

Effect of Global Warming on the Timing of Migration and Breeding of Passerine Birds in the 20th Century

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Abstract—Long-term monitoring of the dates of arrival, breeding, and autumn migration in 25 passerine bird species on the Kurshskaya (Courland) Spit, the Baltic Sea, has shown that spring migration and nesting in most species wintering in Europe or Africa have shifted to earlier dates in the past two decades, whereas the dates of autumn migration in most species studied have not changed significantly. In 16 bird species, a significant negative correlation of the timing of arrival and breeding with the average spring air temperature and the North Atlantic Oscillation index (NAO) in February and March was revealed. In years with early and warm springs, birds arrived at the spit and nested considerably earlier than in years with cold springs. The dates of autumn migration in most species studied largely depended on the timing of nesting but not on weather conditions in autumn. The data obtained indicate that the main factor responsible for long-term changes in the timing of arrival, nesting, and autumn migrations of passerine birds in the Baltic Region is climate fluctuations that led to considerable changes in thermal conditions in the Northern Hemisphere in the 20th century. The hypothesis is proposed that recent climate warming has caused changes in the timing of not only the arrival of birds in Europe but also of their spring migrations from Africa. Further changes in the dates of passerine bird arrival and breeding in the Palearctic in subsequent years will largely depend on the dynamics of winter and spring air temperatures in the Northern Hemisphere, whereas the timing of autumn migrations will be determined mainly by the dates of their arrival and nesting.

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INTRODUCTION

The climate of our planet changes continuously. During the past million years, eight glacial periods during which the giant ice sheet in Europe reached the latitude of Kiev took place. The last glacial period ended approximately 180 000 years ago. The average air temperature near the land surface in the Northern Hemisphere during those times was 5°C below that of the present day (Borisenkov, 1988). Recent warming recorded in both the Northern and the Southern Hemisphere since the 1970s for the most part copies the previous considerable warming of 1910–1945 but has several substantial differences (Borisenkov, 1988; Kondrat'ev, 1992, 1993; Perevedentsev et al., 2002). Thus, according to data obtained by the Intergovernmental Group of Experts in Climate Change, the recent warming has involved the tropical zone, which was not observed during the previous warming (Perevedentsev et al., 2002). Moreover, the tendency toward increasing temperature in the Northern Hemisphere has recently manifested itself mainly in the cold season, whereas warming in the early 20th century occurred in both winter and summer (Figs. 1, 2). Between the 1950s and the 1990s, the minimum night and day air temperatures over the land surface increased by 0.2 and 0.1°C per decade, respectively. The increase in the temperature of

the ocean surface was half as great as that over the land surface. According to observations from satellites, the area of snow cover has decreased by 10% since the end of the 1960s and the surface and thickness of sea ice during the spring and summer seasons in the Northern Hemisphere have decreased by 15%. The mean sea level rose by 0.1–0.2 m in the 20th century (Perevedentsev et al., 2002). The amount of precipitation in most regions at high and middle latitudes of the Northern Hemisphere increased by 0.5–1% per decade. In southern Europe and North Africa, conversely, a considerable reduction of precipitation was observed in the past several decades, which often resulted in severe droughts (Fig. 3).

It is generally accepted that the cyclicity of bird migrations and breeding is based on circannual rhythms that are synchronized with environmental conditions once a year (in the spring, upon photostimulation) but are additionally controlled by changes in the photoperiod throughout the year (Gwinner, 1972, 2003; Berthold et al., 1972; Dol'nik, 1975; Berthold, 2001). As shown in numerous laboratory experiments, the photoperiod in migratory birds controls the annual cycles of the following parameters: (1) the timing and rate of development of sexual activity, (2) the time of onset and the length of the photorefractory period

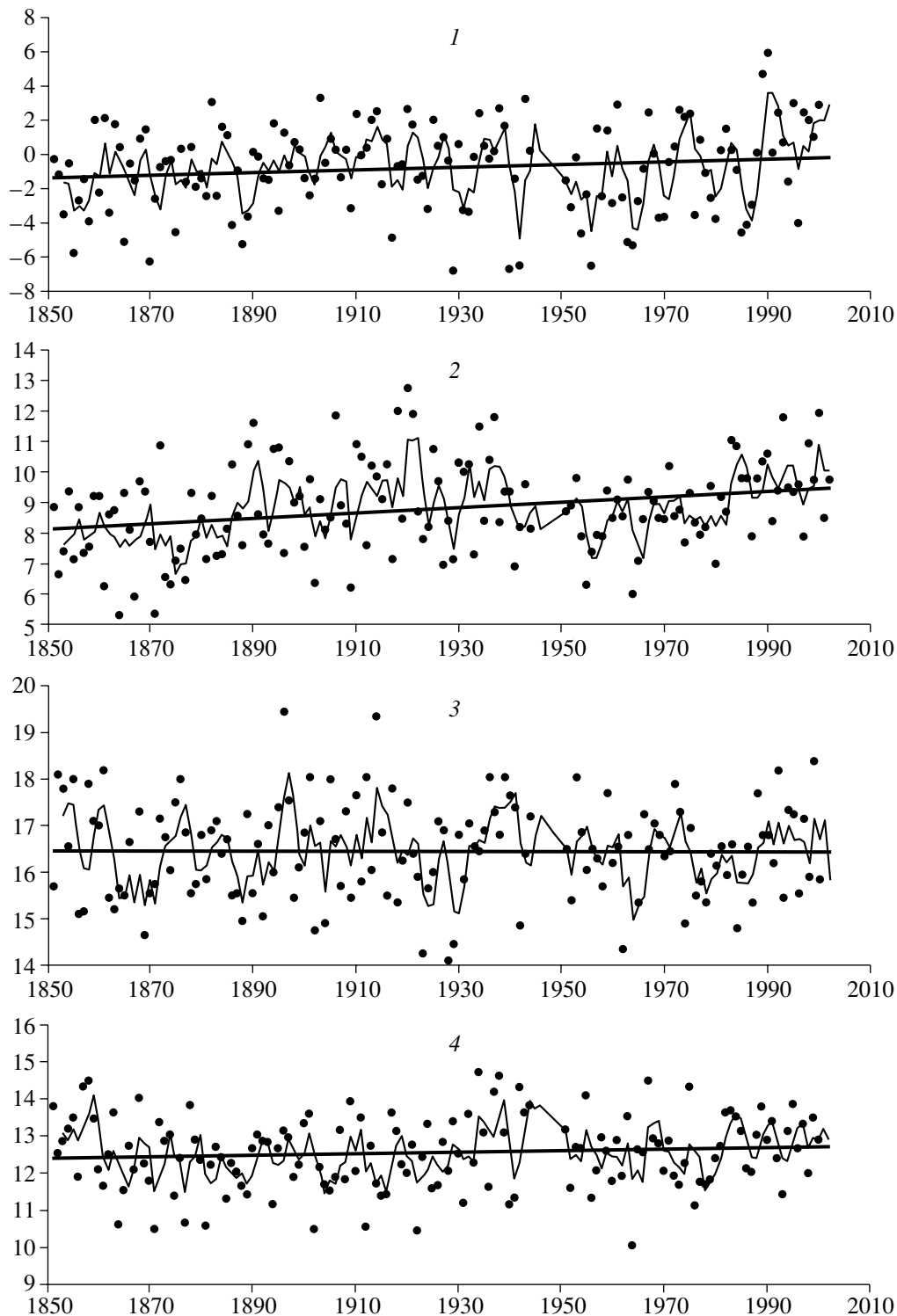


Fig. 1. Dynamics and trends of seasonal air temperatures in the Baltic region (Kaliningrad) smoothed by a three-year moving average: (1) February–March, (2) April–May, (3) June–July, and (4) August–September. Abscissa shows years; ordinate shows average temperatures.

(insensitivity to light) of the regulator of sexual activity, (3) the timing and rate of development of the spring migration status, (4) the duration and time of termination of the refractory period of regulators of spring

migration status, (5) the dates of the onset and termination of postmating molt and its strategy, (6) the timing of the onset and termination of the autumn migration status, and some others (Dol'nik, 1975, p. 237). In

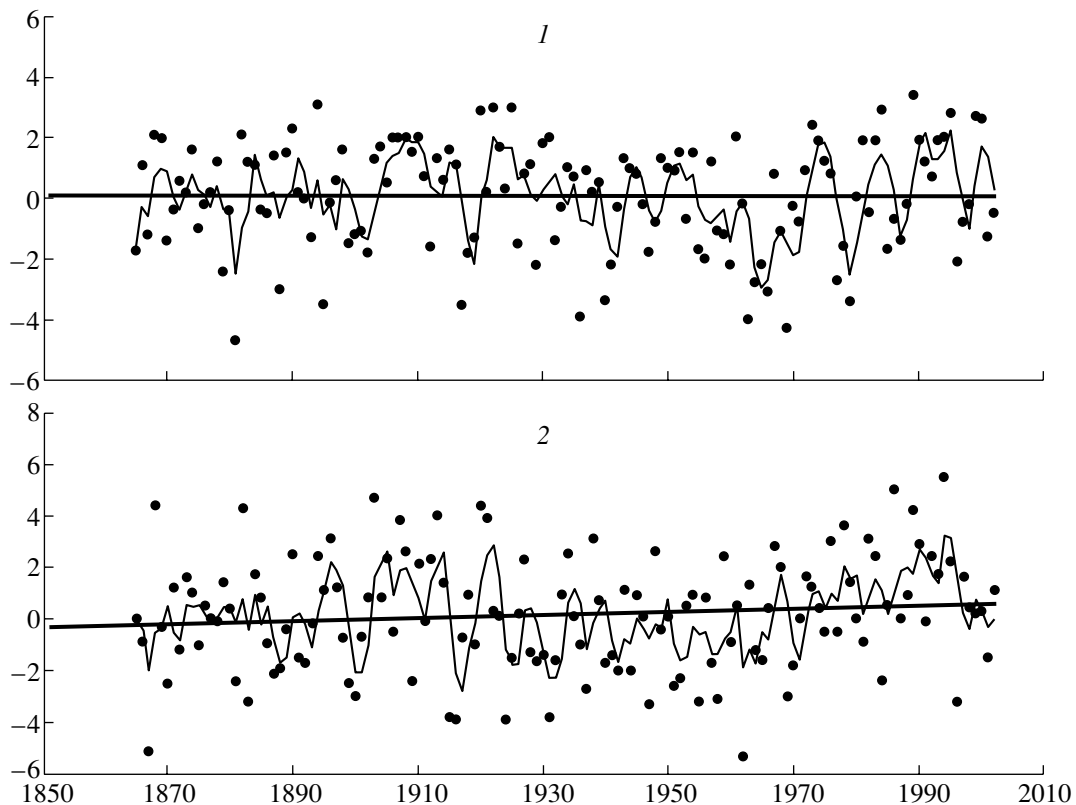


Fig. 2. Dynamics and trend of the North Atlantic Oscillation (NAO) index in (1) December–February and (2) March smoothed by a three-year moving average. Abscissa shows years; ordinate shows NAO values.

transequatorial migrants, spring migration presumably begins after the end of the refractory phase and is stimulated by the decreasing daylight period in the Southern Hemisphere. However, in species wintering near the equator, the spring migration status is spontaneously induced by their endogenous cycles, which are under photoperiodic control during summer and autumn. It is considered that thermoperiodic control of seasonal phenomena is not manifested in birds and that the dependence of migrations on changes in ambient humidity and food resources is characteristic of only certain tropical species rather than Palearctic migrants (Dol'nik, 1975; Gwinner, 2003). Reasoning from this basic concept, most authors suppose that migratory birds, primarily long-distance migrants, start spring migration every year at approximately the same dates, which are genetically specific to each species (population), and that weather conditions in spring have a considerable effect on the rate of migration but not on the date of its onset (Alerstam, 1990; Sparks et al., 2003).

In the past two decades, however, researchers in different countries of Europe, North Asia, North America, and Canada have recorded increasingly earlier arrivals at nesting areas in birds migrating not only within but also between continents, compared to previous decades (Moritz, 1993; Mason, 1995; Root, 1997; Ivanauskas et al., 1997; Loxon and Sparks, 1998; Ahas, 1999; Brad-

ley et al., 1999; Sokolov et al., 1999a; Sparks, 1999; Gatter, 2000; Inouye et al., 2000; Jenkins and Watson, 2000; Sparks and Mason, 2001; Zalakevicius and Zalakeviciute, 2001; Askeyev et al., 2002; Ananin, 2002; Paskhalny, 2002; Gilyasov and Sparks, 2002; Barrett, 2002; Tryjanowski et al., 2002; Fiedler, 2003a; Hüppop and Hüppop, 2003; Ptaszyk et al., 2003). On the other hand, there are also species in which the time of arrival has shifted to later dates, but they are much less numerous (Mason, 1995; Bradley et al., 1999; Sparks and Braslavská, 2001; Peñuelas et al., 2002). Most authors conclude that such a considerable shift in the timing of spring migrations is due to climate warming in the Northern Hemisphere (Brown et al., 1999; Crick and Sparks, 1999; Dunn and Winkler, 1999; Sokolov et al., 1999b, 2001; Forchhammer et al., 1998, 2002; Moss et al., 2001; Sueur and Triplet, 2001; Barrett, 2002; Walther et al., 2002; Hüppop and Hüppop, 2003; Hussell, 2003; Hubálek, 2003, 2004; Golovatin and Paskhalny, 2003).

In addition, many authors have reported a considerable shift to earlier dates in the timing of breeding during the past two decades (Järvinen, 1989; Crick et al., 1997; Winkel and Huddle, 1997; McCleery and Perrins, 1998; Sokolov and Payevsky, 1998; Brown et al., 1999; Crick and Sparks, 1999; Dunn and Winkler, 1999; Slater, 1999; Przybylo et al., 2000; Bairlein and

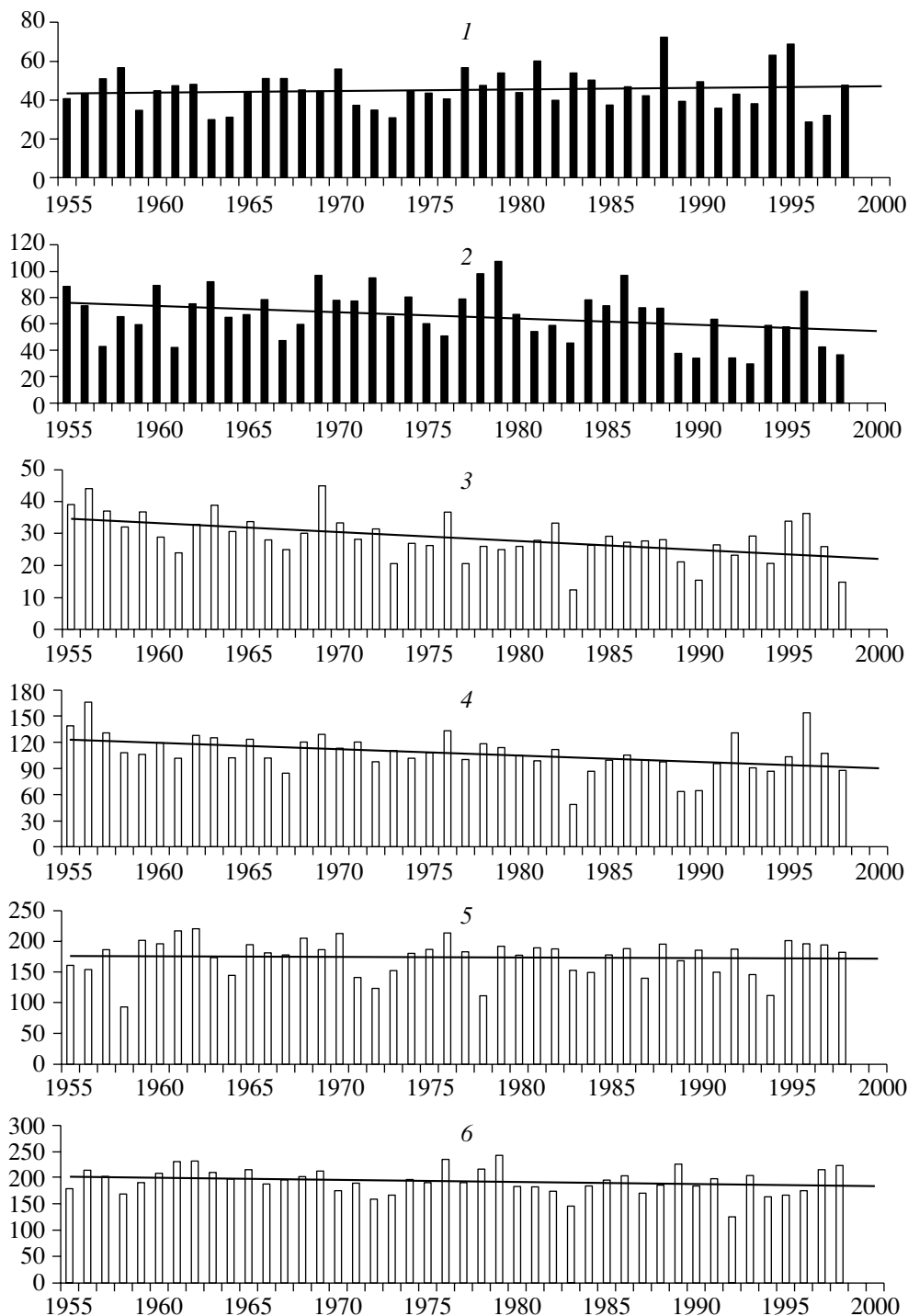


Fig. 3. Dynamics and trends of precipitation in Europe and Africa: (1) northern Europe (52.5° N), (2) southern Europe (42.5° N), (3) northern Africa (7.5° N), and (4–6) Africa (2.5° N, 2.5° S, and 12.5° S). Abscissa shows years; ordinate shows the average amount of precipitation (mm) in January–February.

Winkel, 2001; Koike and Higuchi, 2002; Both et al., 2004). This phenomenon is also attributed to recent climate warming in the Northern Hemisphere.

There are different opinions concerning the long-term change in the timing of autumn migrations. Cer-

tain authors argue that different bird species, including both short-distance and long-distance migrants, depart to their wintering places later than usual because of climate warming in the past decades (Glaubrecht, 1993; Moritz, 1993; Vogel and Moritz, 1995; Sparks and Mason, 2001; Bairlein and Winkel, 2001; Fiedler,

2003a, 2003b). Other authors conclude that the peak of autumn migration in long-distance migrants shifted to earlier dates in the last decade, whereas the timing of migration in most of the short-distance migrants shifted to later dates (Jenni and Kery, 2003). Finally, there is the opinion that the timing of autumn migration in most species of passerine birds has not changed considerably in recent decades (Sokolov et al., 1999c).

It should be kept in mind that the influence of climate and weather on bird migration was noted as early as the 19th and the beginning of the 20th century (Middendorff, 1855; Dikson, 1895; Menzbir, 1904–1909, 1929; Kaigorodov, 1911; Svyatskii, 1926; Loveiko, 1929; Thomson, 1926; Mayr and Meise, 1930). Moreover, long before this, Carolus Linnaeus became the founder of so-called aviphenology, which remained for a long time the only scientific basis for investigation of bird migrations (cited from Steinbacher, 1956, p. 21). Academician M.A. Menzbir in his fundamental book *Ptitsy* (Birds) wrote about the effect of climate on bird migration: “The beginning of migrations apparently dates from the late Pliocene, when winters were growing longer and summers shorter, when the distribution of heat between the seasons of the year had lost its former uniformity and the polar night was about to cover an increasingly greater area. In brief, this was a time preceding a glacial period, during which glaciers covered extensive land areas in the Northern Hemisphere. This directly resulted in the retreat of the faunas of arctic and subarctic countries to the south and indirectly promoted the development of migrations in a more pronounced form” (Menzbir, 1904–1909, p. 122). However, Menzbir did not regard the glacial period as the only factor responsible for the development of migrations. He wrote: “This was only one of the important factors that directly brought new living conditions for birds at certain latitudes and indirectly created new conditions for birds even at latitudes to which its direct effect could not extend” (p. 123). Referring to American authors who believed that spring migrations do not depend on weather changes but are initiated by an inner impulse, Menzbir (1934) in his book *Migratsii ptits* (Bird Migrations) wrote the following: “The fact that climate change is not a factor initiating migration does not allow the conclusion that it has absolutely no influence on migration. Climate change has an effect on food supply to birds, and foraging conditions are among the most important factors determining the time of bird arrival at nesting areas. Consequently, even though it is a physiological stimulus that gives impetus to spring migration, weather changes must have an effect on migration, because they affect foraging conditions. It should also be kept in mind that spring migration is associated with the rise in temperature, whereas autumn migration coincides with its fall” (Menzbir, 1934, p. 34). Pointing out the effect of environmental factors on migration of birds, Menzbir accepts the role of many instinctive features in their behavior, espe-

cially in the tendency to migrate in young birds that have no experience in migration.

The main purpose of this paper is to present arguments in favor of the hypothesis concerning the effect of recent climate warming on long-term changes in the timing of passerine bird migrations and nesting in the Baltic region in the 20th century.

MATERIAL AND METHODS

Studies were performed at the Fringilla field outpost of the Rybachii Biological Station located on the Kurshskaya (Courland) Spit, the Baltic Sea (55°05' N, 20°44' E). Every spring and autumn, a great many birds of different species, mainly passerines, migrate over the spit. Several dozen of these species nest directly in the study area. Large traps (up to 16 m high, 30 m wide, and 70 m long) of the Rybachinskii type (Dol'nik and Payevsky, 1976) were built at the station in 1957 for mass bird capture and banding. Since then, the traps have been installed every year for the period between the end of March and November 1. In certain periods, up to four traps functioned simultaneously. The entrances of two traps faced southwest for capturing birds during spring migration. The entrances of the other two traps faced northwest for capturing birds in autumn. In the nesting period, all four traps functioned simultaneously. During 48 years of investigations at the Rybachii station, specialists have compiled a unique database on the phenology of birds and developed special software allowing long-term data to be processed with due efficiency (Morozov, 1995; Morozov and Efremov, 1997).

In this study, the dates of migrations and breeding of 25 passerine bird species over 44 years (1959–2002) were analyzed. The date of the first capture of a bird and the average date of capture in stationary traps between April 1 and June 1 or 15 (depending on species) in each year were used as parameters characterizing the timing of spring migration. Long-term changes in the dates of spring migrations in 14 species wintering in Europe, 10 species wintering in Africa, and 1 species wintering in India (the common rosefinch *Carpodacus erythrinus*) were analyzed. The timing of nesting in the population of a certain species from the Courland Spit was estimated from the average date of hatching and the date of capture of the first juvenile bird in a trap during the postnesting period. As shown earlier for several passerine species, the time of nesting in local populations can be estimated quite objectively from the date of capture of the first juvenile bird (Sokolov and Payevsky, 1998). The long-term dynamics of the timing of nesting were analyzed in seven species wintering in Europe and in eight species wintering in Africa. The dates of autumn migration in most species were estimated from the average date of bird trapping in the period from August 15 to October 31. Most native birds usually depart from the study region by mid-August (Sokolov, 1991). In the icterine warbler *Hippolais icterina*, an early departing

Table 1. Correlations between monthly average air temperatures in different parts of the Baltic region and the North Atlantic Oscillation (NAO) index between 1873 and 2000 (Sokolov et al., 2003a)

Month	Weather station						
	Stockholm	Helsinki	St. Petersburg	Riga	Vilnius	Kaliningrad	Copenhagen
January	0.52*	0.44*	0.41*	0.44*	0.36*	0.45*	0.53*
February	0.45*	0.45*	0.38*	0.42*	0.39*	0.38*	0.47*
March	0.59*	0.58*	0.53*	0.58*	0.53*	0.58*	0.61*
April	0.14	0.13	0.05	0.04	0.02	0.01	0.15
May	0.22*	0.22*	0.13	0.21*	0.11	0.25	0.18
June	0.11	0.07	-0.04	0.01	-0.06	0.02	0.10
July	0.28*	0.33*	0.25*	0.24*	0.15	0.23*	0.18*
August	0.37*	0.34*	0.18*	0.28*	0.28*	0.33*	0.35*
September	0.34*	0.26*	0.10	0.24*	0.21*	0.30*	0.31*
October	0.33*	0.21*	0.14	0.19*	0.18*	0.23*	0.35*
November	0.37*	0.29*	0.14	0.28*	0.24*	0.27*	0.37*
December	0.41*	0.25*	0.16	0.18*	0.12	0.23*	0.41*

Note: Pearson coefficients of correlation are shown, with values significant at $p < 0.05$ being indicated with asterisks.

species, the autumn migration was estimated to begin on August 1. The date of the last capture in autumn is much less informative in estimating the timing of migration. For this reason, it was not used in this study.

Among environmental factors possibly affecting the timing of migrations and breeding, consideration was given to monthly average air temperatures in the study region (Kaliningrad) and the Mediterranean region (Barcelona, Spain), the North Atlantic Oscillation (NAO) index for different periods of the year, and amounts of precipitation at different latitudes in Europe and Africa. The monthly NAO index is usually used as an indicator of the meteorological situation in Europe, North America, and Canada in winter and early spring (March). In our recent investigations, we used it also for North Africa and Asia (Sokolov and Kosarev, 2003; Sokolov et al., 2004). The NAO index is calculated as the difference between the normalized values of barometric pressure in the regions of the Azores and Iceland for each month separately (Hurrell et al., 2001). At positive values of the NAO index in winter and early spring, weather conditions in Europe are determined by active zonal transfer of warm air masses from the west (from the Atlantic Ocean), which results in the rise of temperature and precipitation in northern Europe (Hurrell, 1995; Visbeck et al., 2001). In Portugal, Spain, and North Africa, conversely, high values of the index are associated with a decreased amount of precipitation in the winter season (Sokolov and Kosarev, 2003). Negative values of the NAO index are indicators of the weakening of westerly winds (meridional transfer) and consequent decrease in temperature and precipitation in northern Europe (Table 1). Monthly NAO indices are available from the National Oceanic and Atmospheric

Administration's Climate Prediction Center website (www.cpc.ncep.noaa.gov/data/teledoc/nao.html).

An analysis of precipitation in different regions of Europe and Africa was performed using the database on monthly amounts of precipitation in sectors extending for five degrees of latitude and longitude for the period from 1900 to 1998 (<http://ingrid.ldeo.columbia.edu/SOURCES/.UEA/.CRU/Hu.../dataset>). For each latitude, data on precipitation in several sectors were summed to calculate the monthly average amount of precipitation from January to April. Data on precipitation in certain countries of eastern Africa were used (Fig. 4). In addition, data of Spanish authors (Peñuelas et al., 2002) on dates of the onset of blossoming in a cultivated apple (*Malus domestica*) in the Mediterranean region (35 km north of Barcelona, Spain) were taken into account, as this is the wintering area for a number of European species migrating via the Baltic region (Payevsky, 1971).

Long-term trends in the timing of migration and nesting relative to monthly average air temperature, NAO index, and amount of precipitation were analyzed by means of correlation and regression analysis. Correlation analysis was also used for revealing connections between the timing of arrival, nesting, and autumn migration, on the one hand, and temperature conditions and the NAO index, on the other hand.

RESULTS

Long-Term Changes in Timing of Spring Migration

The results of long-term monitoring of passerine bird arrival at the Courland Spit show that spring migrations of most species wintering either in Europe or in

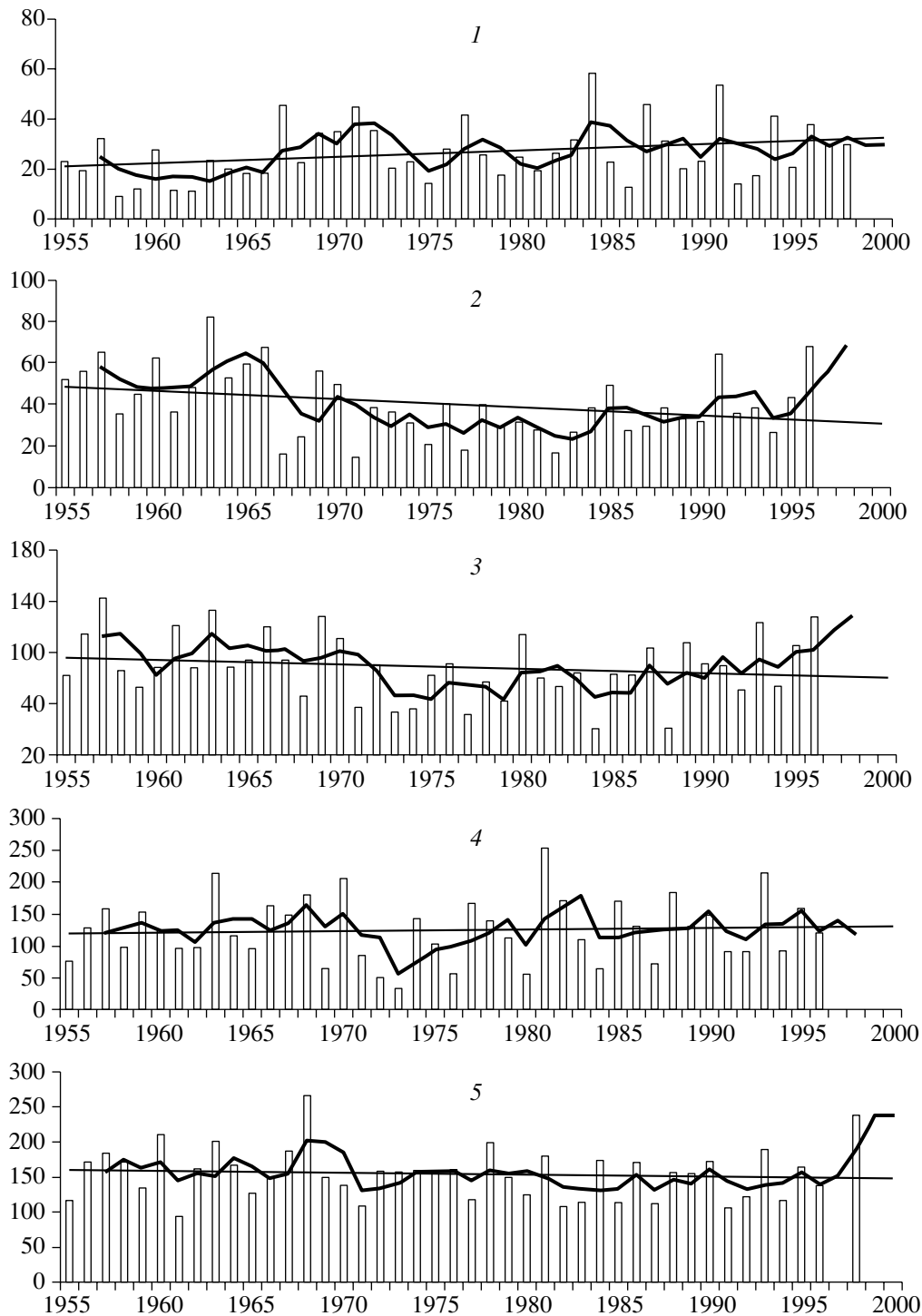


Fig. 4. Dynamics and trends of precipitation in certain countries of eastern Africa: (1) Egypt (27.5° N), (2) Sudan (7.5° N), (3) Ethiopia (7.5° N), (4) Kenya (2.5° N), and (5) Tanzania (7.5° S). Abscissa shows years; ordinate shows the average amount of precipitation (mm) in March–April.

Africa have shifted to earlier dates during the past two decades (Fig. 5, Table 2). On the whole, bird arrival in the 1980s and late 1990s was observed markedly earlier than in the 1970s and part of the 1960s. As follows from the first capture and the average capture dates, the tim-

ing of spring migration in species wintering not only in Europe but also in Africa often differed from year to year by almost one month (Fig. 5).

It has been found that the period (in days) between dates of spring migration in two successive years is not

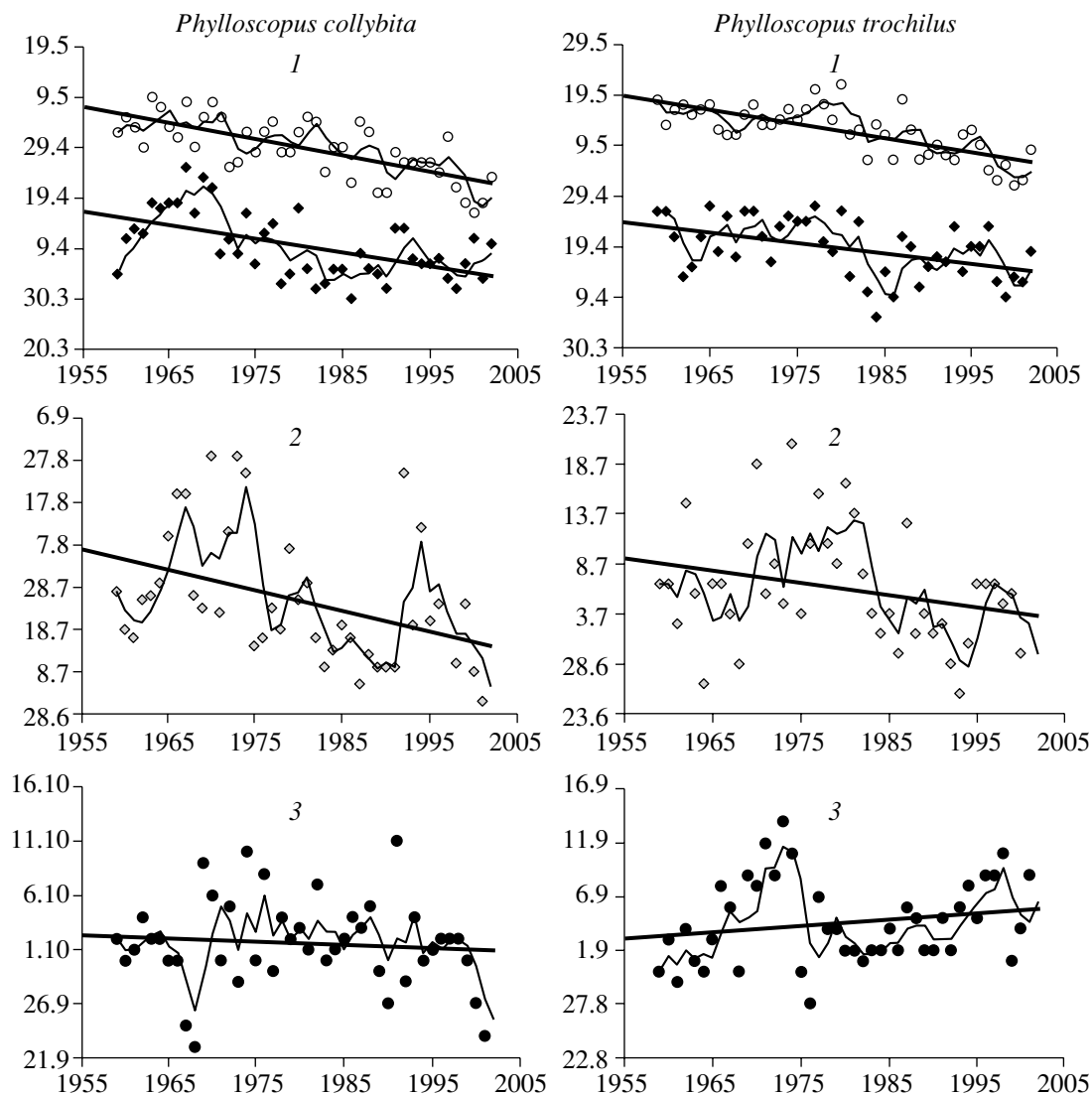


Fig. 5. Dynamics and trends of the timing of migration and nesting in European (chiffchaff *Phylloscopus collybita*) and African (willow warbler *Ph. trochilus*) migrants: (1) spring migration (a, date of first capture; b, average date of flight); (2) date of first juvenile bird capture; and (3) autumn migration (average date of flight). Abscissa shows years; ordinate shows dates. The curves are smoothed by a three-year moving average.

constant but varies significantly depending on the time of migration in the first year (Fig. 6): the period following late migration is significantly shorter than the period following early migration. This is typical for almost all species studied, irrespective of whether they winter in Europe or in Africa.

In 16 species, a significant negative correlation between the timing of migration and air temperatures in spring, mainly in April and May, was revealed (Table 2). In years with warm springs, birds arrived at the Courland Spit markedly earlier than in years with cold springs. A correlation between the dates of spring migration and the NAO index for February and March was revealed in 16 species migrating either within or between continents. In 17 species, these dates correlated with the spring air temperature in the environs of

Barcelona (Spain). Moreover, the dates of arrival at the Courland Spit in 16 species showed a significant positive correlation with the timing of apple blossoming in the same region of Spain (Table 2). Both short-distance and long-distance migrants appeared on the Courland Spit on earlier dates in years with higher air temperatures and earlier apple blossoming in the Mediterranean region.

A significant correlation between the dates of arrival of long-distance migrants and the amounts of precipitation in certain countries of eastern Africa through which many migratory bird species fly in spring was revealed for six out of nine species studied (Table 3). In years with higher spring precipitation levels, these species arrived at the Courland Spit significantly earlier than in relatively dry years (Fig. 4).

Table 2. Correlations between the timing of passerine bird migration in spring on the Courland Spit, the Baltic Sea, and the year, North Atlantic Oscillation (NAO) index, monthly average air temperature (T , °C), and timing of apple (*Malus domestica*) blossoming in the Mediterranean region (Barcelona, Spain) between 1959 and 2002

Species	Date of capture	Year	NAO February–March	Baltic region	Spain	
				T , °C	T , °C	date of apple blossoming
				April (May)	April (May)	
Short- and middle-distance migrants						
<i>Parus major</i>	Average	-0.33*	-0.18	-0.15	-0.36*	0.21
<i>P. caeruleus</i>	Average	-0.19	-0.39**	-0.22	-0.33*	0.20
<i>Regulus regulus</i>	Average	-0.22	-0.31*	-0.32*	-0.35*	0.27
<i>Troglodytes troglodytes</i>	First	-0.47**	-0.31*	-0.17	-0.07	0.40*
	Average	-0.16	-0.25	-0.47**	-0.22	-0.02
<i>Erithacus rubecula</i>	First	-0.13	-0.36*	-0.22	-0.12	0.36*
	Average	-0.22	-0.13	-0.47**	-0.50***	0.06
<i>Turdus merula</i>	First	-0.34*	-0.40**	0.17	0.10	0.30
	Average	-0.55***	-0.27	0.01	-0.19	0.28
<i>T. iliacus</i>	First	-0.59***	-0.37*	-0.18	-0.01	0.45**
<i>T. philomelos</i>	First	-0.37*	-0.14	0.09	0.17	0.25
	Average	-0.54***	-0.18	-0.07	-0.33*	0.26
<i>Fringilla coelebs</i>	Average	-0.51***	-0.35*	-0.35*	-0.27	0.37*
<i>Phoenicurus ochruros</i>	First	-0.38*	-0.18	0.05	-0.03	0.41**
	Average	0.17	0.20	-0.32*	-0.24	-0.12
<i>Carduelis carduelis</i>	First	-0.03	-0.10	0.04	-0.06	0.14
	Average	-0.48**	-0.48**	-0.53***	-0.40**	0.39*
<i>C. spinus</i>	Average	-0.59***	-0.33*	-0.32*	-0.48**	0.49**
<i>Phylloscopus collybita</i>	First	-0.54***	-0.35*	-0.36*	-0.29	0.38*
	Average	-0.71***	-0.48**	-0.54***	-0.40**	0.51***
<i>Sylvia atricapilla</i>	First	-0.54***	-0.36*	-0.38*	(-0.59***)	0.33*
	Average	-0.65***	-0.39**	(-0.30*)	(-0.43**)	0.49**
Long-distance migrants						
<i>Motacilla alba</i>	Average	-0.15	-0.15	-0.37*	-0.35*	0.07
<i>Phoenicurus phoenicurus</i>	First	0.15	-0.19	-0.50***	-0.17	0.04
	Average	-0.20	-0.26	(-0.44**)	-0.40**	0.18
<i>Phylloscopus trochilus</i>	First	-0.46**	-0.29	-0.50***	-0.24	0.30
	Average	-0.72***	-0.56***	(-0.50***)	-0.62***	0.65***
<i>Ph. sibilatrix</i>	Average	-0.32*	-0.12	(-0.07)	-0.17	0.39*
<i>Ficedula hypoleuca</i>	First	-0.48**	-0.37*	-0.57***	-0.40**	0.31
	Average	-0.48**	-0.45**	(-0.41**)	-0.43**	0.45**
<i>Hirundo rustica</i>	First	0.11	-0.01	-0.41**	-0.07	0.11
	Average	-0.36*	-0.30*	(-0.26)	-0.04	0.34*
<i>Sylvia curruca</i>	First	-0.63***	-0.38*	-0.24	-0.37*	0.34*
	Average	-0.42**	-0.38*	-0.32*	-0.60***	0.49**
<i>S. communis</i>	First	-0.20	-0.07	-0.23	-0.23	0.04
	Average	-0.47**	-0.09	(0.01)	-0.31*	0.48**
<i>S. borin</i>	First	0.22	0.03	(0.02)	-0.28	-0.02
	Average	-0.17	0.01	(0.22)	(-0.31*)	0.18
<i>Hippolais icterina</i>	First	0.12	0.04	(-0.19)	0.13	0.11
	Average	-0.54***	-0.44**	(-0.22)	(-0.38*)	0.65***
<i>Carpodacus erythrinus</i>	First	0.28	0.29	(-0.41**)	(0.29)	-0.27
	Average	-0.31*	-0.01	(-0.14)	(0.02)	0.17

Note: Pearson coefficients of correlation are shown. Asterisks indicate that values are significant at * $p < 0.05$, ** $p < 0.01$, or *** $p < 0.001$.

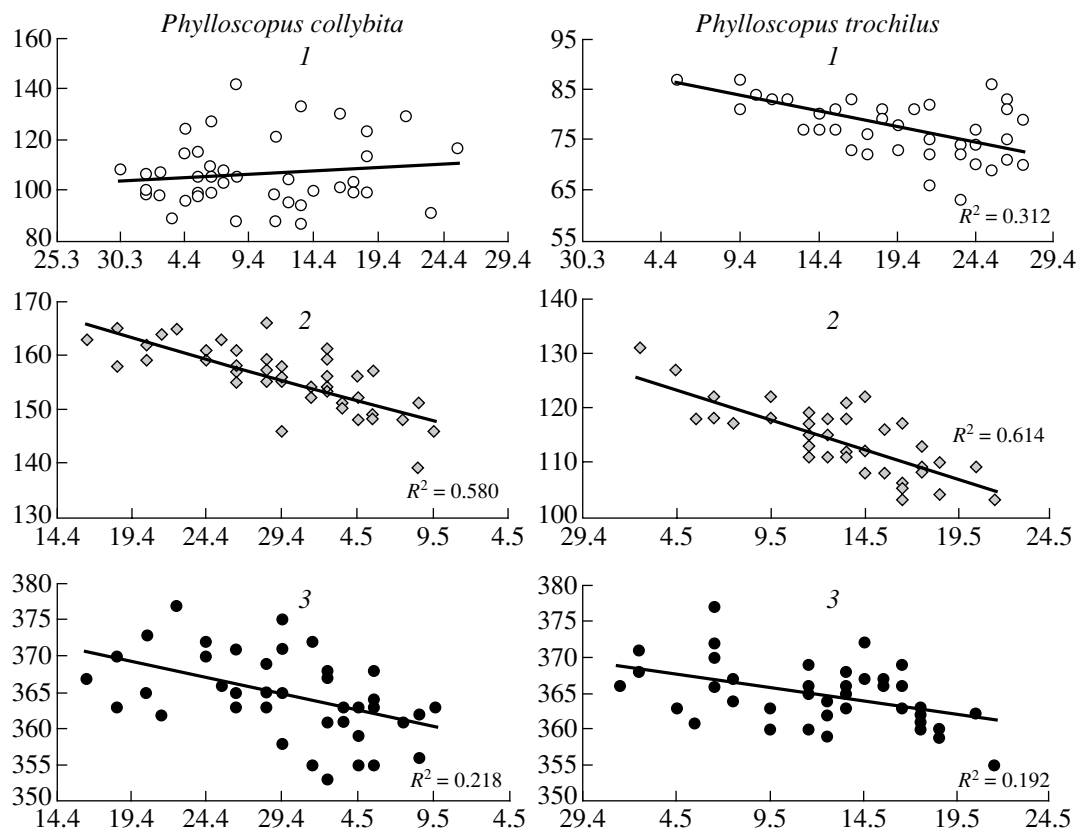


Fig. 6. Numbers of days between the dates of spring migration and (1) nesting (the first juvenile bird capture), (2) autumn migration, and (3) spring migration in the following year as a function of the date of spring migration. Abscissa shows (1) dates of first capture and (2, 3) average dates of spring migration; ordinate shows the number of days.

Long-Term Changes in Timing of Nesting

Long-term data on the dates of nesting in passerine birds on the Courland Spit show that these dates have changed considerably in certain species (Fig. 5, Table 4). In most cases, nesting in the 1980s and the second half of the 1990s occurred earlier than in the late 1960s and 1970s.

A significant positive correlation between the dates of nesting and arrival at the Courland Spit was revealed in 10 out of 15 species (Table 4). In years with early spring migration, the nesting period was also shifted toward earlier dates. Such a correlation was typical for species wintering in Europe or Africa. It was found, however, that the period (in days) between the dates of spring migration and the first capture of a juvenile bird is not constant but significantly depends on the timing of migration (Fig. 6): this period is significantly shorter when spring migration in the previous year occurs later, compared to the case of relatively early migration. This is characteristic of most species studied, irrespective of whether they winter in Europe or Africa.

In all species studied, except for the song thrush *Turdus philomelos*, a significant negative correlation between the dates of nesting and air temperatures in spring, mainly in April and May, was revealed (Table 4).

Bird nesting on the Courland Spit was observed markedly earlier in years with warm springs than in years with cold springs. In eight species, a similar correlation was observed between the timing of nesting and the NAO index in February and March (Table 4). This correlation was equally characteristic of species migrating within or between continents.

Long-Term Changes in Timing of Autumn Migration

In contrast to the spring flight, the timing of autumn migration in most species manifested no significant trend, despite fairly strong fluctuations from year to year (Table 5, Fig. 5). Among species wintering in Europe, the tendency toward later autumn migration was revealed only in the blue tit (*Parus caeruleus*) and blackbird (*T. merula*). Among long-distance migrants, conversely, the pied flycatcher (*Ficedula hypoleuca*) and lesser whitethroat (*Sylvia curruca*) manifested a tendency toward earlier autumn migration (Table 5).

In 11 out of 14 species studied, a significant positive correlation between the timing of breeding and the average date of flight over the Courland Spit was revealed (Table 5). In years with early nesting dates, autumn migration also began earlier. This correlation was equally typical of species wintering in Europe or in

Table 3. Correlations between the timing of arrival of long-distance migrants to the Courland Spit, the Baltic Sea, and the amounts of precipitation in certain countries of eastern Africa (1959–1998)

Species	Date of capture	Egypt, 27.5° N	Sudan, 7.5° N	Ethiopia, 7.5° N	Kenya, 2.5° N	Tanzania, 7.5° S
		March (April)	March (April)	March (April)	March (April)	March
<i>Motacilla alba</i>	Average	0.25	-0.23	-0.08	-0.01	-0.04
<i>Phoenicurus phoenicurus</i>	First	0.05	-0.22	-0.31*	-0.07	-0.17
	Average	0.20	0.20	0.10	(-0.27)	-0.24
<i>Phylloscopus trochilus</i>	First	0.10	-0.04	0.13	0.03	-0.01
	Average	(0.12)	(0.11)	(-0.23)	(-0.20)	-0.19
<i>Ficedula hypoleuca</i>	First	-0.08	-0.21	-0.11	0.03	-0.01
	Average	(-0.05)	-0.10	(-0.24)	(-0.14)	-0.05
<i>Hirundo rustica</i>	First	(-0.37*)	-0.22	0.12	0.03	-0.19
	Average	(0.23)	-0.30	(-0.24)	-0.48**	-0.29
<i>Sylvia curruca</i>	First	-0.25	-0.08	0.09	0.02	-0.12
	Average	(0.32*)	-0.41**	(-0.34*)	(-0.24)	-0.22
<i>S. communis</i>	First	0.10	-0.21	-0.06	0.063	-0.23
	Average	(0.11)	-0.41**	-0.29	(0.03)	-0.13
<i>S. borin</i>	First	0.10	-0.35*	-0.46**	0.01	0.08
	Average	(0.23)	(-0.15)	(-0.06)	(0.10)	-0.09
<i>Hippolais icterina</i>	First	-0.05	-0.22	(-0.21)	-0.29	-0.37*
	Average	(0.16)	(-0.14)	(-0.36*)	(-0.04)	-0.27

Note: Pearson coefficients of correlation are shown. Asterisks indicate that values are significant at * $p < 0.05$ or ** $p < 0.01$.

Africa. The period (in days) between the nesting period and the average date of autumn migration is not constant and markedly depends on the timing of nesting

(Fig. 7): in most species, this period is markedly shorter after late nesting than after early nesting. Moreover, the period between autumn migration and subsequent

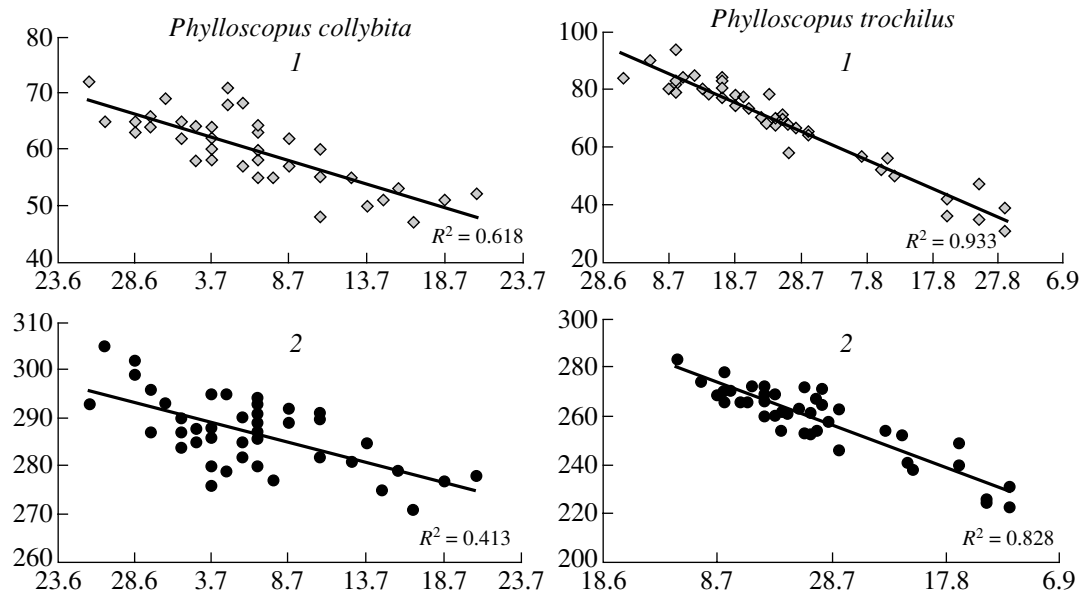


Fig. 7. Numbers of days between the dates of nesting (the first juvenile bird capture) and (1) autumn migration and (2) spring migration in the following year as a function of the dates of nesting. Abscissa shows the date of the first juvenile bird capture; ordinate shows the number of days.

Table 4. Correlation between the timing of breeding of passerine birds and the year, timing of spring migration, North Atlantic Oscillation (NAO) index, and monthly average air temperature (T , °C) on the Courland Spit, the Baltic Sea (1959–2002)

Species	Age	Year	Date of arrival	NAO		T , °C	
				February–March	April–May	February–March	April–May
Short- and middle-distance migrants							
<i>Parus major</i>	Juv.	–0.06	0.03	–0.23		–0.56***	
<i>P. caeruleus</i>	Juv.	–0.28	0.15	–0.42**		–0.39**	
<i>Turdus merula</i>	Juv.	–0.20	0.06	–0.05		–0.61***	
<i>T. philomelos</i>	Juv.	–0.05	–0.14	0.04		–0.18	
<i>Fringilla coelebs</i>	Pull.	–0.35*	0.46**	–0.45**		–0.69***	
	Juv.	–0.28	0.38*	–0.28		–0.62**	
<i>Phylloscopus collybita</i>	Juv.	–0.39**	0.54***	–0.02		–0.41**	
<i>Sylvia atricapilla</i>	Pull.	–0.51**	0.51**	–0.42*		–0.41*	
	Juv.	–0.43**	0.33*	–0.19		–0.50***	
Long-distance migrants							
<i>Motacilla alba</i>	Juv.	–0.04	0.30*	–0.31*		–0.65***	
<i>Phylloscopus trochilus</i>	Pull.	–0.29	0.09	0.05		0.07	
	Juv.	–0.26	0.59***	–0.37*		–0.49**	
<i>Ficedula hypoleuca</i>	Pull.	–0.34	0.70***	–0.29		–0.65***	
	Juv.	–0.54***	0.59***	–0.41**		–0.52***	
<i>Hirundo rustica</i>	Juv.	0.09	0.38*	–0.30		–0.48**	
<i>Sylvia curruca</i>	Pull.	–0.37	0.50*	–0.33		–0.50**	
	Juv.	–0.49**	0.19	–0.51***		–0.52***	
<i>S. communis</i>	Pull.	–0.17	0.63*	–0.16		–0.49*	
	Juv.	0.01	0.03	–0.25		–0.65***	
<i>S. borin</i>	Pull.	–0.56**	0.26	–0.44*		–0.40*	
	Juv.	0.03	–0.05	–0.14		–0.68***	
<i>Hippolais icterina</i>	Pull.	–0.22	0.45**	–0.27		–0.25	
	Juv.	0.24	0.06	–0.07		–0.55***	

Note: Pearson coefficients of correlation are shown. Asterisks indicate that values are significant at * $p < 0.05$, ** $p < 0.01$, or *** $p < 0.001$.

spring migration is also not constant but significantly depends on the timing of autumn migration (Fig. 7).

In nine species, a significant negative correlation was revealed between the timing of autumn migration and temperature conditions in spring but not in autumn (Table 5). In years with warm springs, birds migrated via the Courland Spit on earlier dates than in years with cold springs. A similar correlation with autumn air temperatures was revealed in only two species, the blue tit and common swallow (*Hirundo rustica*). In the garden warbler (*S. borin*), conversely, the timing of autumn migration manifested a positive correlation with temperature conditions in autumn (Table 5). No significant correlation between the timing of autumn migration

and the NAO index was observed in any species included in the study (Table 5).

DISCUSSION

Fluctuations of Climate

Fluctuations of climate may result from different factors, e.g., astronomic (associated with changes in parameters of the Earth's orbit and processes taking place on the Sun or in the solar system), geophysical (conditioned by properties of the Earth as a planet, e.g., by volcanic activity), and circulatory (related to processes in the atmosphere). A number of renowned climatologists consider that certain facts are indicative of the

Table 5. Correlations between the average date of autumn migration of passerine birds and the year, timing of breeding, North Atlantic Oscillation (NAO) index, and monthly average air temperatures (T , °C) in spring and autumn on the Courland Spit, the Baltic Sea (1959–2002)

Species	Year	Date of first juvenile bird capture	NAO	T , °C	T , °C
			August–September (September–October)	April (May)	August–September (September–October)
Short- and middle-distance migrants					
<i>Parus major</i>	0.21	0.41**	(–0.10)	–0.14	(–0.29)
<i>P. caeruleus</i>	0.31*	0.37*	(–0.18)	–0.09	(–0.37*)
<i>Regulus regulus</i>	0.15		(–0.15)	–0.17	(–0.26)
<i>Erithacus rubecula</i>	0.19		(–0.21)	–0.37*	(–0.22)
<i>Turdus merula</i>	0.41**	0.02	(–0.28)	–0.22	(–0.28)
<i>T. iliacus</i>	0.27		(0.11)	0.01	(–0.01)
<i>T. philomelos</i>	0.19	0.60***	(–0.08)	–0.10	(0.15)
<i>Fringilla coelebs</i>	0.07	0.36*	(–0.08)	–0.36*	(0.01)
<i>Phylloscopus collybita</i>	–0.10		(0.13)	–0.39**	(–0.25)
<i>Sylvia atricapilla</i>	0.17	0.16	0.07	–0.14	–0.01
Long-distance migrants					
<i>Motacilla alba</i>	–0.24	0.37*	–0.06	–0.35*	0.08
<i>Phoenicurus phoenicurus</i>	–0.12		–0.10	–0.46**	–0.19
<i>Phylloscopus trochilus</i>	0.19	0.35*	–0.11	–0.35*	–0.09
<i>Ficedula hypoleuca</i>	–0.37*	0.40*	–0.08	–0.34*	–0.12
<i>Hirundo rustica</i>	–0.26	0.31*	–0.05	(–0.34*)	–0.43**
<i>Sylvia curruca</i>	–0.37*	0.13	–0.16	–0.21	–0.24
<i>S. communis</i>	0.16	0.65***	–0.06	–0.59***	0.01
<i>S. borin</i>	0.25	0.31*	0.17	–0.28	0.32*
<i>Hippolais icterina</i>	0.01	0.48**	–0.05	–0.30	–0.12

Note: Pearson coefficients of correlation are shown. Asterisks indicate that values are significant at * $p < 0.05$, ** $p < 0.01$, or *** $p < 0.001$.

connection between climatic events and the 11- and 22-year cycles of solar activity (Borisenkov, 1982, 1988; Kondrat'ev, 1992, 1993). However, this connection is ambiguous, because the climate is under simultaneous influence of many factors. Thus, environmental factors determine climatic fluctuations with different periods (decades, centuries, or longer). On the other hand, many authors are of the opinion that the climate in the 20th century was under considerable influence of anthropogenic factors (Shnaider, 1993; Gorshkov, 1995; Houghton et al., 2001). According to this hypothesis, the consequences of economic activity over the past 100 years (the development of power engineering and other branches of industry, including agriculture; large-scale tree cutting; etc.) include the gradual enrichment of the atmosphere with certain gases (carbon dioxide, methane, chlorofluorocarbons, etc.) that affect the radiation balance of the Earth, shifting it toward heat accumulation in the lower troposphere. This results in the so-called greenhouse effect and, con-

sequently, in the global rise of air temperature. According to recent calculations based on global climate models, the average global temperature will rise by 1.5–5.8°C if the atmospheric CO₂ concentration doubles in this century (Houghton et al., 2001). Proponents of the hypothesis of global warming believe that all these changes will occur gradually, as trends progressing with time against the background of the natural dynamics and cyclicity of the global climatic system, which can overlap anthropogenic effects and amplify or attenuate them. According to different prognoses, however, the 21st century may prove colder than the previous century because of existing near-centennial climatic cycles (Borisenkov, 1982, 1988). Proponents of this concept are far less numerous, however, and their voices are markedly subdued. Unfortunately, the discussion of factors responsible for the recent climate warming has passed from the scientific to the political sphere, where prevailing interests hardly concern science.

Timing of Bird Arrival in Spring

Several papers published in recent years provide evidence for a significant negative correlation between the dates of bird arrival in Europe and the winter NAO index (Forchhammer et al., 2002; Hüppop and Hüppop, 2003; Hubálek, 2003, 2004). It should be noted that this correlation has been revealed not only in species wintering in Europe but also in long-distance migrants wintering in Africa. The question arises as to why the parameter of interest correlates with the NAO index for the winter season, when the birds, long-distance migrants in particular, are still in the regions of wintering. In order to elucidate this question to some extent, we calculated the correlation of the dates of bird arrival at the Courland Spit with both the NAO index averaged over three months (January–March) and its values for each month separately (Sokolov and Kosarev, 2003). The results showed that the NAO index for January strongly correlates not only with winter temperatures in the Baltic region but also with the temperature in April, which has a great impact on the timing of bird arrival at the Courland Spit (Table 2). This fact provides an explanation for the above correlation between the winter NAO index and the dates of bird arrival in central and northern Europe. In this study, I used the NAO index for only two months, February and March, but, nevertheless, identified a similar correlation between the time of arrival and its values for 16 species wintering in Europe and Africa. It can be assumed on the basis of these data that such a correlation is not accidental but can be explained, for instance, by the western transfer of air masses in late winter and early spring (connected with the high NAO index), which may have a considerable effect on early migrating species. It is probable that this can not only accelerate the travel of birds along their route but also stimulate their earlier departure from wintering areas in Europe in years with high air temperatures and, consequently, a high NAO index. Long-term data from monitoring stations indicate that there is a strong positive correlation between the temperature in March and the frequency of westerly and southwesterly winds in Great Britain (Sparks et al., 2001).

Recently, many authors from different countries have devoted attention to the correlation between the dates of bird arrival and spring air temperatures (Temple and Cary, 1987; Sema, 1989; Minin, 1992; Mason, 1995; Huin and Sparks, 1998; Sokolov et al., 1999b; Sokolov, 2001; Sueur and Triplet, 2001; Askeyev et al., 2002; Barrett, 2002; Gilyasov and Sparks, 2002; Tryjanowski et al., 2002; Hussell, 2003; etc.). This is not surprising. As early as the 1920s–1940s, during the previous considerable climate warming in the Northern Hemisphere, many authors noted that different bird species began to arrive markedly earlier than in the 19th century (Svyatskii, 1926; Berg, 1947; Mal'chevskii and Pukinskii, 1983; Sparks and Gill, 2002). As long ago as the early 20th century, Kaigorodov (1911) pointed out

that migratory birds usually arrive in spring along with transfer of warm air masses, whereas cold air (e.g., from the Arctic) delays their travel to the north. Menz-bir (1904–1909, pp. 121–122) presents interesting information concerning the effect of weather conditions on the timing of bird arrival in Russia in spring: *The situation with the return of birds to Russia in 1854 provides convincing evidence that bird migration is determined by real circumstances rather than by foresight or anticipation of future advantages. That year, spring came to central Russia around the usual time; nonetheless, the birds arrived almost a month later.* It turned out that the birds arrived at the northern Black Sea coast in due time but encountered a new spell of cold weather and snowstorms there. Radde gave a good description of suffering and death from this cold weather that befell even ducks, which are generally tolerant to the hardships of our climate. The zone of returning winter weather that barred the birds' way was very narrow, a few hundred versts in width. The birds could have easily overcome this barrier and reached areas with favorable conditions by flying at the proper altitude. But they were not aware of that and could not take any measures to save themselves. Flock after flock attempted to start their journey, expending all their strength in the struggle with the cold and snowstorm in the lower layers of the atmosphere, i.e., trying to fly their usual way, but eventually returned to the Crimea, where it was also cold and food was scarce. However, the birds could not fly south from there, because they did not have enough strength to fly over the sea.

It is still unclear whether the rise of air temperature in spring directly stimulates the departure of birds from European wintering places. An analysis of interannual fluctuations of monthly average temperatures in spring in southern Europe showed that they are fairly strong (Sokolov and Kosarev, 2003). For example, during the past 50 years, the average temperature in March ranged from 5.5 to 13.2°C in Spain (Barcelona), from 1.9 to 8.8°C in France (Nancy), and from 5.5 to 11.4°C in Italy (Milan); the average temperature in April ranged, respectively, from 10.0 to 14.8°C, from 6.6 to 12.0°C, and from 10.9 to 15.8°C. As a rule, spring air temperatures in different European countries strongly correlate with each other (Sinelschikova and Sokolov, 2004). For instance, Spearman's rank coefficient of correlation between March temperatures in Kaliningrad, on the one hand, and Barcelona, Milan and Nancy, on the other, averages 0.38 ($p = 0.01$), 0.47 ($p = 0.002$), and 0.50 ($p = 0.001$); the coefficient for April temperatures averages 0.39 ($p = 0.01$), 0.49 ($p = 0.001$), and 0.25 ($p = 0.09$), respectively. Spanish authors (Peñuelas et al., 2002) demonstrated that the annual average temperature in the region of their investigations (Barcelona, southeastern Spain) increased by 1.4°C between 1952 and 2000. Consequently, buds in certain plant species began to open 16 days earlier, on average. For example, the date of the onset of blossoming in the cultivated apple strongly correlates with air temperature in March. I

revealed significant correlations of the dates of bird arrival at the Courland Spit with spring air temperature and the dates of apple blossoming in the Mediterranean region. This fact supports the hypothesis that birds wintering in this region or flying via it can correctly estimate the general weather and phenological situation in other regions of Europe located along the route of their spring migration.

In principle, a wintering bird can obtain information about approaching fall or rise of temperature from the dynamics of daily average air temperature. Warming may stimulate its earlier departure from the wintering place, whereas cooling may delay the departure. Some time ago, a number of authors using an example of the American night migrant *Zonotrichia leucophrys* demonstrated that a rise of air temperature in the range between 5 and 26°C leads to earlier development of night anxiety in a caged bird. On the contrary, both low and overly high temperatures inhibit the migration activity (Eyster, 1954; Kendeigh et al., 1960; Lewis and Farner, 1973). In this case, however, we deal with the species wintering in the temperate zone rather than in Africa or South America, where the seasonal air temperature remains fairly high throughout the year. In Kenya, for example, where a number of our species migrate for wintering, the winter air temperature throughout the 20th century varied within a one-degree range, between 25 and 26°C (Payevsky et al., 2003). However, recent data show that fluctuations of winter average temperatures in Africa, at 20° N, increased significantly by 0.6°C between 1971 and 2000 (Cotton, 2003).

Thus, what kind of information should the bird wintering in Africa receive in order to start spring migration earlier than usual? In theory, this might be information that spring conditions in the nesting region of breeding are becoming increasingly favorable for early arrival from year to year, which could stimulate the birds to leave the wintering region earlier in years with warm springs and later in years with cold springs. To determine the date of departure from the wintering place, the birds could use their biological clock with an annual cycle, in which a constant number of days until the onset of the next spring migration is counted from the date of the previous migration in adult birds and from the day of birth in young birds. Thus, the bird that was born or started spring migration early in a given year would also start migration early in the following year. However, my calculations show that the number of days between the dates of arrival in two successive years or between the date of breeding and the following spring migration does not remain constant but changes significantly (Figs. 6, 7). When migration or breeding in a certain year occurs early, the number of days elapsed until bird arrival in the following year is significantly greater than in the case of late spring migration. This indicates that the birds preparing for migration from the wintering region apparently do not rely on information received in the previous year but begin the

new cycle of migrations “from a blank sheet,” assessing the current meteorological and phenological situation anew every year. This hypothesis appears to be more probable, because weather and phenological conditions in the region of breeding change unpredictably from year to year, and, therefore, natural selection could hardly lead to the development in birds of a special mechanism for memorizing and using information on the weather and phenological conditions of the previous year. The hypothesis that a considerable shift to earlier dates (by 20 days, on average) in the timing of arrival in most passerine bird species during the past two decades is a direct result of natural selection also appears unlikely. Calculations made by Pulido and Berthold (2003), who analyzed heritability of various elements of migratory behavior in birds, show that, for example, a one-week shift in the timing of autumn migratory activity to later dates can be genetically fixed in the population within nine generations (i.e., years) on condition that 10% of the earliest departing individuals in each generation are eliminated, and about 30 generations are necessary for genetic fixation of a three-week shift. However, data of field research show that the dates of arrival can differ by 14 days or more even in successive years (Fig. 5).

In our recent study (Sokolov and Kosarev, 2003), we proposed that the amount of precipitation in wintering regions might have an effect on the dates of the onset of spring migration in birds wintering in Africa. In Africa north of the equator, mainly in its western part, a considerable decrease in precipitation during the period from January to March, when many migrants from Europe dwell there, has been observed in the past two decades (Fig. 3). In three out of eight long-distance migrants studied, we revealed a significant correlation between the timing of arrival at the Courland Spit and the amount of precipitation in Africa at 2.5°–7.5° N, where these species often winter or stop during spring migration. In years with low precipitation in February at these latitudes, long-distance migrants arrive at the Courland Spit earlier than in years with higher precipitation (Sokolov and Kosarev, 2003). We have no direct evidence in favor of the hypothesis that the amount of precipitation in northern Africa has an effect on the timing of departure of certain long-distance migrant from their wintering regions. However, it is quite probable that migratory passerine birds indeed began leaving Africa substantially later in the past two decades than in the 1970s. Considerable year-to-year fluctuations (by up to one month) in the timing of flight of passerine birds via Eilat (Israel), located at the Israeli–Egyptian border, support this hypothesis (Izhaki and Maitav, 1998; Yosef and Tryjanowski, 2002). In different years, migratory birds in spring arrive in Israel earlier or later; therefore, they apparently cross the Sahara on different dates. It appears that, in very dry years, which were recorded in northern Africa in the 1980s and 1990s, long-distance migrants suffered from an acute shortage of vegetable and animal food in winter and early spring.

This could have made them leave their wintering places earlier than usual and migrate to Europe, where food resources were especially rich in this period because of climate warming in the Mediterranean region (Peñuelas et al., 2002; Sanz, 2002). Curry-Lindahl (1984) noted that severe droughts lasting for several years in Africa, south of the Sahara, forced the birds, particularly waterfowl, to leave their usual wintering places or caused mass mortality among them. The early departure of birds from the Iberian Peninsula in the past two decades, compared to the 1970s, may also be explained by a considerable decrease in the amount of precipitation in this region (Fig. 3). Cotton (2003) revealed a strong negative correlation between the timing of arrival of long-distance migrants in the environs of Oxford and the average winter temperature anomalies in Africa at 20° N between 1971 and 2000. On the basis of available data, he concluded that the timing of arrival of long-distance migrants in Europe apparently depends for the most part on food supply to the birds in Africa and on the dates of their departure from wintering places, rather than on weather conditions in Europe. Likewise, Marra et al. (1998) reported that the date of the onset of spring migration in the American species *Setophaga ruticilla* directly depends on food supply in its wintering places (mangrove thickets) and physical conditions of individual birds (namely, the amount of fat). The more rapidly the birds accumulated the fat necessary for migration, the earlier they left their wintering places.

Unfortunately, direct long-term observations on the timing of bird departure from wintering regions in Africa or Central and South America are practically absent. The only exception is the study by Kok et al. (1991) in which the authors consider the results of visual observations on the arrival and departure of the spotted flycatcher (*Muscicarpa striata*) in the central Orange Free State (29°07' S, 26°13' E), Republic of South Africa, over 36 years (1950–1986). The dates of arrival varied considerably from year to year (between November 5 and 30) but were, on average, earlier in the 1950s (November 5–22) than in subsequent years (November 14–30). The range of variation in the dates of departure was markedly narrower (from March 17 to 27). On the basis of the results of stepwise regression analysis, the authors conclude that the most important factor determining the timing of bird departure from the wintering place is the length of the daylight period. Other environmental factors such as the minimal, maximal, and average air temperatures, the amount of precipitation, and wind velocity have no significant effect on the dates of departure.

Probably, it is not so much the departure from wintering places as the rate of spring flight of birds via Africa that has accelerated in the past decades owing to changes in the ecological situation on the continent. It appears that the birds now fly across dry regions, mainly those in northern Africa, more rapidly than before. The results of some studies corroborate this

supposition. Thus, migrating fat birds, the whitethroat (*Sylvia communis*) in particular, were trapped in web nets installed in the region of Sahel (Nigeria, Lake Chad) on earlier dates in 2000 (the first five days of April) than in the late 1960s (the last five days of April) (Ottosson et al., 2002). In general, there is an increasing body of evidence that Palearctic migrants, such as warblers, do not remain in the same region of Africa but, on the contrary, repeatedly fly from one region to another during winter (Pearson, 1990; Jones, 1995). Depending on the date of onset of the wet season, the same birds can winter in different regions of Africa that are sometimes located hundreds of kilometers away from each other. Migratory birds cross the African continent more rapidly in spring than in autumn, with the duration of travel from South Africa to nesting areas averaging about six weeks (Pearson and Lack, 1992). Most birds migrating over East Africa make a stop and rest for one or two days, but this stopover may be longer if regions rich in food occur on their way. In Kenya, heavy rains usually begin in the middle or end of March (Pearson, 1990), but the central and eastern parts of Kenya may remain dry until early April. In such years, most of wintering migrants leave these regions in search of more favorable places for fattening. The most favorable region for accumulating fat reserves before the long spurt through the Sahara is Ethiopia, where the wet season begins in April (Pearson and Lack, 1992; Jones, 1995). It may well be that the time of onset of the wet season and the duration of the stopover for fattening in this region are major factors determining the dates of flight through the Sahara and the timing of arrival in the Mediterranean region in many species. An analysis of long-term data on precipitation in Ethiopia and Sudan indicates that, in the 1970s, when the birds arrived in the Baltic region on the latest dates, the amounts of precipitation in March and April were far smaller than those in the 1960s, 1980s, and 1990s, when the earliest arrivals of passerines in Europe were recorded (Fig. 4). Palearctic migrants in the 1970s probably had to stay in Ethiopia and Sudan for a longer time in order to accumulate the amount of fat necessary for the flight through the Sahara and the deserts of Saudi Arabia and, consequently, arrived in Europe later. This hypothesis is confirmed by a significant negative correlation that I found between the amounts of precipitation in certain countries of East Africa and the dates on which long-distance migrants appeared on the Courland Spit (Table 3). However, a more detailed analysis of the correlation between the timing of bird arrival in Europe and conditions in the aforementioned part of Africa (the amount of precipitation and the time of onset of the wet season) is necessary for explaining the significant shift to earlier dates in the timing of arrival of long-distance migrants during the past two decades.

Timing of Nesting

Judging from the average date of hatching and the date of the first capture of juvenile birds in the study region, the timing of nesting in many species varies from year to year to the same extent as the timing of spring migration (Fig. 5, Table 4). Similarly to the latter parameter, the timing of nesting significantly correlates with spring air temperatures and the NAO index. Therefore, high temperatures in the spring contribute both to earlier bird arrival in the nesting region and to earlier egg laying and, consequently, earlier hatching of nestlings. Most illustrative in this respect is the year 2000, in which the average temperature in April reached the highest value over the past 48 years (9.7°C in Kalininograd). In that year, the earliest nesting on the Courland Spit over the entire period of our studies was observed not only in species wintering in Europe but also in long-distance migrants such as the pied flycatcher: some females laid the first eggs as early as May 10, and the first nestlings hatched in late May rather than in early June, as had been noted in previous "early" years (Sokolov, 2000). During the past 23 years, the median date of first egg laying in the pied flycatcher on the Courland Spit varied within a 17-day range, from May 19 (2000) to June 5 (1987); the dates of capture of the first flycatchers in spring varied within a similar 18-day range, from April 19 (2000) to May 4 (1988). A comparative analysis of year-to-year variation in the mean date of the onset of egg laying in 25 European pied flycatcher populations, from Spain to northern Finland, showed that nesting in most populations was highly synchronous (Both et al., 2004). As we have shown previously, the dates of spring migration and nesting in passerine birds can synchronously change from year to year in populations living at large distances from each other (Sokolov and Payevsky, 1998; Sokolov et al., 1999a). Recently, many authors have arrived at the conclusion that spring air temperatures can have a significant effect on the timing of nesting as well as on the dates of bird arrival, primarily in passerines (Ellegren, 1990; Ryabitshev, 1993; Rytönen et al., 1993; Morton, 1994; Enemar, 1995; Zając, 1995; Winkel and Huddle, 1997; McCleery and Perrins, 1998; Sokolov and Payevsky, 1998; Brown et al., 1999; Crick and Sparks, 1999; Meijer et al., 1999; Slater, 1999; Sparks et al., 2003; Both et al., 2004). The generally accepted concept is that the photoperiod has the decisive effect on the timing of gonad development and, consequently, breeding in the majority of bird species. However, experimental studies periodically provide evidence that the rate of gonad development and, therefore, the timing of breeding largely depend on temperature (Threadgold, 1960; Lewis and Farnar, 1973; Silverin and Viebke, 1994; Silverin, 1995). Moreover, differences in sensitivity to spring air temperature between populations of the great tit were revealed (Silverin, 1995). Southern populations proved to be more sensitive to low temperature than northern populations: in tits from

Italy, the time of gonad development at 4°C was three to four weeks longer than at 20°C, whereas no such difference was revealed in tits from Sweden.

Timing of Autumn Migration

Long-term monitoring of autumn migration of passerine birds on the Courland Spit revealed considerable fluctuations in the average date of flight in most species, but significant long-term trends in the timing of flight were recorded in only four species (Table 5, Fig. 5). On the whole, in years with warmer springs (the 1960s and 1980s), young and adult birds of many species migrated via the Courland Spit significantly earlier than in years with cold springs (mainly in the 1970s and late 1990s) (Sokolov et al., 1999c). German authors reported that 19 species of short-distance migrants on Helgoland, the North Sea, had the opposite tendency to migrate later than usual (on average, by 10 days) in the warm 1980s, explaining this fact by the influence of current climate warming (Glaubrecht, 1993; Moritz, 1993; Vogel and Moritz, 1995). Other specialists have also noted later dates of autumn migration in some species during the past decades, supposing that in warmer years the birds stay in the region of breeding for a longer time (Gatter, 2000; Sparks and Mason, 2001; Bairlein and Winkel, 2001; Fiedler, 2003a, 2003b). In Germany and other regions of central Europe, some passerine species, primarily short-distance migrants, may indeed remain in their nesting areas for a longer time under favorable weather conditions in autumn. In the Baltic region, however, such a delay of autumn flight during a period of warming was not recorded in short- and long-distance migrants, except for a few species (Table 5) (Sokolov et al., 1999c; Sinelschikova and Sokolov, 2004). Jenni and Keri (2003) analyzed changes in the timing of autumn migration in 65 passerine species on the basis of data on the captures of birds migrating via the Col de Bretolet pass (the Swiss Alps) over 42 years. The authors conclude that the peak of migration in long-distance migrants has shifted to earlier dates, whereas that in 28 species of short-distance migrants has shifted to later dates in recent years. In their opinion, a probable explanation is that short-distance migrants often manage to rear two clutches in favorable years, and, as a result, many individuals born relatively late become involved in the autumn migration. Because of such individuals, the average date of migration (for the species) has shifted to later dates in the past decade. However, the timing of autumn migration has also shifted to earlier dates in 12 species migrating within Europe, including three so-called irruptive species. The authors suppose that global warming may have different effects on irruptive and nonirruptive species. In our recent study on the dates of autumn migration in the long-tailed titmouse *Aegithalos caudatus* (an irruptive species) on the Courland Spit, we failed to reveal any significant trend of changes in the timing of migration over 47 years in this species or in most nonirruptive

species (Sokolov et al., 2004). Only a weak tendency toward the appearance of the first long-tailed titmice on the spit on earlier dates can be traced in the past two decades, which apparently results from earlier breeding of the species in this period.

Let us consider possible factors accounting for annual fluctuations in the average date of autumn migration in long- and short-distance migrants. A comparison of the average dates of autumn migration and breeding shows that these parameters positively correlate in both long- and short-distance migrants (Table 5). Therefore, after early nesting of the population, juvenile and adult birds leave their place of birth (breeding) earlier and, as a consequence, migrate in autumn through the region of our study on earlier dates. A probable explanation for the direct relationship between the timing of breeding and the average date of autumn flight in young birds is that the onset of migration in many passerines (in both long- and middle-distance migrants) is apparently under direct endogenous control (Gwinner, 1972, 2003; Shumakov et al., 1972; Dol'nik et al., 1974; Dol'nik, 1975; Berthold, 1988, 2001). In other words, the date of the onset of autumn migration in young birds depends mainly on their age rather than on some external environmental signals. The study of passerine birds in the Subarctic by Ryzhanskiy (1997) showed that the migratory state in juvenile birds apparently develops under the control of an endogenous temporal program. The author revealed a fairly strong positive correlation between the timing of hatching and departure in the bluethroat (*Luscinia svecica*), willow warbler (*Phylloscopus trochilus*), arctic warbler (*Ph. borealis*), and little bunting (*Emberiza pusilla*) in the period from 1977 to 1982. Ellegren (1990) analyzed the timing of autumn migration in the bluethroat as a function of the dates of breeding in eastern Sweden over 11 years (1972–1982). He revealed a significant positive correlation between the annual median dates of the first egg laying and the median dates of young bird migration through the study region, which varied between August 25 and September 5. It should be taken into account, however, that young birds hatching on later dates have an accelerated program of juvenile molt, which is controlled by the photoperiod. Hence, they can start autumn migration at an earlier age than the individuals born before them (Shumakov et al., 1972; Rymkevich and Bojarinova, 1996; Bojarinova et al., 1999). Bojarinova et al. (2002), who studied the timing of autumn migration in the great tit (*Parus major*) in Leningrad oblast, concluded that the timing of migration in birds from the first broods closely depends on the date of hatching, as all juveniles, irrespective of this date, migrate upon reaching a certain age. Birds from the second broods, conversely, begin to migrate at an earlier age, which varies in accordance with the date of hatching.

According to my calculations, the number of days between the date of hatching (or the date of the first capture of a juvenile bird) and the average date of

autumn migration on the Courland Spit strongly depends on the timing of nesting in the population: the later the timing of nesting, the smaller the number of days elapsed until the average date of autumn migration (Fig. 7). Therefore, in years with late nesting, young birds begin autumn migration at an earlier age, similarly to individuals from late broods. As a result, the difference between the dates of autumn migration in years with early and late nesting levels off to a considerable extent. This is why the average dates of autumn migration in most species have not changed significantly in the study region, irrespective of the significant tendency toward earlier nesting recorded in many long-distance and short-distance migrants on the Courland Spit during last two decades (Table 4, Fig. 5).

According to data of certain authors (Dol'nik, 1975), the timing of the autumn migratory state in adult birds is under the control of an autonomous system of long-term countdown, which is activated in spring owing to an increase in the daylight period. Such a system of control over the onset of autumn migration in adult birds should have reduced the range of variation in the average date of flight compared to that in juveniles. However, our data indicate that the average dates of autumn migration in adult birds (both in short- and long-distance migrants) and juveniles vary from year to year to almost the same extent (Sokolov et al., 1999c). Moreover, the average date of autumn migration in adult birds directly depends on the timing of nesting. Early nesting in the population apparently results in earlier autumn migration of both young and adult birds.

How does the timing of autumn migration respond to the direct influence of weather conditions, primarily temperature? It is generally agreed that the effect of ambient conditions on the departure of birds is virtually absent in long-distance migrants but is fairly strong in short-distance migrants (Berthold, 2001; Schwabl and Silverin, 1990; Gatter, 2000). Curry-Lindahl (1984) considers that the internal rhythms of long-distance migrants tune them to a certain time of departure with an accuracy of about one week, whereas short-distance migrants are more mobile and can change the timing of departure depending on the weather in the autumn of the current year. The departure of short-distance migrants in autumn can be stimulated by a fall in temperature. The sensitivity of these birds to weather also depends on the degree of their readiness to migration: if this degree is high, only a slight environmental influence is enough to provoke the departure. According to this author, the high variability in the timing of autumn migration in short-distance migrants, in contrast to long-distance migrants, is accounted for mainly by their sensitivity to the effect of unstable weather conditions in the period of departure. However, our data do not confirm the opinion that the variation in the dates of autumn migration is greater in short-distance than in long-distance migrants (Sokolov et al., 1999c). As follows from Fig. 5, its range is almost identical in both of these groups. The variation in the average dates of

arrival recorded in the study area in spring is indeed greater in short- and middle-distance than in long-distance migrants (Sokolov et al., 1999a), but this is explained by the fact that migrants wintering in Europe arrive earlier, when air temperature is very unstable. Comparing the average dates of autumn migration with monthly average air temperatures in autumn, I revealed no significant correlation with autumn air temperatures or the NAO index in long- and short-distance migrants, except for three species (Table 5). However, these dates in some species, both short- and long-distance migrants, proved to significantly correlate with air temperatures in spring, especially in April. The most probable explanation for this fact is that the timing of autumn migration largely correlates with the timing of nesting, and the latter, in turn, strongly depends on spring air temperatures (Table 4). This does not mean that weather conditions have no effect on the timing of bird departure in northern regions. For example, observations made by Ryzhanovskii (1997) show that, under favorable conditions, long-distance migrants (the bank swallow *Riparia riparia*, yellow wagtail *Motacilla flava*, and common rosefinch) in the Subarctic usually begin and finish autumn migration in August. In years with a warm and long autumn, the departure of insectivorous birds in the first half of September may be prolonged to some extent, but the bulk of the population leaves the Subarctic on the usual dates owing to the endogenous control of migration timing. In the second half of September, the effect of climatic conditions on the dates of the end of departure increases significantly. When the autumn is warm and long, thrushes (the genus *Turdus*), white wagtails (*M. alba*), meadow pipits (*Anthus pratensis*), and reed buntings (*Emberiza schoeniclus*) occur in small numbers almost until the end of September; if winter comes early, they depart in the second ten-day period of September (Ryzhanovskii, 1997, pp. 257–258).

Thus, based on the data discussed above, I arrived at the principal conclusion that long-term trends of changes in the timing of arrival, nesting, and departure of passerine birds, including both short- and long-distance migrants, in the Palearctic in the 20th century were determined by considerable climatic fluctuations that entailed substantial changes in the thermal regime of the Northern Hemisphere, mainly in winter and spring. Further changes in the timing of bird arrival and nesting will largely depend on the subsequent dynamics of winter and spring air temperatures, whereas the dates of departure to wintering places will mainly depend on the timing of nesting. If climate warming in the Northern Hemisphere were to continue in the 21st century, this would result in still earlier bird arrival and breeding, as early breeding is usually more advantageous for both individuals and the population as a whole, in spite of higher risk of death in early spring in the event of cold spells and sudden worsening of foraging conditions. Many authors have shown that breeding success in passerine birds is considerably higher in years with

early (rather than late) nesting (Lack, 1968; Glue, 1992; Rytönen et al., 1993; Polenets et al., 1995; Järvinen, 1996; Perrins, 1996; Thingstad, 1997; Payevsky, 1999; Sokolov, 1999a; Bairlein and Winkel, 2001; Sokolov et al., 2002). In some cases, however, climate warming may create problems with offspring rearing: the peak of hatching may diverge in time from the peak of abundance of insects, which usually are the main food for nestlings in passerine populations, and their productivity may decrease (Visser et al., 1998; Both and Visser, 2001; Stenseth and Mysterud, 2003). Genetic polymorphism intrinsic to any species provides conditions for successful adaptation of birds to breeding on earlier dates. Recent bird species have repeatedly adapted themselves to new environmental conditions, as the climate of our planet changes continuously, and many of them have survived both glaciations and periods of global warming. Natural selection over hundreds of thousands of years should have provided for the genetic structure of populations that allows their timely restructuring and adaptation to continuously changing environmental factors such as climate.

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SPELL: 1. cyclicality, 2. circannual