

Long-term monitoring of the timing of migration in thrushes (*Turdus philomelos*, *T. iliacus*) in the Eastern Baltic

Alexandra Sinelschikova & Leonid V. Sokolov

Abstract: Sinelschikova, A. & Sokolov, L.V. (2004): Long-term monitoring of the timing of migration in thrushes (*Turdus philomelos*, *T. iliacus*) in the Eastern Baltic. *Avian Ecol. Behav.* 12: 11-30.

Long-term data obtained by trapping in Rybachy-type traps allowed us to analyse the timing of spring and autumn migration in two species of thrushes (Song Thrush *Turdus philomelos* and Redwing *T. iliacus*) in the Eastern Baltic over the last 45 years. Spring passage was shifted towards earlier dates in both species. The onset of migration was related to the March NAO index values. Increasing NAOI values recorded since the middle of the 20th century reflect increased movement of westerly air masses from the Atlantic, causing milder weather in the winter quarters of thrushes and in the Baltic area in early spring. The shift of spring passage towards earlier dates may be due to earlier occurrence of weather conditions favouring migration (increased spring temperatures) and to higher occurrence of following winds enhancing migratory flight.

Timing of autumn passage in the Baltic area did not show any trend in the Song Thrush, even since the 1970s, when a significant trend towards later passage was recorded in Western Europe. Unlike the Song Thrush, the Redwing delayed autumn migration significantly. Neither species showed a relationship between the timing of autumn passage and the temperature regimen in the Baltic area, however this correlation was found with summer temperatures in their presumed breeding area in NW Russia. Later autumn passage of Redwings might be explained by climate change affecting the spring season, causing early spring arrival and prolonged breeding season, and by the relationship between July air temperatures and timing of summer migration of thrushes.

Key words: thrushes, long-term monitoring, timing of migration, climate change, Baltic area.

Address: Biological Station Rybachy, Rybachy 238535, Kaliningrad Region, Russia. E-mail: sinelsch@bioryb.koenig.ru

Received 30 March 2004 / Received in revised form 28 April 2004 / Accepted 11 May 2004.

1. Introduction

An increasing number of publications suggest that many avian migrants, both in Europe and in North America, alter the timing of their migratory arrival. Many birds, primarily passerines, have arrived in the recent decades much earlier than they did in the middle of the 20th century (Mason 1995; Sokolov et al. 1998; Sokolov 2001; Bradley et al. 1999; Jenkins & Watson 2000; Sparks & Mason 2001; Tryjanowski et al. 2001). Earlier arrivals are indicated by first records (captures) and by mean or median dates of spring migration. More evidence becomes available that breeding schedule has also significantly shifted towards earlier dates in a number of bird species (McCleery & Perrins 1998; Brown et al. 1999; Crick & Sparks 1999; Bairlein & Winkel 2001).

Several authors also reported later migratory departures to wintering grounds than in previous decades in many species (Glaubrecht 1993; Moritz 1993; Vogel & Moritz 1995; Sparks & Mason 2001; Bairlein & Winkel 2001; Marchant 2002; Fiedler 2003). Our data based on a long-term trapping project (over 30 years) (Sokolov et al. 2000) did not reveal any significant trends in the timing of autumn migration in most bird species. Unfortunately, few standardised projects which cover the whole autumn migratory season are run over many years in Europe. Therefore, the problem of trends in the timing of migratory departure from the breeding areas remains a debatable one.

Changes in avian phenology are related by many authors to global warming, at least in the 20th century. Ground-level air temperatures in both northern and southern hemispheres show a significant upward trend in the recent decades (Borsenkov 1988; Kondratiev 1992). This trend is especially obvious in winter and in spring. This could not fail to influence avian phenology. Many authors revealed a close relationship between arrival of migrants and spring air temperatures (Mason 1995; Sokolov et al. 1998; Sparks 1999; Barrett 2002; Sparks et al. 2003). High spring air temperatures, as a rule, induce early arrival in both short- and long-distance migrants. Warm and early spring usually promotes early breeding (McCleery & Perrins 1998; Sokolov & Payevsky 1998; Brown et al. 1999; Crick & Sparks 1999; Bairlein & Winkel 2001). However, the relationships between climatic processes and the timing of autumn migration are far from being straightforward (Fiedler 2003).

Long-term monitoring by captures in large Rybachy-type traps makes it possible to analyse the timing of spring and autumn migration. In this paper three aspects of phenology in medium-distance European migrants, the Song Thrush *Turdus philomelos* and the Redwing *T. iliacus*, are studied in the Eastern Baltic.

1. How did timing of spring migration change on the Courish Spit over 45-year period, 1957-2002?
2. Did the timing of autumn migration change?
3. Are any changes in migratory schedule related to climate change in the northern hemisphere?

2. Material and methods

Trapping data from Rybachy-type traps at Fringilla field station (55°05'N, 20°44'E) on the Courish Spit of the Baltic Sea were analysed. The data refer to the period since spring 1957 and autumn 1958 until 2002. The overall numbers of captures are 1,437 Song Thrushes in spring and 16,439 in autumn; 826 Redwings in spring and 3,765 in autumn.

Thrushes arrive early and depart late, therefore the beginning and end of trapping may influence the results. Regression analysis showed no trend towards earlier onset of trapping sessions across 45 years of study ($F = 1.73$, $p = 0.196$).

The mean date of commencing trapping is 28 March. Years when trapping started later than 5 April ($n = 6$) were excluded from the analysis.

To estimate the period of spring migration, time span between the onset of trapping and 1 May was analysed. Furthermore, birds captured during the first two hours after sunrise between 1-20 May were also included.

In some years, nocturnal passage of thrushes may be recorded as early as 10 March (Bolshakov et al. 2002), therefore birds migrating in March are missed. In spring, some 20% of Song Thrushes and 30% of Redwings may be missed from our estimates. However, the main spring migratory period of both species is covered by trapping, as mass nocturnal migration of Song Thrushes occurs on average between 28 March - 29 April, of Redwings - between 24 March - 23 April (Bolshakov et al. 2002).

The timing of autumn migration was estimated on the basis of captures from 1 September until 31 October. According to nocturnal observation in the first 10-day period of November 15% of all migrating Redwings may be missed from our calculations. The percentage of missed Song Thrushes is as low as ca. 2%. The main migratory period of both species is covered by captures. The most intense nocturnal passage of the Song Thrush occurs between 8 September - 17 October; that of the Redwing between 12-23 October (Bolshakov et al. 2002).

Median and mean calendar capture dates in stationary traps were taken as estimates of the timing of migration. The onset of migration was estimated by capturing 5% of all birds, its end by capturing 95%. As the Redwing only occasionally breeds in the study region (Grishanov 2000), the first autumn capture date was also used to characterise the onset of autumn passage. Our long experience shows that in the end of the migratory period birds with physical deformities (one-legged, with deformed beak etc.) are often captured. Therefore we concluded that the timing of autumn passage is better estimated by the mean or median date of autumn captures (Sokolov et al. 1999).

Mean and median capture dates, and capture dates of 5% and 95% of migrants do not accurately reflect the respective parts of migration, but may be used as estimates revealing trends. The only exception is the Song Thrush data for autumn, as practically the whole migratory period of this species is covered by captures in stationary traps.

We used regression analysis to study trends in spring and autumn migration. Correlation analysis was used to analyse the relationships between timing of migration in the study species and NAOI (North Atlantic Oscillation Index), and temperature regimen.

The NAO is a large-scale hemispheric oscillation redistributing atmospheric mass from the Arctic to the subtropical Atlantic and has consequences for regional climate in Europe (Hurrell et al. 2001; Forchhammer et al. 2002). High NAOI numbers (December-March) are associated with increased strength and frequency of westerly winds across the Atlantic and south-westerly winds across Europe.

This, in turn, leads to warm, wet winters in Europe (Nott et al. 2002). In low NAOI winters, the across-Atlantic storm tracks turn south-east resulting in increased strength and frequency of cold and dry winds blowing down south into Europe (Hurrell & van Loon 1997; Visbeck et al. 1998). Europe experiences warmer and wetter winters causing earlier spring emergence of plants and insects during high NAOI winters (Sparks & Carey 1995; Post et al. 2001).

3. Results

3.1. Spring migration

3.1.1. Dynamics of spring migration

Analysis of the mean and median capture dates showed a large interannual variation of the timing of spring migration in both Song Thrush and Redwing. In the former species, the range of variation in the median date was 26 days (31 March – 26 April), in the Redwing it was 22 days (2-24 April).

A strong positive correlation was found between the mean and the median dates in both species (Tab. 1). Both mean and median dates were also significantly positively related to capture dates of 5% and 95% of all birds. Therefore, the earlier passage starts, the earlier the bulk of birds of both species migrate. The end of spring passage in both thrush species is not related to the beginning of migration.

Table 1. Correlations between capture date of 5% of birds (onset of migration), median and mean capture dates and capture date of 95% of birds (end of migration) in the Song Thrush and Redwing during spring passage on the Courish Spit (1961-2002) (Spearman's correlation coefficient: * $p < 0.05$, ** $p < 0.01$).

Species		Median date	Mean date	95% of captures
Song Thrush	5% of captures	0.481*	0.596**	0.142
	Median date		0.805**	
	95% of captures	0.486*	0.704**	
Redwing	5% of captures	0.736**	0.684**	0.321
	Median date		0.961**	
	95% of captures	0.394*	0.482*	

Regression analysis showed significant variation in the timing of spring passage through the study area in 1958-2002 in both species (Fig. 1, 2). Mean and median capture dates, and capture dates of 5% and 95% of birds suggest that thrushes were arriving considerably earlier in the 1980s and 1990s than in the latter half of the 1960s and 1970s. Only in the Redwing was the trend in the end of spring passage (95%) since 1970 close to being significant ($F = 3.63$, $p = 0.06$).

Correlation analysis showed that long-term fluctuations of the timing of migration in the two thrush species are strongly correlated (Tab. 2). This means that if in a particular year early spring passage is recorded on the Courish Spit in the Song Thrush, the migration of the Redwing is likely to occur early, too.

Table 2. Correlation between dates of spring migration (5%, mean, median, 95%) in the Song Thrush and Redwing on the Courish Spit over 23 years (1964-2002) (Spearman's correlation coefficient: * $p < 0.05$, ** $p < 0.001$).

Species	5% capture date	Median date	Mean date	95% capture date
Song Thrush / Redwing	0.474*	0.819**	0.889**	0.455*

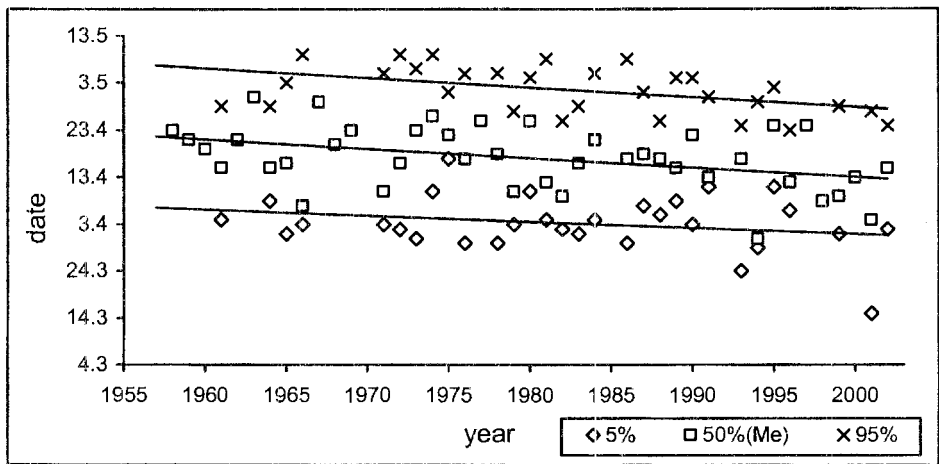


Figure 1. Dynamics of timing of spring passage of the Song Thrush in the Eastern Baltic (1957-2002). Regression analysis: 5% of captures $F = 4.32$, $p = 0.043$; median date $F = 7.56$, $p = 0.008$; mean date $F = 7.28$, $p = 0.009$; 95% of captures $F = 13.5$, $p = 0.001$.

3.1.2. Influence of NAO Index and air temperature

Correlation analysis showed a relationship between the onset of spring migration (capture date of 5% of all birds) and NAO Index in March (Tab. 3, Fig. 3, 4). Neither February nor April index values showed a significant influence on the timing of arrival. No relationship of median and mean dates of passage or capture date of 95% of birds with NAO Index was found (Tab. 3).

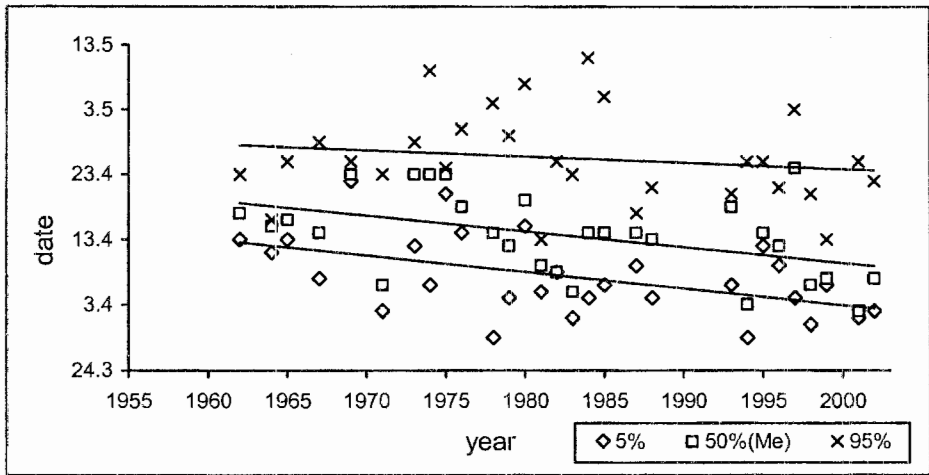


Figure 2. Dynamics of timing of spring passage of the Redwing in the Eastern Baltic (1961-2002). Regression analysis: 5% of captures $F = 7.57$, $p = 0.010$; median date $F = 6.49$, $p = 0.017$; mean date $F = 7.57$, $p = 0.010$; 95% of captures $F = 1.06$, $p = 0.312$.

Table 3. Correlation between dates of spring migration of thrushes on the Courish Spit and mean air temperatures ($^{\circ}\text{C}$) and NAOI (North Atlantic Oscillation Index) during 29 years (1958-2002) (Spearman's correlation coefficient: * $P < 0.05$).

Species	Arrival date	T $^{\circ}\text{C}$ February	T $^{\circ}\text{C}$ March	T $^{\circ}\text{C}$ April	NAOI February	NAOI March	NAOI April
Song	5%	-0.051	-0.234	0.065	-0.154	-0.379*	-0.208
Thrush	Median	0.076	-0.056	-0.195	-0.182	-0.043	0.092
Redwing	5%	-0.157	-0.231	-0.181	-0.218	-0.361*	-0.043
	Median	0.046	-0.155	-0.221	-0.035	-0.138	-0.110

The NAO Index to a large extent reflects the temperature regimen in Europe, our region included, in winter and in early spring, i.e. in March. Long-term dynamics of the NAO Index suggests that the temperature regimen in Europe in March was getting warmer after the 1950s and peaked in the 1980s (Fig. 5). Direct data on temperature in our region also supports the concept of climate warming. March temperature in Kaliningrad shows a significant positive trend over 1955-2002 (Fig. 6).

The comparison of long-term (1913-1993) March temperature data in many European countries (from France to Russia) showed a strong positive relationship between temperature in the Kaliningrad Region and temperatures in various regions of Europe (Fig. 7). This means that if the weather in March in the wintering

quarters of thrushes (France, Belgium, Italy) is warm, it is likely to be warm along the whole migratory route (Germany, Poland, Kaliningrad Region). However, no direct relationship between the timing of passage of thrushes and air temperatures in the Kaliningrad Region in February, March, or April was found (Tab. 3).

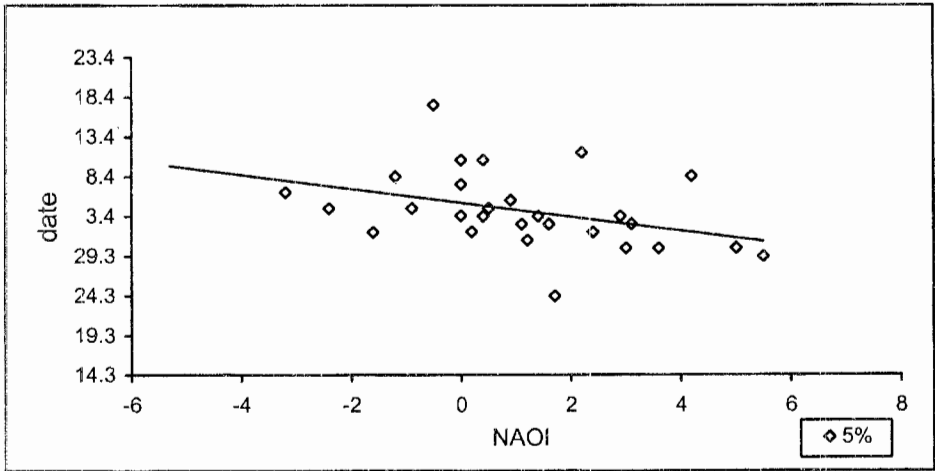


Figure 3. Relationship between the onset of spring passage of the Song Thrush and March NAO Index.

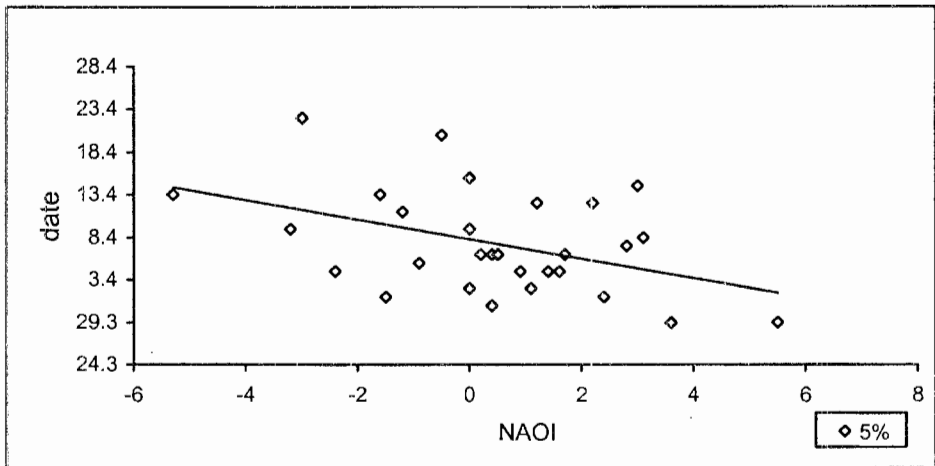


Figure 4. Relationship between the onset of spring passage of the Redwing and March NAO Index.

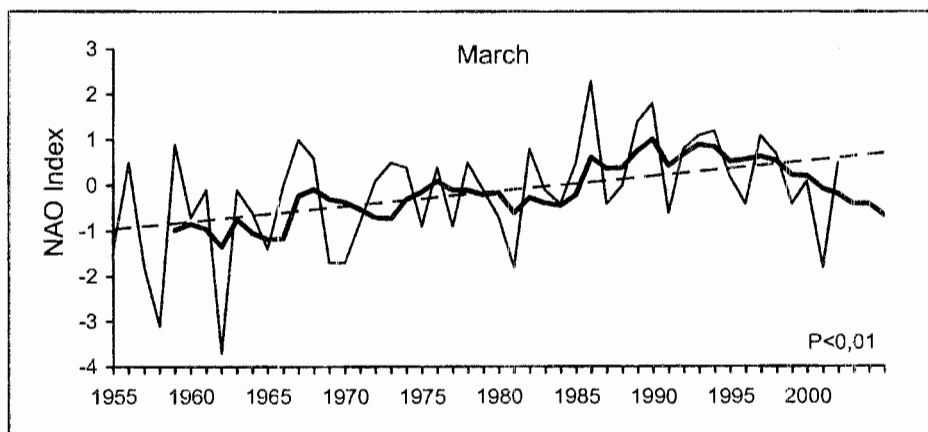


Figure 5. The change in NAO Index in March in 1955-2002. Thin line – NAO Index in each year; thick line – NAO Index smoothed over five years; straight line – the trend over the whole period.

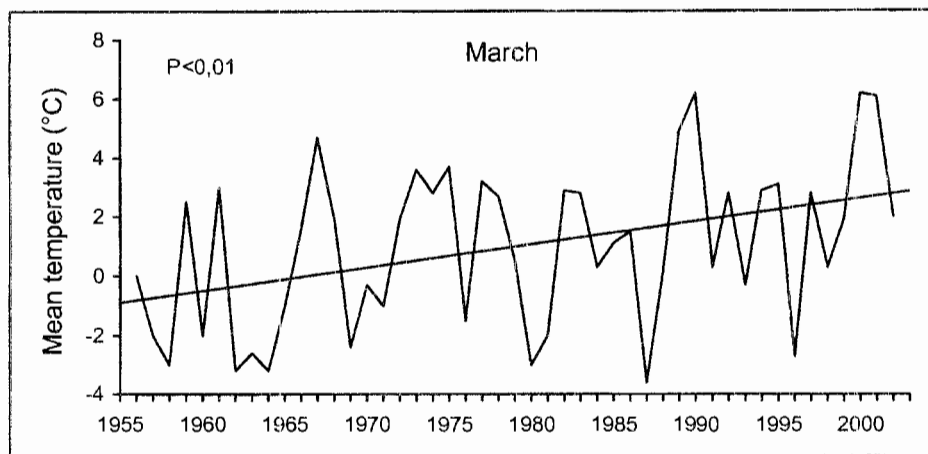


Figure 6. Changes of the mean air temperatures in March on the Courish Spit in 1955-2002.

3.2. Autumn migration

3.2.1. Dynamics of autumn migration

Autumn nocturnal passage of Song Thrushes on the Courish Spit starts in the latter 10-day period of August. However, until the beginning of September, singular individuals are recorded only. Mass passage occurs in late September – mid October. Variation of median capture dates is 22 days (21 September – 13 October) (Bolshakov et al. 2002). The last Song Thrushes are captured until the end of trapping sessions (31 October).

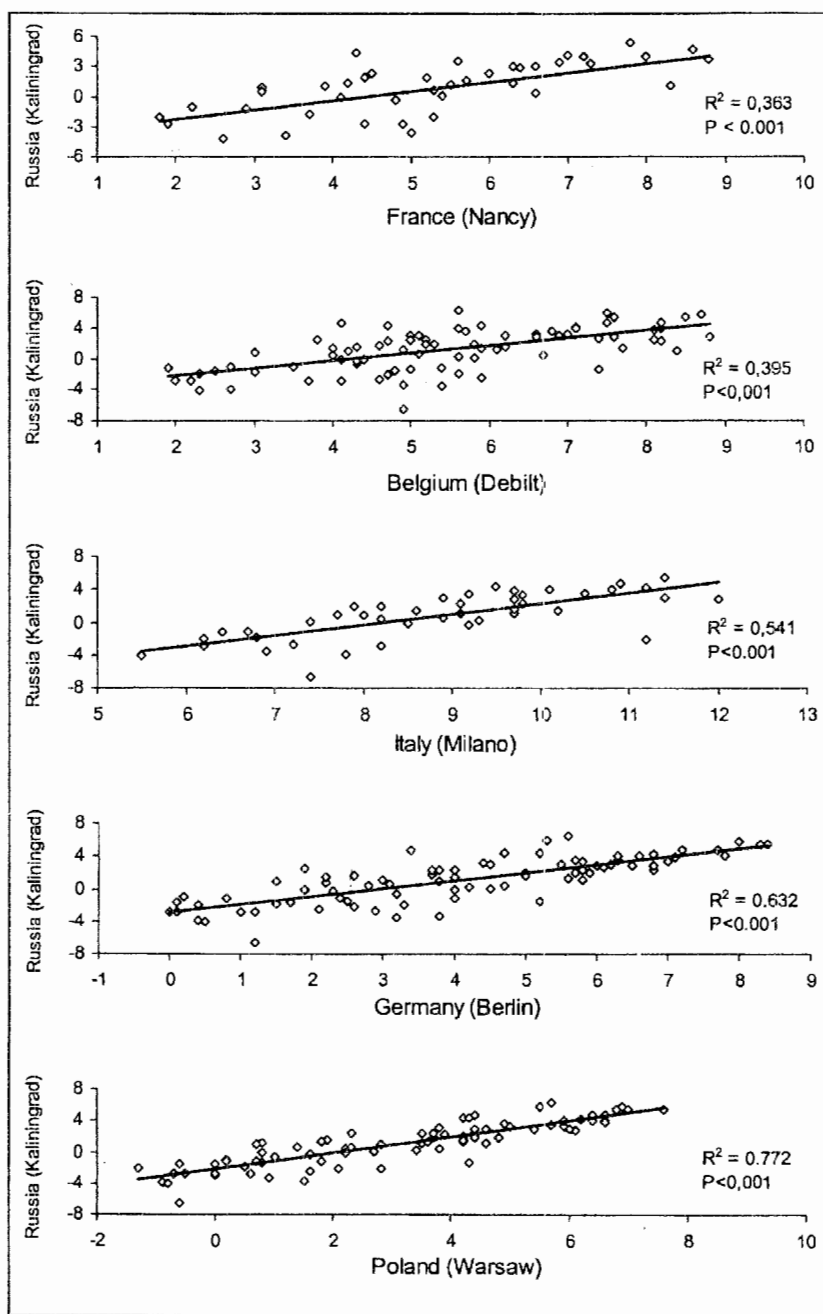


Figure 7. Correlation between mean March air temperatures in different regions of Europe.

First Redwings are usually captured in the latter 10-day period of September. The main passage of this species takes place in the second 10-day period of October. Median capture dates vary within four weeks, between 29 September and 26 October. First-autumn and adult birds pass during the same period (Sokolov et al. 1999; Bolshakov et al. 2002).

In both species mean and median capture dates show a strong positive correlation (Tab. 4). Positive relationship is also found between mean and median capture dates and dates of capturing 5% of birds (and first capture date in the Redwing). The end of autumn passage is not related to the passage of the bulk of birds and the onset of passage (in the Redwing).

Table 4. Correlation between the first capture date, capture of 5% of birds, median and mean capture dates and 95% of captures in the Song Thrush and Redwing during autumn migration on the Courish Spit over 35 years (1961-2002) (Spearman's correlation coefficient: * $p < 0.05$, ** $p < 0.01$).

Species		5% of captures	Median date	Mean date	95% of captures
Song Thrush	5% of captures		0.483*	0.606**	-0.601**
	Median date			0.836**	0.284
	95% of captures			0.305	
Redwing	First capture	0.576**	0.383*	0.353*	0.019
	5% of captures		0.599**	0.637**	0.101
	Median date			0.894**	0.230
	95% of captures			0.222	

In the Song Thrush, regression analysis showed no significant shift in the timing of autumn passage on the Courish Spit in 1958-2002 (Fig. 8). Even during 1970-2001, when a delay of migration was recorded in Western Europe (Fiedler 2003), no significant change occurred on the Courish Spit (median date: $F = 3.81$, $p = 0.06$). In the Song Thrush, which is a common breeder on the Courish Spit, captures of the first 5% of individuals refer to the movements of young birds. No significant shift was recorded in the first 5% of captures, median and mean capture dates. However, time lapse between 5% and 50% of captures increased with years ($F = 5.98$, $p = 0.018$). No increase in overall numbers of birds captured in autumn was recorded in the recent years ($F = 0.12$, $p = 0.73$). To test for the possible effect of the timing of movements of young birds on the median and mean passage dates, we also analysed the long-term dynamics of autumn captures of fat juvenile Song Thrushes (fat score at least 3, Kaiser 1993) in 1972-2002. No significant change in the timing of passage of this subsample group was recorded (for the median date: $F = 3.05$, $p = 0.091$).

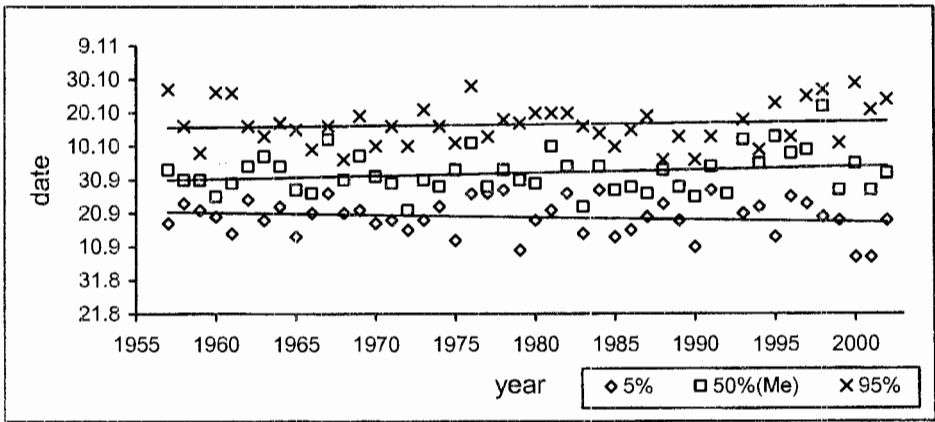


Figure 8. Dynamics of timing of autumn passage of the Song Thrush in the Eastern Baltic (1958-2002). Regression analysis: 5% of captures $F = 2.22$, $p = 0.144$; median date $F = 2.46$, $p = 0.124$; mean date $F = 0.76$, $p = 0.388$; 95% of captures $F = 0.42$, $p = 0.519$.

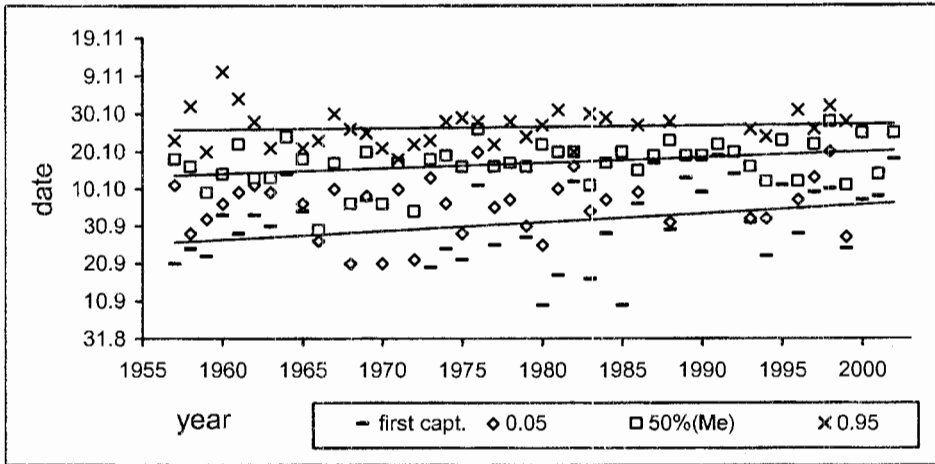


Figure 9. Dynamics of timing of autumn passage of the Redwing in the Eastern Baltic (1958-2002). Regression analysis: first capture $F = 4.57$, $p = 0.038$; 5% of captures $F = 3.05$, $p = 0.089$; median date $F = 5.69$, $p = 0.021$; mean date $F = 4.88$, $p = 0.032$; 95% of captures $F = 1.18$, $p = 0.284$.

Unlike the Song Thrush, the Redwing showed a significant shift towards later autumn passage (Fig. 9). This trend was significant for the mean and median capture dates, and for the first capture in autumn. Numbers of Redwings (unlike other thrushes) have declined sharply in the Baltic region since 1988 (Sokolov et al. 2000). Analysis of correlations between numbers of caught birds and first capture

date, mean and median dates showed a significant relationship with the first capture date only ($r = -0.406$, $p = 0.005$). Therefore, on the Courish Spit the delay of the bulk of birds was not related to decreasing numbers of this species (median date: $r = -0.263$, $p = 0.077$; mean date: $r = -0.173$, $p = 0.27$).

Correlation analysis showed a significant relationship between long-term fluctuations of the median and mean capture dates in both thrush species (Tab. 5). This means that if in a particular year autumn passage occurs late in the Song Thrush, it is most likely to be a year with later passage of the Redwing, too.

Table 5. Correlation between dates of autumn migration (5%, mean, median, 95%) in the Song Thrush and Redwing on the Courish Spit for 35 years (1964-2002) (Spearman's correlation coefficient: * $p < 0.05$, ** $p < 0.001$).

Species	5% capture date	Median date	Mean date	95% capture date
Song Thrush / Redwing	0.297	0.409*	0.495*	0.300

3.2.2. Influence of air temperature

Timing of autumn migration may be indirectly influenced by spring and summer temperatures through breeding schedule. We analysed the relationship of the timing of autumn passage in both thrush species with summer air temperatures in their presumed breeding grounds (Leningrad Region, Russia) as well as with autumn temperatures in our study region. Both species showed weak significant correlation between autumn passage on the Courish Spit and summer temperatures in the presumed breeding areas: June and July temperatures in the Song Thrush, July temperature in the Redwing (Tab. 6). If these correlations are not incidental, this means that a cold summer is followed by late autumn migration.

Table 6. Correlation between dates of autumn migration in thrushes on the Courish Spit and mean air temperatures ($^{\circ}\text{C}$) in the St.Petersburg, Russia in 1959-2002 (35 years) (Spearman's correlation coefficient: * $p < 0.05$).

Species	Date of autumn migration	T $^{\circ}\text{C}$ March	T $^{\circ}\text{C}$ April	T $^{\circ}\text{C}$ May	T $^{\circ}\text{C}$ June	T $^{\circ}\text{C}$ July
Song Thrush	5%	0.023	-0.250	0.055	-0.144	-0.050
	Median	-0.011	-0.077	0.168	-0.418*	-0.342*
	Mean				-0.357*	-0.109
	95%				-0.375*	-0.038
Redwing	5%	0.179	0.006	0.004	-0.017	-0.319*
	Median	0.177	0.092	-0.060	-0.244	-0.103

No significant correlation between autumn air temperatures on the Courish Spit and autumn passage was revealed in both species (Tab. 7).

Table 7. Correlation between dates of autumn migration of thrushes on the Courish Spit and mean autumn temperatures air (°C) in the Kaliningrad Region in 1959-2002.

Species	Date of autumn migration	T °C August	T °C September	T °C October
Song Thrush	5%	0.099	-0.211	-0.060
	Median	-0.007	0.241	0.175
Redwing	5%	-0.031	-0.003	0.105
	Median	-0.088	0.213	-0.098

4. Discussion

4.1. Spring migration

The data of 45-year monitoring of two thrush species by standardised trapping on the Courish Spit of the Baltic Sea show that the timing of spring migration shifted significantly over this period. Song Thrushes and Redwings migrated in spring over the Courish Spit considerably earlier in the 1980s and 1990s than in the 1970s and late 1960s. This is in agreement with the data on many other passerines, both short- and long-distance migrants (Sokolov et al. 1998).

A possible environmental factor affecting the timing of migration is the temperature regimen both in the wintering area and on the route of migration. Air temperature is one of the main meteorological elements characterising climate (Khromov & Mamontova 1974; Weisberg 1976).

We did not find any direct relationship between the timing of thrush passage and spring air temperatures on the Courish Spit. However, a significant correlation with March NAO Index was revealed. The NAO Index is related to temperature regimen in different European regions from France to the Gulf of Finland. The higher March temperatures in Europe are, the earlier the passage of the Song Thrush and the Redwing occurs. Similar patterns have been found in a number of passerine species on the Courish Spit (Sokolov & Kosarev 2003). Our analysis of temperature regimens in March over several decades across a large area from France to Poland and the Kaliningrad Region showed that spring mean monthly temperatures among these countries are strongly correlated. Therefore, if the weather conditions favour migration from the winter quarters, they are likely to be favourable over the large part of migratory route, too. We assume that warm weather in the winter quarters in the beginning of spring may stimulate thrushes to depart earlier. In such years we probably record early migration of thrushes on the Courish Spit. Late and cold spring in the winter quarters, conversely, delays

departure and this retards the whole migratory schedule. Such situations frequently occurred in the 1970s when many passerines, thrushes including, passed through the Courish Spit very late (Sokolov et al. 1998).

Penuelas et al. (2002) studied phenological events in the Mediterranean region, where the thrushes over-winter, and found that average annual temperatures in their study area (Cardedeu, NE Spain) have increased by 1.4 °C over the observation period (1952-2000) while precipitation remained unchanged. A conservative linear treatment of the data shows that leaves unfold on average 16 days earlier, leaves fall on average 23 days later, and plants flower on average 6 days earlier than in 1952. The stronger changes both in temperature and in phenophases timing occurred in the last 25 years.

Forchhammer et al. (2002) analysed and contrasted the effects of climate (NAO Index) and temporal dependence on the long-term (1928-1977) dynamics of springtime arrival in three short-distance (Skylark *Alauda arvensis*, Song Thrush, Starling *Sturnus vulgaris*) and three long-distance (White Wagtail *Motacilla alba*, Swallow *Hirundo rustica*, Cuckoo *Cuculus canorus*) migratory species in Norway. Following high NAOI winters both long- and short-distance migrants arrived earlier than after low NAOI winters. For long-distance migrants, the effect of high NAOI winters was probably indirect through improved foraging conditions in winter quarters, whereas the effect on short-distance migrants may be related both to improved foraging and weather conditions during their northward spring migration.

Mason (1995) found a significant relationship between arrival time and monthly temperature of March and April in eight migrant species in central England over 1942-1991. A negative correlation with March temperature was found in early migrants and with April temperature in late migrants. In England many species show trends of earlier arrival in recent years, consistent with a rise in early spring temperature (Sparks & Mason 2001).

Relationship between migratory schedule of birds and air temperature is often believed to be a direct one. However, other authors suggest that the effect of spring temperature reflects in trophic chains (Sokolov 2000; Both & Visser 2001; Sparks et al. 2003). Ambient temperature governs food abundance and its availability during spring migration. These authors suggest that temperature change just indicates the advent of conditions favourable for avian migration.

Increasing NAO Index in Europe in the last century reflects increasing strength and frequency of westerly winds across the Atlantic which cause high winter and spring temperatures. In Western Europe both air temperature and the frequency of westerly and south-westerly winds increase in March and April in the recent decades (Sparks et al. 2002). Since the general direction of spring migration of thrushes is 044° (Bolshakov et al. 2002), these tailwinds assist the birds in flight. Wind is believed to be a major meteorological agent governing migratory flight activity of birds (Lack 1960; Richardson 1978, 1990; Alerstam 1990). Visual

observations and radar survey show that numbers aloft, especially in passerines, are strongly correlated with tailwinds which are favourable for birds from both energetic and orientational viewpoints (Alerstam 1976, 1990; Alerstam & Lindström 1990; Åkesson & Hedenström 2000). Migrants prefer to fly on the nights with following winds or choose an altitude range with most favourable winds (Liechti & Bruderer 1998). In spring, ca. 85% of thrushes in the Baltic area arrive/depart on tailwinds (Sinelschikova et al. 2003). In some years passage of thrushes may continue during a few "good" nights of following winds (Alerstam 1990).

Therefore, it may be suggested that the significant advance of the timing of spring migration recorded in the recent 50 years may be related to at least two factors: (1) earlier emergence of the conditions enhancing migration due to higher spring temperatures (favouring foraging and fuel deposition) and (2) higher migratory speed over south-western and central European part of their migratory route due to increased frequency of following winds.

4.2. Autumn migration

Timing of autumn migration of the Song Thrush in the Eastern Baltic did not show any significant trend over the last 45 years, in spite of considerable annual fluctuations. Even in 1970-2001, when in Western Europe this species showed significant delay of the timing of autumn passage (Fiedler 2003), no significant trend was revealed on the Courish Spit. Only the Redwing showed a weak but significant trend towards later passage. No relationship between autumn migration and autumn ambient temperature was found in either species. Such a relationship was not found in other passerine species on the Courish Spit, either (Sokolov et al. 2000). However, this does not rule out an effect of climate on the timing of outward migration.

German authors report that on Helgoland (North Sea) 19 species of short-distance migrants showed a tendency to depart later than usual in the 1980s, on average by 10 days (Glaubrecht 1993; Moritz 1993; Vogel & Moritz 1995). These authors relate this to climate change. Later autumn departure was also reported by other authors who suggested that in warm years birds remain in their breeding areas longer (Sparks & Mason 2001; Bairlein & Winkel 2001). Studies of migratory behaviour of caged Blackbirds (*Turdus merula*) from sedentary and migratory German populations showed that migratory activity may be controlled not only by the endogenous programme, but also by environmental factors, in particular by food availability (Partecke & Gwinner 2003). However, decreased migratory activity in good environment was not recorded until their second autumn.

Song Thrushes and Redwings are known to be able to overwinter in their breeding range. Even though in our study area both species are migratory, in warm years solitary birds or small flocks of these birds do occur in the Eastern Baltic in winter (Taurinš 1967; Kumari 1985; Švažas et al. 2000; Raudonikis 2001). In recent years, the Redwing became a common wintering species in the Kaliningrad

Region (Grishanov 2000). The resident urban populations of Blackbird were formed in the Eastern Baltic in the 1950s-1960s (Ivanauskas 1964; Jõgi 1967a; Malchevsky & Pukinsky 1983). A proportion of wintering birds are the winter visitors from northern Europe (Jõgi 1967b; Leuhin & Rootsmäe 1985).

Thus, we cannot rule out that climate warming and associated improvement of food availability may influence later autumn departure in short-distance migrants. This is most obvious in central Europe where some passerines, especially short-distance migrants, under favourable weather conditions indeed remain longer in their breeding area. However, in our more northern area, no delay of departure was recorded in warmer periods either in the Song Thrush or in most other passerines (Sokolov et al. 2000).

Impact of climate change may also act not through autumn temperatures which have undergone slight changes in Europe during the last half-century (Easterling et al. 1997), but rather through spring temperatures. Spring temperatures have increased strongly in Europe during recent decades (Easterling et al. 1997; Walther et al. 2002) and influence the length of reproductive period which has increased due to earlier springtime arrival and breeding. Short-distance migrants achieve higher survival rates and/or obtain higher-quality breeding territories by arriving earlier in spring (Berthold 1990). Short-distance migrants with a variable number of 1 or 2 broods delayed their autumn peak passage mainly due to a higher proportion of pairs raising 2 broods (Jenni & Kéry 2003). The Redwing and Song Thrush are just such species in northern Europe (Khokhlova et al. 1983; Zimin et al. 1993). It is also possible that in Baltic populations of the Song Thrush more pairs are double-brooded annually than in the other populations in Western Europe (Payevsky & Vysotsky 2003).

We found that timing of autumn migration in both species is related not to April or May temperatures, but to summer temperatures in their breeding areas (June and July). Following a cold summer (which become more frequent in the recent years), autumn departure is delayed. Unlike spring, June and July temperatures show no rise in northern Europe, July even became slightly colder. A special feature of the annual cycle of thrushes breeding in NE Europe is their summer nocturnal migration towards the NNE (Bolshakov & Rezvyi 1975, 1981; Rezvyi & Bolshakov 1987). This migration takes place from late June until early August, peaking in mid July. Individual duration of this period is some 7-10 nights between disintegration of broods and the onset of moult, both in adults and juveniles. During this period, a bird may cover 700 km on average. The most likely goal of this migration is utilising berries abundant in northern areas during the premigratory period. It may be assumed that summer temperatures influence fruit ripening and abundance. In years when fruits ripen late (and are probably less abundant) due to cold summers, later passage of thrushes are recorded.

Therefore, we suggest that the delay of autumn passage in thrushes, primarily in the Redwing, is mainly due to the general climate warming, which not only

promotes early spring arrival, but also prolongs reproductive season due to increased frequency of second breeding attempts. Moreover, summer temperatures may govern the timing of summer migration of thrushes, which in its turn may influence the timing of autumn migration.

Acknowledgements

This study was supported by OMPO (France) and the Russian Foundation for Basic Research (grant to Victor Bulyuk no. 04-04-49161 and grant to Leonid Sokolov no. 03-04-49648). The authors are grateful to their colleagues and ringers who have participated in the long-term trapping and ringing of thrushes on the Courish Spit.

Reference

- Åkesson, S. & Hedenström, A. 2000. Wind selectivity of migratory flight departures in birds. *Behav. Ecol. Sociobiol.* 47: 140-144.
- Alerstam, T. 1976. Nocturnal migration of thrushes (*Turdus* spp.) in southern Sweden. *Oikos* 27: 457-475.
- Alerstam, T. 1990. *Bird Migration*. Cambridge Univ. Press.
- Alerstam, T. & Lindström Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. In: E. Gwinner (Ed.). *Bird Migration*. Springer-Verlag, Berlin: 331-359
- Bairlein, F., Jenni, L., Kaiser, A., Karlsson, L., Noordwijk, A., Peach, W., Piastro, W., Spina, F. & Walinder, G. 1995. European-African Songbird Migration Network. Manual of field methods. Wilhelmshaven.
- Bairlein, F. & Winkel, W. 2001. Birds and Climate Change. In: Lozan, J.L., Grassl, H., Hupfer, P. (Eds.). *Climate of the 21st Century: Changes and Risks*. Wissenschaftliche Auswertungen, Hamburg: 278-282.
- Barrett, R.T. 2002. The phenology of spring bird migration to north Norway. *Bird Study*. 49: 270-277.
- Berthold, P. 1990. *Vogelzug*. Darmstadt: Wissenschaftliche Buchgesellschaft.
- Borisenkov, E.P. 1988. Climate Fluctuations during the Last Thousand Years. *Gidrometeorizdat Press, Leningrad* (in Russian).
- Bolshakov, C., Žalakevičius, M. & Švažas S. 2002. Nocturnal migration of thrushes in the Eastern Baltic region. Vilnius.
- Bolshakov, C.V. & Rezvyi, S.P. 1975. About June nocturnal migration of thrushes in Leningrad Region from moon-watch observations. *Proc. All-Union Conf. Bird Migration*. Moscow, 2: 101-104 (in Russian).
- Bolshakov, C.V. & Rezvyi, S.P. 1981. Nocturnal migration of birds in July in Leningrad Region. *Abstr. X Eastern Baltic Ornithol. Confer. Riga*. Part 1: 97-100 (in Russian).
- Both, C. & Visser, M.E. 2001. Adjustment to climate change is constrained by arrival date in long-distance migrant bird. *Nature* 411: 296-298.
- Bradley, N.L., Leopold A.C., Ross, J. & Huffaker, W. 1999. Phenological changes reflect climate change in Wisconsin. *Proc. Nat. Acad. Sci. USA* 96: 9701-9704.
- Brown, J.L., Li, S.-H. & Bhagabati, N. 1999. Long-term trend toward earlier breeding in an American bird: A response to global warming? *Proc. Nat. Acad. Sci.* 97: 5565-5569.

- Crick, H.Q.P. & Sparks, T.H. 1999. Climate change related to egg-laying trends. *Nature* 399: 423-424.
- Sparks, T.H., Roberts D.R. & Crick, H.Q.P. 2002. What is the value of first arrival dates of spring migration in phenology? In: O.A. Zhigalski & L.V. Sokolov (Eds.). Long-term dynamics of bird and mammal populations and global climatic changes. Kazan: 39-46.
- Easterling, D.R., Horton, B., Jones, P.D., Peterson, T.C., Karl, T.R., Parker, D.E., Salinger, N.J., Razuvayev, V., Plummer, N., Jamason, P. & Folland, C.K. 1997. Maximum and minimum temperature trends for globe. *Science* 277: 364-367.
- Fiedler, W. 2003. Changes and stability in timing of autumn passage in 19 passerine species in a stopover site in Southwestern Germany. *Die Vogelwarte*, 4th Conf. EOU: 145-146.
- Forchhammer, M.C., Post, E. & Stenseth, N.C. 2002. North Atlantic Oscillation timing of long-and short-distance migration. *Journal of Animal Ecol.* 71: 1002-1014.
- Glaubrecht, M. 1993. Vogel im Klimastress. *Bild Wiss.* 11: 114-115.
- Hurrell, J.W. & Van Loon, H. 1997. Decadal variations in climate associated with the North Atlantic Oscillation. *Climatic Change* 36: 301-326.
- Hurrell, J.W., Kushnir, Y. & Visbeck, M. 2001. The North Atlantic Oscillation. *Science* 291: 603-605.
- Ivanaukas, T. 1964. Lithuanian birds. Vol. 1-3. Vilnius, Mintis.
- Jenkins, D. & Watson, A. 2000. Dates of first arrival and song of birds during 1974-99 in mid-Deeside, Scotland. *Bird Study* 47: 249-251.
- Jenni, L. & Kéry, M. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proc. R. Soc. Lond. B* 270: 1467-1471.
- Jõgi, A. 1967a. Hibernation of the Blackbird and an invasion of the Fieldfare in Estonia during the winter of 1964/1965. *Comm. Baltic Comm. Study Bird Migration* 4: 128-135 (in Russian with English summary).
- Jõgi, A. 1967b. Migration of the thrushes in Estonia in the light of ringing data. *Comm. Baltic Comm. Study Bird Migration* 4: 136-145 (in Russian with English summary).
- Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. *J. Field Ornithol.* 64: 246-255.
- Kondratiev, K.J. 1992. *The Global Climate*. Nauka Press, St. Petersburg (in Russian).
- Khokhlova, T.Yu., Zakharova, L.S., Zimin, V.B. 1983. Timing and dynamics of seasonal events in the Redwing in Karelia. In: *Fauna and ecology of birds and mammals of northwestern USSR*. (Ivanter, E.V. & Zimin, V.B. Eds.) Petrozavodsk: 11-29 (in Russian).
- Khromov, S.P. & Mamontova, L.I. 1974. *Meteorological dictionary*. Gidrometeoizdat, Leningrad (in Russian).
- Kumari, E. 1985. Wintering in the Baltic area and migratory birds. *Comm. Baltic Comm. Study Bird Migration* 17: 3-13 (in Russian with English summary).
- Lack, D. 1960. Migration across the North Sea studied by radar. Part 2. The spring departure 1956-59. *Ibis* 102: 26-57.
- Leuhin, J. & Rootsmäe, L. 1985. Migratory birds wintering in Estonia. *Comm. Baltic Comm. Study Bird Migration* 17: 99-109 (in Russian with English summary).
- Liechti F. & Bruderer B. 1998. The relevance of wind for optimal migration theory. *Journal of Avian Biology* 29: 561-568.

- Malchevsky, A.S. & Pukinsky, Yu.B. 1983. The birds of Leningrad Region and adjacent areas. Vol. 2. Passerines. Leningrad Univ. Press. Leningrad (in Russian).
- Mason, C.F. 1995. Long-term trends in the arrival dates of spring migrants. *Bird Study* 42: 182-189.
- McCleery, R.H. & Perrins, C.M. 1998. Temperature and egg-laying trends. *Nature* 391: 30-31.
- Middendorff, A. von. 1855. Die Isepiptesen Russlands. Grundlagen zur Erforschung der Zugzeiten und Zugtiantungen der Vogel Russlands. St-Petersburg. Buchdruck d. K. Acad. Der Wiss.
- Moritz, D. 1993. Long-term monitoring of Palaearctic-African migrants at Helgoland (German Bight, North Sea). *Ann. Sci. Zool.* 268: 579-586.
- Partecke, J. & Gwinner, E. 2003. Differences in migratory disposition of urban and forest European blackbirds (*Turdus merula*). *Die Vogelwarte* 42, 4th Conf. EOU: 10.
- Payevsky, V.A. & Vysotsky, V.G. 2003. Migratory Song Thrushes *Turdus philomelos* hunted in Europe: survival rates and other demographic parameters. *Avian Science* 3 (1): 13-20.
- Penuelas, J., Filella, I. & Comas, P. 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology* 8: 531-544.
- Post, E., Forchhammer, M.C., Stenseth, N.C. & Callaghan, T.V. 2001. The timing of life-history events in a changing climate. *Proceedings of the Royal Society London B* 268: 15-23.
- Raudonikis, L. 2001. Species composition changes and their reasons in the terrestrial birds wintering in Lithuania. *Acta Zool. Lituanica* 11: 309-318.
- Rezvyi, S.P. & Bolshakov, C.V. 1987. Summer migration in the annual cycle of thrushes (*Turdus* spp.) from Leningrad Region. In: Potapov, R.L. (Ed.). *Studies in fauna and ecology of Palaearctic birds*. Leningrad: 87-94 (in Russian with English summary).
- Richardson, W.J. 1978. Timing and amount of bird migration in relation to weather: a review. *Oikos* 30: 224-272.
- Richardson, W.J. 1990. Timing of Bird Migration in Relation to Weather: Update Review. E. Gwinner (Ed.). *Bird Migration*. Springer-Verlag, Berlin-Heidelberg: 78-101.
- Sinelschikova, A., Bolshakov, C. & Bulyuk, V. 2003. Nocturnal migration of thrushes (*Turdus* spp.): numbers aloft and the wind. *Die Vogelwarte* 42, 4th Conf. EOU: 100.
- Sokolov, L.V. 2000. Spring ambient temperature as an important factor controlling timing of arrival, breeding, post-fledging dispersal and breeding success of Pied Flycatchers *Ficedula hypoleuca* in Eastern Baltic. *Avian Ecol. Behav.* 5: 79-104.
- Sokolov, L.V. 2001. Climatic influence on year-to-year variation in timing of migration and breeding phenology in passerines on the Courish Spit. *Ring* 23: 159-166.
- Sokolov, L.V. & Payevsky, V.A. 1998. Spring temperatures effects on year-to-year variations in breeding phenology of passerines on the Courish Spit. *Avian Ecol. Behav.* 1: 22-36.
- Sokolov, L.V., Markovets, M.Yu., Shapoval, A.P. & Morozov, Yu.G. 1998. Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* 1: 1-21.
- Sokolov, L.V., Markovets, M.Yu. & Morozov, Yu.G. 1999. Long-term dynamics of the mean date of autumn migration in passerines on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* 2: 1-18.

- Sokolov, L.V., Yefremov, V.D., Markovets, M.Yu., Shapoval, A.P. & Shumakov, M.E. 2000. Monitoring of numbers in passage populations of passerines over 42 years (1958-1999) on the Courish Spit of the Baltic Sea. *Avian Ecol. Behav.* 4: 31-53.
- Sparks, T.H. 1999. Phenology and the changing pattern of bird migration in Britain. *International Journal of Biometeorology* 42: 134-138.
- Sparks, T.H. & Carey, P.D. 1995. The responses of species to climate over two centuries: An analysis of the Marsham phenological record, 1736-1947. *Journal of Ecology* 83: 321-329.
- Sparks, T.H. & Mason, C.F. 2001. Dates of arrivals and departures of spring migrants taken from Essex Bird Reports 1950-1998. *Essex Bird Reports* 1999: 154-164.
- Švažas, S., Jusys, V., Grigonis, R., Patapavičius, R. & Jezerskas, L. 2000. Development of the Ornithological Station "Ventes Ragas" and improvement of bird ringing activities. Report. Vilnius.
- Taurinš, E. 1967. Seasonal distribution and wintering of thrushes on the basis of ringing data in Latvian SSR. *Comm. Baltic Comm. Study Bird Migration* 4: 146-150 (in Russian with English summary).
- Tryjanowski, P., Kuzniak, S. & Sparks, T. 2002. Earlier arrival of some farmland migrants in western Poland. *Ibis* 144: 62-68.
- Visbeck, M., Cullen, H., Krahnemann, G. & Naik, N. 1998. An ocean model's response to North Atlantic Oscillation-like wind forcing. *Geophysical Research Letters* 25: 4521-4524.
- Vogel, D. & Moritz, D. 1995. Langjährige Änderungen von Zugzeiten auf Helgoland. *Jb.Inst. Vogelforschung* 2: 8-9.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.
- Weisberg, J.S. 1976. *Meteorology the Earth and its Weather*. Houghton Mifflin Company.
- Zimin, V.B., Sazonov, S.V., Lapshin, N.V., Khokhlova, T.Yu., Artemiev, A.V., Annenkov, V.G. & Yakovleva, M.V. 1993. *The Avifauna of Karelia*. Petrozavodsk (in Russian).