Formation and Analysis of Long-Term Series of Bird-Population Observations at Key Sites as Way to Study Biodiversity

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Abstract—Studies of 35-year dynamics of the number of bird species and 80-year observations of their arrival on the western macroslope of the Barguzin Ridge have been carried out. A steady decrease in the total abundance of background bird species after 1997–1998 has been revealed. Shifts and cyclic changes in the time of bird arrival have been found. Twenty-six (40.0%) out of 65 species arrived statistically significantly earlier, 7 species (10.8%) arrived later, and 32 species (49.2%) had no statistically significant timing. Correlations have been established between the timing of the first recording of migratory bird species and their local abundance and habitat distribution. Some mechanisms for the formation of the local bird population have been disclosed, including using the redistribution of species breeding density between river valleys and habitats on an altitude profile.

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INTRODUCTION

The study of biodiversity in these regions and in certain key sites makes it possible to reveal the ways and means of the formation and conservation of individual groups of organisms and identify biota responses to long-term climate changes and the effects of anthropogenic factors. Moreover, it is very important to carry out such studies on a long-term basis in the same territories according to unified methods over a long, multiyear period. The territories of state nature reserves, in which the direct influence of human activity is excluded or minimized, can serve first and foremost as a basis for organizing long-term stationary observations. One such sufficiently studied model groups is birds. Long-term stationary observations of the abundance of a species make it possible to identify the peculiarities of its response to certain changes in environmental conditions that develop in a particular year. The organization and implementation of longterm ornithological observations in Russian reserves are focused on recording phenological phenomena in the life cycle of model species; regularly assessing the abundance and distribution of birds in space at constant key sites in the breeding, migration, and winter periods; and identifying the characteristics of the reproductive period, which creates the basis for monitoring biodiversity studies of this model animal group. Currently, highly rated journals are publishing many articles on the impact of climate on the biosphere,

including birds (Sokolov, 2010; Sokolov et al., 2017). Bird populations are considered good indicators of environmental change (Gregory et al., 2005; Stephens et al., 2016), including the phenology of their life cycle. Long-term studies of the timing of migration and development of animals, population dynamics, and the expansion of their habitats have become important scientific areas.

The goals of the study were to identify trends in long-term changes in the abundance of nesting birds on the model territory of the Barguzin Ridge, the transformation of the dates of their spring arrival over an 80-year period, and the discovery of the relationships between the local density of bird species and timing of their arrival.

MATERIALS AND METHODS

The long-term studies of birds were organized and performed in northeastern Baikalia in the territory of the Barguzinsky State Natural Biosphere Reserve $(54^{\circ}01'-54^{\circ}56' \text{ N}, 109^{\circ}28'-110^{\circ}22' \text{ E})$. The Barguzinsky State Reserve was founded in 1916 in a territory that is part of the Lake Baikal region and it has been a UNESCO World Natural Heritage Site since December 1996. It is of interest, first and foremost, as a wild-life territory in Baikalia that has never been exposed to human impact. Being located in undisturbed natural systems, the reserve territory can be considered a reference for identifying biota responses to global changes in the environment and climate.

The quantitative counts of birds on permanent routes in the valleys of three rivers (Bolshaya, Davsha, and Yezovka), which were divided into 11 sections, were carried out in the mountainous, subalpine, and alpine belts of the western macro-slope of the Barguzin Ridge (460-1700 m above sea level) in 1984-2018 (Ananin, 2010). The Bolshaya River has an extended wide valley with a relatively small slope; the counts cover an area of up to 45 km from the shore of Lake Baikal (460–630 m above sea level). The valley of the Davsha River (it flows into the Lake Baikal) has significant areas of meadows of ice origin with deciduous and mixed forests in its lower part; the upper part includes the subalpine and alpine sites (470–1700 m above sea level). The valley of the Yezovka River (which flows into Lake Baikal), which has the lowest heat supply, includes a swampy shore–plain site and a mountain forest belt (460– 1150 m above sea level). The list of accounting sites is given in the notes to Table 2. The total length of walking route surveys is 19290 km, including 8160 km in the nesting period. The abundance of birds was calculated using the method of Ravkin (1967).

Long-term climatic changes in the region were monitored based on measurements at the Barguzinsky Reserve Meteorological Station of the Irkutsk Head Department for Hydrometeorology and Environmental Monitoring in the settlement of Davsha (Ananina and Ananin, 2017), and differences in heat supply in the selected sites were monitored by our year-round observations of air temperatures using automatic thermochron recorders (type DS1921G) (Ananina and Ananin, 2019).

The timing of bird arrivals was estimated for the period from 1938 to 2018 based on our own observations (1984–2018) and using the materials of the Chronicles of Nature of the Barguzinsky Reserve (1936–1983). Nonparametric methods were used to evaluate statistical parameters (the presence of a correlation between the numbers and factors). To assess the strength of the relationship, the Kendall rank correlation coefficient (r_{τ}) was used, and long-term trends of changes in the parameters were assessed by constructing a trend using the linear approximation method (Korosov, 2007). According to Korosov (2007), the values of the approximation coefficient R^2 (the share that the trend occupies in the overall dynamics) in the range from 12 to 51% can be considered statistically significant parameters and make it possible to perform a comparative analysis. Statistical calculations were implemented using the Statistica 10.0 and Excel 7.0 software packages.

RESULTS

Over the past 60 years, significant climate changes have been recorded in the key site (Fig. 1) (Ananina

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and Ananin, 2017). They were manifested in the warming of the spring and summer months and, as a result, in the increase in the average annual air temperature, which coincides with the general logic of global warming. The linear trend of the average annual air temperature is positive ($r_{\tau} = 0.421$, at p < 0.05). The temperature conditions of winter months (with the exception of February) and autumn months (with the exception of September) did not substantially transform (Ananina and Ananin, 2017). The average annual precipitation up to 2013 did not significantly change, and in 2014–2018 precipitation was much less than normal both in winter and in the warm period. Taken together, climate changes have led to increased aridity of the climate and, to some extent, to a growth in its continentality.

The total number of bird species recorded in the territory of the Barguzinsky Reserve is 290; 144 of them have been proven to nest there, and another 11 species are probably nesting. With increasing altitude, the number of species recorded on the accounting routes gradually decreases from 103 on the Baikal terraces (the shore—plain site) to 43 in the alpine belt.

A long-term change in bird abundance in the key site of the Barguzinsky Ridge was considered. A steady decrease in the total bird abundance was revealed in the period after 1997–1998 (Fig. 2).

In the territory of the Barguzinsky Reserve, longterm (1938–2018) shifts in the spring bird-arrival dates were established: of the 65 bird species included in the analysis, 26 (40.0%) began to arrive statistically significantly (p < 0.05) earlier, 7 species (10.8%) began to arrive later, and 32 species (49.2%) did not have any statistical significant change in their timing (Table 1). The timing of the spring arrival was found to have no correlation with wintering places and the length of the migration route.

For many migratory and wintering species, an increase in nesting density was revealed in the years with earlier timing of spring phenophases (Table 2) (Ananin, 2011).

It was hypothesized that there was a correlation between the nesting density of migrant birds and the timing of their arrival at the key site (Ananin, 2010). To test this hypothesis, we analyzed the relationships between the interannual density variations of some bird species in the habitats of the key site of the Barguzin Ridge with the timing of their arrival at the shores of the Lake Baikal in 1984–2018. To assess such an effect, 16 background species were selected as models: 14 distant migrant species: the gray gull (Tringa ochropus (L. 1758)), common sandpiper (Actitis hypoleucos (L. 1758)), eastern turtle dove (Streptopelia orientalis Latham, 1790), cuckoo (Cuculus canorus (L. 1758)), oriental cuckoo (Cuculus optatus (Gould, 1845)), gray wagtail (Motacilla cinerea (Tunstall, 1771)), brown shrike (Lanius cristatus (L. 1758)), Siberian accentor (Prunella montanella (Pall., 1776)), eastern red-breasted flycatcher (Ficedula albicilla (Pall.,



Fig. 1. Time series of average annual air temperature (a), the amount of annual precipitation (b) and their linear trends (with division by decades) on the northeastern shore of Lake Baikal (Barguzinsky Reserve State Meteorological Station, Davsha, 1955–2015).

Order	Number of species							
Oldel	total	species arriving earlier	species arriving later	species arriving on the same dates				
Anseriformes	8	3 (37.5%)	1 (12.5%)	4 (50.0%)				
Falconiformes	8	2 (25.0%)	2 (25.0%)	4 (50.0%)				
Gruiformes	1			1				
Charadriiformes	8	2 (25.0%)		6 (75.0%)				
Columbiformes	1	1						
Cuculiformes	2	2						

15 (41.7%)

25 (38.5%)

4 (26.7%)

21 (42.0%)

 Table 1. Change in the timing of bird arrival in the Barguzinsky Reserve in 1938–2018

1

36

65

15

50

Bucerotiformes

Passeriformes

Near migrants

Distant migrants

Total

4 (11.1%)

7 (10.8%)

4 (26.7%)

3 (6.0%)

1

17 (47.2%)

33 (50.7%)

7 (46.6%)

26 (54.0%)



Fig. 2. Dynamics of the density of the summer bird population in the key site of Barguzin Ridge (1984–2018, the first half of the summer, individuals/km²); the dashed line is a linear trend.

1811)), red-flanked bluetail (*Tarsiger cyanurus* (Pall., 1773)), bramble finch (*Fringilla montifringilla* (L. 1758)), and two near migrant species: the red-throated thrush (*Turdus ruficollis* (Pall., 1776)) and pine bunting (*Emberiza leucocephalos* (Gmelin, 1771)).

Statistically significant correlations of the nesting density of a species with arrival dates in one habitat were recorded for the species that have a maximum abundance in only one area from the entire spectrum of accounting routes in the key site: for the gray gull,

Species	Spring phenophases								
Species	snowy	mixed	bare	green					
Parus ater		MF-D (+)*	LP-B (+)**, LM-B (+)*						
Parus montanus	LM-D (–)*			UM-D (–)*					
Sitta europaea			SP-B (+)*						
Tetrastes bonasia			MF-D (–)*	UM-Y(+)**					
Dendrocopos major	MF-D (-)*, SP-D (-)*, LM-D (-)*								
Phylloscopus proregulus			SP-B (-)*, SP-Y (-)*, LM-D (-)*						
Tarsiger cyanurus	KS (-)*, SP-Y (-)*, LM-Y (-)*		LM-B (+)*, SP-Y (-)**	KS (-)*, UP-B (-)*, LM-Y (-)*					
Anthus hodgsoni	LM-B (+)*	SP-B (+)**, LP-B (+)*	SP-B (+)*						
Spinus spinus	MF-D (+)*, SA-D (+)**								
Phylloscopus trochiloi- des	SP-B (–)*			LM-Y (+)*					
Phylloscopus inornatus	KS (-)*, LM-Y (-)*, SP-D (-)*			SP-B (-)*					
Motacilla cinerea		LP-B (+)**, SP-D (-)*							

Table 2. Correlations of nesting bird abundance with the timing of onset of spring subseasons (r_{τ} , *p < 0.05, **p < 0.01)

* (+) Correlation is positive; (-) correlation is negative. Names of sites: KS, key site; SP, shore-plain site; LP, lower part of the plain moraine site; UP, upper part of the plain moraine site; LM, lower part of the mountain forest belt; UM, upper part of the mountain forest site; MF, mountain-forest site; SA, subalpine-alpine site; D, site in the Davsha River valley; Y, site in the Yezovka River valley; B, site in the Bolshaya River valley; *Parus ater*, designation of wintering bird species.

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Table 3. Assessment of the relationship between the density of some bird species in the habitats of the key site of Barguzin Ridge with the dates of their arrival on the shore of Lake Baikal in 1984–2018 (Kendall tau correlation coefficient (r_{τ}), *p < 0.10, **p < 0.05, and ***p < 0.01; other values are statistically insignificant; they are not shown in the table)

Species/Habitat	1	2	3	4	5	6	7	8	9	10	11	12	13
Tringa ochropus Actitis hypoleucos				0.22*		-0.23*	0.41***		-0.23*				
Streptopelia orientalis				0.23*									0.22*
Cuculus canorus		-0.29**		-0.33**					0.23*				
Cuculus optatus							-0.27^{**}						
Motacilla cinerea								0.24*		0.25**	0.37**	0.41***	0.25**
Lanius cristatus						-0.29**							
Prunella monta- nella			0.26**										
Ficedula albicilla					-0.29**		0.26**					-0.46***	
Tarsiger cyanurus	0.17*									0.18*			
Turdus ruficollis											-0.22*		
Fringilla mon- tifringilla								-0.29**					
Emberiza leucocephalos						0.16*							

*(1) Shore—plain site in the valley, (2) lower part of the mountain forest site of the Davsha River valley, (3) upper part of the mountain forest site of the Davsha River valley, (4) forest belt of the Davsha River valley, (5) subalpine—alpine site of the Davsha River valley, (6) shore—plain site of the Bolshaya River valley, (7) lower part of the plain moraine site of the Bolshaya River valley, (8) upper part of the plain moraine site of the Bolshaya River valley, (9) lower part of the mountain forest site of Bolshaya River valley, (10) lower part of the mountain forest site of the Yezovka River valley, (11) upper part of the mountain forest site of the Yezovka River valley, (12) forest belt of the Yezovka River valley, and (13) entire key site.

brown shrike, Siberian accentor, red-throated thrush, pine bunting, and bramble finch (Table 3).

The common sandpiper, oriental turtle dove, gray wagtail, and eastern red-breasted flycatcher have a maximum abundance in several areas of the key site that cover several habitats; they were revealed to have several territories with statistically significant correlations of abundance with arrival dates.

An increase in the nesting density of different species can be recorded both in the case of an earlier arrival (Oriental cuckoo, brown shrike, red-throated thrush, and bramble finch) and in case of a relatively late arrival (gray gull, oriental turtle dove, gray wagtail, Siberian accentor, red-flanked bluetail, and pine bunting).

For some species, an early arrival is accompanied with an increase in abundance in some areas and its decrease in other high-altitude sections (common sandpiper, cuckoo, and eastern red-breasted flycatcher).

The choice of optimal conditions for a species in a given year can occur by redistribution between sites within the same altitude zone (between river valleys with different heat-supply conditions), as well as due to vertical movements between sites on a vertical ecological profile and between different altitude sections, which may be evidenced by the multidirectional changes in the nesting abundance of species in various habitats.

This hypothesis was considered based on a model group including 35 bird species by analyzing the longterm dynamics of their abundance in seven sites for the period of 1984–2018. It included 9 wintering species. 4 near-migrant species, and 22 distant migrant species wintering mainly in Southeast and South Asia. An analysis of the correlation of long-term changes in the nesting abundance of these species was performed for the shore–plain site (460–520 m above sea level), the lower part of the plain moraine site (520-560 m above the sea level), the upper part of the plain moraine site (560-580 m above sea level), and the lower part of the mountain forest site (580-630 m above sea level) of the Bolshaya River valley, as well as the shore-plain site (470–515 m above sea level), the lower part of the mountain forest site (515–720 m above sea level), and the upper part of the mountain forest site (720-1280 m above sea level) of the Davsha River valley. Each of the sites had a characteristic set of habitats with a different structure of vegetation.

The redistribution of the species population density between the river valleys has been established for two bird species—distant migrants (gray gull and eastern red-breasted flycatcher). This confirms the revealed statistically significant negative correlation of the long-term abundance dynamics of the gray gull in the lower part of the mountain forest belt in the Davsha River valley with changes in the abundance of the species in the lower part of the mountain forest belt $(r_{\tau} = -0.312, p < 0.05)$ and the adjacent upper part of the plaint moraine site $(r_{\tau} = -0.302, p < 0.05)$ in the Bolshaya River valley. The abundance dynamics of the eastern red-breasted flycatcher has a negative correlation between the shore—plain sites of the Bolshaya and Davsha rivers $(r_{\tau} = -0.308, p < 0.05)$.

Altitudinal redistribution that is defined as the presence of a negative correlation of the long-term nesting abundance dynamics for a species between sites located at different levels of the vertical ecological profile was revealed for four long-distance migrant species: the common sandpiper, oriental turtle dove, Indian tree pipit (Anthus hodgsoni (Richmond, 1907)), and greenish warbler (Phylloscopus trochiloides (Sundevall, 1837)), as well as for long-term changes in the summer abundance of one wintering species, the white-winged crossbill (Loxia leucoptera (Gmelin, 1789)). In addition to the existing positive correlations, the white-winged crossbill has a statistically significant negative correlation ($r_{\tau} = -0.277, p < 0.05$) between fluctuations in species abundance in the nesting period in the shore-plain site in the Bolshaya River valley and in the upper part of the mountain forest belt in the Davsha River valley.

Changes in the nesting abundance of the common sandpiper are opposite in direction ($r_{\tau} = -0.378$, p < 0.05) between the sites in the Bolshaya River valley located near the shore of Lake Baikal and the sites that are the most distant from it. A statistically significant negative correlation ($r_{\tau} = -0.392$, p < 0.05) was revealed between fluctuations in nesting abundance of the oriental turtle dove in the shore–plain site of the Bolshava River valley and in the lower part of the mountain forest belt of the Davsha River valley, while a positive correlation was established between the shore-plain sites of the Bolshaya and Davsha River valleys ($r_{\tau} = +0.276$, p < 0.05), indicating the absence of redistribution between the river valleys within the same altitude level. Similar negative correlations were found for the abundance dynamics of the Indian tree pipit ($r_{\tau} = -0.303$, p < 0.05, between the shore-plain site of the Bolshaya River valley and the upper part of the mountain forest site in the Davsha River valley) and the greenish warbler ($r_{\tau} = -0.3007, p < 0.05$, between the lower part of the plain moraine site and the lower part of the mountain forest belt in the Bolshaya River valley).

Positive statistically significant correlations were revealed for long-term changes in nesting abundance of species in various parts of the key site in the group of near migrants: the common wren (*Troglodytes troglodytes* (L., 1758)), Eurasian siskin (*Spinus spinus* (L., 1758)), gray bullfinch (*Pyrrhula cineracea* Cabanis, 1872), and pine bunting, as well as for the background wintering bird species: Eurasian nuthatch (*Sitta europaea* (L., 1758)), coal titmouse (*Parus ater* (L., 1758)), willow tit (*Parus montanus* Conrad von Baldenstein, 1827), Siberian jay (*Perisoreus infaustus* (L., 1758)), hazel grouse (*Tetrastes bonasia* (L., 1758)), great spotted woodpecker (*Dendrocopos major* (L., 1758)), Eurasian long-tailed tit (*Aegithalos caudatus* (L., 1758)), and common treecreeper (*Certhia familiaris* (L., 1758)).

The absence of intervalley and altitudinal redistribution on the western macroslope of the Barguzin Ridge was found for most background bird species from the group of distant migrants: the cuckoo, oriental cuckoo, gray wagtail, taiga flycatcher (Ficedula mugimaki (Temminck, 1835)), brown shrike, Siberian blue robin (Luscinia cyane (Pall., 1776)), Siberian rubythroat (Luscinia calliope (Pall., 1776)), redflanked bluetail, Pallas's warbler (Phylloscopus proregulus (Pall., 1811)), vellow-browed warbler (*Phyllosco*pus inornatus (Blyth, 1842)), dusky leaf warbler (Phylloscopus fuscatus (Blyth, 1842)), Pallas's grasshopper warbler (Locustella certhiola (Pall., 1811)), bramble finch, black-faced bunting (Ocyris spodocephalus (Pall., 1776)), yellow-browed bunting (Ocyris chrysophrys Pall., 1776), and common rosefinch (Carpodacus erythrinus (Pall., 1770)). For these species, only positive correlations were found between fluctuations in nesting abundance in different habitats of the key site.

DISCUSSION

It is believed that certain climate changes can cause long-term changes in bird abundance (Sokolov, 2010; Sokolov et al., 2017), which have an effect on food supply; nesting suitability of the territory; and, through them, on the efficiency of reproduction and mortality in populations. However, in order to identify the effect of climate on the long-term bird abundance dynamics, it is necessary to carry out long-term monitoring of the state of birds in the same region.

A long-term decrease in bird abundance in the key site of the western macroslope of the Barguzin Ridge coincides in time with the arid precipitation phase of the long climate cycle in the region (Noskova et al., 2019), which is accompanied by the development of drought in the vast territories of the Cis-Baikal and Trans-Baikal regions. The humid (wet) phase of this climate cycle was detected in 1983–1998. The periods of high and low abundance in the populations of background bird species in the region are probably caused by this climatic cycle, and a further increase in bird abundance in the observation area is expected.

The phenology of the spring arrival of migratory birds has been intensively studied in many regions of the world (Vähätalo et al., 2004; Rainio et al., 2006; Jonzén et al., 2006; Pulido, 2007; Knudsen et al., 2011; Lehikoinen et al., 2019). The transformations in the seasonal timing of recording the phenological phases in the life cycles of individual bird species can be real responses to long-term climatic changes, which is also confirmed by our studies (Ananin, 2002; Ananin and Sokolov, 2009).

The first arrival dates are known to be sensitive to changes in population size (Mills, 2005; Miller-Rushing et al., 2008; Lindén, 2011; Lehikoinen et al., 2019). Our earlier studies, including observations of bird arrivals up to 2007 (Ananin and Sokolov, 2009) revealed that 28 out of 54 bird species (51.8%) began arriving earlier, 15 species (27.8%) began arriving on average later, and 11 species (20.4%) had no significant changes in the timing. The decrease in the number of species with earlier and later arrival is probably due to a slowdown in regional warming in the last decade (Ananina and Ananin, 2017; Noskova et al., 2019) and the corresponding shift in recording arrival dates to the dates that were noted in the period before the significant increase in spring temperatures in the region. As a result, the dynamics of the timing of arrival has acquired the character of nonperiodic fluctuations for a large number of species or returned to the values of the period before the early 1980s.

Multidirectional changes in the timing of arrival in northeastern Baikalia are noted both in the group of near migrants and in bird species making long-distance flights. Some studies have suggested that near migrants have shifted their arrival dates to a greater extent than distant migrants (Rubolini et al., 2007; Usui et al., 2017), while other studies have not found such a pattern (Jonzén et al., 2006; Knudsen et al., 2011). Our data confirm the hypothesis that the proportion of species that have begun to arrive earlier is higher among distant migrants than among near migrants, but, at the same time, shifts in arrival dates are not statistically significant in about half of species from each group (Table 1).

The analysis of the results of checking the hypothesis about the relationship between the arrival dates of bird species and their nesting abundance in individual sites showed that statistically significant correlations were found in the optimal species habitats in the key site of the Barguzin Ridge. Such territories are regularly used by species for nesting with a high local density. The abundance in suboptimal habitats with a smaller local abundance and its higher interannual variability is usually not statistically related to the dates of the first recording of a species during spring migration.

The factors that have a modifying effect on the formation of the bird population may be the conditions of the current spring, the time frame within which habitats acquire properties such as nesting and feeding suitability. In this case, the readiness of habitats for the start of nesting of a species is determined, in particular, by the timing of the onset of phenological phenomena in a natural complex. Meanwhile, the heatsupply indices can be considered an indicator of the phenological readiness of a habitat for nesting and its food supply (Ananin, 2010). Thus, the proposed hypothesis has been confirmed in the habitats of the key site of the Barguzin Ridge that are optimal for the species.

Returning from wintering places, birds make searching movements in the pre-nesting period, identifying the territories which are the most favorable for nesting in a particular year. Moreover, their actions correspond to the general trend of bird evolution—the development of ways to avoid unfavorable environmental conditions rather than adapt to them. Migratory bird species are significantly more connected with the course of spring phenological processes and heatsupply parameters of the nesting area at the beginning of nesting in the year of observations.

Wintering bird species have low correlations of nesting abundance with the timing of the onset of spring subseasons. This timing of the onset of spring phenological phenomena only slightly affects the formation of a local population. The processes of the formation of a local population for wintering species are implemented mainly during the late summer and autumn movements and migrations and are determined, first and foremost, by the availability of feed in the winter period (Ananin, 2019).

The choice of optimal conditions for a species in the current year is determined by the nesting suitability of the territory and its potential for providing feed for both adult birds and chicks during feeding. In this case, both synchronization of changes in the breeding abundance of birds and redistribution of local density between sites within the same altitude zone (between the river valleys) or between sites on a vertical ecological profile in the form of asynchronous changes in local abundance in different habitats can be observed. The hypothesis of the presence of intervalley and altitudinal redistribution as one of the main ways of choosing breeding habitats has been confirmed only for five distant migrant species and one wintering species, but it has not been confirmed for most other bird species.

The redistribution of bird species between habitats is induced by the heat-supply parameter (sum of active temperatures in spring and early summer). Moreover, the detected asynchronous change in the abundance of the common sandpiper between the sites in the Bolshava River valley that are located within the same altitude level at different distances from the shore of the Lake Baikal was confirmed by the increase in the heat supply in habitats with growing distance from the lake, which was detected using thermochrons (Ananina and Ananin, 2019). In the years with a cold spring, these waders settle in the areas that are predominantly remote from Lake Baikal, and in the warmer years they choose habitats that are closer to the shore. The redistribution of local abundance between the river valleys within the same altitude level was recorded for long-distance migrants-the gray gull and eastern red-breasted flycatcher.

Asynchronous changes in abundance between habitats of different high-altitude sites were detected in local populations of the oriental turtle dove, Indian tree pipit, and greenish warbler. The altitudinal redistribution of white-winged crossbills in the summer is associated with the lack of synchronization of food supply (the presence and amount of the yield of Chekanovsky's larch, Larix czekanowskii Szaf.) on the shore of Lake Baikal and in the upper part of the mountain forest belt on the western macroslope of the Barguzin Ridge in the autumn and winter of the previous year. In other cases, such redistributions also correlate with food supply and readiness of habitats for nest construction (their nesting suitability) in the current year, which are related with differences in the sum of active temperatures in these areas. No asynchronous changes in local abundance were detected in near migrants and most wintering bird species, in which the distribution by habitats is proportional to the size of local populations. This group of bird species is characterized by a rather long period between the appearance at the nesting sites and the beginning of nest construction.

Changes in abundance in local populations of species in different altitude belts and between the river valleys with different conditions most often occur synchronously. They are determined by population changes in species abundance and the number of individuals that have completed migratory movements and settled in the region to nest.

CONCLUSIONS

The analysis of 35-year-old series of bird population dynamics and 80-year observations of the dates of their spring arrival at the key site revealed the patterns of long-term changes in the local abundance of background species on the altitude profile and in the valleys of three rivers with different conditions. The total abundance of background bird species was found to steadily decrease in the period after 1997–1998, which is due to the arid precipitation phase in the long-term climatic cycle in the Cis-Baikal and Trans-Baikal Regions.

Shifts and cyclical changes in the timing of bird arrival were established. Of 65 bird species, 26 species (40.0%) began arriving statistically significantly earlier, 7 species (10.8%) began arriving later, and 32 species (49.2%) had no statistically significant changes in the timing.

Relationships between the arrival dates of migrating bird species and changes in their local abundance and distribution by habitats were revealed. Some mechanisms of the formation of a local bird population were disclosed, including with the use of redistribution of nesting species density between the river valleys and sites located in different altitudinal sections. Intervalley redistribution was recorded in the gray gull and eastern red-breasted flycatcher, and altitudinal redistribution was observed in the Indian tree pipit, greenish warbler, oriental turtle dove, common sandpiper, and white-winged crossbill.

Based on the patterns that were identified, it is possible to build qualitative and quantitative forecasts of responses to long-term climatic changes—changes in the abundance and distribution of local bird populations in mountain conditions.

Returning from wintering places, birds make searching movements in the prenesting period, identifying territories that are the most favorable for nesting in the current year. Compared to wintering bird species, migratory bird species are significantly more connected with the timing of spring phenological processes and the heat-supply parameters of the nesting area in the year of observation. Many migratory species are characterized by increased nesting density in years with earlier periods of spring phenophases.

Wintering species have low correlations of nesting abundance with the timing of the onset of spring subseasons, which only slightly affect the formation of a local population.

As a result, it should be concluded that the diversity of the landscape from the viewpoint of available habitats that is typical for the macroslope of the Barguzin Ridge makes birds react to the unsuitability of conditions by developing ways to avoid unfavorable environmental conditions, rather than adapt to them, which is supposedly the general trend of bird evolution as an individual branch of animal evolution.

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COMPLIANCE WITH ETHICAL STANDARDS

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

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REFERENCES

Ananin, A.A., The influence of climate changes on phenology of birds of Barguzin Nature Reserve, Materialy Mezhdunarodnogo simpoziuma "Mnogoletnyaya dinamika chislennosti ptits i mlekopitayushchikh v svyazi s global'nymi izmeneniyami klimata" (Proc. Int. Symp. "Long-Term Population Dynamics of Birds and Mammals Related with Global Climate Change"), Kazan: Novoe Znanie, 2002, pp. 107–112.

- Ananin, A.A., Pritsy Severnogo Pribaikal'ya: dinamika i osobennosti formirovaniya naseleniya (Dynamics and Population Development of Birds of Northern Cis-Baikal Region), Ulan-Ude: Buryat. Gos. Univ., 2010.
- Ananin, A.A., The influence of spring phenological terms upon formation of the bird nested population in landscape-zone gradient of Northeastern Cis-Baikal Mountains, *Vestn. Tomsk. Gos. Univ., Biol.*, 2011, no. 4 (16), pp. 66–79.
- Ananin, A.A., Long-term changes of the winter bird population in Northeastern Cis-Baikal region, *Vestn. Tversk. Gos. Univ., Ser. Biol. Ekol.*, 2019, no. 1 (53), pp. 7–14.
- Ananin, A.A. and Sokolov, L.V., Long-term arrival trends of 54 avian species to Barguzinsky Nature Reserve in the northeastern Baikal area, *Avian Ecol. Behav.*, 2009, vol. 15, pp. 33–48.
- Ananina, T.L. and Ananin, A.A., Description of the climate of the Barguzin Nature Reserve (Northern Cis-Baikal region) in 1955–2015 and its impact on insects, in *Priroda Baikal'skoi Sibiri* (Nature of Baikal Siberia), Ulan-Ude: Buryat. Nauchn. Tsentr, Sib. Otd., Ross. Akad. Nauk, 2017, no. 2, pp. 117–126.
- Ananina, T.L. and Ananin, A.A., Some results of monitoring the temperature regime in the altitude zone of the Barguzin Ridge (Northern Baikal region), Proc. Int. Conf. "Process Management and Scientific Developments," Birmingham, United Kingdom, November 14, 2019, Birmingham, 2019, pp. 113–121.
- Gregory, R.D., van Strien, A., Voříšek, P., Gmelig-Meyling, A.W., Noble, D.G., Foppen, R.P.B., and Gibbons, D.W., Developing indicators for European birds, *Philos. Trans. R. Soc., B*, 2005, vol. 360, pp. 269–288.
- Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J.O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen E., et al., Rapid advance of spring arrival dates in long-distance migratory birds, *Science*, 2006, vol. 312, no. 5782, pp. 1959–1961.
- Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W.J., Bach, L.A., Coppack, T., Ergon, T., Gienapp, P., Gill, J.A., Gordo, O., Hedenström, A., Lehikoinen, E., et al., Challenging claims in the study of migratory birds and climate change, *Biol. Rev.*, 2011, vol. 86, no. 4, pp. 928–946.
- Korosov, A.V., Spetsial'nye metody biomterii: uchebnoe posobie (Specific Methods in Biometrics: Manual), Petrozavodsk: Petrozvodsk. Gos. Univ., 2007.
- Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T.L., Dunn, E.H., Gregory, G., Karlsson, L., Kristiansen, V., Mackenzie, S., Newman, S., Røer, J.E., Sharpe, C., Sokolov, L.V., Steinholtz, Å., et al., Phenology of the avian spring migratory passage in Europe and North America: asymmetric advancement in time and increase in duration, *Ecol. Indic.*, 2019, vol. 101, pp. 985–991.
- Lindén, A., Using first arrival dates to infer bird migration phenology, Boreal Environ. Res., 2011, vol. 16, suppl. B, pp. 49–60.

- Mills, A.M., Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming, *Ibis*, 2005, vol. 147, no. 2, pp. 259–269.
- Miller-Rushing, A.J., Lloyd-Evans, T.L., Primack, R.B., and Satzinger, P., Bird migration times, climate change and changes in population sizes, *Global Change Biol.*, 2008, vol. 14, no. 9, pp. 1959–1972.
- Noskova, E.V., Vakhnina, I.L., and Kurganovich, K.A., Analysis of moistening conditions of drainless lakes of the Torei Plain using meteorological data, *Vestn. Zabaik. Gos. Univ.*, 2019, vol. 25, no. 3, pp. 22–30.
- Pulido, F., Phenotypic changes in spring arrival: evolution, phenotypic plasticity, effect of weather and condition, *Clim. Res.*, 2007, vol. 35, nos. 1–2, pp. 5–23.
- Rainio, K., Laaksonen, T., Ahola, M., Vähätalo, A.V., and Lehikoinen, E., Climatic responses in spring migration of boreal and arctic birds in relation to wintering area and taxonomy, *J. Avian Biol.*, 2006, vol. 37, no. 5, pp. 507–515.
- Ravkin, Yu.S., Registration of birds in forest landscapes, in *Priroda ochagov kleshchevogo entsefalita na Altae* (Nature of Tick-Born Encephalitis Foci in Altai), Novosibirsk: Nauka, 1967, pp. 66–75.
- Rubolini, D., Møller, A.P., Rainio, K., and Lehikoinen, E., Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species, *Clim. Res.*, 2007, vol. 35, nos. 1–2, pp. 135–146.
- Sokolov, L.V., *Klimat v zhizni rastenii i zhivotnykh* (Climate in Life of the Plants and Animals), St. Petersburg: Tessa, 2010.
- Sokolov, L.V., Markovets, M.Yu., and Shapoval, A.P., Effect of climate on long-term dynamics of bird population in Baltic region, *Materialy Vserossiiskoi nauchnoi konferentsii "Dinamika chislennosti ptits v nazemnykh landshaftakh," 17–21 marta 2017 g.* (Proc. All-Russ. Sci. Conf. "Dynamics of Bird Population in Terrestrial Landscapes," March 17–21, 2017), Moscow: KMK, 2017, pp. 25–33.
- Stephens, P.A., Mason, L.R., Green, R.E., Gregory, R.D., Sauer, J.R., Alison, J., Aunins, A., Brotons, L., Butchart, S.H.M., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., et al., Consistent response of bird populations to climate change on two continents, *Science*, 2016, vol. 352, no. 6281, pp. 84–87.
- Usui, T., Butchart, S.H.M., and Phillimore, A.B., Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis, *J. Anim. Ecol.*, 2017, vol. 86, no. 2, pp. 250–261.
- Vähätalo, A.V., Rainio, K., Lehikoinen, A., and Lehikoinen, E., Spring arrival of birds depends on the North Atlantic oscillation, *J. Avian Biol.*, 2004, vol. 35, pp. 210–216.

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