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Sex-specific differences in spring migration timing of Song Thrush *Turdus philomelos* at the Baltic coast in relation to temperatures on the wintering grounds

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Abstract

Environmental factors influencing the timing of bird migration frequently affect age and sex groups differently. We applied discriminant functions to determine the sex of adult Song Thrushes ringed during spring migration in 1968–2019 at Hel on the Polish Baltic coast. We aimed to determine any differences between the sexes in the timing of spring migration and changes in protandry, and to identify any relationships between migration timing and temperatures at the wintering grounds. We analysed relationships between the date of migration and the year and monthly mean minimum temperatures in December–February by sex, using multiple quantile regression for q10, q50 and q90 of spring passage. On average males migrated six days before females. Spring protandry increased over 1968–2019 and with warm winters. The sexes responded differently to winter temperatures, likely because of the species' mating strategy. For males the warmer the winter, especially in February, the earlier spring migration began and the later it ended, prolonging its duration. The influence of February's temperature on the beginning of males' migration is likely explained by selective pressure for their early arrival to establish territories. The later end of their arrival with a warm winter might reflect more low-quality males surviving, and migrating later than high-quality males, than with cold winters. For females December and January temperatures had no effect on the beginning and the end of spring migration; but the warmer the February, the earlier migration started and the later it ended. Females probably benefitted from improved conditions in a warm February in two ways: early-arriving females maximized their breeding success with a chance to raise a second brood, and late-arriving females maximized their chances of surviving migration by prolonging fuelling and stopovers, which extended females' arrivals.

Keywords: *Sex-differential migration, spring passage, Song Thrush,* Turdus philomelos*, climate warming*

Introduction

Environmental factors influence the timing of bird migration (Berthold 1993; Newton 2008). Temperature or rainfall at the wintering grounds and on passage influence the timing of spring migration (e.g. Ahola et al. 2004; Norris et al. 2004; Marra et al. 2005; Tøttrup et al. 2010; Tryjanowski et al. 2013; Halupka & Halupka 2017; Lehikoinen et al. 2019), but these factors frequently affect a species' age and sex groups differently (Newton 2008). Age-specific differences in migration timing have been observed in many bird species (e.g. Woodrey & Chandler 1997; MacMynowski & Root 2007; Jarjour et al. 2017), as have sex-differential migration patterns (e.g. Morbey & Ydenberg 2001; Nam et al. 2011). Males of many passerines, especially short- and medium-distance migrants, tend to be less migratory than females: more males stay at the breeding grounds in winter, others migrate shorter distances and arrive earlier in spring (Francis & Cooke 1986; Kokko 1999; Morbey & Ydenberg 2001; Komar et al. 2005; Catry et al. 2006). Differences in the sexes' migration patterns might be related to each species' mating system and to the sexes' different roles in reproduction (Kokko et al. 2006; Payevsky 2009). Social monogamy is the most common mating strategy in passerines (Orians 1969; Johnson & Burley

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1998), and often requires the male to establish a territory and then attract a female by song or other displays (Gill 1995). Thus, males benefit by arriving early at the breeding grounds in spring when more optimum territories are available or by retaining a high-quality territory throughout the year if they do not migrate (Ketterson & Nolan 1983; Lozano et al. 1996; Kokko 1999; Morbey & Ydenberg 2001; Spottiswoode et al. 2006; Rainio et al. 2007). Females are less pressed to arrive early; therefore, they might migrate farther than the males to avoid low temperatures and the risk of food shortages (Kokko 1999; Rubolini et al. 2004; Catry et al. 2006; Jarjour et al. 2017). They can arrive at the breeding grounds later when the weather in spring is most optimal (Ketterson & Nolan 1983; Francis & Cooke 1986; Morbey & Ydenberg 2001; Kokko et al. 2006; Spottiswoode et al. 2006). Therefore, protandry, where the males of a species arrive on the breeding grounds earlier in spring than the females, occurs in many European passerines such as Pied Flycatcher *Ficedula hypoleuca* (Rubolini et al. 2004; Rainio et al. 2007; Harnos et al. 2015a), Blackcap *Sylvia atricapilla* (Rainio et al. 2007), Common Redstart *Phoenicurus phoenicurus* (Rubolini et al. 2004; Rainio et al. 2007), Northern Wheatear *Oenanthe oenanthe* (Maggini & Bairlein 2012) and Common Blackbird *Turdus merula* (Bakken et al. 2006). Age and sex groups might respond differently to environmental conditions (Newton 2008; Hedlund et al. 2015). For example, temperatures during spring migration influence the sexes differently, with a stronger effect on the migration timing of the sex that migrates earlier (Newton 2011; Jarjour et al. 2017). Older male passerines typically arrive at the breeding grounds earlier than all other sex and age groups (Francis & Cooke 1986; Lozano et al. 1996; Kokko 1999). Temperatures in spring have a weaker effect on inexperienced young males, which usually arrive at the breeding grounds later than their older cohorts (Lundberg & Alatalo 1992; Møller 2004; Spottiswoode et al. 2006; Rainio et al. 2007; Newton 2008). Most observations of sex-differential migration in passerines consider species with well-pronounced sexual dimorphism (Newton 2008). If migration timing differs between the sexes they might respond differently to temperature, so differences in arrival timing might be greater in warm springs than in cold springs when the population generally arrives later (Francis & Cooke 1986; Newton 2008). Thus, the sexes likely respond differently to climate warming, as do Willow Warblers *Phylloscopus trochilus*, whose males returned earlier to the island of Gotland, Sweden, in 1990–2012 than the females (Hedlund et al. 2015). The males migrate shorter distances than the females in nine species of small passerines wintering in Mexico (Komar et al. 2005), as do Greenfinch *Chloris chloris*, Goldcrest *Regulus regulus* and Chaffinch *Fringilla coelebs* in Europe (Fransson & Hall-Karlsson 2008). Reed Bunting *Emberiza shoeniclus* males migrate a shorter distance than females and return to the breeding grounds earlier (Fransson & Hall-Karlsson 2008). In monomorphic species, which are difficult to sex in the field, sex-differential migration has been reported for few species such as Chiffchaff *Phylloscopus collybita* (Catry et al. 2005; Csörgo & Harnos 2011), Willow Warbler (Hedlund et al. 2015), Little Stint *Calidris minuta* (Mazur et al. 2020) and Wood Sandpiper *Tringa glareola* (Remisiewicz & Wennerberg 2006). The most reliable method to distinguish males and females in monomorphic species is by DNA sexing (Dubiec & Zagalska-Neubauer 2006). With a sample of DNA-sexed individuals as a guide, researchers can later use classification methods such as Discriminant Function Analysis of morphometrics to distinguish males and females in a data set by a combination of morphological measurements (Tabachnick & Fidell 1996; Mazur et al. 2020). These functions can be applied to determine the sex of previously measured individuals and to allow further analysis of sex-differential migration if biometric datasets collected in a standardised manner over the entire migration season for many years are available.

The Song Thrush *Turdus philomelos* is a medium-sized passerine that is widespread across the entire Western Palearctic (Cramp 1988; Collar 2005). Song Thrushes that migrate in spring across the southern Baltic coast belong to the nominate subspecies *philomelos* and are medium-distance migrants returning from wintering quarters in the Iberian Peninsula, France and the Western Mediterranean to their breeding grounds in Scandinavia, Finland and northwestern Russia (Busse & Maksalon 1986; Milwright 2006; Redlisiak et al. 2018). In northern and central Europe this species' spring migration has shifted earlier over the past decades (Sinelschikova & Sokolov 2004; Tøttrup et al. 2006; Lehikoinen & Sparks 2010; Vengerov 2017), but this had not been confirmed for Song Thrush populations migrating across the Polish Baltic coast (Redlisiak et al. 2018). We found no published studies on any sex differences in the migration timing of the Song Thrush, probably because the species is difficult to sex in the field for it lacks any clear sexual dimorphism in plumage or size (Svensson 1992; Demongin 2016). However, discriminant functions we recently developed (Redlisiak et al. 2020) enable the sexing of Song Thrushes migrating across the southern Baltic coast by a combination of measurements. We applied these functions to our dataset from 1968 to 2019 to determine any sex differences in the timing of Song Thrush spring migration across the southern Baltic coast and to check if the protandry we expected showed any change over these years. We also aimed to identify any relationships between the timing of the sexes' spring migration and temperatures at their wintering grounds that would explain any changes we might reveal.

Materials and methods

We used morphometrics of Song Thrushes caught at the Hel ringing station (54°44′N, 18°34′E, Figure 1) as a part of the Operation Baltic research project (Nowakowski et al. 2012) during spring migration in 1968–2019. We assumed 26 March–15 May as the period of spring migration of the Song Thrush across the Baltic coast, as in Redlisiak et al. (2018). The birds were caught from dawn to dusk in 35–50 mist nets in a standardized manner each year in the same coastal habitat (Busse & Meer 2015; Redlisiak et al. 2018). The number of nets remained stable during each season, but changed between years. Our bird ringing was conducted with the authorization of the Polish Academy of Sciences and with the approval of the General Directorate for Environmental Protection, Poland (DZP-WG. 6401.03.97.2017.jro). Field research at Hel was approved by the Marine Office, Gdynia (1/BN-P/ 2017). We used measurements of wing length by the maximum chord method (Svensson 1992), and the distance between the tip of the first primary and the tip of the longest primary covert (P1-PC) (Eck et al. 2011; Demongin 2016). We analysed only the measurements of Song Thrushes aged by plumage as adults hatched two or more years before capture (Svensson 1992; Demongin 2016) because this was the only age group for which the discriminant functions were reliable (Redlisiak et al. 2020).

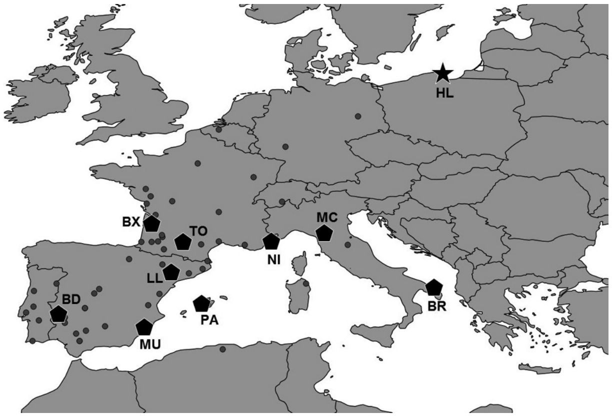

Figure 1. Locations of Hel ringing station, ring recoveries and weather stations used in the study. HL – Hel. Weather stations: BD – Badajoz/Talavera la Real (38°53′N, 6°50′W), MU – Murcia (38°00′N, 1°10′W), BX – Bordeaux-Merignac (44°50′N, 0° 41′W), LL – Lleida (41°38′N, 0°36′E), TO – Toulouse-Blagnac (43°37′N, 1°23′E), PA – Palma de Mallorca CMT (39°33′N, 2° 38′E), NI – Nice (43°39′N, 7°13′E), MC – Monte Cimone (44° 12′N, 10°42′E), BR – Brindisi (40°38′N, 17°56′E), and the distribution of ring recoveries (dark grey circles) of Song Thrushes ringed at Hel and recovered elsewhere in December–February 1960–2018.

For adults whose wing length and P1–PC we had measured we applied the following discriminant function, after Redlisiak et al. (2020):

$$\mathbf{D_1 = 35.828 + 0.423 * P1 - PC - 0.256 * Wing}$$

If $D_1 < 0.1675$ the bird was classified as a male and if $D_1 > 0.1675$ as a female (Redlisiak et al. 2020). In 1972–1973 and 1992–2010 the P1–PC was not measured in any birds, thus for these years we were not able to sex any Song Thrushes using this discriminant function and we had no alternative function with the required accuracy for reliable sexing (Redlisiak et al. 2020). Thus, we used data on the sexed birds from 31 springs during 1968–2019 (Suppl. Table S1), but only after we confirmed that neither wing length nor P1–PC showed any significant changes during this period (Suppl. Figures S1 and S2). For the sexed birds in analyses, we used the Julian dates when they were ringed.

To determine any relationship between the spring migration timing of male and female Song Thrushes and weather at their wintering grounds we used the minimum daily temperatures provided by the Royal Netherlands Meteorological Institute (European Climate Assessment and Dataset 2018) for nine weather stations at the wintering grounds (Figure 1). We determined the wintering grounds of the populations of Song Thrushes that migrate across the Polish Baltic coast (Busse & Maksalon 1986; Milwright 2006) from literature and from the distribution of ringing recoveries of Song Thrushes ringed at Hel and recovered while wintering (December–February) (Figure 1). We used the minimum daily temperatures because Redlisiak et al. (2018) showed that those temperatures were related to the spring migration timing of the Song Thrush, but mean daily temperatures were not.

From the daily data collected at each weather station, we calculated a monthly mean of minimum temperatures at the wintering grounds for each of the three winter months in each year between 1968 and 2019.

We checked if these mean minimum temperatures were correlated across the three winter months in the 31 years we analysed using Pearson's correlation, then checked for any multi-year trends in these temperatures over 1968–2019 using least square linear regression (Zar 2010). Then, we analysed the relationships between these monthly mean temperatures in the months preceding the spring migration and the timing of the Song Thrushes' passage across the Baltic coast by using the migration dates of all the 1154 sexed Song Thrushes caught in 31 springs during 1968–2019 (Table S1). The distributions of migration dates for each sex departed from normal and we considered if different fractions of the population might be affected by winter temperatures in different ways, so we used quantile regression to investigate any relationships (Koenker & Bassett 1978; Cade & Noon 2003; Koenker 2004). We applied quantile regression to 10th (q10), 50th (q50) and 90th (q90) quantiles (Cade & Noon 2003) of the spring migration dates (further in the text called "start date", "middle or mid" and "end date", respectively) to estimate any relationships of these parts of spring passage in each sex with winter temperatures. We used multiple quantile regression with the Julian date of migration (Day, 1 January = Day 1) as the response variable, the sex (Sex) as the categorical factor, the year (Year as the year number, 1968 = year 1) and the monthly means of minimum temperatures of December (TDec), January (TJan) and February (TFeb) as continuous factors with four interactions between the sex and each remaining factor as explanatory variables to estimate any relationships between these temperatures and the timing of the spring passage of male and female Song Thrushes. We retained the year in our models and used it as a continuous fixed explanatory variable, rather than a random factor (Dytham 2011). We kept the sequence of years because some temperatures showed multi-year trends and we aimed to control for the effect of the year while estimating the effects of the temperatures (Frost 2019). We included interactions between Sex and Year to check for any differences between the sexes in their multi-year trends of migration timing, and between Sex and each monthly temperature to check for any differences between the sexes in relationships between their migration timing and these temperatures. To present any sexual differences revealed in response patterns to winter temperatures and the year, we show quantile regressions of migration timing for each sex against these variables separately. We considered the differences in the slopes of regression lines for q10, q50 and q90 as proxies for the degree of protandry. The statistical analyses were conducted in R 4.0.3 (R Core Team 2020), and we used the package "lqmm 1.5.5" (Geraci 2014, 2019) to perform the quantile regression.

Results

Temperatures at wintering grounds

Temperatures from the weather stations at the Song Thrush wintering grounds (Figure 1) were strongly positively correlated (Suppl. Tables S2–S4), so we used temperatures averaged for the nine stations in each month as a proxy for the temperature on the wintering grounds in December, January and February, as in Redlisiak et al. (2018). Over the 31 years, we analysed the temperatures were not significantly correlated between these three months and their correlations with the year were $|r| < 0.41$ (Table S5), thus multicollinearity caused little if any bias to our results (Dormann et al. 2013). December and January means of minimum temperatures on the wintering grounds increased by nearly 2°C over 1968–2019, but February temperatures showed no significant trend over the years (Figure S1).

Sex differences in multi-year trends in the timing of spring migration

We sexed 1154 adult Song Thrushes (499 males, 655 females) captured during 31 springs in 1968–2019 (Figure 2, Table S1). The median dates of migration were on average six days earlier for males (13 Apr) than for females (19 Apr) (Mann-Whitney U-test: $Z = 6.80$, $p < 0.0001$).

According to the full models by quantile regression (Table I), the interactions between Sex and Year, and between Sex and December and February temperatures were significant for the start (q10), middle (q50) and the end (q90) of Song Thrush passage. For each of these quantiles the males migrated earlier than the females, as indicated by the negative coefficient for the Sex factor, but the effect of Sex alone was not significant (Table I). The best models (Tables I, Tables II) selected by AIC (Tables S6–S8) confirmed that these three interactions were significant, which indicated that males and females differed in the relationship of their migration date against the year, and against the December and February temperatures (Tables I, Tables II).

According to the best models, the start, middle and end dates of spring migration for both sexes combined shifted earlier by 0.15 to 0.27 days

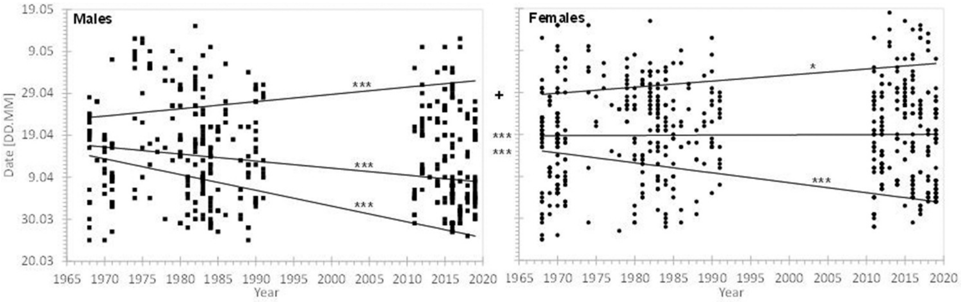

Figure 2. Spring migration dates of Song Thrushes by sex against year at Hel, N Poland, in 31 springs between 1968 and 2019, and linear trends by quantile regression. Bottom lines – q10, middle lines – q50, top lines – q90. Symbols between left and right figures indicate significant differences in the slopes of regression lines between males and females from the models with interaction between Sex and Year, symbols above each line indicate statistical significance of the trend from models for each sex separately (Tables III, S9). *** – p < 0.001, ** – p < 0.01, * – p < 0.05, + – 0.05 < p < 0.1.

Table I. Full models of the relationships between the migration timing of adult male and female Song Thrushes at Hel, N Poland, in 31 springs between 1968 and 2019 with the year and the mean minimum daily temperatures in winter months at the wintering grounds, by quantile regression. TDec – mean temperatures in December, TJan – in January, TFeb – in February, q10 – 10th quantile, q50 – 50th quantile, q90 – 90th quantile. The temperatures for each winter month were averaged for nine weather stations (Figure 1). The 31 springs we analysed are shown at Figure 2 and listed in Suppl. Table S1. Estimate – coefficients (ß) from quantile regression, SE – standard error of the estimates, *P* – significance of each estimate, p < 0.05 marked in bold face, 0.05 < p < 0.1 marked in *italics*.

Quantile	q10			q50			q90		
Factors	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
	Full model			Full model			Full model = Best model		
Intercept	107.72	2.02	<0.0001	108.10	2.00	<0.0001	108.90	2.22	<0.0001
Sex	−2.04	2.61	0.4380	−1.88	2.61	0.4755	−1.51	2.81	0.5927
Year	−0.19	0.07	0.0076	−0.27	0.04	<0.0001	−0.15	0.06	0.0092
TDec	1.37	0.45	0.0036	2.08	0.41	<0.0001	2.47	0.45	<0.0001
TJan	−1.20	0.42	0.0064	−0.37	0.40	0.3623	0.72	0.42	*0.0919*
TFeb	−2.10	0.42	<0.0001	−0.80	0.38	0.0434	0.36	0.36	0.3213
Sex:Year	0.16	0.05	0.0009	0.18	0.05	0.0012	0.14	0.06	0.0303
Sex:TDec	−1.25	0.50	0.0167	*−0.93*	*0.51*	*0.0744*	−1.40	0.52	0.0090
Sex:TJan	−0.37	0.62	0.5497	−0.08	0.63	0.8992	0.38	0.52	0.4732
Sex:TFeb	1.01	0.45	0.0281	1.63	0.45	0.0007	1.52	0.52	0.0054

per year on average, thus 8 to 14 days over 1968–2019 (Tables I, Tables II). But in the males alone the start of migration shifted earlier by 19 days and in the females by 12 days, thus the degree of protandry increased on average by 7 days over these 52 years (Figure 2, Tables III, S9). The middle of migration also shifted earlier in males, by 9 days over 1968–2019 on average, but did not change in females. This difference between the sexes was significant, thus the protandry in q50 also increased (Figure 2, Tables III, S9). The end of migration shifted later, in males by 9 days and in females by 8 days over the 52 years. This difference between the sexes was not significant, thus protandry remained in q90 but decreased slightly (Figure 2, Tables III, S9). Because the start of migration shifted earlier and the end of migration shifted later the average migration period became prolonged over 1968–2019 in both sexes, by 28 days in males and by 20 days in the females (Figure 2, Tables III, S9).

Sex differences in spring migration timing in response to temperatures at wintering grounds

The timing of Song Thrushes' spring migration was related to temperatures of each winter month in a different way (Tables I, Tables II). The start and the middle of passage shifted earlier with higher December and January temperatures, but later with higher February temperatures (Table II). The end of migration shifted later with higher temperatures in all winter months, with the effect of December temperatures being the strongest (Table I). The sexes responded

Table II. The best models of the relationships between the migration timing of adult male and female Song Thrushes at Hel, N Poland, in 31 springs between 1968 and 2019 with the year and the mean minimum daily temperatures in winter months at the wintering grounds, by the quantile regression, for the 10th quantile (q10) and the 50th quantile (q50). For the 90th quantile (q90) the best model = full model presented in Table I. Model selection by AIC is shown in Tables S6–S8. Symbols as in Table I.

Factors	Estimate	SE	P
Quantile	q10		
Intercept	106.64	1.36	<0.0001
Year	−0.15	0.05	0.0067
TDec	1.33	0.42	0.0028
TJan	−1.35	0.27	<0.0001
TFeb	−2.01	0.40	<0.0001
Sex:Year	0.13	0.05	0.0173
Sex:TDec	−1.36	0.55	0.0182
Sex:TFeb	*0.60*	*0.33*	*0.0768*
Quantile	q50		
Intercept	108.10	1.84	<0.0001
Sex	−1.89	2.42	0.4381
Year	−0.27	0.04	<0.0001
TDec	2.13	0.45	<0.0001
TJan	−0.43	0.27	0.1238
TFeb	−0.80	0.39	0.0474
Sex:Year	0.17	0.06	0.0092
Sex:TDec	−0.91	0.61	0.1393
Sex:TFeb	1.61	0.50	0.0025

differently in their migration timing to the temperatures in December and February, as indicated by the significant interactions between Sex and these variables (Tables I, Tables II, Figure 3). The relationship of migration timing and January temperatures were significant, but did not differ between the sexes for any of the quantiles (Tables I, Tables II).

The sexes differed in their responses to the mean minimum temperatures of each winter month (Figure 3, Tables III, S10–S12). In both sexes the temperature in February had the strongest effect on the beginning of migration, but only in the females on the end of migration. December temperatures had the strongest effect of any of the three months for the end of migration in the males. Thus, males' migration was prolonged the most with a warm February and December. In the females migration was most prolonged by a warm February, but responded less to a warm December or January. A warm December prolonged migration in the males by 3.3 days per 1°C increase, about four times more than for the females. A warm January and February prolonged migration by 1–2 days per 1°C more for the males than for the females.

The sexes differed in the pattern of their responses in each quantile of migration to the mean minimum temperatures of each winter month (Figure 3, Tables III, S10–S12). For males migration on average started 1.3–2.5 days earlier per 1°C increase in temperature of each winter month, with the strongest response to temperatures in February. The dates of mid-migration for males shifted earlier by 1.6 days per 1°C increase in January temperatures, but were not related to temperatures in December and February. The end of migration for males was on average 1.0—2.0 days later per 1°C increase in temperatures of each month, with the strongest response to December temperatures. Because the beginning of migration advanced and the end was delayed the duration of the males' spring passage was extended by 2.8—3.5 days per 1°C increase in temperatures of each month, with the greatest change in response to February temperatures. Contrary to the males' pattern, for females the beginning of spring migration was not related to temperatures in December and January, and the shift to an earlier passage with higher February temperatures was significantly smaller than in males. In contrast to the males, the females' mid-migration shifted later by 0.9–1.1 day per 1°C increase in December and February temperatures, but was not related to temperatures in January. In females, the end of migration was on average 0.9–1.0 day later per 1°C increase in January and February temperatures, similarly as in males, which was indicated by parallel regression lines and no significant interactions (Figure 3, Tables III, S10–S12). The end of the females' migration was also delayed with an increase in December temperatures, but this shift was smaller than in the males, as indicated by significant interaction and the different slopes of the regression lines for each sex (Figure 3, Tables III, S10–S12).

The degree of protandry at the start (q10) and in the middle (q50) of migration, indicated by steeper negative slopes of regression lines for the males than for the females (Figure 3), and the positive interactions between Sex and monthly temperatures (Tables III, S10–S12), extended with an increase in temperatures of each winter month. The protandry at the beginning of migration increased by 1.1–1.5 day per 1°C increase in temperature of each winter month. Though the start of males' migration responded the most to a warm February on the wintering grounds, protandry increased the most with an increase in January temperatures, because q10 shifted earlier in the males but not in the females. The protandry in the middle of migration extended with an increase in the temperatures of all winter months, but responded the most to a warm February. The end of migration (q90) shifted later in both sexes, but significantly more in females than in males, thus the protandry at the end of

Table III. The rate of change in migration timing of adult male and female Song Thrushes at Hel, N Poland, in 31 springs between 1968 and 2019 in relation to the year and to temperatures of three winter months, by the quantile regression. The 31 springs we analysed are shown in Figure 2 and listed in Table S1. q10 – 10th quantile, q50 – 50th quantile, q90 – 90th quantile. ß – coefficients from quantile regression, according to the models with sex and one other factor and their interaction (Tables S9–S12), presented in Figures 2 and 3; ß * 52 years – estimated change of timing in days over 1968–2019, negative values reflect advance of migration. Protandry – the interaction between the sex and each factor, which indicates the difference in the slopes of regression lines for each sex; a positive interaction indicates a greater shift to earlier migration in the males than in the females. Change in duration of migration was calculated as the combined shift of q90 and q10. $p < 0.05$ marked in bold face, $0.05 < p < 0.1$ marked in *italics*.

	Change (days) per year or 1°C (ß)			52 years * ß (days)		
Factor	Males	Females	Protandry	Males	Females	Protandry
q10						
Year	−0.38	−0.24	0.14	−19.52	−12.32	7.20
TDec	−1.29	−0.23	1.06			
TJan	−1.62	−0.10	1.52			
TFeb	−2.51	−1.24	1.27			
q50						
Year	−0.17	0.01	0.17	−8.72	0.35	9.07
TDec	0.03	*0.93*	0.89			
TJan	−1.58	−0.36	1.22			
TFeb	−0.70	1.07	1.77			
q90						
Year	0.17	0.14	−0.03	8.92	7.51	−1.41
TDec	1.99	*0.50*	−1.49			
TJan	1.21	*0.89*	−0.32			
TFeb	0.96	1.05	0.09			
Duration of migration						
Year	0.55	0.38	0.17	28.44	19.83	8.61
TDec	3.28	0.73	2.55			
TJan	2.84	1.00	1.84			
TFeb	3.46	2.29	1.18			

migration remained, but decreased, especially with a warm December (Figure 3, Tables III, S10–S12).

Discussion

The first novel outcome of our study is the evidence of spring protandry in the Song Thrush, and of the increase in that protandry over 1968–2019 with warmer winters at the wintering grounds. Secondly, we revealed that the sexes responded differently to winter temperatures. The warmer the December and January at the wintering grounds, the earlier the males began their migration and the later they ended it, so prolonging their passage; the females responded weakly to temperatures in these months. The warmer the February at the wintering grounds, the earlier both sexes started migration and the later they ended it, but migration was most prolonged for the males, the middle of migration shifted earlier in the males but later in the females, increasing protandry. We discuss these sexual differences in responses to winter temperatures in the context of mating strategies and different sexual selection pressures on the males and the females in spring.

Protandry in spring migration of Song Thrush

Spring protandry has been described in many passerines, such as Pied Flycatcher (Rubolini et al. 2004; Rainio et al. 2007; Harnos et al. 2015a, 2015b), Blackcap (Rainio et al. 2007), Common Redstart (Rubolini et al. 2004; Rainio et al. 2007), Red-backed Shrike *Lanius collurio* (Rainio et al. 2007), Eastern Great Reed Warbler *Acrocephalus orientalis* (Nisbet & Medway 1972), Common Blackbird (Bakken et al. 2006), Chiffchaff (Catry et al. 2005; Csörgo & Harnos 2011) and Willow Warbler (Hedlund et al. 2015). Our results provide the first evidence of protandry in Song Thrushes during their spring migration, which could have been suspected but had not been proven, most likely because the species is difficult to sex.

The earlier arrival of males than females is a result of social monogamy, the most common mating system in

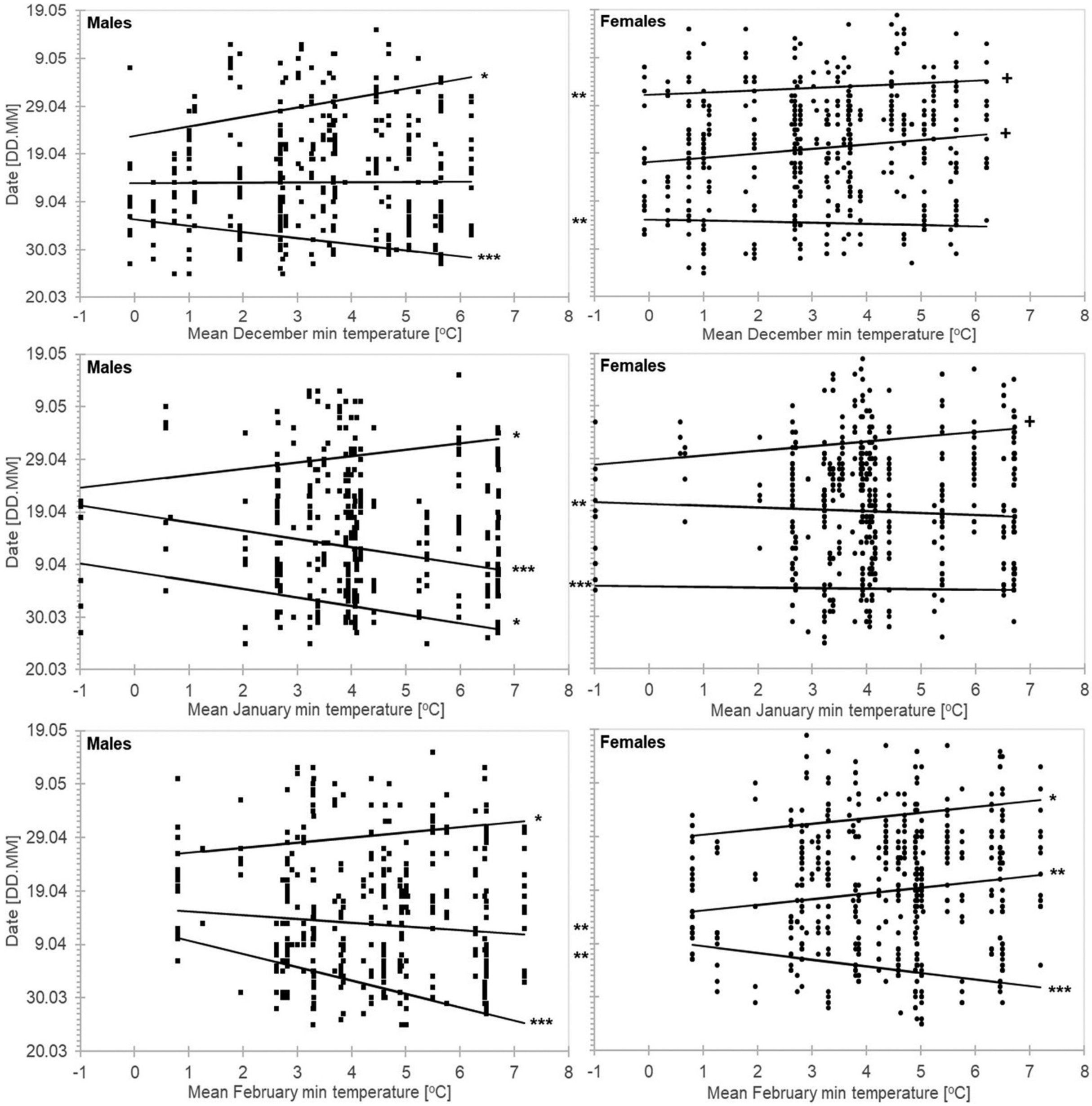

Figure 3. Spring migration dates of Song Thrushes at Hel, N Poland, by sex against the monthly means of minimum temperatures in December, January and February at the wintering grounds in 31 seasons between 1968 and 2019. Bottom lines – q10, middle lines – q50, top lines – q90. Symbols between left and right figures indicate significant differences in the slopes of regression lines between males and females from the models with interaction between Sex and temperature of each month, symbols above each line indicate statistical significance of the trend from the models for each sex separately (Tables III, S10–S12). *** – p < 0.001, ** – p < 0.01, * – p < 0.05, + – 0.05 < p < 0.1.

passerines (Kokko 1999; Payevsky 2009). Males establish territories at the breeding grounds that they defend against competing males and to which they attract females by displays (Kokko 1999; Morbey & Ydenberg 2001; Møller 2004; Rubolini et al. 2004; Newton 2008). They sing to attract females and then form monogamous pairs (Cramp 1988; Clement et al. 2000). Thus, males arriving early benefit by taking the best territories, which increases their chances of finding a mate (Morbey & Ydenberg 2001; Møller 2004; Spottiswoode et al. 2006) and even of having a second clutch if the weather allows (Najmanová & Adamík 2009). These strategies maximize their reproductive success (Cramp 1988). However, early spring migration and early arrival at the breeding grounds does involve risk, because food might be less abundant than later in the season and sudden cold spells might kill or starve males that arrive too soon (Morbey & Ydenberg 2001; Møller 2004; Spottiswoode et al. 2006).

Our results show that the degree of protandry in migrating adult Song Thrushes varied in relation to temperatures at the wintering grounds: in years with a cold December and February the males migrated as late as the females, but after warm winters the males migrated ahead of the females (Figure 3). This shows greater flexibility in migration timing for the males than for the females, which affects the degree of protandry in the Song Thrush that increased with warm winters (Figure 3, Table III). A warm February advanced mid-migration for males, but delayed it for females (Figure 3), which suggests that each sex takes advantage differently of a warm end to winter, with the bulk of males arriving early and some females delaying their migration, which we discuss later. The response of both sexes to year-to-year changes in February temperatures cannot explain any multi-year trends in migration timing (Figure 2) because temperatures for this month showed no trend over the years (Figure S3). However, the increase of December and January temperatures on the wintering grounds over 1968–2019 (Figure S3), and the relationships between these temperatures and the migration timing of both sexes (Figure 3, Table III), likely partly explain the multi-year increase in protandry in the Song Thrush (Figure 2, Table III). A multi-year increase in protandry has been shown for a few European passerines, e.g. Barn Swallow *Hirundo rustica* (Møller 2004), Chiffchaff (Csörgo & Harnos 2011) and Pied Flycatcher (Harnos et al. 2015a), but not confirmed in other species, though it was suggested by a greater advance in the arrival of males than females (Spottiswoode et al. 2006; Rainio et al. 2007; Tøttrup & Thorup 2008; Hedlund et al. 2015). To enable comparisons, we present the change in spring migration timing for male and female Song Thrush over the years and with winter temperatures using similar methods to these studies, i.e. trends by least square regression for selected percentiles (10%, 50%, 90%) of migration in sequential years (Figures S4–S6, Table S13). We provide clear evidence of the multi-year increase in protandry in the Song Thrush because we analysed the change over 52 years (Figure 2), a much longer time-series than in the other studies. The increase in spring protandry in Barn Swallow, Chiffchaff and Pied Flycatcher were linked to an increase of local spring temperatures on the birds' arrival at their breeding grounds (Møller 2004; Csörgo & Harnos 2011; Harnos et al. 2015a). We explained the spring protandry of Song Thrush with milder winters at its wintering grounds as an effect of climate warming, though local spring temperatures likely do contribute to the pattern.

Influence of temperatures at wintering grounds on migration timing of males and females

Temperature is one of many environmental factors that influence the migration timing of birds (e.g. Huin & Sparks 2000; Ahola et al. 2004). The timing of spring migration might be related to temperatures before the birds' depart from the wintering grounds and on their passage, especially in short- and medium-distance migrants (e.g. Ahola et al. 2004; Gordo & José Sanz 2008; Balbontin et al. 2009; Tøttrup et al. 2010; Robson & Barriocanal 2011; Briedis et al. 2017). Environmental conditions such as temperature before and during migration might influence each sex differently if the males and the females differ in migration timing (Møller 2004; Rainio et al. 2007). Spring migration in response to climate warming tends to advance more in species where sexual selection is based on female choice, as in Song Thrush, than in species with other mating strategies (Spottiswoode et al. 2006). We found no literature evidence of any sex-specific influence of the conditions at the wintering grounds on Song Thrush migration timing, probably because the species lacks sexually dimorphic characters. In Blackbird, the only species of the genus Turdus with clear sexual dimorphism, some adult males, which dominate adult females, forgo migration altogether with favourable conditions at the breeding grounds, an extreme shift in migration timing; the females, however, still migrate (Lundberg 1985). Though a general advance in the spring migration timing of Song Thrush over the past few decades has been reported from other locations in Europe (Forchhammer et al. 2002; Hüppop & Hüppop 2003; Lehikoinen & Sparks 2010) and in the Baltic region (Sinelschikova & Sokolov 2004; Tøttrup et al. 2006), we found no similar tendency at Hel, probably because of a different population mixture and the more recent period we analysed than those covered in other studies (Redlisiak et al. 2018). Spring migration dates of male and female Song Thrushes at the Polish coast were related to temperatures at the wintering grounds, mostly at the beginning of winter in December and just before they depart these areas in February (Scebba et al. 2014; Muscianese et al. 2018). The relationship of the duration and the end of males' migration to December temperatures is likely explained as an effect of winter temperatures on the survival of males (Newton 1998; Elkins 2004; Salewski et al. 2013; Pearce-Higgins & Green 2014). Lower-quality males are less likely to establish territories that will sustain them through a cold winter, but in a warm December would be more likely to find suitable winter territories. Additionally, in warm winters birds expend less energy on thermoregulation than in cold winters, improving survival rates (Alerstam & Högstedt 1982; Santangeli & Lehikoinen 2017). Low-quality males forage less efficiently and require more time to accumulate a fuel supply sufficient to depart the wintering grounds. They also need more time to refuel at stopover sites than top-quality males (Caldow et al. 2002). In a spring following a warm winter higher quality males are able to migrate early, but lower-quality males usually migrate later, hence the prolonged migration and the delayed end to the Song Thrush males' passage across the Baltic coast (Figure 3, Table III). In contrast, December temperatures weakly affected the females' migration, but the small delays in the middle and the end of their migration with warm Decembers (Figure 3, Table III) might be explained by better survival and later migration of lower-quality females, as for the males.

For short- and medium-distance migrants conditions at the wintering grounds before departure might suggest the conditions they will encounter on passage and at the breeding grounds (Ahola et al. 2004). Environmental conditions likely fine tune the timing of the migrants' departure, generally controlled by the changing day length in spring (Berthold 1996; Newton 2008). Conditions at the wintering grounds largely determine the birds' condition and thus the timing of their departure as well as the number and the duration of stopovers on their return passage, and hence the speed of their migration (Katti & Price 1999; Marra et al. 2005). Both sexes would generally accumulate greater fuel deposits in a warm February at the wintering grounds, enabling them to migrate faster than in years with a cold February. This would explain the relationship of an earlier start to the migration of both sexes with February temperatures (Figure 3, Table III). The influence of temperature on the start and the middle of the males' migration is likely explained by the selective pressure for early arrival and the benefits of establishing a territory as early as possible (Møller 1994; Kokko 1999). The effect of a warmer February on the migration timing of females is more complex. The breeding season of many passerines, which tend to multibrood, has lengthened in the northern hemisphere over recent decades in response to climate warming (Najmanová & Adamík 2009; Halupka & Halupka 2017). The Song Thrush's breeding season in central and eastern Europe has also been prolonged over the past decades because of an earlier start to breeding, enabled by early arrivals, and a delay in the median and end dates of breeding because of more second broods in warm springs (Najmanová & Adamík 2009; Vengerov 2017). The reproductive success of Song Thrushes has also increased in relation to warmer springs by larger clutches and more synchronous breeding, which reduce predation pressure (Vengerov 2017). Females would therefore also benefit from departing for the breeding grounds earlier in a warm spring, which would improve their chances of mating with a male holding a good territory and the chances of raising a second brood (Vengerov 2017). Both these benefits would increase the females' overall reproductive success (Møller 1994; Kokko 1999; Newton 2008). This would explain the effect of February temperatures on the beginning of female migration that we determined (Figure 3, Table III). It seems that a warm February at the wintering grounds also delays the departure of a part of females' cohort or that they then migrate slower than the males, considering the delayed middle and end of females' passage that we found (Figure 3, Table III). We suggest that females use the improved conditions of a warm February at the wintering grounds and on migration to prolong the period of pre-migratory fuelling before migration or to use longer or more frequent stopovers that improve their chances of survival during migration. Because of that pattern, the average duration of females' migration has increased with climate change and their migration speed has probably decreased. Delayed arrival at the breeding grounds as an effect of extended stopovers during drought on migration routes in Africa was reported in Red-backed Shrike and Thrush Nightingale *Luscinia luscinia* (Tøttrup et al. 2012). Differences in migration speed and fuelling rates between the sexes, promoting protandry, were revealed in the *leucorhoa* subspecies of the Northern Wheatear (Schmaljohann et al. 2016). We suggest that the female Song Thrushes we studied adjust to conditions at stopovers, as in those studies, and slow their passage to take advantage of good conditions. Both prolonged pre-migratory fuelling and more frequent or longer stopovers during a warm February would allow female Song Thrushes to accumulate larger energy reserves for producing their eggs. Larger reserves would improve their chances in case of a food shortage on arriving at the breeding grounds. The relationships we have shown (Figure 3, Table III), alongside literature data, suggest that mild winters in southwestern Europe extend protandry and prolong the breeding period of the Song Thrush, allowing a higher proportion of the northeastern European populations to raise multiple broods.

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Supplementary material

Supplemental data for this article can be accessed here.

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