Effect of environmental temperatures and intraspecific factors on migration timing of Song Thrush *Turdus philomelos* through the southern

Michał Redlisiak

Introduction

Bird migration, a cyclical phenomenon of nature, has been the subject of scientific research since the beginnings of the natural sciences. Many factors, internal and external [1, 2], influence birds' migration. The elements of migration that these factors influence include its timing, rate, distance, direction and more [1]. Internal factors are mainly genetic as an innate "programme" that regulates the timing, direction and distance of migration [1, 3, 4]. This "programme" might be shared by all individuals of a species, but might also vary between populations [4]. Other internal factors that influence migration are related to the individual traits of each migrant, such as sex or age [5, 6]. Protandry, the earlier return of males than females to the breeding areas in spring from wintering grounds [6, 7, 8, 9], is one example of these influences. External factors that influence bird migration are mostly environmental, such as daylength, weather (e.g. temperature, rainfall), snow depth and food availability [10, 11, 12, 13, 14, 15]. One clear example of the influence that external factors play on bird migration is the recent earlier dates of spring migration and return to the breeding grounds observed in many species, which is associated with an increase in Europe's temperatures with global warming [16, 17, 18]. The influence of internal factors often results in external factors exerting different influences on the migration of individuals from different age and sex groups [2, 19]. One example is the stronger influence of temperatures on male spring migration than on that of females reported in different species [2, 20, 21].

This thesis examines the influence of external factors (temperature along the migration route, at breeding areas and on wintering grounds) and internal factors (sex) on the dates of spring and autumn migration of the Song Thrush (*Turdus philomelos*) across the southern Baltic coast in 1960–2019. The Song Thrush is a medium-sized passerine that is common across almost the entire Western Palearctic [22, 23]. Individuals that migrate across the southern coast of the Baltic originate from breeding populations in Fennoscandia and northern Russia [24, 25]. These birds are medium-distance migrants that traverse an average distance of about 2,500 km [26]. Earlier spring migration of Song Thrushes has been reported from sites in northern and central Europe [18, 26, 27], but potential differences in the migration timing of males and females and protandry in this species had not been explored. The main reason for these lacunae had been the difficulty in determining the sex of this species in the field. Male and female Song Thrushes show no clear sexual dimorphism [28, 29]. The slight dimorphism in size [29] was considered too weak to allow any reliable determination of the sex of an individual by morphological features measured while bird ringing. The small size dimorphism, however, did allow the development of functions by discriminant analysis that enabled the sex of Song Thrushes to be determined using morphological measurements [30].

Aims and hypotheses

This dissertation aimed to determine the influence of selected external factors (temperature on the migration route, the wintering and the breeding grounds) and an internal factor (sex) on the timing of Song Thrush migration across the southern coast of the Baltic.

Paper no. 1 examined multiyear trends in the timing of Song Thrush spring and autumn migration across the Polish coast of the Baltic, and determined if this timing was related to temperatures trends along migration routes and at the breeding areas in 1975–2014. A multiyear trend to an earlier spring migration had previously been reported from other parts of the Baltic region [18, 26, 27]. Advancing dates to the beginning of autumn migration had previously been reported only from the bird-ringing station on the Baltic island of Christiansø, near Bornholm [31]. Trends in the timing of spring and autumn migration had not been related to temperatures at any of the Song Thrush's breeding areas or on its migration routes, though such relationships had been determined for other migratory passerines [15, 32]. We therefore expected to find long-term trends in the dates of the Song Thrush's spring and autumn migrations across the southern Baltic, as well as a relationship between these trends and any long-term changes in temperatures at different parts of the species' range.

Paper no. 2 verified sexual dimorphism in the morphometrics of Song Thrushes and attempted to develop discriminant functions that would allow the species to be sexed using biometrics. The literature had indicated small sexual dimorphism in the measurements of Song Thrushes [29, 33]. These data, however, were obtained from a small sample of individuals originating from the breeding population in Spain [33], far from the populations we were studying around the Baltic Sea. We nevertheless expected populations of Song Thrushes migrating through the Baltic region to exhibit sexual size dimorphism, though specific values of morphological measurements might well differ from conspecifics in Spain due to an inter-population variation in size [33]. We also expected that any sexual size dimorphism of Song Thrushes migrating through the southern Baltic region would be sufficient to develop effective discriminant functions allowing for the sexual determination of this species from its biometrics.

Paper no. 3 used the discriminant functions developed in Paper no. 2 to verify the hypotheses about the differences in the dates of male and female spring migration and to determine the differential influence on both sexes of temperatures at the wintering grounds on the dates of spring migration. Spring protandry is common in migrating passerines [9, 19, 21, 34, 35], so we expected to find this phenomenon in the Song Thrush. Many passerines in Europe now migrate earlier in spring [16, 17, 18] , thus we expected that higher temperatures on the wintering grounds would lead to earlier spring migration in the Song Thrush. Weather conditions during spring migration most affect the fraction of a population that migrates earlier [2], so it could be expected that any protandry in Song Thrushes migrating across the southern Baltic coast in spring would indicate that males, which migrate earlier, would be more influenced by the temperatures at their winter quarters than the females.

Materials and methods

Research presented in this thesis was enabled by many years of data collected by the Operation Baltic research project, coordinated by the Bird Migration Research Station, and by data available from other sources.

The following data sets were used:

1. A ringing and biometry database covering 1968–2019 from Operation Baltic's ringing stations at Hel and at Mierzeja Wiślana. Source: Bird Migration Research Station, University of Gdańsk, Poland.
2. European Climate Assessment and Dataset, provided by the Royal Netherlands Meteorological Institute. Source: www.ecad.eu.

3. Results of molecular sex determination of Song Thrushes ringed on spring and autumn migration at Hel and Mierzeja Wiślana in 2015 and 2016. Source: own research.
4. A database of recoveries of Song Thrushes ringed in the Baltic region over 1960–2010 was used to visualize the geographical distribution of the birds' migration routes, breeding areas and winter quarters. Source: EURING, Operation Baltic, Polish Ringing Centre, Lithuanian Ringing Centre, Latvian Ringing Centre, Falsterbo Bird Observatory.

In Paper no. 1 multiyear trends in migration dates and temperatures were determined using Generalized Additive Models (GAM) [36, 37]. The significance of the trends obtained was checked using a permutation test [38]. The relationships between migration dates and temperatures were investigated using Pearson's product-moment correlation [39]. To determine the factors influencing the change in migration dates, linear regression was used with many explanatory variables [39, 40]. Statistical analysis were performed in Statistica 13.1 [41] and R 3.3.2 [42] software.

In Paper no. 2, DNA for molecular sexing was isolated from blood samples collected from Song Thrushes ringed and measured at Operation Baltic's ringing stations in 2015 and 2016. PCR [43] was used to amplify the two variants of the CHD gene located on the birds' Z and W sex chromosomes [44]. Individuals from different populations might differ genetically [45, 46], so two primer pairs were used: P2/P8 [44] and F2/R1 [47]. The products of the PCR were then separated on agarose gel using electrophoresis and sex was determined by the presence of the amplified CHD genes. For males only the CHD-Z variant was present, which produced one band on the gel; females had both the CHD-Z and CHD-W variants, which was visible on the gel after electrophoresis as two bands [44]. The results from molecular sexing were combined with the individual's measurements taken in the field. The discriminant analysis was applied to the combined data to develop functions to determine the sex of Song Thrushes based on a combination of biometrics [30].

In Paper no. 3 the discriminant functions developed in Paper no. 2 were applied to determine the sex of Song Thrushes captured in 1968–2019 at the Hel ringing station. Quantile regression was applied [48] to identify the relationship between temperatures at the winter quarters and the timing of male and female spring migration and also to determine the degree of protandry[48, 49]. The statistical analyses were performed using R 4.0.3 software [50].

Results and discussion

Paper no. 1 – Effect of temperatures on migration route and at breeding grounds on dates of spring and autumn Song Thrush migration through Baltic Region.

The dates Song Thrushes undertake their spring migration across and along the southern Baltic coast were correlated with temperatures on their migration routes in Germany and Austria. The higher the April average minimum daily temperatures on the migration routes, the earlier their spring migration through the Operation Baltic ringing stations on the southern Baltic coast; the lower these April temperatures, the later Song Thrushes migrated. No significant multiyear trends in the dates of spring migration were found, though these dates did fluctuate from year to year. This finding was inconsistent with observations from other locations in the Baltic region [18, 26, 27] . These fluctuating dates of spring migration through the Operation Baltic stations alternated between advancements and delays. Yet a significant

advancement in the start of immature Song Thrushes' autumn migration was detected over the past 50 years, as at the Danish ringing station at Christiansø [31]. The higher the average minimum daily temperatures in July at the breeding grounds, the earlier was the beginning of autumn migration of young Song Thrushes across the Polish Baltic coast. The lack of a significant long-term trend in spring migration dates, despite such trends elsewhere around the Baltic Sea, probably resulted from the longer period of data analysed for this paper, because periods of overlapping data from Operation Baltic's ringing stations and from other locations did correlate with trends in migration dates observed over shorter periods at other stations. The correlation of the dates of spring migration with temperatures on the migration route suggested that Song Thrushes can adjust the timing of their spring migration to the environmental conditions they encounter *en route*. This indicates the species' phenological plasticity and shows that this species' migration is regulated by external and internal factors [1, 51]. The earlier starting dates of young Song Thrushes' autumn migration probably resulted from the increased breeding success and additional broods fostered by a warming climate in the breeding areas. Higher temperatures in the breeding season (e.g. in July) increase breeding success, which results in an increased number of young birds [52, 53]. That would increase competition for food with adult birds feeding their second broods. Young birds would therefore probably benefit by leaving the breeding grounds early, despite the favourable conditions prevailing there.

Paper no. 2 – Development of discriminant functions allowing the sexing of Song Thrushes by their morphological measurements.

This paper confirmed the sexual size dimorphism of Song Thrushes migrating in spring and autumn across the Polish Baltic coast. Males were generally larger than females, as indicated by wing length. Despite their longer wings, males had a significantly shorter vestigial primary than females. Using measurements of Song Thrushes collected in the field combined with molecular sex determination from blood samples, discriminant functions were developed allowing adult Song Thrushes migrating across the southern coast of the Baltic in spring and autumn to be sexed on biometric criteria with acceptable accuracy (> 80% efficiency). For young birds in immature plumage the functions were too inaccurate (about 60%) to be applicable in practice.

Paper no. 3 – Effect of wintering grounds temperatures on the dates of spring migration of males and females and the degree of protandry in Song Thrushes migrating in spring across the southern Baltic coast.

The study showed clear spring protandry in the Song Thrush, which increased over 1968–2019. The degree of protandry and the dates of each sex's spring migration were related to the monthly mean minimum daily temperatures at the wintering grounds in December–February. After cold winters at the wintering grounds, males and females migrated at similar times through the Baltic region in spring. But after warm winters males on average migrated in spring earlier than females. For males warm winters advanced the beginning of migration and delayed its end, resulting in an extended spring migration. Females' spring migration dates showed a similar but weaker relationship to temperatures. Protandry in the Song Thrush results from the species' mating system, where the male occupies and defends a territory to which he attracts the female [7, 54, 55]. Males therefore benefit from returning to the breeding area as early as possible [6, 7, 8, 9]. Returning too early, however, risks adverse weather making food less abundant than later in the season [6, 8, 20]. Males therefore probably delay spring migration after cold winters. The increasing degree of protandry in Song Thrushes migrating across the southern Baltic coast over the past 50 years most likely results from climate change

and global warming. Protandry has also increased in several other European passerines [20, 35, 56], so it is likely a widely occurring phenomenon. Males' prolonged migration after a warm winter probably relates to two factors. Warm winters enable the males to start spring migration earlier than after a cold winter, which enables them to reach the breeding grounds earlier. Warm winters also increase the survival prospects of lower-quality males, which need more time to accumulate sufficient energy reserves for migration. They therefore migrate later than males in better condition [57, 58, 59]. Fewer lower-quality males survive cold winters, hence there is no observable delay in the end of migration after cold winters. Females also benefit by returning earlier to the breeding grounds because they improve their prospects of selecting a male in good condition holding a good territory; an early return also allows for additional broods [60]. Some females might use improved conditions at the wintering grounds to prolong their period of intensive pre-migratory fuelling before migration to improve their chances of surviving their passage. Some females likely also extend their stopovers during migration. Females' later passage across the Baltic Sea after warm winters might result from a combination of both these phenomena.

Conclusions

This thesis demonstrated the influence of temperatures at the wintering grounds, on migration routes and at the breeding areas, as well as sex, on the timing of Song Thrush migration across the southern coast of the Baltic Sea. The influence that temperatures on the migration route has on the timing of spring migration (earlier migration with higher temperatures and *vice versa*) was determined. An earlier beginning to the autumn migration of young Song Thrushes was also demonstrated, along with its relationship to a multiyear increase of July temperatures on the breeding grounds caused by climate warming. With the use of discriminant functions, which enabled the sexing of Song Thrushes from biometrics gathered over decades at Operation Baltic's ringing stations, it became possible for the first time to determine the effect of sex on the migration timing of the Song Thrush and the different influences of temperatures on the migration of each sex.

One novel outcome of the dissertation was in confirming protandry in the Song Thrush and proving that temperatures at wintering grounds have a different effect on the spring migration of males and females. This paper also highlighted possibilities for further studies on how climatic conditions influence the phenology of monomorphic passerine migrants in relation to the sex of individuals. Developing discriminant functions for sexing Song Thrushes provided further possibilities to study the effects of sex on migration and on other elements of this species' biology. The thesis also showed the value of multiyear data series, such as Operation Baltic's data on bird morphology and migration timing. Combined with weather data, multiyear data series allow studies on the effects of climate change on living organisms.

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