

## **Spring temperatures influence year-to-year variations in the breeding phenology of passerines on the Courish Spit, eastern Baltic**

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Abstract: Sokolov, L.V. & V.A. Payevsky (1998): Spring temperatures influence year-to-year variations in the breeding phenology of passerines on the Courish Spit, eastern Baltic. *Avian Ecology and Behaviour* 1: 22-36.

A significant positive correlation between average hatching dates and average catching dates of local juveniles (before August 15) in stationary Rybachy-type traps on the Courish Spit was revealed for 10 bird species over a period of 10-29 years. Timing of breeding may thus be estimated from dates of trapping local juveniles during juvenile dispersal. Analysis of the annual fluctuations of average dates for the first five catches, and of all catches in 19 species of local breeders in sedentary (Crested Tit *Parus cristatus* and Marsh Tit *Parus palustris*) and migratory populations during four decades revealed a trend towards later breeding in the 1970s and 1990s compared to the 1960s and 1980s. We compared the timing of breeding and of juvenile dispersal in 36 species with the monthly average temperatures in spring and summer. Early arriving species showed a significant negative correlation with average March and April temperatures, as did late arriving long-distance migrants with average temperatures in April and May. In two of the earliest breeders, Common Crossbill *Loxia curvirostra* and Siskin *Carduelis spinus*, similar relationships with February and March temperatures were found. For four species a relationship with the temperature of June was revealed. Five species showed a positive correlation between arrival dates and the timing of juvenile dispersal. On the basis of our material and literature sources we show that the long-term trends in the timing of breeding and juvenile dispersal that were observed in the Baltic region in sedentary and migratory passerines in the 20th century were caused mainly by climatic fluctuations. These occurred in the form of long-term variations in spring temperatures and various phenological events. The rising of spring temperatures in the 1960s and 1980s caused not only a significant shift towards earlier spring migration in many passerines (Sokolov et al., this volume), but earlier breeding and earlier dispersal as well. Colder periods in the 1960s and partly in the 1990s caused a shift towards later breeding and dispersal in sedentary birds, as well as in short- and long-distance migrants.

Key words: passerines, timing of breeding, air temperatures, long-term trends

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### **1. Introduction**

Much information concerning timing of breeding in many bird species has been published, but the results of long-term monitoring (over 10 years) are presented infrequently (Kania 1994). In a number of publications authors establish relationships between breeding of birds and certain phenological events, e.g. disappearance of snow cover and ice, opening of leaves in trees and bushes, flowering of plants, etc. (Ellegren 1990, Nystrom 1991, Morton 1994, Wiklander et al. 1994, Watson 1996). Nevertheless, the impact of spring temperatures on long-term trends in the timing of breeding and especially in the timing of juvenile dispersal, is insufficiently studied. This problem is discussed in this paper.

## 2. Material and methods

The study was conducted at the Biological Station Rybachy's field site „Fringilla" on the Courish (or Curonian) Spit of the Baltic (55°05' N 20°44' E) over the period of 1959-1998. At this site regular nest searches were conducted, and nestlings ringed (Payevsky 1985, Sokolov 1991). Average hatching dates were used as estimates of timing of breeding. Sufficient data on the timing of breeding was collected for 10 species (Tab. 1).

Timing of juvenile dispersal was estimated on the basis of trapping in stationary Rybachy-type traps (for detailed description of the traps see; Dolnik & Payevsky 1976). The date of the first catch, average date of first five catches, and average trapping date of juveniles mainly of local origin (trapped before August 15) were used. During the summer period usually two Rybachy-type traps were operated that trapped birds moving either towards the NE or the SW.

In order to reveal long-term trends in the variation of timing of juvenile dispersal three time intervals were used: 1959-1974 (16 years); 1975-1990 (16 years), and 1988-1998 (11 years). For statistical treatment Spearman's rank correlation  $r_s$  was used (Lloyd & Ledermann 1984).

For the analysis of temperature influence average air temperatures in February, March, April, May, and June during the period 1959-1990 were used. The data for the Kaliningrad Region (Russia) was kindly provided by R.V.Abramov (Institute of Oceanology). Correlation analysis was used to reveal relationships between timing of breeding, dispersal, and air temperature.

## 3. Results

### 3.1. Relationships between average hatching date and timing of juvenile dispersal

First it was necessary to find out whether catches during the period of dispersal can be used to estimate timing of breeding. If so, it would be possible to estimate the timing of breeding in a number of species over four decades, as Rybachy-type traps supplied the data on timing of juvenile dispersal over this period for more than 30 passerine species.

This analysis was done for 10 species, both sedentary and migratory, that breed on the Courish Spit in sufficient numbers. A significant positive correlation between average hatching dates and dates of catches of local juveniles before August 15 was found in all 10 species during long enough periods of 10 to 29 years (Tab. 1). This relationship suggests that early hatching is followed by earlier post-fledging movements. Thus, timing of juvenile dispersal may be an estimate of timing of breeding in both sedentary and migratory species.

### 3.2. Trends in the timing of juvenile dispersal

The analysis of annual fluctuations of average catching dates of first five and of all juveniles during the post-fledging period (before August 1) showed significant trends in many species (Fig.). A significant trend towards earlier dispersal in the 1960s compared to the 1970s was revealed in 12 species out of 19 (Tab. 2). A similar trend was found when comparing the 1980s with the 1970s. In almost all studied species, except for Lesser Whitethroat *Sylvia curruca*, juvenile dispersal took place later in the 1970s than in the 1980s (Tab. 2). A trend towards later breeding in the 1990s compared to the 1980s was found in 14 species (Tab.2).

Table 1. The correlation between mean dates of hatching birds and captures of local young birds before 15 August at the Courish Spit ( $r_s$  = Spearman's rank correlation coefficient; \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ )

Species	Number of years	$r_s$
<i>Parus palustris</i>	10	0.70*
<i>Parus major</i>	20	0.62*
<i>Fringilla coelebs</i>	29	0.60***
<i>Phylloscopus trochilus</i>	20	0.50*
<i>Phylloscopus sibilatrix</i>	16	0.48*
<i>Ficedula hypoleuca</i>	20	0.59**
<i>Sylvia borin</i>	20	0.45*
<i>Sylvia nisoria</i>	18	0.51*
<i>Hippolais icterina</i>	16	0.44*
<i>Carpodacus erythrinus</i>	18	0.61**

Table 2. The tendency to change in the timing of postbreeding dispersal of young birds at the Courish Spit revealed by the correlation between dates of captures of young birds and the years (Spearman's rank correlation coefficient, +  $p < 0.10$ , \*  $p < 0.05$ , \*\*  $p < 0.05$ , \*\*\*  $p < 0.001$ )

Species	1959-1974		1975-1990		1988-1998	
	Years first five youngs	all youngs	Years first five youngs	all youngs	Years first five youngs	all youngs
<i>Parus cristatus</i>	0.52*	0.52*	-0.83**	-0.75**	0.78**	0.77**
<i>Parus palustris</i>	0.54*	0.65*	-0.76**	-0.70**	0.69*	0.47
<i>Parus major</i>	0.34	0.36	-0.45 <sup>+</sup>	-0.64*	0.54*	0.89***
<i>Parus caeruleus</i>	0.33	0.53*	-0.61*	-0.65*	0.86***	0.43
<i>Fringilla coelebs</i>	0.63*	0.41	-0.54*	-0.57*	0.23	0.33
<i>Emberiza citrinella</i>	-0.07	0.50*	-0.38	-0.67*	0.85***	0.76**
<i>Phoenicurus ochruros</i>	0.17	0.17	0.77**	-0.59*	0.32	-
<i>Phylloscopus collybita</i>	0.62*	0.62*	-0.66*	-0.31	0.55*	-
<i>Motacilla alba</i>	0.18	-0.10	-0.73**	-0.80**	0.50 <sup>+</sup>	0.51 <sup>+</sup>
<i>Anthus trivialis</i>	0.13	0.21	-0.57*	-0.60*	0.45	0.40
<i>Phylloscopus trochilus</i>	0.21	0.03	-0.60*	-0.61*	0.35	0.10
<i>Phylloscopus sibilatrix</i>	0.76**	0.59*	0.57*	-0.69**	0.58*	0.65*
<i>Ficedula hypoleuca</i>	0.46 <sup>+</sup>	0.36	-0.56*	-0.65*	0.74**	0.84**
<i>Sylvia atricapilla</i>	0.34	0.69**	-0.64*	-0.61*	0.71**	0.46
<i>Sylvia curruca</i>	-0, 18	0.47 <sup>+</sup>	-0.40	-0.41	0.61*	0.20
<i>Sylvia communis</i>	0.56*	0.75**	-0.69**	-0.49*	0.52 <sup>+</sup>	0.23
<i>Sylvia borin</i>	0.71**	0.59*	-0.49 <sup>+</sup>	-0.12	0.85***	0.35
<i>Hippolais icterina</i>	0.73**	0.90***	-0.50 <sup>+</sup>	-0.54*	0.74**	0.81**
<i>Carpodacus erythrinus</i>	0.61*	-0.51*	0.09			

First five youngs - mean date of five first captures of young birds, all youngs - mean date of captures of all young birds before 15 August.

Figure 1. Changes in the summer dispersal date of juveniles on the Courish Spit.

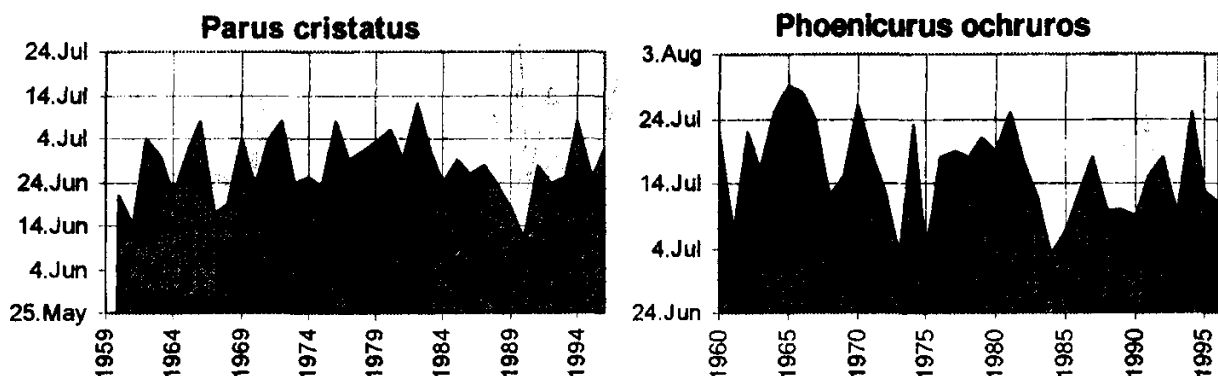


Figure 1. Continued

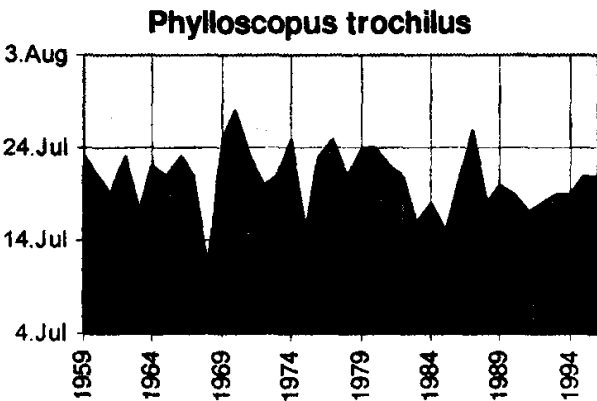
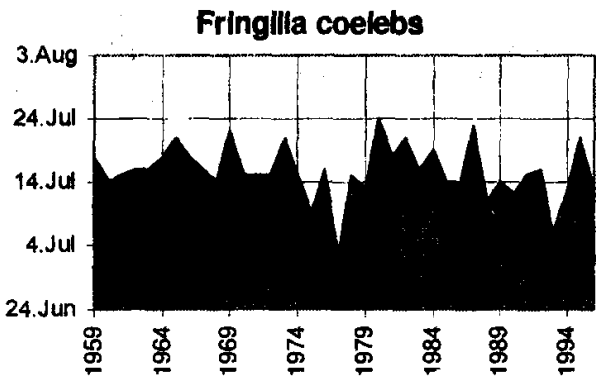
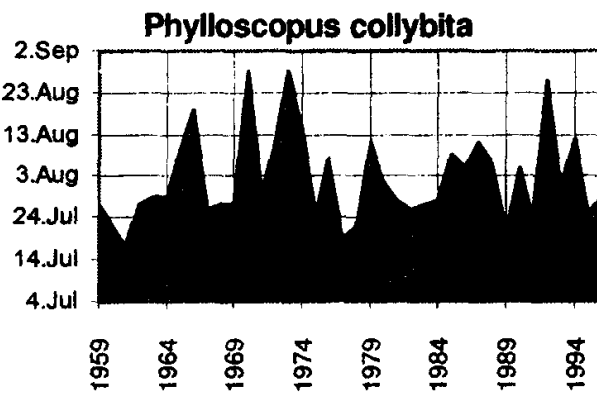
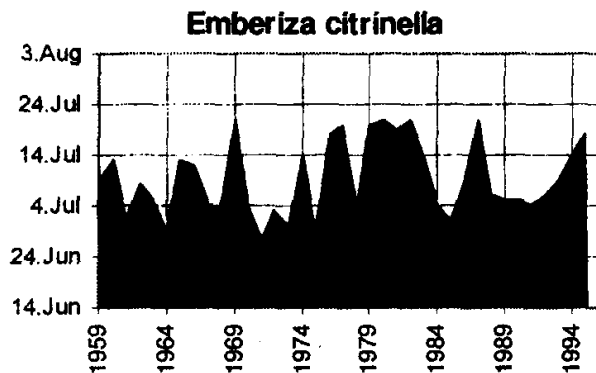
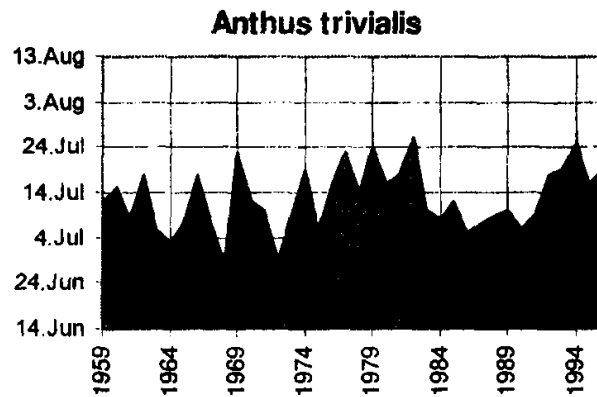
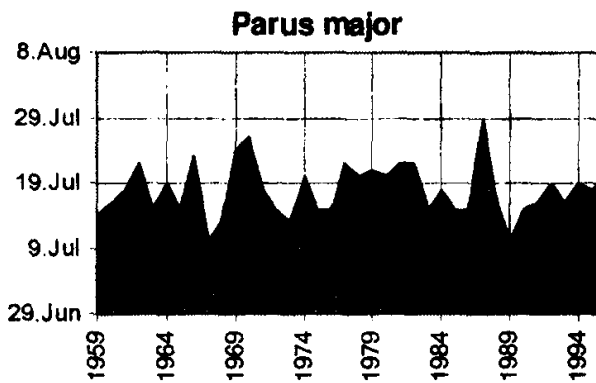
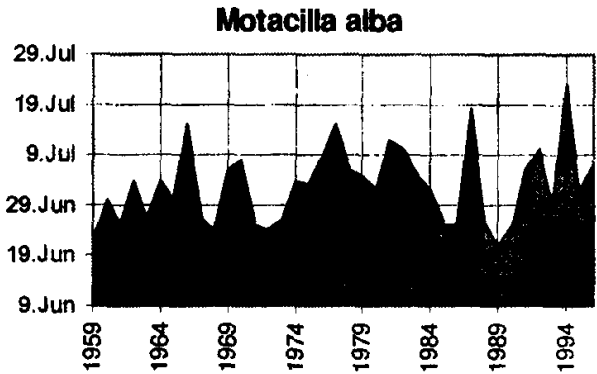
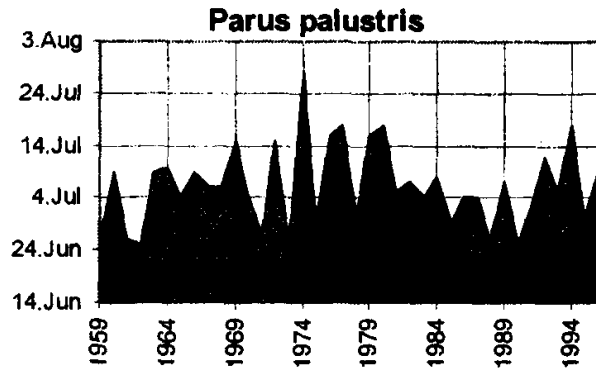
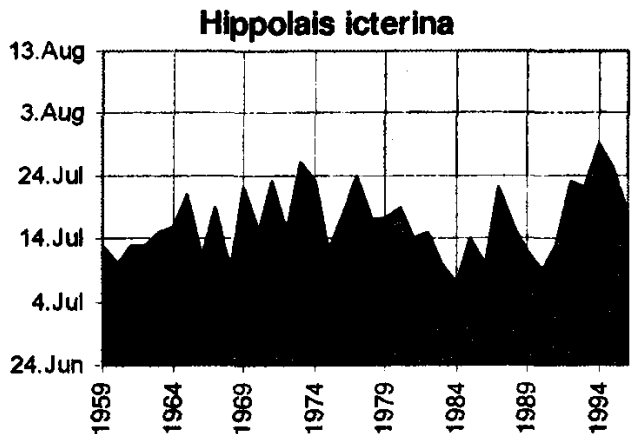
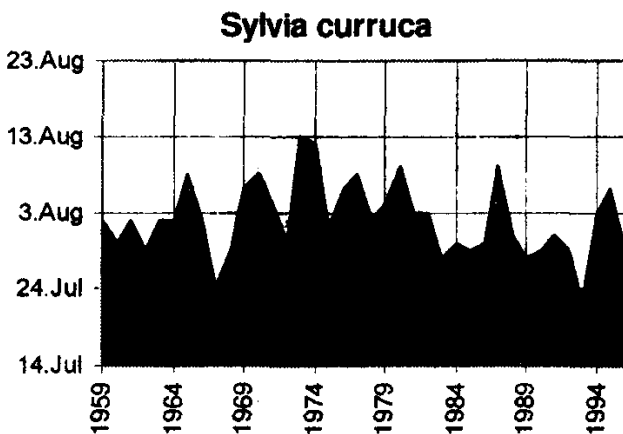
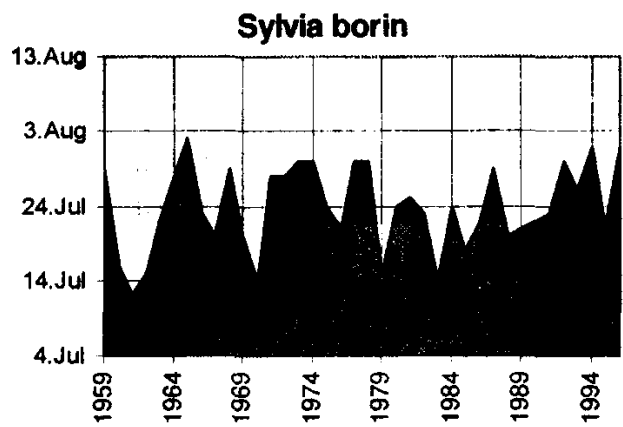
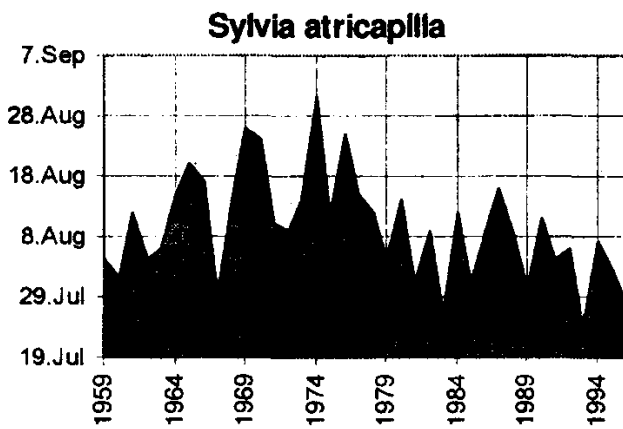
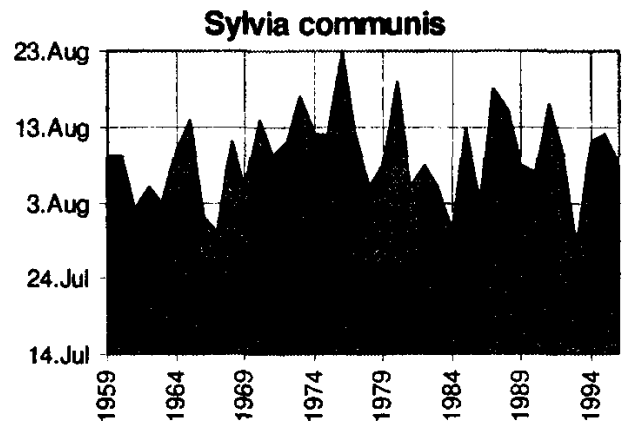
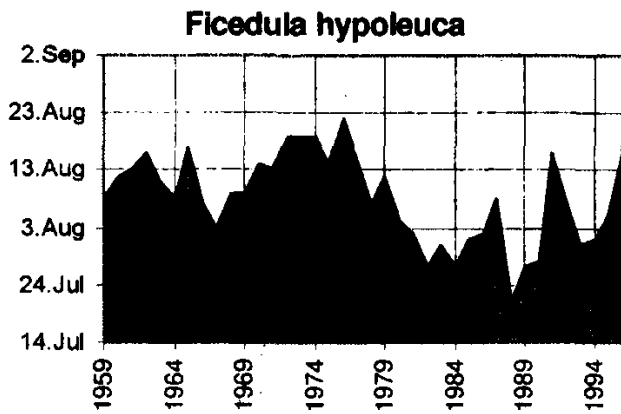
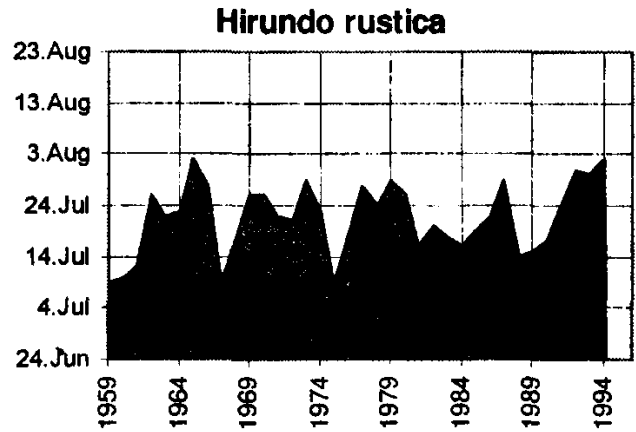
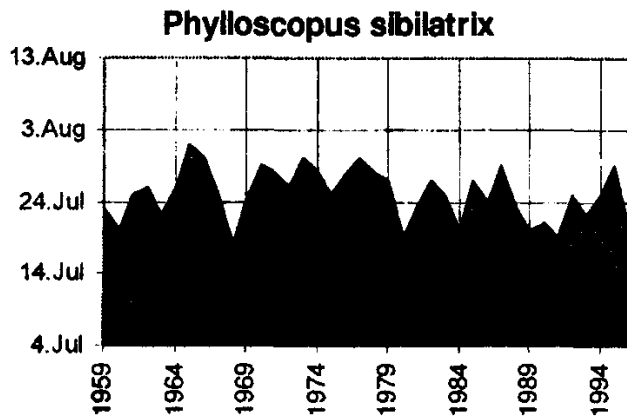


Figure 1. Continued



Thus, timing of breeding in the species studied, sedentary, short and long-distance migrants was earlier in the 1960s and the 1980s compared to the 1970s and the 1990s, with the exception of some years (Fig. 1).

### 3.3. Relationship between hatching dates and spring and summer air temperatures

Comparing average temperatures of spring and summer months with the timing of breeding for 12 species revealed a negative relationship in 10 species (Tab. 3). High temperatures in spring months caused early hatching. A correlation with March average temperature was found in the Great Tit *Parus major* and Chaffinch *Fringilla coelebs* which arrive early, Significant or barely significant correlation with April temperature was revealed in six species. In seven species, mainly long-distance migrants, this correlation was found with May temperature, and June temperature influenced timing of breeding only in the Whitethroat *Sylvia communis*. Median hatching date in the sedentary Marsh Tit *Parus palustris* population on the Courish Spit was correlated to average April temperature ( $r_s = -0.77$ ;  $p < 0.05$ ;  $n = 10$ ), but not to May temperature ( $r_s = -0.18$ ;  $p > 0.05$ ;  $n = 10$ ) (Markovets, unpubl.).

Table 3. The correlation between mean hatching date of nestling and air temperatures during spring and summer months in some species at the Courish Spit ( Spearman's rank correlation coefficient; +  $p < 0.10$ , \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ )

Species	Number of years	t°C March	t°C April	t°C May	t°C June
<i>Parus major</i>	20	-0.39*	-0.42*	-0.58*	-0.53*
<i>Fringilla coelebs</i>	29	-0.38*	-0.40*	-0.66***	-0.22
<i>Phylloscopus trochilus</i>	20	-0.30	-0.28	-0.61**	-0.03
<i>Phylloscopus sibilatrix</i>	18	-0.38	-0.61*	-0.49*	0.12
<i>Ficedula hypoleuca</i>	20	-0.21	-0.45*	-0.59**	-0.23
<i>Sylvia atricapilla</i>	18	-0.18	-0.40*	-0.26	-0.02
<i>Sylvia curruca</i>	20	-0.21	-0.45*	-0.33	-0.37
<i>Sylvia communis</i>	16	0.11	-0.07	-0.38	-0.62*
<i>Sylvia borin</i>	20	-0.03	-0.16	-0.51*	-0.26
<i>Sylvia nisoria</i>	18	-0.08	-0.32	-0.65**	0.05
<i>Hippolais icterina</i>	16	-0.10	-0.24	-0.34	-0.28
<i>Carpodacus erythrinus</i>	18	-0.13	-0.22	-0.75**	0.09

### 3.4. Correlation between timing of juvenile dispersal and air temperature in spring and in summer

Comparing the timing of first captures with average monthly temperatures in spring and summer showed a negative correlation with March temperature in 11 species, with April temperature in 25 species, with May temperature in 17 species and with June temperature in just one species (Tab. 4). Timing of first captures of juveniles was correlated with March temperatures mostly in early breeders. In two earliest breeders, Common Crossbill *Loxia curvirostra* and Siskin *Carduelis spinus*, average dates of first five captures were negatively correlated with average February temperature ( $r_s = -0.39$ ;  $p < 0.05$ ;  $n = 29$  and  $r_s = -0.36$ ;  $p < 0.05$ ;  $n = 29$ , correspondingly).

Significant negative correlation was found mainly between average trapping dates during dispersal and air temperatures in April and May (Tab. 4). A better correlation with March temperature was found for the timing of first captures than for the timing of the whole dispersal.

Table 4. The correlation between mean dates of postbreeding dispersal movements of birds and mean air temperatures during spring and summer months at the Courish spit, 1959-1990 (Spearman's rank correlation coefficient,+ p<0.10, \* p<0.05, \*\* p<0.01,\*\*\* p<0.001)

<i>Species</i>	Date's category	t°C March	t°C April	t°C May	t°C June
<i>Parus cristatus</i>	first young	-0.32*	-0.50**	-0.24	0.11
	five youngs	-0.23	-0.64***	-0.16	-0.08
	all youngs	-0.28	-0.61***	-0.03	-0.22
<i>Parus palustris</i>	first	-0.22	-0.46*	-0.38*	-0.05
	five	0.03	-0.34*	-0.13	0.08
	all	0.06	-0.29	-0.21	-0.05
<i>Parus montanus</i>	first	-0.63***	-0.27	-0.30*	-0.14
	five	-0.42*	-0.36*	-0.20	0.03
<i>Parus major</i>	first	-0.53**	-0.63***	-0.20	-0.15
	five	-0.44*	-0.67***	-0.27	0.01
	all	-0.33*	-0.57**	-0.56**	0.03
<i>Parus caeruleus</i>	first	-0.42*	-0.49**	-0.05	-0.46**
	five	-0.31*	-0.63***	-0.07	-0.33*
	all		-0.64***	-0.41*	-0.34*
<i>Regulus regulus</i>	first	-0.37*	-0.26	-0.10	
	five	-0.39*	-0.33*	-0.17	0.10
<i>Sturnus vulgaris</i>	first	-0.28	-0.55**	-0.22	-0.19
	five	-0.26	-0.48**	-0.16	-0.14
<i>Lullula arborea</i>	first	0.12	-0.55*	-0.04	-0.18
	five	0.19	-0.67**	-0.11	-0.21
<i>Erithacus rubecula</i>	first	-0.30*	-0.31*	-0.22	-0.01
	five	-0.41*	-0.39*	-0.33*	0.04
<i>Turdus merula</i>	first	-0.07	-0.43*	-0.39*	-0.12
	five	-0.30*	-0.49**	-0.32*	-0.01
<i>Turdus philomelos</i>	first	-0.24	-0.33*	-0.05	-0.26
	five	-0.25	-0.21	0.06	-0.19
<i>Fringilla coelebs</i>	first	-0.23	-0.69***	-0.23	-0.25
	five	-0.31*	-0.63***	-0.40*	-0.18
	all	-0.23	-0.53**	-0.60***	-0.14
<i>Emberiza citrinella</i>	first	-0.01	-0.42*	-0.25	-0.01
	five	-0.19	-0.48***	-0.26	-0.15
	all	-0.37*	-0.50**	-0.27	-0.07
<i>Carduelis spinus</i>	first	-0.32*	-0.29	-0.01	-0.24
	five	-0.36*	-0.21	0.03	-0.25
<i>Loxia curvirostra</i>	first	-0.34*	0.08	0.03	-0.23
	five	-0.50**	0.01	-0.08	-0.23
<i>Phoenicurus ochruros</i>	first	-0.25	-0.58***	-0.58**	0.13
	five	-0.35*	-0.59***	-0.51**	0.16
	all	-0.36*	-0.56**	-0.49**	0.10
<i>Phylloscopus collybita</i>	first	-0.10	-0.31*	-0.29	0.29
	five	-0.15	-0.40*	-0.19	0.21
	all	0.08	-0.28	-0.02	0.21
<i>Motacilla alba</i>	first	-0.13	-0.63***	-0.17	-0.09
	five	-0, 32*	-0.68***	-0.29	-0.09
	all	-0.42*	-0.52**	-0.33*	-0.10
<i>Anthus trivialis</i>	first	-0.05	-0.45*	-0.21	-0.22
	five	-0.24	-0.60***	-0.22	-0.21
	all	-0.27	-0.73***	-0.52**	-0.08
<i>Phylloscopus trochilus</i>	first	-0.32*	-0.63***	-0.46**	-0.25
	five	-0.39*	-0.63***	-0.49**	-0.24
	all	-0.45*	-0.52**	-0.60***	-0.07

<i>Phylloscopus sibilatrix</i>	first	-0.13	-0.69***	-0.36*	-0.13
	five	-0.20	-0.68***	-0.46**	-0.19
	all	-0.22	-0.56**	-0.50**	-0.26
<i>Ficedula hypoleuca</i>	first	-0.01	-0.53**	-0.41*	0.12
	five	-0.23	-0.59***	-0.46**	-0.13
	all	-0.04	-0.53**	-0.51**	-0.17
<i>Phoenicurus phoenicurus</i>	first	-0.33*	-0.17	-0.06	-0, 02
	five	-0.31*	-0.19	-0.09	0.00
<i>Sylvia atricapilla</i>	first	-0.33*	-0.34*	-0.66***	0.12
	five	-0.34*	-0.46**	-0.62***	0.00
	all	-0.24	-0.65***	-0.56**	-0.08
<i>Sylvia curruca</i>	first	-0.43*	-0.42*	-0.35*	-0.09
	five	-0.50**	-0.56**	-0.16	-0.06
	all	-0.24	-0.54**	-0.44*	0.07
<i>Hirundo rustica</i>	first	-0.23	-0.27	-0.48**	0.01
	five	-0.36*	-0.27	-0.20	0.08
<i>Delichon urbica</i>	first	-0.04	-0.18	-0.23	0.00
	five	0.04	-0.25	-0.41*	-0.08
<i>Riparia riparia</i>	first	-0.08	0.29	-0.24	0.28
	five	-0.12	0.15	-0.24	-0.11
<i>Sylvia communis</i>	first	-0.16	-0.68***	-0.53**	-0.08
	five	-0.17	-0.68***	-0.39*	-0.05
	all	-0.11	-0.57**	-0.32*	-0.11
<i>Muscicapa striata</i>	first	0.05	-0.24	-0.25	-0.18
	five	-0.07	-0.31*	-0.36*	-0.27
<i>Muscicapa parva</i>	first	-0.36	-0.50*	-0.19	-0.52*
	five	-0.26	0.57*	-0.14	-0.29
<i>Luscinia luscinia</i>	first	-0.25	0.09	-0.31*	-0.27
<i>Sylvia borin</i>	first	-0.13	-0.52**	-0.53**	-0.25
	five	-0.11	-0.60***	-0.50**	-0.09
	all	-0.06	-0.45*	-0.40*	-0.05
<i>Sylvia nisoria</i>	first	-0.01	-0.39*	-0.47*	0.09
	five	0.02	-0.31	-0.29	0.16
	all	-0.15	-0.57**	-0.40*	0.11
<i>Hippolais icterina</i>	first	-0.11	-0.62***	-0.41*	-0.01
	five	-0.22	-0.68***	-0.43*	-0.06
	all	-0.03	-0.66***	-0.41*	-0.23
<i>Carpodacus erythrinus</i>	first	-0.13	-0.39*	-0.48**	0.03
	five	-0.17	-0.51**	-0.59***	0.05

The species are listed in the order of their appearing in the region of summer stay. First young - first date of capture of young bird, five youngs - mean date of first captures of young birds, all youngs - mean date of captures of all young birds before 15 August.

### 3.5. Correlation between spring arrival and timing of juvenile dispersal

Comparison of average arrival dates with dates of first five captures of juveniles, and with average trapping dates of local juveniles in 12 species showed a significant positive correlation between these variables in early arriving species (Tab. 5). This suggests that in years when these species arrive early they start breeding earlier which causes earlier juvenile dispersal. No such relationship was revealed in birds arriving late (Tab. 5), timing of their breeding and of juvenile dispersal shows no correlation with tuning of arrival.

## 4. Discussion

Analysis of data from over 40 years (1959-1998) long-term monitoring of timing of seasonal



events in various birds species showed that during two decades (1960s and 1980s) early breeding prevailed, and during two other decades (1970s and 1990s) late breeding was recorded more frequently (Fig. 1). This pattern was observed in both early and late arriving migrants.

Table 5. The correlation between mean dates of spring migration and postbreeding dispersal of young birds in some species at the Courish spit ( $r_s$  = Spearman's rank correlation coefficient; +  $p < 0.10$ , \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ )

Species	Date's category	$r_s$
<i>Fringilla coelebs</i>	all youngs	0.34*
<i>Phoenicurus ochruros</i>	five youngs	0.45*
	all youngs	0.34*
<i>Phylloscopus collybita</i>	five	0.31*
	all	0.04
<i>Anthus trivialis</i>	five	0.24
	all	0.38*
<i>Phylloscopus trochilus</i>	five	0.65***
	all	0.70***
<i>Ficedula hypoleuca</i>	five	0.45*
	all	0.39*
<i>Sylvia atricapilla</i>	five	0.42*
	all	0.27
<i>Sylvia curruca</i>	five	0.07
	all	0.22
<i>Sylvia communis</i>	five	-0.10
	all	-0.08
<i>Sylvia borin</i>	five	-0.14
	all	-0.15
<i>Sylvia nisoria</i>	five	-0.20
	all	-0.09
<i>Hippolais icterina</i>	five	-0.01
	all	0.02

The legends of date's category see footnote for table 2.

It has been shown (Sokolov et al., this volume) that in the 1960s and the 1980s early migrants arrived to the study area on average 1-2 weeks earlier than in the 1950s, 1970s, and 1990s. In late migrants arriving in May significantly earlier arrival was recorded only in 1980s compared to the 1970s. In this study we investigated the relationship between the timing of breeding and of juvenile dispersal with timing of spring arrival. Such correlation was found in early arriving species; when they arrive early, they start breeding earlier (Tab. 5). No such relationship was found in late arriving birds, although a significant negative correlation between timing of breeding and spring temperatures was revealed. Positive correlation between timing of breeding and timing of arrival was reported by several authors, e.g. in the Red-backed Shrike *Lanius collurio* from France (Grisser 1995). In Poland early arriving male Willow Warblers *Phylloscopus trochilus* find mates and start breeding earlier (Michalak 1994).

Timing of breeding in various species in our area appeared to depend mainly on spring, not on summer temperatures. In sedentary species, as well in early arriving birds, both short and long-distance migrants, a significant negative correlation between timing of breeding and mostly March

and April temperatures was found. In late arriving long-distance migrants a relationship mainly with April and May temperatures was revealed. In Common Crossbills and Siskins that breed very early (Cramp & Perrins 1994), similar relationships with average February and March temperatures were found.

Other authors also report relationships between timing of breeding and spring temperatures. According to Mikhantiev & Selivanova (1996), in western Siberia egg laying dates in Mallards *Anas platyrhynchos* are correlated with temperatures in the first half of April ( $r = -0.77$ ;  $p < 0.001$ ;  $n = 22$ ). Egg laying in this species is more intensive during warm springs not interrupted by cold spells. In the Kurgan Region (Russia) in cold springs of 1992 and 1993 falling average daily temperatures of 4-6°C delayed laying dates in gulls and waterfowl for 1-2 weeks (Kalinin 1994). Weak insolation forced gulls to prolong incubation up to 28-31 days, the norm being 18-22 days. Influence of spring temperature was also found in a number of passerines. Rytönen et al. (1993) predict timing of breeding of Rooks *Corvus frugilegus* in northern Finland on the basis of temperature dynamics in May and of occurrence of ground frost. Nager & van Noordwijk (1995) reported that in the Great Tit ultra-population variation in the timing of breeding was mainly determined by spring temperatures. Low temperatures during the expected laying period and the abundance of caterpillars also played a role in shaping the variation in time of breeding. Zajac (1995) analysed timing of breeding of Great and Blue Tits near Krakow and suggested that the weather, especially air temperature and precipitation, was most important in shaping this process. In the Treecreeper *Certhia familiaris* in SW Sweden the length of incubation correlated negatively to average air temperature during egg laying and the first five days of incubation (Enemar 1995). The author suggests that under adverse weather birds started incubation later. In western Switzerland egg laying for Pied Flycatcher *Ficedula hypoleuca* started significantly later than at other central European sites and was dependent on the cumulated air temperatures in April and early May (Ravussin & Neet 1995). In the northernmost breeders the snow cover has a strong effect on the timing of breeding. In Swedish Lapland the time when snow cover melts is subject to considerable inter-annual variation, which greatly influences the timing of breeding for Bluethroat *Luscinia svecica* (Ellegren 1990). In Scotland average hatching date for Snow Bunting *Plectrophenax nivalis* is dependent on the snow cover in early June which may vary from 15% (1981) to 98% (1977) (Watson 1996). In the sub-Arctic Yamal Peninsula (Russia) the timing of snow melting varies a great deal which causes considerable inter-annual variation in the timing of breeding for many bird species (Ryabitsev 1993).

The dependence of timing of breeding on spring temperatures on the Courish Spit probably reflects the condition of the ecosystem, which is closely connected with the development of vegetation when birds occupy breeding territories, nest building, egg laying, incubation and other parameters. Vegetation development is influenced by spring temperatures (Shulz 1981). On the basis of data on flowering of 24 plant species in Sumy Region (Ukraine) and on average monthly air temperatures in a neighbouring Cherkassy Region (Grischenko & Yablonovska-Grischenko 1996) we found negative correlations between the timing of flowering of some plants and air temperatures: *Tussilago farvara* ( $r_s = -0.73$ ;  $p < 0.01$ ;  $n = 13$ ) and *Corylus avellana* ( $r_s = -0.85$ ;  $p < 0.001$ ;  $n = 14$ ) with March temperature; *Cerasus vulgaris* ( $r_s = -0.80$ ;  $p < 0.001$ ;  $n = 14$ ) and *Armeniaca vulgaris* ( $r_s = -0.86$ ;  $p < 0.001$ ;  $n = 14$ ) with April temperature; *Filipendula denudata* ( $r_s = -0.65$ ;  $p < 0.01$ ;  $n = 14$ ) and *Malus domestica* ( $r_s = -0.68$ ;  $p < 0.05$ ;  $n = 11$ ) with May temperature.

Fesenko et al. (1996) revealed strong correlations between the arrival of birds and flowering of plants. The authors believe that flowering shows not only the trophic capacities of an ecosystem,

but also the condition of possible breeding territories. It is further evidenced by stronger association with habitats when nests are built than with foraging habitats. According to Nystrom (1991), the first peak of Willow Warblers' prey (caterpillars and aphid *Aphidoidea* larvae) in spring in Sweden is recorded two days before the opening of birch leaves. The first male Willow Warblers are recorded several days before birch leaves open, and females appeared during the peak of insect abundance. Significant correlation between the flowering of *Allium validum* and egg laying in White-crowned Sparrow *Zonotrichia leucophrys oriantha* and the snow situation was found in Sierra Nevada (California):  $r = 0.87$ ;  $p < 0.01$ ;  $n = 21$  (Morton 1994). The beginning of egg laying in the Lesser Spotted Woodpecker *Dendrocopos minor* in southern Sweden was subject to considerable inter-annual variation, but always coincided with opening of oak leaves (Wiktander et al. 1994).

Few data is available on the inter-annual fluctuations of the timing of juvenile dispersal and on factors influencing this process. This is caused by methodological difficulties. At our site the timing of juvenile dispersal is monitored for 40 years by catching birds in Rybachy-type traps (Sokolov 1991). Our data suggests that the timing of juvenile dispersal estimated by first catches and by average trapping date of local birds vary greatly between the years. They depend on when the population breeds: early breeding is followed by early catches of young birds (Tab. 1). These are individuals that had already gained independence, i.e. first catches of juvenile occur at the age of 30-40 days. There are reasons to believe that the age of beginning juvenile dispersal is under endogenous control (Berndt & Sternberg 1968, Lance 1970, Dolnik 1975, Sokolov 1991). Arctic Warblers *Phylloscopus borealis* depart from sub-Arctic areas (Polar Urals, Russia) at the age of 29-35 days, and Willow Warblers at the age of 31-40 days (Ryzhanovsky 1997). The author reveals a significant relationship between the timing of departure and the timing of hatching which he believes suggests an endogenous control over the timing of departure. We believe that the correlation between the timing of juvenile dispersal and the timing of hatching explain the dependence of dispersal timing on spring temperatures that was found in this study (Tab. 4).

We should like to emphasize the following. On the basis of our material and other literary data we conclude that the long-term trends in the timing of breeding and dispersal for sedentary and migratory passerines that were recorded in the 20th century, were caused mainly by climatic fluctuations in the northern hemisphere. These fluctuations occurred in the form of inter-annual variations of spring air temperatures and various phenological events, including the timing of spring migration (Sokolov et al., this volume).

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