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**WPLYW TEMPERATURY ŚRODOWISKA
I CZYNNIKÓW WEWNĄTRZGATUNKOWYCH
NA TERMINY MIGRACJI ŚPIEWAKA *TURDUS
PHILOMELOS* PRZEZ POŁUDNIOWE WYBRZEŻE
BAŁTYKU**

**EFFECT OF ENVIRONMENTAL TEMPERATURES AND INTRASPECIFIC
FACTORS ON MIGRATION TIMING OF SONG THRUSH *TURDUS PHILOMELOS*
THROUGH THE SOUTHERN BALTIC COAST**

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Redlisiak M, Mazur A, Remisiewicz M (2020).	33
Size dimorphism and sex determination in the song thrush (<i>Turdus philomelos</i>) migrating through the southern Baltic coast. Ann. Zool. Fennici 57: 31–40, doi: 10.5735/086.057.0104	
Redlisiak M, Remisiewicz M, Mazur A (2021).	44
Sex-specific differences in spring migration timing of Song Thrush <i>Turdus philomelos</i> at the Baltic coast in relation to temperatures on the wintering grounds. The European Zoological Journal 88:1, 191-203, doi: 10.1080/24750263.2020.1869842	
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Streszczenie

Wstęp

Wędrowki ptaków, jako cykliczny fenomen przyrody, są przedmiotem badań naukowych od początków nauk przyrodniczych. Wiele czynników, zarówno wewnętrznych jak i zewnętrznych, ma wpływ na migrację ptaków^{1, 2}. Czynniki te wpływają na parametry migracji takie jak jej termin, tempo, odległość czy kierunek¹. Czynniki wewnętrzne mają głównie podłoże genetyczne i charakter wrodzonego „programu” regulującego terminy, kierunek czy odległość migracji^{1, 3, 4}. Ten „program” może być jednakowy dla wszystkich osobników danego gatunku, ale może też różnić się między populacjami⁴. Inne wewnętrzne czynniki wpływające na migracje są związane z cechami migrujących osobników, jak ich płeć lub wiek^{5, 6}. Przykładem takiego wpływu jest zjawisko protandrii, czyli wcześniejszego wiosennego powrotu samców niż samic z zimowisk na obszary lęgowe^{6, 7, 8, 9}. Czynniki zewnętrzne wpływające na migrację ptaków to przede wszystkim rozmaite parametry środowiska w którym przebywają ptaki, takie jak długość dnia, pogoda (np. temperatura, opady), grubość pokrywy śnieżnej, dostępność pokarmu itp.^{10, 11, 12, 13, 14, 15}. Przykładem wpływu tych czynników na migrację ptaków jest zjawisko coraz wcześniejszych terminów wiosennej wędrowki i powrotów na lęgowiska obserwowane u wielu gatunków, związane ze wzrostem temperatur w Europie i z globalnym ociepleniem^{16, 17, 18}. Ze względu na wpływ czynników wewnętrznych, czynniki zewnętrzne mogą mieć różny wpływ na migracje ptaków z różnych grup wiekowych i płciowych^{2, 19}. Przykładem jest silniejszy wpływ temperatur na wiosenną migrację samców niż samic^{2, 20, 21}.

W niniejszej rozprawie badano wpływ czynników zewnętrznych (temperatury na trasie wędrowki, obszarach lęgowych oraz zimowiskach) oraz wewnętrznych (płeć) na terminy wiosennej i jesiennej migracji śpiewaka (*Turdus philomelos*) przez południowe wybrzeże Bałtyku, w okresie 1960–2019. Śpiewak to średniej wielkości przedstawiciel ptaków wróblowych *Passeriformes* pospolity w całej zachodniej Palearktyce^{22, 23}. Populacje tego gatunku migrujące przez południowe wybrzeże Bałtyku, pochodzące z populacji gniazdujących na obszarze Fennoskandii i północnej Rosji^{24, 25}, to migranty średniodystansowe o dystansie wędrowki przeciętnie około 2500 km²⁶. Dotychczas wykazano przyspieszenie terminów wiosennego przelotu śpiewaków w północnej i środkowej Europie^{18, 26, 27}. Natomiast potencjalne różnice w migracji obu płci i zjawisko protandrii nie były dotąd badane u tego gatunku. Było to wynikiem trudności w oznaczeniu płci u tego gatunku w terenie, ponieważ u śpiewaka nie występuje dymorfizm w wyglądzie samców i samic^{28, 29}. Niewielki dymorfizm występuje w wielkości osobników²⁹. Jest on zbyt mały aby umożliwić oznaczenie płci ptaków według wielkości jednego z pomiarów morfologii, jak te zbieranych podczas obrączkowania ptaków. Daje natomiast podstawę do zastosowania analizy dyskryminacyjnej i opracowania równań dyskryminacyjnych, które umożliwią oznaczanie płci śpiewaków na podstawie kombinacji kilku cech biometrii³⁰.

Cele i hipotezy

Celem niniejszej rozprawy było określenie wpływu wybranych czynników zewnętrznych (temperatura na trasie migracji, zimowiskach i lęgowiskach) oraz wewnętrznych (płeć) na terminy przelotu śpiewaków przez południowe wybrzeże Bałtyku.

W pierwszej kolejności (Artykuł nr 1) sprawdzono czy istnieją wieloletnie trendy w terminach wiosennego i jesienno przelotu śpiewaka przez polskie wybrzeże Bałtyku, a także czy terminy te mają związek z wieloletnimi zmianami temperatur na trasach wędrowki i obszarach lęgowych, w latach 1975–2014. Trendy wieloletnie polegające na przyspieszeniu wiosennej migracji u śpiewaka były wcześniej stwierdzane w innych

rejonach wybrzeża Bałtyku^{18, 26, 27}. Przyspieszenie początku jesiennej migracji stwierdzono jedynie w stacji obrączkowania ptaków na wyspie Christiansø na Bałtyku, w pobliżu Bornholmu³¹. Jednak trendy te, zarówno dla wędrówki wiosennej jak i jesiennej, nie zostały dotąd powiązane z temperaturami na konkretnych obszarach lęgowych i trasach migracji śpiewaków. Takie zależności stwierdzono jednak u innych wędrownych gatunków ptaków wróblowych^{15, 32}. Dlatego można oczekiwać wystąpienia wieloletnich trendów w terminach zarówno wiosennego jak i jesienno-przeletu śpiewaka przez południowe wybrzeże Bałtyku oraz związku tych trendów z wieloletnimi zmianami temperatur w różnych częściach zasięgu tego gatunku.

W drugim etapie (Artykuł nr 2) zbadano występowanie dymorfizmu płciowego rozmiarów ciała śpiewaków oraz podjęto próbę opracowania równań dyskryminacyjnych pozwalających na oznaczanie płci śpiewaków na podstawie ich biometrii. Dostępne dane literaturowe wskazują na istnienie pewnego dymorfizmu płciowego w wielkości osobników śpiewaka^{29, 33}. Są to jednak wyniki uzyskane z niewielkiej liczby osobników pochodzących z populacji lęgowej z Hiszpanii³³, daleko od badanego rejonu Morza Bałtyckiego. Z tego powodu można się spodziewać, że dymorfizm płciowy w wielkości będzie również występował u osobników migrujących przez rejon Bałtyku, mimo iż wartości konkretnych wymiarów ciała mogą się różnić od śpiewaków z Hiszpanii, ze względu na międzypopulacyjne zróżnicowanie wielkości osobników³³. Można więc oczekiwać, że zróżnicowanie biometryczne samców i samic śpiewaka migrujących przez rejon Bałtyku będzie wystarczające do opracowania skutecznych równań dyskryminacyjnych pozwalających oznaczać płeć u tego gatunku.

W trzecim etapie (Artykuł nr 3) zastosowano równania opracowane w Artykule nr 2 do zweryfikowania hipotez o różnicach w terminach wiosennej migracji samców i samic, oraz o różnym wpływie temperatur na zimowiskach na terminy wiosennego przeletu samców i samic. Protandria to powszechne zjawisko u ptaków wróblowych^{9, 19, 21, 34, 35}, można więc oczekiwać jej wystąpienia również u śpiewaka. Ponieważ u wielu gatunków nastąpiło przyspieszenie wiosennej migracji przez Europę^{16, 17, 18}, można się spodziewać, że również u śpiewaka wyższe temperatury na zimowiskach będą wpływać na ich wcześniejszą wiosenną wędrówkę w danym roku. Warunki pogodowe podczas wiosennej migracji najsilniej wpływają na frakcję populacji migrującą najwcześniej², można więc oczekiwać, że jeśli u tego gatunku występuje protandria, to temperatury te będą silniej wpływać na samce, które wędrują wcześniej, niż na samice.

Materiały i metody

Badania składające się na rozprawę przeprowadzono w oparciu o wieloletnie dane programu badawczego Akcja Bałtycka, prowadzonego przez Stację Badania Wędrówek Ptaków UG, oraz udostępnione dane z innych źródeł.

Do przygotowania niniejszej rozprawy wykorzystano następujące zbiory danych:

1. Baza danych obrączkowania i biometrii z lat 1968–2019 ze stacji obrączkowania ptaków „Hel” oraz „Mierzeja Wiślana” działających w ramach programu badawczego Akcja Bałtycka. Źródło: Stacja Badania Wędrówek Ptaków UG.
2. Baza danych klimatycznych European Climate Assessment and Dataset udostępniona przez Holenderski Królewski Instytut Meteorologiczny. Źródło: www.ecad.eu.
3. Wyniki molekularnego oznaczania płci śpiewaków chwytnych w trakcie wiosennej i jesiennej wędrówki w stacjach obrączkowania ptaków Akcji Bałtyckiej „Hel” i „Mierzeja Wiślana” w latach 2015–2016. Źródło: badania własne.

4. Dodatkowo, do wizualizacji tras migracji, zimowisk i lęgówisk śpiewaków migrujących przez rejon Bałtyku wykorzystano bazę wiadomości powrotnych o śpiewakach obrączkowanych w rejonie Bałtyku w latach 1960–2010, w tym w 14 stacjach obrączkowania ptaków. Źródła: EURING, Akcja Bałtycka, Polska Centrala Obrączkowania Ptaków, Litewska Centrala Obrączkowania Ptaków, Łotewska Centrala Obrączkowania Ptaków, Falsterbo Bird Observatory.

W Artykule nr 1 wyznaczono wieloletnie trendy terminów przelotu i temperatur z użyciem uogólnionych modeli addytywnych (*Generalised Additive Models, GAM*)^{36, 37}. Istotność uzyskanych trendów sprawdzono za pomocą testu permutacji³⁸, a tempo wieloletnich zmian określono wykorzystując współczynnik nachylenia β z regresji liniowej³⁹. Związek terminów wędrówki z temperaturami zbadano za pomocą współczynnika korelacji Pearsona³⁹. W celu określenia czynników wpływających na zmianę terminów migracji zastosowano regresję liniową z wieloma zmiennymi objaśniającymi^{39, 40}. Analizy statystyczne przeprowadzono w programach Statistica 13.1⁴¹ oraz R 3.3.2⁴².

W Artykule nr 2 W celu molekularnego oznaczenia płci śpiewaków najpierw przeprowadzono izolację DNA z krwi pobranej od śpiewaków schwytanych i zmierzonych w stacjach obrączkowania ptaków Akcji Bałtyckiej w trakcie migracji w latach 2015 i 2016. Następnie zastosowano metodę PCR⁴³ w celu amplifikacji genów CHD które u ptaków są zlokalizowane na chromosomach płci i występują w dwóch wariantach: CHD-Z i CHD-W, zlokalizowanych odpowiednio na chromosomach płci Z i W⁴⁴. Ponieważ osobniki z różnych populacji mogły różnić się genetycznie^{45, 46}, w celu zwiększenia skuteczności oznaczenia płci wykorzystano dwie pary primerów: P2/P8⁴⁴ oraz F2/R1⁴⁷. Następnie rozdzielono produkty reakcji PCR za pomocą elektroforezy w żelu agarozowym. Płeć osobników określano na podstawie obecności amplifikowanych genów CHD. Dla samców obecny był tylko wariant CHD-Z, który dawał jeden prążek na żelu, natomiast u samic stwierdzano oba warianty CHD-Z i CHD-W, co było widoczne na żelu po elektroforezie jako dwa prążki⁴⁴. Po molekularnym oznaczeniu płci śpiewaków od których pobrano próbki krwi, połączono wyniki tych oznaczeń z pomiarami osobników wykonanymi w terenie. Do tak przygotowanych danych zastosowano analizę dyskryminacyjną, w celu opracowania równań dyskryminacyjnych pozwalających oznaczać płeć śpiewaków na podstawie kombinacji kilku pomiarów ich morfologii³⁰.

W Artykule nr 3 zastosowano równania dyskryminacyjne opracowane w Artykule nr 2 do oznaczenia płci śpiewaków obrączkowanych w latach 1968–2019 na stacji a obrączkowania ptaków Akcji Bałtyckiej „Hel”. W celu określenia wpływu temperatur na zimowiskach na terminy wiosennej migracji samców i samic oraz wyznaczenia zakresu protandrii zastosowano regresję kwantylową^{48, 49}. Analizy statystyczne przeprowadzono w programie R 4.0.3⁵⁰.

Wyniki i dyskusja

Artykuł nr 1 – Wpływ temperatur na trasie migracji i lęgówiskach na terminy wiosennego i jesiennego przelotu śpiewaków przez rejon Bałtyku.

Stwierdzono związek terminów wiosennej wędrówki śpiewaków migrujących przez południowe wybrzeże Bałtyku z temperaturami na ich trasie migracji (Niemcy, Austria). Im wyższa była kwietniowa średnia z minimalnych dobowych temperatur na trasach migracji, tym wcześniejszy był wiosenny przelot śpiewaków przez stacje Akcji Bałtyckiej na południowym wybrzeżu Bałtyku, a im niższe były temperatury kwietnia tym śpiewaki wędrowały później. Nie stwierdzono istotnych wieloletnich trendów terminów migracji wiosennej, a raczej znaczną zmienność terminów z roku na rok, co nie jest zgodne z wynikami dla innych lokalizacji z regionu Bałtyku^{18, 26, 27}. Zmienność terminów

wiosennego przelotu przez stacje Akcji Bałtyckiej miała jednak formę naprzemiennych okresów przyspieszania i opóźniania terminu wędrówki. Stwierdzono natomiast istotne przyspieszenie początku jesiennego przelotu młodych śpiewaków w ciągu ostatnich 50 lat, podobnie jak w duńskiej stacji obrączkowania ptaków Christiansø³¹. Dodatkowo, im wyższa była średnia temperatura w lipcu na lęgowiskach tym wcześniejszy był początek jesiennego przelotu przez polskie wybrzeże Bałtyku. Brak istotnego trendu wieloletniego terminów wiosennej wędrówki przy obecności takich trendów w innych miejscach nad Bałtykiem to prawdopodobnie efekt dłuższego okresu danych analizowanych w tej rozprawie, ponieważ przy zestawieniu danych z okresów wspólnych dla polskiego wybrzeża i innych lokalizacji trendy terminów przelotu były zbieżne. Korelacja terminów wiosennego przelotu z temperaturami na trasie wędrówki sugeruje, że śpiewaki dostosowują terminy migracji do napotkanych warunków środowiska, co świadczy o ich plastyczności oraz wskazuje na to, że fenologia migracji tego gatunku jest regulowana nie tylko przez czynniki wewnętrzne, ale też przez czynniki zewnętrzne^{1, 51}. Przyspieszenie początku jesiennego przelotu młodych śpiewaków było prawdopodobnie wynikiem zwiększonego sukcesu lęgowego i dodatkowych lęgów, które były możliwe w związku z ociepleniem klimatu na obszarach lęgowych. Wyższe temperatury w okresie lęgowym (m.in. w lipcu) zwiększają sukces lęgowy, co skutkuje zwiększoną liczebnością młodych osobników w środowisku^{52, 53} i może powodować zwiększoną konkurencję o pokarm między młodymi osobnikami, oraz między młodymi a dorosłymi ptakami karmiącymi kolejny lęg. Z tego powodu wczesne opuszczenie lęgowisk jest prawdopodobnie korzystne dla młodych ptaków mimo panujących tam pozornie dobrych warunków.

Artykuł nr 2 – Opracowanie równań dyskryminacyjnych pozwalających na oznaczanie płci śpiewaków na podstawie biometrii.

Potwierdzono występowanie dymorfizmu płciowego w wielkości osobników u śpiewaków migrujących zarówno wiosną jak i jesienią przez polskie wybrzeże Bałtyku. Samce były generalnie większe niż samice na co wskazywały ich wartości pomiaru długości skrzydła. Pomimo przeciętnie dłuższych skrzydeł samce miały jednak istotnie krótsze zewnętrzne lotki pierwszorzędowe niż samice. Wykorzystując pomiary śpiewaków w terenie i ich płęć oznaczoną molekularnie, opracowano równania dyskryminacyjne pozwalające oznaczać z akceptowalną dokładnością (>80% skuteczności) płęć dorosłych śpiewaków obrączkowanych zarówno wiosną jak i jesienią. W przypadku młodych ptaków (w szacie immaturalnej) otrzymane równania miały zbyt małą skuteczność (około 60%) aby można było je zastosować w praktyce.

Artykuł 3 – Wpływ temperatur na zimowiskach na terminy wiosennego przelotu w zależności od płci oraz zakres protandrii u śpiewaków migrujących wiosną przez południowe wybrzeże Bałtyku.

W pracy stwierdzono wyraźną wiosenną protandrię u śpiewaka oraz jej zwiększenie w latach 1968–2019. Zakres protandrii oraz terminy wiosennego przelotu każdej z płci były powiązane ze średnimi temperaturami na zimowiskach w miesiącach grudzień–luty. W przypadku niskich temperatur na zimowiskach samce i samice migrowały wiosną przez rejon Bałtyku w podobnych terminach. Natomiast po ciepłych zimach samce wędrowały wiosną zdecydowanie wcześniej niż samice. U samców cieplejsze zimy powodowały zarówno przyspieszenie początku przelotu, jak i opóźnienie jego końca, i w efekcie wydłużenie okresu wiosennego przelotu. U samic występowała podobna ale słabsza zależność. Występowanie protandrii u śpiewaka wynika ze strategii rozrodczej tego gatunku, gdzie samiec zajmuje i broni terytorium, na które następnie „zwabia” samice^{7, 54, 55}. Z tego powodu dla samców korzystny jest jak najwcześniejszy powrót na lęgowisko^{6, 7, 8, 9}. Jednak zbyt wczesny powrót może być ryzykowny w wypadku gorszych warunków pogodowych, gdyż samce mogą

dotrzeć na lęgowiska gdy wciąż panują na nich niekorzystne temperatury i zanim jeszcze rozwinie się tam baza pokarmowa^{6, 8, 20}. Z tego powodu samce prawdopodobnie opóźniają migrację wiosenną po mroźnej zimie. Wzrost poziomu wiosennej protandrii u śpiewaków migrujących wiosną przez południowe wybrzeże Bałtyku w ciągu ostatnich 50 lat jest najprawdopodobniej efektem zmian klimatycznych i globalnego ocieplenia. Wzrost poziomu protandrii stwierdzono u kilku innych gatunków europejskich ptaków wróblowych^{20, 35, 56}, jest to więc najprawdopodobniej zjawisko powszechne. Natomiast „rozszerzenie” okresu przelotu samców po cieplejszej zimie wynika prawdopodobnie z dwóch czynników. Ciepła zima powoduje, że samce rozpoczynają migrację wcześniej niż po chłodnej zimie, co umożliwia im wcześniejsze dotarcie na lęgowiska. Dodatkowo, ciepła zima prawdopodobnie zwiększa przeżywalność frakcji samców w gorszej kondycji, które potrzebują więcej czasu na zgromadzenie rezerw energetycznych potrzebnych do wędrówki i migrują później niż samce w lepszej formie^{57, 58, 59}. Przy chłodnych zimach słabsze samce prawdopodobnie nie przeżywają okresu zimowania, stąd brak opóźnienia końca przelotu po chłodnych zimach. W przypadku samic wcześniejszy powrót na tereny lęgowe jest również korzystny, gdyż umożliwia wybór samca w dobrej kondycji i z dobrym terytorium, oraz umożliwia dodatkowe lęgi⁶⁰. Jednak część samic może wykorzystywać cieplejsze warunki na zimowiskach by wydłużyć okres intensywnego żerowania przed wędrówką i zwiększyć swoje szanse przetrwania migracji. Możliwe też, że część samic zatrzymuje się na dłuższe okresy postoju w trakcie migracji. Późniejszy przelot samic przez rejon Bałtyku po ciepłych zimach może być wynikiem kombinacji obu zjawisk.

Podsumowanie

Niniejsza praca doktorska wykazała wpływ temperatur środowiska na zimowiskach, trasach migracji i lęgowiskach, oraz płci na terminy wędrówki śpiewaka przez południowe wybrzeże Bałtyku. Stwierdzono wpływ temperatur na trasach migracji na terminy wiosennego przelotu śpiewaków przez południowe wybrzeże Bałtyku (wcześniejszy przelot przy wyższych temperaturach i *vice versa*). Wykazano też przyspieszenie początku jesiennego przelotu młodych śpiewaków i jego związek ze wzrostem temperatur w lipcu na lęgowiskach spowodowanym przez ocieplenie klimatu. Dzięki zastosowaniu równań dyskryminacyjnych, które pozwoliły na oznaczenie płci śpiewaków obrączkowanych przez dziesięciolecia na terenowych stacjach obrączkowania ptaków Akcji Bałtyckiej, po raz pierwszy było możliwe określenie wpływu płci na terminy przelotu śpiewaka oraz różnic we wpływie temperatury na migracje każdej z płci. Nowatorskim wynikiem rozprawy było potwierdzenie występowania protandrii u śpiewaka, oraz wykazanie, że temperatury na zimowiskach mają różny wpływ na wiosenną migrację samców i samic. Niniejsza praca stanowi podstawę do szerszych badań wpływu warunków klimatycznych na fenologię migracji ptaków wróblowych, z uwzględnieniem płci osobników. Opracowanie równań dyskryminacyjnych pozwalających oznaczać płeć u śpiewaków migrujących przez polskie wybrzeże otwiera dalsze możliwości badań wpływu płci na migrację i na inne elementy biologii tego gatunku. Rozprawa także pokazała wartość wieloletnich serii danych, takich jak dane Akcji Bałtyckiej dotyczące morfologii i terminów wędrówek ptaków, oraz dane klimatyczne, w badaniach wpływu zmian klimatu na organizmy żywe.

Summary

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 more¹. 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 populations⁴. 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 km²⁶. 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 size²⁹ 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 measurements³⁰.

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 Bornholm³¹. 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 Spain³³, 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 size³³. 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 earlier², 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 broods⁶⁰. 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.

Literatura

1. Berthold P. 1996. Control of bird migration. London: Chapman & Hall
2. Newton I. 2008. The migration ecology of birds. London: Academic Press
3. Merlin C, Liedvogel M. 2019. The genetics and epigenetics of animal migration and orientation: birds, butterflies and beyond. *Journal of Experimental Biology* 222: 1–11. DOI: 10.1242/jeb.191890
4. Zhao T, Ilieva M, Larson K, Lundberg M, Neto JM, Sokolovskis K, Åkesson S, Bensch S. 2020. Autumn migration direction of juvenile willow warblers (*Phylloscopus t. trochilus* and *P. t. acredula*) and their hybrids assessed by qPCR SNP genotyping. *Movement Ecology* 8, Article number: 22. DOI: 10.1186/s40462-020-00209-7
5. Woodrey M, Chandler C. 1997. Age-Related Timing of Migration: Geographic and Interspecific Patterns. *The Wilson Bulletin* 109 (1): 52–67.
6. Morbey YE, Ydenberg RC. 2001. Protandrous arrival timing to breeding areas: a review. *Ecology Letters* 4: 663–673. DOI:10.1046/j.1461-0248.2001.00265.x
7. Kokko H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68: 940–950. DOI: 10.1046/j.1365-2656.1999.00343.x
8. Spottiswoode CN, Tøttrup AP, Coppack T. 2006. Sexual selection predicts advancement of avian spring migration in response to climate change. *Proceedings of the Royal Society of London B* 273: 3023–3029
9. Rainio K, Tøttrup AP, Lehikoinen E, Coppack T. 2007. Effects of climate change on the degree of protandry in migratory songbirds. *Climate Research* 35: 107–114. DOI: 10.3354/cr00717
10. Tryjanowski P, Kuźniak S, Sparks TH. 2002 Earlier arrival of some farmland migrants in western Poland. *Ibis* 144: 62–68, DOI: 10.1046/j.0019-1019.2001.00022.x
11. Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London B* 271: 59–64
12. Marra PP, Francis CM, Mulvihill RS, Moore FR. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142: 307–315. DOI: 10.1007/s00442-004-1725-x
13. Tøttrup AP., Rainio K, Coppack T, Lehikoinen E, Rahbek C, Thorup K. 2010. Local Temperature Fine-Tunes the Timing of Spring Migration in Birds. *Integrative and Comparative Biology* 50 (3): 293–304. DOI:10.1093/icb/icq028
14. Robson D, Barriocanal C. 2011. Ecological conditions in wintering and passage areas as determinants of timing of spring migration in trans-Saharan migratory birds. *Journal of Animal Ecology* 80: 320–331. DOI: 10.1111/j.1365-2656.2010.01772.x
15. Lehikoinen A, Lindén A, Karlsson M, Andersson A, Crewe TL, Dunn EH, Gregory G, Karlsson L, Kristiansen V, Mackenzie S, Newman S, Røer JE, Sharpe C, Sokolov LV, Steinholtz A, Stervander M, Tirri IS, Tjørnløv RS. 2019. Phenology of the avian spring migratory passage in Europe and North America:

- Asymmetric advancement in time and increase in duration. *Ecological Indicators* 101:985–991. DOI: 10.1016/j.ecolind.2019.01.083
16. Forchhammer MC, Post E, Stenseth NC. 2002. North Atlantic Oscillation timing of long- and short-distance migration. *Journal of Animal Ecology* 71:1002–1014. DOI: 10.1046/j.1365-2656.2002.00664.x
 17. Hüppop O, Hüppop K. 2003. North Atlantic oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London B* 270: 233–240. DOI: 10.1098/rspb.2002.2236
 18. Lehikoinen E, Sparks TH. 2010. Changes in migration. In: Møller AP, Fiedler W, Berthold P, editors. *Effects of Climate Change on Birds*. Oxford: Oxford University Press. pp. 89–112.
 19. Hedlund JSU, Jakobsson S, Kullberg C, Fransson T. 2015. Long-term phenological shifts and intra-specific differences in migratory change in the willow warbler *Phylloscopus trochilus*. *Journal of Avian Biology* 46: 97–106. DOI: 10.1111/jav.00484
 20. Møller AP. 2004. Protandry, sexual selection and climate change. *Global Change Biology* 10: 2028–2035
 21. Rubolini D, Spina F, Saino N. 2004. Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behavioral Ecology* 15: 592–601. DOI: 10.1093/beheco/arh048
 22. Cramp S. 1988. *The birds of the Western Palearctic*. Vol. V. Oxford: Oxford University Press.
 23. Collar N. 2005. Song Thrush. In: del Hoyo J, Elliott A, Sargatal J, Christie D, de Juana E, editors. *Handbook of the Birds of the World*. Barcelona: Lynx Edicions. pp. 637–638.
 24. Busse P, Maksalon L. 1986. Wędrowniki europejskich populacji drozda śpiewaka *Turdus philomelos*. *Notatki Ornitologiczne* 27: 1–2.
 25. Milwright RDP. 2006. Post-breeding dispersal, breeding site fidelity and migration/wintering areas of migratory populations of Song Thrush *Turdus philomelos* in the Western Palearctic. *Ringling & Migration* 23: 21–32. DOI: 10.1080/03078698.2006.9674340
 26. Tøttrup AP, Thorup K, Rahbek C. 2006. Patterns of change in timing of spring migration in North European songbird populations. *Journal of Avian Biology* 37:84–92, DOI: 10.1111/j.0908-8857.2006.03391.x
 27. Sinelschikova A, Sokolov LV. 2004 Long-term monitoring of the timing of migration in thrushes (*Turdus philomelos*, *T. iliacus*) in the Eastern Baltic. *Avian Ecology and Behavior* 12: 11–30.
 28. Svensson, L. 1992. *Identification Guide to European Passerines*. British Trust for Ornithology, The Nunnery, UK.
 29. Demongin, L. 2016. *Identification guide to Birds in the Hand*. Beauregard-Vendon.
 30. Tabachnick, B.G. & Fidell, L.S. 1996. *Using multivariate statistics*. 3rd ed. Harper Collins Publishers, New York.

31. Tøttrup AP, Thorup K, Rahbek C. 2006. Changes in timing of autumn migration in North European songbird populations. *Ardea* 94: 527–536.
32. Ahola M, Laaksonen T, Sippola K, Eeva T, Rainio K, Lehikoinen E. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology* 10: 1610–1617. DOI: 10.1111/j.1365-2486.2004.00823.x
33. Guallar S, Quesada J, Gargallo G, Herrando S, Romero JM. 2010. Use of discriminant analysis in the sex determination of passerines breeding in the western Mediterranean. *Revista Catalana d'Ornitologia* 26: 38–50.
34. Bakken V, Runde O, Tjørve E. 2006. Norsk ringmerkingsatlas. Vol. 2. Stavanger: Stavanger Museum.
35. Csörgo T, Harnos A. 2011. Change of migration timing of Chiffchaff (*Phylloscopus collybita*) during 23 years. *Ornis Hungarica* 9(1–2): 53–63.
36. Hastie TJ, Tibshirani RJ. 1990. Generalized additive models. Chapman and Hall, London.
37. Wood S. 2017. Generalized Additive Models: An Introduction with R. 2nd edn. Chapman & Hall. CRC Press, Taylor & Francis Group, Florida, US.
38. Manly BFJ. 2007. Randomization, bootstrap, and Monte Carlo methods in biology. 3rd edn. Chapman & Hall, London, pp 64–65
39. Zar JH. 2010. Biostatistical Analysis. 5th edition. New Jersey: Pearson Prentice Hall. pp: 400–402.
40. Biecek P. 2013. Analiza danych z programem R: modele liniowe z efektami stałymi, losowymi i mieszanymi. Wydawnictwo Naukowe PWN.
41. TIBCO Software Inc. 2017. Statistica 13.1.0
42. R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
43. Saiki R, Scharf S, Faloona F, Mullis K, Horn G, Erlich H, Arnheim N. 1985. Enzymatic amplification of beta-globin genomic sequences and restriction site analysis for diagnosis of sickle cell anemia. *Science* 230 (4732): 1350–1354. DOI:10.1126/science.2999980.
44. Griffiths R, Double MC, Orr K, Dawson RJG. 1998. A DNA test to sex most birds. *Molecular Ecology* 7: 1071–1075. DOI: 10.1046/j.1365-294x.1998.00389.x
45. Ball RM, Avise JC. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. *The Auk* 109: 626–636
46. Bensch S, Andersson T, Åkesson S. 1999. Morphological and molecular variation across a migratory divide in Willow warblers, *Phylloscopus trochilus*. *Evolution* 53: 1925–1935.
47. Bantock TM, Prys-Jones RTP, Lee PLM. 2008. New and improved molecular sexing for museum bird specimens. *Molecular Ecology Notes* 8: 519–528.
48. Cade BS, Noon BR. 2003. A Gentle Introduction to Quantile Regression for Ecologists. *Frontiers in Ecology and the Environment* 1(8): 412–420.

49. Koenker R. 2004. Quantile regression for longitudinal data. *Journal of Multivariate Analysis* 91:74–89.
50. R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
51. Knudsen E, Lindén A, Both C, Jonzén N, Pulido F, Saino N, Sutherland WJ, Bach LA, Coppack T, Ergon T, Gienapp P, Gill JA, Gordo O, Hedenström A, Lehikoinen E, Marra PP, Møller AP, Nilsson ALK, Péron G, Ranta E, Rubolini D, Sparks TH, Spina F, Studds CE, Sæther SA, Tryjanowski P, Stenseth NC. 2011. Challenging claims in the study of migratory birds and climate change. *Biol Rev* 86: 928–946, DOI: 10.1111/j.1469-185X.2011.00179.x
52. Lack D. 1972. *Ecological Adaptations for Breeding in Birds*. Chapman and Hall, London.
53. Dunn P. 2004. Breeding dates and reproductive performance. *Adv Ecol Res* 35: 67–86, DOI: 10.1016/S0065-2504(04)35004-X
54. Orians G. 1969. On the Evolution of Mating Systems in Birds and Mammals. *The American Naturalist* 103(934): 589–603.
55. Gill F. 1995. *Ornithology*. New York: WH Freeman and Co.
56. Harnos A, Lang Z, Fehérvári P, Csörgő T. 2015. Sex and age dependent migration phenology of the Pied Flycatcher in a stopover site in the Carpathian Basin. *Ornis Hungarica* 23(2): 10–19. DOI: 10.1515/orhu-2015-0010
57. Elkins N. 2004. *Weather and Bird behavior*. London: T&A D Poyser.
58. Salewski V, Hochachka WM, Fiedler W. 2013. Multiple Weather Factors Affect Apparent Survival of European Passerine Birds. *PLoS One* 8(4): e59110. DOI: 10.1371/journal.pone.0059110
59. Pearce-Higgins JW, Green RE. 2014. *Birds and climate change: impacts and conservation solutions*. Cambridge, UK: Cambridge University Press.
60. Vengerov PD. 2017. Effect of rise in spring air temperature on the arrival dates and reproductive success of the Song Thrush, *Turdus philomelos* (C.L. Brehm, 1831) in the forest-steppe of the Russian Plain. *Russian Journal of Ecology* 48 (2): 178–184. DOI: 10.1134/S1067413617020102

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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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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

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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

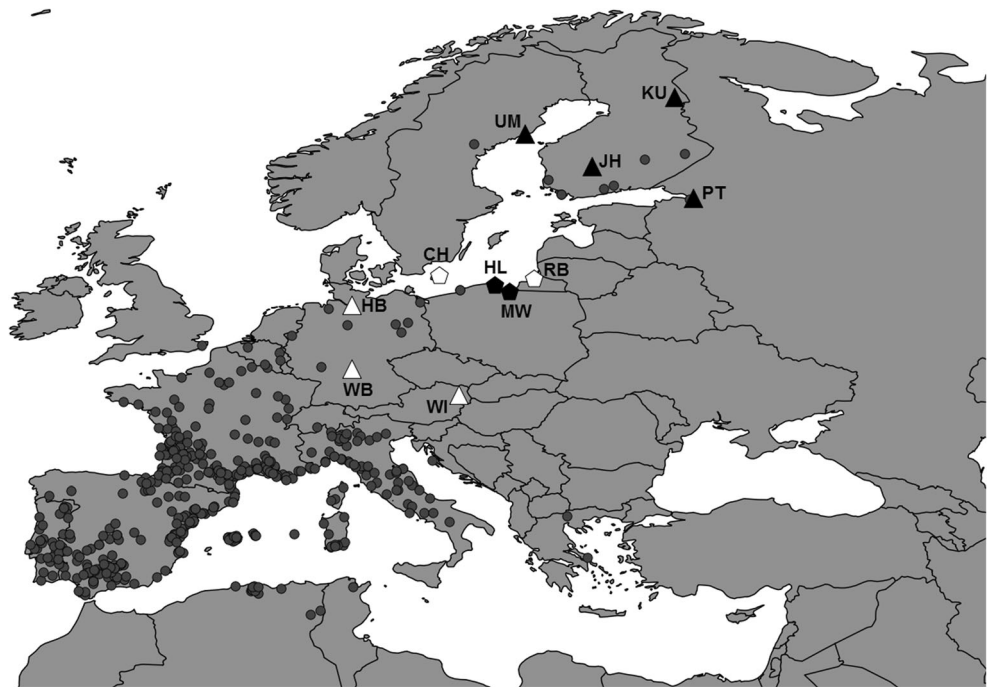
Wiślana (54° 21' N, 19° 17'–19° 23' E), on the Vistula Spit in the south of the Gulf of Gdańsk, which operated during autumn migration from mid-August to the beginning of November.

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).

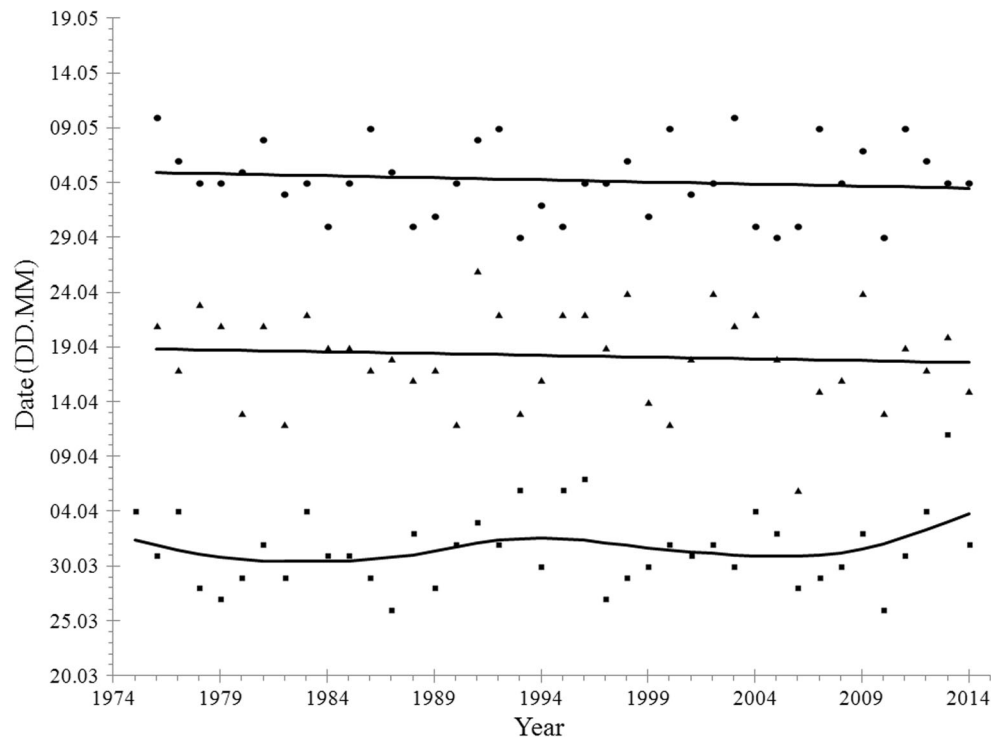
Comparison of migration through Polish and other Baltic stations

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

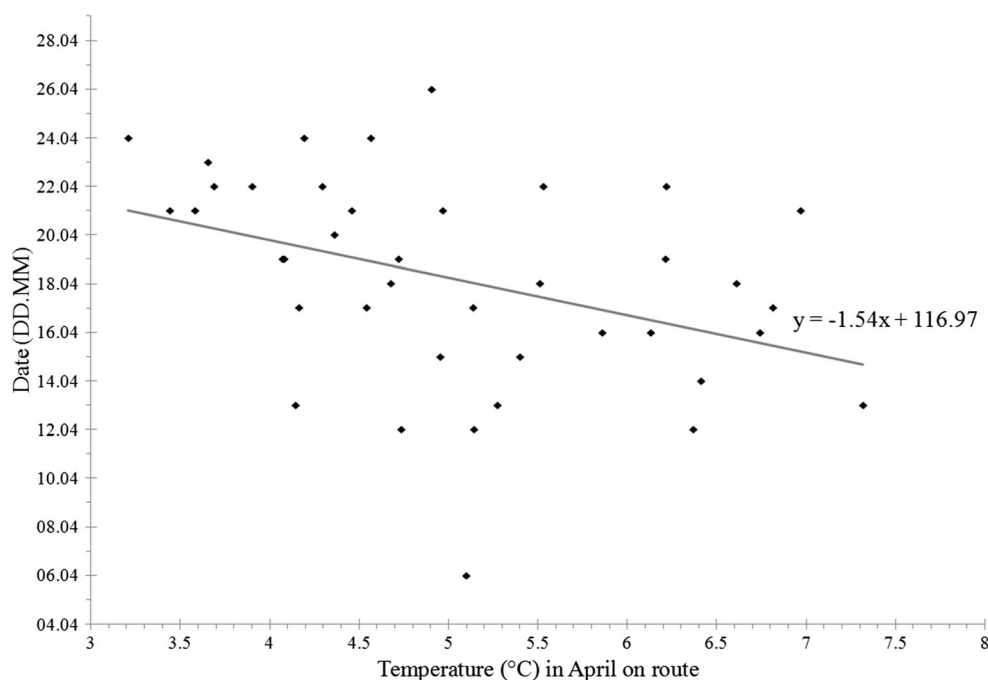
Table 1 Slope coefficients β from linear regressions of dates when 5, 50 and 95% of Song Thrushes migrated through Hel in spring in 1975–2014 with the April mean of minimum daily temperatures, and the April mean of mean daily temperatures averaged for the three weather stations

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

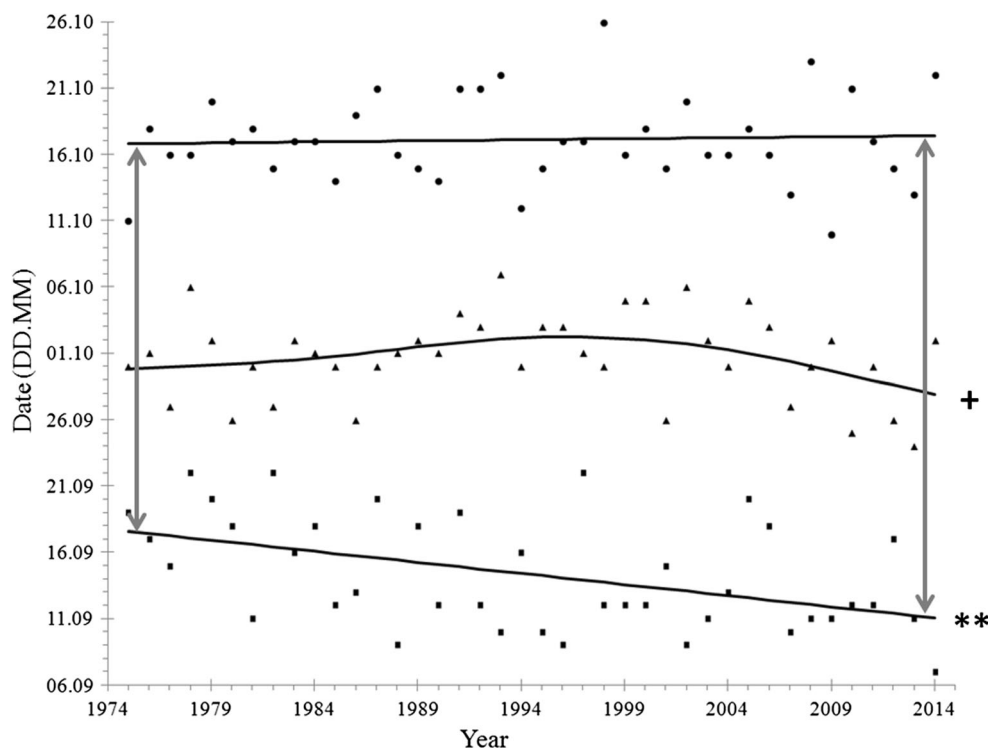


Table 2 Slope coefficients β from linear regressions of dates when 5, 50 and 95% of Song Thrushes migrated in autumn through Mierzeja Wiślana in 1975–2014 with the July mean of minimum daily temperatures at the

breeding 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)

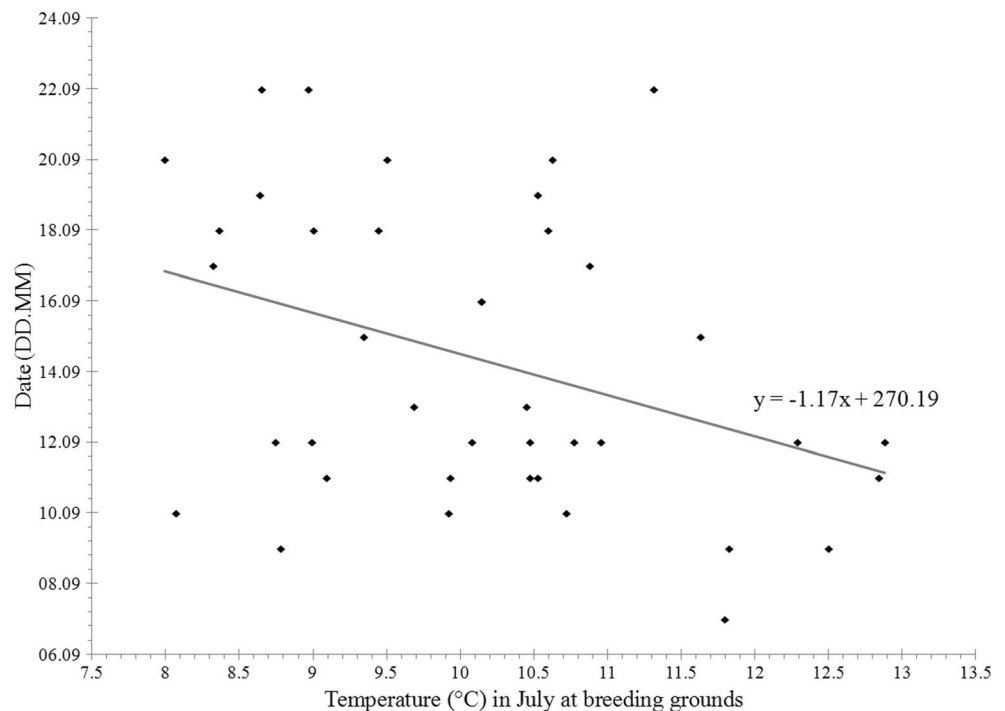


Table 3 Slope coefficients β from linear regressions of dates when 5, 50 and 95% of Song Thrushes migrated in spring through Hel and Rybachy in 1976–1997, against the year. p , comparison of the slope coefficients β by ANCOVA

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.

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References

- Ahola M, Laaksonen T, Sippola K, Eeva T, Rainio K, Lehikoinen E (2004) Variation in climate warming along the migration route uncouples arrival and breeding dates. *Glob Chang Biol* 10:1610–1617. <https://doi.org/10.1111/j.1365-2486.2004.00823.x>
- Allison PD (1999) Multiple Regression: A Primer. Pine Forge Press, Thousand Oaks, p 142
- Askeyev OV, Sparks TH, Askeyev IV, Tryjanowski P (2007) Is earlier spring migration of Tatarstan warblers expected under climate warming? *Int J Biometeorol* 51:459–463. <https://doi.org/10.1007/s00484-007-0085-8>
- Berthold P (1998) Vogelwelt und Klima: Gegenwärtige Veränderungen. *Naturwissenschaftliche Rundschau* 51:337–346
- Berthold P (1996) Control of bird migration. Chapman & Hall, London
- Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migrant. *Nature* 441:81–83. <https://doi.org/10.1038/nature04539>
- Briedis M, Hahn S, Adamik P (2017) Cold spell *en route* delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecol* 17:11. <https://doi.org/10.1186/s12898-017-0121-4>
- Busse P (2000) Bird Station manual. Southeast European bird migration network. University of Gdańsk, Choczewo
- Busse P, Maksalon L (1986) Wędrowki europejskich populacji drozda śpiewaka *Turdus philomelos*. *Notatki Ornitologiczne* 27:1–2
- Chodkiewicz T, Meissner W, Chylarecki P, Neubauer G, Sikora A, Pietrasz K, Cenian Z, Betleja J, Kajtoch Ł, Lenkiewicz W, Ławicki Ł, Rohde Z, Rubacha S, Smyk B, Wieloch M, Wylegała P, Zielińska M, Zieliński P (2016) Monitoring Ptaków Polski w latach 2015–2016. *Biuletyn Monitoringu Przyrody* 15:1–86
- Clement P, Hathway R, Byers C, Wilczur J (2000) Thrushes. Christopher Helm Publishers Ltd, London
- Cotton PA (2003) Avian migration phenology and global climate change. *PNAS* 100:12219–12222. <https://doi.org/10.1073/pnas.1930548100>

- Cramp S (ed) (1988) The birds of the Western Palearctic. Vol V. Oxford University Press, Oxford, pp 989–1000
- Crawley MJ (2013) The R book, 2nd edn. John Wiley & Sons, Ltd, Hoboken, pp 586–588
- Crick HQP, Sparks TH (1999) Climate change related to egg-laying trends. *Nature* 399:423. <https://doi.org/10.1038/20839>
- Demongin L (2016) Identification guide to birds in the hand. Beauregard-Vendon, pp 266
- Dunn P (2004) Breeding dates and reproductive performance. *Adv Ecol Res* 35:67–86. [https://doi.org/10.1016/S0065-2504\(04\)35004-X](https://doi.org/10.1016/S0065-2504(04)35004-X)
- Ehnbom S, Karlsson L, Ylvén R, Åkesson S (1993) A comparison of autumn migration strategies in Robins *Erithacus rubecula* at a coastal and an inland site in southern Sweden. *Ring. Migr* 14:84–93. <https://doi.org/10.1080/03078698.1993.9674049>
- Elkins N (2004) Weather and bird behavior. T&A D Poyser, London
- European Climate Assessment and Dataset (2015) Daily mean and minimum temperatures: <http://eca.knmi.nl/dailydata/predefinedseries.php>. Accessed 15 Aug 2015
- Forchhammer MC, Post E, Stenseth NC (2002) North Atlantic oscillation timing of long- and short-distance migration. *J Anim Ecol* 71:1002–1014. <https://doi.org/10.1046/j.1365-2656.2002.00664.x>
- Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Sage, Thousand Oaks
- Fransson T, Hall-Karlsson S (2008) Svensk ringmärkningsatlas. Vol. 3. Stockholm, pp 85–90
- Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim Res* 35:37–58. <https://doi.org/10.3354/cr00713>
- Gordo O, Tryjanowski P, Kosicki JZ, Fulin M (2013) Complex phenological changes and their consequences in the breeding success of a migratory bird, the white stork *Ciconia ciconia*. *J Anim Ecol* 82:1072–1086. <https://doi.org/10.1111/1365-2656.12084>
- Harvard University Center for the Environment (HUCE) (2013) Extreme weather & climate change. HUCE Newsletter 5:18–21
- Hastie TJ, Tibshirani RJ (1990) Generalized additive models. Chapman and Hall, London
- Howell DC (2015) Randomization Test on Two Independent Samples. <https://www.uvm.edu/~dhowell/StatPages/Randomization%20Tests/Random2Sample/twoindependentsamples.html>. Accessed 16 June 2016
- Huin N, Sparks TH (2000) Spring arrival patterns of the Cuckoo *Cuculus canorus*, nightingale *Luscinia megarhynchos* and spotted flycatcher *Muscicapa striata* in Britain. *Bird Study* 47:22–31. <https://doi.org/10.1080/00063650009461157>
- Hüppop O, Hüppop K (2003) North Atlantic oscillation and timing of spring migration in birds. *Proc R Soc Lond B* 270:233–240. <https://doi.org/10.1098/rspb.2002.2236>
- Knudsen E, Lindén A, Both C, Jonzén N, Pulido F, Saino N, Sutherland WJ, Bach LA, Coppack T, Ergon T, Gienapp P, Gill JA, Gordo O, Hedenström A, Lehikoinen E, Marra PP, Møller AP, Nilsson ALK, Péron G, Ranta E, Rubolini D, Sparks TH, Spina F, Studds CE, Sæther SA, Tryjanowski P, Stenseth NC (2011) Challenging claims in the study of migratory birds and climate change. *Biol Rev* 86:928–946. <https://doi.org/10.1111/j.1469-185X.2011.00179.x>
- Kokko H (1999) Competition for early arrival in migratory birds. *J Anim Ecol* 68:940–950. <https://doi.org/10.1046/j.1365-2656.1999.00343.x>
- Lack D (1972) Ecological adaptations for breeding in birds. Chapman and Hall, London
- Lehikoinen E, Sparks TH (2010) Changes in migration. In: Møller AP, Fiedler W, Berthold P (eds) Effects of Climate Change on Birds. Oxford University Press, Oxford, pp 89–112
- Manly BFJ (2007) Randomization, bootstrap, and Monte Carlo methods in biology, 3rd edn. Chapman & Hall, London, pp 64–65
- Marra PP, Francis CM, Mulvihill RS, Moore FR (2005) The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142:307–315. <https://doi.org/10.1007/s00442-004-1725-x>
- Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kübler K, Bissolli P, Braslavská O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl Å, Defila C, Donnelly A, Filella Y, Jatczak K, Måge F, Mestre A, Nordli Ø, Peñuelas J, Pirinen P, Remišová V, Scheifinger H, Striz M, Susnik A, Van Vliet AJH, Wielgolaski F-E, Zach S, Zust ANA (2006) European phenological response to climate change matches the warming pattern. *Glob Chang Biol* 12:1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>
- Miller-Rushing AJ, Lloyd-Evans TL, Primack RB, Sazinger P (2008) Bird migration times, climate change, and changing population sizes. *Glob Chang Biol* 14:1959–1972. <https://doi.org/10.1111/j.1365-2486.2008.01619.x>
- Milwright RDP (2006) Post-breeding dispersal, breeding site fidelity and migration/wintering areas of migratory populations of Song Thrush *Turdus philomelos* in the Western Palearctic. *Ring. Migr* 23:21–32. <https://doi.org/10.1080/03078698.2006.9674340>
- Mitrus C, Sparks TH, Tryjanowski P (2005) First evidence of phenological change in a transcontinental migrant overwintering in the Indian sub-continent: the red-breasted flycatcher *Ficedula parva*. *Orn Fenn* 82:13–19
- Møller AP, Fiedler W, Berthold P (2010) Introduction. In: Møller AP, Fiedler W, Berthold P (eds) Effects of climate change on birds. Oxford University Press, Oxford, pp 3–5
- Moritz D (1993) Long-term monitoring of Palearctic-African migrants at Helgoland (German Bight, North Sea). *Ann Sei Zool* 268:579–586
- Nowakowski JK, Remisiewicz M, Keller M, Busse P, Rowiński P (2005) Synchronisation of the autumn mass migration of passerines: a case of Robins *Erithacus rubecula*. *Acta Ornithol* 40:103–115. <https://doi.org/10.3161/068.040.0206>
- Payevsky VA (1998) Age structure of passerine migrants at the eastern Baltic coast: the analysis of the “coastal effect”. *Ornis Svecica* 8:171–178
- Portal of Finnish bird ringing services and bird monitoring. (2017). <https://rengastus.helsinki.fi/tuloksia/Pistelaskenta/tilasto/TURPHI> Accessed 15 July 2017
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- Rainio K, Tøttrup AP, Lehikoinen E, Coppack T (2007) Effects of climate change on the degree of protandry in migratory songbirds. *Clim Res* 35:107–114. <https://doi.org/10.3354/cr00717>
- Remisiewicz M, Tree AJ, Underhill LG, Burman MS (2017) Age-specific variation in relationship between moult and pre-migratory fuelling in Wood Sandpipers *Tringa glareola* in southern Africa. *Ibis* 159:91–102. <https://doi.org/10.1111/ibi.12436>
- Rubolini D, Spina F, Saino N (2004) Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behav Ecol* 15:592–601. <https://doi.org/10.1093/beheco/arih048>
- Sinelschikova A, Sokolov LV (2004) Long-term monitoring of the timing of migration in thrushes (*Turdus philomelos*, *T. iliacus*) in the Eastern Baltic. *Avian Ecol Behav* 12:11–30
- Sokolov LV, Markovets MY, Shapoval AP, Morozov YG (1998) Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. *Avian Ecology and Behavior* 1:1–21
- Sparks TH, Tryjanowski P (2005) The detection of climate impacts: some methodological considerations. *Int J Climatol* 25:271–277. <https://doi.org/10.1002/joc.1136>
- Sparks TH, Tryjanowski P (2007) Patterns of spring arrival dates differ in two hirundines. *Clim Res* 35:159–164. <https://doi.org/10.3354/cr00722>
- Svensson L (1992) Identification guide to European passerines, British Trust for Ornithology, The Nunnery, pp 152–153

- Tøttrup AP, Thorup K, Rahbek C (2006a) Patterns of change in timing of spring migration in North European songbird populations. *J Avian Biol* 37:84–92. <https://doi.org/10.1111/j.0908-8857.2006.03391.x>
- Tøttrup AP, Thorup K, Rahbek C (2006b) Changes in timing of autumn migration in North European songbird populations. *Ardea* 94:527–536
- Tryjanowski P, Kuźniak S, Sparks TH (2002) Earlier arrival of some farmland migrants in western Poland. *Ibis* 144:62–68. <https://doi.org/10.1046/j.0019-1019.2001.00022.x>
- Valkama J, Saurola P, Lehtikoinen A, Lehtikoinen E, Piha M, Sola P, Velmala W (2014) The Finnish Bird Ringing Atlas. Vol II. Finnish Museum of Natural History and Ministry of Environment, Helsinki, pp 445–450
- Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York
- Wood S (2017a) Generalized additive models: an introduction with R, 2nd edn. Chapman & Hall. CRC Press, Taylor & Francis Group, Florida
- Wood S (2017b) Package ‘mgcv’. <https://cran.r-project.org/package=mgcv>
- Zar JH (2010) Biostatistical analysis, 5th edn. Pearson Prentice Hall, New Jersey, pp 400–402

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IF = 1.46

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Size dimorphism and sex determination in the song thrush (*Turdus philomelos*) migrating through the southern Baltic coast

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Age and sex are key information to interpret results of studies on birds' biology. As sexing monomorphic species is difficult, in this study we aimed to determine the degree of sexual size dimorphism in song thrushes migrating across the southern Baltic coast, and to develop reliable sexing criteria for future studies of this species. We ringed, measured and took blood samples of song thrushes at the Polish coast. Then we used molecular techniques to determine the sex of ringed individuals and to calculate functions from morphometrics for sexing birds from different age groups. Our results showed a degree of size dimorphism between sexes, more pronounced in adults than in immatures. Dimorphism was clearest in the size of the vestigial outermost primary, which was longer in females despite their smaller size, a likely result of different selection pressures during the breeding season. Differences between sexes were greater in adults than immatures, probably because the immatures are not exposed to selection pressures acting on older birds during migration and breeding. We developed equations allowing to estimate sex correctly of 81.5% of adults in spring and 81% in autumn, and of 63.3% immatures in spring and 63.6% in autumn. Thus, the equation for adults can be used with confidence, while those for immatures with caution.

Introduction

The age and sex of individuals are often key factors to interpret results of many studies on bird biology. Ageing criteria for most Western Palearctic species are well known, but sexing monomorphic species can be problematic (Prater *et al.* 1977, Baker 1993, Svensson 1998, Demongin 2016). In dimorphic species,

such as the blackbird (*Turdus merula*), the chaffinche (*Fringilla coelebs*) and the great tit (*Parus major*), the sexes clearly differ in size or in plumage (Svensson 1998, Demongin 2016). However, species with monomorphic plumage and subtle size differences are difficult to sex in the field because the ranges of morphological measurements overlap (Wilson 1999, Shealer & Cleary 2007, Kulaszewicz *et al.* 2013, Jakubas

et al. 2014, Meissner & Krupa 2016). For some species with no sex differences in plumage, some sexing methods usually based on wing length exist (Svensson 1992, Demongin 2016), but these methods might be population-specific and should be applied with caution (Ellrich et al. 2009). Sexing by DNA is the most reliable method to distinguish between males and females (Dubiec & Zagalska-Neubauer 2006), but it is limited to individuals that were sampled, and is rather expensive and time consuming. However, if a sample of sexed individuals and a set of their morphometrics are available, discriminant function analysis can be used to produce equation which can be used to assess the sex of a bird (Tabachnick & Fidell 2007). The discriminant functions might be subsequently applied to distinguish males from females of unsexed individuals and address the questions considering functions of sexes in monomorphic species in various aspects of their biology, for example in parental care (Wojczulanis-Jakubas et al. 2009), moult (Kulaszewicz & Jakubas 2015, Niemc et al. 2018), or differences between sexes in migration behaviour (Francis & Cooke 1986, Kokko 1999, Morbey & Ydenberg 2001, Nam et al. 2011).

The song thrush, *Turdus philomelos*, is a common migrant passerine widespread in the Western Palearctic (Cramp 1988, Clement et al. 2000), and one of the most frequently ringed birds in the Baltic region during its spring and autumn migrations (Bolshakov et al. 2005, Augustyn 2008, Karlsson 2011, Hellström et al. 2013). Individuals migrating across the southern Baltic coast breed mainly in Scandinavia, Finland and northwestern Russia (Busse & Maksalon 1986, Milwright 2006). Males and females are monomorphic in plumage, but show subtle differences in morphometrics that are too small to sex the birds based on any single measurement (Cramp 1988, Svensson 1998, Demongin 2016). The difficulty with sexing explains why many potential differences in the species' biology outside the breeding season remain unknown. One example might be the extent of protandry during spring and autumn migrations, which has been described for such sexually dimorphic species as the blackbird (*Turdus merula*), the redstart (*Phoenicurus phoenicurus*), the blackcap (*Sylvia atricapilla*) and the red-backed shrike (*Lanius collurio*) (Bakken et al. 2006, Rainio et al. 2007), but remains unknown in the monomorphic thrushes, including the song thrush.

I this study, we aimed to determine the degree of sexual size dimorphism in immature and adult song thrushes migrating across the southern Baltic coast, and to develop reliable sexing criteria by means of discriminant function analysis using measurements data from DNA-sexed individuals.

Material and methods

We captured and ringed song thrushes at the two following Operation Baltic ringing stations (<https://operbalt.ug.edu.pl/>) located on the coast of Gdańsk Bay (southern Baltic, Poland):

1. Hel (54°44'N, 18°33'E), located on the Hel Peninsula. The station operates during the spring migration of passerines, from the last week of March to mid-May. We collected samples at this station in spring 2015 and 2016.
2. Mierzeja Wiślana (54°21'N, 19°23'E), located on the Vistula Spit (south Gdańsk Bay). The station operates during autumn migration, from mid-August to the beginning of November. We collected samples at this station in autumn 2015.

Based on their plumage, we classified all captured individuals either as immatures (between the first post-juvenile moult shortly after leaving the nest and the first complete post-breeding moult), or as adults (after the first complete post-breeding moult) (see Svensson 1992, Demongin 2016).

From each bird we took the set of measurements required by Operation Baltic's standard protocol (Busse & Meissner 2015), and some additional measurements (Kipp 1959, Eck et al. 2011, Svensson 1992, Demongin 2016). These measurements were as follows:

1. Wing length (henceforth "wing"): the distance between the carpal joint and the tip of the longest primary feather of a closed

wing, using the “maximum chord measurement” of the flattened and straightened wing method (Busse & Meissner 2015), also called the “maximum length” (Svensson 1992, Demongin 2016).

2. The distance between the tips of the first and the second primaries (“P1–P2”) (Eck *et al.* 2011).
3. The distance between the tip of the first primary and the tip of the primary coverts (“P1–PC”). This is the distance between the tip of the outermost, vestigial, primary and the tip of the longest primary covert, measured on the folded wing (Eck *et al.* 2011, Demongin 2016). If the first primary is shorter than the longest primary covert, as in the song thrush, the distance is recorded as a negative value.
4. Kipp’s distance (henceforth “kipp”): the distance between the tip of the longest primary and the tip of the outermost secondary, measured on the closed wing (Kipp 1959).
5. The tarsus length (henceforth “tarsus”) which is the distance between the tarsal joint and the distal end of the tarso-metatarsus (Svensson 1992, Demongin 2016).

Experienced Operation Baltic ringers with valid ringing licences issued by the Polish Ringing Centre, each of whom was calibrated against the others, took all measurements. The measurements were taken with a ruler to the nearest 1 mm, except for tarsus, which was measured to the nearest 0.1 mm with callipers.

We also collected blood samples from the brachial vein (Owen 2011) from as many individuals as possible taking care not to put the birds’ well-being at risk. The blood samples were taken with permission from the Local Ethics Committee for Animal Experimentation in Gdańsk, Poland (permission no. 35/2013 issued on 22 July 2013). All blood samples were preserved in 96% ethanol for later DNA sexing. We sampled 136 adults and 131 immatures in the 2015 and 2016 spring seasons, and 81 adults and 136 immatures during autumn 2016.

To sex the song thrushes, we isolated DNA from blood samples using the Blood Mini Kit (A&A Biotechnology), and then conducted PCR analyses with two pairs of primers: P2/P8 (Griffiths *et al.* 1998) and F2/R1 (Bantock *et al.* 2008).

We used two pairs of primers to improve the number of successfully sexed individuals since birds from different populations can differ in their genetic structure (Ball & Avise 1992, Bensch *et al.* 1999, Irwin *et al.* 2005). First we used P2/P8 for all samples, then F2/R1 for samples that were not sexed by the first pair of primers. We also used the F2/R1 primers on 38 samples successfully sexed by the P2/P8 primers to confirm that we obtained the same results with both pairs of primers. We used 16 µl PCR reaction mix containing 2 µl of DNA sample, 1 µl of each primer (10 mM), 1 µl of additional MgCl₂ solution (25 mM), 3.5 µl of sterile-filtered H₂O and 7.5 µl of REDTaq® ReadyMix™ PCR Reaction Mix (Sigma-Aldrich). All PCRs were performed on a T100™ Thermal Cycler (Bio-Rad). We separated the PCR products using horizontal gel electrophoresis. Amplicons obtained using P2/P8 primers were separated on a 3.5% agarose gel for 120 min at 75 V. Amplicons obtained by applying F2/R1 primers were separated on 4% agarose gel for 60 min at 110 V. To visualize DNA bands we added Midori Green Advanced DNA Stain (Nippon Genetics). We assessed the length of the products with a GeneRuler 50 bp DNA Ladder (Thermo Scientific).

For the analyses, we combined the results of sexing from the two spring seasons, and compared measurements between males and females within each age group (immature, adult) at each station by means of the *t*-test (Zar 2010). We then calculated a sexual size dimorphism index (SSD% = [100 × (♂ mean size/♀ mean size) – 1]) to determine the degree of sexual size dimorphism in each measurement (Aradis *et al.* 2015). Positive SSD values indicated that males were larger than females.

Next, we used discriminant function analysis to obtain the best set of measurements to predict the sex of birds in each age group for each station. All the assumptions of the analysis were met, i.e. data were normally distributed, variances were homogenous and variance-covariance matrices were equal for groups (Tabachnick & Fidell 2007). We analysed birds captured in spring and in autumn separately because different patterns of feather abrasion in these seasons could affect the results. We used a stepwise method that included measurements after their pairwise cor-

relation to avoid multicollinearity (Tabachnick & Fidell 2007) and a jack-knife procedure to validate our results (Dechaume-Moncharmont *et al.* 2011). We calculated Cohen's kappa statistic (Titus & Mosher 1984) to check the effectiveness of the functions we obtained because of unequal numbers of males and females. We calculated a cutting score separating males and females as a weighted average of the groups' centroids (Hair *et al.* 1995). Statistical analyses were performed in IBM SPSS Statistics for Windows ver. 23.0 (IBM Corp., Armonk, NY). For each discriminant function we calculated the probabilities of correctly sexing samples by the D score. All tests were two-tailed and the results were considered significant at $p < 0.05$.

Results

Molecular sexing

We successfully sexed 460 of 484 samples (95%) by molecular methods. This included 132 adults (51 males and 81 females) and 131 immatures (63 males and 68 females) caught in spring, and 77 adults (44 males and 33 females) and 120 immatures (64 males and 56 females) captured in autumn (Appendix). All samples for which we used both pairs of primers produced identical results.

Sexual size dimorphism in song thrush

Males had significantly longer wings and a greater P1–P2 distance than the females (Table 1) in all seasons and all age groups. Kipp's distance was significantly greater in males of all groups, except in adult birds in spring. The P1–PC distance was significantly greater in adults in spring and autumn; similar was found for immatures but the difference was not significant. All measurements, except tarsus length, differed between the sexes with males on average larger than females (Table 1). The greatest difference between the sexes in all groups was in P1–PC distance, as evidenced by the greatest SSD%, which indicated a greater distance between the tips of these feathers in males

than in females (Table 1). Sexual dimorphism was stronger in adults than in immatures in most measurements, except for Kipp's distance in spring. In spring and autumn immatures were generally smaller than adults (Table 1).

Discriminant functions for song thrushes

We obtained four discriminant functions, one for each age group in spring and in autumn (Table 2 and Fig. 1). The functions for adults correctly sexed more birds than those for immature birds. The procedure corrected for the unequal numbers of males and females indicated that the classification using these functions improved the efficiency of sexing in adults by 60%–70%, (Kappa values; *see* Table 2) as compared with random allocation of the sex; for immatures the functions improved sexing by 27%–38% (Table 2). For each of the four function, the probability of correctly sexing an individual was higher for birds with extreme D values (Fig. 1).

Discussion

We showed sexual size dimorphism in the song thrush migrating across the southern Baltic coast, which was more pronounced in adults than in immatures. Our functions can help field biologists determine the sex of individual birds from their morphological measurements, but should be applied with caution to immatures because of lower accuracy. Thus, we suggest that any application of our functions should be preceded by adjusting them to the local population using a sample of song thrushes sexed by DNA. Our novel finding that the length of the vestigial outer primary differs between the sexes suggests different selection pressures on males than females during the breeding period

Sex differences in morphological features

Male song thrushes had longer wings than females, as previously reported by Demongin (2016). Wing length can be used as a proxy for the size of an individual (Gosler *et al.* 1995),

Table 1. Characteristics of adult and immature male and female song thrushes captured at Hel (HL) in spring 2015–2016 and at Mierzeja Wiśniana (MW) in autumn 2015. All measurements are in mm. SSD = sexual size dimorphism index.

Group	Measurement	Males			Females			t-test		SSD (%)		
		n	mean	SD	range	n	mean	SD	range		t	p
Spring HL adult	Wing length	50	120.76	2.34	116 to 126	81	118.33	2.31	112 to 123	-5.81	<0.001	2.1
	P1–P2 distance	51	71.92	1.81	67 to 76	79	69.37	2.51	60 to 74	-6.29	<0.001	3.7
	P1–PC distance	51	-13.71	1.76	-10 to -18	80	-11.63	1.84	-17 to -7	6.43	<0.001	17.9
	Kipp's distance	50	37.30	2.21	31 to 41	80	37.03	1.93	34 to 42	-0.75	0.46	0.7
	Tarsus length	50	32.39	0.98	30.0 to 34.5	78	32.66	0.94	30.6 to 35.5	1.56	0.12	-0.8
Spring HL immature	Wing length	61	118.97	2.07	114 to 123	67	117.15	2.57	112 to 124	-4.38	<0.001	1.6
	P1–P2 distance	59	69.27	2.03	65 to 75	66	67.83	2.47	62 to 74	-3.52	<0.001	2.1
	P1–PC distance	59	-10.41	1.60	-7 to -16	66	-9.95	1.86	-17 to -6	1.45	0.15	4.5
	Kipp's distance	56	36.75	2.44	30 to 42	65	35.57	2.65	30 to 41	-2.54	0.01	3.3
	Tarsus length	59	32.45	1.01	29.7 to 34.8	64	32.42	1.15	29.1 to 36.1	-0.15	0.88	0.1
Autumn MW adult	Wing length	42	121.36	2.09	117 to 127	31	119.48	2.93	113 to 125	3.19	<0.001	1.6
	P1–P2 distance	32	72.56	1.85	69 to 76	26	69.81	2.02	66 to 74	5.41	<0.001	3.9
	P1–PC distance	33	-12.70	1.42	-9 to -16	26	-11.58	1.75	-14 to -8	-2.71	0.01	9.7
	Kipp's distance	34	39.00	1.83	36 to 44	26	36.96	1.28	34 to 39	4.85	<0.001	5.5
	Tarsus length	34	32.43	0.93	29.5 to 34.3	27	32.36	1.02	30.4 to 34.5	0.27	0.79	0.2
Autumn MW immature	Wing length	64	118.58	2.44	112 to 124	54	117.56	2.60	110 to 122	2.20	0.03	0.9
	P1–P2 distance	64	68.73	2.22	62 to 74	53	67.55	2.61	56 to 71	2.66	0.01	1.8
	P1–PC distance	63	-10.11	1.39	-6 to -13	53	-9.66	1.73	-13 to -5	-1.55	0.12	4.7
	Kipp's distance	64	37.45	2.24	33 to 48	54	36.43	1.80	32 to 42	2.71	0.01	2.8
	Tarsus length	64	32.68	1.06	30.4 to 36.0	55	32.51	1.29	28.8 to 37.0	0.78	0.44	0.5

Table 2. Results of discriminant function analysis for different age groups (AD = adult, IM = immature) of the song thrush ringed in spring and autumn.

Group	Cut-off values	Correctly sexed indiv. (%)			Cohen's kappa statistic			
		Males	Females	Standard	Jack-knife	Kappa	SE	p <
AD spring	$D_1 < 0.1675$	81.5	$D_1 > 0.1675$	81.5	81.5	0.601	0.095	0.001
IM spring	$D_2 > 0.0265$	63.3	$D_2 < 0.0265$	63.3	63.3	0.262	0.089	0.001
AD autumn	$D_3 > -0.0945$	81	$D_3 < -0.0945$	81	81	0.762	0.133	0.001
IM autumn	$D_4 > -0.0370$	63.6	$D_4 < -0.0370$	63.6	63.6	0.387	0.093	0.001

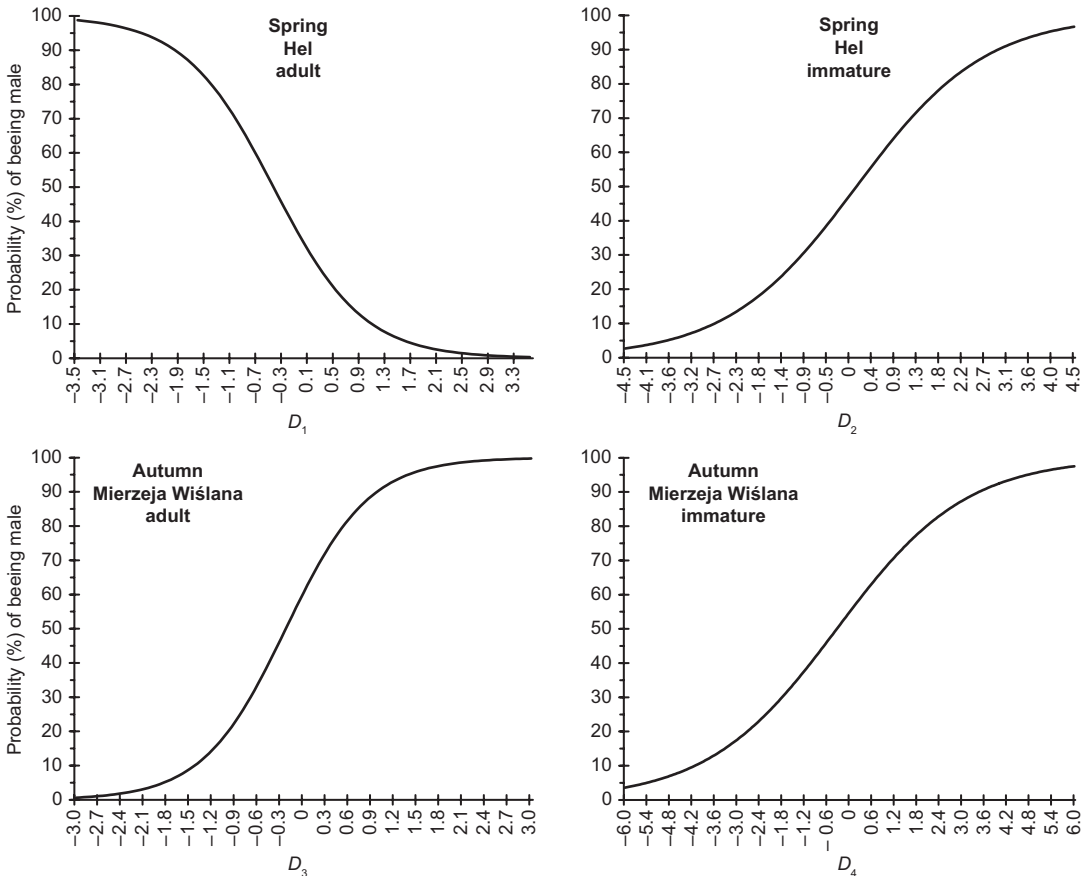


Fig. 1. Probabilities of being a male for adult and immature song thrushes in spring and autumn based on D values. Probability of an individual being a female = $1 -$ probability of an individual being male.

thus the longer wing indicates that males are generally larger than females. We also observed sexual dimorphism in Kipp's distance, P1–PC and P1–P2 distances (Table 1), which have not been previously described. Kipp's distance was greater in males than in females, reflecting differences in wing length, while P1–PC and P1–P2 distances characterise wing shape better than size because they depend on the length of the vestigial outermost primary (P1). This primary is much shorter than the others in most passerines that retain it, including the song thrush (Jenni & Winkler 1994, Hall 2005).

Little has been published on the function of this primary in flight. Its length affects general wing shape because a longer first primary makes wings more rounded, which improves rapid take-off and manoeuvrability but makes flight less energy efficient (Swaddle & Lockwood 2003).

The longer the first primary, the shorter the P1–P2 and P1–PC distances. Though female song thrushes had shorter wings, they had longer first primaries than the males, as indicated by these two distances. This sexual dimorphism in the length of P1 might be explained by the differences in the breeding biology of male and female song thrushes. Females incubate eggs, brood the chicks and spend more time on the nest (Cramp 1988, Clement *et al.* 2000, Demongin 2016), where they are vulnerable to attacks by predators. The relatively longer first primary would improve their ability to take off rapidly thus improving their survival during the breeding period by allowing them to better escape predator attacks when on the nest. Males do not incubate and spend little time on the nest when the female is absent (Cramp 1988, Clement *et al.* 2000), so they are probably less selected for

rapid takeoff and hence have a shorter P1. The longer P1 in females than in males indicates that selection during the breeding period affects their wing shape more than selection during migration. Similar sex differences in P1–P2 were reported in populations of both the migratory and sedentary stonechat *Saxicola torquata* (Baldwin *et al.* 2010), which suggests that the length of P1 is related to the birds' general flight performance.

Efficiency and application of the discriminant functions

The reliable discriminant functions might be a useful tool enabling studies of various aspects of biology in monomorphic species, for example parental duties between the sexes (Wojczulanis-Jakubas *et al.* 2009), differences in moult patterns (Kulaszewicz & Jakubas 2015), or sex-differential migration patterns (Francis & Cooke 1986, Kokko 1999, Morbey & Ydenberg 2001, Remisiewicz & Wennerberg 2006, Sikora & Dubiec 2007, Nam *et al.* 2011). The mean acceptable discriminant rate for sexing reported in literature is ~80% (Dechaume-Moncharmont *et al.* 2011). The functions we derived for adult birds, in spring and in autumn, met this criterion, but the ones for immatures did not (Table 1).

The difference in accuracy can be due to differences in feather quality and wear between age groups. Immature birds' wing feathers are generally of lower quality than those in adults (Francis & Wood 1989, Jenni & Winkler 1994, Merilä & Hemborg 2000, Alonso & Arizaga 2006, De La Hera *et al.* 2010). All first-generation flight feathers in juvenile song thrushes grow simultaneously while birds are still in the nest, only the last stage of feather growth is completed after the fledglings leave the nest (Jenni and Winkler 1994). During the last stages of development in the nest the large, mostly immobile and noisy fledglings are an easy target for nest predators (Ricklefs 1968). This puts pressure on young birds to fledge and leave the nest as soon as possible, even at the cost of poor-quality non-durable flight feathers (Martin 1995, Butler *et al.* 2008, Martin 2015). The development of feathers in nestlings also depends on how well their parents feed them, which is affected

by many factors, such as the parents' own quality, food availability and weather. These factors combined lead to immatures with very different feather quality. Migration, the next step in their annual life cycle, requires intense flight, which results in worn feathers (Swaddle *et al.* 1996, Flinks & Salewski 2012, Echeverry-Galvis & Hau 2013). Individuals with lower-quality plumage are more vulnerable to feather abrasion, which affects the morphometrics of flight feathers and masks any sexual size dimorphism. Adults undergo a full moult before autumn migration, which is spread in time as feathers grow in sequence (Jenni & Winkler 1994). Experienced adult song thrushes are less vulnerable to inclement weather and food shortages (Skórka *et al.* 2016).

Another explanation for the lower accuracy of the discriminant functions for immatures is that the young of small passerines tend to have shorter and more rounded wings than the adults (Slagsvold 1980, Alonso and Arizaga 2003), probably because of the high risk of predation after leaving the nest. Shorter and more rounded wings improve takeoff speed and flight manoeuvrability, decreasing predation vulnerability (Swaddle & Lockwood 1998). The lack of clear differences between the sexes might be because all the young benefit from rounder wings in the same way regardless of their sex. Activities during the breeding period likely affect nesting males and females in different ways, determined by their parental duties. This in turn might lead to sexual dimorphism in wing shape, which is thus easier to detect in adults than in immatures. Additionally, worsening conditions at the breeding grounds in late autumn would force immatures from late broods to start migrating before their wings had fully grown, affecting the results of discriminant function analysis.

The discriminant functions we derived for immatures should be used with caution because they are less robust than those for adults. We recommend molecular sexing as still the most reliable method to sex song thrushes, especially immatures, whenever feasible. On the other hand, the functions we developed for sexing adult song thrushes in spring and autumn are suitable for practical application in studies of the sexual aspects of the song thrush biology. We, however, recommend adjusting the functions for

local populations using a sample of DNA-sexed birds from the population in focus, as the measurements might differ between teams of ringers or be population-specific (Ellrich *et al.* 2010).

Conclusions

We proved sexual size dimorphism in wing length and shape in the song thrush. Males were generally larger than females, as indicated by wing length. However, despite having longer wings, males had a significantly shorter vestigial primary than females. This might be an effect of different selective pressures on the sexes during the breeding season, related to their different parental roles. Sexual size dimorphism was more pronounced in adults than immatures, which had not yet been exposed to any sex-specific pressures during breeding or migration, and whose flight feathers were less durable and often more worn, limiting reliability of their measurements. Our novel application of P1–P2, P1–PC and Kipp's distances, in combination with traditionally used wing length, provides a useful tool for other researchers to facilitate studies of sex-related aspects of biology in the song thrush, and other monomorphic species of passerines.

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References

- Alonso, D. & Arizaga, J. 2006: Biometrics of citril finch *Serinus citrinella* in the west Pyrenees and the influence of feather abrasion on biometric data. — *Ringing & Migration* 23: 116–124.
- Aradis, A., Landucci, G., Tagliavia, M. & Bultrini, M. 2015: Sex determination of Eurasian woodcock *Scolopax rusticola*: a molecular and morphological approach. — *Avocetta* 39: 83–89.
- Augustyn, A. 2008: Sprawozdanie z prac Akcji Bałtyckiej w latach 1994–2005. — *Notatki Ornitologiczne* 49: 186–202.
- Baker, K. 1993: *Identification guide to European non-passerines*. — British Trust for Ornithology, The National Centre for Ornithology.
- Bakken, V., Runde, O. & Tjorve, E. 2006: *Norsk ringmergingsatlas*, vol. 2. — Stavanger Museum, Stavanger.
- Baldwin, M. W., Winkler, H., Organ, C. L. & Helm, B. 2010: Wing pointedness associated with migratory distance in common garden and comparative studies of stonechats (*Saxicola torquata*). — *Journal of Evolutionary Biology* 23: 1050–1063.
- Ball, R. M. & Avise, J. C. 1992: Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. — *The Auk* 109: 626–636.
- Bantock, T. M., Prys-Jones, R. T. P. & Lee, P. L. M. 2008: New and improved molecular sexing for museum bird specimens. — *Molecular Ecology Notes* 8: 519–528.
- Bensch, S., Andersson, T. & Akesson, S. 1999: Morphological and molecular variation across a migratory divide in willow warblers, *Phylloscopus trochilus*. — *Evolution* 53: 1925–1935.
- Bowlin, M. S. & Wikelski, M. 2008: Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. — *PLoS ONE* 3: e2154, <https://doi.org/10.1371/journal.pone.0002154>.
- Busse, P. & Meissner, W. 2015: *Bird ringing station manual*. — De Gruyter Open Ltd., Warsaw.
- Busse, P. & Maksalon, L. 1986: Wędrówki europejskich populacji drozda śpiewaka *Turdus philomelos*. — *Notatki Ornitologiczne* 27: 1–2.
- Butler, L. K., Rohwer, S. & Speidel, M. G. 2008: Quantifying structural variation in contour feathers to address functional variation and life history trade-offs. — *Journal of Avian Biology* 39: 629–639.
- Bolshakov, C. V., Shapoval, A. P. & Zelenova, N. P. 2005: Results of bird trapping and ringing by the Biological Station “Rybachy” on the Courish Spit in 2004. — *Avian Ecology and Behaviour* 13: 4–95.
- Clement, P., Hathway, R., Byers, C. & Wilczur, J. 2000: *Thrushes*. — Christopher Helm Publishers Ltd., London.
- Cramp, S. (ed.) 1988: *The birds of the Western Palearctic*, vol. V. — Oxford University Press, Oxford.
- De La Hera, I., Hedenström, A., Pérez-Tris, J. & Tellería, J. L. 2010: Variation in the mechanical properties of flight feathers of the blackcap *Sylvia atricapilla* in relation to migration. — *Journal of Avian Biology* 41: 342–347.
- Dechaume-Moncharmont, F.X., Monceau, K. & Cézilly, F. 2011: Sexing birds using discriminant function analysis: a critical appraisal. — *The Auk* 128: 78–86.
- Demongin, L. 2016: *Identification guide to birds in the hand*. — Published by the author.
- Dubiec, A. & Zagalska-Neubauer, M. 2006: Molecular techniques for sex identification in birds. — *Biological Letters* 43: 3–12.
- Eck, S., Töpfer, T., Fiebig, J., Heynen, I., Fiedler, W., Nicolai, B., van den Elzen, R., Winkler, R. & Woog, F. 2011:

- Measuring birds*. — Christ Media Natur, Minden.
- Echeverry-Galvis, M. A. & Hau, M. 2013: Flight performance and feather quality: paying the price of overlapping moult and breeding in a tropical highland bird. — *PLoS ONE* 8(5): e61106, <https://doi.org/10.1371/journal.pone.0061106>.
- Ellrich, H., Salewski, V. & Fiedler, W. 2009: Morphological sexing of passerines: not valid over larger geographical scales. — *Journal of Ornithology* 151: 449–458.
- Flinks, H. & Salewski, V. 2012: Quantifying the effect of feather abrasion on wing and tail lengths measurements. — *Journal of Ornithology* 153: 1053–1065.
- Francis, C. M. & Wood, D. S. 1989: Effects of age and wear on wing length of wood-warblers. — *Journal of Field Ornithology* 60: 495–503.
- Gosler, A. G., Greenwood, J. J. D., Baker, J. K. & King, J. R. 1995: A comparison of wing length and primary length as size measures for small passerines. — *Ringing & Migration* 16: 65–78.
- Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G. 1998: A DNA test to sex most birds. — *Molecular Ecology* 7: 1071–1075.
- Hall, K. S. S. 2005: Do nine-primaried passerines have nine or ten primary feathers? The evolution of a concept. — *Journal of Ornithology* 146: 121–126.
- Hedenström, A. 2002: Aerodynamics, evolution and ecology of avian flight. — *Trends in Ecology and Evolution* 17: 415–422.
- Hellström, M., Ottvall, R., Andersson, A., Magnusson, C., Waldenström, J. & Lindström, Å. 2013: *Fågelräkning och ringmärkning vid Ottenby fågelstation (2013)*. — Ottenby Bird Observatory, Swedish Ornithological Society.
- Irwin, D. E., Bensch, S., Irwin, J. H. & Price, T. D. 2005: Speciation by distance in a ring species. — *Science* 307: 414–416.
- Jakubas, D., Wojczulanis-Jakubas, K., Foucher, J., Dziarska-Palac, J. & Dugué, H. 2014: Age and sex differences in fuel load and biometrics of aquatic warblers *Acrocephalus palaudicola* at an autumn stopover site in the Loire Estuary (NW France). — *Ardeola* 61: 15–30.
- Jenni, L. & Winkler, R. 1994: *Moult and ageing of European passerines*. — Academic Press, London.
- Karlsson, L. 2011: *Ringing at Falsterbo Bird Observatory 2011*. — Falsterbo Bird Observatory.
- Kipp, F. A. 1959. Der Handflügel-Index als flugbiologisches Maß. — *Vogelwarte* 20: 77–86.
- Kulaszewicz, I., Jakubas, D. & Wojczulanis-Jakubas, K. 2013: Sex discrimination in the Savi's warbler (*Locustella luscinioides*) using morphometric traits. — *Ornis Fennica* 90: 203–210.
- Kulaszewicz I. & Jakubas D. 2015: Factors affecting post-breeding moult in the Savi's warbler *Locustella luscinioides* in northern Poland. — *Ardea* 103: 61–68.
- Martin, T. E. 1995: Avian life history evolution in relation to nest sites, nest predation and food. — *Ecological Monographs* 65: 101–127.
- Martin, T. E. 2015: Age-related mortality explains life history strategies of tropical and temperate songbirds. — *Science* 349: 966–970.
- Meissner, W. & Krupa, R. 2016: Identifying the sex of the common sandpiper (*Actitis hypoleucos*) by linear measurements. — *Annales Zoologici Fennici* 53: 175–182.
- Meissner, W., Pinchuk, P., Karlionova, N., Fisher, I. & Pilacka, L. 2018: Sexual size dimorphism and sex determination by external measurements in the redshank *Tringa tetanus*. — *Turkish Journal of Zoology* 42: 1–5.
- Merilä, J. & Hemborg, C. 2000: Fitness and feather wear in the collared flycatcher *Ficedula albicollis*. — *Journal of Avian Biology* 31: 504–510.
- Milwright, R. D. P. 2006: Post-breeding dispersal, breeding site fidelity and migration/wintering areas of migratory populations of song thrush *Turdus philomelos* in the Western Palearctic. — *Ringing & Migration* 23: 21–32.
- Mönkkönen, M. 1995: Do migrant birds have more pointed wings?: a comparative study. — *Evolutionary Ecology* 9: 520–528.
- Niemc, A., Remisiewicz, M., Avni, J. & Underhill, L. G. 2018: Sexual dimorphism in adult Little Stints (*Calidris minuta*) revealed by DNA sexing and discriminant analysis. — *PeerJ* 6: e5367, <https://doi.org/10.7717/peerj.5367>.
- Owen, J. C. 2011: Collecting, processing, and storing avian blood: a review. — *Journal of Field Ornithology* 82: 339–354.
- Prater, T., Marchant, J. & Vuorinen, J. 1977: *Guide to the identification and ageing of Holarctic waders*. — British Trust for Ornithology.
- Remisiewicz, M. & Wennerberg, L. 2006: Differential migration strategies of the wood sandpiper (*Tringa glareola*) — genetic analyses reveal sex differences in morphology and spring migration phenology. — *Ornis Fennica* 83: 1–10.
- Ricklefs, R. E. 1968: Patterns of growth in birds. — *Ibis* 110: 419–451.
- Sikora A. & Dubiec A. 2007: Sex identification of jack snipe *Lymnocyptes minimus* by discriminant analysis of morphometric measurements. — *Ardea* 95: 125–133
- Shealer, D. A. & Cleary, C. M. 2007: Sex determination of adult black terns by DNA and morphometrics: tests of sample size, temporal stability and geographic specificity in the classification accuracy of discriminant function models. — *Waterbirds* 30: 180–188.
- Skórka, P., Lenda, M. & Sutherland, W. J. 2016: Response of young and adult birds to the same environmental variables and different spatial scales during post breeding period. — *Landscape Ecology* 31: 2063–2078.
- Slagsvold, T. 1982: Morphology of the hooded crow *Corvus corone cornix* in relation to locality, season and year. — *Fauna Norvegica C* 3: 16–35.
- Swaddle, J. P., Witter, M. S., Cuthill, I. C., Budden, A. & McCowen, P. 1996: Plumage condition affects flight performance in common starlings: implications for developmental homeostasis, abrasion and moult. — *Journal of Avian Biology* 27: 103–111.
- Swaddle, J. P. & Lockwood, R. 1998: Morphological adaptations to predation risk in passerines. — *Journal of Avian Biology* 29: 172–176.
- Swaddle, J. P. & Lockwood, R. 2003: Wingtip shape and flight performance in the European starling *Sturnus vulgaris*. — *Ibis* 145: 457–464.

- Svensson, L. 1992: *Identification guide to European passerines*. — British Trust for Ornithology.
- Tabachnick, B. G. & Fidell, L. S. 1996: *Using multivariate statistics*, 3rd ed. — Harper Collins Publishers, New York.
- Titus, K. & Mosher, J. A. 1984: Chance-corrected classification for use in discriminant analysis: ecological application. — *The American Midland Naturalist* 111: 1–7.
- Wilson, R. R. 1999: Sex determination of the acadian flycatcher using discriminant analysis. — *Journal of Field Ornithology* 70: 514–519.
- Wojczulanis-Jakubas, K., Jakubas D. & Stempniewicz L. 2009: Sex-specific parental care by incubating little auks (*Alle alle*). — *Ornis Fennica* 86: 140–148.
- Zar, J. H. 2010: *Biostatistical analysis*, 5th ed. — Pearson Prentice Hall, New Jersey.

Appendix. Numbers of DNA-sexed adult and immature song thrushes captured at Hel in spring 2015–2016 and at Mierzeja Wiślana in autumn 2015.

Station (season)	Age group	Number of all samples	Number of sexed samples	Number of males	Number of females
Hel (spring)	adult	136	132	51	81
	immature	131	131	63	68
Mierzeja Wiślana (autumn)	adult	81	77	44	33
	immature	136	120	64	56

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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 (Orlans 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-Karlssohn 2008). Reed Bunting *Emberiza schoeniclus* males migrate a shorter distance than females and return to the breeding grounds earlier (Fransson & Hall-Karlssohn 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).

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

$$D_1 = 35.828 + 0.423 * P1 - PC - 0.256 * Wing$$

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 & Maksimalon 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.



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.

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

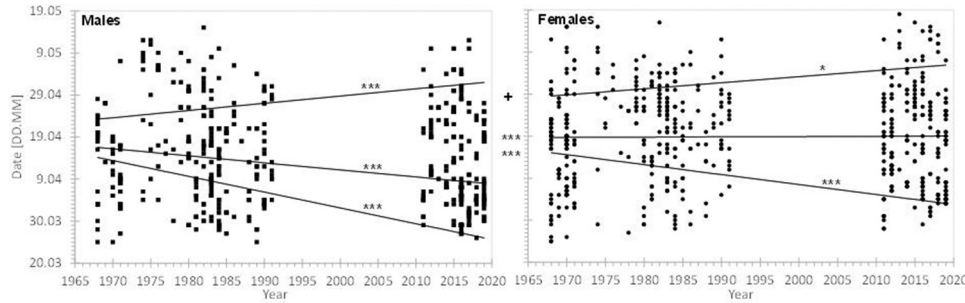


Figure 2. Spring migration dates of Song Thrushes by sex against year at Hel, N Poland, in 31 springs between 1968 and 2019, and linear trends by quantile regression. Bottom lines – q10, middle lines – q50, top lines – q90. Symbols between left and right figures indicate significant differences in the 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 (β) 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		
	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	<i>0.0919</i>
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	<i>-0.93</i>	<i>0.51</i>	<i>0.0744</i>	-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. β – 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; $\beta * 52$ 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*.

Factor	Change (days) per year or 1°C (β)			52 years * β (days)		
	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	<i>0.93</i>	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	<i>0.50</i>	–1.49			
TJan	1.21	<i>0.89</i>	–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

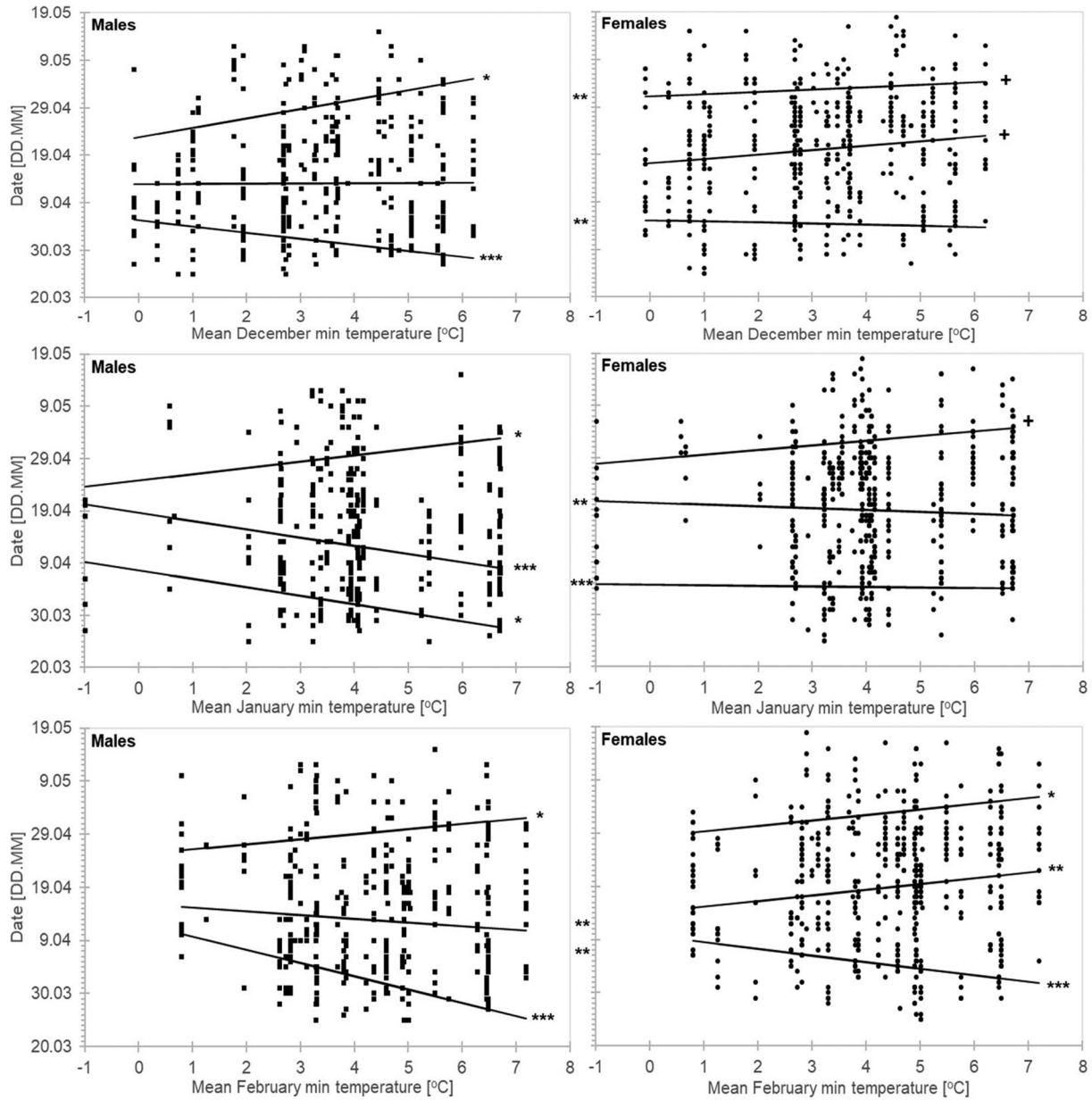


Figure 3. Spring migration dates of Song Thrushes at Hel, N Poland, by sex against the monthly means of minimum temperatures in December, January and February at the wintering grounds in 31 seasons between 1968 and 2019. Bottom lines – q10, middle lines – q50, top lines – q90. Symbols between left and 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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References

- Ahola M, Laaksonen T, Sippola K, Eeva T, Rainio K, Lehikoinen E. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology* 10:1610–1617. DOI: [10.1111/j.1365-2486.2004.00823.x](https://doi.org/10.1111/j.1365-2486.2004.00823.x).
- Alerstam T, Högstedt G. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. *Ornis Scandinavica* 13:25–37. DOI: [10.2307/3675970](https://doi.org/10.2307/3675970).
- Bakken V, Runde O, Tjørve E. 2006. Norsk ringmerkingatlas. Vol. 2. Stavanger: Stavanger Museum.
- Balbotin J, Møller AP, Hermosell IG, Marzal A, Reviriego M, de Lope F. 2009. Divergent patterns of impact of environmental conditions on life history traits in two populations of a long-distance migratory bird. *Oecologia* 159:859–872. DOI: [10.1007/s00442-008-1267-8](https://doi.org/10.1007/s00442-008-1267-8).
- Berthold P. 1993. Bird migration. A general survey. Oxford: Oxford University Press.
- Berthold P. 1996. Control of bird migration. London: Chapman & Hall.
- Briedis M, Hahn S, Adamik P. 2017. Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird. *BMC Ecology* 17(1):11. DOI: [10.1186/s12898-017-0121-4](https://doi.org/10.1186/s12898-017-0121-4).
- Busse P, Maksalon L. 1986. Wędrowniki europejskich populacji drozda śpiewaka *Turdus philomelos*. Notatki Ornitologiczne 27:1–2. (in Polish with English summary).
- Busse P, Meer W. 2015. Bird ringing station manual. Berlin, Boston: De Gruyter.
- Cade BS, Noon BR. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1(8):412–420. DOI: [10.1890/1540-9295-\(2003\)001\[0412:AGITQR\]2.0.CO;2](https://doi.org/10.1890/1540-9295-(2003)001[0412:AGITQR]2.0.CO;2).
- Caldow RWG, Goss-Custard JD, Stillman RA, Dit Durell SE, Swinfen R, Bregnballe T. 2002. Individual variation in the competitive ability of interference-prone foragers: The relative importance of foraging efficiency and susceptibility to interference. *Journal of Animal Ecology* 68(5):869–878. DOI: [10.1046/j.1365-2656.1999.00334.x](https://doi.org/10.1046/j.1365-2656.1999.00334.x).
- Catry P, Lecoq M, Araujo A, Conway G, Felgueiras M, King JMB, Rumsey S, Salima H, Tenr P. 2005. Differential migration of chiffchaffs *Phylloscopus collybita* and *P. ibericus* in Europe and Africa. *Journal of Avian Biology* 36:184–190. DOI: [10.1111/j.0908-8857.2005.03445.x](https://doi.org/10.1111/j.0908-8857.2005.03445.x).
- Catry P, Phillips R, Croxall JP. 2006. Sexual segregation in birds: Patterns, processes and implications for conservation. In: Ruckstuhl KE, Neuhaus P, editors. *Sexual segregation in vertebrates*. Cambridge: Cambridge University Press; pp. 351–378.
- Clement P, Hathway R, Byers C, Wilczur J. 2000. Thrushes. London: Christopher Helm Publishers Ltd.
- Collar N. 2005. Song Thrush. In: Del Hoyo J, Elliott A, Sargatal J, Christie D, de Juana E, editors. *Handbook of the birds of the world*. Barcelona: Lynx Edicions. pp. 637–638.
- Cramp S. 1988. The birds of the Western palearctic. Vol. V. Oxford: Oxford University Press.
- Csörgo T, Harnos A. 2011. Change of migration timing of Chiffchaff (*Phylloscopus collybita*) during 23 years. *Ornis Hungarica* 9(1–2):53–63. (in Hungarian with English summary).
- Demongin L. 2016. Identification guide to birds in the hand. Beaugard-Vendon: Demongin. pp. 266.
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carr G, Garc JR, Gruber B, Lafourcade B, Leit PJ, Tamara M, McClean C, Osborne PE, Der BS, Skidmore AK, Zurell D, Lautenbach S. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46. DOI: [10.1111/j.1600-0587.2012.07348.x](https://doi.org/10.1111/j.1600-0587.2012.07348.x).
- Dubiec A, Zagalska-Neubauer M. 2006. Molecular techniques for sex identification in birds. *Biological Letters* 43:3–12.
- Dytham C. 2011. Choosing and using statistics: A biologist's guide. 3rd ed. Chichester, UK: Wiley-Blackwell.
- Eck S, Töpfer T, Fiebig J, Heynen I, Fiedler W, Nicolai B, van den Elzen R, Winkler R, Woog F. 2011. Measuring birds. Vögel vermessen. Deutsche Ornithologen-Gesellschaft, Wilhelmshaven.
- Elkins N. 2004. Weather and bird behavior. London: T&A D Poyser.
- European Climate Assessment and Dataset. 2018. Daily mean and minimum temperatures. Available: <http://eca.knmi.nl/dailydata/predefinedseries.php>. Accessed May 2018 15.

- Forchhammer MC, Post E, Stenseth NC. 2002. North Atlantic oscillation timing of long- and short-distance migration. *Journal of Animal Ecology* 71:1002–1014. DOI: 10.1046/j.1365-2656.2002.00664.x.
- Francis CM, Cooke F. 1986. Differential timing of spring migration in wood warblers (Parulinae). *Auk* 103:548–556.
- Fransson T, Hall-Karlsson S. 2008. Svensk ringmärkningsatlas. Vol. 3. Stockholm: Naturhistoriska riksmuseet & Sveriges Ornitologiska Forening.
- Frost J. 2019. Regression analysis. An intuitive guide for using and interpreting linear models. 1st ed. US: Statistics By Jim Publishing. Available: statisticsbyjim.com. Accessed Oct 2020 08.
- Geraci M. 2014. Linear quantile mixed models: The lqmm package for Laplace quantile regression. *Journal of Statistical Software* 57(13):1–29. DOI: 10.18637/jss.v057.i13.
- Geraci M. 2019. Package ‘lqmm’. Linear Quantile Mixed Models. Available: <https://cran.r-project.org/web/packages/lqmm/lqmm.pdf>. Accessed Oct 2020 8.
- Gill F. 1995. Ornithology. New York: WH Freeman and Co.
- Gordo O, José Sanz J. 2008. The relative importance of conditions in wintering and passage areas on spring arrival dates: The case of long-distance Iberian migrants. *Journal of Ornithology* 149:199–210. DOI: 10.1007/s10336-007-0260-z.
- Halupka L, Halupka K. 2017. The effect of climate change on the duration of avian breeding seasons: A meta-analysis. *Proceedings of the Royal Society of London B* 284:1710. DOI: 10.1098/rspb.2017.1710.
- Harnos A, Lang Z, Fehérvári P, Csörgő T. 2015a. Sex and age dependent migration phenology of the Pied Flycatcher in a stopover site in the Carpathian Basin. *Ornis Hungarica* 23(2):10–19. DOI: 10.1515/orhu-2015-0010.
- Harnos A, Nóra Á, Kovács S, Lang Z, Csörgő T. 2015b. Increasing protandry in the spring migration of the Pied Flycatcher (*Ficedula hypoleuca*) in Central Europe. *Journal of Ornithology* 156(2):543–546. DOI: 10.1007/s10336-014-1148-3.
- Hedlund JSU, Jakobsson S, Kullberg C, Fransson T. 2015. Long-term phenological shifts and intra-specific differences in migratory change in the willow warbler *Phylloscopus trochilus*. *Journal of Avian Biology* 46:97–106. DOI: 10.1111/jav.00484.
- Huin N, Sparks TH. 2000. Spring arrival patterns of the Cuckoo *Cuculus canorus*, Nightingale *Luscinia megarhynchos* and spotted Flycatcher *Muscicapa striata* in Britain. *Bird Study* 47:22–31. DOI: 10.1080/00063650009461157.
- Hüppop O, Hüppop K. 2003. North Atlantic oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London B* 270:233–240. DOI: 10.1098/rspb.2002.2236.
- Jarjour C, Frei B, Elliott KH. 2017. Associations between sex, age and species-specific climate sensitivity in migration. *Animal Migration* 4(1):23–36. DOI: 10.1515/ami-2017-0004.
- Johnson K, Burley N. 1998. Mating tactics and mating systems of birds. *Ornithological Monographs* 49:21–60. DOI: 10.2307/40166717.
- Katti M, Price T. 1999. Annual variation in fat storage by a migrant warbler overwintering in the Indian tropics. *Journal of Animal Ecology* 68(4):815–823. DOI: 10.1046/j.1365-2656.1999.00331.x.
- Ketterson ED, Nolan VJ. 1983. The evolution of differential bird migration. In: Johnston RF, editor. *Current ornithology*. Vol. 1. New York: Plenum Press. pp. 357–402.
- Koenker R. 2004. Quantile regression for longitudinal data. *Journal of Multivariate Analysis* 91:74–89. DOI: 10.1016/j.jmva.2004.05.006.
- Koenker R, Bassett G. 1978. Regression quantiles. *Econometrica* 46(1):33–50. DOI: 10.2307/1913643.
- Kokko H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68:940–950. DOI: 10.1046/j.1365-2656.1999.00343.x.
- Kokko H, Gunnarsson TG, Morrell LJ, Gill JA. 2006. Why do female migratory birds arrive later than males? *Journal of Animal Ecology* 75:1293–1303. DOI: 10.1111/j.1365-2656.2006.01151.x.
- Komar O, O’Shea BJ, Peterson AT, Navarro-Sigüenza AG. 2005. Evidence of latitudinal sexual segregation among migratory birds wintering in Mexico. *The Auk* 122(3):938–948. DOI: 10.1093/auk/122.3.938.
- Lehikoinen A, Lindén A, Karlsson M, Andersson A, Crewe TL, Dunn EH, Gregory G, Karlsson L, Kristiansen V, Mackenzie S, Newman S, Røer JE, Sharpe C, Sokolov LV, Steinholtz A, Stervander M, Tirri IS, Tjørnløv RS. 2019. Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. *Ecological Indicators* 101:985–991. DOI: 10.1016/j.ecolind.2019.01.083.
- Lehikoinen E, Sparks TH. 2010. Changes in migration. In: Møller AP, Fiedler W, Berthold P, editors. *Effects of climate change on birds*. Oxford: Oxford University Press. pp. 89–112.
- Lozano G, Perreault S, Lemon R. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. *Journal of Avian Biology* 27(2):164–170. DOI: 10.2307/3677146.
- Lundberg A, Alatalo RV. 1992. The pied flycatcher. London, UK: T & A D Poyser.
- Lundberg P. 1985. Dominance behaviour, body weight and fat variations, and partial migration in European blackbirds *Turdus merula*. *Behavioral Ecology and Sociobiology* 17:185–1889.
- MacMynowski DP, Root TL. 2007. Climate and the complexity of migratory phenology: Sexes, migratory distance, and arrival distributions. *International Journal of Biometeorology* 51:361–373. DOI: 10.1007/s00484-006-0084-1.
- Maggini I, Bairlein F. 2012. Innate sex differences in the timing of spring migration in a songbird. *PLoS ONE* 7(2):e31271. DOI: 10.1371/journal.pone.0031271.
- Marra PP, Francis CM, Mulvihill RS, Moore FR. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142:307–315. DOI: 10.1007/s00442-004-1725-x.
- Mazur AE, Remisiewicz M, Underhill LG. 2020. Sex-specific patterns of fuelling and pre-breeding body moult of little stints *Calidris minuta* in South Africa. *Ibis*. DOI: 10.1111/ibi.12840.
- Milwright RDP. 2006. Post-breeding dispersal, breeding site fidelity and migration/wintering areas of migratory populations of Song Thrush *Turdus philomelos* in the Western Palearctic. *Ringing & Migration* 23:21–32. DOI: 10.1080/03078698.2006.9674340.
- Møller AP. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology* 35:115–122. DOI: 10.1007/BF00171501.
- Møller AP. 2004. Protandry, sexual selection and climate change. *Global Change Biology* 10:2028–2035. DOI: 10.1111/j.1365-2486.2004.00874.x.
- Morbey YE, Ydenberg RC. 2001. Protandrous arrival timing to breeding areas: A review. *Ecology Letters* 4:663–673. DOI: 10.1046/j.1461-0248.2001.00265.x.
- Muscianese E, Martino G, Sgro P, Scebba S, Sorrenti M. 2018. Timing of pre-nuptial migration of the Song Thrush *Turdus philomelos* in Calabria (Southern Italy). *Ring* 40:19–30. DOI: 10.1515/ring-2018-0002.

- Najmanová L, Adamík P. 2009. Effect of climatic change on the duration of the breeding season in three European thrushes. *Bird Study* 56(3):349–365. DOI: 10.1080/00063650902937305.
- Nam HY, Choi CY, Park JG, Hong GP, Won IJ, Kim SJ, Bing GC, Chae HY. 2011. Protandrous migration and variation in morphological characters in *Emberiza buntings* at an East Asian stopover site. *Ibis* 153:494–501. DOI: 10.1111/j.1474-919X.2011.01134.x.
- Newton I. 1998. Population limitation in birds. London: Academic Press.
- Newton I. 2008. The migration ecology of birds. London: Academic Press.
- Newton I. 2011. Migration within the annual cycle: Species, sex and age differences. *Journal of Ornithology* 152(Suppl 1): S169–S185. DOI: 10.1007/s10336-011-0689-y.
- Nisbet ICT, Medway L. 1972. Dispersion, population ecology and migration of Eastern great reed warblers *Acrocephalus orientalis* wintering in Malaysia. *Ibis* 114:451–494. DOI: 10.1111/j.1474-919X.1972.tb00850.x.
- Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London B* 271:59–64. DOI: 10.1098/rspb.2003.2569.
- Nowakowski JK, Muś K, Stępniewski K, Manikowska-Ślepowska B, Szulc J. 2012. Internetowa Baza Danych Programu Badawczego “Akcja Bałtycka”. Stacja Badania Wędrówek Ptaków, Uniwersytet Gdański (in Polish). Available: <http://akbalt.ug.edu.pl>. Accessed Oct 2018 10.
- Orians G. 1969. On the evolution of mating systems in birds and mammals. *The American Naturalist* 103(934):589–603. DOI: 10.1086/282628.
- Payevsky VA. 2009. Songbird demography. Sofia – Moscow: Pensoft Publishers.
- Pearce-Higgins JW, Green RE. 2014. Birds and climate change: Impacts and conservation solutions. Cambridge, UK: Cambridge University Press.
- R Core Team. 2020. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available: <https://www.R-project.org>. Accessed Oct 2020 12.
- Rainio K, Tøttrup AP, Lehikoinen E, Coppack T. 2007. Effects of climate change on the degree of protandry in migratory songbirds. *Climate Research* 35:107–114. DOI: 10.3354/cr00717.
- Redliski M, Mazur A, Remisiewicz M. 2020. Size dimorphism and sex determination in the song thrush (*Turdus philomelos*) migrating through the southern Baltic coast. *Annales Zoologici Fennici* 57:31–40. DOI: 10.5735/086.057.0104.
- Redliski M, Remisiewicz M, Nowakowski JK. 2018. 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. *International Journal of Biometeorology* 62:1595–1605. DOI: 10.1007/s00484-018-1559-6.
- Remisiewicz M, Wennerberg L. 2006. Differential migration strategies of the Wood Sandpiper (*Tringa glareola*) – Genetic analyses reveal sex differences in morphology and spring migration phenology. *Ornis Fennica* 83:1–10.
- Robson D, Barriocanal C. 2011. Ecological conditions in wintering and passage areas as determinants of timing of spring migration in trans-Saharan migratory birds. *Journal of Animal Ecology* 80:320–331. DOI: 10.1111/j.1365-2656.2010.01772.x.
- Rubolini D, Spina F, Saino N. 2004. Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behavioral Ecology* 15:592–601. DOI: 10.1093/beheco/arh048.
- Salewski V, Hochachka WM, Fiedler W. 2013. Multiple weather factors affect apparent survival of European passerine birds. *PLoS One* 8(4):e59110. DOI: 10.1371/journal.pone.0059110.
- Santangeli A, Lehikoinen A. 2017. Are winter and breeding bird communities able to track rapid climate change? Lessons from the high North. *Diversity & Distributions* 23:308–316. DOI: 10.1111/ddi.12529.
- Scebba S, Soprano M, Sorrenti M. 2014. Timing of the spring migration of the Song Thrush *Turdus philomelos* through southern Italy. *The Ring* 36(1):23–31. DOI: 10.2478/ring-2014-0002.
- Schmaljohann H, Meier C, Arlt D, Bairlein F, van Oosten H, Morbey YE, Åkesson S, Buchmann M, Chernetsov N, Desaeveer R, Elliott J, Hellström M, Liechti F, López A, Middleton J, Ottosson U, Pärt T, Spina F, Eikenaar C. 2016. Proximate causes of avian protandry differ between subspecies with contrasting migration challenges. *Behavioral Ecology* 27:321–331. DOI: 10.1093/beheco/arv160.
- Sinelschikova A, Sokolov LV. 2004. Long-term monitoring of the timing of migration in thrushes (*Turdus philomelos*, *T. iliacus*) in the Eastern Baltic. *Avian Ecology and Behavior* 12:11–30.
- Spottiswoode CN, Tøttrup AP, Coppack T. 2006. Sexual selection predicts advancement of avian spring migration in response to climate change. *Proceedings of the Royal Society of London B* 273:3023–3029.
- Svensson L. 1992. Identification guide to European passerines. The Nunnery, UK: British Trust for Ornithology. pp. 152–153.
- Tabachnick BG, Fidell LS. 1996. Using multivariate statistics. 3rd ed. New York: Harper Collins Publishers.
- Tøttrup AP, Klaassen RHG, Kristensen MW, Strandberg R, Vardanis Y, Lindström A, Rahbek C, Alerstam T, Thorup K. 2012. Drought in Africa caused delayed arrival of European songbirds. *Science* 338:1307. DOI: 10.1126/science.1227548.
- Tøttrup AP, Rainio K, Coppack T, Lehikoinen E, Rahbek C, Thorup K. 2010. Local temperature fine-tunes the timing of spring migration in birds. *Integrative and Comparative Biology* 50(3):293–304. DOI: 10.1093/icb/icq028.
- Tøttrup AP, Thorup K. 2008. Sex-differentiated migration patterns, protandry and phenology in North European songbird populations. *Journal of Ornithology* 149:161–167. DOI: 10.1007/s10336-007-0254-x.
- Tøttrup AP, Thorup K, Rahbek C. 2006. Patterns of change in timing of spring migration in North European songbird populations. *Journal of Avian Biology* 37:84–92. DOI: 10.1111/j.0908-8857.2006.03391.x.
- Tryjanowski P, Sparks TH, Kuźniak S, Czechowski P, Jerzak L. 2013. Bird migration advances more strongly in urban environments. *PLoS ONE* 8(5):e63482. DOI: 10.1371/journal.pone.0063482.
- Vengerov PD. 2017. Effect of rise in spring air temperature on the arrival dates and reproductive success of the Song Thrush, *Turdus philomelos* (C.L. Brehm, 1831) in the forest-steppe of the Russian Plain. *Russian Journal of Ecology* 48(2):178–184. DOI: 10.1134/S1067413617020102.
- Woodrey M, Chandler C. 1997. Age-related timing of migration: Geographic and interspecific patterns. *The Wilson Bulletin* 109(1):52–67.
- Zar JH. 2010. Biostatistical analysis. 5th ed. New Jersey: Pearson Prentice Hall. pp. 400–402.

Zakres udziału poszczególnych autorów w publikacjach naukowych wchodzących w skład rozprawy i oświadczenia autorów

Redlisiak M, Remisiewicz M, Nowakowski JK (2018). 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. *International Journal of Biometeorology* 62: 1595, doi: 10.1007/s00484-018-1559-6

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3. Redlisiak M, Remisiewicz M, Mazur A (2021). Sex-specific differences in spring migration timing of Song Thrush *Turdus philomelos* at the Baltic coast in relation to temperatures on the wintering grounds. *The European Zoological Journal*, 88:1, 191–203, doi: 10.1080/24750263.2020.1869842

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Lista publikacji i osiągnięć nie będących przedmiotem rozprawy

Artykuły naukowe:

1. **Redlisiak M**, Kajzer K, Wardecki Ł, Elas M (2014) Gniazdowanie gawrona *Corvus frugilegus* w Warszawie w latach 2013-2014. Kulon 19: 81–113.
2. **Redlisiak M**, Wardecki Ł, Karpińska O, Hayatli F, Kajzer K (2018) Sprawozdanie z projektu znakowania krzyżówki *Anas platyrhynchos* na obszarze aglomeracji warszawskiej w latach 2015-2018. Kulon 23: 177–186.

Artykuły popularnonaukowe:

1. Kośmicki A, Niemc A, **Redlisiak M**, Rosińska K, Rubacha S, Stępniewska K, Stępniewski K, Szulc J (2015) Pomorze Gdańskie Ptasią Autostradą – znaczenie regionu w europejskim systemie wędrówek ptaków. Broszura edukacyjna wydana przez Fundację Akcja Bałtycka dzięki dofinansowaniu ze środków Województwa Pomorskiego.

Doniesienia konferencyjne:

1. **Redlisiak M**, Remisiewicz M (2014) Wintering areas of Song Thrushes *Turdus philomelos* migrating in autumn through five ringing stations in western and southern Baltic region. International Bird Observatories Conference 1, 28.08-1.09.2014, Falsterbo, Szwecja [poster].
2. **Redlisiak M** (2015) Akcja Bałtycka – 55 lat wiadomości powrotnych. Konferencja „Współczesne obrączkowanie ptaków – aspekt naukowy i etyczny”, 28.11.2015, Gdańsk. [prezentacja].
3. Niemc A, **Redlisiak M** (2016) Równania dyskryminacyjne w ornitologii i ich zastosowanie na przykładzie biegusa malutkiego *Calidris minuta* i śpiewaka *Turdus philomelos*. III Zjazd Krajowej Sieci Stacji Obrączkowania Ptaków, 05-06.03.2016, Kraków. [prezentacja].
4. **Redlisiak M**, Remisiewicz M, Nowakowski JK (2016) Long-term changes in timing of autumn migration through southern Baltic in first-year Song Thrush related to temperatures at breeding grounds. Konferencja Bird Numbers 2016 “Birds in a changing world”, 5-9.09.2016, Halle, Niemcy [poster].
5. Remisiewicz M, Maciąg T, Nowakowski JK, **Redlisiak M** (2016) Long-term ringing shows fluctuating populations of forest passerines migrating through the Polish Baltic coast. Konferencja Bird Numbers 2016 “Birds in a changing world”, 5-9.09.2016, Halle, Niemcy [poster].
6. **Redlisiak M**, Remisiewicz M, Nowakowski JK (2016) Akcja Bałtycka na początku XXI wieku: stare i nowe metody badania wędrówek ptaków. Sympozjum Młodych Ornitologów, 21-23.10.2016. Spała [prezentacja].
7. **Redlisiak M**, Remisiewicz M, Nowakowski JK (2017) Wieloletnie zmiany terminów wiosennej i jesiennej migracji śpiewaka *Turdus philomelos* przez polskie wybrzeże Bałtyku. II Zjazd Obrączkarzy, 17-19.11.2017, Gdańsk-Sobieszewo [prezentacja].

8. Maciąg T, Remisiewicz M, **Redlisiak M**, Nowakowski JK (2017) Trendy liczebności wybranych gatunków wróblowych Passeriformes wędrujących przez stacje Akcji Bałtyckiej w latach 1965-2012. II Zjazd Obrączkarzy, 17-19.11.2017, Gdańsk-Sobieszewo [prezentacja].
9. Karpińska O, Wardecki Ł, **Redlisiak M**, Kajzer K (2018) Wstępne wyniki projektu kolorowego obrączkowania krzyżówki *Anas platyrhynchos* w aglomeracji warszawskiej. XVII Zjazd Mazowiecko-Świętokrzyskiego Towarzystwa Ornitologicznego, 24-25.02.2018, Izabelin [prezentacja].
10. **Redlisiak M**, Remisiewicz M, Mazur A, Nowakowski JK (2018) Wpływ temperatury na zimowiskach na terminy wiosennego przelotu samców i samic śpiewaka *Turdus philomelos* przez polskie wybrzeże Bałtyku. II Sympozjum Młodych Ornitologów, 9-11.11.2018, Rogów [prezentacja]
11. **Redlisiak M**, Karpińska O, Wardecki Ł, Hayatli F, Kajzer K (2018) Wstępne wyniki projektu kolorowego obrączkowania krzyżówki *Anas platyrhynchos* w aglomeracji warszawskiej. II Sympozjum Młodych Ornitologów, 9-11.11.2018, Rogów [wyróżniony poster].
12. **Redlisiak M**, Remisiewicz M, Nowakowski JK, Mazur A (2018) Effect of temperature on spring and autumn migration timing of Song Thrush *Turdus philomelos* at the Polish Baltic coast. Konferencja Migrant Birds as Indicators of Climate Change, 13-16.12.2018, Gdańsk-Sobieszewo [prezentacja].

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