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Long-term dynamics of the mean date of autumn migration in passerines on the Courish Spit of the Baltic Sea

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The analysis of the mean date of autumn migration in juveniles in 26 passerine species over 40 years (1959-1998) revealed considerable inter-annual variation in the majority of species. In many species the mean date of autumn migration varied in parallel. In the 1960s eleven bird species migrated earlier through the Courish Spit compared with the 1970s. In the 1980s, compared with the 1970s, such a trend was revealed in 15 species. In the 1990s, compared with the 1980s, a tendency towards later migration was recorded in eight species. Similar trends were also found in adults in eight species. A comparison of the timing of autumn migration of juveniles with mean monthly ambient temperatures in spring, summer and autumn showed a significant or nearly significant negative correlation in 14 species, mainly with April temperature. A significant positive relationship between the timing of autumn migration and post-fledging dispersal was revealed in nine species out of 13 tested. In the Great Tit *Parus major* and Chaffinch *Fringilla coelebs* we found a significant positive relationship between the timing of breeding and the mean date of autumn passage of adults. We conclude that the main reason of long-term variation of the timing of autumn passage in passerines in our study area are long-term climate fluctuations in Europe in the 20th century. Warmings observed in the northern hemisphere in the 1960s and even more pronounced in the 1980s caused a shift towards earlier arrival in spring and earlier breeding in many passerines (Sokolov et al. 1998, Sokolov & Payevsky 1998). This caused a respective shift in the timing of autumn migration in a number of species. Colder periods in the 1970s and to some extent in the 1990s, to the contrary, resulted in later migration in some passerines. Future trends will depend on annual dynamics of spring ambient temperature in Europe.

Key words: autumn migration, dynamics of the timing of migration, mean date of migration, ambient temperature, climate, passerines.

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1. Introduction

In previous publications (Sokolov et al. 1998, Sokolov & Payevsky 1998) we showed that the timing of spring migration and breeding in many passerines in Europe varied in the 20th century along with considerable climate fluctuations in the northern hemisphere. It is necessary to test the possible effect of these events on the timing of autumn migration.

Timing of arrival to and departure from the breeding range is known to be subject to inter-annual variation (Curry-Undahl 1975, Gavrilov 1979, Sema 1989, Alerstam 1990, Ellegren 1990, Ryzhanovsky 1997, Heldbjerg & Karlsson 1997). However, apparently few researchers possess long-term standardised data that could be a tool for studying long-term trends in the timing of autumn migration. We managed to find few studies (Glaubrecht 1993, Moritz 1993, Vogel & Moritz 1995, Bairlein & Winkel 1998) reporting pronounced trends in the timing of autumn migration. E.g. in Germany in 19 species of short-distance migrants a tendency was found over the last 14 years to commence autumn migration on average 10 days later than usual, which is explained by climate warming (Glaubrecht 1993, Vogel & Moritz 1995). Particular data on inter-annual variation in the timing of autumn migration in juveniles and adults is even more scarce.

Much attention is paid to factors that influence the onset of autumn migration. It is widely believed that in long-distance migrants the beginning of autumn migration is under endogenous control and practically independent from environmental stimuli (for reviews see: Gwinner 1975, 1986, 1990, 1996; Dolnik 1975, Berthold 1988, 1993, 1996). Dolnik (1975) reported that in several species, e.g. in the Chaffinch *Fringilla coelebs* which winters within Europe the timing of developing first autumn migratory disposition is also under endogenous control and depends on bird's age, not on environmental stimuli.

A number of authors suggest that in short-distance migrants, in contrast to those migrating longer distances, the onset of autumn migration may be to a large extent shaped by the weather (Curry-Undahl 1975, Gavrilov 1979, Sema 1989, Alerstam 1990). However, the impact of the weather on the timing of autumn migration of species that migrate within Europe is insufficiently studied.

The aims of this study were:

1) to estimate the scope of inter-annual variation in the mean date of autumn migration in species migrating for varying distances;

2) to determine long-term trends in the variation of the timing of autumn migration in juveniles and adults;

3) to test relationships between the mean dates of migration and spring, summer, and autumn air temperature in the study area;

4) to study the relationship between the timing of migration and timing of breeding.

2. Material and methods

Birds migrating over the Courish Spit of the Baltic Sea have been regularly trapped since 1957 at the field site Fringilla (55° 08' N, 20° 42' E) in 2-3 large Rybachy-type traps, oriented towards NE and SW. Trapping data are stored in a computerised database which is unique in the respect of its size (Morozov 1995).

Timing of autumn migration was estimated as the mean trapping date within the period between August 15 and October 31. The bulk of local birds usually leaves the study area before August 15 (Sokolov 1997, Sokolov & Payevsky 1998). The majority of species under study departs from the Courish Spit before November 1 (Payevsky 1985). In earliest migrants (Icterine Warbler *Hippolais icterina.* Wood Warbler *Phylloscopus sibilatrix.* Tree Pipit *Antfus trivialis* and Red-backed Shrike *Lanius coUurio)* we calculated the mean trapping date from August 1 onwards. We used the mean trapping date following the approach applied for the study of timing of spring migration, breeding, and juvenile dispersal of passerines on the Courish Spit (Sokolov et al. 1998, Sokolov & Payevsky 1998).

Long-term trends of the mean date of autumn migration of juveniles were analysed in 26 passerine species that migrate within Europe or to sub-Saharan winter quarters (Tab. 1). Timing of migration of adults was analysed in eleven species, in which ageing criteria in autumn are most reliable. In 25 species attempts were made to reveal long-term trends in the timing of autumn migration over the period 1959-1998.

To reveal long-term trends, three partly overlapping periods were considered: 1959-1976 (18 years), 1976-1990 (15 years), and 1985-1998 (14 years). The second and the third periods overlap, as we needed long enough series - over 10 years. Trends in adults were analysed within two periods: 1966-1980 (15 years) and 1976-1990 (16 years). When choosing intervals we tried to have similarly long periods, including years from neighbouring decades (Sokolov et al. 1998, Sokolov & Payevsky 1998).

Statistical significance of trends was tested by Spearman rank correlation (Lloyd & Ledermann 1984). For the analysis of inter-annual variation regression analysis was applied.

When testing relationships between autumn migration and ambient temperature we used mean monthly air temperature of March, April, May, June, August, September, and October in the Kaliningrad Region. Elsewhere it was shown that spring temperatures are correlated over a huge area from Byelorussia and Poland up to Finland and Kola Peninsula (Sokolov et al. 1998). The bulk of passerines migrating over the Courish Spit in autumn breed predominantly in the Baltic area (Payevsky 1973). To reveal relationships between the mean date of autumn migration and air temperature we used rank correlation analysis. The same statistics were applied to study correlations between spring and in autumn air temperatures.

3. Results

3.1. Inter-annual variation in the mean date of autumn migration in juveniles and in adults

In nearly all species out of the 26 concerned a considerable inter-annual variation in the mean date of autumn migration in juveniles was recorded (Tab. 1). This variation was not dependent on the timing of migration over the Courish Spit, or on distance covered (Fig. 1).

Table 1. Mean dates of autumn migration in juveniles on the Courish Spit, 1959-1997.

Species	Mean number of birds	Mean date	Range of mean dates	SD
	Long-distance migrants			
Hippolais icterina	32	13 Aug.	6 Aug. - 19 Aug.	2.9
Phylloscopus sibilatrix	68	23 Aug.	16 Aug. - 3 Sep.	4.3
Anthus trivialis	58	24 Aug.	13 Aug. - 2 Sep.	5.2
Lanius collurio	16	25 Aug.	10 Aug. - 5 Sep.	6.4
Sylvia cunvca	103	27 Aug.	19 Aug. - 5 Sep.	4.3
Sylvia communis	17	28 Aug.	19 Aug.-12 Sep.	4.6
Hirundo rustica	56	29 Aug.	15 Aug. - 13 Sep.	7.0
Motacilla alba	66	30 Aug.	10 Aug.-11 Sep.	7.5
Ficedula hypoleuca	72	31 Aug.	21 Aug.-11 Sep.	5.3
Sylvia borin	63	3Sep.	25 Aug.-11 Sep.	4.0
Phylloscopus trochilus	2300	3Sep.	27 Aug. - 13 Sep.	3.9
Muscicapa striata	105	5 Sep.	27 Aug. - 16 Sep.	5.0
Phoenicurus phoenicurus	140	16 Sep.	7 Sep. - 26 Sep.	5.8
	Medium- and short-distance migrants			
Sylvia alricapilla	37	16 Sep.	3 Sep. - 1 Oct.	6.9
Erithacus rubecula	790	29 Sep.	21. Sep.-5 Oct.	3.5
Phylloscopus collybita	64	2 Oct.	22 Sep.-11 Oct.	3.9
Prunella modularis	18	2 Oct.	24 Sep.-11 Oct.	4.5
Fringilla coelebs	12800	2 Oct.	24 Sep.-12 Oct.	4.2
Parus caeruleus	1140	4 Oct.	25 Sep. - 12 Oct.	6.3
Anthus pratensis	196	4 Oct.	27 Sep. - 14 Oct.	4.0
Emberiza schoemclus	8	8 Oct.	30 Sep. - 20 Oct.	5.3
Parus major	3290	10 Oct.	23 Sep. - 16 Oct.	5.0
Fringilla montifrinylla	1460	11 Oct.	4 Oct.-19 Oct.	3.9
Regains regulus	5861	11 Oct.	29 Sep. - 21 Oct.	4.4
Chhris chloris	122	17 Oct.	9 Oct. - 25 Oct.	4.8
Pyrrhula pyrrhula	996	23 Oct.	11 Oct.-30 Oct.	4.0

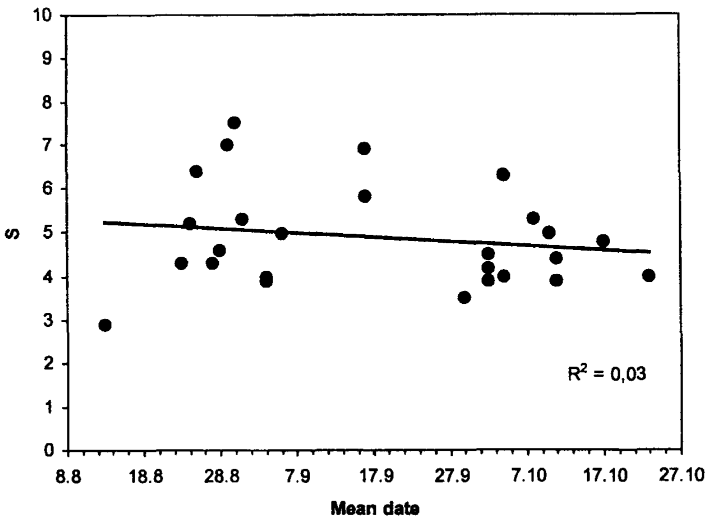

Figure 1. Annual variation of the mean date of autumn migration for some species of the Courish Spit. S - standard deviation.

Table 2. Mean dates of autumn migration in adults birds on the Courish Spit, 1966-1996.

Species	Mean number of birds	Mean mean dates	Range date of	SD
		Long-distance migrants		
Phylhscopus trochilus	76	4 Sep.	27 Aug.-21 Sep.	5.8
Phoenicurus phoenicurus	8	15 Sep.	1 Sep. - 30 Sep.	6.7
		Medium- and short-distance migrants		
Erithacus rubecula	70	4 Oct.	21 Sep.-15 Oct.	5.6
Fringilla coelebs	8100	5 Oct.	24 Sep. - 13 Oct.	7.8
Parus caeruleus	147	7 Oct.	19 Sep. - 17 Oct.	5.8
Fringilla montifringilla	576	9 Oct.	30 Sep. - 17 Oct.	3.9
Parus major	275	11 Oct.	21 Sep. - 19 Oct.	7.8
Regulus regulus	247	14 Oct.	5 Oct. - 22 Oct.	3.8

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n eight species this trait was analysed in adults (Tab. 2). Mean date of autumn migration over the whole study period (1966-1996) was later than in juveniles in a number of species. The scale of year-to-year fluctuations of the mean date was at least of the same magnitude as in juveniles. High variability in the timing of autumn migration was recorded in both short- and long-distance migrants.

Average autumn trapping figures varied broadly between species, from several individuals to several thousand (Tab. I). Nevertheless, we revealed no relationships between year-to-year variation of the timing of migration and trapping figures.

3.2. Trends in the variation of the mean date of autumn migration in juveniles and in adults

The analysis of trends in the timing of autumn migration over 40 years (1959-1998) in 25 species showed earlier migration in the 1960s compared with the 1970s in 11 species (Tab. 3, Fig. 2). This tendency was revealed in both short- and long-distance migrants.

In 15 species the mean date of autumn migration of juveniles was significantly earlier in the 1980s compared with the 1970s. This trend was also recorded in birds with a different migratory distance (Tab. 3). In the 1990s a shift towards later migration in juveniles was recorded in nine species. It was valid for both short- and long-distance migrants.

Timing of autumn migration of adults varied in a similar fashion. In four species out of eight studied a trend towards earlier migration in the 1960s compared with the 1970s was recorded (Fig. 3, Tab. 4). In the 1980s compared with the 1970s adults showed significant or nearly significant trends towards earlier migration.

Long-term dynamics of mean dates of autumn migration in juveniles and adults were highly significantly correlated in 11 species (Tab. 5).

3.3. Relationships between the timing of migration in juveniles and ambient temperature

We compared mean dates of autumn migration of juveniles in 23 species with mean monthly air temperatures of March, April, and May over the period 1959-1990 (Tab. 6). In not a single species was a significant correlation with March temperature revealed. In 11 species we revealed significant or nearly significant negative relationships with April temperature, including both short- and long-distance migrants. Similar relationship with May temperature was recorded in three species, two of them showing correlation also with April values. In four species a relationship with June temperature was recorded, three of them also showing correlation with April or May temperatures (Tab. 6).

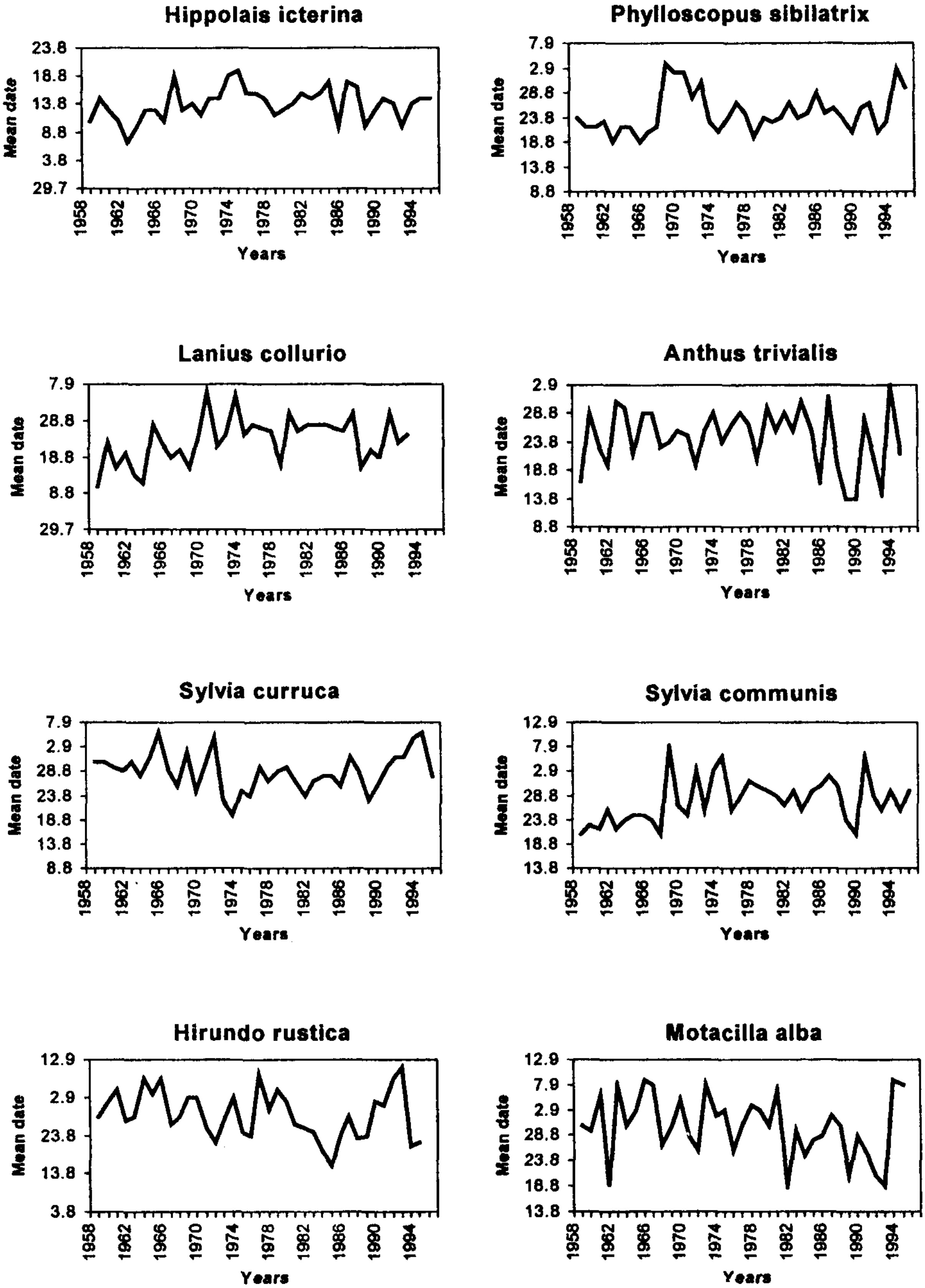
The analysis of relationships between the timing of autumn migration of juveniles and autumn ambient temperature revealed significant negative correlation with August values for the Chaffinch and Brambling *Fringilla montifringilla* (Tab. 6). In not a single species was a correlation with September or October temperatures recorded.

The comparison of mean monthly temperatures in spring and in autumn revealed a significant positive correlation only between May and August temperatures (Tab. 7). September and October temperatures reached maxima most frequently in the 1960s and 1980s (Fig. 4).

Table 3. Trends to change of mean date of autumn migration in juveniles (Spearman's rank correlation coefficient: + p<0.10, * p<0.05, ** p<0.01, ******* p<0.001).

Species	Years 1959-1976	Years 1976-1990	Years 1985-1998
	Long-distance migrants		
Hippolais icterina	0.68**	-0.30	0.04
Phylloscopus sibilatrix	0.57*	0.04	0.38
Anthus trivialis	0.10	-0.48*	0.28
Sylvia curruca	-0.10	-0.68**	0.64*
Sylvia communis	0.07	-0.40	0.67*
Hirundo rustica	-0.17	-0.52*	-
Motacilla alba	-0.16	-0.63**	0.27
Kcedula hypoleuca	0.09	-0.34	0.54*
Sylvia borin	0.51*	-0.11	0.70"
Phylloscopus trochilus	0.74***	-0.41	0.86***
Phoenicurus phoenicurus	0.73***	-0.59**	0.09
	Medium- and short-distance migrants		
Sylvia atricapilla	0.48*	-0.31	0.68**
Erithacus rubecula	0.47*	-0.76**	0.51*
Turdus iliacus	0.37	-0.39	-
Turdus philomelos	0.48	-0.52*	-
Stumus vulgaris	0.59*	-0.61*	-
Prunella modularis	0.26	-0.52*	-
Fringilla coelebs	0.32	-0.67**	0.31
Parus caervleus	0.54*	-0.79***	0.46+
Anthus pratensis	0.52*	-0.41	-
Embema schoeniclus	0.44+	-0.58*	-
Parus major	0.33	-0.37	0.41
Fringilla montifringilla	0.19	-0.35+	0.33
Regulus regulus	0.37	-0.45+	0.37
Chloris chloris	0.36	-0.52*	-

Figure 2. Mean passage date of young birds in some species on the Courish Spit.



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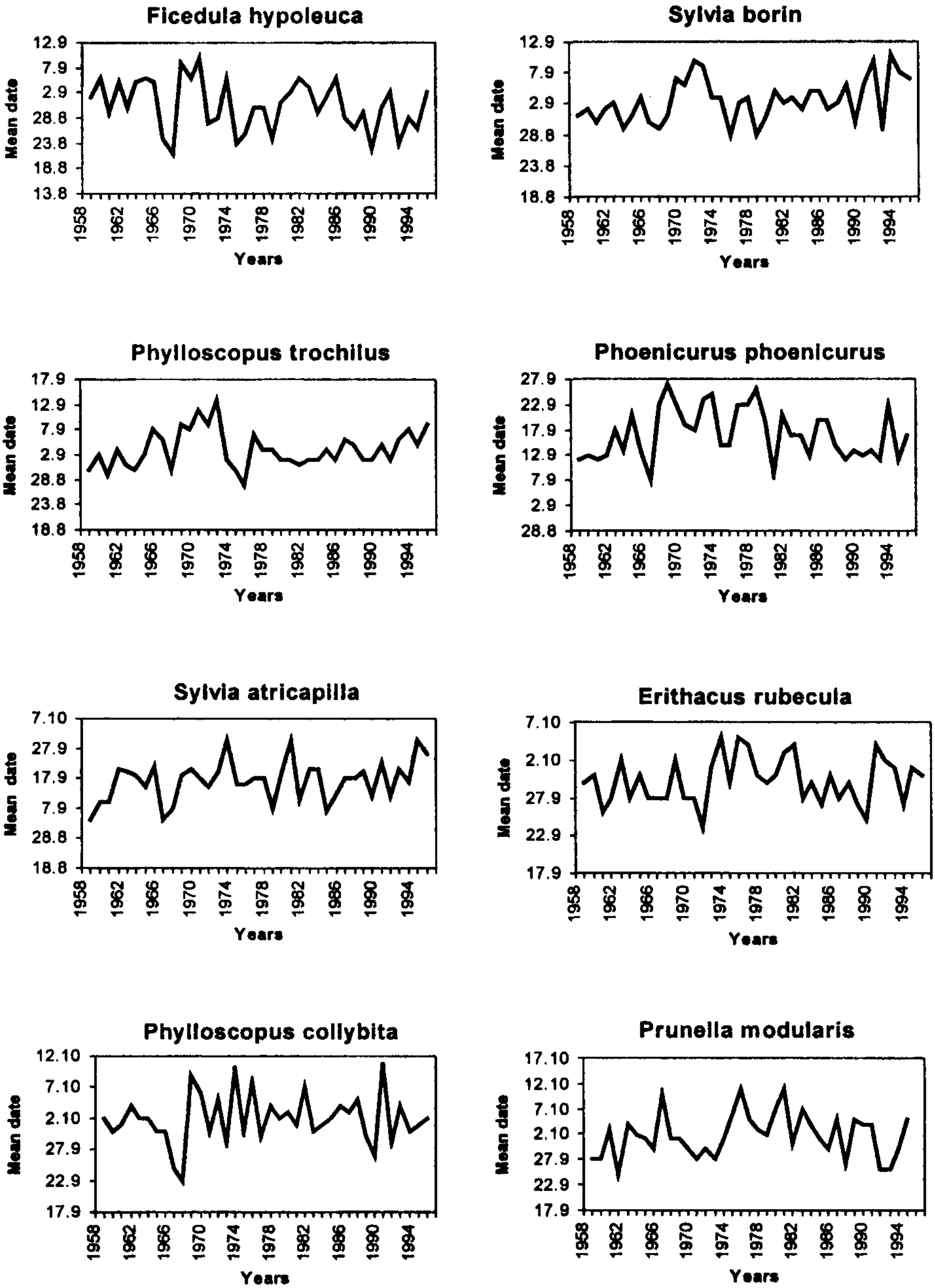

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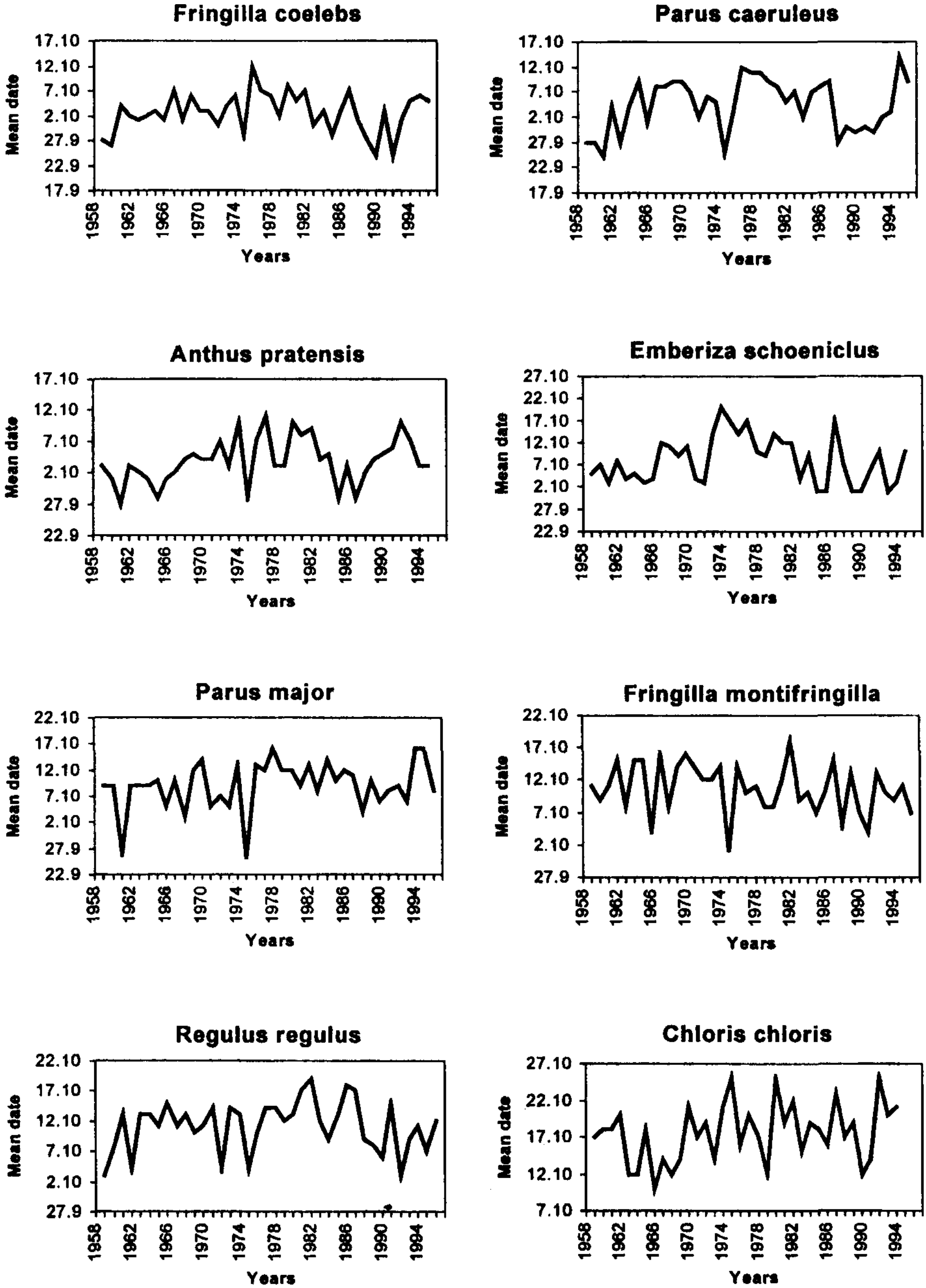

Table 4. The tendency to change of mean date of autumn migration in adult birds of some passerines on the Courish Spit (Spearman's rank correlation: + p<0.10. * p<0.05, ****** p<0.01).

Species	Years 1966-1980	Years 1976-1990
Long-distance migrants		
Phylloscopus trochilus	0.46	-0.52*
Phoenicunis phoenicurus	0.54*	-0.71 **
Medium- and short-distance migrants		
Erithacus rubecula	0.58*	-0.57+
Fringilla coelebs	0.18	-0.54*
Parus caeruleus	0.30	-0.37
Fringilla montifringilla	-0.41	-0.48+
Parus major	0.61 *	-0.35
Regulus regulus	0.60*	-0.62*

Table 5. Correlation between mean dates of autumn migration in juveniles and adults, 1966-1996 (r_s - Spearman's rank correlation: * p<0.05, ****** p<0.01, ******* p<0.001).

Species	r_s
Long-distance migrants	
Phylloscopus trochitus	0.45*
Phoenicurus phoenicurus	0.39*
Medium- and short-distance migrants	
Erithacus rubecula	0.73***
Turdus iliacus	0.75***
Turdus phuomehs	0.74***
Stumus vulgaris	0.85***
Fringilla coelebs	0.85***
Parus caeruleus	0.66***
Parus major	0.86***
Fringilla montifringilla	0.77***
Regulus regulus	0.74***

Table 6. Correlation between mean date of autumn migration and spring, summer and autumn temperatures in juveniles (Spearman's rank correlation coefficient: + p<0.10, * p<0.05, ** p<0.01).

Species	T°C March	T°C April	T°C May	T°C June	T°C August	T°C Sep-	T°C October
Long-distance migrants							
Hippolais icterina	0.07	-0.19	-0.28	-0.16	0.09		
Phylloscopus sibilatrix	-0.14	-0.33+	-0.06	-0.20	-0.01		
Lanius collurio	-0.07	-0.29	-0.30+	-0.43*	0.02		
Anthus trivialis	-0.33+	-0.37*	-0.19	-0.16	-0.08	0.16	
Sylvia curruca	-0.15	-0.30+	-0.08	0.06	0.05	-0.02	
Sylvia communis	0.02	-0.30+	-0.23	-0.09	-0.06	0.08	
Motacilla alba	0.01	-0.28	-0.04	0.20	0.08	0.16	
Ficedula hypoleuca	-0.27	-0.27	-0.01	-0.19	-0.18	-0.17	
Sylvia borin	0.01	-0.18	0.04	-0.16	0.20	-0.11	
Phylloscopus trochilus	-0.09	-0.44*	-0.12	0.16	0.01	-0.25	
Muscicapa striata	-0.05	-0.28	-0.12	-0.16	0.04	-0.20	
Phoenicurus phoemcurus	-0.11	-0.39*	-0.15	-0.02	0.01	-0.15	
Medium- and short-distance migrants							
Sylvia atricapilla	-0.16	-0.08	-0.10	-0.14	0.07	-0.01	
Erithacus rubecula	-0.02	-0.39*	-0.21	-0.31+	-0.01	0.04	-0.19
Phylloscopus collybita	-0.18	-0.33+	-0.15	-0.36*	-0.26	-0.19	
Prunella modularis	0.14	-0.05	-0.01	-0.12	0.05	0.23	0.20
Fringilla coelebs	-0.20	-0.38*	-0.35*	-0.17	-0.36*	-0.11	-0.05
Parus caeruleus	-0.01	-0.27	-0.17	-0.08	-0.28	-0.25	0.08
Anthus pratensis	0.05	-0.15	-0.15	-0.23	0.05	-0.14	-0.10
Emberiza schoeniclus	-0.09	-0.38*	-0.39*	-0.19	-0.22	0.09	-0.25
Parus major	-0.11	-0.26	-0.26	-0.31+	-0.28	-0.05	0.05
Fringilla montifringilla	-0.06	-0.04	-0.28	-0.27	-0.33+	0.04	-0.09
Regulus regulus	-0.14	-0.36*	-0.02	-0.04	-0.14	-0.15	0.02

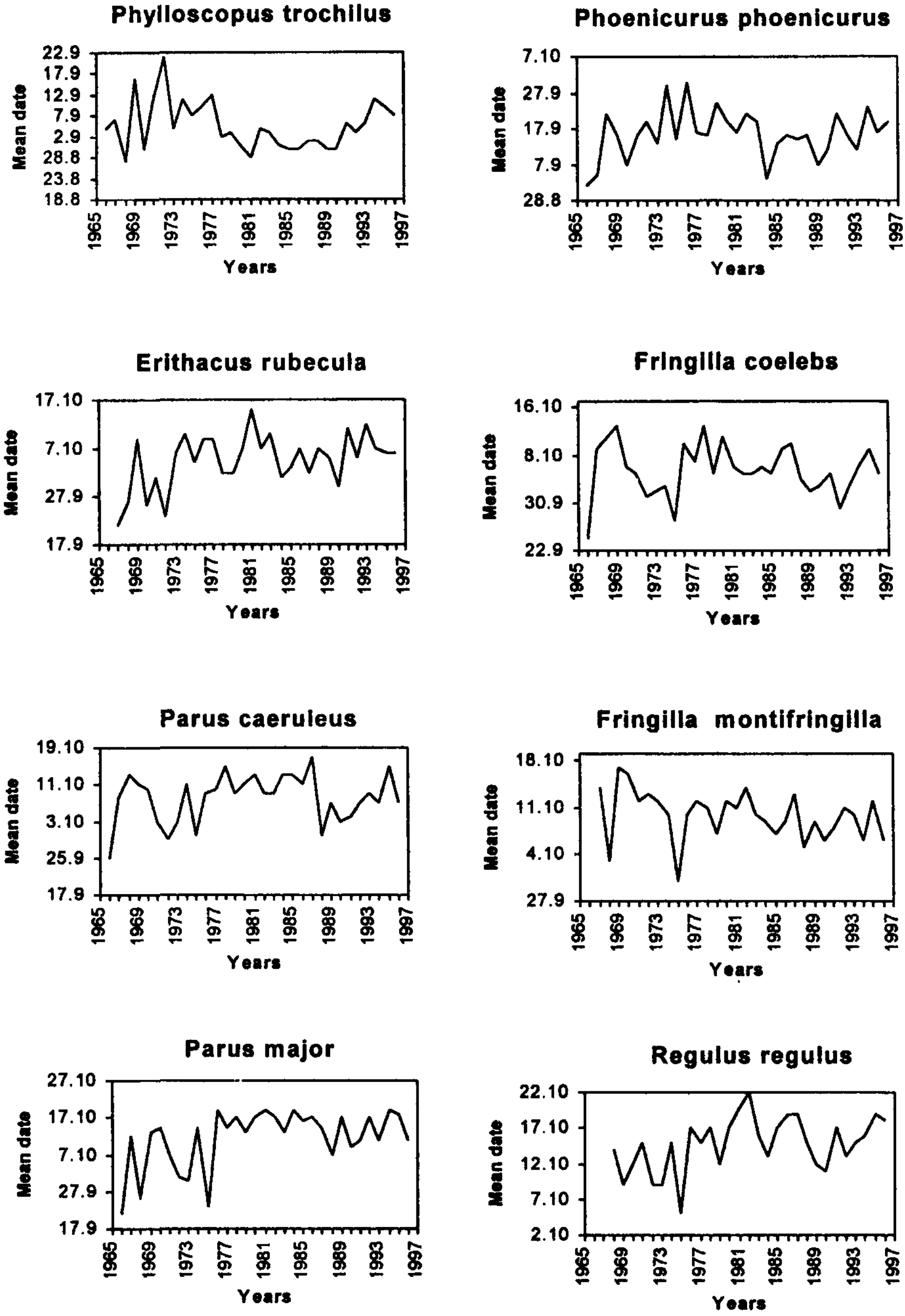

Figure 3. Mean passage date of adult birds in some species on the Courish Spit.

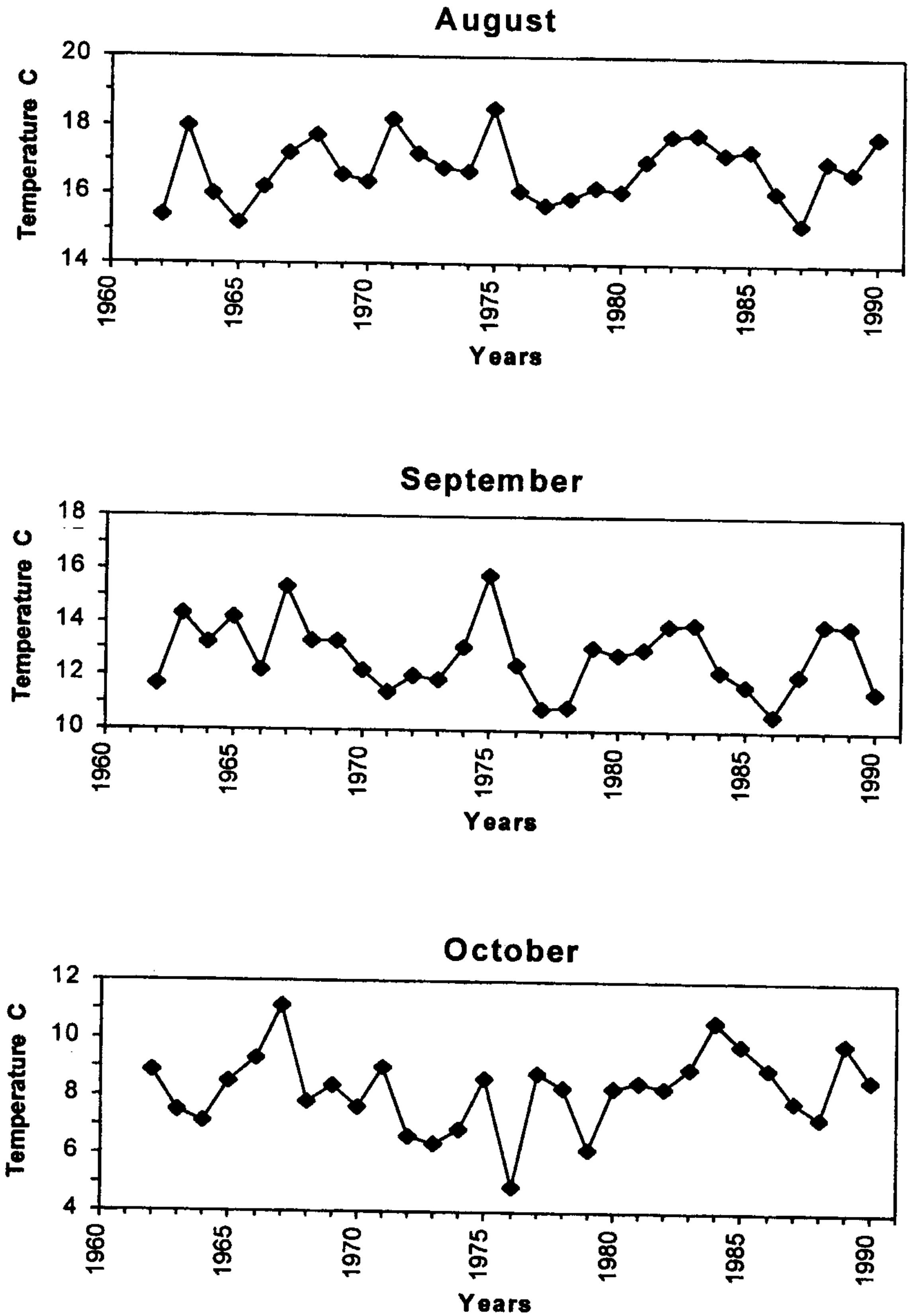

Figure 4. Changes mean monthly air temperatures in the Kaliningrad region.

Table 7. Correlations between mean spring, summer and autumn temperatures on the Courish Spit, 1962-1990 (Spearman's rank correlation: ** p<0.01).

Month	August	September	October
March	0.26	0.06	0.25
April	0.20	0.04	0.30
May	0.51"	0.07	0.30
June	-0.05	0.06	-0.27

3.4. Correlations between the mean date of autumn migration and the timing of breeding and post-juvenile dispersal

In nine species out of 13 studied a significant or nearly significant correlation between the timing of autumn passage of northern populations and the timing of post-fledging movements of local juveniles was revealed (Tab. 8). This relationship was found in both short- and long-distance migrants.

In the Great Tit *Parus major* and Chaffinch a positive relationship was found between the mean date of autumn migration of adults and the timing of breeding (mean hatching date) of the Courish population (Tab. 9).

4. Discussion

In the majority of species studied we found long-term significant synchronous trends in the variation of the mean date of autumn passage. In the 1960s and 1980s in a number of species adults and juveniles migrated through our study area significantly earlier than in the 1970s and 1990s. A similar pattern of spring passage has previously been reported from the Courish Spit (Sokolov et al. 1998). The timing of breeding in our study area was also shifted towards earlier season in the 1960s and 1980s (Sokolov & Payevsky 1998). German authors reported a trend towards later onset of autumn migration in the 1980s from Heligoland, Northern Sea, in 19 species of short-distance migrants. The difference reached as much as 10 days, which the authors explain by the climate warming (Glaubrecht 1993, Moritz 1993, Vogel & Moritz 1995). It is possible that in Germany some passerines, primarily short-distance migrants, indeed remain longer in the study area in autumn under favourable weather conditions. In our more NE region no migration delay was recorded in short- and medium-distance migrants in warm periods.

The comparison of average dates of autumn migration and of breeding shows a significant positive correlation between these parameters in both short- and long-distance migrants (Tab. 8, 9). It suggests that after an early breeding season adults and juveniles depart from breeding/natal areas and pass through our region earlier. Such direct dependence between the timing of breeding and the average date of autumn migration is caused by the fact that the onset of migration in young birds of many passerines, long- and medium-distance migrants, is under direct endogenous control (Gwinner 1975, 1986, 1990, 1996, Shumakov et al. 1972, Dolnik et al. 1974, Dolnik 1975, Berthold 1988, 1993, 1996, Ket-terson & Nolan 1985). Thus, the onset of autumn migration of juveniles depends on their age, not on environmental stimuli. In sub-Arctic areas the initiation of migratory disposition in juvenile passerines is under endogenous control (Ryzhanovsky 1997). The author reports positive correlation between hatching dates and timing of departure in the Blu-ethroat *Lusicinia svecica*, Willow Warbler *Phylloscopus trochilus*, Arctic Warbler *Ph. bore-alis*, and Little Bunting *Embema pusilla* over the period 1977-1982. Ellegren (1990) studied the timing of autumn migration and timing of breeding in Bluethroats in eastern Sweden over 11 years (1972-1982). He found a significant positive correlation (r; =0.65; p<0.025) between median dates of laying the first egg and median trapping dates of juve-niles that varied between August 25 and September 5.

Table 8. Correlations between mean dates of autumn migration and post-fledging dispersal, 1959-1991 (Г, - Spearman's rank correlation coefficient: + p<0.10, * p<0.05).

Species	T_s
Long-distance migrants	
Hippolais icterina	0.42*
Phylloscopus sibilatrix	0.32+
Anthus trivialis	0.21
Sylvia curruca	0.05
Sylvia communis	0.40*
Motacilla alba	0.29+
Kcedula hypoleuca	0.11
Sylvia borin	0.06
Phylloscopus trochilus	0.34*
Medium- and short-distance migrants	
Sylvia atricapilla	0.29+
Fringilla coelebs	0.35*
Parus caeruleus	0.38*
Parus major	0.28+

According to several studies (Dolnik & Gavrilov 1972, Dolnik et al. 1974, Dolnik 1975), timing of autumnal migratory disposition in adult birds is controlled by a long-term endogenous time counter, triggered at the beginning of the period of photoperiodic stimulation in spring. Such a control mechanism of the onset of autumn migration should make variation of the average date of migration in adults more restricted than in juveniles. However, our data demonstrates that the timing of autumn migration varies in adults no less than in juveniles (Tab. 2). The mean date of autumn migration in adults is directly related to the timing of breeding. Early breeding probably causes early autumn migration in juveniles and adults. Thus, the existence of endogenous control mechanism of the onset of autumnal migration in adults, though recorded in the laboratory, is not confirmed by our field data.

Table 9. Correlations between mean dates of autumn migration and breeding in adults (Fg - Spearman's rank correlation coefficient: * p<0.05, ****** p< 0.01).

Species	Number of years	r_s
Phylloscopus trochilus	20	0.24
Fringilla coelebs	26	0.52**
Parus major	23	0.46*

How does the weather, primarily temperature, influence the timing of autumn migration? It is usually assumed that the weather has practically no impact on the departure of long-distance migrants, but it influences the behaviour of short-distance migrants. Curry-Lindahl (1975) believes that long-distance migrants are pre-programmed to depart within an interval of approx. one week, due to their endogenous rhythm. Short-distance migrants are more flexible and can adjust the timing of departure to weather conditions. The author suggests that their departure may be caused by cold spells. Weather sensitivity depends on their migratory disposition. When birds are in strong migratory mood their departure may be triggered by stimuli of low intensity. Curry-Lindahl (1975) suggests that highly variable timing of autumn migration in short-distance migrants, as opposed to those migrating over large distances, is explained by the impact of unpredictable weather conditions. Our data do not confirm higher variation in the timing of autumn migration in short-distance migrants (Tab. 1). Variation is roughly the same in both groups (Fig. 1). In spring we indeed recorded higher variation in short- and medium-distance migrants, as opposed to long-distance migrants (Sokolov et al. 1998). This is caused by earlier arrival of birds that spend their winter within Europe, when temperature is variable and unpredictable.

When comparing average dates of autumn migration in juveniles with mean monthly temperatures in autumn we did not find any significant relationship in any group of migrants, neither with September nor with October temperature (Tab. 6). However, timing of autumn migration is indeed related to spring temperatures, primarily to the temperature of April in a number of species. The reason is probably that the timing of autumn migration is related to the timing of breeding which depends heavily on ambient temperature in spring (Sokolov & Payevsky 1998).

Thus, we can conclude that the main cause of long-term trends in fluctuations of the timing of autumn migration in our area are climate fluctuations observed in Europe in the 20th century. This holds true for both juveniles and adults, for short- and long-distance migrants. Considerable warmings in the northern hemisphere recorded in the 1960s and especially 1980s caused significant shifts towards earlier arrival and breeding in many passerines (Sokolov et al. 1998, Sokolov & Payevsky 1998). These events resulted in earlier autumn migration in a number of species migrating for varying distances. Colder periods in the 1970s and to some extent in the 1990s, on the contrary, shifted autumn migration towards later season. Further development of the timing of autumn migration in passerines in our region will be to a large extent determined by year-to-year fluctuations of spring temperatures in Europe.

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