



Long-term changes in migration timing of Song Thrush *Turdus philomelos* at the southern Baltic coast in response to temperatures on route and at breeding grounds

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Received: 31 July 2017 / Revised: 7 May 2018 / Accepted: 8 May 2018
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Abstract

Climate warming causes the advancement of spring arrival of many migrant birds breeding in Europe, but the effects on their autumn migration are less known. We aimed to determine any changes in the timing of Song Thrush captured during spring and autumn migrations at the Polish Baltic coast from 1975 to 2014, and if these were related to long-term changes of temperature at their breeding grounds and migration routes. The timing of spring migration at Hel ringing station in 1975–2014 did not show long-term advance, but they had responded to environmental conditions on the year-to-year basis. The warmer the temperatures were in April on their migration route, the earlier were the dates of the median and the end of spring migration at Hel. The beginning of autumn migration at the Mierzeja Wiślana ringing station advanced by 5 days between 1975 and 2014. The warmer the April on route, and the July at the Song Thrushes' breeding grounds, the earlier young birds began autumn migration across the Baltic coast. We suggest this was a combined effect of adults' migration and breeding early during warm springs and young birds getting ready faster for autumn migration during warm summers. The average time span of 90% of the autumn migration was extended by 5 days, probably because of early migration of young birds from first broods and late of those from second broods enabled by warm springs and summers. The response of Song Thrushes' migration timing to temperatures on route and at the breeding grounds indicated high plasticity in the species and suggested it might adapt well to climate changes.

Keywords Migration timing · Climate change · Song Thrush · *Turdus philomelos* · Temperature response

Introduction

The effect of climate change on the biology and the ecology of living organisms is a seminal topic of contemporary science (Møller et al. 2010), and changes in the timing of short- and long-distance bird migration are manifestations of these species' response to climate warming (Lehikoinen and Sparks 2010). One potential effect of climate warming on bird

migration is an earlier spring passage and therefore earlier arrival at their breeding grounds (Forchhammer et al. 2002, Hüppop and Hüppop 2003, Lehikoinen and Sparks 2010). An advance of spring migration in the Baltic region of Europe has been reported for many species of passerines (Moritz 1993, Sokolov et al. 1998, Tryjanowski et al. 2002, Mitrus et al. 2005, Tøttrup et al. 2006a). A similar advance in spring migration has been reported from North America (Marra et al. 2005, Miller-Rushing et al. 2008). Timing of migration and arrival at the breeding grounds might be influenced by conditions on the wintering grounds, on the migration route and at the breeding grounds, and has been shown to correlate with large-scale climate indicators like the North Atlantic Oscillation Index (Huin and Sparks 2000, Forchhammer et al. 2002, Ahola et al. 2004, Hüppop and Hüppop 2003). Early arrival at the breeding grounds is frequently associated with earlier reproduction (Dunn 2004, Elkins 2004), but reported exceptions (Ahola et al. 2004) have shown this does not always benefit the migrants (Both et al. 2006) and can vary spatially and temporally (Gordo et al. 2013). The early arrival

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00484-018-1559-6>) contains supplementary material, which is available to authorized users.

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at the breeding grounds might enable early breeding, early maturity of young and thus early departure from the breeding grounds (Crick and Sparks 1999). The effect of climate change on the timing of autumn migration in the northern hemisphere is less known (Lehikoinen and Sparks 2010). Some authors suggest birds' autumn migration could be delayed by a longer breeding period in response to climate warming (Dunn 2004, Lehikoinen and Sparks 2010 after Berthold 1998), but other studies show an earlier start to autumn migration (Tøttrup et al. 2006b).

Song Thrushes *Turdus philomelos* migrating through the Polish Baltic coast in spring and autumn are medium-distance migrants with an average passage of 2500 km (Tøttrup et al. 2006a). These birds originate from breeding grounds in Fennoscandia and northern Russia (Busse and Maksalon 1986, Milwright 2006, Operation Baltic – unpublished data). Some authors have suggested that the spring migration of Song Thrushes through the Baltic Sea region has advanced during the second half of the twentieth century (Sinelschikova and Sokolov 2004, Tøttrup et al. 2006a, Lehikoinen and Sparks 2010), as with other passerines. The response in the timing of autumn migration to climate change trends is unclear, as Song Thrushes ringed at Rybachy station on the eastern Baltic coast showed no clear tendencies (Sinelschikova and Sokolov 2004), but at Christiansø in the western Baltic, the passage advanced in 1976–1997 (Tøttrup et al. 2006b). The published records of bird migration timing end at Rybachy in 2002 and at Christiansø in 1997; thus, it remains unknown if the tendencies observed earlier have persisted. It is also unclear if similar advances have occurred in the population of Song Thrushes in the eastern Baltic, which hosts birds of partially different breeding origins than those passing through Christiansø (Busse and Maksalon 1986). We therefore aimed to determine any multiyear trends in the timing of Song Thrushes' spring and autumn migration across the Polish Baltic coast in the 40 years between 1975 and 2014, and to correlate any tendencies with long-term temperature changes on the migration routes and the breeding grounds of these populations. Correlations would help us to determine if any observed tendencies might be the reaction of Song Thrushes to temperatures on migration routes and at breeding grounds.

Material and methods

We determined the timing of Song Thrush migration through the Polish Baltic coast from 1975 to 2014 by analysing the dynamics of yearly catches at two Operation Baltic ringing stations (Fig. 1): (1) Hel (54° 44'–54° 46'N, 18° 28'–18° 33' E), on the Hel Peninsula in the northwest Gulf of Gdańsk, which operated during spring migration, from the end of March to the second half of May; and (2) Mierzeja

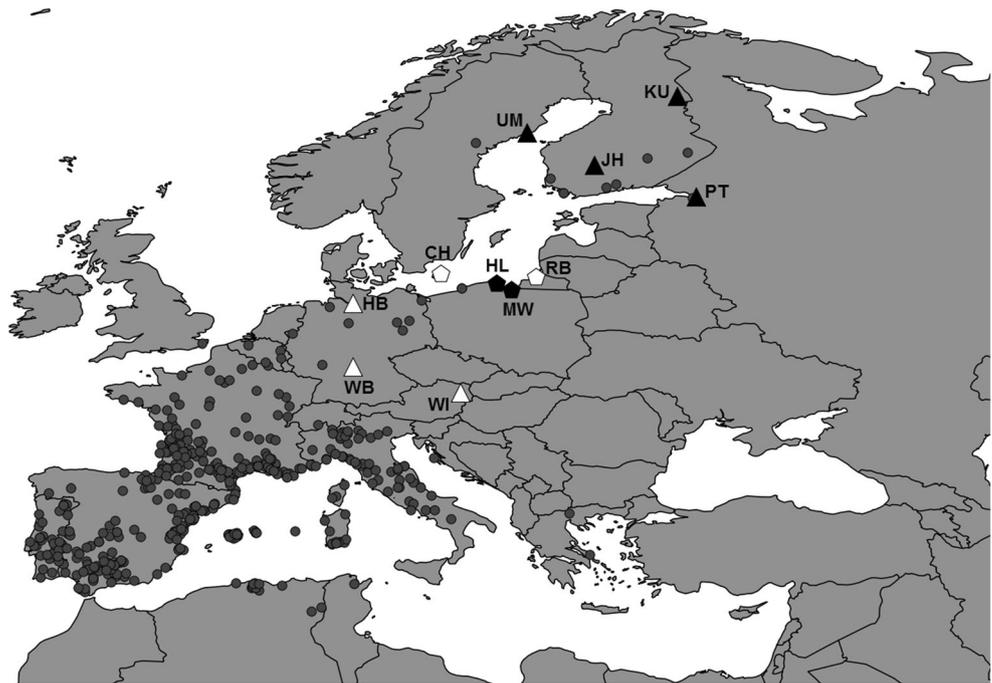
Wiślana (54° 21' N, 19° 17'–19° 23' E), on the Vistula Spit in the south of the Gulf of Gdańsk, which operated during autumn migration from mid-August to the beginning of November.

Both stations used the same standard protocol throughout the years of our study (Busse 2000). Birds were caught from dawn till dusk in 35 to 89 mist nets. The number of nets varied over the years but remained constant in each season. Both stations changed locations within a few kilometres over the years as habitat changed, but these were small moves within the same immediate area of the coastal zone that channels the birds' passage, so we combined data from all locations for each station as one dataset.

After a preliminary analysis of the catch dynamics in each year at each station, we accepted the period of Song Thrush spring migration as 26 March–15 May and the autumn migration as 5 September–31 October. These dates excluded from analysis most local Song Thrush that breed in the vicinity, which were at most two pairs, and thus several offsprings (Operation Baltic unpubl. data). In both seasons, the stations' operations spanned the whole period of Song Thrush migration. We used data only from young birds identified by immature plumage that persists after a partial post-juvenile moult and worn by the birds until their first complete post-breeding moult in about June–July of their first year (Svensson 1992, Demongin 2016). These immature individuals constituted on average 88% of all Song Thrushes ringed each season (Operation Baltic, unpubl. data). Too few adult birds were caught in most seasons to analyse as a representative sample; birds of unknown age were excluded from analyses. We filled small gaps in data on days when ringing was suspended for random reasons such as heavy storms that made mistnetting dangerous for birds and people. We imputed the missing data, as frequently done in other studies based on data from ringing stations (Tøttrup et al. 2006a, 2006b, Sokolov et al. 1998), by calculating the mean number of birds ringed on those dates in the 6 consecutive years before and after any year. These gaps constituted no more than 4 days per season and occurred in 10 years at Hel and in 6 years at Mierzeja Wiślana. After filling the data gaps, we calculated the dates when 5, 50 and 95% of all young Song Thrushes were ringed during each spring and autumn migration in 1975–2014. We used these dates to determine the long-term trends in the timing of the beginning, the median and the end of the Song Thrush migration.

To determine the effect of weather on Song Thrush migration timing, we used the temperatures for 1975–2014 from the European Climate Assessment and Dataset (2015) provided by the Royal Netherlands Meteorological Institute (<http://www.ecad.eu>). We used the minimum and mean daily temperatures at three weather stations on the Song Thrushes' migration route from the wintering grounds in southwestern Europe to the Baltic coast—Hamburg-Botanischer Garten (Germany, 53° 33' N, 9° 59' E), Würzburg (Germany, 49°

Fig. 1 Locations of Operation Baltic's Polish ringing stations (black pentagons: HL Hel, MW Mierzeja Wiślana), Christiansø and Rybachy ringing stations (white pentagons: CH and RB) and weather stations used in the study (black triangles: stations at the breeding grounds UM Umea Flygplats, JH Juupajoki Hyytiälä, KU Kuusamo Kiutakongas, PT St. Petersburg; white triangles: stations on spring migration route HB Hamburg-Botanischer Garten, WB Würzburg, WI Wien), and distribution of ringing recoveries of Song Thrushes ringed at the HL and MW stations (dark grey circles) in 1960–2015



46° N, 9° 57' E) and Wien (Austria, 48° 13' N, 16° 21' E)—and at four stations in the presumed breeding areas of the population of Song Thrushes that migrate across the Baltic Sea—Umea Flygplats (Sweden, 63° 47' N, 20° 17' E), Juupajoki Hyytiälä (Finland, 61° 51' N, 24° 17' E), Kuusamo Kiutakongas (Finland, 66° 22' N, 20° 19' E) and St. Petersburg (Russia, 59° 58' N, 30° 18' E) (Fig. 1). We determined the migration route and breeding zones of this population based on the distribution of ringing recoveries of Song Thrushes ringed at the Polish coast (Fig. 1) and literature on their distribution (Busse and Maksalon 1986, Milwright 2006). Using minimum and mean daily temperatures from these weather stations, we calculated the monthly means, which we used in further analysis. We also checked for correlations between these monthly mean temperatures at the weather stations on the migration route and between the stations at the breeding grounds (Fig. 1).

We assumed that Song Thrushes that migrate through the Baltic region in spring on their way back from wintering grounds cross areas southwest of the Baltic in March–April (Cramp 1988, Clement et al. 2000). We correlated the dates of spring migration at the Polish stations with the temperatures in March and April on the part of the species' spring migration route ca. 350 km southwest of the Polish Baltic coast. We also assumed that Song Thrushes breed and fledge in May–August (Cramp 1988, Clement et al. 2000). So we correlated the dates of their autumn migration through the Polish stations with the temperatures in May, June, July and August at the breeding grounds of this species (Fig. 1).

Most studies analysing changes in migration timing use a linear approach (e.g. Sokolov et al. 1998; Tøttrup et al. 2006a,

2006b; Marra et al. 2005, Miller-Rushing et al. 2008). We calculated long-term trends in migration dates of 5, 50 and 95% of the passage using quantile regression, as Tøttrup et al. (2006a, 2006b). Our preliminary analysis of Song Thrushes' migration timing along the Polish coast showed that migration dates varied widely from year to year, which made a linear approach unsuitable for some analyses of this dataset because the determination coefficients (R^2) of their linear regressions against the year were close to 0, and thus explained a small proportion of variation. To identify possible curved smoothed trends in the datasets, we thus used generalised additive models (GAM) (Hastie and Tibshirani 1990, Wood 2017a). We used the package “mgcv 1.8-22” (Wood 2017b) in R 3.3.2 (R Core Team 2016).

We checked the significance of any change by comparing the dates for the percentiles we analysed between the first and the last 10 years of the period using a permutation test with 1000 repetitions (Manly 2007) and an R script by Howell (2015) as in Remisiewicz et al. (2017). To correlate the migration dates with temperatures for the data series, we used Pearson's product-moment correlation (Zar 2010). For those variables where GAM indicated linear trends over the years, we used the slope coefficients β from the linear regressions to show the rate of the long-term changes. We compared the slope coefficients β at our station Hel with those at Rybachy using analysis of covariance (ANCOVA) in R (Crawley 2013). In our search for factors that cause the change in autumn migration timing, we used multiple regression with the dates of autumn passage as the response variable, and the year, the dates of spring passage and spring and autumn temperatures as explanatory variables. We chose the best model using

stepwise model selection by Akaike Information Criteria (AIC) in *R* package “MASS 7.3-49” (Venables & Ripley 2002). We calculated the variance inflation factor (VIF) using *R* package “car 2.1-6” (Fox and Weisberg 2011) to check how much the potential correlations between these variables might affect the results; VIF > 10 indicates high multicollinearity (Allison 1999).

Results

Temperatures on migration route and at breeding grounds

Mean and minimum daily temperatures were significantly correlated (see Suppl. Table S1 and S2) among the weather stations located on the migration route southwest of the Baltic (Fig. 1). Thus, we used the mean and minimum monthly mean temperatures averaged for the three stations as a proxy for the temperatures on route. The minimum April temperatures on route increased by 1.7 °C on average over the 40 years we analysed ($\beta = 0.042$; $p = 0.003$), and the mean temperatures increased by 3.0 °C ($\beta = 0.076$; $p < 0.0001$). Mean and minimum daily temperatures were also correlated (see Suppl. Table S3 and S4) among the weather stations at the breeding grounds (Fig. 1). However, temperatures at Saint Petersburg weather station were significantly higher, on average by 4.8 °C for the minimum daily temperature and by 3.3 °C for the mean daily temperature, than those at the other three stations. So we used the monthly mean temperatures averaged for the three cooler northwestern stations, as a proxy for conditions at the northwestern part of the Song Thrush breeding grounds, and the monthly means from Saint Petersburg as a proxy for conditions in the eastern part of the breeding grounds. The mean July temperatures at the three northwestern stations on average increased by 2.5 °C ($\beta = 0.062$; $p = 0.0002$), and the mean July temperatures in Saint Petersburg increased by 3.5 °C ($\beta = 0.076$; $p < 0.0001$) over the 40 years.

Timing of spring migration at Hel

The timing of Song Thrush spring migration at Hel in 1975–2014 showed no significant trends (Fig. 2).

The dates of spring migration were related with the temperatures on the migration route. The warmer the April on their migration route, the earlier were the dates of the median (50%) and the end (95%) of Song Thrushes' spring migration at Hel. These migration dates advanced by about 1 day per 1 °C increase in the April means of daily minimum and of daily mean temperatures (Table 1) on the Song Thrushes' route from the wintering grounds to the Polish Baltic coast (Table 1, Fig. 3).

Timing of autumn migration at Mierzeja Wiślana

The beginning (first 5% of year's migrants) of autumn migration at Mierzeja Wiślana advanced significantly during 1975–2014 (Fig. 4), by 5 days on average from 19 September in 1975–1984 to 14 September in 2005–2014 (permutation test: $p = 0.009$). The median (50% of year's migrants) dates of autumn migration advanced after 1999 (Fig. 4). The dates of the end of migration (95% of year's migrants) showed no significant trend (Fig. 4). Because the date when the first 5% of migrants advanced, but the 95% end of migration remained relatively constant, the average time span of the autumn passage of 90% of migrants, on average extended 5 days longer between the first 10 (1975–1984) and the last 10 (2005–2014) years of the study (permutation test: $p = 0.046$; Fig. 4).

The warmer the July at the Song Thrushes' breeding grounds, the earlier autumn migration of young birds began at the Baltic coast (Table 2). The dates of 5% of autumn migration at Mierzeja Wiślana advanced by about 1 day per 1 °C increase in the mean of July minimum daily temperatures at the breeding grounds (Fig. 5). Migration dates were not correlated with the mean daily temperatures (Table 2).

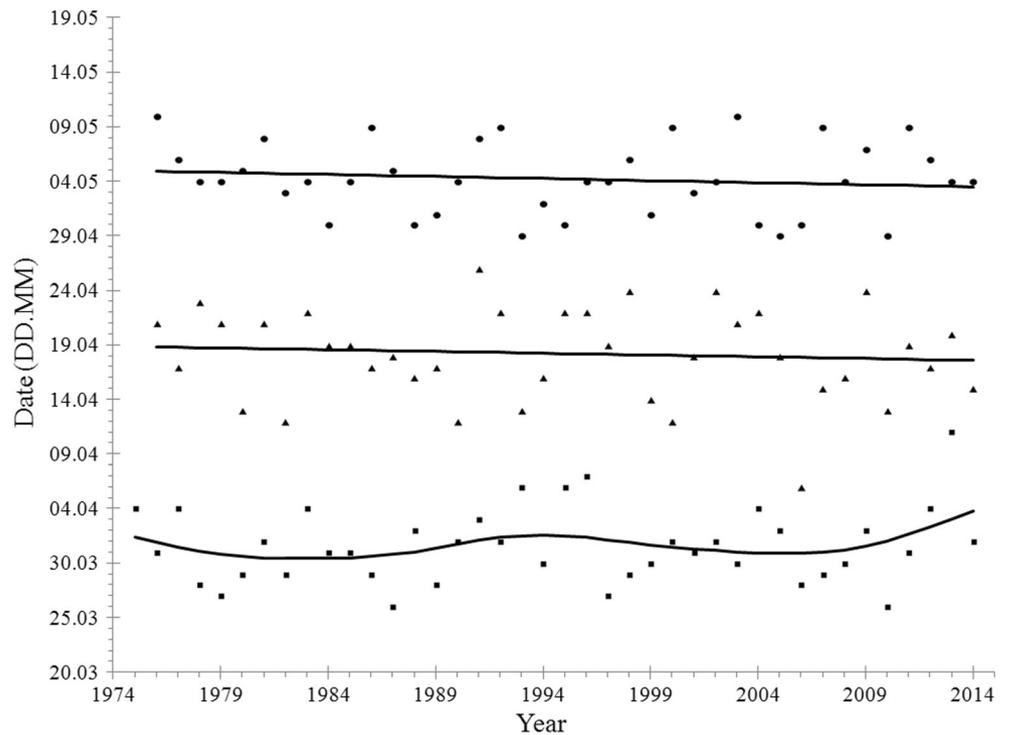
Comparison of migration through Polish and other Baltic stations

To compare our results with those from Christiansø, we fitted a linear regression to the dates of 5, 50 and 95% of the spring migration in 1976–1997 at Hel and in Rybachy (from Sinelschikova and Sokolov 2004). At both stations over that period, the tendency was the delay of 5 and 50% of passage, significant for 5% of passage at Hel (Table 3); the slopes did not differ between Hel and Rybachy (Table 3). The dates when 50% of the migrants had passed were positively correlated between these stations ($r = 0.394$, $p = 0.086$). The dates of the ends (95%) of passage tend to advance at both stations, although the trends were not significant.

Relationship between the timing of autumn and spring migration and spring and autumn temperatures

The warmer April on route and the warmer July at the north-west of the breeding grounds, the earlier was the median (50%) of the autumn passage of young Song Thrushes at Mierzeja Wiślana, after we controlled for the effect of the year (Table 4). The dates of median (50%) of spring migration had no significant effect on the dates of autumn migration (Table 4, full model). The combined effect of April temperatures on route and July temperatures at the breeding grounds explained 35% of variation in timing of the median of autumn passage at the Baltic coast (Table 4, best model). Low variance inflation

Fig. 2 Dates of the beginning (5%; squares), median (50%; triangles) and end (95%; circles) of spring migration of Song Thrushes at Hel and the multiyear trends of these dates by GAM (Wood 2017b). For all GAM significance of the effect of the year: $p > 0.4$



factors (VIF) indicated that multicollinearity had small effect on the results from these models.

Discussion

We found no long-term advance in the timing of Song Thrush spring migration, in contrast to a clear advance of its spring migration observed at the other ringing stations on the southern Baltic coast. However, spring migration dates of Song Thrush in subsequent years were correlated with spring temperatures on the migration route before they arrived at the Baltic coast. The beginning of autumn migration clearly advanced over the 40 years we studied and was correlated with the temperatures on spring migration route and summer temperatures at the breeding grounds. Neither pattern has been reported previously for this species. We explain these patterns

in the timing of spring and autumn migration in the context of the species’ breeding biology, the life stage that links both migrations.

Temperatures on route and multiyear trends in spring migration at the Baltic coast

Our results on the timing of Song Thrush spring migration were not consistent from those at other locations in the Baltic region (Tøttrup et al. 2006a, Sinelschikova and Sokolov 2004). At Christiansø, ca 250 km west of Hel, Song Thrush migration advanced in 1976–1997 for the first 5% of birds by 0.33 days a year ($\beta = -0.33$), 0.18 days for the first 50% and 0.33 days for the end of migration (Fig. 1, Tøttrup et al. 2006a). An advancement in 1957–2002 was reported for Song Thrushes migrating through Rybachy, ca 150 km east of Hel (Fig. 1, Sinelschikova and Sokolov

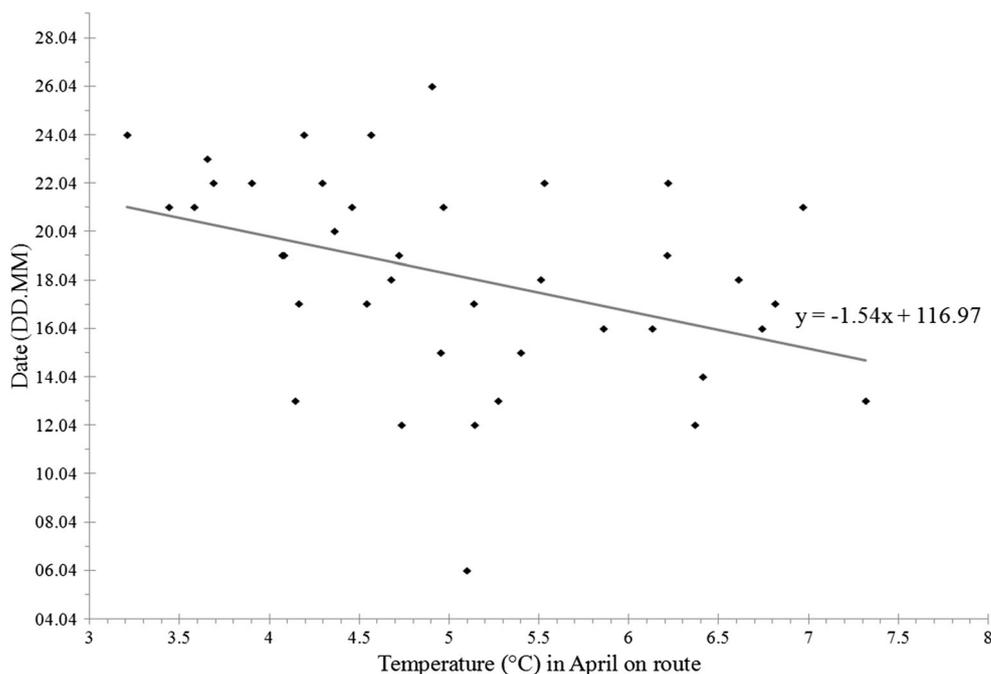
Table 1 Slope coefficients β from linear regressions of dates when 5, 50 and 95% of Song Thrushes migrated through Hel in spring in 1975–2014 with the April mean of minimum daily temperatures, and the April mean of mean daily temperatures averaged for the three weather stations

Temperatures	Start of passage (5%)		Median of passage (50%)		End of passage (95%)	
	β	R^2	β	R^2	β	R^2
April mean of minimum daily temperatures	0.497	0.001	-1.154*	0.132	-1.036*	0.087
April mean of mean daily temperatures	0.362	0.004	-1.146*	0.123	-0.896*	0.017

* $p < 0.05$

on the migration route. β indicates the rate of change in migration timing per 1 °C increase in April mean temperatures; R^2 indicate the proportion of the variance in migration dates explained by these temperatures

Fig. 3 Relationship between the dates of 50% of spring migration of Song Thrush at Hel and the mean minimum temperatures of April on route (grey line regression line, equation regression equation)



2004). However, during the same period as at Christiansø (1976–1997) the start (5%) of passage at Hel and Rybachy tended to delay (Table 3). This common delay and the correlated timing of 50% migration at Hel and Rybachy might be the effect of a synchronised passage of the same populations over a wider area, as reported for Robin *Erithacus rubecula* (Nowakowski et al. 2005). The inconsistency in trends between

Christiansø and the two more eastern stations might be caused by different proportions of birds returning from different wintering grounds or heading to different breeding grounds from these stations. Climate change might influence the migration timing of birds from different source areas with different intensity, considering that spring advanced more in the southwestern part of Europe than in the rest of continent (Menzel et al. 2006).

Fig. 4 Dates of the beginning (5% of year's birds; squares), median (50%; triangles) and end (95%; circles) of of Song Thrush autumn migration at Mierzeja Wiślana and the multiyear trends of these dates by GAM (Wood 2017b). Significance of the effects of the year: $**p = 0.0023$ and the trend explained 21.8% of deviance in data; $+p = 0.0827$ and the trend explained 20.6% of deviance. Grey arrows show the duration of migration during the first and the last 10 years of the studied period

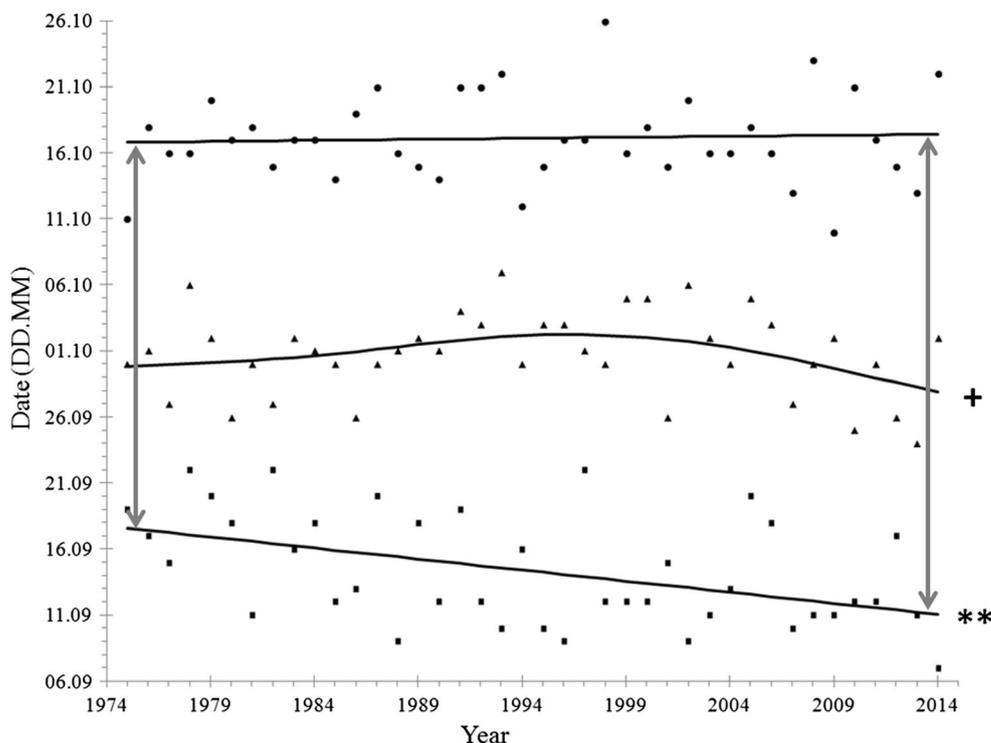


Table 2 Slope coefficients β from linear regressions of dates when 5, 50 and 95% of Song Thrushes migrated in autumn through Mierzeja Wiślana in 1975–2014 with the July mean of minimum daily temperatures at thebreeding grounds (Fig. 1). β indicates the rate of change in migration timing per 1 °C increase in July mean temperatures; R^2 indicate the proportion of the variance in migration dates explained by these temperatures

Temperatures	Start of passage (5%)		Median of passage (50%)		End of passage (95%)	
	β	R^2	β	R^2	β	R^2
July minimum daily temperature:						
NW of breeding grounds	-1.169*	0.112	-0.186	0.020	0.322	0.010
Saint Petersburg	-0.851*	0.092	-0.338	0.006	0.117	0.023
July mean daily temperature:						
NW of breeding grounds	-0.445	0.003	-0.239	0.015	0.087	0.025
Saint Petersburg	-0.544	0.037	-0.295	0.005	0.031	0.026

* $p < 0.05$

At Rybachy, the spring migration dates did not correlate with the local mean temperatures (Sinelschikova and Sokolov 2004). Our results showed that the temperatures in April on route influenced timing of 50 and 95% of the spring passage at Hel (Table 1), probably for ecological and physiological reasons. Song Thrushes feed mainly on small invertebrates, hunted on and drawn from the ground (Cramp 1988, Clement et al. 2000). Even short-term temperature decreases might halt these invertebrates' activity and impede the birds' foraging (Elkins 2004). Low temperatures also exact a higher energy cost for thermoregulation and require extra food to be collected to meet these demands (Elkins 2004). For individuals on migration, which already bear a large energy cost for extended flight, low temperatures might halt migration until

thermal and foraging conditions improve (Berthold 1996, Elkins 2004, Marra et al. 2005, Briedis et al. 2017). The correlation of Song Thrushes' spring migration timing at the Polish coast with temperatures on their route suggested that these birds were able to adjust the pace of their passage to the environmental conditions they encountered at stopover sites. This indicated that Song Thrush migration was regulated not only by endogenous factors, but also responded to exogenous conditions (Berthold 1996, Knudsen et al. 2011). Arriving at breeding grounds as early as possible in spring benefits individual birds, especially males (Rubolini et al. 2004, Rainio et al. 2007) competing for territories and partners (Kokko 1999). Thus, a quick response in migratory behavior to conditions on route would have an adaptive advantage by enabling early

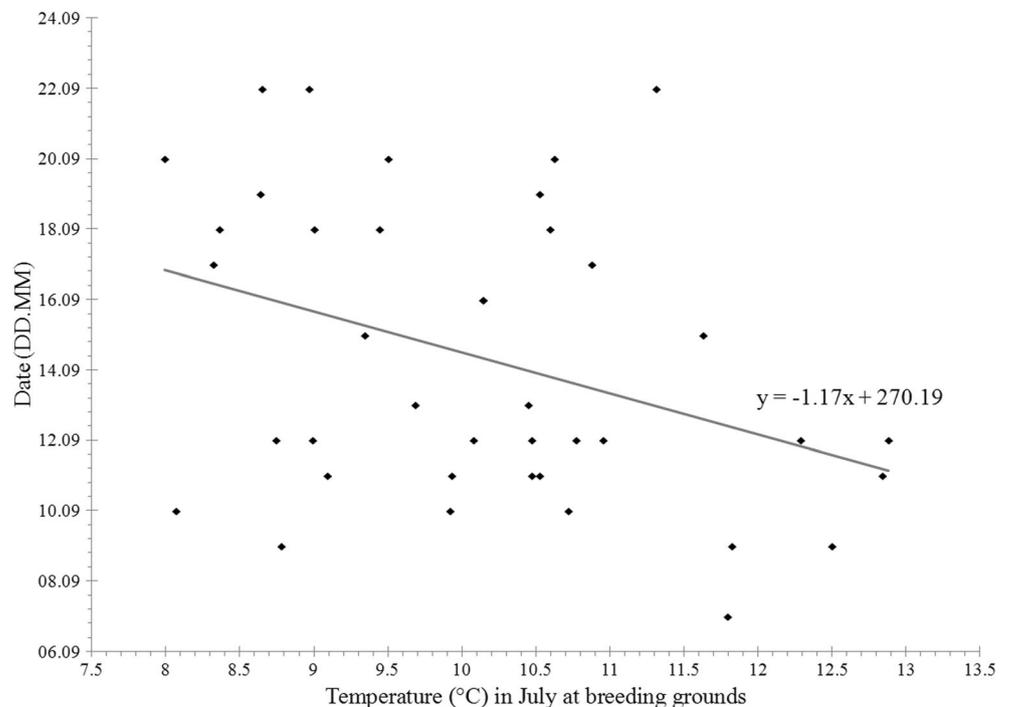
Fig. 5 Relationship between the dates of 5% of autumn migration of Song Thrush at Mierzeja Wiślana and mean minimum temperatures of July averaged for three weather stations northwest of the breeding grounds (grey line, regression line; equation, regression equation)

Table 3 Slope coefficients β from linear regressions of dates when 5, 50 and 95% of Song Thrushes migrated in spring through Hel and Rybachy in 1976–1997, against the year. p , comparison of the slope coefficients β by ANCOVA

Station	Start of passage (5%)		Median of passage (50%)		End of passage (95%)	
	β	p	β	p	β	p
Hel	0.249*	0.931	0.042	0.697	-0.106	0.969
Rybachy	0.268		-0.097		-0.117	

* $p < 0.05$

arrivers to benefit from an early and warm spring at the breeding grounds.

Multiyear trends in the dates of Song Thrush spring migration at Hel differed from trends reported for other passerines in the northern hemisphere. Spring migration has advanced in recent decades for many species at many European sites (Moritz 1993, Sokolov et al. 1998, Tryjanowski et al. 2002, Cotton 2003, Mitrus et al. 2005, Tøttrup et al. 2006a, Askeyev et al. 2007, Lehikoinen and Sparks 2010) and in North America (Marra et al. 2005, Miller-Rushing et al. 2008). In the Baltic region, an earlier spring migration was reported for ten species passing through the German island of Helgoland (Moritz 1993), 12 passerine species ringed at Rybachy (Fig. 1, Sokolov et al. 1998) and 25 species of passerines ringed at Christiansø (Fig. 1, Tøttrup et al. 2006a). The trends from linear regression might depend on the range of years being analysed (Sparks and Tryjanowski 2005), as we demonstrated for Rybachy and Hel. The pattern of change in migration timing might also be non-linear, as suggested by our trends for dates of 5% spring passage at Hel (Fig. 2) and for 50% of autumn passage at Mierzeja Wiślana (Fig. 3), and shown for

other species (Sparks and Tryjanowski 2005, 2007). Our results did not confirm an overall advancement in Song Thrush migration at Hel over the whole period of 1976–2014 and in 1976–1997. Besides the spring temperatures, other factors, e.g. changes in the population size (Gordo 2007), might contribute to year-to-year variation in spring migration timing, and probably obscured any long-term trends.

Temperatures on the breeding grounds and multiyear trends in autumn migration at the Baltic coast

The effects of climate on the timing of birds' autumn migration are less known than on spring migration (Lehikoinen and Sparks 2010). Birds' autumn migration might be delayed by climate warming that prolongs the breeding season (Dunn 2004, Lehikoinen and Sparks 2010 after Berthold 1998). However, at Mierzeja Wiślana, Song Thrushes' autumn migration advanced during the period we studied, as at Christiansø in 1976–1997 (Tøttrup et al. 2006b). The first-year birds, which we analysed, constituted on average 88% of all Song Thrushes ringed each autumn season (Operation Baltic, unpubl. data). This high proportion of immature birds is probably caused by a "coastal effect", i.e. young inexperienced birds concentrated along the coast, which they use as a landmark during migration (Ehnbom et al. 1993, Payevsky 1998). Because of this effect, first-year birds probably also dominated the Song Thrushes ringed at Christiansø, though they were not analysed by age (Tøttrup et al. 2006b). At Christiansø, the timing of 5, 50 and 95% of autumn migration advanced, but at Mierzeja Wiślana, only the beginning (5%) of migration advanced. The inconsistency between the stations in migration timing for the second half of autumn might reflect the varying influence of climate changes on the different breeding populations of Song Thrush. At Mierzeja

Table 4 Relationship between the dates of start (5%) of Song Thrushes autumn passage through Mierzeja Wiślana in 1975–2014 (dependent variable), and the year, the April mean of minimum daily temperatures on route, July mean of minimum daily temperatures at the northwest of

the breeding grounds (independent variables) and the dates of median (50%) of spring passage at Hel, by multiple regression. Estimate, coefficients from multiple regression; SE, standard error of the estimates; VIF, variance inflation factor

Factor	Estimate	SE	VIF
Best model ($F_{3,36} = 7.262$ $p < 0.001$, $R^2 = 0.351$)			
Intercept	277.407***	4.786	
April mean of minimum daily temperatures	-1.822**	0.518	1.017
July minimum daily temperature NW of breeding grounds	-0.974*	0.426	1.017
Full model ($F_{4,35} = 5.514$, $p = 0.0015$, $R^2 = 0.387$)			
Intercept	393.338**	124.907	
Year	-0.050	0.065	1.850
April mean of minimum daily temperatures	-1.874**	0.635	1.528
July minimum daily temperature NW of breeding grounds	-0.700	0.514	1.487
Date of median (50%) of spring passage at Hel	-0.164	0.143	1.200

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Wiślana, located further east than Christiansø (Fig. 1), birds that originated from the north-eastern part of the breeding range most likely formed a higher proportion of migrants (Busse and Maksalon 1986, Fransson and Hall-Karlsson 2008, Valkama et al. 2014).

The advanced beginning of autumn migration by first-year Song Thrushes over the 40 years might be caused by combined effect of climate warming in Europe in spring and autumn, as our results indicated. Warmer spring on route might enable adults to arrive at the breeding grounds and start breeding early. Warmer summers also enable their offspring to grow faster and to prepare for migration earlier (Elkins 2004). Such a domino effect has been described in other medium-distance migrants, such as Dunnock *Prunella modularis* and European Robin *Erithacus rubecula* (Crick and Sparks 1999). Climate change might influence autumn migration also in other ways. Warm breeding seasons generally enhance breeding productivity and the survival rate of nestlings (Lack 1972, Dunn 2004). Advanced beginning of autumn migration that we showed at Mierzeja Wiślana, with no change in the timing of the median and the end of migration, might be caused by the population of Song Thrushes migrating across the Baltic from northeastern Europe more often attempting second broods with spring and summers at the breeding grounds becoming earlier and warmer over the years. Song Thrushes from the northern part of the breeding range usually have one brood, but birds from southwestern Europe have up to three broods (Cramp 1988). With the species' potential for multi-brooding, second broods might occur at the north in years with an early and warm spring. Extra broods in the population breeding northeast of the Baltic might prolong autumn migration by the early passage of young from first broods that are ready to migrate earlier than those from later broods. Single broods, with breeding success enhanced by a warm summer, and additional broods, would both increase the numbers of young birds at the breeding grounds and thus cause more competition for food. This might induce young birds that hatched early to depart earlier, despite the extended period of favourable conditions at the breeding grounds as an effect of climate warming.

Conclusions

Short- and medium-distance migrants, such as Song Thrush, Blackbird *Turdus merula*, Goldcrest *Regulus regulus*, Redwing *Turdus iliacus*, European Robin and Dunnock, had been shown to advance spring migration more than long-distance migrants, such as Thrush Nightgale *Luscinia luscinia* and Willow Warbler *Phylloscopus trochilus* (Tøttrup et al. 2006a). Yet, our results showed no apparent advancement in Song Thrushes' spring migration, probably because of its high variation on the year-to-year basis, which made the long-term

trends unclear. The year-to-year response of Song Thrush migration timing to spring temperatures on route and to summer temperatures at the breeding grounds indicated high plasticity in the species. This plasticity might help the species to adapt well to climate changes, which include not only general warming but also more frequent weather anomalies (HUCE 2013). Increasing numbers of Song Thrushes in Poland (Chodkiewicz et al. 2016) and in Finland (Portal of Finnish bird ringing services and bird monitoring 2017) indicate that the species might indeed have benefitted from climate change in the Baltic region over the past few decades.

Acknowledgements We are grateful to Marc Burman for advice on statistical procedures. We are grateful to Joel Avni for valuable comments and editing. We are grateful to the Editor and three anonymous reviewers for helpful comments to the earlier version of the paper.

Funding information This paper was supported by the research grant from the National Research Foundation (NRF) in South Africa and the National Centre for Research and Development (NCBiR) in Poland, within the Poland-South Africa Agreement in Science and Technology (PL-RPA/BEW/01/2016). The field data used in this study was collected with the support of the grants from the Polish Ministry of Higher Education to the Bird Migration Research Station (SPUB).

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