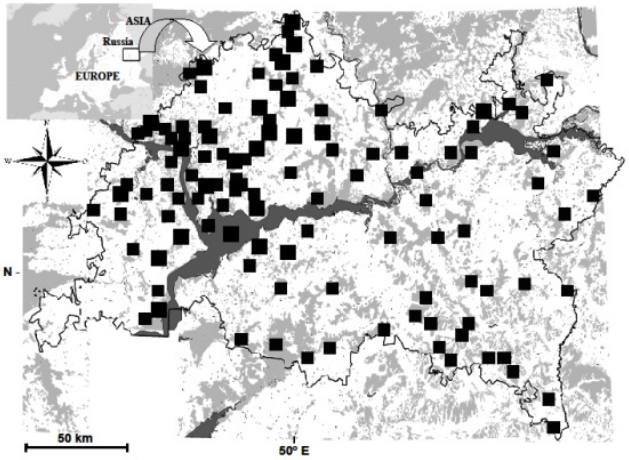


Figure 1. Distribution of sampling plots in the Tatarstan Republic (inset shows location within Europe). Forest cover is shaded in grey.

Bombycilla garrulus (Linnaeus, 1758). Most individuals of the studied species breed to the north of our study region and are winter visitors. Hence, we used summer temperature from a large area of European Russia to the north of the city of Kazan (the Tatarstan capital) for analysis. We calculated the average summer temperature (May-August) using data from the following meteorological stations: Arkhangelsk, Syktyvkar, Naryan Mar, Salekhard, Kirov, Perm and Kazan. Monthly winter temperatures, and the date of establishment of permanent snow cover, were obtained from five stations within the Tatarstan Republic. When recording bird counts, without exception, the weather conditions and the abundance of seeds (visual observations on the Kapper scale (Table 1) (Kapper 1926) of Birch *Betula* spp., Rowan *Sorbus aucuparia* (Linnaeus, 1753), Scots Pine *Pinus sylvestris* (Linnaeus, 1753), hereafter Pine) and two species of Spruce: Siberian Spruce *Picea obovata* (Ledebour, 1833) and Norway Spruce *Picea abies* ((Linnaeus) H. Karst, 1881) were also recorded. All seed data from all plots were averaged to produce an annual mean score for the region.

Table 1 A summary of the Kapper scale for describing seed crops

Score	Description	Yield: individual and forest edge trees	Yield: forest interior
0	No crop	None	None
1	Very bad	Low	None
2	Poor	Satisfactory	10-20%
3	Average	Considerable	30-40%
4	Good	Heavy	50-70%
5	Very good	Heavy	80-100%

Data analysis

We divided winter into two periods centred around the winter solstice; the first half with daylength decreasing, and the second half with daylength increasing. Bird densities were calculated separately for each. Changes in densities of each species over time were assessed using linear regression in each of the two winter periods.

We used Principal Component Analysis (PCA) to determine the similarity of long-term bird population dynamics across species in the first and second half of winter. We wanted to see if these trends show synchronous long-term changes. We then used Canonical Correspondence Analysis (CCA) to examine the factors that influence densities in the first half of winter. In this analysis, we examined the influence of the following environment variables: abundance of seeds of Birch, Rowan, Pine and Spruce, the date of the start of permanent snow cover, and summer air temperature (breeding season: May-August). We subsequently used generalized linear models with a normal error structure to determine the environmental factors affecting the long-term dynamics of the abundance of the bird species. We checked predictor variables for multicollinearity using Variance Inflation Factor (VIF) and Tolerance values. The following variables were predictors in this analysis: abundance of seeds of Birch, Rowan, Pine and Spruce, the date of the start of permanent snow cover, and summer temperature. The best-fit model was selected based on lowest Akaike Information Criterion (AIC). Only statistically significant variables were retained in these models. In a fourth step, we used similar generalized linear models to identify the variables that determined bird densities in the second half of winter. We included in these models: average minimum winter temperature (November-February), winter severity (defined as the number of days with minimum temperature below -20 °C), the date of the start of permanent snow cover, and the abundance of seeds of Birch, Rowan, Pine and Spruce. Calculation and visualization were done in PAST version 4.04 and XLSTAT 2021.

RESULTS

Climate dynamics

Between 1991 and 2020 there was a significant (P=0.03) increase in the summer temperature (May-August) of the large territory north of Kazan, equating to an increase of 1.5 °C (Figure 2). The winter of 2019/20 was the first in which temperatures recorded in met stations close to Kazan did not fall below -20°C. The maximum number (38) of such days was recorded in the winter of 2002–2003.

Bird number dynamics

The density of the studied species varied greatly from year to year, by several orders of magnitude. The greatest inter-annual changes were recorded for Common Redpoll and Bohemian Waxwing in both halves of winter. Two of the four bird species had significant increases in densities in the first half of

Figure 2. Changes in mean summer temperature (a) and winter severity (number of days below -20 °C) (b). Regression line indicated by the solid line. Regression equation, correlation coefficient and significance are shown.

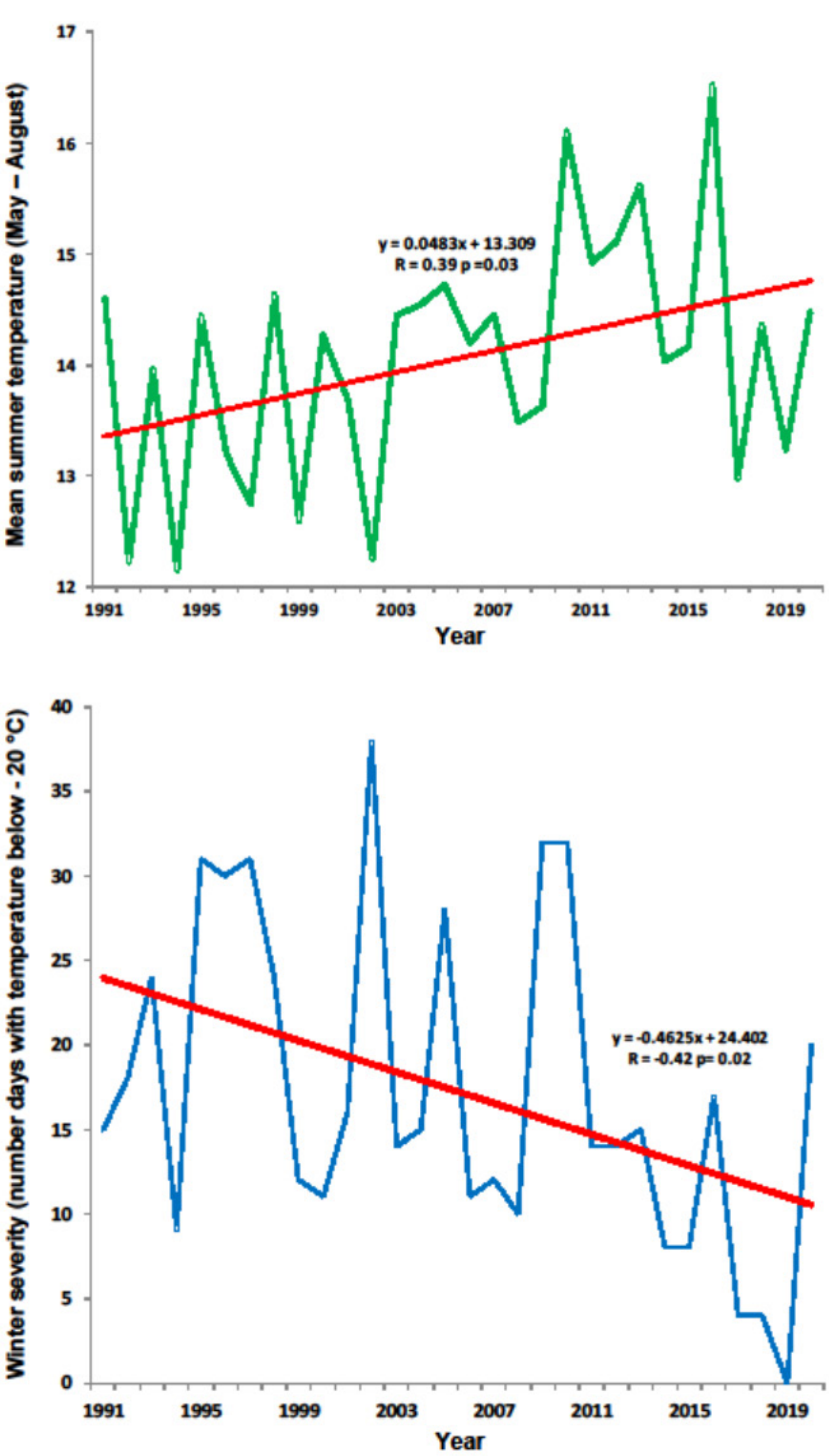


Table 2 Changes in bird populations in the first half of winter (a) (numbers per square km ± SD) and second half of winter (b) in Tatarstan, 1991/2-2020/1. Regression coefficients (b ± SE) represent changes in bird density per year. Statistically significant changes are shown in bold

(a)

Species	Abbreviation	Mean ± SD density (km^{-2})	Slope of regression	
			b ± SE	P
Red Crossbill	RC	4.1±5.6	0.019±0.018	0.318
Eurasian Siskin	ES	18.8±24.1	**0.050±0.022**	**0.001**
Common Redpoll	CR	35.4±33.9	0.023±0.017	0.187
Bohemian Waxwing	BW	24.4±35.8	**0.041±0.019**	**0.010**

(b)

Species	Mean ± SD density (km^{-2})	Slope of regression	
		b ± SE	P
Red Crossbill	3.8±5.4	**0.053±0.022**	**0.019**
Eurasian Siskin	13.7±18.8	**0.061±0.023**	**0.010**
Common Redpoll	38.1±48.4	**0.025±0.012**	**0.048**
Bohemian Waxwing	16.2±15.1	**0.051±0.017**	**0.005**

winter, and all four species in the second half (Table 2 a,b). Common Redpoll was the most abundant species in both halves of winter. There were no significant decreases in the numbers of any of the studied species.

Long-term dynamics of the number of four bird species

The first two components of the PCA explained 72.7% and 72.5% of the total variance in numbers of the four species in the first half and second half of winter respectively (Figure 3). All selected species were significantly and positively correlated with the first axis, which explained 46.5% and 49.7% of the variation in the first half and second half of winter respectively. The second axis explained 26.1% and 22.8% of the variation in the two halves of winter, and species were significantly correlated with this. The sequence on the first axis shows that dynamics have followed long-term positive trends. On the left side are years with low winter densities and on the right side are years with high densities of birds (Figure 3a,b). The second axis reflects ecological differences in population dynamics. Separate positions on this axis are marked for the "coniferous" species (Red Crossbill and Eurasian Siskin) and mainly "deciduous-mixed" species (Common Redpoll and Bohemian Waxwing).

Bird densities and environmental factors

The first two components of the analysis (CCA) explained 91.9% of the total variance of long-term dynamics of the densities of the species in the first half of winter. Axis 1 explained 66.6% (Figure 4) and was associated with all selected factors with the exception of the date of the start of permanent snow cover. Axis 2 explained 25.3% and was associated with the date of the start of permanent snow cover, summer temperature and the abundance of Birch seeds (Figure 4).

The analysis showed that the abundance of some species in the first half of winter was reliably associated with specific environmental variables. For example, the abundance of Common Redpoll was mainly associated with date of the start of permanent snow cover and abundance of Birch seeds. The numbers of Red Crossbill were more associated with abundance of Pine and Spruce seeds. Density of Eurasian Siskin was related to summer temperature, and Bohemian Waxwing was more associated with the abundance of Rowan seeds.

Figure 3. Biplots of Principal Component Analysis (PCA) performed on time series of the bird species abundance in the first half (**A**) and second half (**B**) of winter. Species presented as vectors. For species abbreviations see Table 1.

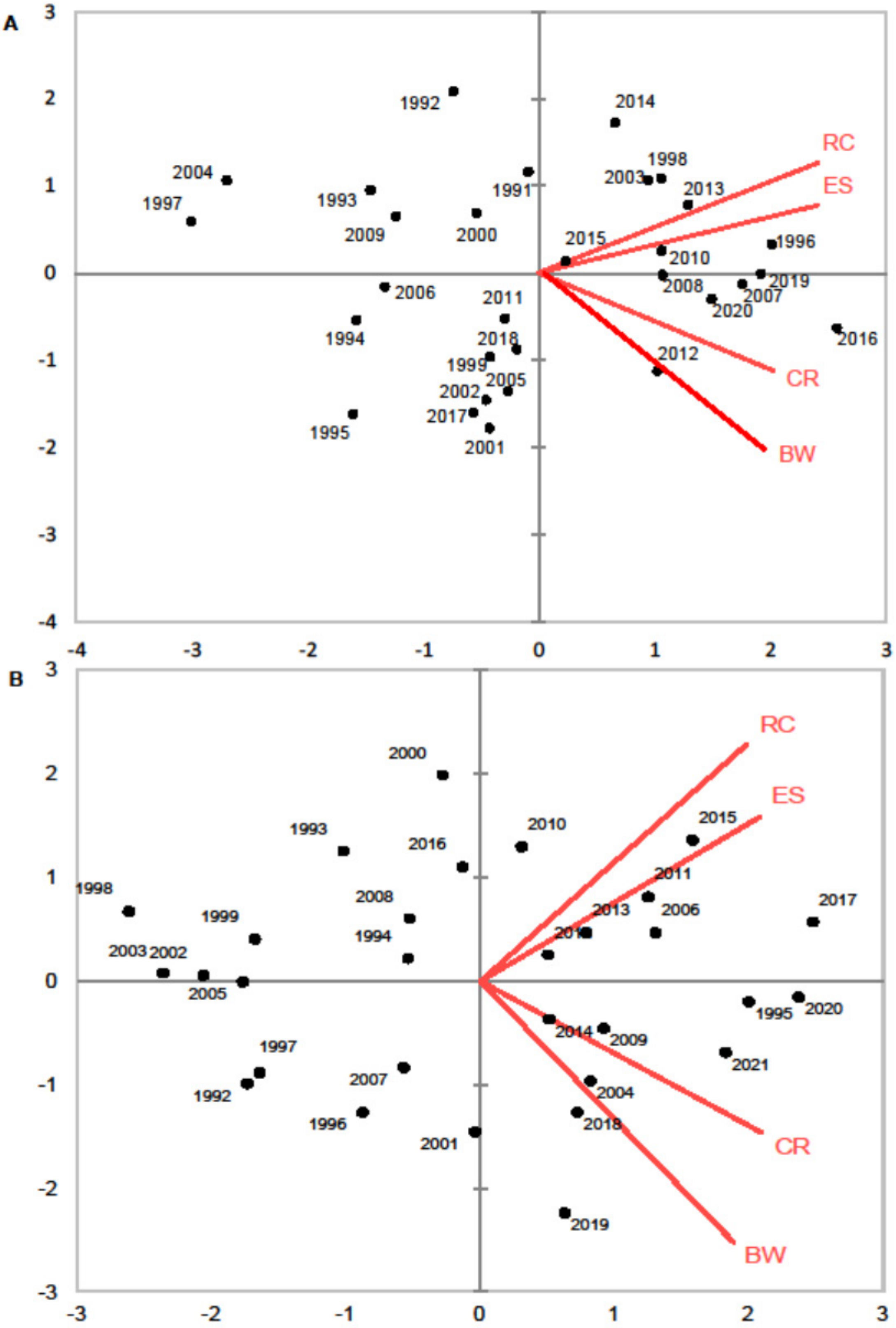
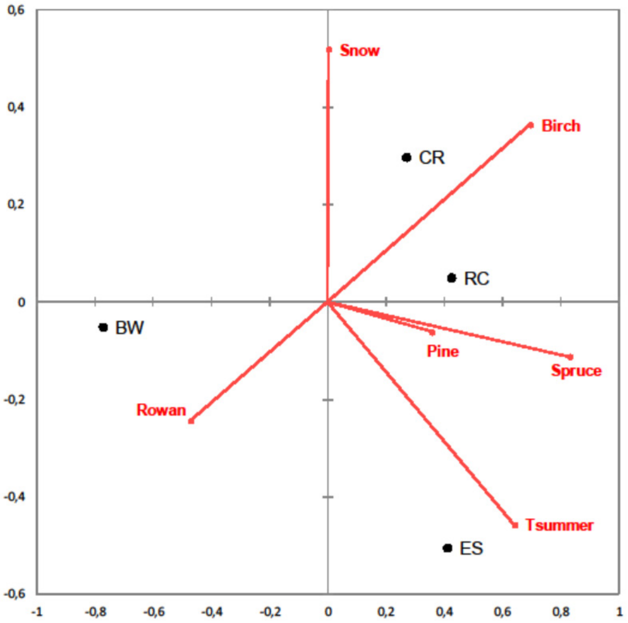


Figure 4. Biplots of Canonical Correspondence Analysis (CCA), showing the relative influence of each environmental variable on the densities of bird species in the first half of winter. Environmental variables indicated by red arrows: summer (May-August) temperatures (Tsummer), date of the start of permanent snow cover (Snow), abundance of seeds of Birch (Birch), Rowan (Rowan), Pine (Pine) and Spruce (Spruce). Species symbols shown in black.



Factors explaining bird dynamics in the first half of winter

Checking for multicollinearity revealed low VIF and Tolerance values, so all six variables were retained. Annual fluctuations in densities for all species showed statistically significant relationships with two or more of the investigated environmental variables (Table 3). Environmental variables explained from 15.4 to 52.0% of the variability (R^2) in the changes in densities of different species (Table 3). Three species were associated with the date of the start of permanent snow cover, two species with the abundance of Spruce seeds and summer temperature, one species with the abundance of seeds of Birch, Rowan and Pine (Table 3). The abundance of Pine and Spruce seeds, and the date of the start of permanent snow cover significantly influenced the abundance of Red Crossbill. Eurasian Siskin densities in the first half of winter depended on summer temperature and the abundance of Spruce seeds. The abundance of Birch seeds and the date of the start of permanent snow cover significantly influenced the abundance of Common Redpoll. Long-term dynamics of the abundance of Bohemian Waxwing were mainly associated with the abundance of Rowan seeds, summer temperature and the date of the start of permanent snow cover.

Table 3 The best explanatory models of bird species densities in the first half of winter. Environmental variables included in models are abbreviated as follows: abundance of seeds of Birch (Birch), Rowan (Rowan), Pine (Pine), and Spruce (Spruce), summer (May-August) temperature (Summer), and the date of permanent snow cover (Snow)

	coefficients									
Species	Const.	Birch	Rowan	Pine	Spruce	Summer	Snow	R^2	AIC	P
Red Crossbill	-3.6			0.88	2.56		1.94	0.46	92.34	<0.001
Eurasian Siskin	-3.9				2.19	2.60		0.52	174.39	<0.001
Common Redpoll	-4.3	1.41					0.93	0.48	196.91	<0.001
Bohemian Waxwing	3.3		2.72			1.81	0.67	0.15	216.95	0.238

Table 4 The best explanatory models of bird species densities in the second half of winter. Environmental variables included in models are abbreviated as follows: abundance of Birch (Birch), Rowan (Rowan) and Spruce (Spruce) seeds, average minimum winter temperature (Winter), winter severity, defined as the number of days with minimum temperature below −20 °C (Severity), and date of the start of permanent snow cover (Snow)

	Coefficients									
Species	Const.	Birch	Rowan	Spruce	Winter	Severity	Snow	R^2	AIC	P
Red Crossbill	-3.4			1.89		-1.96	0.21	0.46	89.84	<0.001
Eurasian Siskin	3.9			1.40		-0.26		0.25	174.74	0.042
Common Redpoll	-4.4	3.09				-0.41	1.59	0.22	232.21	0.079
Bohemian Waxwing	3.7		1.27		1.61	-0.54		0.34	157.56	0.010

Winter severity and bird densities in the second half of winter

Checking for multicollinearity revealed low VIF and Tolerance values, so all six variables were retained. Annual fluctuations in the densities for all species showed statistically significant relationships with two or three of the variables (Table 4). Environmental variables explained from 22.4 to 46.1% of the variability (R^2) of the changes in densities of different species (Table 4). Abundance of all bird species was negatively associated with winter severity, two species were positively related with the abundance of Spruce seeds and the date of the start of permanent snow cover, and the abundance of one species was associated with the abundance of Birch and Rowan seeds, and average minimum winter temperature (Table 4).

Discussion

Winter numbers of the four studied species were subject to considerable annual fluctuations making it harder to identify population changes. However, contrary to the opinion that climate warming will contribute to a decrease in the populations of boreal species, our study showed that the numbers of the studied bird species increased significantly in the east of Europe. The increase in the number of birds in our study was mainly due to an increase in temperature during the summer nesting period, a later start of winter, a decrease in the number of severe cold days, and tree seed abundance. Yields of Birch, Rowan, Pine, and Spruce seeds tended to increase, but any trend was masked by substantial annual fluctuations. The seed yield of the selected tree species is also controlled by climate change (Gallego Zamorano et al. 2018). In our region the densities of the bird species changed between years by several orders of magnitude, thus long term studies are necessary to detect any underlying trend. In our study, the Common Redpoll had the largest fluctuations in abundance. Elsewhere in Europe, the winter bird populations of these species also changed significantly during the last three decades, again against a background of considerable fluctuations from year to year. However, for most of the studied species, trends in other European countries differed markedly from those presented here. In Sweden in the middle of winter (Christmas census), numbers of Eurasian Siskin, Common Redpoll and Red Crossbill significantly decreased (Lehikoinen et al. 2016; Green et al. 2021). In Finland, also in mid-winter, Common Redpoll and Red Crossbill decreased (Lehikoinen et al. 2016; Lehikoinen & Tirri 2021). In Denmark, Red Crossbill (particularly in the last 10 years), Eurasian Siskin and Common Redpoll significantly decreased (Lehikoinen et al. 2016; Eskildsen et al. 2021) and in the Netherlands, Eurasian Siskin and Common Redpoll decreased (Lehikoinen et al. 2016; Indexen wintervogels www.sovon.nl 2021). In Estonia (Elts 2016), the numbers of Common Redpoll and Bohemian Waxwing fluctuated by too much to determine a clear trend; but the numbers of Eurasian Siskin were stable over the studied period. Our results for these species differ markedly, with trends in the opposite direction. However, changes in numbers of Bohemian Waxwing (in Finland and Sweden), Eurasian Siskin (in Finland) and Red Crossbill (in the Netherlands) were very similar. In other European countries, no unambiguous reasons for the changes in the numbers of winter forest birds have been found so far (Fraixedas et al. 2015; Meller et al. 2016; Ferry et al. 2020). It is likely that the reasons will be complex (Ram et al. 2017; Askeyev et al. 2018, 2022).

PCA revealed that there were both similarities and dissimilarities in the long-term dynamics of the studied species. Separate positions in the first two components were shown for “coniferous” species (Eurasian Siskin and Red Crossbill) and for mainly “deciduous-mixed” species (Common Redpoll and Bohemian Waxwing) in winter. This clearly shows differentiation in the dynamics of their densities. Similar responses to environmental factors that regulate abundance affect species within the same group. We can thus identify with confidence those environmental factors playing a major role in influencing population dynamics.

Our analysis using CCA identified factors affecting the densities of seed-eating birds during the first half of winter. The temperatures in summer and food supply at, and before, the beginning of winter were key drivers. We then tested hypotheses about the influence of environmental factors on long-term dynamics of the populations, where we analyzed the effect of seed yield, seasonal phenomena of the start of winter, and temperature regime during the breeding season on the populations of seed-eating birds. The densities of two bird species, Eurasian Siskin and Bohemian Waxwing, were significantly related to summer temperature. This is very consistent with the fact that, during the nesting period, these two species feed their chicks mainly with insects. In warm summers the productivity of these bird species is therefore likely to increase. Positive relationships were found between the date of the start of winter (permanent snow cover) and the densities of Red Crossbill, Common Redpoll and Bohemian Waxwing in the first half of winter, i.e. if winter started later, densities were higher. Apparently, snow cover does not limit the availability of food for these species (Newton 2008). However, staying in one place while there is enough food, and moving on along the migration route when food runs out, as previously suggested (Haila et al. 1986; Payevsky 2015), is, in our opinion, not the complete picture of the winter life of these species. An early start of severe frosts in combination with snow cover on branches of trees and very short daylight hours will encourage birds to migrate further south. Birds seem to have mechanisms to look beyond the "event horizon" allowing them to predict the future development of the situation. Therefore, the idea that birds simply move progressively further from their breeding areas during winter, stripping seed and fruit crops as they go (Newton 2008) may be too simple an explanation. Our 30-year monitoring suggests that higher numbers of these species in the first half of winter are influenced by warmer summers in the nesting area, an abundant food supply, and a later onset of winter.

In contrast to many others, we do not suggest that only a single factor influences bird densities during winter. Most studies devoted to the dynamics of the number of birds in winter broadly interpret the change in the numbers of these four species as influenced by the food supply. In Finland, there was a strong correlation between Bohemian Waxwing abundance and Rowan yield (Lehikoinen et al. 2010; Fraixedas et al. 2015; Suhonen & Jokimäki 2015; Kanerva et al. 2020). In addition, it was noted that a strong drop in numbers at the end of winter, compared to the first half, occurred because Bohemian Waxwings ate all the Rowan berries and departed (Lehikoinen et al. 2010). Many authors have noted a very strong relationship between the abundance of Eurasian Siskin and the seed productivity of Spruce and Birch (Hogstad 1967; Formozov 1976; Sjöberg et al. 2007; Newton 2008; Lehikoinen et al. 2010; Fraixedas et al. 2015). The winter numbers of Common Redpoll in Finland (Lehikoinen et al. 2010) and in Norway (Dale 2021) depends on the seed yield of Birch. Common Redpoll numbers frequently fell in Finland in the second half of winter (Lehikoinen et al. 2010). During winter, Red Crossbill concentrates in areas where spruce cones are abundant (Newton 1998, 2008) and it is well known that their winter numbers depend on the yield of Spruce (Reinikainen 1937; Formozov 1976; Lehikoinen et al. 2010; Fraixedas et al. 2015). Compared to insectivorous bird species in winter in Eastern Europe (Askeyev et al. 2018), the population trend in seed-eaters was more pronounced in the second half of winter than in the first. The drop in numbers in the second half of winter is smaller than that of insectivores. However, our data show a very strong relationship between winter severity and the number of seed-eating birds in the second half of the winter. Granivorous birds can, of course, cope with severe frosts better than, for example, Goldcrest or Tits. However, it is likely that mortality is almost certainly heavy in severe winters. Strong adhesion of snow and ice to tree branches can make it difficult for even seed-eaters to get food. This combination, with a decrease in seeds towards the end of winter, increases mortality. We suggest that only a combination of the influence of various environmental factors can cause such responses in birds. The idea that low bird abundance in winter is determined only by the availability of food is not sufficiently comprehensive. Indeed, in some years when there are rich seed crops, birds from the north do not migrate to our study region, but likely settle in good feeding areas further north. Certainly, changes in snow depth can affect bird movements in winter, but can also affect migration patterns and change in species ranges (Bosco et al. 2022; Deshpande et al. 2022). Without taking into account seasonality or monthly changes in the natural environment, merely interpreting numbers of seed-eating birds has limitations. Using counts from only a short time window (e.g. Christmas census) can lead to unreliable information about the actual number of birds. For example, if we used only data on Bohemian Waxwing at the start of January, we might conclude that densities in the second half of winter were higher than at the start of winter. But the pattern in the second half of winter can be completely different. There are pronounced seasonal dynamics that can indicate significant spatial movements of bird populations during winter and for the correct estimation of numbers we need to census throughout the season.

We have shown clear trends in the winter densities of seed-eating birds in this region of Russia, and the influence of climate change and the food supply on those changes. For most of these birds living in Tatarstan, winter movements and mortality can play an important role in regulating numbers. In addition, the observed food supply in recent years has met the energy needs of seed-eating species during our harsh winters. At the present time, for many forest birds in Eastern Europe, an era of "great abundance" may have begun. The number of both granivorous and insectivorous bird species of various sizes and orders has been growing rapidly (Askeyev et al. 2018, 2020, 2022). But how long will this "golden age" last, and will it all collapse in a biblical manner? Despite the obvious favourable trend of climate change in Eastern Europe, nature continues to present "surprises". For example, after an incredibly hot and dry summer in 2010, the following winter was one of the snowiest, with snow still more than 1 m deep in March 2011. Weather contrasts, within a month or even a single week, can reach catastrophic levels, and record breaking maximum and minimum temperatures (in a 200 year climate history) can be experienced in the same year. Climate change in the boreal zone can lead to very complex changes in ecosystems and in the numbers of individual bird species (Dale 2021). The answers to many questions on birds and climate can only be provided by long-term monitoring of abundance across a large territory and throughout all seasons of the year.

References

Askeyev, O.V., Sparks, T.H., Askeyev, I.V. & Tryjanowski, P. (2009) Spring migration timing of Sylvia warblers in Tatarstan (Russia) 1957-2008. Central European Journal of Biology, 4, 595-602. DOI: 10.2478/s11535-009-0046-9

Askeyev, A., Askeyev, O. & Askeyev. I. (2017a) Long-term woodpecker winter population dynamics in the Tatarstan Republic. Vogelwelt, 137, 130-133.

Askeyev, O., Askeyev, A. & Askeyev. I. (2017b) Bird winter population dynamics at the eastern edge of Europe. Vogelwelt, 137, 134-142.

Askeyev, O., Askeyev, A. & Askeyev. I. (2018) Recent climate change has increased forest winter bird densities in East Europe. Ecological Research, 33, 445-456. DOI 10.1007/s11284-018-1566-4

Askeyev, O., Askeyev, A., Askeyev. I. & Sparks, T. (2020) Rapid climate change has increased post-breeding and autumn bird density at the eastern limit of Europe. Ecological Research, 35, 235-242. DOI: 10.1111/1440-1703.12079

Askeyev, A.O., Askeyev, O.V, Askeyev. I.V. & Sparks, T.H. (2022) Woodpecker populations in winter in the interior of the European continent are highly dependent on climate change and its consequences. Journal of Ornithology, 163, 481-493. DOI: 10.1007/s10336-021-01960-3

Bosco, L., Xu, Y., Deshpande, P. & Lehikoinen, A. (2022) Range shifts of overwintering birds depend on habitat type, snow conditions and habitat specialization. Oecologia, 199, 725-736. DOI: 10.1007/s00442-022-05209-5

Dale, S. (2021) Mass occurrence and habitat selection of Common Redpolls (Carduelis flammea) after a large seed crop year: snow-covered ground facilitates food access. Journal of Ornithology, 162, 1087-1099. DOI: 10.1007/s10336-021-01912-x

Deshpande, P., Lehikoinen, P., Thorogood, R. & Lehikoinen, A. (2022) Snow depth drives habitat selection by overwintering birds in built-up areas, farmlands and forests. Journal of Biogeography, 49, 630-639. DOI: 10.1111/jbi.14326

Elts, J. (2016) A review of 29 years of mainland winter bird counts in Estonia. Technical report. Tartu: Estonian Ornithological Society Tartu.

Eskildsen, D.P., Vikstrøm, T. & Jørgensen M.F. (2021) Overvågning af de almindelige fuglearter i Danmark 1975-2020. Årsrapport for Punkttællingsprogrammet. Dansk Ornitologisk Forening. (in Danish).

Ferry, B., Rune, H., Andersson, U. & Green, M. (2020) Increasing numbers of wintering forest birds in Swedish Lapland 1986-2017 show stronger correlations with forest development than with local weather. Ornis Svecica, 30, 13-30. DOI: 10.34080/os.v30.19633

Formozov, A.N. (1960) La production de graines dans les forêts de conifères de la taiga de l'USSR et l'envahissement de l'Europe occidentale par certaines espèces d'oiseaux. Proceedings of the International Ornithological Congress, 12, 216-229. (in Russian).

Formozov, A.N. (1976) Animals, birds and their relationship with the habitat. Moscow: Nauka. (in Russian).

Fraixedas, S., Lehikoinen, A. & Lindén, A. (2015) Impacts of climate and land use change on wintering bird populations in Finland. Journal of Avian Biology, 46, 63-72. DOI: 10.1111/jav.00441

Gallego Zamorano, J., Hokkanen, T. & Lehikoinen, A. (2018) Climate-driven synchrony in seed production of masting deciduous and conifer tree species. Journal of Plant Ecology, 11, 180-188. DOI: 10.1093/jpe/rtw117

Green, M., Haas, F., Lindström, Å. & Nilsson, L. (2021) Övervakning av fåglarnas populationsutveckling Årsrapport för 2020 (Monitoring population changes of birds in Sweden. Annual report for 2020), Lund: Lund University Department of Biology.

Haest, B. Hüppop, O., van de Pol, M. & Bairlein, F. (2019) Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects. Global Change Biology, 25, 4064-4080. DOI: 10.1111/gcb.14746

Haila, Y. Tiainen J. & Vepsäläinen, K. (1986) Delayed autumn migration as an adaptive strategy of birds in northern Europe: evidence from Finland. Ornis Fennica, 63, 1-9.

Hogstad, O. (1967) Density fluctuations of Carduelis spinus in relation to the cone crops of Norway Spruce. Sterna, 7, 255-260.

Indexen wintervogels. (2021) (bron: Netwerk Ecologische Monitoring, Sovon Vogelonderzoek Nederland & CBS, www.sovon.nl

Kanerva, A.M., Hokkanen, T., Lehikoinen, A., Norrdahl, K. & Suhonen, J. (2020) The impact of tree crops and temperature on the timing of frugivorous bird migration. Oecologia, 193, 1021-1026. DOI: 10.1007/s00442-020-04726-5

Kapper, V. (1926) Business crop in forestry in USSR Moscow: Nauka. (in Russian).

Koenig, W.D. & Knops, J.M.H. (2000) Patterns of annual seed production by Northern Hemisphere trees: a global perspective. American Naturalist, 155, 59-69. DOI: 10.1086/303302

Koenig, W.D. & Knops, J.M.H. (2001) Seed crop size and eruptions of North American boreal seed-eating birds. Journal of Animal Ecology, 70, 609-620. DOI: 10.1046/j.1365-2656.2001.00516.x

Lehikoinen, A., Väisänen, R.A & Hokkanen, T. (2010) Siemen-ja marjalintujen runsaus Suomessa erilaisina puiden satotalvina 1957-2009. Linnut-vuosikirja, 90-99. (in Finnish).

Lehikoinen, A., Foppen, R.P.B., Heldbjerg, H., Lindström, Å., van Manen, W., Piirainen, S., et al. (2016) Large-scale climatic drivers of regional winter bird population trends. Diversity and Distributions, 22, 1163–1173. DOI: 10.1111/ddi.12480

Lehikoinen, A. & Tirri, I. (2021) Changes in regional wintering abundances of birds in Finland. Linnut vuosikirja, 18-29. (in Finnish).

Meller, K., Vähätalo, A.V., Hokkanen, T., Rintala, J., Piha, M. & Lehikoinen, A. (2016) Interannual variation and long-term trends in proportions of resident individuals in partially migratory birds. Journal of Animal Ecology, 85, 570-580. DOI: 10.1111/1365-2656.12486

Newton, I. (1972) Finches. London: Collins.

Newton, I. (1998) Population limitation in birds. San Diego: Academic Press.

Newton, I. (2006) Advances in the study of irruptive migration. Ardea, 94, 433-460.

Newton, I. (2008) The migration ecology of birds. London: Academic Press.

Payevsky, V.A. (2015) True finches of the world. Moscow: KMK Scientific Press Ltd. (in Russian).

Piersma, T., Pérez-Tris, J., Mouritsen, H., Bauchinger, U. & Bairlein, F. (2005) Is there a ‘migratory syndrome’ common to all migrant birds? Annals of the New York Academy of Sciences, 1046, 282-294. DOI: 10.1196/annals.1343.026

Ram, D., Axelsson, A.L., Green, M., Smith, H.G. & Lindström, Å. (2017) What drives current population trends in forest birds – forest quantity, quality or climate? A large-scale analysis from northern Europe. Forest Ecology and Management, 385, 177-188. DOI: 10.1016/j.foreco.2016.11.013

Ravkin, Y.S. (1967) On the procedure of bird census in forest landscapes. Priroda ochagov kleshchevogo entsefalita na Altae, pp 66-75. (in Russian).

Reinikainen, A. (1937) The irregular migrations of the Crossbill, Loxia c. curvirostra, and their relation to the cone-crop of the conifers. Ornis Fennica, 14, 55-64.

Robinson, R.A. Crick, H.Q.P., Learmonth, J.A., Maclean, I.M.D., Thomas, C.D., Bairlein, F. et al. (2009) Travelling through a warming world: climate change and migratory species. Endangered Species Research, 7, 87-99.

Sjöberg, K., Pettersson, R.B., Ball, J.P. & Sundströmet, T. (2007) Seed crops of Norway spruce and winter habitat quality for boreal birds: old-growth compared with managed forests. Annales Zoologici Fennici, 44, 486-495.

Suhonen, J. & Jokimäki, J. (2015) Fruit removal from rowanberry (Sorbus aucuparia) trees at urban and rural areas in Finland: a multi-scale study. Landscape and Urban Planning, 137, 13-19. DOI: 10.1016/j.landurbplan.2014.12.012

Tishin, D. (2006) Influence of natural and climate factors on radial growth of main trees in Middle Volga region. PhD thesis, Kazan State University, Kazan, Russia. (in Russian).