

Wydział Biologii
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Wpływ czynników klimatycznych i
wewnątrzgatunkowych na terminy
migracji dwóch gatunków z rodzaju *Sylvia*:
gajówki i kapturki, przez
południowe wybrzeże Bałtyku

The influence of climatic and intraspecific factors on
the migration timing of two *Sylvia* species: the Garden
Warbler and the Eurasian Blackcap across the southern
Baltic coast

Praca przedstawiona
Radzie Dyscypliny Nauki biologiczne Uniwersytetu Gdańskiego
celem uzyskania stopnia doktora
w dziedzinie nauk ścisłych i przyrodniczych
w dyscyplinie nauki biologiczne

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Stacja Badania Wędrówek Ptaków

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Podziękowania

Powstanie niniejszej rozprawy nie byłoby możliwe bez pomocy i wsparcia wielu osób, którym w tym miejscu pragnę podziękować.

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Streszczenie po polsku

Wstęp

Wiele gatunków ptaków migruje dwa razy w roku między lęgowiskami a zimowiskami, wykorzystując miejsca odpoczynku na trasach wędrówki do żerowania i odbudowy zapasów energetycznych (Newton 2008). Warunki środowiska na tych trasach wpływają na przebieg i terminy tych wędrówek (Gordo 2007). Zmiany klimatu w Europie i Afryce wpływają na terminy ptasich wędrówek w obrębie palearktyczno-afrykańskiego systemu migracji (Jenni i Kéry 2003; Lehikoinen i in. 2019). Chociaż terminy ptasich wędrówek są uwarunkowane genetycznie, mogą być modyfikowane przez temperatury na zimowiskach i wzdłuż tras przelotu, które oddziałują na ptaki bezpośrednio, wpływając na koszty termoregulacji, oraz pośrednio, kształtując dostępność ich bazy pokarmowej (Newton 2008). Poza regionalnymi temperaturami, na wędrówkę ptaków wpływają także systemy cyrkulacji atmosferycznej, które kształtują temperatury, oraz opady i wiatry nad Europą i Afryką (Saji i Vinayachandran 1999; Hurrell i in. 2003). Wielkoskalowe wskaźniki klimatyczne, takie jak Oscylacja Północnoatlantycka (NAO), Oscylacja Skandynawska (SCI), Oscylacja Śródziemnomorska (MOI) oraz Dipol Oceanu Indyjskiego (IOD), które odzwierciedlają wzorce cyrkulacji atmosferycznej na dużych obszarach obu kontynentów, są powiązane z terminami wędrówek ptaków (Stenseth i in. 2002; Jonzén i in. 2007). Ponieważ klimat stale się zmienia, odpowiedź populacji ptaków na warunki pogodowe może ulegać modyfikacjom na przestrzeni dziesięcioleci (Jonzén i in. 2006; Romano i in. 2023).

Jednym z efektów ocieplenia klimatu na ptasie wędrówki jest ich coraz wcześniejszy przelot wiosenny, a co za tym idzie, wcześniejsze przybycie na lęgowiska na północy (Forchhammer i in. 2002). Choć przyspieszenie terminów wiosennej migracji jest dobrze udokumentowane, zwłaszcza w Europie, wędrówce jesiennej poświęcono mniej uwagi, przez co mniej wiadomo o tym, jak zmiany klimatu wpłynęły na terminy tej wędrówki (Gallinat i in. 2015). Fenologia jesiennej wędrówki różnych gatunków ptaków wróblowych w odmienny sposób dostosowała się do zmian klimatu, wykazując przyspieszenie lub opóźnienie terminów przelotu (Jenni i Kéry 2003). Badania nad wpływem pogody napotkanej przez dorosłe migranty podczas wiosennej wędrówki na jesienną migrację kolejnego pokolenia, czyli ich potomstwa, są nieliczne (Jenni i Kéry 2003; Tomotani i in. 2018). Ciepłe wiosny mogą sprzyjać wczesnemu przylotowi dorosłych osobników na lęgowiska i ich wczesnemu gniazdowaniu, co prowadzi do wczesnego wyklucia i odlotu młodych ptaków na południe

(Hałupka i in. 2017). Większość badań do tej pory skupiała się na międzygatunkowych różnicach w fenologii migracji, podczas gdy zmienność wewnątrzgatunkowa, w tym możliwe różnice między płciami, pozostaje słabo zbadana (Nakazawa i in. 2023). U wielu migrujących ptaków wróblowych protandria, czyli wcześniejszy przylot samców niż samic na lęgowiska, występuje już w trakcie wiosennej migracji, i zaznacza się na miejscach odpoczynku (Morbey i Ydenberg 2001; Rubolini i in. 2004). Głównym mechanizmem wyjaśniającym protandrię jest hipoteza „szansy na znalezienie partnerki” (*mate opportunity hypothesis*), według której wcześniejszy przylot pozwala samcom zająć najlepsze terytoria, co zwiększa ich szanse na zdobycie samic i sukces lęgowy (Kokko 1999; Møller 2004). Wcześniejszy przylot samców na miejsca odpoczynku i lęgowiska może również wynikać z przestrzennego rozdzielania płci w sezonie pozalęgowym, jeśli samce i samice korzystają z częściowo różnych zimowisk lub tras wędrówek (Catry i in. 2006). Różnice w terminach wędrówek są również powiązane z odmiennymi strategiami zarządzania energią w trakcie migracji u obu płci, ponieważ samice muszą utrzymać zapasy tłuszczu i białka do produkcji jaj oraz unikać zbyt wczesnego przylotu na lęgowiska podczas surowych wiosen, co mogłoby wyczerpać te zasoby (Francis i Cooke 1986; Schmaljohann i in. 2016). Natomiast produkcja plemników jest mniej wymagająca energetycznie, co pozwala samcom podjąć ryzyko związane z niekorzystną pogodą, w celu zdobycia najlepszych terytoriów i partnerek (Péczely 2017). Dlatego wiosną samce często stosują strategię minimalizacji czasu wędrówki (*time-minimization strategy*), stawiając na szybkie tempo wędrówki ponad oszczędzanie energii, podczas gdy samice stosują strategię minimalizacji wydatków energii na wędrówkę (*energy-minimization strategy*), aby utrzymać dobrą kondycję ciała, która jest kluczowa do produkcji jaj (Dierschke i in. 2005).

Dla zbadania tych złożonych reakcji migrantów na zmieniający się klimat wybrałam jako gatunki modelowe dwa spokrewnione gatunki małych ptaków wróblowych z rodzaju *Sylvia*, które korzystają z podobnych siedlisk w okresie lęgowym i migrują przez południowe wybrzeże Bałtyku, ale różnią się dystansem wędrówki oraz liczbą lęgów w roku (Cramp i Brooks 1992). Kapturka (*Sylvia atricapilla*) to ptak o wyraźnym dymorfizmie płciowym, który może wyprowadzać do kilku lęgów w roku, zimuje w południowej Europie oraz zachodniej i wschodniej Afryce, a także wykazuje w ostatnich dziesięcioleciach niezwykłą plastyczność w dostosowywaniu wędrówek do zmian klimatu przez skracanie dystansu migracji i tworzenie nowych zimowisk, położonych coraz bliżej lęgów (Pulido i Berthold 2004; Spina i in. 2022). Natomiast gajówka (*Sylvia borin*) to gatunek monomorficzny, u

którego płcie nie różnią się zewnętrznie, wyprowadzający jeden lęg w roku, ale o dłuższym dystansie wędrówki niż kapturka, między Fennoskandią a Afryką subsaharyjską i środkową (Maciąg i in. 2017; Spina i in. 2022).

Cele i hipotezy

Celem niniejszej rozprawy jest określenie wpływu wybranych czynników zewnętrznych (temperatur regionalnych i wielkoskalowych oscylacji klimatycznych) oraz wewnątrzpopulacyjnych (płci) na terminy wiosennej i jesiennej wędrówki dwóch gatunków z rodzaju *Sylvia* przez południowe wybrzeże Morza Bałtyckiego, z wykorzystaniem unikalnych danych z obrączkowania ptaków od lat 1960-tych w ramach projektu Akcja Bałtycka.

Po pierwsze, zbadalam wieloletnie zmiany w terminach wędrówek: fenologię wiosennej migracji samców i samic kapturki (1982–2025) oraz terminy jesiennej migracji gajówki (1967–2018). Wcześniejsze prace wykazały, że terminy wiosennej wędrówki kapturki na terenie Europy uległy przyspieszeniu pod koniec XX wieku. Dlatego postawiłam hipotezę o dalszym przyspieszeniu terminów wiosennej wędrówki u obu płci. Biorąc pod uwagę wcześniejsze badania pokazujące coraz wcześniejszą jesienną wędrówkę gajówek przez Europę, spodziewałam się przyspieszenia terminów jesiennego przelotu tego gatunku na polskim wybrzeżu Bałtyku w latach 1967–2018.

Po drugie, celem badań było określenie dla obu gatunków zależności między terminami ich wędrówek a zmianami klimatu. W przypadku gajówki zbadalam zależności między terminami jesiennej wędrówki a temperaturami na lęgowiskach oraz wzdłuż tras wiosennej i jesiennej wędrówki. Zmienność w terminach jesiennej wędrówki do tej pory wiązano z biologią lęgową i dystansem migracji poszczególnych gatunków, jednak rzadko badano jej związek z temperaturami napotykanymi przez dorosłe ptaki podczas wędrówki wiosennej. Dlatego wysunęłam hipotezę, że terminy jesiennej wędrówki młodych gajówek są powiązane z temperaturami, jakich doświadczyły na lęgowiskach i podczas tej wędrówki, jak również z temperaturami, jakie dorosłe ptaki (ich rodzice) napotkały wcześniej, podczas wiosennej wędrówki na lęgowiska. W przypadku kapturki, celem badań było określenie zależności między terminami wiosennej wędrówki a wielkoskalowymi wskaźnikami klimatycznymi (NAO, SCI, MOI i IOD), a także regionalnymi temperaturami zimą i wiosną w Europie i Afryce. Oczekiwałam, że te wielkoskalowe wskaźniki klimatyczne oraz

temperatury regionalne mają wpływ na terminy wiosennej wędrówki kapturki na południowym wybrzeżu Bałtyku.

Po trzecie, chciałam zweryfikować hipotezę, że stopień protandrii w trakcie wiosennej wędrówki u kapturki zmienił się w okresie 1982–2025 oraz określić wpływ czynników klimatycznych na każdą z płci. Spodziewałam się zwiększenia stopnia protandrii w badanym okresie, biorąc pod uwagę bardziej gwałtowne zmiany klimatu i wzrosty temperatur w ciągu ostatnich dekad. Ponadto spodziewałam się, że samce i samice mogą inaczej reagować na te zmiany klimatyczne.

Po czwarte, podzieliłam wieloletnie dane dotyczące samców i samic kapturki na dwa okresy (1982–2004 oraz 2005–2025), aby sprawdzić, czy wieloletnie trendy, stopień protandrii oraz specyficzny dla płci wpływ regionalnych temperatur na terminy migracji, różniły się między tymi okresami. Ponieważ w poprzedniej pracy z tej rozprawy wykazałam, że kapturki przyspieszyły terminy wiosennej wędrówki w ciągu całych 44 lat badań, postawiłam hipotezę, że trendy wieloletnie będą podobne między tymi dwoma okresami. Spodziewałam się również, że regionalne temperatury zimą i wiosną w Europie i Afryce będą wpływać na terminy migracji w obu okresach.

Materialy i metody

W badaniach przedstawionych w tej rozprawie wykorzystałam wieloletnie dane zebrane podczas codziennego chwytania ptaków w sieci ornitologiczne według standardu metodycznego projektu badawczego Akcja Bałtycka (Busse i Meissner 2015) na Terenowej Stacji Obrączkowania Ptaków Bukowo-Kopań na polskim wybrzeżu Morza Bałtyckiego. Analizowany materiał obejmował dane z obrączkowania (pierwsze schwytanie) gajówek podczas jesiennej wędrówki (14 sierpnia – 15 października) w latach 1967–2018, oraz kapturek podczas wiosennej wędrówki (26 marca – 16 maja) w latach 1982–2025. Gajówki są wiosną nieliczne na stacji Bukowo-Kopań, co uniemożliwiło porównanie wiosennej wędrówki obu gatunków. W celu określenia regionów, w których badane populacje przebywają na kolejnych etapach swojego rocznego cyklu, naniosłam na mapę wiadomości powrotne o osobnikach z tych gatunków schwytanych na wszystkich stacjach Akcji Bałtyckiej, w tym Bukowo-Kopań, na polskim wybrzeżu, a następnie porównałam je z danymi z literatury (Spina et al. 2022). Średnie dzienne temperatury oraz wielkoskalowe wskaźniki klimatyczne (NAO, SCI, MOI, IOD) dla regionów geograficznych

wyodrębnionych w obrębie zasięgów tych gatunków, uzyskałam z baz danych European Climate Assessment and Dataset (ECA&D), NOAA oraz KNMI Climate Explorer.

Terminy wędrówki określiłam za pomocą dat (wyrażonych jako numery dnia w roku), w których schwytano 10%, 50% i 90% ptaków w danym sezonie. Daty te obliczyłam dla przelotu jesiennego młodych gajówek (Publikacja 1), a dla przelotu wiosennego kapturek oddzielnie dla samców i samic (Publikacje 2, 3). Ponadto, aby ocenić międzysezonowe zmiany w terminach jesiennych wędrówek wszystkich gajówek łącznie, obliczyłam anomalię roczną (Annual Anomaly, AA) dla każdej jesieni jako odchylenie dziennej skumulowanej krzywej przelotu w danym roku od średniej wieloletniej krzywej przelotu (Publikacja 1). Aby oszacować wieloletnie trendy tych parametrów przelotu, zastosowałam regresję liniową. Dla kapturki oszacowałam trendy wieloletnie oddzielnie dla samców i samic. Następnie podzieliłam dane o wiosennej wędrówce kapturki na dwa okresy (1982–2004 i 2005–2025), aby sprawdzić różnice między nimi w trendach wieloletnich, wykorzystując modele regresji liniowej, w których zmiennymi objaśniającymi były: rok, płeć, okres badań i ich interakcje (Publikacja 3).

Aby określić wpływ czynników klimatycznych na terminy migracji, zbudowałam modele wielorakiej regresji liniowej. W tych modelach zmiennymi objaśnianymi były daty przelotu 10%, 50% i 90% ptaków, i dodatkowo AA dla gajówki. Zmienne objaśniające obejmowały numer roku oraz czynniki klimatyczne odpowiednio wybrane dla każdego gatunku. Aby sprawdzić wpływ temperatur regionalnych (Publikacje 1, 3), jako zmienne objaśniające wykorzystałam dwumiesięczne średnie temperatury wiosną, latem i jesienią na terenach lęgowych i wzdłuż tras migracji dla gajówki (Publikacja 1), oraz trzymiesięczne średnie temperatury regionalne zimą i wiosną w Europie i Afryce dla kapturki (Publikacja 3). Aby ocenić wpływ wielkoskalowych wskaźników klimatycznych na wędrówkę kapturki (Publikacja 2), zmiennymi objaśniającymi były trzymiesięczne średnie zimowe oraz wiosenne wielkoskalowych wskaźników klimatycznych. Wszystkie zmienne objaśniające zostały zestandaryzowane, ponieważ miały różne skale. Ponieważ zmiennych klimatycznych było zbyt wiele, aby uwzględnić je we wspólnym modelu, najpierw stworzyłam modele cząstkowe dla każdego sezonu osobno (wiosna, lato i jesień dla gajówki; zima i wiosna dla kapturki). Następnie połączyłam zmienne objaśniające z najlepszych modeli sezonowych we wspólne modele dla obu sezonów. Najlepsze z tych wspólnych modeli poddałam dalszej interpretacji. Aby zbadać, czy zależności między terminami migracji a temperaturami u kapturki zmieniły się między dwoma okresami, stworzyłam modele porównujące te okresy. Te modele

uwzględniały kombinacje zmiennych temperaturowych z najlepszych wspólnych modeli "zimowych i wiosennych", a także interakcje między okresem badań a tymi zmiennymi (Publikacja 3). Aby określić różnice między płciami we wpływie tych czynników klimatycznych na wiosenną wędrówkę kapturki, w tych modelach uwzględniłam interakcje między czynnikami klimatycznymi a płcią (Publikacje 2, 3). Aby sprawdzić występowanie protandrii i przetestować, czy jej stopień zmienił się na przestrzeni lat, wykonałam modele wielorakiej regresji liniowej obejmujące płeć, rok (numer roku od 1982) i ich interakcję (Publikacje 2, 3), oraz przetestowałam różnice w protandrii między dwoma podokresami, włączając do modeli podokres badań jako czynnik (Publikacja 3). Wszystkie modele wielorakiej regresji liniowej wykorzystane w tej rozprawie zbudowałam przy użyciu podejścia „all-subsets” (sprawdzającego wszystkie kombinacje zmiennych), a modele zostały uszeregowane za pomocą Kryterium Informacyjnego Akaikego skorygowanego dla małych prób (AICc). Najlepszym modelem w każdej analizie był ten z najniższą wartością AICc. Wszystkie analizy statystyczne przeprowadziłam w programie R (wersje 4.1.2, 4.4.2 i 4.6.1).

Wyniki i dyskusja

Publikacja nr 1:

U gajówki termin całego przelotu jesiennego (AA) młodych ptaków uległ przyspieszeniu o 7 dni, a daty przelotu 50% i 90% schwytanych ptaków uległy przyspieszeniu o 6–11 dni, w latach 1967–2018, co doprowadziło do skrócenia okresu migracji. Prawdopodobnie jest to wynikiem skrócenia sezonu lęgowego, w którym ten gatunek, wyprowadzający jeden lęg w roku, dostosował termin składania jaj do szczytu zasobów pokarmowych, który również przesunął się na wcześniejszy termin w odpowiedzi na rosnące temperatury (Hałupka i in. 2017). Cały przelot (AA) oraz daty przelotu 10%, 50% i 90% schwytanych ptaków jesienią na wybrzeżu Bałtyku były wczesne przy ciepłych wiosnach na trasach wiosennej wędrówki we Włoszech, lub późne przy niskich temperaturach we Włoszech, ponieważ te zależności działają w obie strony. Taka zależność sugeruje międzypokoleniowy efekt przeniesienia (*carry-over effect*), ponieważ ciepłe wiosny sprzyjają szybkiej wędrówce, a tym samym wczesnemu przylotowi i gniazdowaniu dorosłych ptaków powracających na lęgowiska, co prowadzi do wcześniejszego klucia i szybszego wzrostu młodych (Tomotani i in. 2018). Ponadto, wysokie temperatury latem na terenach lęgowych w południowej Szwecji i Norwegii były powiązane z wcześniejszym jesiennym przelotem gajówek przez Bukowo-Kopań. Ciepłe lato sprzyja szybkiemu dojrzewaniu, pozwalając

młodym ptakom szybciej rosnać i opuścić terenów lęgowe wcześniej niż po chłodnym lecie (Sparks i Crick 1999). Jednak wysokie temperatury lata w Finlandii opóźniały środkową fazę (50%) i cały jesienny przelot (AA) na stacji Bukowo-Kopań. Te wyniki sugerują, że dobre warunki żerowania podczas ciepłych lat na tych lęgowskich i miejscach postojowych opóźniały przelot, ponieważ niedoświadczone młode ptaki wykorzystywały te warunki do zgromadzenia zapasów tłuszczu przed wędrówką na południe (Ożarowska 2015).

Publikacja nr 2:

U kapturki, zarówno u samców, jak i u samic, terminy początkowej fazy (10%) i mediany (50%) wiosennego przelotu uległy przyspieszeniu o 7–9 dni w latach 1982–2025. Podobne przyspieszenie u obu płci sugeruje, że wcześniejszy wiosenny przelot przynosi im równe korzyści, umożliwiając samcom maksymalizację szans na znalezienie partnerki, a samicom wydłużenie sezonu lęgowego pozwalające na drugie lęgi (Fontaine and Martin 2006). Ponieważ obie płcie podobnie zmieniły terminy migracji, stopień protandrii w pierwszej fazie (10%) migracji pozostał stabilny, a samce wędrowały średnio o około 2 dni wcześniej niż samice w całym okresie badań. Ten stabilny stopień protandrii jest zgodny z hipotezą szansy na znalezienie partnerki (*mating opportunity hypothesis*) wskazując, że presja selekcyjna utrzymuje różnice w terminach wędrówki między płciami niezależnie od zmienności warunków pogodowych w poszczególnych latach (Tøttrup i Thorup 2008). Samce i samice wykazywały podobne relacje z wielkoskalowymi wskaźnikami klimatycznymi, co sugeruje, że warunki pogodowe na dużych obszarach wpływają na terminy migracji obu płci w podobny sposób, nawet jeśli stosują one różne strategie inwestycji energii podczas wędrówki lub zimują na nieco innych terenach. Dodatkowo wartości NAO zimą i wiosną oraz SCI wiosną, odzwierciedlające ciepłe i wilgotne zimy oraz wiosny w Europie, były skorelowane z wczesnym przelotem 10% i 50% schwytanych ptaków, a dodatni wskaźnik IOD zimą wiązał się z opóźnionym przelotem 90% schwytanych ptaków. Wskazuje to, że kolejne grupy migrantów przybywają z obszarów znajdujących się pod wpływem różnych czynników klimatycznych, dostosowując tempo wędrówki do różnych układów cyrkulacji w Europie i Afryce, podobnie u obu płci.

Publikacja nr 3:

Porównanie terminów wiosennej migracji kapturki między dwoma okresami (1982–2004, 2005–2025) pokazało, że dwudniowa protandria w początkowej fazie przelotu (10%)

utrzymywała się w obu okresach. Jednak protandria nie zaznaczyła się już w medianach (50%) przelotu samców i samic. Stabilna protandria na początku przelotu utrzymuje się prawdopodobnie dlatego, że wcześniej przylatujące samce mają większe szanse na znalezienie partnerki, niezależnie od postępującego ocieplenia. Brak protandrii w środkowej (50%) i końcowej (90%) fazie przelotu prawdopodobnie odzwierciedla strategię minimalizacji wydatków energetycznych na wędrówkę u niedoświadczonych młodych ptaków, które dominują na miejscach odpoczynku na wybrzeżach, takich jak Bukowo-Kopań (Neate-Clegg i Tingley 2023). Mediany przelotu obu płci uległy przesunięciu o 10 dni wcześniej w latach 1982–2004, ale ustabilizowały się w okresie 2005–2025. Początkowa (10%) faza i mediana (50%) przelotu obu płci były wczesne podczas ciepłych wiosen w Europie Środkowej i Afryce Wschodniej. Sugeruje to, że te wczesne migranty dynamicznie dostosowują się do warunków środowiskowych, opuszczając wysychające siedliska w Afryce i wykorzystując korzystne warunki wiosenne do przyspieszenia przelotu przez Europę (Aloni i in. 2019). Co istotne, wpływ wiosennych temperatur w Europie Środkowej na medianę przelotu był słabszy w drugim okresie (2005–2025), mimo że ocieplenie w tym regionie postępowało. Ta słabsza zależność i niedawna stabilizacja środkowej fazy przelotu wskazują, że część migrującej populacji osiągnęła biologiczną granicę przyspieszania terminu wiosennej migracji. Wpływ rosnących temperatur na przyspieszenie szczytu dostępności bazy pokarmowej ma swoje ograniczenia, gdyż fenologia roślin i owadów na lęgowskich ostatecznie zależy również od czynników środowiska, które się nie zmieniają, takich jak fotoperiod (Tougeron i in. 2019). Obserwowana stabilizacja terminów przelotu zapobiega przedwczesnemu pojawianiu się ptaków na lęgowskich, co pozwala im uniknąć drastycznego niedopasowania ekologicznego do dostępności pożywienia u progu sezonu lęgowego (Romano i in. 2023). Z kolei późna faza przelotu (90%) opóźniała się przy ciepłych zimach w zachodnim rejonie Morza Śródziemnego. Ciepłe zimy na tym obszarze często powodują wczesny rozwój roślinności (Solakis-Tena i in. 2025), przez co szczyt liczebności owadów przypada zbyt wcześnie dla osobników wędrujących późno w sezonie. Przez to mają one trudności z odbudową zapasów energii i muszą robić dłuższe postoje w tym regionie (Mayor i in. 2017; Maggini i in. 2020), stąd ich opóźniony przelot na wybrzeżu Bałtyku.

Wnioski

W niniejszej rozprawie wykazałam wpływ czynników klimatycznych i wewnątrzgatunkowych na fenologię wędrówek dwóch gatunków pokrzewek z rodzaju *Sylvia*,

przelatujących wiosną lub jesienią przez południowe wybrzeże Morza Bałtyckiego. Analiza wieloletnich serii danych dotyczących terminów wędrówek w zestawieniu z danymi klimatycznymi pokazała, jak te spokrewnione gatunki ptaków reagują na globalne zmiany klimatu. U gajówki terminy jesiennej wędrówki młodych ptaków są bezpośrednio kształtowane przez warunki środowiska na terenach lęgowych, a pośrednio przez wpływ temperatur wiosną na wiosenną wędrówkę ich rodziców, przez międzypokoleniowy efekt przeniesienia (*transgenerational carry-over effect*). U kapturki dwudniowa protandria na początku wiosennego przelotu utrzymywała się przez 44 lata badań oraz w obu podokresach. Jest to zgodne z hipotezą szansy na znalezienie partnerki (*mate opportunity hypothesis*), co wskazuje, że presja selekcyjna pozwala zachować różnice w wiosennej fenologii między płciami, niezależnie od postępującego ocieplenia klimatu. Ponadto, pomimo odmiennych strategii wędrówki, zarówno samce, jak i samice kapturki podobnie odpowiadały na zmiany regionalnych temperatur i wielkoskalowych wskaźników klimatycznych. Jednakże, chociaż zmiana terminów wędrówki jest powszechną reakcją ptaków na zmieniający się klimat, ta zdolność do adaptacji fenologicznej wydaje się ograniczona przez limity ekologiczne i niższą skuteczność żerowania niedoświadczonych młodych ptaków, które dominują podczas wędrówki wzdłuż wybrzeża. Przyspieszenie terminów wiosennego przelotu w latach 1982–2004 oraz stabilizacja tych terminów w latach 2005–2025 wskazują na osiągnięcie przez kapturkę biologicznej granicy plastyczności fenologicznej. Prawdopodobnie zapobiega to ekologicznemu niedopasowaniu pojawienia się migrantów do szczytu dostępności pokarmu na miejscach postojowych i lęgowiskach.

Porównanie tych dwóch gatunków z rodzaju *Sylvia* wskazuje, jak różnice w dystansie wędrówki i liczbie lęgów kształtują ich reakcje na zmiany klimatu. Kapturka, która migruje na krótsze odległości i może wyprowadzać kilka lęgów w roku, wykazuje niezwykle plastyczność. Ta plastyczność fenologiczna pozwoliła na znaczne przyspieszenie terminu wiosennego przelotu kapturki w minionych dziesięcioleciach, dla maksymalizacji sukcesu lęgowego. W przeciwieństwie do niej, wyprowadzająca jeden lęg i wędrująca na większe dystanse gajówka ma bardzo napięty roczny terminarz kolejnych etapów życia w ciągu roku. Przy takich ograniczeniach, jej adaptacja do zmieniających się warunków środowiskowych przejawiała się w skróceniu okresu jesienno-wiosennego przelotu, prawdopodobnie w wyniku coraz bardziej skoncentrowanego sezonu lęgowego. Wszystkie te wyniki podkreślają, że mimo iż ptaki wędrowne podlegają wpływom ocieplenia klimatu, ich adaptacje fenologiczne są ograniczone przez ich biologię lęgową i dystans wędrówki. Zrozumienie, w jaki sposób te

biologiczne ograniczenia kształtują specyficzne dla danego gatunku reakcje na zmiany klimatu, jest niezbędne do przewidywania ich podatności na zagrożenia i opracowania skutecznych strategii ochrony wędrownych ptaków.

English summary

Introduction

Many bird species migrate twice a year between their breeding and wintering grounds, relying on stopover sites to feed and rebuild energy reserves on their way (Newton 2008). The environmental conditions along these routes influence the progress and timing of their migration (Gordo 2007). Climate change in Europe and Africa affects the timing of bird migrations within the Palearctic-African migration system (Jenni and Kéry 2003; Lehikoinen et al. 2019). Although the timing of bird migrations is genetically determined, it can be modified by temperatures at wintering grounds and along migration routes, which act directly by altering birds' thermoregulatory costs and indirectly by shaping the availability of their food base (Newton 2008). Besides temperatures at subsequent locations visited by birds, their migration is influenced by atmospheric circulation patterns that shape temperatures, precipitation, and winds over large areas (Saji and Vinayachandran 1999; Hurrell et al. 2003). Large-scale climate indices, such as the North Atlantic Oscillation (NAO), Scandinavian Index (SCI), Mediterranean Oscillation Index (MOI), and Indian Ocean Dipole (IOD), which reflect circulation patterns within large areas of Europe and Africa, are related to bird migration timing (Stenseth et al. 2002; Jonzén et al. 2007). Because regional climate changes continuously, the responses of bird populations to weather might shift over the decades (Jonzén et al. 2006; Romano et al. 2023).

One of the effects of climate warming on bird migration is their generally earlier spring passage and therefore earlier arrival at their breeding grounds in the Northern Hemisphere (Forchhammer et al. 2002). While the advancement of spring migration is well documented, especially in Europe, autumn migration has received less attention, so less is known about how these changes have affected the phenology of post-breeding southward migration (Gallinat et al. 2015). Autumn migration in different passerine species has adjusted to climate change in varied ways, ranging from an advance to a delay of passage (Jenni and Kéry 2003). Studies showing how weather that one generation of migrants encounters during their spring migration to the breeding grounds might affect autumn migration of their offspring are few (Jenni and Kéry 2003; Tomotani et al. 2018). Warm springs might promote early arrival of adults at the breeding grounds and early nesting, leading to early hatching and departure of immatures to the south (Halupka et al. 2017). Most studies have focused on interspecific differences in phenological shifts, while intraspecific variation, including

possible sex differences, remains poorly understood (Nakazawa et al. 2023). In many migrant passerines, protandry, which is an earlier arrival of males than females at the breeding grounds, occurs already at stopover sites during spring migration (Morbey and Ydenberg 2001; Rubolini et al. 2004). The main mechanism explaining protandry is the mate opportunity hypothesis, where earlier arrival allows males to secure high-quality territories, increasing their chances of attracting females and improving reproductive success (Kokko 1999; Møller 2004). The earlier arrival of males at stopover and breeding sites may also result from spatial sex segregation during the non-breeding season, when males and females use different wintering grounds or migration routes (Catry et al. 2006). These differences in migration timing are also linked to the varied energy management strategies of the sexes, because females must maintain fat and protein reserves for egg production and avoid too early arrival at the breeding grounds during harsh springs, which could deplete these resources (Francis and Cooke 1986; Schmaljohann et al. 2016). In contrast, sperm production is less demanding, allowing males to risk exposure to adverse weather to secure the best territories and mates (Péczeley 2017). Thus, in spring, males often act as time minimisers, prioritising migration speed over energy saving, whereas females behave as energy minimisers to preserve good body condition, which is crucial for egg production (Dierschke et al. 2005).

I selected two related species from the genus *Sylvia* that use similar habitats and migrate through the southern Baltic coast to northern breeding grounds, but differ in migration distance and the number of broods per year, as our model species to investigate these complex responses of migrants to changing climate (Cramp and Brooks 1992). The Eurasian Blackcap (*Sylvia atricapilla*) is a sexually dimorphic passerine that can raise multiple broods in a year, overwinters across southern Europe, West and East Africa, and shows remarkable plasticity in adjusting its migrations to climate change by shortening migration distances and establishing new wintering areas increasingly closer to the breeding grounds in recent decades (Pulido and Berthold 2004; Spina et al. 2022). In contrast, the Garden Warbler (*Sylvia borin*) is a monomorphic, single-brooded migrant with an even twice as long migration distance between Fennoscandia and sub-Saharan Africa and central Africa (Maciąg et al. 2017; Spina et al. 2022).

Aims and hypotheses

This dissertation aims to determine the influence of selected external factors (regional temperatures and large-scale climate patterns) and an intra-population factor (sex) on the

timing of spring and autumn migration of two *Sylvia* species across the southern coast of the Baltic Sea, using the unique long-term bird ringing dataset of the Operation Baltic project collected since 1961.

Firstly, I examined long-term changes in the timing of migration: the spring migration phenology of male and female Eurasian Blackcaps (1982–2025), and the autumn migration timing of Garden Warblers (1967–2018). Earlier studies showed that spring migration of blackcaps advanced during the late 20th century. Therefore, I expected further advancement of spring migration in both sexes. Given advances in autumn migration timing of Garden Warblers in other locations, I expected a shift to earlier autumn passage of this species on the Baltic coast of Poland over 1967–2018.

Secondly, I aimed to determine relationships between migration timing and external environmental conditions for both species. For Garden Warblers, I determined relationships between the timing of autumn migration and temperatures on the breeding grounds and along spring and autumn migration routes. Shifts in autumn migration timing have been previously attributed to breeding biology and migration distance of a species, but rarely linked to temperatures encountered by adults during spring migration to the breeding grounds. Therefore, I hypothesised that the timing of immature Garden Warblers' autumn migration would be related not only to the temperatures they experienced at the breeding grounds and during autumn migration, but also to temperatures the adults had encountered earlier, during their spring migration. For Eurasian Blackcaps, I aimed to determine relationships between spring migration timing and large-scale climate indices (NAO, SCI, MOI, and IOD), as well as winter and spring regional temperatures across Europe and Africa. I expected that these large-scale climate indices and regional temperatures influence spring migration timing of blackcaps on the southern Baltic coast.

Thirdly, I aimed to test if the degree of protandry has changed over 1982–2025 in Eurasian Blackcaps, and to determine sex-specific responses to the environmental conditions. I expected an increase in protandry over the study period, considering more rapid recent climate change and temperature increases. Furthermore, I expected that males and females might respond differently to these environmental conditions.

Fourthly, I divided the long-term dataset of male and female Eurasian Blackcaps into two periods (1982–2004 and 2005–2025) to test if multi-year trends, the degree of protandry,

and sex-specific responses to regional temperatures differed between past and recent decades. Because in the previous paper I revealed that blackcaps constantly advanced their migration over 44 years, I tested a hypothesis that the multi-year trends would not differ between the two periods, expecting a continuous advancement of spring migration. I also expected that winter and spring regional temperatures across Europe and Africa would influence migration timing in both periods. Thus, I aimed to determine these relationships, and test whether they changed between the two periods, considering the species' plasticity.

Materials and methods

Research presented in this thesis was based on long-term data collected during daily standardised mist-netting from dawn to dusk at the Bukowo-Kopań bird ringing station on the Polish Baltic Sea coast, following the standard methods of the Operation Baltic research project (Busse and Meissner 2015). The analysed dataset included the ringing records (first capture) during autumn migration (14 August–15 October) for Garden Warblers (1967–2018) and during spring migration (26 March–16 May) for Eurasian Blackcaps (1982–2025). Garden Warblers are infrequent on spring passage at Bukowo-Kopań, which impeded direct comparison of spring migration patterns between these two species. To identify the regions visited by the studied populations across their annual cycle, the ringing recoveries of individuals of these two species captured at all Operation Baltic stations on the Polish coast, including Bukowo-Kopań, were mapped and compared with literature data. I obtained daily mean temperatures and large-scale climate indices (NAO, SCI, MOI, IOD) for geographic regions I distinguished within the species' ranges, from the European Climate Assessment and Dataset (ECA&D), NOAA climate databases, and KNMI Climate Explorer.

The timing of migration was quantified using the dates when 10%, 50%, and 90% of the birds were captured each season, expressed as Julian days. This was calculated for immature Garden Warblers in autumn (Paper 1), and separately for male and female Blackcaps in spring (Papers 2, 3). Additionally, to assess overall passage shifts for Garden Warblers, I calculated an Annual Anomaly (AA) for each autumn as the departure of the daily cumulative curve for each year from the many-year average daily cumulative curve (Paper 1). I applied linear regression to estimate multi-year trends in these parameters of passage. For Blackcaps, I estimated multi-year trends separately for males and females. Furthermore, spring migration data on Blackcaps were divided into two sub-periods (1982–2004 and 2005–

2025) to test differences in multi-year trends between them, using linear regression models with year, sex, study period, and their interactions as explanatory variables (Paper 3).

To determine the effects of climate factors on migration timing, I built multiple linear regression models. In these models, the response variables were the dates when 10%, 50%, and 90% of the birds were captured, and additionally AA for Garden Warblers. The explanatory variables consisted of the year number and the selected climate factors relevant for each species. To test the effects of regional temperatures (Papers 1, 3), the explanatory variables were bi-monthly averages of spring, summer, and autumn temperatures at the breeding grounds and along the migration routes for Garden Warblers (Paper 1), and tri-monthly averages of winter and spring regional temperatures across Europe and Africa for Blackcaps (Paper 3). To assess the influence of large-scale climate indices on Blackcaps (Paper 2), the explanatory variables were the tri-monthly averages of winter and spring large-scale climate indices. All explanatory variables were standardised, as they were on different scales. Because the explanatory variables representing climate factors were too many to include in one model, I first ran partial models for each season separately (spring, summer, and autumn for Garden Warblers; winter and spring for Blackcaps). Then, the variables from the best seasonal models were integrated into final combined models. I then interpreted these best combined models. Finally, to investigate whether the relationships between migration timing and temperatures changed between the periods for Blackcaps, I formulated period-comparison models. These period-comparison models included the combinations of temperature variables selected by the best combined "winter and spring" models, testing the interaction between the study period and these variables (Paper 3). To determine differences between sexes in the effect of these climate factors on Blackcap spring migration, I included interactions between the climate factors and sex in the respective models (Papers 2, 3). To check for protandry and test whether its degree changed over the years, I ran multiple linear regression models including sex, year (as the year number since 1982), and their interaction (Papers 2, 3), and tested for differences in protandry between the two sub-periods by including the study period in the models (Paper 3). All multiple linear regression models used in this dissertation were built using the "all-subsets approach", and models were ranked by the Akaike Information Criterion corrected for small sample sizes (AICc). The best model was the one with the lowest AICc. All statistical analyses were conducted in R software (versions 4.1.2, 4.4.2, and 4.6.1).

Results and discussion

Paper no. 1:

In the Garden Warbler, the overall autumn passage (AA) of immatures advanced by 7 days, and the dates of the 50% and 90% of passage advanced by 6–11 days over 1967–2018, which led to a shorter migration period. This likely reflects a condensed breeding season, in which this single-brooded species adjusts egg-laying timing to match the peak of food resources, which also shifted earlier, in response to increasing temperatures (Halupka et al. 2017). The overall passage (AA) and the dates of 10%, 50% and 90% of autumn passage at the Baltic coast were early with higher spring temperatures on the spring migration route in Italy, or late with low temperatures in Italy, as these relationships work both ways. This relationship suggests a trans-generational carry-over effect, as warm springs encourage fast migration, and thus early arrival and nesting of returning adults, leading to earlier hatching and faster growth of juveniles (Tomotani et al. 2018). Furthermore, warm summers at the breeding grounds in southern Sweden and Norway were related to an earlier autumn passage. Warm summers support early maturity, allowing immatures to grow faster and depart earlier from their breeding grounds than after cold summers (Sparks and Crick 1999). However, high summer temperatures in Finland delayed the median and the overall autumn passage at Bukowo-Kopań. I suggest that favourable feeding conditions during warm summers at these breeding grounds and stopover sites delayed the passage because these inexperienced young birds took advantage of the conditions to accumulate fuel before migrating south (Ożarowska 2015).

Paper no. 2:

In Blackcaps, both males and females advanced the first (10%) and median (50%) phases of spring passage by 7–9 days during 1982–2025. Similar advancements of both sexes suggest that earlier spring passage benefits both sexes equally, enabling males to maximise mating opportunities and females to extend the breeding season for potential second broods (Fontaine and Martin 2006). Because both sexes shifted their timing at the same rate, the degree of protandry remained stable, with males migrating about 2.2 days earlier than females. This stable degree of protandry supports the mate opportunity hypothesis, indicating that selective pressures preserve the timing differences between sexes regardless of the interannual variation in weather conditions (Tøttrup and Thorup 2008). Males and females

showed uniform responses to the large-scale climate indices, suggesting that broad weather conditions influence migration timing of both sexes similarly, even if they adopt different strategies of energy allocation during migration or overwinter in slightly different areas. Positive winter and spring NAO and spring SCI, reflecting warm and wet winters and springs in Europe, were related to early 10% and 50% of passage, while positive winter IOD was associated with a delayed 90% of passage. This indicates that successive migrating cohorts arrive from areas under different climatic influences, adjusting their migration pace to different broad atmospheric patterns across Europe and Africa, similarly in both sexes.

Paper no. 3:

Comparing spring migration timing between two sub-periods (1982–2004, 2005–2025) revealed that the 2.2-day protandry in Blackcaps at the first phase of passage (10%) remained stable across both time periods, but did not manifest in the median (50%) of passage. The stable protandry among the first migrants is likely maintained by the increased mating opportunities of males arriving early, regardless of continuous warming. The lack of protandry at the median and late (90%) phases of passage probably reflects the energy-minimising strategy of inexperienced young birds, which dominate on the coastal stopover sites, such as Bukowo-Kopań (Neate-Clegg and Tingley 2023). The median (50%) of passage of both sexes shifted earlier by 10 days during 1982–2004, but stabilised during 2005–2025. The first (10%) and median (50%) phases of passage were early with warm springs in Central Europe and Eastern Africa. I suggest that these early migrants dynamically adapt to environmental cues by escaping drying environments in Africa and utilising favourable spring conditions to speed up their passage across Europe (Aloni et al. 2019). Notably, the influence of Central European spring temperatures on the median of passage weakened during the second period (2005–2025), even though warming in this region continued. This weaker response and the recent stabilisation of the median of passage indicate that parts of the migrating population reached a biological threshold of advancing spring passage. Since the advancement of the food peak at the breeding grounds is ultimately constrained by photoperiod (Tougeron et al. 2019), this stabilisation prevents birds from arriving too early, thereby avoiding a severe ecological mismatch between breeding and food availability, despite continuous climate warming (Romano et al. 2023). In contrast, the late phase (90%) was delayed with high winter temperatures in the Western Mediterranean. Warm winters in the Western Mediterranean region frequently cause vegetation to develop early (Solakis-Tena et al. 2025), shifting the peak abundance of insects too early for the late migrants, which

struggle to refuel and have to make longer stopovers in this region (Mayor et al. 2017; Maggini et al. 2020), hence their delayed passage at the Baltic coast.

Conclusions

This dissertation demonstrated the influence of climatic and intraspecific factors on the migration phenology of two species of *Sylvia* warblers passing in spring or autumn through the southern Baltic Sea coast. Analysing long-term data series on bird migration timing against the climate data revealed how these related species respond to global climate change. In the Garden Warbler, the autumn migration timing of immatures is shaped directly by environmental conditions at the breeding grounds and indirectly by the influence of spring temperatures on spring migration of their parents, through a trans-generational carry-over effect. For the Eurasian Blackcap, the two-day protandry at the beginning of spring passage remained stable over 44 years of study, and across both sub-periods. This is in line with the mate opportunity hypothesis, showing that selective pressures preserve differences in spring phenology between sexes, regardless of continuous climate warming. Furthermore, despite their different energy allocation strategies during migration, both male and female Blackcaps responded uniformly to regional temperatures and large-scale climate indices. However, while shifting migration is a universal population response to changing regional climates, this adaptability seems to be restricted by ecological limits and lower foraging efficiency of inexperienced young birds, which prevail during migration along the coast. This was evident in Blackcaps, where the spring migration timing for the majority of the population advanced during 1982–2004 but stabilised during 2005–2025. This recent stabilisation indicates that migrants have reached a biological threshold in their phenological flexibility, which likely prevents ecological mismatches with their peak food availability on stopovers and breeding grounds.

Ultimately, comparing these two *Sylvia* species highlights how their differences in migration distance and the number of broods shape their responses to climate change. The Eurasian Blackcap, which migrates over shorter distances and can raise even two broods a year, exhibits remarkable plasticity. This plasticity enabled Blackcaps to significantly advance their spring passage over the past decades, to maximise reproductive success. In contrast, the single-brooded, long-distance Garden Warbler operates under a tight annual schedule of subsequent life stages. With such time constraints, its adaptation to changing environmental conditions manifested as a shortened period of autumn passage, likely due to the condensed

breeding season. Together, these findings emphasise that while migratory birds are affected by climate warming, their phenological adaptations are limited by their breeding biology and migration distance. Understanding how these biological constraints shape species-specific responses to climate change is essential for predicting their vulnerability and developing effective conservation strategies for migratory birds.

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Rozdział 1

Long-term changes in autumn migration timing of Garden Warblers *Sylvia borin* at the southern Baltic coast in response to spring, summer and autumn temperatures

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Long-term changes in autumn migration timing of Garden Warblers *Sylvia borin* at the southern Baltic coast in response to spring, summer and autumn temperatures

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Abstract

Many migrant European birds have been departing their breeding grounds earlier in recent decades in response to rising temperatures from climate change. We examined long-term changes in the autumn migration timing of immature Garden Warblers using data from ringing station Bukowo-Kopań on the Polish Baltic coast in 1967–2018. We calculated an Annual Anomaly (AA) of migration and the dates when 10%, 50% and 90% of migrating birds were caught at each station. We modelled AA and the dates of these percentiles of passage for each station against the year and bi-monthly spring, summer and autumn temperatures as explanatory variables in multiple linear regression models. The overall passage (AA) of immature Garden Warblers advanced by 7 days and the dates of the 50th and 90th passage percentiles advanced by 6–11 days. Overall passage, and dates for 50% of passage occurred later the higher summer temperatures rose in Finland. We suggest favourable foraging conditions in warm summers at these breeding grounds and at first stopover sites delayed the passage because these inexperienced birds took advantage of the conditions to accumulate fuel before migrating south. The overall passage, and the dates of 10%, 50% and 90% of autumn passage occurred the earlier the higher were spring temperatures on spring migration route in Italy, and the higher were mean summer temperatures at breeding grounds in southern Sweden and Norway. We suggest a trans-generation carry-over effect, as warm springs encourage early arrival and nesting of returning adults, thus earlier broods and hatching of juveniles, which also grow faster in warm summers. These effects enable immatures to migrate earlier in autumn after a warm breeding season. The long-term increase in Europe's spring and summer temperatures thus help explain the shift in Garden Warblers' migration timing.

Keywords: Climate change, autumn migration, migration phenology, carry-over effect, *Sylvia borin*

Introduction

The timing of bird migration is driven by an endogenous rhythm controlled by seasonal changes in photoperiod (e.g. Gwinner 1996; Coppack & Pulido 2004; Dawson 2008; Knudsen et al. 2011), but external factors such as temperatures or feeding conditions often modify the timing of birds' life stages, including migration, breeding and wintering (e.g. Tryjanowski et al. 2002; Storde 2003; Newton 2008; Ockendon et al. 2013; Briedis et al. 2019; Lehikoinen et al. 2019). The timing of migrant passerines' passages and breeding has changed over recent decades in the northern hemisphere in response to climate change (e.g. Sokolov et al. 1999, Jenni & Kéry 2003; Tøttrup et al. 2006a,

2006b, Miles et al. 2017; Klun et al. 2017; Lehikoinen et al. 2019).

Most studies show that progressively earlier arrivals in spring are more pronounced in short-distance migrants than in their long-distance counterparts (e.g. Hüppop & Hüppop 2003; Jenni & Kéry 2003; Tøttrup et al. 2006a). Yet many long-distance migrants are also arriving earlier in the northern European spring, for example the Willow Warbler *Phylloscopus trochilus* and the Blackcap *Sylvia atricapilla* (Remisiewicz & Underhill 2020, 2022a, 2022b). In many migrants the shift to an earlier spring passage has been attributed to higher winter and spring temperatures in the north,

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including Pied Flycatchers *Ficedula hypoleuca* in Finland (Ahola et al. 2004) and Song Thrushes *Turdus philomelos* at the Baltic coast in Poland (Redlisiak et al. 2021), among tens of other species across Europe and North America (Lehikoinen et al. 2019).

Researchers have focused on how climate change has affected the phenology of spring migration, but autumn migration has received less attention, so less is known about how these changes have affected the phenology of southward migration (Gallinat et al. 2015; Rivrud et al. 2016; Haest et al. 2019). Passerines have responded to climate in varied ways, ranging from earlier to later autumn passages (Jenni & Kéry 2003; Gallinat et al. 2015; Miles et al. 2017). These shifts in autumn migration timing over recent decades have been attributed to individual species' breeding biology, including the number of clutches they lay a season (Halupka & Halupka 2017), and to migration distance (Jenni & Kéry 2003). In single-brooded species, if adults begin and end breeding early in a warm spring the immatures often depart the breeding grounds early in autumn (Halupka & Halupka 2017), as documented in Bluethroats *Luscinia svecica* in Sweden (Ellegren 1990) and Garden Warblers *Sylvia borin* in Denmark (Tøttrup et al. 2006b). In contrast, multiple-brooded species might use the breeding period extended by a warm spring to lay additional clutches, such as Barn Swallows *Hirundo rustica* in Denmark (Møller 2002). Immatures from additional clutches would be ready to depart the breeding grounds later than those from the first clutches and thus show a delayed autumn migration, as do Song Thrushes in Poland (Redlisiak et al. 2018) and Great Tits *Parus major* in Russia (Bojarinova et al. 2002). Short-distance migrants are under different pressures from long-distance migrants in autumn, with different effects on the timing of their migrations and other life stages (Jenni & Kéry 2003; Gordo 2007). For short-distance European migrants environmental conditions on their non-breeding grounds, often around the Mediterranean, improve as autumn progresses, bringing rainfall that ameliorates the effects of summer droughts (Gordo 2007). Yet short-distance migrants that arrive at their non-breeding grounds too early might face unfavourable conditions, including phenological mismatches affecting foraging success, which would reduce their chances for survival: thus they might benefit from staying longer at the breeding grounds (Jonzén et al. 2007; Newton 2008; Halupka et al. 2017). Long-distance migrants usually begin autumn migration right after breeding to take advantage of the peak abundance of food in early autumn at their

stopovers and later at their non-breeding grounds (Morel 1973 cited by Gordo 2007, Redlisiak et al. 2018). Jenni and Kéry (2003) suggested that in response to climate change autumn migration has shifted later in short-distance migrants but earlier in long-distance migrants. Nevertheless, long-distance migrant passerines have adopted divergent strategies to cope with these changes: autumn migration of Blackcaps *Sylvia atricapilla* in Denmark shifted earlier over 1976–1997, but autumn migration of Wood Warblers *Phylloscopus sibilatrix* in Denmark and Willow Warblers and Whinchats *Saxicola rubetra* in the UK shifted later over 1955–2014, and no long-term change occurred among Common Whitethroats *Sylvia communis* in the UK in this period (Cotton 2003; Tøttrup et al. 2006b; Miles et al. 2017).

Few researchers have yet studied phenological shifts in the autumn migration of passerines, which vary widely (Gallinat et al. 2015). Responses to climate change might vary within a family, as among *Sylvia* warblers, even between the different migration phases of individual species (Fransson 1995, Tøttrup et al. 2006b). For example, in Garden Warblers the first half of autumn migration has advanced, but in Lesser Whitethroat *Sylvia curruca* the second half of passage shifted later at Fair Isle over 1955–2014, though these shifts have not been attributed to climate (Miles et al. 2017).

Garden Warblers are single-brooded, long-distance migrants that pass through Poland from the beginning of August to mid-September on their way south from breeding grounds in Fennoscandia (Norway, Sweden, Finland) to sub-Saharan Africa (Cramp 1992; Maciąg et al. 2017). We used monitoring data on migrant Garden Warblers collected during 1967–2018 at bird ringing station Bukowo-Kopań, on the Baltic coast of Poland. The ringing recoveries indicate that Garden Warblers migrating through this station come from the breeding grounds in Sweden, Norway and Finland (Figure 1; Spina et al. 2022). These migratory populations breed mostly in June–July, migrate in autumn from August to mid-November, visit the non-breeding grounds from mid-November to mid-March, and migrate north in spring from mid-March to the end of May (Cramp 1992).

Most studies examining how climate change affects autumn migration focus on the influences of local weather that directly affect this passage, such as local summer temperatures on the breeding grounds (e.g. Cotton 2003; van Buskirk et al. 2009; Horev et al. 2010; Smith et al. 2011; Chambers et al. 2014; Ellwood et al. 2015; Bozó et al. 2018). Temperatures can serve as proxies for the myriad ecological

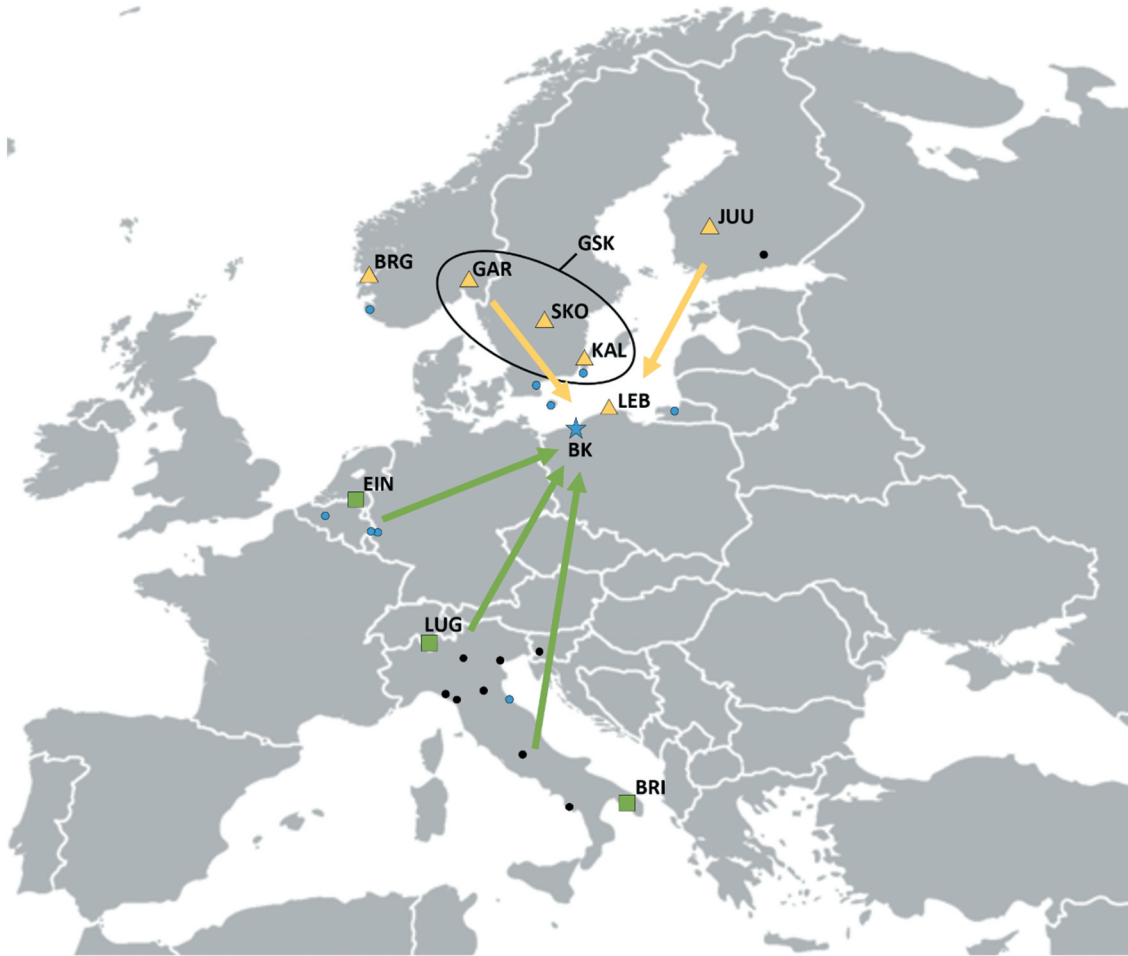


Figure 1. Location of ringing and weather stations used in the study, and recoveries of Garden Warblers ringed at Operation Baltic stations but recovered elsewhere. Blue star – Bukowo-Kopań ringing station (BK). Blue circles – recoveries of birds caught at Bukowo-Kopań, black circles – recoveries of birds caught at two other coastal stations (Hel, Mierzeja Wiślana), after Maciąg et al. (2017). Yellow triangles – weather stations near breeding grounds and on autumn migration routes: LEB – Leba, JUU – Juupajoki, BRG – Bergen, KAL – Kalmar, GAR – Gardermoen, SKO – Skovde, GSK – group of three weather stations combined (Gardermoen, Skovde and Kalmar). Green squares – weather stations on spring migration routes: BRI – Brindisi, LUG – Lugano, EIN – Eindhoven. Arrows – general directions of migration of Garden Warblers towards the Polish coast from the breeding grounds in autumn (yellow arrows), and from the non-breeding grounds in spring (green arrows).

conditions that govern a migrant's success, from the availability of suitable habitat to foraging conditions (Walther et al. 2002; Julliard et al. 2004; Thackeray et al. 2016). But few studies have examined the cumulative influence on migrants of factors such as temperatures along spring migration routes that might affect autumn migration indirectly through carry-over effects of phenological shifts in one life stage altering the timing of a later stage (e.g. Sokolov 2006; Barshep et al. 2011; Tomotani et al. 2018). We aimed to identify any multiyear and year-to-year changes in the timing of Garden Warblers' autumn migration. Given advances in autumn migration timing of Garden Warbler over 60 years at Fair Isle (Miles et al. 2017), we expected a shift to earlier autumn passage of this species at Poland's Baltic

coast over 1967–2018. Considering the limited literature evidence of carry-over effects of temperatures on migrants, we aimed to determine any relationship between the timing of Garden Warblers' autumn migration and temperatures not only on the breeding grounds and along autumn migration routes, but also on previous spring migration routes. We expected the timing of immature Garden Warblers' autumn migration to be related to the temperatures they had experienced at the breeding grounds in Fennoscandia, and which the adults had encountered earlier during their spring migration to these areas. With this study we aim to fill in a gap in knowledge on a trans-generational carry-over effects of temperatures in migrant birds, which would extend our understanding of the ways the climate change might

affect migrants at subsequent stages of their life in different parts of their range.

Materials and methods

We used the autumn migration dates of immature Garden Warblers caught at Operation Baltic's ringing station Bukowo-Kopań (54°19'38"–54°27'54"N; 16°13'33"–16°25'15"E) on the southern Baltic coast (Figure 1). This station is mostly a stop-over site for migrating Garden Warblers from the breeding grounds in Fennoscandia, but locally recaptured individuals (Nowakowski 2017) indicate that some birds come from local populations, which breed in nearby riparian broadleaved forest (Remisiewicz & Underhill 2022b). Data were collected for the period when these warblers migrate south through Poland, from 14 August to 15 October, in 1967–2018. Bukowo-Kopań station used the same standard data-collection protocol throughout this period (Busse & Meissner 2015). Migrating birds were caught daily in mist nets from dawn till dusk. The number of mist nets remained constant in each season, but ranged from 25 to 89 over the years. Birds were ringed, measured, and Garden Warblers caught in autumn were aged as immatures or adults by their plumage (Svensson 1992; Demongin 2016).

We used the daily numbers of immature Garden Warblers caught each autumn because too few adults were caught to analyse. We noted only the first capture of a bird in the season. The few gaps in data on days when catching was suspended for different reasons, mostly storms, were imputed with the mean number of birds caught at the station on those dates in the six previous years and the six following years, as in previous studies (Redlisiak et al. 2018; Remisiewicz & Underhill 2020, 2022a, 2022b). These gaps occurred in 12 years of the study and there was no more than three gap days in any season. We analysed data only for years in which more than 30 immature Garden Warblers were captured in autumn (Table S1), for a total of 4407 birds.

For each year we determined how many immature Garden Warblers were caught on each day of the season. Then we calculated this number as a percentage of the autumn total of immature Garden Warblers. These cumulative percentages were then converted to a scale of 0–1 for our statistical analyses. Based on these values we drew the daily cumulative curves, reflecting the pattern of autumn migration in each year of the study (Redlisiak et al. 2018; Remisiewicz & Underhill 2020). We determined the Annual Anomaly (AA) of passage in each autumn as the departure of the

daily cumulative curve in that year from the many-year (1967–2018) average daily cumulative curve, as in Remisiewicz and Underhill (2020). A negative Annual Anomaly showed that overall passage that autumn occurred earlier than the many-year average pattern, and a positive AA showed that season's passage had occurred later than the average (Remisiewicz & Underhill 2020, 2022a).

To show changes in autumn migration timing in more detail, from the daily cumulative curves we derived the dates when 10%, 50% and 90% of the season's immature Garden Warblers were captured, as in other studies (e.g. Tøttrup et al. 2006b; Miles et al. 2017; Lehtikoinen et al. 2019). These dates were used in further analyses as Julian days – the number of days from 1 January. We also calculated the duration of passage for 80% of the Garden Warblers each year as the difference (in days) between the dates when 10% and 90% of the birds had passed. We then used linear regression to check for any multiyear trends in the dates of 10% (beginning), 50% (middle) and 90% (end) of immatures' migration and the duration of migration for each year we studied.

To determine the relationship between temperatures and the timing of autumn migration we used mean temperatures from weather stations on the Garden Warblers' spring migration routes, at their breeding grounds and on their autumn migration routes (Table I, Figure 1). We selected these locations based on the distribution of ringing recoveries of Garden Warblers caught at three Operation Baltic's field stations: Bukowo-Kopań, and at Hel and Mierzeja Wiślana, located ca 150–200 km respectively, to the east (Figure 1, Maciąg et al. 2017). Using mean daily temperatures from the selected weather stations from April to September 1967–2018 (<http://www.ecad.eu>, 2018) we calculated bi-monthly mean temperatures of April–May, June–July and August–September, periods that corresponded with consecutive stages in the life cycle of the Garden Warbler (Table I). Strongly correlated temperature data from three weather stations in south Scandinavia for June–July and for August–September we combined as a single variable, GSK (Figure 1, Table S2). We checked if temperatures on the spring migration routes, at the breeding grounds and on the autumn migration routes showed any trends over 1967–2018 by using linear regression of the temperature variables against the year.

The variables were in different measurement units, so we standardised the AA, the Julian dates for the percentiles of passage and temperature variables so that each had a mean of 0 and a standard deviation of 1. We also checked for any correlations between the temperature variables using Pearson's correlation

Table I. Weather stations on Garden Warblers' spring migration routes and breeding grounds, from which we used the mean bi-monthly temperatures of months when the area was used by the birds. Abbreviations – symbols of the temperature variables used in the study, indicating weather station or grouping (as in Figure 1) and season.

Region (months = SEASON)	Weather station (country)	Abbreviations
Spring migration routes (April–May = SPRING)	Brindisi (Italy)	BRI_SPR
	Lugano (Switzerland)	LUG_SPR
	Eindhoven (Netherlands)	EIN_SPR
	Łeba (Poland)	LEB_SPR
Breeding grounds (June–July = SUMMER),	Łeba (Poland)	LEB_SUM
		LEB_AUT
Autumn migration routes (August–September = AUTUMN)	Kalmar (Sweden)	GSK_SUM
	Skovde (Sweden)	GSK_AUT
	Gardermoen (Norway)	
	Bergen (Norway)	BRG_SUM
		BRG_AUT
	Juupajoki (Finland)	JUU_SUM
		JUU_AUT

coefficient to check for multicollinearity (Dormann et al. 2013), which we considered in the interpretation of our results.

We determined if spring, summer and autumn temperatures had influenced the timing of the immature Garden Warblers' autumn migration across the southern Baltic coast by building multiple linear regression models in which the AA and dates for 10%, 50% and 90% of passage (further in the text: “measures of migration timing”) were response variables in the model against 13 explanatory variables of the bi-monthly mean temperatures at the weather stations (Table I) and the year. Our calculations included many explanatory variables, so as our first step we analysed each response variable against the year and temperature variables from the weather stations for spring, summer and autumn separately. Most correlation coefficients between the temperature variables were within the acceptable level of $|r| < 0.7$ (Dormann et al. 2013), but eight variables were correlated within spring and summer season above this threshold (Table S2), which might cause a bias to the results of our models (Dormann et al. 2013), so we applied an iterative approach. Thus, in the second step we created two sets of partial models for each of these seasons, where we included only uncorrelated variables (Quinn & Keough 2008). We then assessed whether the explanatory variables selected in the best models derived from these partial models differed from the best models derived from the full models and we evaluated if the values and signs of the effects for each variable differed between the best models derived by these two approaches. When the sign and the strength of each effect were the same in the best models derived in these two ways, we assumed that any multicollinearity in the full model did not affect the selection of the model. Thus we used the best

model derived from the full model in further considerations. When the best models derived from the partial models showed no significant effect of any variable, but these derived from the full model included the correlated variables, we further used this latter best model, which indicated that such variables might have a combined influence on bird migration timing. In our third step we analysed each response variable against the year and those temperature variables found to be significant in the best models for spring, summer and autumn. We plotted the residuals of the best models to verify if the models met the assumptions of multiple regression (Crawley 2013). To further evaluate any multicollinearity we calculated the variance inflation factor (VIF), which in all full and partial models and in the best multiple regression models for spring, summer and both seasons combined were all < 10 , indicating that any multicollinearity was low and did not harm our results (Quinn & Keough 2008; Dormann et al. 2013).

We selected the best models by Akaike Information Criteria corrected for small sample size (AICc) with “all subsets” of the variables using the dredge function in the package “MuMIn 1.43.17” (Bartoń 2020). Using the adjusted determination coefficient (AdjR^2) we evaluated the percentage of variation explained by all the explanatory variables of the best models. To evaluate the percentage of variation for each explanatory variable in the models we also determined partial regression coefficients (partial R^2) using the package “heplots 1.3–5” (Fox et al. 2007). We then plotted all the temperature variables that had any significant effect on the timing of the immature Garden Warblers' autumn migration against corresponding response variables to examine the influence of each temperature variable separately. The statistical analyses followed Remisiewicz and Underhill (2020) and

were conducted in R 4.1.2 (R Core Team 2021) and RStudio 2021.9.2–382 (RStudio, Inc. 2021).

Results

Multiyear trends in timing of immature Garden Warblers' autumn migration across Polish Baltic coast

The overall autumn migration timing (AA) of immature Garden Warblers through Bukowo-Kopań shifted earlier by 7 days on average over 1967–2018 (Figure 2(a), Table S3). The timing of the 50th percentile of passage advanced by 6 days over these 52 years and of the 90th percentile by 11 days (Figure 2(b), Table S3). The duration of these immature Garden Warblers' autumn migration shortened by 9 days on average over 1967–2018, because the dates of the end (last 90%) of passage shifted earlier but those of the beginning (first 10%) of migration did not change (Fig. S1, Table S3).

Relationship between temperatures on spring migration north and at breeding grounds and timing of following autumn migration across Baltic coast

All the spring, summer and autumn temperatures we analysed increased significantly by 1.3 to 2.9°C over 1967–2018, except for summer temperatures at Juupajoki in Finland (Table S4). The first step of our analysis showed that autumn migration occurred earlier with higher spring temperatures, and higher summer temperatures were related to earlier or later dates for the median and end of passage at Bukowo-Kopań. Autumn temperatures showed no significant effects. The full models with four spring temperature variables and the year indicated a significant negative relationship between spring temperatures in Brindisi, Italy, and AA as well as the dates of 90% of passage (Tables S5–S10). The full models with four summer temperature variables and the year indicated that summer temperature at Juupajoki, Finland, had a significant positive relationship with the dates on which the median (50%) of immatures migrated through Bukowo-Kopań (Tables S11–S12). The dates for the end of migration (90%) at this station showed a significantly negative relationship with summer temperatures in Łeba, Poland (Tables S11–S12). The best models derived from the full models for spring (Table S6) and summer (Table S12) corresponded well with those derived from the partial models (Tables S8, S10, S14, S16). This showed that multicollinearity did not bias the model selection process, thus we used the best models derived from full models (Tables S5–S6, S11–S12). The models examining four autumn temperature variables and the year

as explanatory variables showed no significant relationships with any of the measures of migration timing at Bukowo-Kopań (Tables S17–S18), so we excluded autumn temperatures from the next step of our analysis. In the third step, the best multiple regression models with those spring and summer temperatures found significant in the first step included from one to four temperature variables and explained 13%–35% of the variation in AA and in the dates of the percentiles of passage (Table II, Tables S19–S20). When combined in a single model, the higher were temperatures the preceding spring the earlier all phases of autumn passage occurred, but high summer temperatures were related to early or late timing in different phases of the autumn passage (Table II). The higher the spring temperatures on the migration route in Brindisi in Italy, the earlier Garden Warblers arrived the next autumn at Bukowo-Kopań, as indicated by the negative relationships between these temperature variables and all our measures of migration timing, especially the end (90%) of passage (Table II, Figure 3(a)). The higher the summer temperatures at GSK stations in south Scandinavia the earlier overall passage (AA), beginning (10%) and median (50%) of migration of Garden Warblers occurred at Bukowo-Kopań in autumn (Table II, Figure 3(b)). The higher the summer temperatures at Bergen, Norway the earlier the end (90%) of immature Garden Warblers' passage occurred at Bukowo-Kopań (Table II, Fig. S6(b)). But the higher the summer temperatures in Łeba, Poland, the later the first 10% of migrating Garden Warblers occurred (Table II, Fig. S6(a)). Also the higher the summer temperatures on the breeding grounds in Juupajoki, Finland, the later was the median (50%) and the overall passage of the immature Garden Warbler (Table II, Figure 3(c)).

Discussion

We found that immature Garden Warblers' autumn passage at Polish Baltic coast had ended progressively earlier over the five decades of our study and thus the duration of their passage had shortened. Our results showed that these changes likely occurred in response to summer temperatures at the species' breeding grounds in Fennoscandia and Poland and to temperatures the previous spring on their migration routes in Italy. We discuss how the timing of Garden Warblers' autumn migration might respond to temperatures in spring, months before the immatures we examined had hatched, through a carry-over effect across the generations, and also through the direct effects on the immatures of conditions at the breeding grounds.

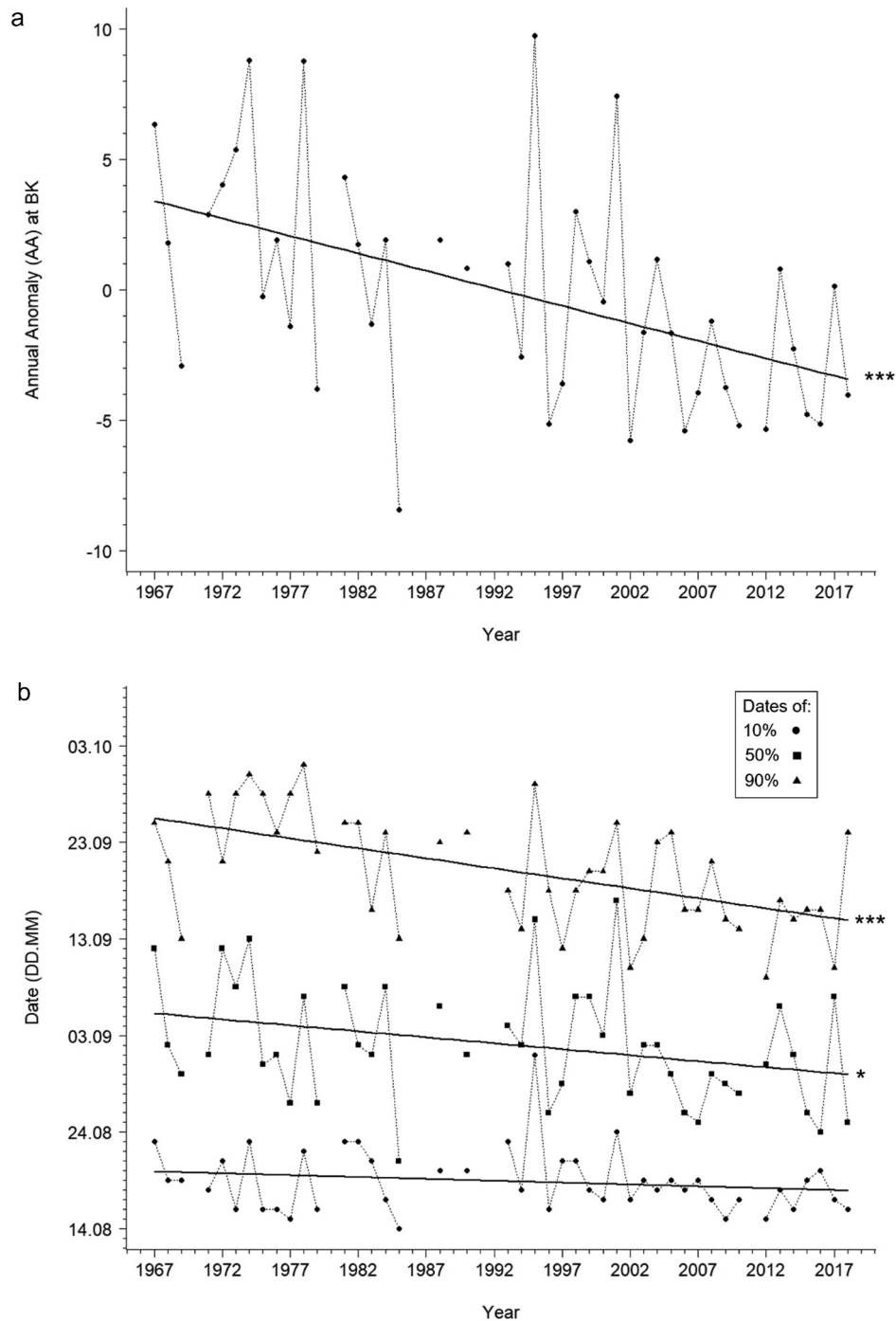


Figure 2. Trends in overall Annual Anomaly (AA) and dates of sequential percentiles of autumn passage at Bukowo-Kopań over 1967–2018. (a) Annual Anomaly and the trend by linear regression. (b) Dates of 10th, 50th and 90th percentiles of autumn passage and their trends by linear regression. *** – $p < 0.001$, * – $p < 0.05$. Statistics for regression equations in Table S3.

Shifts in timing of autumn migration on southern Baltic coast compared with other European sites

Our study showed that the timing of the end (90%) of Garden Warblers' autumn passage at the southern

part of Baltic coast in Poland advanced over 1967–2018, as it had in 1976–1997 at the Danish island of Christiansø on the southern Baltic ca 130 km northwest of Bukowo-Kopań (Tøttrup et al. 2006b). Garden Warblers' earlier median date of autumn

Table II. Relationships between overall Annual Anomaly (AA) and migration dates of 10th, 50th and 90th percentiles of autumn migration by immature Garden Warbler at Bukowo-Kopań over 1967–2018 with the temperature variables and year in the best models selected by Akaike Information Criteria (AICc). Statistics for the best model: AdjR² – adjusted coefficient of determination, F – result of GLM, p – significance of the best model, Estimate – coefficients of multiple regression, SE – standard error of the estimates, t – t-test, P – significance of each estimate, VIF – variance inflation factor, R² – partial determination coefficient for each estimate. p < 0.05 marked in **bold** face and 0.05 < p < 0.1 in *italics*. Symbols of explanatory variables as in Table I.

Response variable	AdjR ²	F	p	Explanatory variable	Estimate	SE	t	P	VIF	R ²
AA	0.35	F _{3,41} = 8.87	<0.001	BRI_SPR	−0.502	0.129	−3.90	<0.001	1.07	0.27
				GSK_SUM	−0.466	0.163	−2.86	0.007	1.85	0.17
				JUU_SUM	0.426	0.166	2.57	0.014	1.84	0.14
10%	0.13	F _{3,41} = 3.16	0.035	BRI_SPR	−0.454	0.173	−2.62	0.012	1.45	0.14
				GSK_SUM	−0.642	0.273	−2.35	0.024	3.87	0.12
				LEB_SUM	0.706	0.304	2.32	0.025	4.71	0.12
50%	0.25	F _{3,41} = 5.96	0.002	BRI_SPR	−0.341	0.138	−2.47	0.018	1.07	0.13
				GSK_SUM	−0.519	0.175	−2.98	0.005	1.85	0.18
				JUU_SUM	0.551	0.178	3.10	0.003	1.84	0.19
90%	0.30	F _{2,42} = 10.6	<0.001	BRI_SPR	−0.499	0.131	−3.80	0.000	1.04	0.26
				BRG_SUM	−0.224	0.126	−1.77	0.083	1.04	0.07

passage in 1967–2018 at Bukowo-Kopań was similar to the trend for mean autumn passage over 1960–2014 at Heligoland Island, Germany (Haest et al. 2019) ca 540 km west of Bukowo-Kopań (Table S3). This might indicate similar effects of common environmental factors, including the temperatures we analysed, for the species' autumn migration through the Baltic and the North Sea region. As in our study, the last autumn departure dates advanced in 1971–2000 at Oxfordshire, England, (Cotton et al. 2003) though studies at other locations in Europe have shown different patterns. For example, the dates when 5%, 10%, 25% and 50% of Garden Warblers on passage were caught at Fair Island, Scotland, shifted significantly earlier over 1955–2014, but the dates for 75%–95% of passage did not (Miles et al. 2017), in contrast to our results.

The median date of autumn passage (50%) of immature Garden Warblers caught at Ottenby Bird Observatory in Sweden showed no significant shift over 1950–2008 (Iwajomo et al. 2012), in contrast to our results, where the median passage shifted earlier (Table S3, Figure 2). At Rybachy station on the Courish Spit, Russia, about 315 km east of Bukowo-Kopań, the mean dates of this species' autumn migration shifted later over 1959–1976 and 1985–1998, but no trend was found in 1976–1990 (Sokolov et al. 1999), in contrast to the significant trend towards earlier median date and overall (AA) autumn passage over 1967–2018 at Bukowo-Kopań (Table S3, Figure 2). These different trends between neighbouring stations in the Baltic region likely resulted from the different periods being studied.

Changes in autumn migration timing might vary even for different phases of the same passage (e.g.

Tøttrup et al. 2006b; Miles et al. 2017; Barton et al. 2018). Similarly, when the beginning and end of migration are advanced or delayed the duration of the passage might lengthen or shorten. The duration of Song Thrush migration in spring and autumn lengthened (Redlisiak et al. 2018 2021), as it did in Lesser Whitethroat (Miles et al. 2017) and in the spring migration of Willow Warbler (Remisiewicz & Underhill 2020). The duration of passage might also shorten, as for Redstart *Phoenicurus phoenicurus* (Miles et al. 2017). We suggest that the duration of immature Garden Warblers' autumn passage at Bukowo-Kopań field station shortened over the five decades we studied because of the earlier departures of the last cohorts of Garden Warblers from their breeding grounds and thus the last phases of their passage at stopover sites shifted earlier. This finding contrasted with those for most other short- and long-distance migrants in the temperate and boreal zones of the northern hemisphere, whose autumn migrations have extended because of an earlier beginning and a later end of passage compared with earlier decades (Lehikoinen et al. 2019). Meta-analysis of the duration of breeding has revealed that single-brooded species in the northern hemisphere have shortened their breeding season in the past few decades in response to increasing temperatures, in contrast to multi-brooded species, which have extended their breeding period (Halupka & Halupka 2017). The condensed breeding season observed in single-brooded species likely results from them fine-tuning their egg-laying dates to match the maximum energetic demands of their offspring with the peak of food resources. Insects now often appear earlier in spring as temperatures trend upwards and foraging opportunities might be

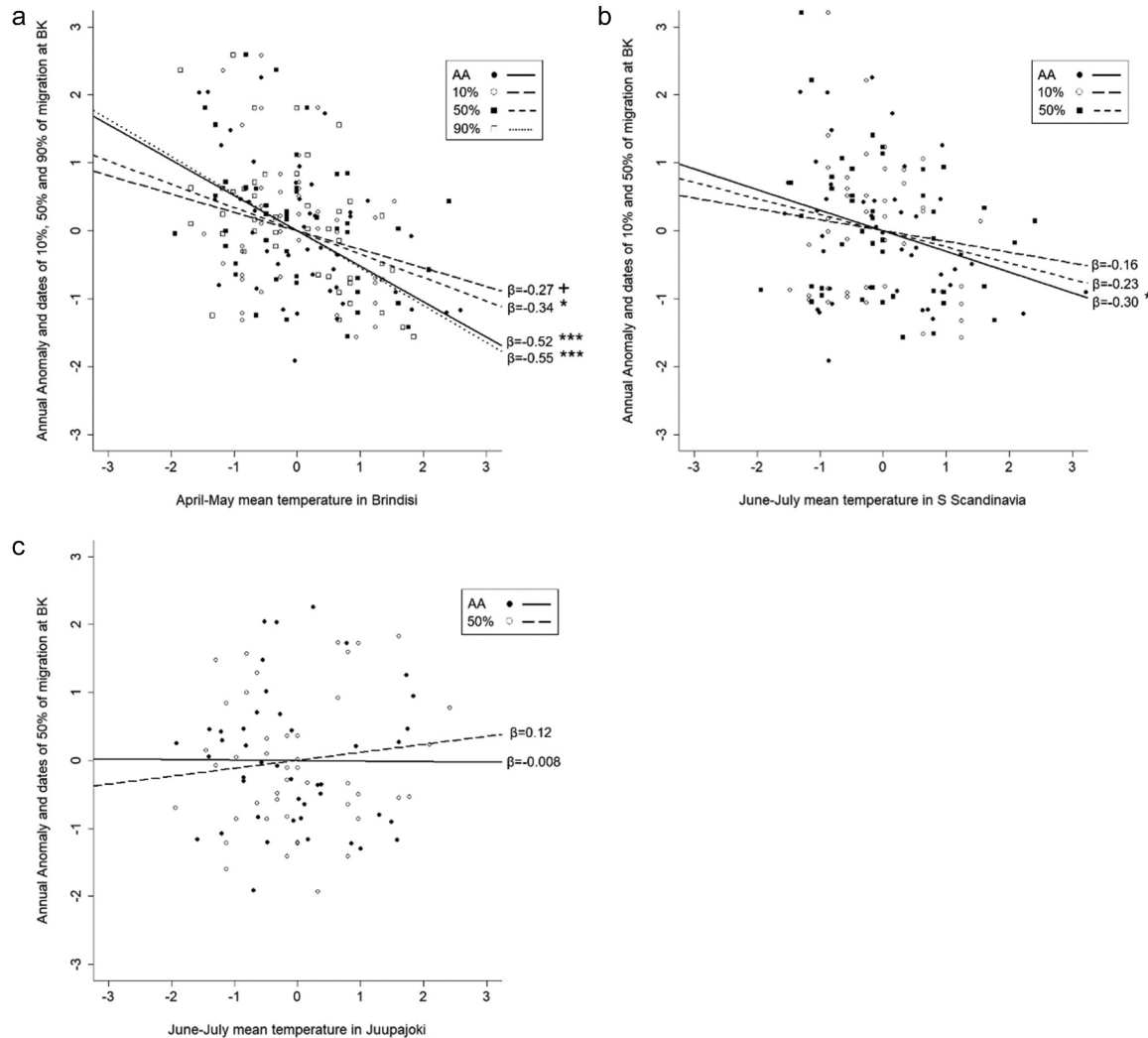


Figure 3. Overall Annual Anomaly (AA) and dates of 10th, 50th and 90th percentiles of autumn migration by immature Garden Warbler at Bukowo-Kopań over 1967–2018 against temperature variables selected in best models (Table II) with trends by linear regression. β – regression coefficient. *** – $p < 0.001$, * – $p < 0.05$, + – $p < 0.1$. All variables are presented as standardised values. (a) AA and 10th, 50th and 90th percentiles against April–May mean temperature in Brindisi, (b) AA and 10th and 90th percentiles against June–July mean temperature in South Scandinavia, (c) AA and 50th percentile against June–July mean temperature in Juupajoki.

a limiting factor for insectivorous birds that breed late in spring (Halupka & Halupka 2017). Thus the shorter autumn migration period we found in Garden Warblers, a single-brooded, insectivorous, long-distance migrant that arrives on the breeding grounds in northeastern Europe in mid-May – late compared with other passerines – likely reflects a shortening of its breeding period.

Timing of autumn migration in relation to temperatures on spring migration

Few studies have examined how the effects of weather encountered by one generation of birds might be carried-over to the timing of autumn

migration in the next generation (e.g. Sokolov 2006; Tomotani et al. 2018). Yet our results suggest that the timing of immature birds' autumn migration might be indirectly affected by temperatures their parents encountered at different stages in their life, including on spring migration routes. We found that the higher were spring temperatures in Italy on the Garden Warblers' migration northwards, the earlier the immatures migrating south arrived in autumn on the Polish Baltic coast. This influence could only be indirect, because the immatures we analysed would have hatched after spring, so these conditions could only have affected their parents. Warm springs might encourage the earlier arrival of adults at the breeding grounds and earlier

nesting than in years with a cold spring (Tomotani et al. 2018), thus the earlier hatching of the immatures followed by an earlier departure of both age groups from the breeding grounds (Ellegren 1990; Sokolov et al. 1999; Gordo 2007). The early spring passage of Garden Warblers at Hanko Bird Observatory in Finland corresponds with high temperatures in May on the migration routes north, confirming that a warm spring encourages the early arrival of adults at the breeding grounds (Halkka 2011).

Timing of autumn migration in relation to temperatures on breeding grounds

Several studies have shown that high summer temperatures at the breeding grounds affect the timing of autumn migration, but most of these studies have focused on temperatures at a single breeding area (e.g. Cotton 2003; Ellwood et al. 2015; Bozó et al. 2018). Few studies have investigated the effect of temperatures at widespread breeding grounds on subsequent autumn migration timing (e.g. Redlisiak et al. 2018; Haest et al. 2019), as we did. We found that temperatures at the different breeding areas in Fennoscandia directly influenced the migration timing of immature Garden Warblers at the southern Baltic coast. Warm summers enable immatures to grow faster, thus depart earlier from the breeding grounds, and thus then appear earlier at autumn stopover sites than after cold and rainy summers (Crick and Sparks 1999; Redlisiak et al. 2018). This effect likely explains why the overall passage (AA) and the first half (10%, 50%) of migrating immature Garden Warblers shifted earlier at Bukowo-Kopań in autumns after higher summer temperatures on the breeding grounds in south Scandinavia (GSK stations) in June–July (Table II). An earlier end (90%) of Garden Warblers' passage through Bukowo-Kopań corresponded with higher summer temperatures in Norway (BRG) in June–July (Table II), as in Oxfordshire, UK, where the last 95% of Garden Warblers passed through earlier with higher local summer temperatures (Cotton 2003).

The positive relationship between temperatures at local breeding grounds in Poland and the timing of the beginning of Garden Warblers' passage (10%) at Bukowo-Kopań (Table II), indicating later passage, probably accounted for the lack of a clear trend in the timing of this cohort of migrants. We found the later overall passage (AA) and median (50%) of migration at Bukowo-Kopań with higher summer temperatures in Finland (Table II), which suggests that warm summer at the breeding grounds and at

early stopover sites might delay passage at the southern Baltic coast because the migrants take advantage of favourable feeding conditions to accumulate fuel for their long trip to sub-Saharan Africa. Garden Warblers gradually accumulate fuel reserves along their migration route and their median fat score in autumn at Bukowo-Kopań was a modest 2 on a scale from 0 to 7 (Ożarowska 2015). These inexperienced birds accumulated this fat at the breeding grounds or at their first stopover sites. Nevertheless, the timing of end of Garden Warblers' migration clearly shifted earlier, despite higher summer temperatures at some breeding grounds corresponded with a later passage of the first half of migrants. We suggest that temperatures that advance autumn migration – such as higher temperatures along the northward migration routes the previous spring, and at the breeding grounds in Norway and southern Sweden – have a stronger overall effect than the delay incurred at certain breeding grounds (Finland, Polish coast) on a cohort of immature migrants.

Different influences of summer temperatures at various breeding areas on subsequent stages of Garden Warblers' migration suggest that different cohorts arrive at the southern coast of the Baltic from different parts of the breeding grounds (Figure 1) (Maciąg et al. 2017; Spina et al. 2022). Our results show that the higher the summer temperatures on the breeding grounds in southern Scandinavia, the earlier immature Garden Warblers arrive in autumn. If we assume that most Garden Warblers ringed at Bukowo-Kopań come mostly from southern Scandinavia as suggested by ringing recoveries (Figure 1) (Maciąg et al. 2017; Spina et al. 2022), this, combined with the earlier passage related to high spring temperatures, would explain the general trend towards an overall earlier autumn passage at this station.

Many-year trends and year-to-year variation in timing of immature Garden Warbler's autumn migration as a response to temperature

Spring temperatures on migration routes and summer temperatures at the Garden Warblers' breeding grounds rose over 1967–2018 (Table S4), likely as an effect of global climate change (Blunden & Boyer 2021). Considering the many different relationships between these temperatures and the timing of the species' migration that we found, the multiyear trend of rising temperatures partly explains the many-year trend towards an earlier end of the immatures' autumn passage and its shorter duration at the southern Baltic coast. The timing of bird migration

is generally determined genetically (e.g. Coppack & Pulido 2004; Dawson 2008) but can be modified by temperature (e.g. Tryjanowski et al. 2002; Ockendon et al. 2013; Lehikoinen et al. 2019), therefore birds can fine-tune their migrations to adapt to climate change in the northern hemisphere (e.g. Jenni & Kéry 2003; Tøttrup et al. 2010). In several other long-distance migrants between Africa and northern Europe, the timing of spring migration at Bukowo-Kopań was shaped by the combined influence of certain climate variables showing long-term trends and others showing no trends (Remisiewicz & Underhill 2020, 2022a, 2022b). Similarly, the timing of immature Garden Warblers' autumn migration through the Baltic coast is likely a combination of their response to temperature variables showing long-term trends and to factors which showed no such trend, as summer temperatures in Finland (Table S4).

Conclusions

The relationship we found in Garden Warblers between an earlier end to the immature's autumn passage south at the Baltic coast and a warm spring during the adults' migration north to the breeding grounds suggests a carry-over effect with the timing of the life stages of one generation on the next. Tomotani et al. (2018) showed a similar carry-over effect in another migrant passerine, the Pied Flycatcher, where adults breeding early aided the survival of their offspring. To our knowledge no other study has shown a trans-generational carry-over effect of temperatures influencing the migration timing of immature birds. In addition, the offspring respond directly to summer temperatures at the breeding grounds. Warm summers aid early maturity, thus early departure from the breeding grounds on autumn migration, but the birds might daily to take advantage of optimal foraging opportunities before heading south to sub-Saharan Africa. The many-year trend to an earlier end of autumn migration by immature Garden Warblers at Poland's Baltic coast along with the year-to-year variations we revealed are therefore likely shaped by the combined effects of the indirect influence of spring temperatures on adults en route to their breeding grounds and the direct influence of summer temperatures on their offspring.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Supplementary material

Supplemental data for this article can be accessed online at <https://doi.org/10.1080/24750263.2023.2192239>

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Long-term changes in autumn migration timing of Garden Warblers *Sylvia borin* at the southern Baltic coast in response to temperatures in spring and summer

**Supplementary Information
Figures S1-S6 and Tables S1-S20**

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Table S1. The number of immature Garden Warblers caught each year between 14 August and 15 October at Bukowo-Kopań station, over 1967-2018; “-” – years in which fewer than 30 individuals were caught.

Year	Total
1967	100
1968	106
1969	82
1970	-
1971	60
1972	102
1973	52
1974	122
1975	64
1976	52
1977	75
1978	86
1979	53
1980	-
1981	151
1982	103
1983	42
1984	50
1985	37
1986	-
1987	-
1988	56
1989	-
1990	55
1991	-
1992	-
1993	60
1994	84
1995	111
1996	199
1997	247
1998	148
1999	178
2000	67
2001	236
2002	214
2003	133
2004	68
2005	147
2006	159
2007	110
2008	104
2009	66
2010	126
2011	-
2012	69
2013	67
2014	91
2015	105
2016	43
2017	89
2018	38
Grand total	4407

Table S2. Pearson's correlation coefficients for bi-monthly mean daily temperatures in April–May, June–July and August–September from weather stations on spring migration routes and at breeding grounds of Garden warblers and the year (1967–2018). $p < 0.05$ marked in **red**. Symbols of variables as in Table 1.

Variable	Year	LUG_SPR	BRI_SPR	EIN_SPR	LEB_SPR	LEB_SUM	GSK_SUM	BRG_SUM	JUU_SUM	LEB_AUT	GSK_AUT	BRG_AUT
LUG_SPR	0.622											
BRI_SPR	0.558	0.476										
EIN_SPR	0.647	0.789	0.476									
LEB_SPR	0.645	0.558	0.621	0.739								
LEB_SUM	0.538	0.538	0.502	0.434	0.432							
GSK_SUM	0.332	0.404	0.290	0.314	0.246	0.846						
BRG_SUM	0.465	0.418	0.139	0.406	0.210	0.647	0.700					
JUU_SUM	0.084	0.113	0.175	0.059	-0.018	0.637	0.660	0.375				
LEB_AUT	0.485	0.449	0.243	0.311	0.311	0.588	0.536	0.568	0.308			
GSK_AUT	0.416	0.418	0.168	0.217	0.199	0.511	0.514	0.548	0.275	0.874		
BRG_AUT	0.426	0.358	0.175	0.213	0.152	0.391	0.319	0.460	0.135	0.660	0.821	
JUU_AUT	0.462	0.434	0.223	0.263	0.230	0.532	0.491	0.460	0.351	0.847	0.793	0.612

Figure S1. Trend in duration of autumn migration of immature Garden Warbler at Bukowo-Kopań over 1967–2018 by linear regression. ** – $p < 0.01$. Statistics for the regression equation in Table S3.

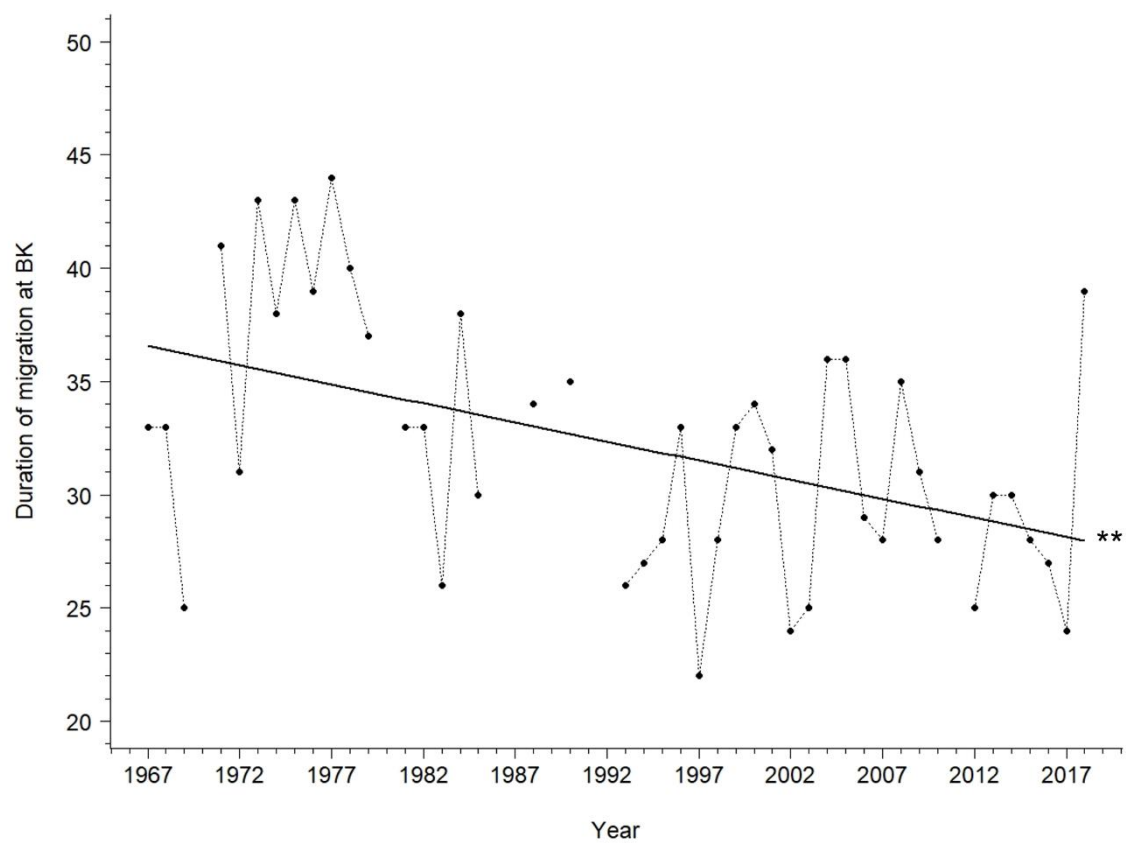


Table S3. Coefficients from regression equations for parameters affecting autumn migration timing of immature Garden Warblers (Figure 2) and duration of migration (Figure S1) at Bukowo-Kopań against the year over 1967–2018; a – intercept, β – slope of regression line, SE – standard error, p – statistical significance, $52*\beta$ – change in autumn migration dates and duration of migration (in days) over 52 years, negative values indicate earlier arrival and or shorter duration. p < 0.05 marked in **bold** face.

Parameter	Mean arrival date	a	β	SE	p	R ²	$52*\beta$
AA	-	3.54	-0.134	0.038	0.001	0.23	-7
10%	19 Aug	231.96	-0.039	0.032	0.231	0.03	-2
50%	2 Sep	248.42	-0.124	0.058	0.038	0.10	-6
90%	20 Sep	268.69	-0.207	0.049	< 0.001	0.30	-11
Duration	-	36.73	-0.168	0.049	0.001	0.22	-9

Table S4. Coefficients from regression equations for bi-monthly mean spring, summer and autumn temperatures on migration routes and at breeding grounds of Garden Warblers against the year over 1967–2018 (Figure 1, Table 1); a – intercept, β – slope of regression line, SE – standard error, p – statistical significance, $52*\beta$ – change in temperatures (in °C) over 52 years, positive values indicate increased temperature. $p < 0.05$ marked in **bold** face.

Parameter	Mean bi-monthly temperature	a	β	SE	p	R^2	$52*\beta$
LUG_SPR	13.6	12.43	0.044	0.009	<0.001	0.33	2.3
BRI_SPR	16.5	15.39	0.041	0.009	<0.001	0.31	2.2
EIN_SPR	11.3	9.86	0.052	0.009	<0.001	0.41	2.7
LEB_SPR	8.5	6.99	0.054	0.008	<0.001	0.45	2.9
LEB_SUM	15.7	14.83	0.032	0.007	<0.001	0.28	1.7
GSK_SUM	15.7	14.98	0.025	0.009	0.009	0.12	1.3
BRG_SUM	13.9	13.02	0.034	0.009	<0.001	0.21	1.8
JUU_SUM	14.8	14.57	0.007	0.011	0.525	0.01	0.4
LEB_AUT	15.2	14.39	0.031	0.007	<0.001	0.25	1.6
GSK_AUT	13.5	12.58	0.033	0.009	<0.001	0.20	1.8
BRG_AUT	13.3	12.39	0.034	0.010	0.001	0.18	1.8
JUU_AUT	11.4	10.40	0.037	0.010	<0.001	0.21	1.9

Table S5. Relationships between overall Annual Anomaly (AA) and the dates of 10th, 50th and 90th percentiles of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, four spring temperature variables and the year in full model. Statistics for the full model: AdjR² – adjusted coefficient of determination, F – result of GLM, P – significance of best model, Estimate – coefficients of multiple regression, SE – standard error of the estimates, t – t-test, p – significance of each estimate, VIF – variance inflation factor. p < 0.05 marked in **bold** face. Symbols of explanatory variables as in Table 1.

Response variable	AdjR ²	F _{5,39}	p	Explanatory variable	Estimate	SE	t	P	VIF
AA	0.20	3.22	0.016	BRI_SPR	-0.452	0.173	-2.62	0.013	1.58
				LUG_SPR	-0.296	0.235	-1.26	0.215	2.54
				EIN_SPR	0.180	0.284	0.64	0.529	4.15
				LEB_SPR	-0.044	0.245	-0.18	0.858	2.96
				Year	-0.001	0.005	-0.13	0.899	1.30
10%	-0.03	0.71	0.621	BRI_SPR	-0.260	0.197	-1.32	0.194	1.58
				LUG_SPR	-0.131	0.267	-0.49	0.626	2.54
				EIN_SPR	0.236	0.323	0.73	0.469	4.15
				LEB_SPR	-0.131	0.279	-0.47	0.641	2.96
				Year	0.001	0.006	0.11	0.913	1.30
50%	0.04	1.35	0.266	BRI_SPR	-0.314	0.190	-1.65	0.107	1.58
				LUG_SPR	-0.202	0.258	-0.78	0.438	2.54
				EIN_SPR	-0.049	0.311	-0.16	0.876	4.15
				LEB_SPR	0.139	0.269	0.52	0.608	2.96
				Year	0.000	0.005	-0.07	0.945	1.30
90%	0.25	3.95	0.005	BRI_SPR	-0.419	0.168	-2.50	0.017	1.58
				LUG_SPR	-0.345	0.227	-1.52	0.138	2.54
				EIN_SPR	0.307	0.275	1.12	0.270	4.15
				LEB_SPR	-0.219	0.237	-0.92	0.363	2.96
				Year	-0.001	0.005	-0.15	0.885	1.30

Table S6. Model selection by “all subsets”, from the full models for spring temperatures (Table S5). The models describe relationships between overall Annual Anomaly (AA) and dates of the 10th, 50th and 90th percentiles of immature Garden Warblers’ autumn migration at Bukowo-Kopań over 1967–2018, four spring temperature variables and the year. The models were ranked by corrected Akaike’s Information Criteria for small samples size (AICc) and the table shows those with $\Delta\text{AICc} < 2$: k – number of estimated parameters in the model, ΔAICc – difference from the model with lowest AICc, weight – the Akaike weight. Symbols of explanatory variables as in Table 1.

Variable	Models	BRI_SPR	EIN_SPR	LEB_SPR	LUG_SPR	Year	k	AICc	ΔAICc	weight
AA	1	-0.521	-	-	-	-	2	114.92	0.00	0.61
	2	-0.448	-	-	-0.185	-	3	115.81	0.89	0.39
10%	1	-0.271	-	-	-	-	2	124.93	0.00	0.62
	2	-	-	-0.102	-	-	1	125.95	1.02	0.38
50%	1	-0.344	-	-	-	-	2	122.86	0.00	0.40
	2	-0.266	-	-	-0.197	-	3	123.83	0.97	0.25
	3	-	-	-	-0.317	-	2	124.28	1.42	0.20
	4	-0.300	-0.100	-	-	-	3	124.79	1.93	0.15
90%	1	-0.546	-	-	-	-	2	113.35	0.00	0.40
	2	-0.468	-	-	-0.198	-	3	113.98	0.63	0.29
	3	-0.483	-	-0.117	-	-	3	115.14	1.78	0.16
	4	-0.515	-	-	-	-0.003	3	115.32	1.96	0.15

Table S7. Relationships between overall Annual Anomaly (AA) and the dates of 10th, 50th and 90th percentiles of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, three spring temperature variables and the year in the partial model, excluding correlated variables (Table S2). Statistics for the partial model: AdjR² – adjusted coefficient of determination, F – result of GLM, p – significance of best model, Estimate – coefficients of multiple regression, SE – standard error of the estimates, t – t-test, P – significance of each estimate, VIF – variance inflation factor. p < 0.05 marked in bold face and 0.05 < p < 0.1 in italics. Symbols of explanatory variables as in Table 1.

Response variable	AdjR ²	F _{4,40}	P	Explanatory variable	Estimate	SE	t	p	VIF
AA	0.21	3.99	0.008	BRI_SPR	-0.464	0.171	-2.72	0.010	1.56
				LUG_SPR	-0.196	0.173	-1.13	0.265	1.40
				LEB_SPR	0.057	0.185	0.31	0.759	1.71
				Year	-0.001	0.005	-0.17	0.863	1.29
10%	-0.02	0.76	0.558	BRI_SPR	-0.276	0.195	-1.42	0.164	1.56
				LUG_SPR	-0.001	0.198	0.00	0.998	1.40
				LEB_SPR	0.001	0.211	0.01	0.995	1.71
				Year	0.000	0.005	0.06	0.953	1.29
50%	0.06	1.72	0.165	BRI_SPR	-0.310	0.187	-1.66	0.104	1.56
				LUG_SPR	-0.229	0.189	-1.21	0.233	1.40
				LEB_SPR	0.112	0.202	0.55	0.583	1.71
				Year	0.000	0.005	-0.06	0.953	1.29
90%	0.25	4.60	0.004	BRI_SPR	-0.440	0.167	-2.63	0.012	1.56
				LUG_SPR	-0.174	0.170	-1.03	0.310	1.40
				LEB_SPR	-0.046	0.181	-0.25	0.800	1.71
				Year	-0.001	0.005	-0.22	0.824	1.29

Table S8. Model selection by “all subsets”, from the partial models for spring temperatures (Table S8). The models describe relationships between overall Annual Anomaly (AA) and dates of the 10th, 50th and 90th percentiles of immature Garden Warblers’ autumn migration at Bukowo-Kopań over 1967–2018, three spring temperature variables and the year. The models were ranked by corrected Akaike’s Information Criteria for small samples size (AICc) and the table shows those with $\Delta AICc < 2$: k – number of estimated parameters in the model, $\Delta AICc$ – difference from the model with lowest AICc, weight – the Akaike weight. Symbols of explanatory variables as in Table 1.

Variable	Models	BRI_SPR	LEB_SPR	LUG_SPR	Year	k	AICc	$\Delta AICc$	weight
AA	1	-0.521	-	-	-	2	114.92	0.00	0.61
	2	-0.448	-	-0.185	-	3	115.81	0.89	0.39
10%	1	-0.271	-	-	-	2	124.93	0.00	0.62
	2	-	-	-	-	1	125.95	1.02	0.38
50%	1	-0.344	-	-	-	2	122.86	0.00	0.47
	2	-0.266	-	-0.197	-	3	123.83	0.97	0.29
	3	-	-	-0.317	-	2	124.28	1.42	0.23
90%	1	-0.546	-	-	-	2	113.35	0.00	0.40
	2	-0.468	-	-0.198	-	3	113.98	0.63	0.29
	3	-0.483	-0.117	-	-	3	115.14	1.78	0.16
	4	-0.515	-	-	-0.003	3	115.32	1.96	0.15

Table S9. Relationships between overall Annual Anomaly (AA) and the dates of 10th, 50th and 90th percentiles of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, two remaining uncorrelated spring temperature variables (Table S2) and the year in partial model. Statistics for the partial model: AdjR² – adjusted coefficient of determination, F – result of GLM, p – significance of best model, Estimate – coefficients of multiple regression, SE – standard error of the estimates, t – t-test, P – significance of each estimate, VIF – variance inflation factor. p < 0.05 marked in bold face and 0.05 < p < 0.1 in italics. Symbols of explanatory variables as in Table 1.

Response variable	AdjR ²	F _{3,41}	P	Explanatory variable	Estimate	SE	t	p	VIF
AA	0.21	4.88	0.005	BRI_SPR	-0.487	0.159	-3.07	0.004	1.34
				EIN_SPR	-0.035	0.159	-0.22	0.827	1.31
				Year	-0.001	0.005	-0.32	0.751	1.23
10%	0.01	1.10	0.359	BRI_SPR	-0.303	0.178	-1.70	<i>0.096</i>	1.34
				EIN_SPR	0.075	0.178	0.42	0.675	1.31
				Year	0.000	0.005	-0.03	0.976	1.23
50%	0.06	1.88	0.148	BRI_SPR	-0.296	0.173	-1.71	<i>0.095</i>	1.34
				EIN_SPR	-0.097	0.174	-0.56	0.580	1.37
				Year	0.000	0.005	-0.08	0.938	1.12
90%	0.24	5.65	0.002	BRI_SPR	-0.500	0.156	-3.22	0.003	1.34
				EIN_SPR	-0.041	0.156	-0.27	0.792	1.37
				Year	-0.002	0.005	-0.50	0.623	1.12

Table S10. Model selection by “all subsets”, from the partial models for spring temperatures (Table S10). The models describe relationships between overall Annual Anomaly (AA) and dates of the 10th, 50th and 90th percentiles of immature Garden Warblers’ autumn migration at Bukowo-Kopań over 1967–2018, two spring temperature variables and the year. The models were ranked by corrected Akaike’s Information Criteria for small samples size (AICc) and the table shows those with $\Delta\text{AICc} < 2$: k – number of estimated parameters in the model, ΔAICc – difference from the model with lowest AICc, weight – the Akaike weight. Symbols of explanatory variables as in Table 1.

Variable	Models	BRI_SPR	EIN_SPR	Year	k	AICc	ΔAICc	weight
AA	1	-0.521	-	-	2	114.92	0.00	1.00
10%	1	-0.271	-	-	2	124.93	0.00	0.62
	2	-	-	-	1	125.95	1.02	0.38
50%	1	-0.344	-	-	2	122.86	0.00	0.72
	2	-0.300	-0.100	-	3	124.79	1.93	0.28
90%	1	-0.546	-	-	2	113.35	0.00	0.73
	2	-0.515	-	-0.003	3	115.32	1.96	0.27

Table S11 . Relationships between overall Annual Anomaly (AA) and the dates of the 10th, 50th and 90th percentiles of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, four summer temperature variables and the year in the full summer model. Statistics for the full model: AdjR² – adjusted coefficient of determination, F – result of GLM, P – significance of best model, Estimate – coefficients of multiple regression, SE – standard error of the estimates, t – t-test, p – significance of each estimate, VIF – variance inflation factor. p < 0.05 marked in **bold** face, 0.05 < p < 0.1 in *italics*. Symbols of explanatory variables as in Table 1.

Response variable	AdjR ²	F _{5,39}	p	Explanatory variable	Estimate	SE	t	P	VIF
AA	0.11	2.09	<i>0.087</i>	BRG_SUM	0.088	0.216	0.41	0.684	2.38
				GSK_SUM	-0.377	0.300	-1.26	0.217	4.60
				JUU_SUM	0.439	0.222	1.98	<i>0.055</i>	2.41
				LEB_SUM	-0.316	0.307	-1.03	0.310	4.71
				Year	-0.003	0.005	-0.61	0.544	1.24
10%	-0.04	0.67	0.647	BRG_SUM	0.068	0.233	0.29	0.771	2.38
				GSK_SUM	-0.521	0.325	-1.60	0.117	4.60
				JUU_SUM	0.185	0.240	0.77	0.446	2.41
				LEB_SUM	0.246	0.332	0.74	0.462	4.71
				Year	-0.003	0.005	-0.53	0.601	1.24
50%	0.10	2.00	<i>0.099</i>	BRG_SUM	0.027	0.217	0.13	0.900	2.38
				GSK_SUM	-0.521	0.302	-1.73	<i>0.092</i>	4.60
				JUU_SUM	0.531	0.223	2.38	0.022	2.41
				LEB_SUM	-0.094	0.309	-0.31	0.762	4.71
				Year	-0.001	0.005	-0.24	0.816	1.24
90%	0.16	2.64	0.038	BRG_SUM	-0.111	0.210	-0.53	0.599	2.38
				GSK_SUM	0.219	0.292	0.75	0.459	4.60
				JUU_SUM	0.311	0.216	1.44	0.158	2.41
				LEB_SUM	-0.695	0.299	-2.33	0.025	4.71
				Year	-0.002	0.005	-0.43	0.666	1.24

Table S12. Model selection by “all subsets”, according to AICc, from the full models for summer temperatures (Table S8). The models describe relationships between overall Annual Anomaly (AA) and dates of the 10th, 50th and 90th percentiles of immature Garden Warblers’ autumn migration at Bukowo-Kopań over 1967–2018, four summer temperature variables and the year. The models were ranked by corrected Akaike’s Information Criteria for small samples size (AICc) and the table shows those with $\Delta AICc < 2$: k – number of estimated parameters in the model, $\Delta AICc$ – the difference from the model with the lowest AICc, weight – the Akaike weight. Symbols of explanatory variables as in Table 1.

Variable	Models	BRG_SUM	GSK_SUM	JUU_SUM	LEB_SUM	Year	k	AICc	$\Delta AICc$	weight
AA	1	-	-	0.3982	-0.578	-	3	122.02	0.00	0.27
	2	-	-0.546	0.3664	-	-	3	122.33	0.31	0.23
	3	-	-0.307	0.4502	-0.352	-	4	123.00	0.98	0.16
	4	-	-0.498	0.3324	-	-0.005	4	123.64	1.62	0.12
	5	-	-0.305	-	-	-	2	123.72	1.70	0.11
	6	-	-	-	-0.304	-	2	123.84	1.81	0.11
10%	1	-	-	-	-	-	1	125.95	0.00	0.35
	2	-	-0.160	-	-	-	2	126.97	1.02	0.21
	3	-0.100	-	-	-	-	2	127.69	1.74	0.15
	4	-	-0.323	0.249	-	-	3	127.73	1.78	0.14
	5	-	-	-	-	-0.003	2	127.78	1.83	0.14
50%	1	-	-0.573	0.511	-	-	3	120.65	0.00	1.00
90%	1	-	-	0.399	-0.665	-	3	118.62	0.00	1.00

Table S13. Relationships between overall Annual Anomaly (AA) and the dates of the 10th, 50th and 90th percentiles of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, three summer temperature variables and the year in the partial summer model. Statistics for the partial model: AdjR² – adjusted coefficient of determination, F – result of GLM, p – significance of best model, Estimate – coefficients of multiple regression, SE – standard error of the estimates, t – t-test, P – significance of each estimate, VIF – variance inflation factor. p < 0.05 marked in bold face, 0.05 < p < 0.1 in italics. Symbols of explanatory variables as in Table 1.

Response variable	AdjR ²	F _{4,40}	p	Explanatory variable	Estimate	SE	t	P	VIF
AA	0.11	2.35	0.071	BRG_SUM	0.038	0.210	0.18	0.857	2.26
				GSK_SUM	-0.529	0.262	-2.02	0.050	3.48
				JUU_SUM	0.340	0.200	0.70	<i>0.098</i>	1.96
				Year	-0.005	0.005	-1.03	0.310	1.09
10%	-0.03	0.71	0.589	BRG_SUM	0.108	0.226	0.48	0.636	2.26
				GSK_SUM	-0.402	0.281	-1.43	0.160	3.48
				JUU_SUM	0.262	0.215	1.22	0.230	1.96
				Year	-0.001	0.005	-0.29	0.772	1.09
50%	0.12	2.54	0.055	BRG_SUM	0.012	0.208	0.06	0.953	2.26
				GSK_SUM	-0.567	0.259	-2.18	0.035	3.48
				JUU_SUM	0.501	0.199	2.52	0.016	1.96
				Year	-0.002	0.005	-0.37	0.716	1.09
90%	0.06	1.75	0.157	BRG_SUM	-0.222	0.215	-1.03	0.308	2.26
				GSK_SUM	-0.117	0.268	-0.44	0.665	3.48
				JUU_SUM	0.093	0.205	0.45	0.653	1.96
				Year	-0.006	0.005	-1.25	0.220	1.09

Table S14. Model selection by “all subsets”, according to AICc, from the partial models for summer temperatures (Table S14). The models describe relationships between overall Annual Anomaly (AA) and dates of the 10th, 50th and 90th percentiles of immature Garden Warblers’ autumn migration at Bukowo-Kopań over 1967–2018, three summer temperature variables and the year. The models were ranked by corrected Akaike’s Information Criteria for small samples size (AICc) and the table shows those with $\Delta\text{AICc} < 2$: k – number of estimated parameters in the model, ΔAICc – the difference from the model with the lowest AICc, weight – the Akaike weight. Symbols of explanatory variables as in Table 1.

Variables	Models	BRG_SUM	GSK_SUM	JUU_SUM	Year	k	AICc	ΔAICc	weight
AA	1	-	-0.546	0.366	-	3	122.33	0.00	0.42
	2	-	-0.498	0.332	-0.005	4	123.64	1.32	0.22
	3	-	-0.305	-	-	2	123.72	1.39	0.21
	4	-	-0.272	-	-0.006	3	124.27	1.94	0.16
10%	1	-	-	-	-	1	125.95	0.00	0.35
	2	-	-0.160	-	-	2	126.97	1.02	0.21
	3	-0.100	-	-	-	2	127.69	1.74	0.15
	4	-	-0.323	0.249	-	3	127.73	1.78	0.14
	5	-	-	-	-0.003	2	127.78	1.83	0.14
50%	1	-	-0.573	0.511	-	3	120.65	0.00	1.00
90%	1	-0.322	-	-	-	2	123.15	0.00	0.38
	2	-0.271	-	-	-0.006	3	123.61	0.46	0.30
	3	-	-	-	-0.009	2	124.80	1.65	0.17
	4	-	-0.209	-	-0.007	3	125.00	1.84	0.15

Table S15. Relationships between overall Annual Anomaly (AA) and the dates of the 10th, 50th and 90th percentiles of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, three summer temperature variables and the year in the partial summer model. Statistics for the partial model: AdjR² – adjusted coefficient of determination, F – result of GLM, p – significance of best model, Estimate – coefficients of multiple regression, SE – standard error of the estimates, t – t-test, P – significance of each estimate, VIF – variance inflation factor. p < 0.05 marked in bold face, 0.05 < p < 0.1 in italics. Symbols of explanatory variables as in Table 1.

Response variable	AdjR ²	F _{4,40}	p	Explanatory variable	Estimate	SE	t	P	VIF
AA	0.10	2.19	<i>0.088</i>	BRG_SUM	-0.034	0.194	-0.18	0.861	1.89
				LEB_SUM	-0.506	0.269	-1.88	<i>0.067</i>	3.57
				JUU_SUM	0.360	0.215	1.68	0.101	2.22
				Year	-0.002	0.005	-0.47	0.642	1.22
10%	-0.07	0.19	0.942	BRG_SUM	-0.101	0.212	-0.48	0.636	1.89
				LEB_SUM	-0.016	0.294	-0.06	0.956	3.57
				JUU_SUM	0.075	0.235	0.32	0.750	2.22
				Year	-0.002	0.005	-0.34	0.736	1.22
50%	0.06	1.68	0.174	BRG_SUM	-0.142	0.198	-0.72	0.477	1.89
				LEB_SUM	-0.357	0.275	-1.30	0.202	3.57
				JUU_SUM	0.421	0.219	1.92	<i>0.062</i>	2.22
				Year	0.000	0.005	-0.04	0.971	1.22
90%	0.17	3.19	0.023	BRG_SUM	-0.040	0.186	-0.22	0.829	1.89
				LEB_SUM	-0.585	0.259	-2.26	0.029	3.57
				JUU_SUM	0.357	0.206	1.73	<i>0.091</i>	2.22
				Year	-0.003	0.005	-0.53	0.602	1.22

Table S16. Model selection by “all subsets”, according to AICc, from the partial models for summer temperatures (Table S16). The models describe relationships between overall Annual Anomaly (AA) and dates of the 10th, 50th and 90th percentiles of immature Garden Warblers’ autumn migration at Bukowo-Kopań over 1967–2018, three summer temperature variables and the year. The models were ranked by corrected Akaike’s Information Criteria for small samples size (AICc) and the table shows those with $\Delta\text{AICc} < 2$: k – number of estimated parameters in the model, ΔAICc – the difference from the model with the lowest AICc, weight – the Akaike weight. Symbols of explanatory variables as in Table 1.

Variables	Models	BRG_SUM	JUU_SUM	LEB_SUM	Year	k	AICc	ΔAICc	weight
AA	1	-	0.398	-0.578	-	3	122.02	0.00	0.71
	2	-	-	-0.304	-	2	123.84	1.81	0.29
10%	1	-	-	-	-	1	125.95	0.00	0.55
	2	-0.100	-	-	-	2	127.69	1.74	0.23
	3	-	-	-	-0.003	2	127.78	1.83	0.22
50%	1	-	0.453	-0.477	-	3	124.20	0.00	0.36
	2	-0.231	-	-	-	2	125.66	1.46	0.17
	3	-0.314	0.235	-	-	3	125.71	1.51	0.17
	4	-	-	-	-	1	125.95	1.75	0.15
	5	-0.142	0.424	-0.360	-	4	126.06	1.86	0.14
90%	1	-	0.399	-0.665	-	3	118.62	0.00	1.00

Table S17. Relationships between overall Annual Anomaly (AA) and dates of the 10th, 50th and 90th percentiles of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, four autumn temperature variables and the year in the full autumn model. Statistics for the full model: AdjR² – adjusted coefficient of determination, F – result of GLM, p – significance of best model, Estimate – coefficients of multiple regression, SE – standard error of the estimates, t – t-test, P – significance of each estimate, VIF – variance inflation factor. p < 0.05 marked in **bold** face, 0.05 < p < 0.1 in *italics*. Symbols of explanatory variables as in Table 1.

Response variable	AdjR ²	F _{5,39}	p	Explanatory variable	Estimate	SE	t	P	VIF
AA	0.07	1.69	0.161	LEB_AUT	0.094	0.340	0.28	0.784	5.50
				BRG_AUT	-0.026	0.266	-0.10	0.921	3.09
				GSK_AUT	-0.067	0.395	-0.17	0.865	7.24
				JUU_AUT	-0.389	0.277	-1.40	0.168	3.39
				Year	-0.004	0.005	-0.82	0.417	1.15
10%	-0.08	0.36	0.876	LEB_AUT	-0.147	0.367	-0.40	0.691	5.50
				BRG_AUT	-0.173	0.287	-0.60	0.550	3.09
				GSK_AUT	0.440	0.426	1.04	0.307	7.24
				JUU_AUT	-0.215	0.299	-0.72	0.476	3.39
				Year	-0.002	0.005	-0.35	0.725	1.15
50%	-0.03	0.77	0.581	LEB_AUT	0.171	0.358	0.48	0.635	5.50
				BRG_AUT	0.101	0.280	0.36	0.719	3.09
				GSK_AUT	-0.226	0.415	-0.54	0.590	7.24
				JUU_AUT	-0.282	0.292	-0.97	0.339	3.39
				Year	-0.003	0.005	-0.55	0.582	1.15
90%	0.07	1.71	0.155	LEB_AUT	-0.062	0.339	-0.18	0.855	5.50
				BRG_AUT	-0.273	0.265	-1.03	0.311	3.09
				GSK_AUT	0.113	0.394	0.29	0.775	7.24
				JUU_AUT	-0.197	0.277	-0.71	0.480	3.39
				Year	-0.005	0.005	-0.93	0.359	1.15

Table S18. Model selection by “all subsets”, according to AICc, from the full models for autumn temperatures (Table S18). The models describe relationships between the overall Annual Anomaly (AA) and migration dates of the 10th, 50th and 90th percentiles of immature Garden Warblers’ autumn migration at Bukowo-Kopań over 1967–2018, four autumn temperature variables and the year. The models were ranked by corrected Akaike’s Information Criteria for small samples size (AICc) and the table shows those with $\Delta\text{AICc} < 2$: k – number of estimated parameters in the model, ΔAICc – the difference in AICc from the model with lowest AICc, weight – the Akaike weight. Symbols of explanatory variables as in Table 1.

Variable	Models	BRG_AUT	GSK_AUT	JUU_AUT	LEB_AUT	Year	k	AICc	ΔAICc	weight
AA	1	-	-	-0.414	-	-	2	120.52	0.00	0.68
	2	-	-	-0.373	-	-0.004	3	121.99	1.46	0.32
10%	1	-	-	-	-	-	1	125.95	0.00	0.55
	2	-	-	-0.108	-	-	2	127.67	1.72	0.23
	3	-	-	-	-	-0.003	2	127.78	1.83	0.22
50%	1	-	-	-0.285	-	-	2	124.70	0.00	0.38
	2	-	-0.233	-	-	-	2	125.74	1.04	0.23
	3	-	-	-	-	-	1	125.95	1.25	0.20
	4	-	-	-	-0.212	-	2	126.11	1.40	0.19
90%	1	-0.372	-	-	-	-	2	122.13	0.00	0.15
	2	-	-	-0.351	-	-	2	122.78	0.66	0.11
	3	-	-0.341	-	-	-	2	122.83	0.70	0.11
	4	-0.258	-	-0.215	-	-	3	122.84	0.72	0.10
	5	-0.315	-	-	-	-0.005	3	123.04	0.91	0.09
	6	-	-	-	-0.328	-	2	123.13	1.00	0.09
	7	-	-0.286	-	-	-0.006	3	123.48	1.36	0.08
	8	-0.261	-	-	-0.173	-	3	123.48	1.36	0.08
	9	-	-	-0.294	-	-0.006	3	123.49	1.36	0.08
	10	-	-	-	-0.272	-0.006	3	123.76	1.63	0.07
	11	-0.254	-0.143	-	-	-	3	124.07	1.94	0.06

Table S19. Relationships between overall Annual Anomaly (AA) and dates of the 10th, 50th and 90th percentiles of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, eight spring and summer temperature variables and the year in the full model. Statistics for the full model: AdjR² – adjusted coefficient of determination, F – result of GLM, p – significance of best model, Estimate – coefficients of multiple regression, SE – standard error of the estimates, t – t-test, P – significance of each estimate, VIF – variance inflation factor. p < 0.05 marked in **bold** face and 0.05 < p < 0.1 in *italics*. Symbols of explanatory variables as in Table 1.

Response variable	AdjR ²	F _{9,35}	P	Explanatory variable	Estimate	SE	t	p	VIF
AA	0.26	2.75	0.015	BRI_SPR	-0.582	0.183	-3.19	0.003	1.91
				LUG_SPR	-0.161	0.247	-0.65	0.518	3.03
				EIN_SPR	0.195	0.282	0.69	0.494	4.44
				LEB_SPR	-0.002	0.246	-0.01	0.995	3.23
				LEB_SUM	0.172	0.331	0.52	0.606	6.62
				BRG_SUM	-0.009	0.210	-0.04	0.966	2.73
				GSK_SUM	-0.568	0.281	-2.02	<i>0.051</i>	4.86
				JUU_SUM	0.408	0.221	1.85	<i>0.073</i>	2.87
				Year	0.001	0.005	0.11	0.913	1.36
10%	0.02	1.10	0.389	BRI_SPR	-0.439	0.211	-2.08	0.045	1.91
				LUG_SPR	-0.134	0.284	-0.47	0.641	3.03
				EIN_SPR	0.314	0.325	0.97	0.340	4.44
				LEB_SPR	-0.191	0.284	-0.67	0.505	3.23
				LEB_SUM	0.672	0.382	1.76	<i>0.087</i>	6.62
				BRG_SUM	-0.052	0.242	-0.21	0.832	2.73
				GSK_SUM	-0.676	0.324	-2.09	0.044	4.86
				JUU_SUM	0.142	0.255	0.56	0.580	2.87
				Year	0.000	0.005	0.08	0.936	1.36
50%	0.17	2.01	<i>0.068</i>	BRI_SPR	-0.499	0.194	-2.58	0.014	1.91
				LUG_SPR	-0.058	0.262	-0.22	0.827	3.03
				EIN_SPR	-0.022	0.299	-0.08	0.941	4.44
				LEB_SPR	0.200	0.261	0.77	0.449	3.23
				LEB_SUM	0.232	0.351	0.66	0.514	6.62
				BRG_SUM	-0.020	0.223	-0.09	0.930	2.73
				GSK_SUM	-0.670	0.298	-2.25	0.031	4.86
				JUU_SUM	0.544	0.234	2.32	0.026	2.87
				Year	0.001	0.005	0.22	0.830	1.36
90%	0.24	2.58	0.021	BRI_SPR	-0.450	0.185	-2.43	0.020	1.91
				LUG_SPR	-0.181	0.250	-0.72	0.474	3.03
				EIN_SPR	0.340	0.285	1.19	0.242	4.44
				LEB_SPR	-0.168	0.249	-0.68	0.503	3.23
				LEB_SUM	-0.263	0.335	-0.78	0.439	6.62
				BRG_SUM	-0.230	0.213	-1.08	0.288	2.73
				GSK_SUM	0.065	0.284	0.23	0.820	4.86
				JUU_SUM	0.268	0.223	1.20	0.239	2.87
				Year	0.001	0.005	0.24	0.814	1.36

Table S20. Model selection by “all subsets”, according to AICc, from the full models (Table S20). The models describe relationships between overall Annual Anomaly (AA) and the migration dates of 10th, 50th and 90th percentiles of immature Garden Warblers’ autumn migration at Bukowo-Kopań over 1967–2018, eight spring and summer temperature variables and the year. The models were ranked by corrected Akaike’s Information Criteria for small samples size (AICc) and the table shows models with $\Delta AICc < 2$: k – number of estimated parameters in the model, $\Delta AICc$ – the difference in AICc from the model with lowest AICc, weight – the Akaike weight. Symbols of explanatory variables as in Table 1.

Variable	Models	BRI_SPR	LUG_SPR	EIN_SPR	LEB_SPR	BRG_SUM	GSK_SUM	JUU_SUM	LEB_SUM	Year	k	AICc	$\Delta AICc$	weight
AA	1	-0.502	-	-	-	-	-0.466	0.426	-	-	4	110.88	0.00	0.56
	2	-0.554	-	0.121	-	-	-0.514	0.470	-	-	5	112.73	1.85	0.22
	3	-0.570	-	-	0.123	-	-0.496	0.465	-	-	5	112.81	1.93	0.21
10%	1	-0.454	-	-	-	-	-0.642	-	0.706	-	4	123.74	0.00	0.52
	2	-0.271	-	-	-	-	-	-	-	-	2	124.93	1.19	0.29
	3	-0.442	-	-	-	-	-0.680	0.151	0.628	-	5	125.69	1.95	0.20
50%	1	-0.341	-	-	-	-	-0.519	0.551	-	-	4	116.96	0.00	0.48
	2	-0.459	-	-	0.213	-	-0.572	0.619	-	-	5	117.88	0.92	0.30
	3	-0.423	-	-	-	-	-0.705	0.491	0.293	-	5	118.46	1.50	0.22
90%	1	-0.499	-	-	-	-0.224	-	-	-	-	3	112.48	0.00	0.26
	2	-0.417	-	-	-	-	-	0.320	-0.418	-	4	113.16	0.68	0.19
	3	-0.546	-	-	-	-	-	-	-	-	2	113.35	0.87	0.17
	4	-0.524	-	-	-	-0.273	-	0.152	-	-	4	113.61	1.13	0.15
	5	-0.468	-0.198	-	-	-	-	-	-	-	3	113.98	1.50	0.12
	6	-0.459	-	-	-	-	-	-	-0.178	-	3	114.10	1.62	0.12

Figure S2. Model diagnostics for the best model (Table 2). The model describes relationships between overall Annual Anomaly (AA) of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, eight spring and summer temperature variables and the year. The plots of residuals follow Crawley (2013).

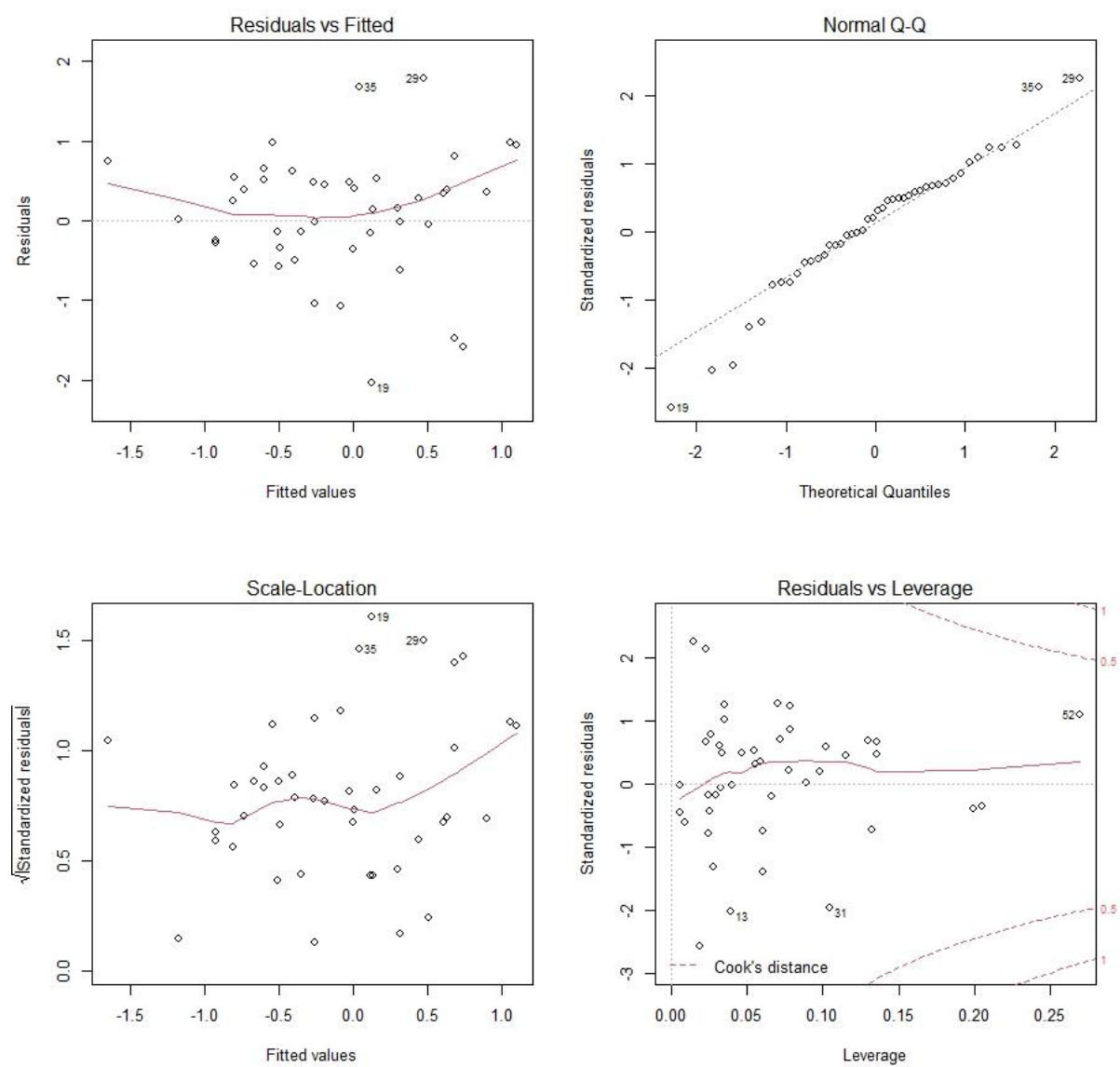


Figure S3. Model diagnostics for the best model (Table 2). The model describes relationships between migration dates of 10th percentile of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, eight spring and summer temperature variables and the year. The plots of residuals follow Crawley (2013).

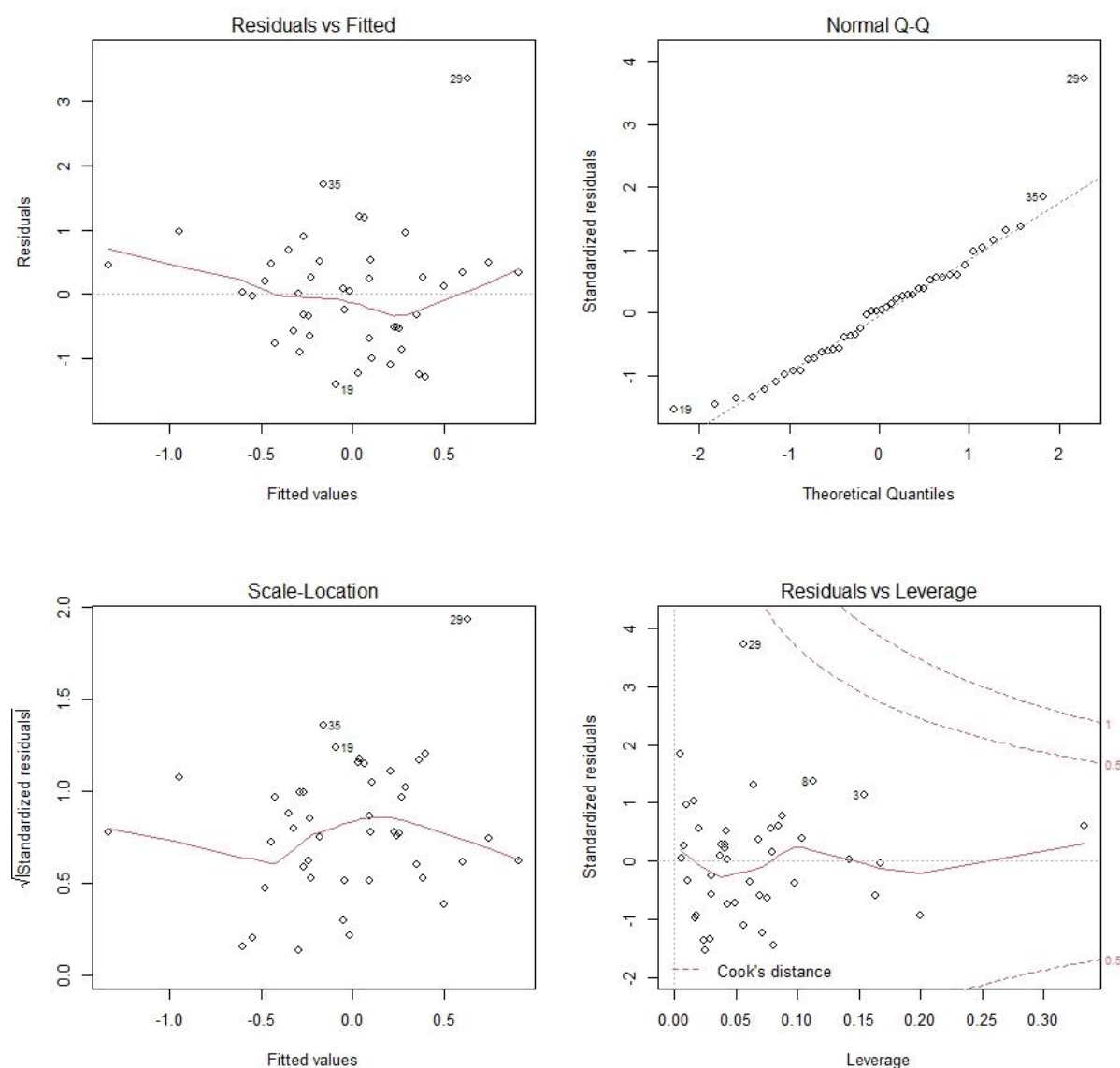


Figure S4. Model diagnostics for the best model (Table 2). The model describes relationships between migration dates of 50th percentile of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, eight spring and summer temperature variables and the year. The plots of residuals follow Crawley (2013).

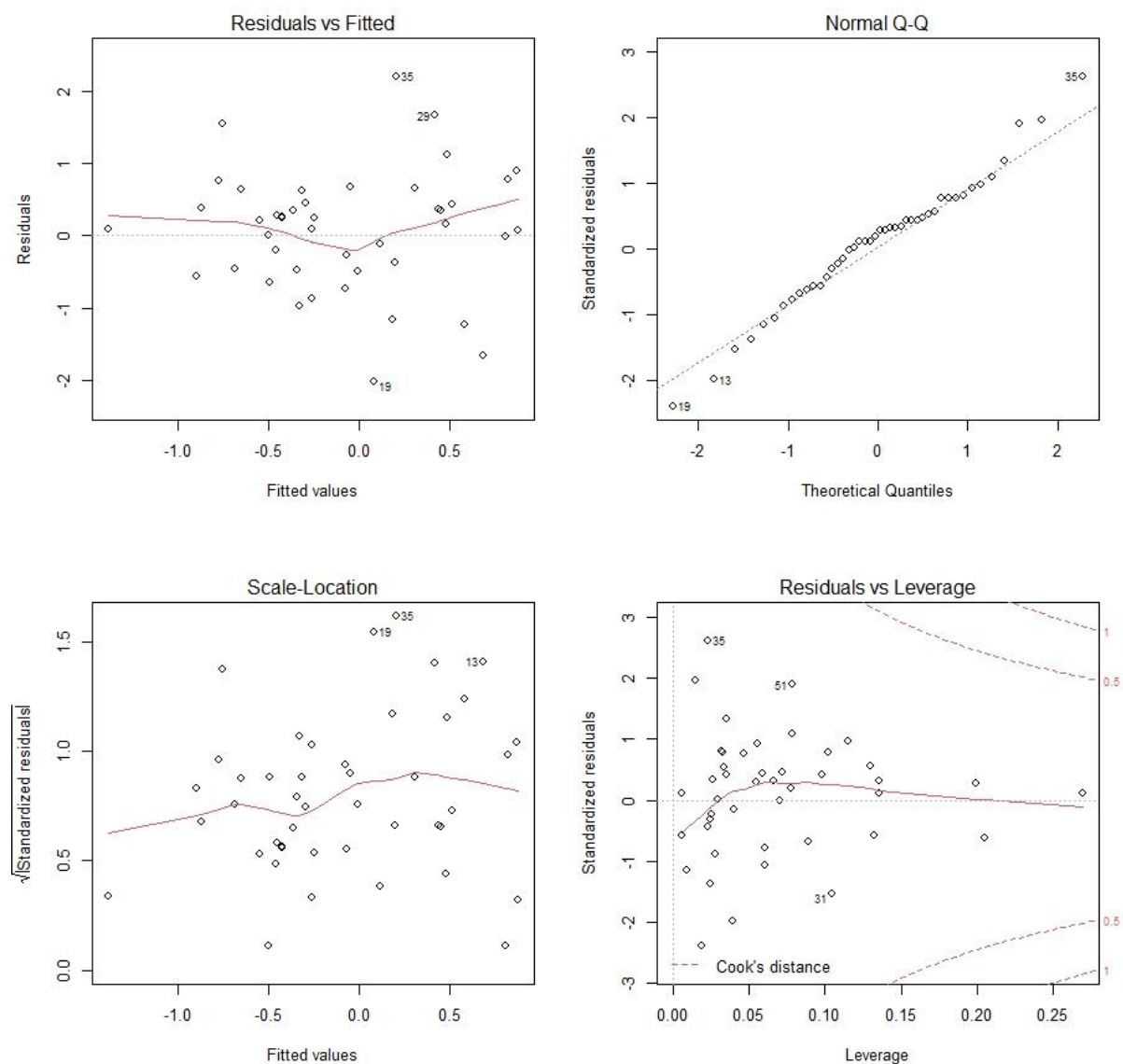


Figure S5. Model diagnostics for the best model (Table 2). The model describes relationships between migration dates of 90th percentile of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018, eight spring and summer temperature variables and the year. The plots of residuals follow Crawley (2013).

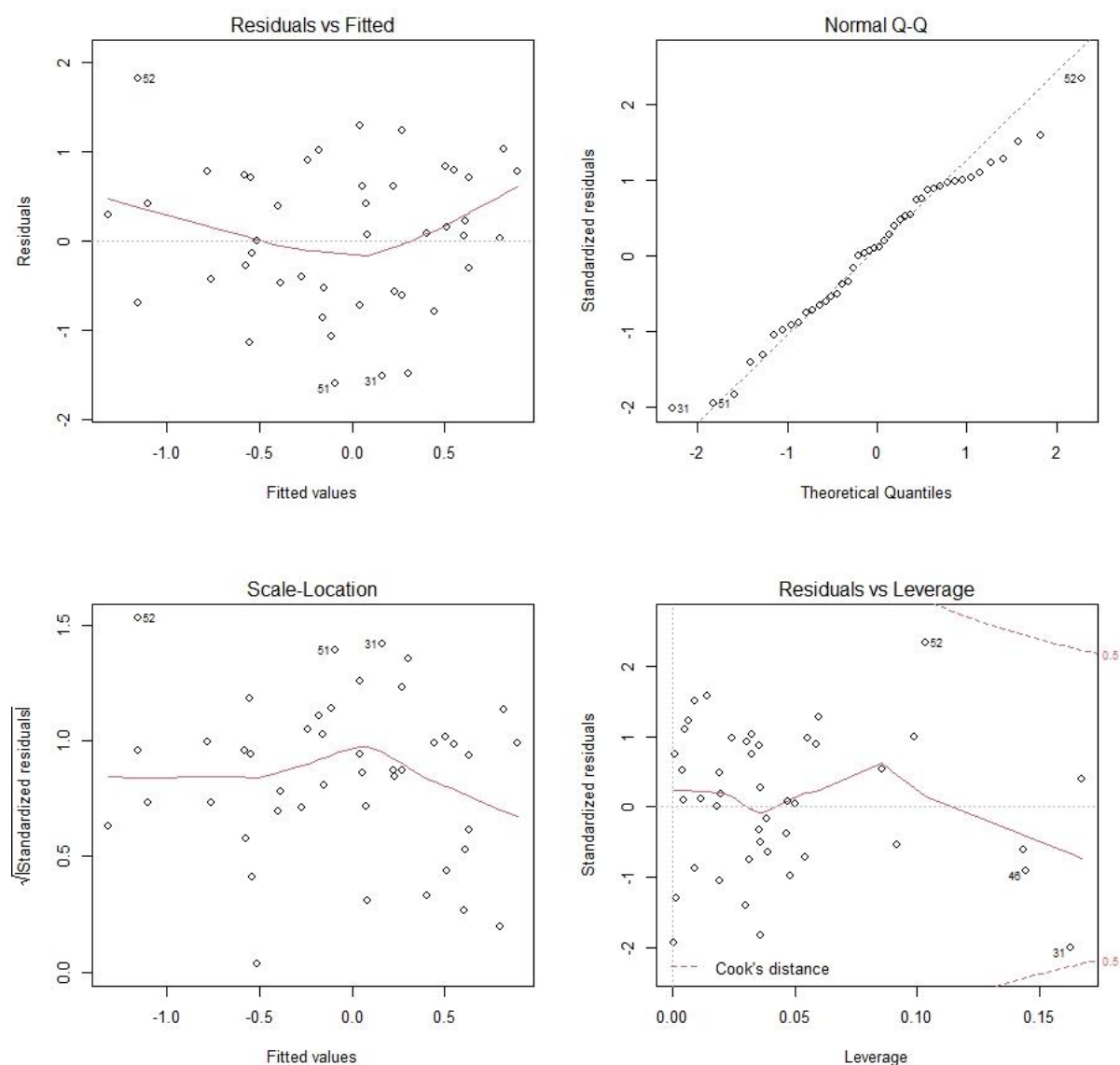
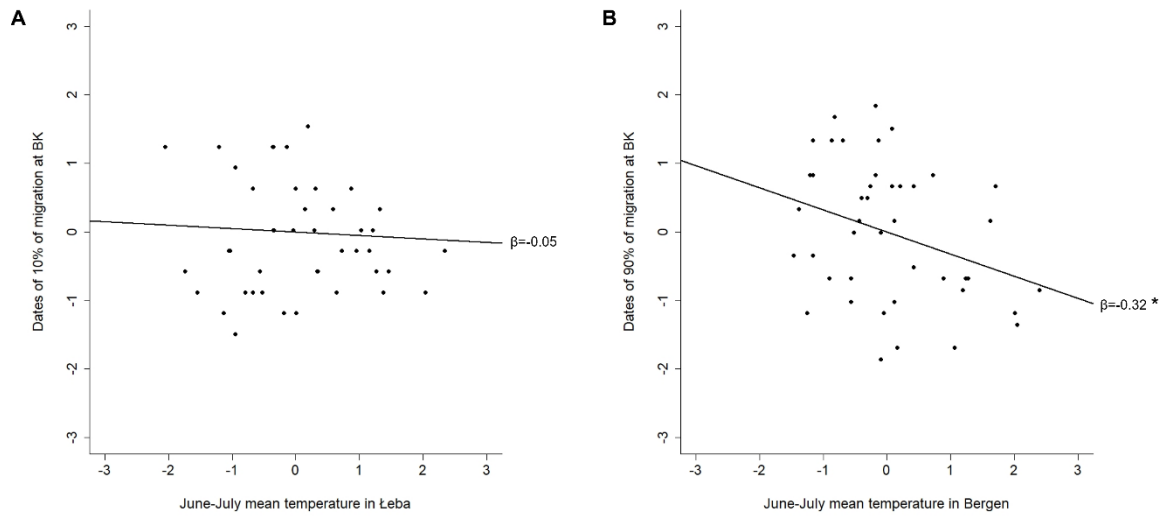


Figure S6. Dates of the 10th and 90th percentiles of immature Garden Warblers' autumn migration at Bukowo-Kopań over 1967–2018 against the temperature variables selected in the best models (Table 2) and trends by linear regression. β – regression coefficient. * – $p < 0.05$. All variables presented as standardised values. (A) 10th percentile of autumn passage against June–July mean temperature in Łeba, (B) 90th percentile of autumn passage against June–July mean temperature in Bergen.



Rozdział 2

The Influence of Winter and Spring Large-Scale Climate Patterns on the Timing of Male and Female Blackcap Spring Passage at the Baltic Coast

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Article

The Influence of Winter and Spring Large-Scale Climate Patterns on the Timing of Male and Female Blackcap Spring Passage at the Baltic Coast

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Simple Summary

Climate change shifts the timing of bird migration, yet whether these environmental pressures affect males and females differently remains poorly understood. We investigated how large-scale climate indices: the North Atlantic Oscillation (NAO), Scandinavian Pattern (SCI), and Indian Ocean Dipole (IOD), which shape weather conditions across Europe and Africa, influence the spring passage of Eurasian blackcaps at the Baltic coast of Poland. Analyses of data from daily standardised mist netting during spring migration (26 March–16 May) at Bukowo–Kopań bird ringing station showed that both sexes have advanced the early and median phases of passage by 7–9 days during 1982–2025. Because both sexes shifted their timing at the same rate, the degree of protandry has remained stable over these 44 years, with males migrating about two days earlier than females. Males and females showed uniform responses to the large-scale climate indices, and migrated later after dry winters in Africa, but earlier after warm winters and springs in Europe. Understanding the extent of adaptability within a migratory species helps to predict how their demography would respond to climate change at different locations, and to inform better international conservation strategies.

Abstract

Sex-specific adjustments of bird migration phenology to climate change are understudied. We analysed blackcap migration timing using spring (26 March–16 May) ringing data from Bukowo–Kopań (N Poland) in 1982–2025. We assessed the influence of large-scale climate indices in winter (December–February) and spring (March–May) at the beginning (p10), median (p50), and end (p90) of passage of each sex, using multiple regression. Protandry (earlier arrival of males) at the beginning of passage averaged 2.2 days and remained stable over 44 years, because p10 dates advanced by 9 days in both sexes. This aligns with 22-year studies from northern Europe, and with the mating opportunity hypothesis. The median (p50) of passage advanced by 7–9 days, but p90 showed no trends during 1982–2025. Positive winter and spring North Atlantic Oscillation (NAO) and spring Scandinavian Pattern (SCI) were associated with early p10 and p50, and positive winter Indian Ocean Dipole (IOD) with delayed p90, in both sexes alike. These similar responses likely occur because these climate patterns affect broad non-breeding areas of both sexes. We suggest that female blackcaps are as adaptive as males, and advanced migration maximises reproductive success and the chance of second broods in both sexes.

Keywords: spring phenology; protandry; sex-specific migration; climate change; bird migration



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1. Introduction

Spring migration of birds within the Palearctic–African migration system is an evolutionary adaptation that enables them to benefit from the abundance of food and breeding sites in spring and summer at northern latitudes, where harsh winter limits their year-round residence [1–5]. To maximise individual fitness, migrants time their migration to match local food availability, such as spring vegetation growth and the peak of insects, at their spring destinations [3,6]. However, the optimal timing of spring migration might differ between the sexes, because of different selection pressures on males and females [1,7–12]. Climate change in the Northern Hemisphere affects the timing of bird migrations [13–18]. However, most studies have focused on the interspecific differences in phenological shifts, while intraspecific variation, including possible sex differences, in responses to climate change remains poorly understood [19].

In many migrant passerines, protandry, which is an earlier arrival of males than females at the breeding grounds, manifests at stopover sites during spring migration [8–10,12,20,21]. Changing environmental conditions might influence the degree of protandry (difference in arrival dates of males and females), modifying the costs and benefits of early arrival for each sex [2,10,22–24]. Although protandry is common among migrants, differences in arrival times between the sexes are shaped by the selective pressures of a species' mating system [6,11]. The main mechanism explaining protandry is the mating opportunity hypothesis, where earlier arrival allows males to occupy high-quality territories, increasing their chances of attracting females and improving their reproductive success [7,10,25,26]. Evolutionary models support this hypothesis, suggesting that selection for the timing of male and female arrivals is the main driver of asynchronous sex-specific arrival times [6,21,27]. Differences in arrival timing can also be explained by energy management of each sex. Females in spring should maintain sufficient reserves to meet high nutritional demands of egg production, which often cannot be provided by local foraging [5]. Arriving too early under harsh spring conditions could deplete these reserves, leading to smaller clutches or lower-quality eggs [5,10]. In contrast, sperm production by males is far less energetically demanding, allowing them to take the risk of arriving early [5,11]. The evolutionary advantages of securing the best territories and mates outweigh the potential costs of adverse weather, especially during warmer springs [7,8,10]. This leads to sex-specific migration strategies, in which males prioritise speed of arrival (time-minimising), while females optimise energy costs (energy-minimising) to maintain sufficient body condition [5,11].

The earlier arrival of males at stopover and breeding sites may also result from spatial sex segregation during the non-breeding season, when males and females use separate wintering grounds or different migration routes [6,11,12,28–32]. However, studies using geolocators show that even when the sexes overwinter in the same regions, protandry is driven by behavioural differences [11,33]. In particular, males often depart from their wintering grounds earlier and stay ahead of females throughout the migration [6,33]. Furthermore, migration speed may be sex-specific, as in some species males migrate faster due to a higher rate of energy replenishment or morphological adaptations, such as more pointed wings [5,11].

Over the past few decades, the effects of climate change have become increasingly evident in the Northern Hemisphere, leading to long-term shifts in temperatures and weather patterns [13,15,34]. These climatic changes can directly influence the timing of spring migration [35] and potentially alter the degree of protandry by modifying the costs and benefits of early arrival for each sex [2,22–24]. The timing of migration is influenced by environmental factors, such as food abundance or weather conditions at subsequent locations visited by migrants [17,18,22,36,37]. Large-scale climate indices, which are differences in air pressure between distant locations, such as the North Atlantic Oscillation

(NAO), Mediterranean Oscillation Index (MOI), and Scandinavian Index (SCAND, hereafter: SCI), or in sea surface temperatures, such as the Indian Ocean Dipole (IOD), reflect atmospheric circulation that shapes winds, temperatures and precipitation over Europe and Africa [17,18,38–41]. These climate patterns influence the timing of spring migration in many migrant bird species in Europe [17,18,38–41]. High winter and spring NAO, which bring warm winters and springs to Europe, are associated with early spring arrivals of both short- and long-distance migrants across the continent in such years. The spring phenology of the first group shows a stronger relationship to NAO, attributed to its direct influence on conditions at their wintering and stopover sites in Europe [38,42–46]. However, the arrival timing of long-distance migrants, including the Eurasian blackcap (*Sylvia atricapilla*) (thereafter: blackcap), in southern Europe is also related to winter NAO, likely in response to its influence on conditions across Africa [47]. At our study site in central Europe, the timing of the overall spring passage of six species of long-distance migrants, including blackcap (both sexes jointly), was early with positive winter or spring NAO, and was also related to spring SCI and winter IOD [17]. Recently, spring phenology of the Eurasian wren (*Troglodytes troglodytes*) at our study site was linked to annual variation in winter and spring MOI [18]. These studies guided our choice of climate indices to use as proxies for environmental conditions that blackcaps encounter across their wintering grounds and spring migration routes between Africa and Europe.

Among studies on shifts in avian migration phenology, the possibility of different responses of males and females to changes in climatic conditions has attracted some attention. Earlier analyses of species exhibiting sexual dimorphism showed that in short-distance migrants such as the goldcrest (*Regulus regulus*), the blackbird (*Turdus merula*) and the reed bunting (*Schoeniclus schoeniclus*), the first and middle phases of passage advanced in both sexes between 1976 and 1997 [10]. In long-distance migrants, including the redstart (*Phoenicurus phoenicurus*), the whinchat (*Saxicola rubetra*), the red-backed shrike (*Lanius collurio*), the pied flycatcher (*Ficedula hypoleuca*), and the blackcap, the shifts were less pronounced, and all phases of spring migration advanced in both sexes at a similar rate, thus their degree of protandry remained unchanged over 1976–1997 [10]. However, more recent studies show that, with progressively warmer winters and springs, males begin their migration much earlier than females, leading to an increasing difference in arrival dates, especially in long-distance migrants, such as the pied flycatcher [42,43], the barn swallow (*Hirundo rustica*) [44], the willow warbler (*Phylloscopus trochilus*) [48], the chiffchaff (*Phylloscopus collybita*) [49], and a medium-distance migrant—the song thrush (*Turdus philomelos*) [45]. Uneven shifts in migration timing might result from different responsiveness of the sexes to the same conditions, or from slightly different environmental conditions they experience at non-breeding grounds due to spatial or temporal segregation, or from both mechanisms. The consequent carry-over effects can modify reproductive success, with long-term implications for local population dynamics [12,50].

The Eurasian blackcap, a common migrant passerine with prominent sexual dimorphism, shows remarkable flexibility in adjusting migrations to climate change. This plasticity manifests in shorter migration distances and the establishment of new wintering grounds in the British Isles over recent decades [51–54]. Additionally, it has been suggested that migrations of the eastern European populations have recently shifted from their traditional wintering grounds in the eastern Mediterranean to more western parts of their wintering range [55]. In earlier studies on the relationships between spring migration phenology of blackcaps and climate indices, the sexes were treated jointly, so potential sex differences have not been considered [17,41]. For these reasons, we selected the blackcap to investigate hypotheses of a potential increase in protandry and sex-specific responses to climate change, similar to those found in other long-distance migratory passerines.

Earlier studies based on about 20 years of data from the late 20th century found no evidence of increasing protandry in the blackcap [10]. Using twice as long a dataset on its spring migration, we set out to reassess this pattern. Firstly, we set out to identify any long-term trends in the spring migration phenology of male and female blackcaps, using a 44-year data series (1982–2025) from the southern Baltic coast. By comparing these trends between the sexes, we aimed to test if the degree of protandry has changed over this period. We expected an increase in protandry over a longer period, considering more rapid climate change and temperature increases across Europe in recent decades. Secondly, we aimed to determine relationships between spring migration timing and large-scale climate indices for male and female blackcaps, and to test if the sexes differ in their relationships to any climate indices. We expected such differences, bearing in mind blackcaps' protandry and intraspecific differences in sensitivity to environmental conditions in other migrants.

2. Materials and Methods

2.1. Study Species

The Eurasian blackcap is a small passerine easily sexed by plumage and size: females have a brown crown, and males are slightly larger with a characteristic black cap [56]. Blackcaps commonly breed across Europe (Figure 1) in habitats with dense undergrowth, such as parks, gardens, and deciduous or mixed woodlands [56].

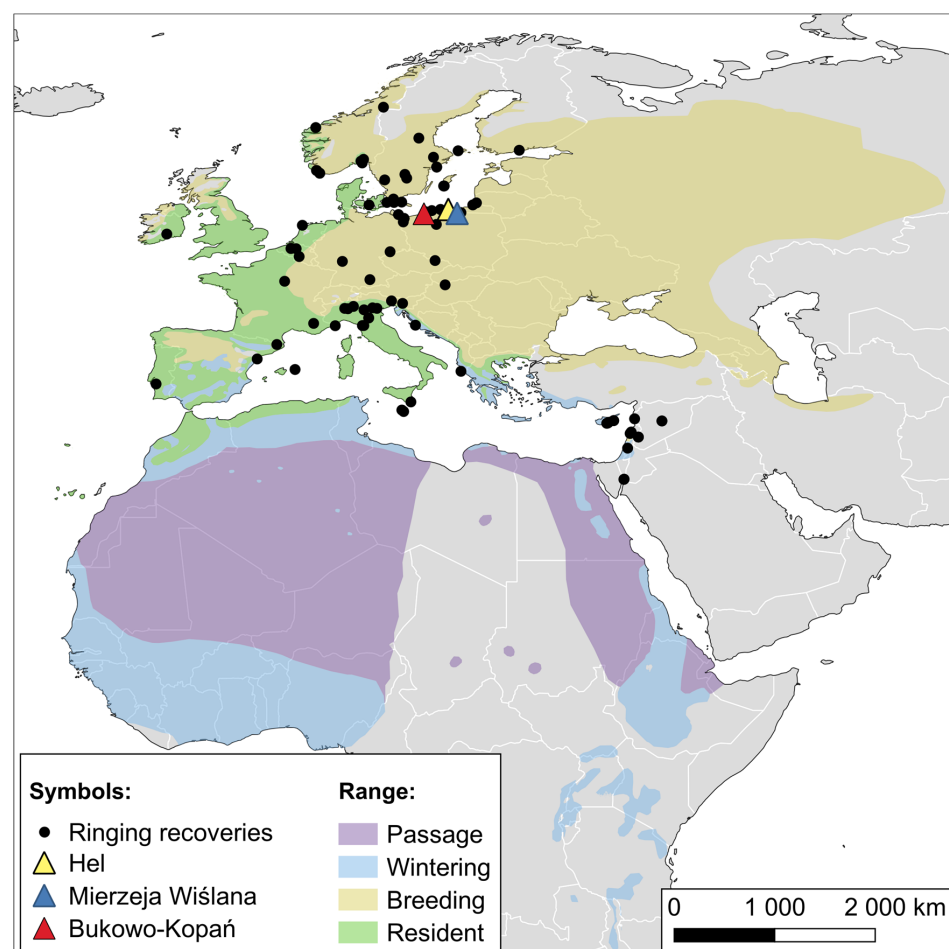


Figure 1. Spatial context of the study. The map shows the locations of the Bukowo–Kopań ringing station ($54^{\circ}19'38''$ – $54^{\circ}27'54''$ N, $16^{\circ}13'33''$ – $16^{\circ}25'15''$ E) and two other stations of the Operation Baltic Project: Mierzeja Wiślana ($54^{\circ}21'57''$ N, $19^{\circ}23'30''$ E) and Hel ($54^{\circ}44'29''$ N, $18^{\circ}33'40''$ E), and ringing recoveries of Eurasian blackcaps ringed or recovered at these stations during September 1960–June 2025, against the species' range [57].

They are mainly insectivorous, but their pre-migratory fattening is supported by a highly flexible diet including fruits; during periods of invertebrate scarcity they can switch to pollen, nectar, and fruit [56,58]. Blackcaps exhibit considerable variation in migration habits, ranging from completely resident populations breeding in the south and west of Europe (Figure 1) to obligatory long-distance, trans-Saharan migrants in the north and east of the breeding range [56,59]. Central Europe features a migratory divide separating southwest-bound and southeast-bound autumn migration routes, with intermediate populations moving south [60,61]. Additionally, a recent evolutionary shift has led some birds breeding in central and northwestern Europe to winter in the British Isles rather than in their traditional southern wintering grounds [51–53,60,62]. The eastern European populations have recently shown some shifts from their historical wintering grounds in the eastern Mediterranean region to more western areas of Europe, closer to the breeding grounds [55]. Populations breeding in western Europe are only partially migratory [56,62].

Blackcaps passing through the southern Baltic coast, which are the focus of this study, originate primarily from populations breeding in Scandinavia and the Baltic region, including local birds breeding near the study site (Figure 1) [61,63]. These populations overwinter across the Iberian Peninsula, northwest Africa, and the eastern Mediterranean region (particularly the Levant), with some individuals migrating as far as west Africa [60,61,63–65]. The annual phenology of these populations includes the spring migration from these wintering quarters to the northern breeding grounds during March to mid-May, the breeding season (May to August, with one or two broods), the autumn migration (mid-August to November), and the wintering period (December to February) [56].

2.2. Study Site and Methods of Catching Birds

Fieldwork was conducted at the Bukowo–Kopań ringing station, situated on the Baltic Sea coast of Poland (Figure 1), as a part of the long-term Operation Baltic research project. This coastal area, overgrown by mixed forests with fruit bushes, serves as a stopover site for blackcaps heading in spring to northern and northeastern breeding territories and also supports a local breeding population [60,63]. Following the Operation Baltic standard [66], birds were caught in mist nets daily from dawn until dusk. The number of mist nets remained constant within each spring season, but interannual variation ranged from 35 to 61 nets (Supplement Table S1). Upon capture, each bird received a ring, and birds' sex and age were recorded before release. The station's habitats and procedures are described in detail by Remisiewicz and Underhill [17].

Our analysis covers spring migration data collected between 26 March and 16 May 1982–2025. Fieldwork was suspended during the springs of 2011 and 2020 due to logistical constraints and the COVID-19 pandemic, resulting in 42 active seasons. Blackcaps caught after 16 May were mostly local breeding individuals, confirmed by their high recapture rates and the presence of brood patches.

To identify geographical regions used by the studied blackcap populations at different life stages, we analysed a supplementary dataset of 105 ringing recoveries. This dataset includes birds ringed at three Operation Baltic stations (Figure 1) and subsequently found elsewhere, as well as foreign-ringed individuals controlled at these stations, between September 1960 and June 2025. We mapped these ringing recoveries (Figure 1) against the species' geographical distribution [57] using QGIS v. 3.44.5 [67].

2.3. Large-Scale Climate Indices

We analysed seven large-scale climate indices that represent climatic conditions across the non-breeding areas and spring migration routes of the blackcap populations we studied.

To match these indices to the species' annual cycle, we calculated seasonal means from monthly values of these indices for two periods: the wintering period (December–February) and spring migration (March–May). These large-scale indices serve as proxies for ecological conditions experienced by blackcaps during these life stages. We provide their brief descriptions below, focused on their positive phases; the negative phase usually brings opposite regional climate effects, but we specify when this pattern occasionally differs.

2.3.1. Mediterranean Oscillation Index (MOI)

The Mediterranean Oscillation Index we used in this study is the difference in air pressure between Algiers and Cairo [68–70]. The positive winter MOI brings stable, dry, and warm weather across the western and central Mediterranean basin to the Balkan Peninsula, but opposite conditions in the easternmost Mediterranean (Figure 2a) [71–75].

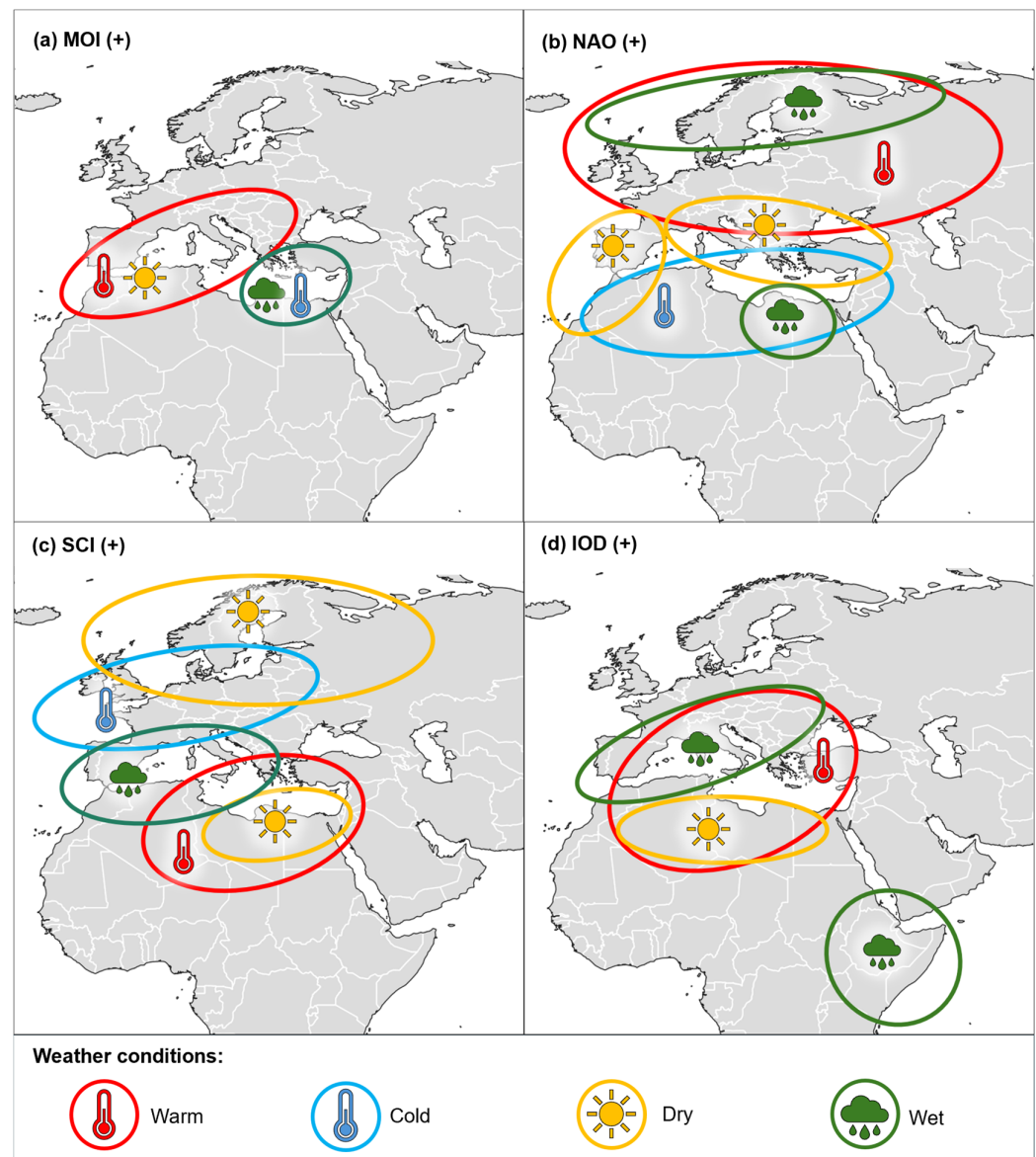


Figure 2. Spatial extent of typical weather conditions associated with the positive phase of the analysed large-scale climate indices in winter and spring (December–May). (a) Weather conditions associated with the positive phase of the Mediterranean Oscillation (MOI); (b) weather conditions associated with the positive winter and spring North Atlantic Oscillation (NAO); (c) weather conditions associated with the positive winter and spring Scandinavia pattern (SCI); (d) weather conditions associated with the positive winter and spring Indian Ocean Dipole (IOD).

The positive spring MOI maintains dry conditions in the central Mediterranean [76], but with regional exceptions, such as increased precipitation in April and May in Morocco [72], and brings cooler or humid conditions in the Balkan Peninsula [73]. The negative MOI in winter and spring increases precipitation across the western and central Mediterranean [71,74], promoting vegetation and increasing primary production [77,78]. Monthly MOI values were downloaded from the Climatic Research Unit of the University of East Anglia database [79].

2.3.2. North Atlantic Oscillation (NAO)

The North Atlantic Oscillation is the surface sea-level pressure difference between the Azores High and the Icelandic Low [80,81]. The positive winter NAO (Figure 2b) produces strong westerly winds that bring warm, moist winters in northern, central, and eastern Europe. This causes warm winters and significantly reduces the extent, depth, and duration of snow cover across northern, western, and central Europe [82,83]. The northerly airflow exposes southern Europe, the Mediterranean, and North Africa to colder conditions [80,81,84–88]. During positive NAO, winter precipitation increases in northern Europe and the central coast of North Africa, while western and southern Europe, the Balkans, and western North Africa remain drier [80,81,88,89]. In northwestern Africa, this drought can be compounded by dry eastward winds [89], reducing vegetation growth and decreasing primary production [90]. In early spring, the positive NAO maintains these weather patterns [84,91]. Monthly values of NAO index were retrieved from the NOAA Climate Prediction Center database [92].

2.3.3. Scandinavian Pattern Index (SCI)

The Scandinavian Pattern Index is shaped by a pressure difference between Scandinavia and southern Europe (Figure 2c) [93–96]. The positive winter SCI leads to cold and dry winters across Scandinavia and western, central, and eastern Europe. At the same time, southeastern Europe and the eastern Mediterranean basin experience warm conditions; the whole southern and western Europe, especially the Iberian and Apennine Peninsulas, experience increased rainfall [93,94,97]. The positive spring SCI in spring continues its cooling effect on European weather [98] and maintains dry conditions in the eastern Baltic Sea region [95]. It also generates southerly winds across central and western Europe [99,100] and promotes faster melting of snow cover [94]. During the negative SCI phase, the spatial influence remains identical to the positive phase, but the temperature and precipitation effects are opposite [94,95,97,98]. Monthly SCI values were retrieved from the NOAA Climate Prediction Center database [101].

2.3.4. Indian Ocean Dipole (IOD)

The Indian Ocean Dipole reflects the difference in ocean surface temperatures between the western and southeastern tropical Indian Ocean, which affects the climate in this region directly and the weather patterns in Europe indirectly (Figure 2d) [102]. The positive winter IOD brings above-average rainfall, which increases primary productivity and vegetation growth, in the Horn of Africa and East Africa, but extremely high IOD may cause torrential rains and floods there, which spoil maturing crops [102–106]. In contrast, in southeastern Africa, positive IOD causes droughts and reduces plant productivity [102–104]. Positive IOD brings warm winters to most of Europe and North Africa, and increases winter precipitation in southern and western Europe, particularly on the Iberian Peninsula and at the western coast of North Africa [107,108]. Drier conditions occur across the rest of North Africa and the eastern Mediterranean basin (Figure 2d) [108]. High spring IOD, especially in May, leads to unusually warm temperatures across Europe [102,109,110], and increases rainfall in the Horn of Africa [111,112]. The negative winter IOD causes drought in this

region [102], as well as in southwestern and eastern Europe and the eastern Mediterranean (Figure 2d) [107,108]. It also brings cold winters to the western and central Mediterranean region and north Africa, but warm conditions in northern and eastern Europe [107,108]. Monthly values of IOD were retrieved from the NOAA international ocean monitoring datasets [113].

2.3.5. Long-Term Trends of Large-Scale Climate Indices and Their Correlations

We checked for multi-year trends in all large-scale climate indices over the study period using simple linear regression models. The spring SCI had the only statistically significant trend and decreased over 1982–2025 (Figure S1). We also checked if these large-scale climate indices were correlated using Pearson's correlation coefficient, applying Benjamini and Hochberg's [114] correction for multiple comparisons. Only three correlations were statistically significant (Table 1), and the strongest correlation between the winter NAO and winter MOI was $r = 0.68$, thus we did not include these two variables in one multiple regression model to reduce multicollinearity.

Table 1. Pearson's correlation coefficients between the winter (December–February; indicated as WIN) and spring (March–May, indicated as SPR) temperature variables in 1982–2025. Bold values indicate statistically significant correlations, after Benjamini–Hochberg correction for multiple comparisons with an accepted 5% level of false positives.

Climate Variable	NAO_SPR	IOD_WIN	IOD_SPR	SCI_WIN	SCI_SPR	MOI_WIN	MOI_SPR
NAO_WIN	0.19	−0.17	0.03	−0.55	−0.11	0.68	−0.16
NAO_SPR		−0.25	−0.10	−0.42	0.06	0.33	−0.02
IOD_WIN			0.37	0.07	0.10	−0.18	0.18
IOD_SPR				0.09	−0.23	−0.16	0.29
SCI_WIN					0.01	−0.55	0.14
SCI_SPR						−0.03	−0.32
MOI_WIN							−0.31

All correlation coefficients were lower than the recommended threshold of $|r| = 0.7$, indicating that the effects of multicollinearity on the results of models including these climate variables would be negligible [115].

2.4. Methods of Data Analysis

2.4.1. Analysis of Long-Term Trends in Spring Migration Phenology and Protandry

We used only the data from the initial capture for each bird within a season and excluded any unsexed individuals from analyses. We combined all age classes for analyses (adults, second-calendar-year birds, and full-grown), because if the birds from the last, less accurate age category were excluded, the sample sizes in the age/sex groups, especially of adult females, were too small to analyse in one third of the years. Thus, we combined all the age groups, assuming that all blackcaps caught during spring were migrating to their breeding grounds. However, we analysed males and females separately, as this study focuses on sex differences in spring phenology.

First, we used individual capture data to calculate the dates at which 10%, 50% and 90% of all males or females were ringed in each year (Figure S2). We used these dates for each sex, expressed as the day number (1 January = Day 1), as parameters reflecting the timing of three phases of migration: the date of the 10th percentile (p10) as the beginning, the 50th percentile as the middle, and the 90th percentile (p90) as the end phase of passage, as in other studies [10,16,116–119]. We excluded four years from the analyses when fewer than 5 females were captured, as females were fewer than males among captures (Table S1).

Thus, we finally analysed data from 38 springs during 1982–2025, including 2912 females and 4345 males, in total 7257 blackcaps (Table S1).

To estimate multi-year trends in migration timing for each sex, we used linear regression of the dates of p10, p50 and p90 for each sex against the year number from 1982 (YearN), used as a continuous explanatory variable. Our selection of the linear regression approach, used in other studies [10,16,116–119], was supported by an initial data examination using General Additive Models (GAMs), which showed that multi-year trends of all these dates were nearly linear. We considered the degree of protandry in subsequent phases of passage as the difference in the dates of these percentiles between males and females, as in Tøttrup and Thorup [10]. To check for protandry and to test whether its degree had changed over the years, we ran three multiple linear regression models, one for each of the time series of these percentiles' dates, including the standardised year (YearSt) and sex (SexN, coded as 0 = males, 1 = females), and their interaction as explanatory variables. We applied the “all subsets” approach using the “dredge” function in the “MuMIn” package [120], and we ranked the models using the Akaike Information Criterion corrected for small sample sizes (AICc). The model with the lowest AICc was considered the best model, which we interpreted.

2.4.2. Estimating the Effects of Large-Scale Climate Indices on Different Phases of Blackcap Spring Migration

To test the effects of large-scale climate indices on the timing of these three phases of passage, we ran multiple linear regression models where the time series of the dates of p10, p50 and p90 in 1982–2025 were response variables, and the explanatory variables included the year, the four large-scale climate indices (NAO, MOI, SCI, IOD) in winter and spring, and the interactions of these climate variables with sex. We selected the multiple regression approach as in other studies [10,17,121] to enable comparisons of results. We used the year as the continuous explanatory variable, not as a random effect, to account for long-term trends in the dataset [16,17,40,122]. All explanatory variables were standardised before being included in the models, because they had different scales. Because these variables were too many to include in one model, we first ran the models separately using the indices for winter months (December–February) in the “winter models” and the indices for spring months (March–May) in separate “spring models”. Because winter MOI and winter NAO were correlated at $r = 0.68$ (Table 1), to avoid multicollinearity, we ran the partial winter models for two sets of variables: one excluding winter MOI, and the other excluding winter NAO. Thus, we ran nine models: two “winter” models and one “spring” model for each of three migration phases. We conducted the model selection using the “all subsets” approach and model ranking according to AICc, using the “MuMIn” package [120], as previously described.

Comparing these partial “winter” models, we found that models including winter NAO consistently explained a higher proportion of the variation in the migration timing, as they had higher Adjusted R^2 (Adj R^2) values than the models including winter MOI. Therefore, in the second step, we used the variables selected in the best “winter” models including winter NAO (not winter MOI), and in the best “spring” models.

Next, for each migration phase (p10, p50, and p90), we ran “winter and spring” models combining winter and spring climate indices selected by the best “winter” and “spring” models. In these multiple regression models, we included those interactions of these indices with sex that were retained by the respective “winter” or “spring” best models in the first step. We applied the same “all subsets” approach and AICc model ranking as earlier, to identify the final best “winter and spring” models. To determine the percentage of explained variation in the response variable, we extracted Adj R^2 for each final model using the “broom” package [123].

We evaluated multicollinearity in these models using the Variance Inflation Factor (VIF) from the “car” package [124]. In all models, $VIF < 3$, which indicated no harmful effects of multicollinearity on the results [125]. To test for potential overfitting, we cross-validated the final best models using a three-step approach recommended by [122]: (1) visual inspection of diagnostic plots to identify outliers and highly influential data points based on Cook’s distance; (2) evaluation of the ratio of Adj R^2 to the multiple coefficient of determination (R^2), where a ratio approaching 1 indicates an optimal model fit; and (3) comparison of Adj R^2 with the Predictive R^2 ($predR^2$). The $predR^2$ was calculated from the Predicted Residual Error Sum of Squares (PRESS) using a Leave-One-Out Cross-Validation procedure using custom R functions [126]. In this approach, each data point is sequentially removed, the model is refitted, and its ability to predict the omitted observation is evaluated. A minimal difference between Adj R^2 and $predR^2$ indicates that the model is stable and not overfitted [126]. Additionally, we evaluate the presence of first-order temporal autocorrelation in the model residuals, using the Durbin–Watson test. This application of multiple regression, evaluation of final models’ multicollinearity and stability followed earlier studies [18,40,41]. The final “winter and spring” models provided estimates of the effect of each selected climate variable on the dates of p10, p50, and p90 of the spring passage. We visualised these effects as scatter plots showing relationships of these variables to the dates of these phases of passage and fitted linear regression lines, using the “ggplot2” package [127]. All statistical analyses were conducted in R 4.4.2 [128].

3. Results

3.1. Protandry and Sex-Specific Long-Term Trends in the Timing of Spring Migration of Blackcaps

During 1982–2025, the dates of the beginning (p10) of spring passage for both sexes shifted earlier by 9 days (Figure 3; Table S2). Protandry in blackcaps at Bukowo–Kopań occurred at the beginning of spring passage because p10 was on average 2.2 days earlier for males than females (Figure 3; Tables S3 and S4). This degree of protandry remained stable over 1982–2025 (Figure 3, Tables S3 and S4), as indicated by the parallel regression lines (Figure 3) and a lack of the YearSt:SexN interaction in the best model for p10 (Table S4). The median dates (p50) of passage did not differ between the sexes (Figure 3), as confirmed by the absence of the sex effect (SexN) in the best model (Table S4). The p50 dates for males shifted earlier by 9 days and for females by 7 days, over 1982–2025 (Figure 3; Table S2). These advancing trends were similar, as indicated by no YearSt:SexN interaction in the best model (Table S4). The dates of the end of migration (p90) showed no trends over time and did not differ between the sexes (Figure 3; Table S3), as shown by no effect of sex (SexN) in the best model (Table S4).

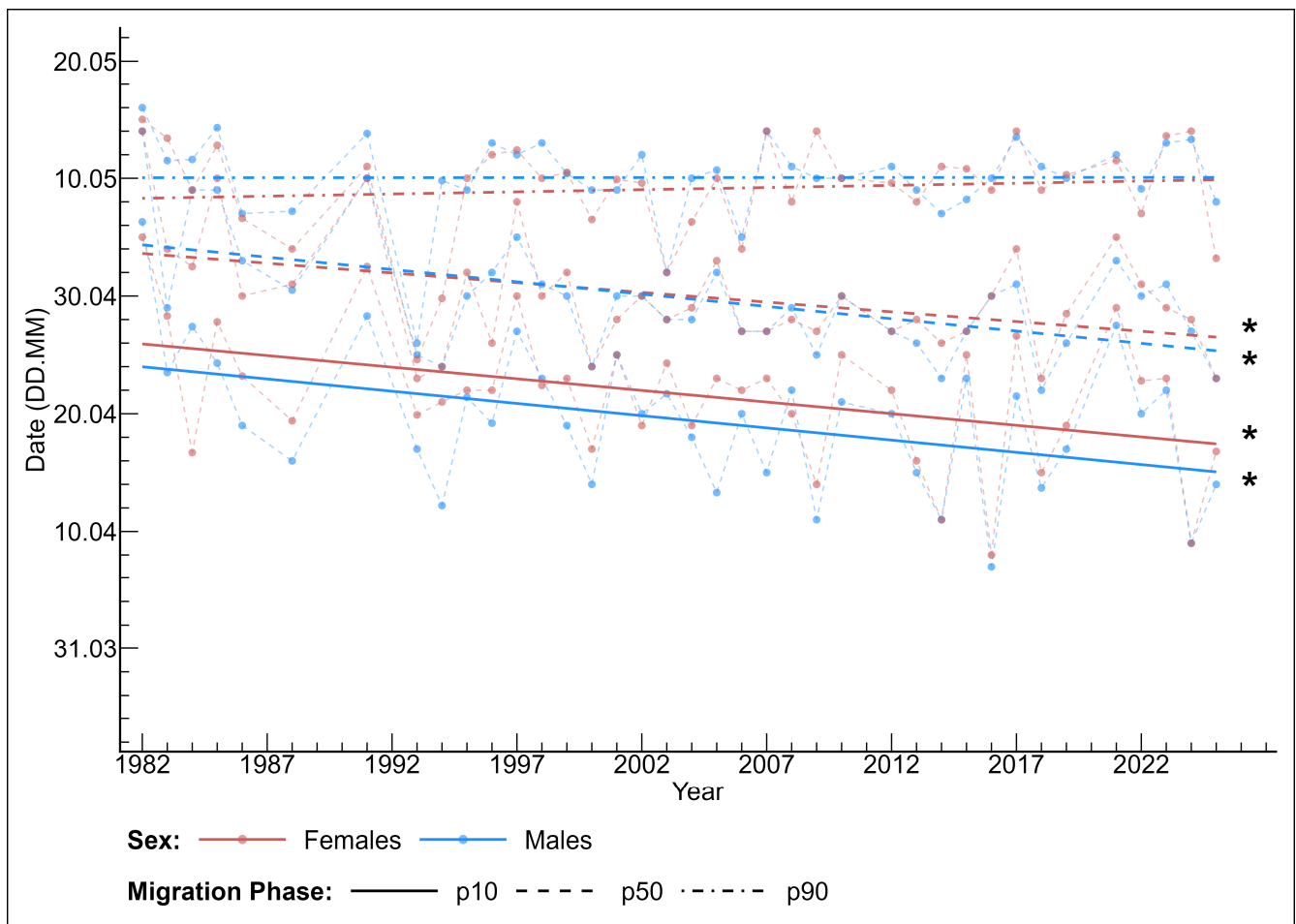


Figure 3. Multi-year trends in the timing of the first (p10), median (p50), and last (p90) phases of spring migration for male and female Eurasian blackcaps at Bukowo-Kopań in 1982–2025. Circles represent the dates of the respective percentiles of passage in each year plotted against the year, for each sex separately. Lines show fitted linear regression trends; asterisks (*) indicate statistically significant trends. The details of the regression are in Table S2.

3.2. Effects of Large-Scale Climate Indices on Spring Migration Timing

The “winter” models including NAO (but not MOI) explained 7–27% of the variation in the timing of different phases of spring migration (Table S6), while the models including MOI (but not NAO) explained 7–25% of this variation (Table S8). Because the “winter” models including winter NAO consistently explained a higher proportion of the variation than those including MOI (Tables S6 and S8), we used the outcome from the first approach in the combined “winter and spring” models. The best “spring” models explained from 0% to 44% of the variation in the timing of p90 and p10, respectively (Table S10).

The best “winter and spring” model (Table S11) explained 48% of the variation in the date of the beginning of passage (p10) at Bukowo-Kopań during 1982–2025 (Table S12). We found no differences between the sexes in the relationships of p10 to the climate indices. For both sexes, p10 was early with high winter NAO (Figure 4a) and high spring SCI (Figure 4b), or late with low values of these indices, as these relationships work both ways (Tables S12 and S13).

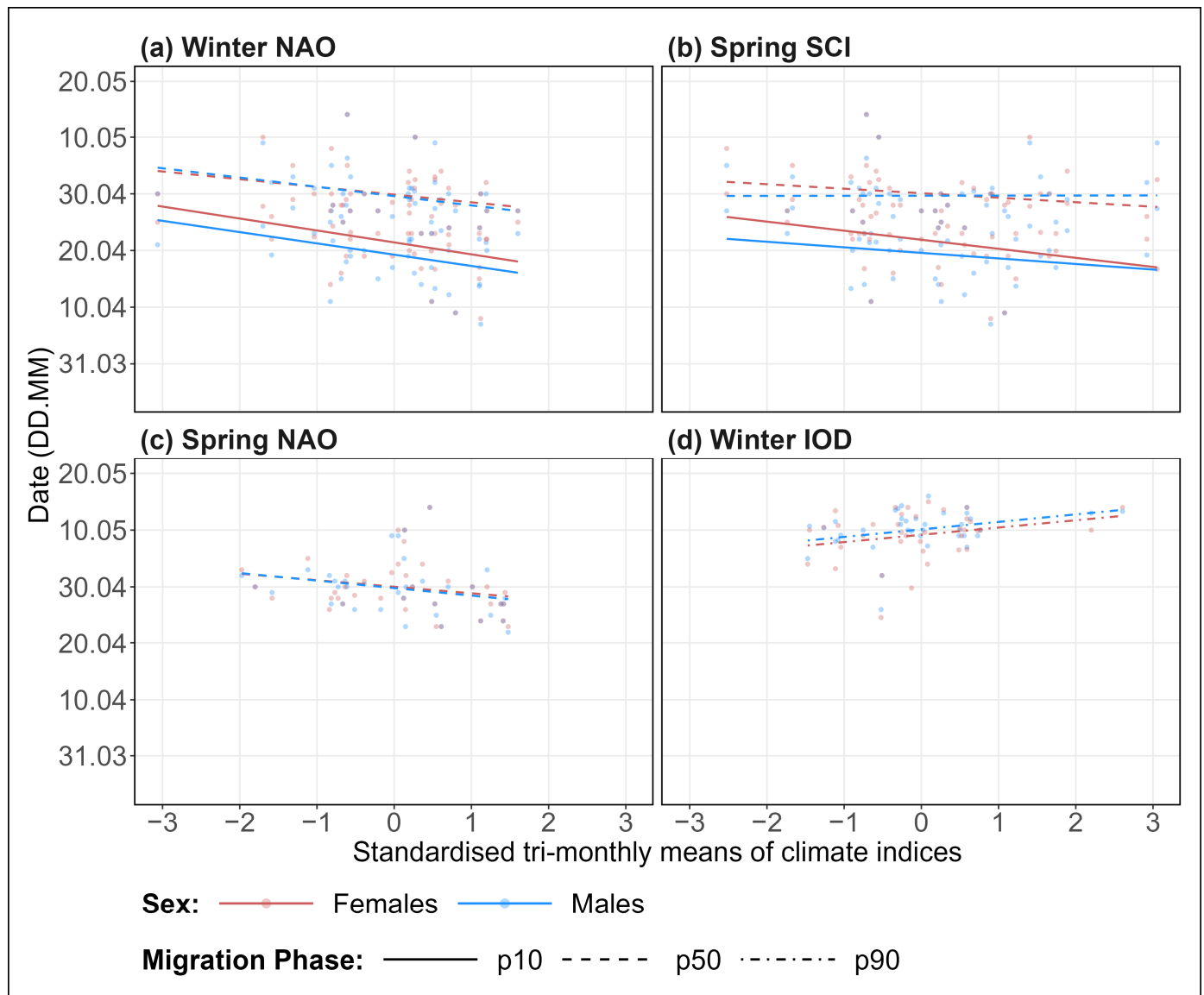


Figure 4. Relationships between the timing of the selected percentiles (p10, p50, p90) of spring migration for male and female Eurasian blackcaps at Bukowo–Kopań in 1982–2025 and the large-scale climate indices selected in the best “winter and spring” models (Table S13). Points represent the dates of the respective percentiles of passage plotted against the values of the climate index in a given year. Linear regression lines show the modelled trends. (a) The effect of the winter NAO on the first (p10) and median (p50) phases of passage; (b) the effect of the spring SCI on the first (p10) and median (p50) phases of passage; (c) the effect of the spring NAO on the median (p50) phase of passage; and (d) the effect of the winter IOD on the end (p90) phase of passage.

For the median date of passage (p50), the best model explained 39% of its variation in 1982–2025 (Table S12). No sex-specific differences occurred in the effects of large-scale climate indices. The median for both sexes was early with high winter NAO (Figure 4a, Table S13), high spring NAO (Figure 4c, Table S13), and high spring SCI (Figure 4b, Table S13). The best model for the end of passage (p90) explained 7% of its variation over the 44 years (Table S12). The sexes did not differ in their relationships to any of the climate indices. The date of p90 for both sexes was late with high winter IOD, or early with low IOD (Figure 4d; Tables S12 and S13).

Diagnostic tests confirmed the stability of the final “winter and spring” models (Table S14, Figure S3). Minimum discrepancies between Adj R^2 and pred R^2 and high

ratios of Adj R^2 to R^2 (range: 0.84–0.94) indicated that the models were not overfitted (Table S14). Visual inspection of diagnostic plots confirmed that the assumptions of the regression models were met, with no highly influential outliers (Figure S3). The Durbin–Watson test indicated positive autocorrelation in the residuals (DW statistics: 0.91–1.25, Table S14). Such autocorrelation is common in multi-decadal ecological time series, as successive years often share similar environmental conditions [129,130]. However, given the high stability of our models, this did not affect the reliability of the identified climatic relationships (Table S14).

4. Discussion

Our study shows that both male and female blackcaps advanced their spring passage through the southern Baltic coast over 1982–2025 at similar rates. The first phase of passage (p10) shifted earlier by 9 days in both sexes, thus protandry remained stable over these 44 years, opposite to what we expected, considering the changes in protandry in other passerines [45,48,131]. The two-day protandry, the most apparent at the first phase, decreased at the subsequent phases of blackcaps' passage, although the median phase advanced for males and females by 9 and 7 days, respectively. Contrary to our expectations, annual variation in migration timing was related to large-scale climate indices in both sexes similarly, but the timing of subsequent phases of passage in both sexes was shaped by different climate indices. The first (p10) and median (p50) phases of passage were early with positive winter and spring NAO, and spring SCI, but the last phase (p90) was delayed after positive winter IOD, in males and females alike, suggesting that successive cohorts of both sexes arrived along different migration routes. We discuss these findings in the context of the mating opportunity hypothesis and changing climate conditions across blackcap wintering grounds and migration routes.

4.1. Long-Term Phenological Trends in Both Sexes and Drivers of Spring Protandry

Protandry is common among migratory birds, driven mainly by the selective pressures of the mating system [6,11]. The mating opportunity hypothesis explains that earlier arrival enables males to occupy high-quality territories to improve reproductive success [10,26]. These phenological differences are related to energy management. Females must maintain sufficient fat and protein reserves for egg production, so they optimise energy costs and avoid harsh conditions early in spring that could deplete these essential reserves [5]. In contrast, males prioritise migration speed over energy saving [11]. Thus, blackcap males exhibit a time-minimising strategy and females an energy-maximising strategy during spring migration [132]. Furthermore, the earlier passage of males may result from spatial sex segregation at the non-breeding grounds. In blackcaps, males might winter in greater proportion at more northern latitudes than females, having a shorter migration distance to cross [30,133,134].

We suggest that both mechanisms contribute to the spring protandry we found at the first phase (p10) of passage at Bukowo–Kopań over 1982–2025, in line with earlier studies [10,135]. The protandry among the first migrants supports the mating opportunity hypothesis. Competition for breeding opportunities creates evolutionary pressure on males [7,136], as the first-arriving individuals secure the best territories and attract the earliest females [137–139]. In contrast, the timing of the median (p50) and the end (p90) phases of passage at our station was similar for both sexes, suggesting that the pressure for early male arrival fades as the season progresses. The lack of protandry in the median dates of passage contrasts with results from Helgoland (North Sea, Germany) and Christiansø (Baltic Sea, Denmark), where this phase of passage was significantly earlier in males than in females [135]. This discrepancy might result from differences in the composition of

populations passing through these stations compared to Bukowo–Kopań, or the different time periods analysed (1982–2025 in our study vs. 1976–1997 in Rainio et al. [135]).

The degree of protandry at the first phase of passage (p10) did not change over our 44-year study period, as males and females advanced their migration timing at a similar rate. Furthermore, the median of passage (p50) advanced similarly for males and females, by 9 and 7 days, respectively, despite no clear protandry at that phase of migration. This uniform phenological shift aligns with earlier studies, which also reported no changes in the degree of protandry over 1976–1997, both for the combined data from Helgoland and Christiansø [135], and for Christiansø alone [10]. The similar advancements of both sexes suggest that they respond to similar environmental conditions shaped by oscillation patterns over large areas, where the sexes likely occur in a close sequence [134]. Males and females probably also fine-tune the progress of passage across Europe using the same external cues, like temperature or food availability at stopover areas, rather than sex-specific cues [10,140,141]. The parallel phenological shifts suggest that among early arrivals both sexes compete for mates [10] and earlier spring passage benefits both sexes equally. Mild springs might enable males to reach breeding grounds early to maximise mating opportunities, and allow females to lay eggs earlier, extending the breeding season and increasing chances of raising two clutches for both sexes [20,26].

Interestingly, resident birds such as great tit (*Parus major*) and blue tits (*Cyanistes caeruleus*) exhibit similar phenological plasticity, shifting their breeding dates earlier [142,143]. These populations utilise local environmental cues, such as springtime warming and early leafing, to synchronise their reproduction with the accelerated peak of food resources [144].

The advancement of the start of migration by 9 days (for both sexes) and of the median by 7–9 days at Bukowo–Kopań is consistent with the shift to earlier median migration dates during 1976–1997 for combined data from Helgoland and Christiansø [135]. Our results also correspond with the trends observed at Christiansø alone [10] that indicated an advance in arrival at all migration phases (5%, 50%, and 95%); though, these trends were not significant, likely because of a shorter time series than ours. More recently the first and last 5% of blackcaps' passage significantly advanced during 1984–2022 at the Blåvand bird observatory in Denmark; however, unlike our study, this analysis combined males and females [119]. The lack of any multi-year trend in the timing of p90 in our study differs from the significant trend at Blåvand [119], probably because at Bukowo–Kopań the local breeding blackcaps occurring at the end of spring masked any trends. A weaker phenological shift with the progress of the passage is a common pattern across all the mentioned stations [10,119]. This might result from a slower migration of birds in the “tail” of passage, which often includes weaker individuals, which likely were “outcompeted” by the preceding fitter individuals, but might still be able to raise some chicks [145], hence smaller time pressure. Furthermore, this late phase mainly consists of females and young males [131,146]. These individuals face weaker selection pressure to migrate early because females do not establish territories and young males have lower chances to secure prime breeding spots than adults [7,8,21]. The overall shift to earlier passage for the first half of the population suggests that blackcaps respond to increasingly mild conditions on their wintering grounds and along spring migration routes [2,10,22], which increases their chances to raise two clutches during extended breeding season [26]. While our results highlight the role of large-scale climate patterns, we suggest that these phenological shifts might be co-influenced by other ecological factors. These could include habitat changes along the flyways, fluctuations in stopover site quality, and broader population-level shifts, such as the increasing numbers of blackcaps wintering in western and northern Europe [52–55]. Similar advancement suggests that earlier spring passage benefits both sexes equally. Mild springs might enable males to reach breeding grounds early to maximise

mating opportunities, and allow females to lay eggs earlier, extending the breeding season and increasing chances of raising two clutches for both sexes [20,26].

4.2. *Similar Responses of Both Sexes to Large-Scale Climate Indices*

Our key finding is a lack of differences in male and female blackcap relationships to any of the large-scale climate indices. This differs from our initial expectations that males should respond more strongly to some climate patterns, especially those that shape winter and spring conditions in Europe, as male blackcaps generally winter closer to their breeding grounds than females [6,11,12,28–32]. Unlike the song thrush, in which after warm winters and springs the males arrived in the Baltic region much earlier than the females [45], in the blackcap the relationships of both sexes to climatic conditions were similar, despite the protandry at the first phase of passage (p10) at Bukowo–Kopań. This difference might reflect species-specific phenological plasticity, with the song thrush and both sexes of the blackcap showing the same level of flexibility in response to changing conditions. Both species share part of their wintering grounds in the Mediterranean region, but Redlisiak et al. [45] analysed regional mean temperatures in southern and southwestern Europe, unlike our study. If male and female song thrushes are partly segregated across the wintering grounds, as other passerines, they might be exposed to varied local temperatures, which could affect their migration differently. This contrasts with the large-scale climate factors we analysed for blackcaps, which have a climatic footprint over much larger areas of the blackcap wintering range from northern Africa through the Mediterranean to central Europe [80,147]. Even though females winter farther south than males due to spatial segregation [11,30], both sexes likely experience the same broad weather conditions dictated by these large-scale oscillations and adjust their migration timing accordingly. Additionally, female blackcaps appear to be as phenologically adaptive as males, likely because the benefits of advancing spring migration and increasing the chance for second broods balance the risks posed by cold spells in spring similarly in both sexes [20,26]. This uniform response of males and females is consistent with findings from Helgoland and Christiansø, where the winter NAO did not affect the degree of protandry in blackcaps [135], and with the conclusion that both sexes respond similarly to changing climatic conditions [10]. However, this uniform response is atypical compared to other passerines, for example the barn swallow, the willow warbler, the chiffchaff and the song thrush, which show increasing differences in arrival dates between the sexes with progressively warmer winters and springs [42–45,48,49]. This suggests that uneven shifts in migration timing are not a common pattern among all migratory birds. In species with remarkable flexibility, such as the blackcap, the benefits of early arrival, such as occupying high-quality territories for males [7,10] and extending the breeding season for females [20,26], likely create similar selective pressures on both sexes, allowing them to adjust to changing environmental conditions and maximise reproductive success. Protandry in blackcaps appears to be maintained by the selective pressures described by the mating opportunity hypothesis [7,10,20], regardless of the weather conditions in a given season.

4.3. *Effect of the North Atlantic Oscillation (NAO) on Spring Migration Timing*

Positive winter NAO was related in both sexes to an advanced first (p10), and, with a weaker effect, to the median (p50) phases of passage, but not to its end phase (p90), a pattern similar to the responses to winter NAO in blackcaps migrating through other locations [10,116,119,135]. Our results for the first phase of passage contrast with no significant relationship between the first arrival dates of blackcaps and winter NAO shown by long-term (1881–2007) observations from the Czech Republic [148]. This suggests that

first blackcaps arrive there from areas under a weaker climatic influence of NAO, like the eastern Mediterranean or southeast of Europe [61], than the first migrants at more northern and coastal locations in Europe, including Bukowo–Kopań. The relationship between NAO and the first phase of passage at our station suggests that the first migrants winter close to the breeding grounds, in areas where positive NAO brings mild winters, such as western and central Europe [80,88]. Warm winters reduce energy expenditure on thermoregulation and lead to an earlier availability of insect prey, allowing these short-distance migrants to reach migration condition faster and depart early. The relationship we found between winter NAO and advancement of p50 contrasts with earlier results from Helgoland and Christiansø, where no analogous effect was found [135], possibly because they analysed a shorter time series. The relationship we revealed might also reflect a more recent shift in wintering patterns of the eastern population of blackcap, from eastern to more western wintering grounds [55], which are under climatic influence of NAO. Positive spring NAO was related to the early median phase of passage (p50) for both sexes, in line with earlier results showing such a relationship for both sexes jointly [17]. Positive NAO brings south-westerly winds and warm spring across central and western Europe [80,84,85,91]. This effect of NAO is most pronounced in March, about the time that migrant blackcaps moving northward enter this region. Winds from the southwest can assist migrants in their movement across Europe to the northeast. Warm conditions might benefit migrants more indirectly, accelerating the development of spring vegetation and increasing insect abundance at stopover sites [22,149]. Additionally, the reduced snow cover across western and central Europe [82,83] makes these stopover sites accessible earlier in the spring. All these effects of positive NAO favour quick fuel accumulation along migration routes, allowing birds to maintain their early passage.

4.4. Effect of the Scandinavian Pattern Index (SCI) on Spring Migration Timing

Positive spring SCI, which brings warm weather and thus likely favourable food conditions to the central and western Mediterranean [93,94,97], was associated with earlier first (p10) and median (p50) phases of passage of both sexes at Bukowo–Kopań. This suggests the first half of migrants benefit from these conditions, which allow for quick fuel accumulation and thus shorter stopovers during spring migration. Following the mating opportunity hypothesis [7,10,20], we suggest that the migrants that form the first phase of passage (p10) winter close to the breeding grounds, probably at the northern edges of the central and western Mediterranean region. With positive SCI, they might experience the spring peak in food availability in these areas, which enables an early departure for migration. Birds that form the middle phase (p50) of passage, arriving from more southern wintering areas, might experience such conditions during their stopovers in these areas, which results in an analogous phenological shift. Furthermore, the south-westerly and southerly winds across western and central Europe during positive spring SCI can directly assist early migrants in their movement across Europe to the northeast, contributing to the earlier beginning (p10) and median (p50) of passage at our station. This earlier arrival is beneficial, as positive SCI accelerates spring snowmelt across central Europe and Scandinavia [99,150], making subsequent stopover sites and northern breeding grounds accessible earlier in the season. These phase-specific responses align with the previously found relationship between the positive spring SCI and advancement of the overall spring passage of the blackcap at Bukowo–Kopań [17]. By dividing the migration into phases, our study reveals that this overall relationship has been primarily driven by a response of the first half of migrants to environmental conditions shaped by SCI.

4.5. Effect of the Indian Ocean Dipole (IOD) on Spring Migration Timing

Positive winter IOD, which brings high rainfall to East Africa [111] but dry spells to the eastern Mediterranean [108,151], was related to the delayed end of migration (p90) in both sexes. This suggests that blackcaps that form the end of spring passage at Bukowo–Kopań arrive from the eastern part of wintering grounds or stopover areas in the eastern Mediterranean region, as indicated by ringing recoveries (Figure 1) [61]. The delayed last phase (p90) of blackcaps' passage after high winter IOD corresponds to late overall spring passage of the common redstart and the pied flycatcher, and a late end of the chiffchaff's passage at Bukowo–Kopań with such conditions [17,41]. These delays might be attributed to heavy rains and floods in East Africa with extremely high winter IOD, as in 2019/2020 [111]. Rainfall and temperature conditions in Africa in February–March can affect migrants' departure from these areas, directly by influencing their energy requirements during fuelling, and indirectly by affecting resource availability and conditions for birds [47,152]. High IOD, related to a lack of rain in the Mediterranean region, limits vegetation growth and food availability [153,154]. Such unfavourable conditions might extend the time the birds need to build fuel reserves and delay their departure from wintering or stopover sites in this area. Analogies between the patterns in blackcap and other species indicate that IOD similarly influences several long-distance migrants, probably those that arrive at the southern Baltic coast from the southeast, along similar spring migration routes. Unfavourable conditions for birds related to extremely high winter IOD in East Africa and the eastern Mediterranean might compound the delay in birds' migration along this route and ultimately delay their arrival at the Baltic coast.

4.6. Study Limitations and Broader Ecological Context

Although our 44-year study provides clear long-term trends, some methodological limitations should be considered while interpreting our results. Furthermore, annual capture numbers of males and females could be influenced by local and interannual changes in habitat and stopover site quality. Capture probabilities might also be affected by minor variations in catching effort; although we aimed for methodological consistency, the exact number of mist nets varied between seasons (Table S1), and the location of mist netting slightly shifted over the 44-years. With the available data, we could not isolate the effects of individual body condition or age on the timing of passage. Our findings, such as the stable degree of protandry and uniform responses to climate indices, align with patterns from nearby Baltic and North Sea stations like Christiansø and Helgoland [10,135], but our data come from a single ringing station. Thus, they represent a location-specific mix of blackcaps arriving there along the western and the eastern flyways, and of local breeding birds and individuals migrating farther north to Scandinavia [60–63]. Therefore, the phenological patterns we observed might not fully capture the dynamics along all flyways across Europe, and might differ at other locations, thus comparisons with patterns at other stations might lead to further interesting findings.

5. Conclusions

We showed that both male and female blackcaps advanced the first half of their spring migration on the Baltic coast at similar rates; thus, the two-day protandry in the first phase of their passage remained stable over the 44 years of our study. This stable protandry can be explained by the mating opportunity hypothesis, which suggests that selective pressures preserve the difference in spring timing between the sexes, regardless of the interannual variation in weather conditions. Despite this protandry, males and females responded uniformly to winter and spring climate patterns, suggesting that these conditions similarly affect broad non-breeding grounds of both sexes. We suggest that

females are as phenologically adaptive as males, to maximise a common reproductive outcome for both sexes. Such phenological response to climate change apparently benefits the species, considering its almost threefold increase in numbers across Europe, including the Baltic region, since the 1980s [128].

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/biology15171518/s1>, Figure S1: Long-term trends in large-scale climate indices used in the analysis. Statistically significant trends are indicated by an asterisk (*) next to the variable abbreviation; Figure S2: Visual representation of the method of calculating the dates of spring migration phases (p10, p50, and p90) for males and females of Eurasian blackcaps, using the 2009 spring season as an example. The solid stepped lines illustrate the cumulative curve of passage (left y-axis), while the bars show the daily number of captured individuals (right y-axis). The horizontal and vertical lines show how the capture of 10%, 50%, and 90% of all males or females indicated the dates of the respective migration phases. (a) Visual representation of deriving the dates of the three phases of passage for males; (b) visual representation of deriving the dates of the three phases of passage for females; Figure S3: Diagnostic plots for the final best “winter and spring” linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration. The plots present residuals versus fitted values, normal Q-Q plots, scale-location plots, and residuals versus leverage to assess regression assumptions, including linearity, normality of residuals, and identification of highly influential data points (Cook’s distance); Table S1: Numbers of captured males, females, and all Eurasian blackcaps (*Sylvia atricapilla*) caught, and of the nets used during each spring migration season (26 March–16 May) at Bukowo–Kopań in subsequent years of the period 1982–2025. Grey fields—seasons which were excluded from analyses, because the station did not operate or fewer than five females were caught. Total for analyses (in both font) indicates the numbers of individuals considered in analyses; Table S2: Linear regression parameters for the long-term trends in the dates for the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcaps at Bukowo–Kopań in 1982–2025 (Figure 3). The table presents the slope coefficient (β), intercept, standard error (SE), and significance level (p). ‘ $\beta \times \text{years}$ ’ is the estimated total shift in arrival timing (in days) during the analysed period, calculated by multiplying the slope coefficient by the number of years (44 years). A negative β value indicates an advance in the date of the analysed percentile over time; Table S3: Model selection for the linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring passage, used as response variables. The explanatory variables in the full models included sex (SexN), standardised year (YearSt), and their interaction (YearSt:SexN). The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with a delta AICc < 2. Bold digits indicate variables selected in the best model. Parameters of these best models are presented in more detail in Table S4; Table S4: Parameters of the best linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration used as response variables, and the explanatory variables: standardised year (YearSt), sex (SexN), and their interaction (YearSt:SexN). The best models were selected based on the lowest AICc (Table S4). The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), and significance level (p) for the intercept and explanatory variables selected in the best models. The estimates for the YearSt:SexN interaction indicate the change in the degree of protandry over the years; Table S5: Model selection for the “winter” models including NAO (without MOI) of relationships between dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo–Kopań and winter large-scale climate indices, excluding the winter MOI variable, in 1982–2025. The candidate explanatory variables are listed in the table heading. Abbreviations of the temperature variables are provided in Table 1. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion

corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Bold digits indicate variables selected for the best partial “winter” model. Parameters of this best model are presented in more detail in Table S6; Table S6: Parameters of the best “winter” linear regression models including NAO (without MOI), for the dates of the beginning (p10), median (p50), and end (p90) of spring migration and winter variables in 1982–2025. The best model had the lowest AICc. The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), and significance level (p), and the Variance Inflation Factor (VIF) for the intercept and the explanatory variables selected by the best model, as well as the Adjusted R² (Adj R²) for the entire model; Table S7: Model selection for the “winter” models of relationships including MOI (without NAO) between dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo–Kopań and winter large-scale climate indices, excluding the winter NAO variable, in 1982–2025. The candidate explanatory variables are listed in the table heading. Abbreviations of the temperature variables are provided in Table 1. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Bold digits indicate variables selected for the best partial “winter” model. Parameters of this best model are presented in more detail in Table S8; Table S8: Parameters of the best “winter” linear regression models including MOI (without NAO), for the dates of the beginning (p10), median (p50), and end (p90) of spring migration at Bukowo–Kopań in 1982–2025 and winter variables in 1982–2025. The best model had the lowest AICc. The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), and significance level (p), and Variance Inflation Factor (VIF) for the intercept and the explanatory variables selected by the best model, as well as the Adjusted R² (Adj R²) for the entire model; Table S9: Model selection for the “spring models” of relationships between dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo–Kopań and spring large-scale climate indices in 1982–2025. The candidate explanatory variables are listed in the table heading. Abbreviations of the temperature variables are provided in Table 1. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with a delta AICc < 2. Bold digits indicate variables selected for the best “spring” model. Parameters of this best model are presented in more detail in Table S10; Table S10: Parameters of the best “spring” linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration at Bukowo–Kopań and spring variables, in 1982–2025. The best model had the lowest AICc. The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), and significance level (p), and the Variance Inflation Factor (VIF) for the intercept and the explanatory variables selected by the best model, as well as the Adjusted R² (Adj R²) for the entire model; Table S11: Model selection for the “winter and spring” models of relationships between dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo–Kopań and for combined winter and spring temperature variables, in 1982–2025. The candidate explanatory variables are listed in the table heading. Abbreviations of the climate indices are provided in Table 1. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with a delta AICc < 2. Bold digits indicate variables selected for the best “winter and spring” model. Parameters of this best model are presented in more detail in Table S12; Table S12: Parameters of the best “winter and spring” linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo–Kopań and winter and spring large-scale climate indices selected in

the best “winter” and “spring” models, in 1982–2025. The best model had the lowest AICc. The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), significance level (p), and Variance Inflation Factor (VIF) for the intercept and the explanatory variables selected by the best model, as well as the Adjusted R^2 (Adj R^2) for the entire model; Table S13: Linear regression parameters for the relationships between the dates of the beginning (p10), median (p50), and end (p90) of spring migration of males and females of the Eurasian blackcaps at Bukowo–Kopań in 1982–2025 and the selected large-scale climate indices (Figure 4). The table presents the slope coefficient (β), intercept, standard error (SE), and significance level (p). The slope coefficient (β) estimates the shift in arrival timing (in days) per one-unit increase in the standardised climate index. A negative β value indicates an advance in the date of the analysed percentile with higher values of the climate index; Table S14: Diagnostic tests for the final best “winter and spring” linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration. The table presents the multiple coefficient of determination (R^2), adjusted R^2 , (Adj R^2) the ratio of Adj R^2 to R^2 , predictive R^2 (Pred R^2) calculated based on the Predicted Residual Error Sum of Squares (PRESS) to evaluate model overfitting, and the Durbin–Watson statistic (DW) along with its p-value (DW_p) to assess first-order autocorrelation in the residuals.

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Abbreviations

The following abbreviations are used in this manuscript:

NAO	North Atlantic Oscillation
MOI	Mediterranean Oscillation Index
SCI	Scandinavian Index
IOD	Indian Ocean Dipole
WIN	Winter (December–February)
SPR	Spring (March–May)

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The Influence of Winter and Spring Large-Scale Climate Patterns on the Timing of Male and Female Blackcap Spring Passage at the Baltic Coast

Supplementary materials: Figures S1–S3 and Tables S1–S14

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Figure S1 Long-term trends in large scale climate indices used in the analysis. Statistically significant trends are indicated by an asterisk (*) next to the variable abbreviation.

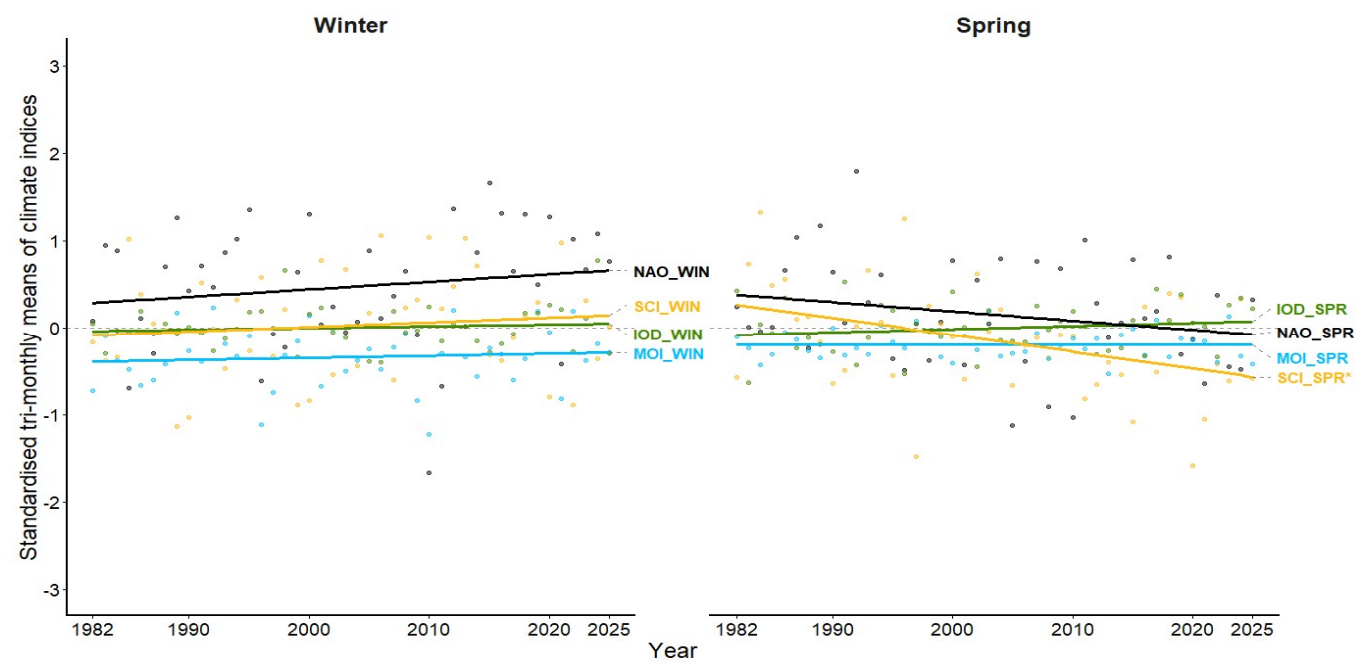


Figure S2. Visual representation of the method of calculating the dates of spring migration phases (p10, p50, and p90) for males and females of Eurasian blackcaps, using the 2009 spring season as an example. The solid stepped lines illustrate the cumulative curve of passage (left y-axis), while the bars show the daily number of captured individuals (right y-axis). The horizontal and vertical lines show how the capture of 10%, 50%, and 90% of all males of females indicated the dates of the respective migration phases. a) Visual representation of deriving the dates of the three phases of passage for males; (b) Visual representation of deriving the dates of the three phases of passage for females.

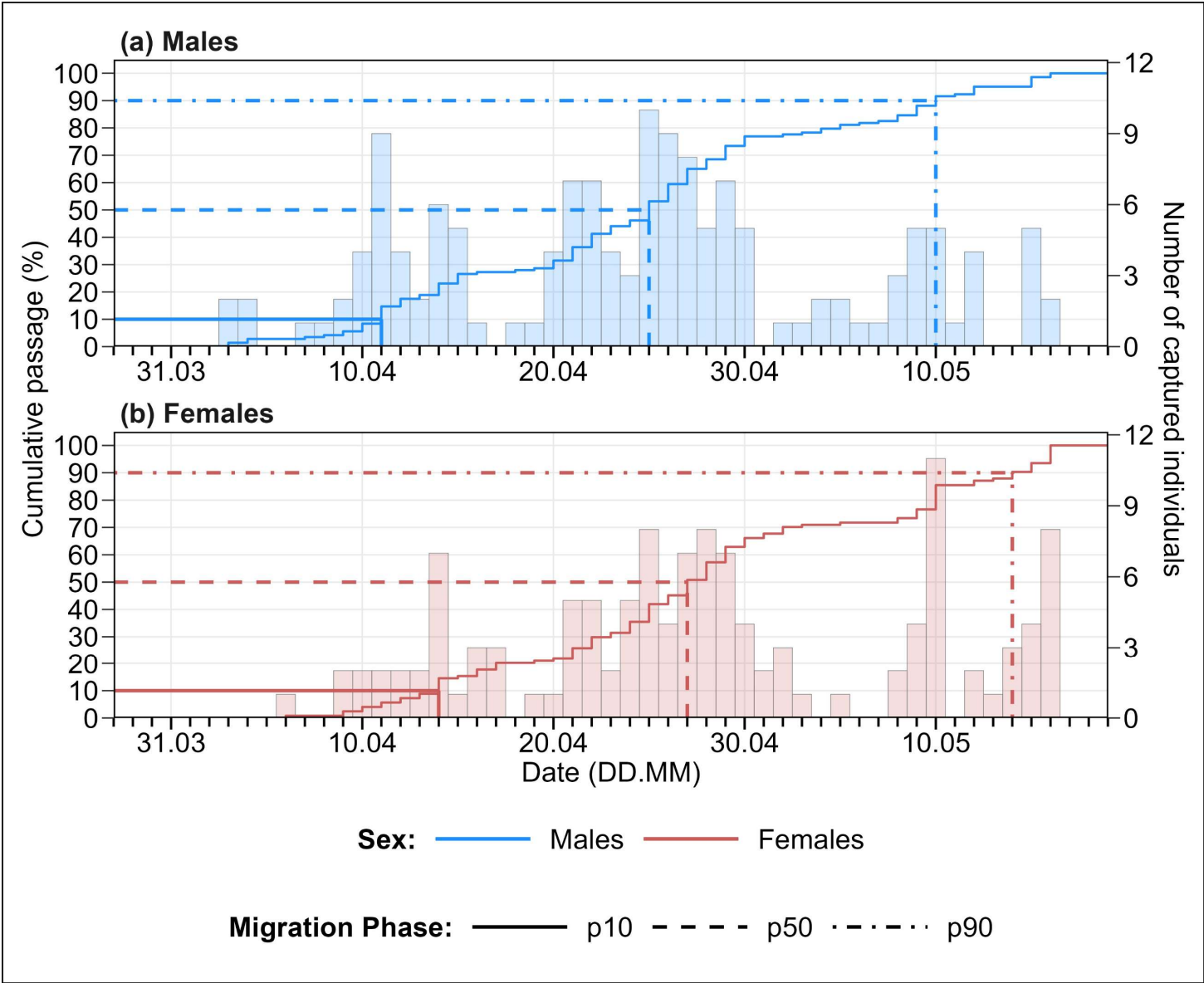


Figure S3. Diagnostic plots for the final best “winter and spring” linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration. The plots present residuals versus fitted values, normal Q-Q plots, scale-location plots, and residuals versus leverage to assess regression assumptions, including linearity, normality of residuals, and identification of highly influential data points (Cook’s distance).

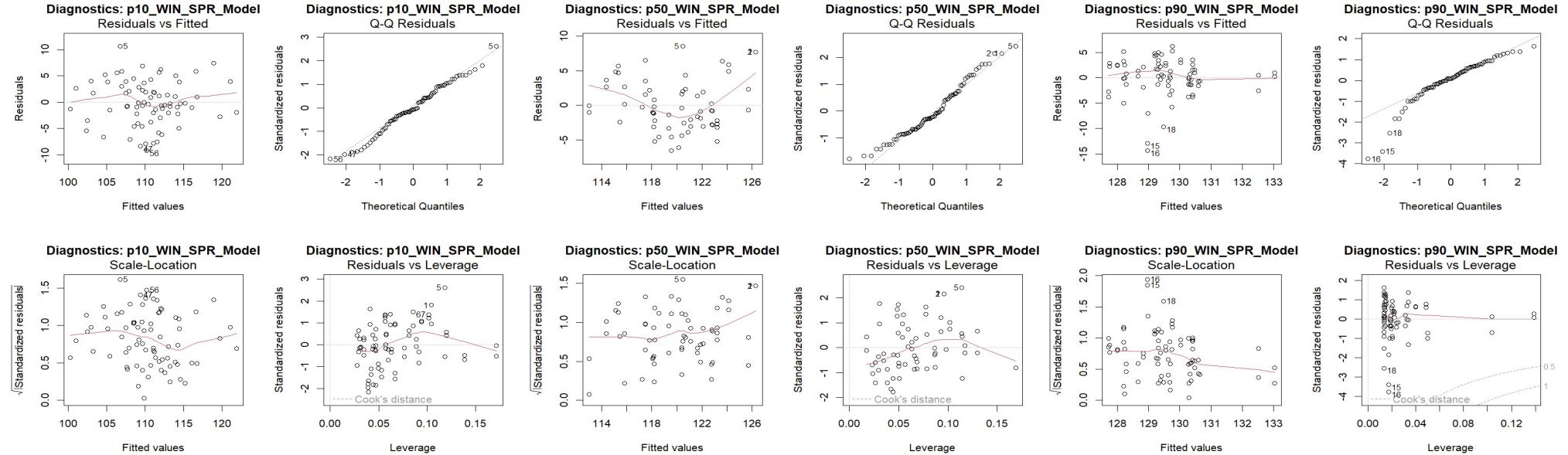


Table S1. Numbers of captured males, females, and all Eurasian blackcaps (*Sylvia atricapilla*) caught, and of the nets used during each spring migration season (26 March–16 May) at Bukowo-Kopań in subsequent years of the period 1982–2025.

Grey fields – seasons which were excluded from analyses, because the station did not operate or fewer than 5 females were caught. Total for analyses shows the numbers of individuals considered in analyses.

Year	Females	Males	Total	N nets
1982	44	54	98	57
1983	34	46	80	57
1984	8	13	21	57
1985	5	8	13	42
1986	13	11	24	51
1987	3	5	8	50
1988	15	20	35	45
1989	3	8	11	45
1990	4	4	8	45
1991	6	22	28	45
1992	3	12	15	45
1993	8	11	19	37
1994	23	35	58	47
1995	17	18	35	47
1996	32	32	64	47
1997	47	62	109	47
1998	48	71	119	47
1999	56	77	133	47
2000	38	81	119	47
2001	72	110	182	47
2002	43	91	134	57
2003	54	88	142	51
2004	68	94	162	46
2005	124	154	278	50
2006	133	162	295	50
2007	89	119	208	50
2008	59	91	150	54
2009	124	143	267	50
2010	149	143	292	46
2011	0	0	0	0
2012	105	175	280	35
2013	162	273	435	44
2014	77	140	217	41
2015	73	119	192	48
2016	151	230	381	51
2017	77	126	203	52
2018	123	258	381	52
2019	128	225	353	53
2020	0	0	0	0
2021	156	196	352	46
2022	119	180	299	57
2023	145	165	310	47
2024	148	298	446	48
2025	139	204	343	61
Grand total	2925	4374	7299	
Total for analyses	2912	4345	7257	

Table S2. Linear regression parameters for the long-term trends in the dates for the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcaps at Bukowo-Kopań in 1982–2025 (Figure 3). The table presents the slope coefficient (β), intercept, standard error (SE), and significance level (p). ' $\beta \times \text{years}$ ' is the estimated total shift in arrival timing (in days) during the analysed period, calculated by multiplying the slope coefficient by the number of years (44 years). A negative β value indicates an advance in the date of the analysed percentile over time.

Percentile	Sex	β	$\beta \times 44$	Intercept	SE	p
p10	Males	-0.208	-9	114.20	0.07	0.0058
	Females	-0.197	-9	116.13	0.07	0.0076
p50	Males	-0.209	-9	124.55	0.05	0.0004
	Females	-0.165	-7	123.78	0.06	0.0065
p90	Males	0.001	0	130.05	0.05	0.9899
	Females	0.037	2	128.26	0.06	0.5203

Table S3. Model selection for the linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring passage, used as response variables. The explanatory variables in the full models included sex (SexN), standardized year (YearSt), and their interaction (YearSt:SexN). The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with a delta AICc < 2. Bold digits indicate variables selected in the best model. Parameters of these best models are presented in more detail in Table S4.

Percentile	(Intercept)	SexN	YearSt	SexN:YearSt	df	AICc	delta AICc	weight
p10	107.89	2.17	-2.05		4.00	477.04	0.00	0.61
	108.97		-2.05		3.00	477.96	0.91	0.39
p50	118.44		-1.89		3.00	439.33	0.00	1.00
	129.59				2.00	428.49	0.00	0.51
p90	130.06	-0.95			3.00	429.55	1.07	0.30
	129.72		0.19		3.00	430.39	1.90	0.20

Table S4. Parameters of the best linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration used as response variables, and the explanatory variables: standardized year (YearSt), sex (SexN), and their interaction (YearSt:SexN). The best models were selected based on the lowest AICc (Table S4). The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), and significance level (p) for the intercept and explanatory variables selected in the best models. The estimates for the YearSt:SexN interaction indicate the change in the degree of protandry over the years.

Percentile	p10				p50				p90			
Variable	Estimate	SE	t	p	Estimate	SE	t	p	Estimate	SE	t	p
(Intercept)	107.89	0.94	114.38	<0.0001	118.44	0.56	211.23	<0.0001	129.59	0.46	284.42	<0.0001
YearSt	-2.05	0.50	-4.10	0.0001	-1.89	0.39	-4.82	<0.0001				
SexN	2.17	1.24	1.76	0.0833								
YearSt:SexN												

Table S5. Model selection for the “winter” models including NAO (without MOI) of relationships between dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo-Kopań and winter large scale climate indices, excluding the winter MOI variable, in 1982–2025. The candidate explanatory variables are listed in the table heading. Abbreviations of the temperature variables are provided in Table 1. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Bold digits indicate variables selected for the best partial “winter” model. Parameters of this best model are presented in more detail in Table S6.

Percentile	(Intercept)	SexN	YearSt	IOD_WIN	NAO_WIN	SCI_WIN	IOD_WIN:SexN	NAO_WIN:SexN	SCI_WIN:SexN	SexN:YearSt	df	AICc	delta AICc	weight
p10	107.97	2.17	-1.83		-1.64						5	472.52	0.00	0.46
	107.97	2.17	-1.78	-0.82	-1.84						6	473.51	0.99	0.28
	109.06		-1.83		-1.64						4	473.65	1.14	0.26
p50	118.50		-1.75		-1.11						4	436.63	0.00	0.72
	118.49		-1.70		-1.34	-0.39					5	438.47	1.85	0.28
p90	129.65			1.30							3	424.34	0.00	0.49
	130.12	-0.95		1.30							4	425.37	1.03	0.30
	129.63			1.21	-0.34						4	426.05	1.71	0.21

Table S6. Parameters of the best “winter” linear regression models including NAO (without MOI), for the dates of the beginning (p10), median (p50), and end (p90) of spring migration and winter variables in 1982–2025. The best model had the lowest AICc. The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), and significance level (p), and Variance Inflation Factor (VIF) for the intercept and the explanatory variables selected by the best model, as well as the Adjusted R² (Adj R²) for the entire model.

Percentile	Variable	Estimate	SE	t	p	VIF	AdjR ²
p10	(Intercept)	107.97	0.91	118.82	<0.0001	-	25%
	SexN	2.17	1.19	1.82	0.0723	1.00	
	YearSt	-1.83	0.49	-3.76	0.0003	1.03	
	NAO_WIN	-1.64	0.63	-2.60	0.0113	1.03	
p50	(Intercept)	118.50	0.55	216.58	<0.0001	-	27%
	YearSt	-1.75	0.39	-4.50	<0.0001	1.03	
	NAO_WIN	-1.11	0.50	-2.21	0.0301	1.03	
p90	(Intercept)	129.65	0.44	294.26	<0.0001	-	7%
	IOD_WIN	1.30	0.51	2.53	0.0135	-	

Table S7. Model selection for the “winter” models of relationships including MOI (without NAO) between dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo-Kopań and winter large scale climate indices, excluding the winter NAO variable, in 1982–2025. The candidate explanatory variables are listed in the table heading. Abbreviations of the temperature variables are provided in Table 1. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Bold digits indicate variables selected for the best partial “winter” model. Parameters of this best model are presented in more detail in Table S8.

Percentile (Intercept)	SexN	YearSt	IOD_WIN	MOI_WIN	SCI_WIN	IOD_WIN:SexN	MOI_WIN:SexN	SCI_WIN:SexN	SexN:YearSt	df	AICc	delta AICc	weight
p10	107.91	2.17	-1.92		-1.09					5.00	476.43	0.00	0.20
	107.96	2.17	-2.09			0.98				5.00	476.87	0.45	0.16
	107.89	2.17	-2.05							4.00	477.04	0.62	0.15
	109.00		-1.92		-1.09					4.00	477.40	0.97	0.13
	109.04		-2.09			0.98				4.00	477.83	1.40	0.10
	108.97		-2.05							3.00	477.96	1.53	0.09
	107.95	2.17	-1.98		-0.77	0.57				6.00	478.19	1.76	0.08
	107.91	2.17	-1.89	-0.50	-1.17					6.00	478.27	1.85	0.08
p50	118.47		-1.78		-0.95					4.00	437.97	0.00	0.66
	118.44		-1.89							3.00	439.33	1.36	0.34
p90	129.65			1.30						3.00	424.34	0.00	0.47
	130.12	-0.95		1.30						4.00	425.37	1.03	0.28
	129.61			1.22	-0.47					4.00	425.54	1.20	0.26

Table S8. Parameters of the best “winter” linear regression models including MOI (without NAO), for the dates of the beginning (p10), median (p50), and end (p90) of spring migration at Bukowo-Kopań in 1982–2025 and winter variables in 1982–2025. The best model had the lowest AICc. The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), and significance level (p), and Variance Inflation Factor (VIF) for the intercept and the explanatory variables selected by the best model, as well as the Adjusted R² (Adj R²) for the entire model.

Percentile	Variable	Estimate	SE	t	p	VIF	AdjR ²
p10	(Intercept)	107.91	0.93	115.80	<0.0001	-	21%
	SexN	2.17	1.22	1.78	0.0797	1.00	
	YearSt	-1.92	0.50	-3.85	0.0003	1.02	
	MOI_WIN	-1.09	0.65	-1.68	0.0979	1.02	
p50	(Intercept)	118.47	0.55	214.79	<0.0001	-	25%
	YearSt	-1.78	0.39	-4.56	<0.0001	1.02	
	MOI_WIN	-0.95	0.51	-1.88	0.0644	1.02	
p90	(Intercept)	129.65	0.44	294.26	<0.0001	-	7%
	IOD_WIN	1.30	0.51	2.53	0.0135	-	

Table S9. Model selection for the “spring models” of relationships between dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo-Kopań and spring large scale climate indices in 1982–2025. The candidate explanatory variables, listed in the table heading. Abbreviations of the temperature variables are provided in Table 1. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with a delta AICc < 2. Bold digits indicate variables selected for the best “spring” model. Parameters of this best model are presented in more detail in Table S10.

Percentile	(Intercept)	SexN	YearSt	IOD_SPR	MOI_SPR	NAO_SPR	SCI_SPR	IOD_SPR:SexN	MOI_SPR:SexN	NAO_SPR:SexN	SCI_SPR:SexN	SexN:YearSt	df	AICc	delta	weight
p10	107.75	2.17	-2.90		1.13	-0.98	-2.08						7	452.89	0.00	0.35
	107.71	2.17	-2.87		1.08		-2.16						6	453.66	0.78	0.24
	107.85	2.17	-3.02			-0.93	-2.43						6	454.61	1.72	0.15
	107.79	2.09	-2.90		0.73	-0.98	-2.08		0.79				8	454.78	1.90	0.14
	107.68	2.32	-2.90		1.13	-0.98	-1.77				-0.62		8	454.82	1.93	0.13
p50	118.46		-2.45			-1.31	-1.27						5	425.80	0.00	0.57
	118.44		-2.43	0.56		-1.40	-1.12						6	426.40	0.60	0.43
	129.59												2	428.49	0.00	0.17
	129.64						-0.57						3	429.29	0.80	0.11
	129.69							-0.44					3	429.30	0.81	0.11
	130.06	-0.95											3	429.55	1.07	0.10
	129.55				0.44								3	429.78	1.30	0.09
	129.58			0.38									3	429.88	1.39	0.09
	129.72		0.19										3	430.39	1.90	0.07
	130.11	-0.95				-0.57							4	430.39	1.91	0.07
	129.73					-0.52	-0.39						4	430.40	1.92	0.07
	130.17	-0.95					-0.44						4	430.41	1.92	0.07
	129.63			0.44		-0.63							4	430.46	1.98	0.06
p90																

Table S10. Parameters of the best “spring” linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration at Bukowo-Kopań and spring variables, in 1982–2025. The best model had the lowest AICc. The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), and significance level (p), and Variance Inflation Factor (VIF) for the intercept and the explanatory variables selected by the best model, as well as the Adjusted R² (Adj R²) for the entire model.

Percentile	Variable	Estimate	SE	t	p	VIF	AdjR ²
p10	(Intercept)	107.75	0.79	136.99	<0.0001	-	44%
	SexN	2.17	1.03	2.11	0.0383	1.00	
	YearSt	-2.90	0.46	-6.35	<0.0001	1.21	
	MOI_SPR	1.13	0.57	1.98	0.0513	1.14	
	NAO_SPR	-0.98	0.56	-1.74	0.0868	1.01	
	SCI_SPR	-2.08	0.50	-4.18	0.0001	1.36	
p50	(Intercept)	118.46	0.51	234.33	<0.0001	-	37%
	YearSt	-2.45	0.38	-6.37	<0.0001	1.18	
	NAO_SPR	-1.31	0.48	-2.73	0.0079	1.01	
	SCI_SPR	-1.27	0.40	-3.20	0.0021	1.19	
p90	(Intercept)	129.59	0.46	284.42	<0.0001	-	0%

Table S11. Model selection for the “winter and spring” models of relationships between dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo-Kopań and for combined winter and spring temperature variables, in 1982–2025. The candidate explanatory variables are listed in the table heading. Abbreviations of the climate indices are provided in Table 1. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with a delta AICc < 2. Bold digits indicate variables selected for the best “winter and spring” model. Parameters of this best model are presented in more detail in Table S12.

Percentile	(Intercept)	SexN	YearSt	MOI_SPR	NAO_SPR	NAO_WIN	SCI_SPR	IOD_WIN	df	logLik	AICc	delta AICc	weight
p10	107.89	2.17	-2.79				-1.75	-2.55	6	-216.61	446.43	0.00	0.55
	107.81	2.17	-2.72	0.76			-1.61	-2.31	7	-215.60	446.85	0.42	0.45
p50	118.49		-2.34		-1.00	-0.81	-1.31		6	-206.06	425.34	0.00	0.45
	118.46		-2.45		-1.31		-1.27		5	-207.47	425.80	0.46	0.36
	118.46		-2.27			-1.17	-1.39		5	-208.06	426.98	1.64	0.20
p90	129.65							1.30	3	-209.00	424.34	0.00	1.00

Table S12. Parameters of the best “winter and spring” linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration of the Eurasian blackcap at Bukowo-Kopań and winter and spring large scale climate indices selected in the best “winter” and “spring” models, in 1982–2025. The best model had the lowest AICc. The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), significance level (p), and Variance Inflation Factor (VIF) for the intercept and the explanatory variables selected by the best model, as well as the Adjusted R² (Adj R²) for the entire model.

Percentile	Variable	Estimate	SE	t	p	VIF	AdjR ²
q10	(Intercept)	107.89	0.76	142.15	<0.0001	-	48%
	NAO_WIN	-1.75	0.53	-3.31	0.0015	1.03	
	SCI_SPR	-2.55	0.45	-5.68	<0.0001	1.18	
	SexN	2.17	0.99	2.18	0.0323	1.00	
	YearSt	-2.79	0.44	-6.33	<0.0001	1.21	
q50	(Intercept)	118.49	0.50	236.99	<0.0001	-	39%
	NAO_SPR	-1.00	0.51	-1.96	0.0541	1.17	
	NAO_WIN	-0.81	0.50	-1.64	0.1057	1.20	
	SCI_SPR	-1.31	0.39	-3.34	0.0013	1.20	
	YearSt	-2.34	0.39	-6.07	<0.0001	1.22	
q90	(Intercept)	129.65	0.44	294.26	<0.0001	-	7%
	IOD_WIN	1.30	0.51	2.53	0.0135	-	

Table S13. Linear regression parameters for the relationships between the dates of the beginning (p10), median (p50), and end (p90) of spring migration of males and females of the Eurasian blackcaps at Bukowo-Kopań in 1982–2025 and the selected large-scale climate indices (Figure 4). The table presents the slope coefficient (β), intercept, standard error (SE), and significance level (p). The slope coefficient (β) estimates the shift in arrival timing (in days) per one-unit increase in the standardised climate index. A negative β value indicates an advance in the date of the analysed percentile with higher values of the climate index.

Percentile	Climate index	Sex	β	Intercept	SE	p
p10	NAO_WIN	Males	-1.99	109.26	0.98	0.050
		Females	-2.11	111.43	0.95	0.033
	SCI_SPR	Males	-0.98	109.58	0.80	0.230
		Females	-1.60	111.90	0.76	0.042
p50	NAO_WIN	Males	-1.64	119.60	0.79	0.047
		Females	-1.36	119.86	0.80	0.098
	NAO_SPR	Males	-1.32	119.79	0.84	0.125
		Females	-1.15	120.02	0.84	0.180
	SCI_SPR	Males	0.02	119.67	0.67	0.982
		Females	-0.79	120.11	0.65	0.227
p90	IOD_WIN	Males	1.32	130.12	0.65	0.051
		Females	1.28	129.17	0.80	0.119

Table S14. Diagnostic tests for the final best “winter and spring” linear regression models for the dates of the beginning (p10), median (p50), and end (p90) of spring migration. The table presents the multiple coefficient of determination (R^2), adjusted R^2 , (Adj R^2) the ratio of Adj R^2 to R^2 , predictive R^2 (Pred R^2) calculated based on the Predicted Residual Error Sum of Squares (PRESS) to evaluate model overfitting, and the Durbin-Watson statistics (DW) along with its p-value (DW_p) to assess first-order autocorrelation in the residuals.

Percentile	R^2	Adj R^2	Adj R^2/R^2	Pred R^2	PRESS	DW	DW_p
p10	0.506	0.478	0.945	0.433	1525.44	1.069	0.000
p50	0.422	0.389	0.923	0.337	1155.22	0.913	0.000
p90	0.08	0.067	0.844	0.043	1132.46	1.250	0.000

Rozdział 3

Effect of long-term temperature changes at non-breeding grounds on phenological shifts in spring migration timing of male and female blackcaps on the southern Baltic coast

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Effect of long-term temperature changes at non-breeding grounds on phenological shifts in spring migration timing of male and female blackcaps on the southern Baltic coast

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ABSTRACT

Increasing temperatures across Europe and Africa have altered avian migrations, but sex differences in spring phenology shifts and responses to temperature remain understudied. We analysed spring migration timing of male and female Eurasian blackcaps using daily (26 March–16 May) ringing data from Bukowo-Kopań (N Poland) in 1982–2025. Using multiple regression, we estimated multi-year trends and effects of winter and spring temperatures in five non-breeding regions in Europe and Africa on the dates of the first (p10), median (p50), and end (p90) phases of passage for each sex, in two periods (1982–2004, 2005–2025). The first phase advanced by 9 days in both sexes over 1982–2025, maintaining 2.2-day protandry across both periods. We suggest that competition for mates among early males maintains protandry regardless of warming. Despite different migration strategies, both sexes responded uniformly to temperatures. The p10 dates in both sexes were early with warm springs in Eastern Africa, Eastern Mediterranean and Central Europe, suggesting they use the eastern flyway. No protandry occurred for p50, which for both sexes advanced by 10 days during 1982–2004, but stabilised during 2005–2025. The influence of Central European spring temperatures on p50

weakened during 2005–2025, despite continued regional warming, suggesting the population has reached its biological limit of phenological flexibility. The p90 dates were late after warm winters in the Western Mediterranean. This relationship, and no protandry for p50 and p90, likely reflects a high proportion of energy-minimising, inexperienced young birds migrating along the Baltic coast.

Keywords: climate change, temperature increase, sex-differential migration, avian protandry, spring phenology.

1. Introduction

In migratory birds, males often arrive at the breeding grounds before females, a pattern called protandry (Morbey and Ydenberg 2001; Møller 2004; Rubolini et al. 2004; Kokko et al. 2006; Briedis and Bauer 2018). The primary evolutionary driver for this behaviour is the competition for mates, described by the mating opportunity hypothesis, where early arrival allows males to occupy high-quality territories, thereby increasing their chances of attracting females and improving reproductive success (Kokko 1999; Møller 2004; Fontaine and Martin 2006; Tøttrup and Thorup 2008; Briedis and Bauer 2018; Briedis et al. 2019).

These differences in arrival timing reflect different energy management strategies of the sexes, with females acting as energy minimisers during migration, maintaining fat and protein reserves for egg production and avoiding arriving too early at the breeding grounds during harsh springs that could deplete these resources (Francis and Cooke 1986; Smith and Moore 2005; Schmaljohann et al. 2016; Péczely 2017). In contrast, less demanding sperm production allows males to act as time minimisers, prioritising migration speed and risking adverse weather to secure the best territories and mates (Francis and Cooke 1986; Kokko et al. 2006; Schmaljohann et al. 2016; Péczely 2017).

Protandry may also result from spatial segregation of the sexes during the non-breeding season, when males winter closer to the breeding grounds or use different migration routes than females (Cristol et al. 1999; Marra and Holmes 2001; Komar et al. 2005; Catry et al. 2006). However, even when both sexes overwinter in the same region, behavioural differences drive protandry, as males often depart from their wintering areas earlier and maintain that advance throughout the spring passage (Schmaljohann et al. 2016; Briedis et al. 2019; Pedersen et al. 2019). Because of these different migration strategies and mechanisms, changing

environmental conditions can alter the degree of protandry by modifying the costs and benefits of early arrival for each sex (Newton 2008; Tøttrup and Thorup 2008; Messmer et al. 2021). If temperatures along the migration route change over decades, the responses of males and females might become different, leading to long-term shifts in the timing of migration for each sex (Møller 2004; Harnos et al. 2014; Redlisiak et al. 2021; Neate-Clegg and Tingley 2023).

Rising temperatures across the Northern Hemisphere alter the timing of spring migration, leading many bird species to migrate earlier as springs become warmer (Tryjanowski et al. 2002; Jonzén et al. 2006; Gordo 2007; Hurlbert and Liang 2012; Neate-Clegg and Tingley 2023). Temperatures along migration routes and weather conditions at wintering areas influence these arrival dates (Stenseth et al. 2002; Gordo 2007; Haest et al. 2020; Gołębiewski and Remisiewicz 2026). Both short- and long-distance migrants adjust their passage to temperatures and environmental conditions at subsequent stages of their passage (Gordo 2007; Tøttrup et al. 2008; Haest et al. 2020; Remisiewicz and Underhill 2025). Among short-distance migrants, arrival timing is often shaped by temperatures at their wintering grounds and en route (Forchhammer et al. 2002; Cotton 2003; Saino and Ambrosini 2008). For example, the common chiffchaff (*Phylloscopus collybita*) and European wren (*Troglodytes troglodytes*) advanced migration in response to warmer regional temperatures across their migration routes (Croxton et al. 2005; Sokolov 2006; Gołębiewski and Remisiewicz 2026). Similarly, long-distance migrants fine-tune their passage to conditions encountered en route and at their breeding grounds (Tøttrup et al. 2010). For instance, the willow warbler (*Phylloscopus trochilus*), Eurasian blackcap (*Sylvia atricapilla*) and pied flycatcher (*Ficedula hypoleuca*) arrive earlier when springs en route are warmer, and respond to conditions at their wintering grounds (Croxton et al. 2005; Sokolov 2006; Valtonen et al. 2017; Remisiewicz and Underhill 2020).

However, responses to temperature vary among species and locations (Møller 2004; Newton 2008; Tøttrup and Thorup 2008; Podhrázký et al. 2017). Because regional climates change continuously, the responses of bird populations to weather might shift over the decades (Jonzén et al. 2006; Usui et al. 2017; Romano et al. 2023). While most studies assume that phenological responses to climate remain constant over the years, comparing time periods within long-term datasets can reveal hidden varied shifts in migration timing (Croxton et al. 2005; Sparks and Tryjanowski 2005; Bozó and Csörgő 2020). For example, some species, such as the lesser whitethroat (*Sylvia curruca*) and the pied flycatcher (*Ficedula hypoleuca*), advanced their migration only during 1959–1981, while others, like the common whitethroat

(*Sylvia communis*) and the barn swallow (*Hirundo rustica*), shifted more in 1982–2005 (Croxtton et al. 2005). Yet, we still know very little about possible changes in the actual effect of temperature on migration over time (Hurlbert and Liang 2012; Usui et al. 2017; Fraser et al. 2019; Helm et al. 2019), or on any differences between males' and females' adaptations to these shifting conditions (Møller 2004; Tøttrup and Thorup 2008; Neate-Clegg and Tingley 2023).

The Eurasian blackcap (*Sylvia atricapilla*) is a common passerine that shows remarkable flexibility in adjusting its migrations to climate change (Berthold and Terrill 1988; Jonzén et al. 2006; Rolshausen et al. 2010; Pulido and Berthold 2010). This plasticity manifests in their shortening migration distances and the establishment of new wintering areas in the British Isles over recent decades (Berthold and Terrill 1988; Kopiec and Ożarowska 2012; Ożarowska and Meissner 2024). Some studies also suggest that eastern European populations have recently shifted from their traditional wintering grounds in the eastern Mediterranean to more western parts of their wintering range (Wynn et al. 2026). In our previous study, we demonstrated that the degree of protandry at the beginning of spring migration of blackcaps at the Bukowo-Kopań ringing station on the southern Baltic coast remained stable over 44 years, with males migrating about two days earlier than females (Pinszke and Remisiewicz 2026). We also showed that the first phase and the median of their spring migration advanced at similar rates in both sexes, which responded uniformly to variation in large-scale climate patterns (Pinszke and Remisiewicz 2026). Building on these results, we divided the dataset into two periods to test the hypothesis that the shifts in migration timing of male and female blackcaps differed between the two earlier and the two recent decades. We also examined how the timing of spring passage for each sex at the Baltic coast was related to regional temperatures on blackcaps' wintering areas and along their spring migration routes. We expected that the responses of male and female blackcaps to temperatures would differ, and that these relationships might change between the two study periods.

2. Materials and Methods

2.1. Study Species

The Eurasian blackcap (hereafter: blackcap) is a common passerine with a prominent sexual dimorphism and a flexible diet (Cramp and Brooks 1992). This species exhibits considerable variation in migration habits, ranging from completely resident populations breeding in the south and west of Europe to obligatory long-distance, trans-Saharan migrants

from the north and east of the breeding range (Cramp and Brooks 1992; del Hoyo et al. 2006). Additionally, a recent evolutionary shift has led some blackcaps breeding in central and northwestern Europe to winter in the British Isles (Berthold and Terrill 1988; Pulido and Berthold 2004; Kopiec and Ożarowska 2012; Delmore et al. 2020). The eastern European populations have shown some recent shifts from their historical wintering grounds in the Eastern Mediterranean region to more western areas of southern Europe, closer to the breeding grounds (Wynn et al. 2026).

Blackcaps passing through the southern Baltic coast originate primarily from populations breeding in Scandinavia and the Baltic region, including local birds breeding near the study site (Fig. 1) (Delmore et al. 2020; Spina et al. 2022; Maciąg et al. 2017). These populations overwinter across the Iberian Peninsula, northwest Africa, and the eastern Mediterranean region, with some individuals migrating as far as West Africa (Bakken et al. 2006; Fransson et al. 2008; Spina et al. 2022; Maciąg et al. 2017). The annual phenology of these populations includes the spring migration from these wintering quarters to the northern breeding grounds (March – May), the breeding season (May – August), the autumn migration (mid-August – November), and the wintering period (December–February) (Cramp and Brooks 1992).

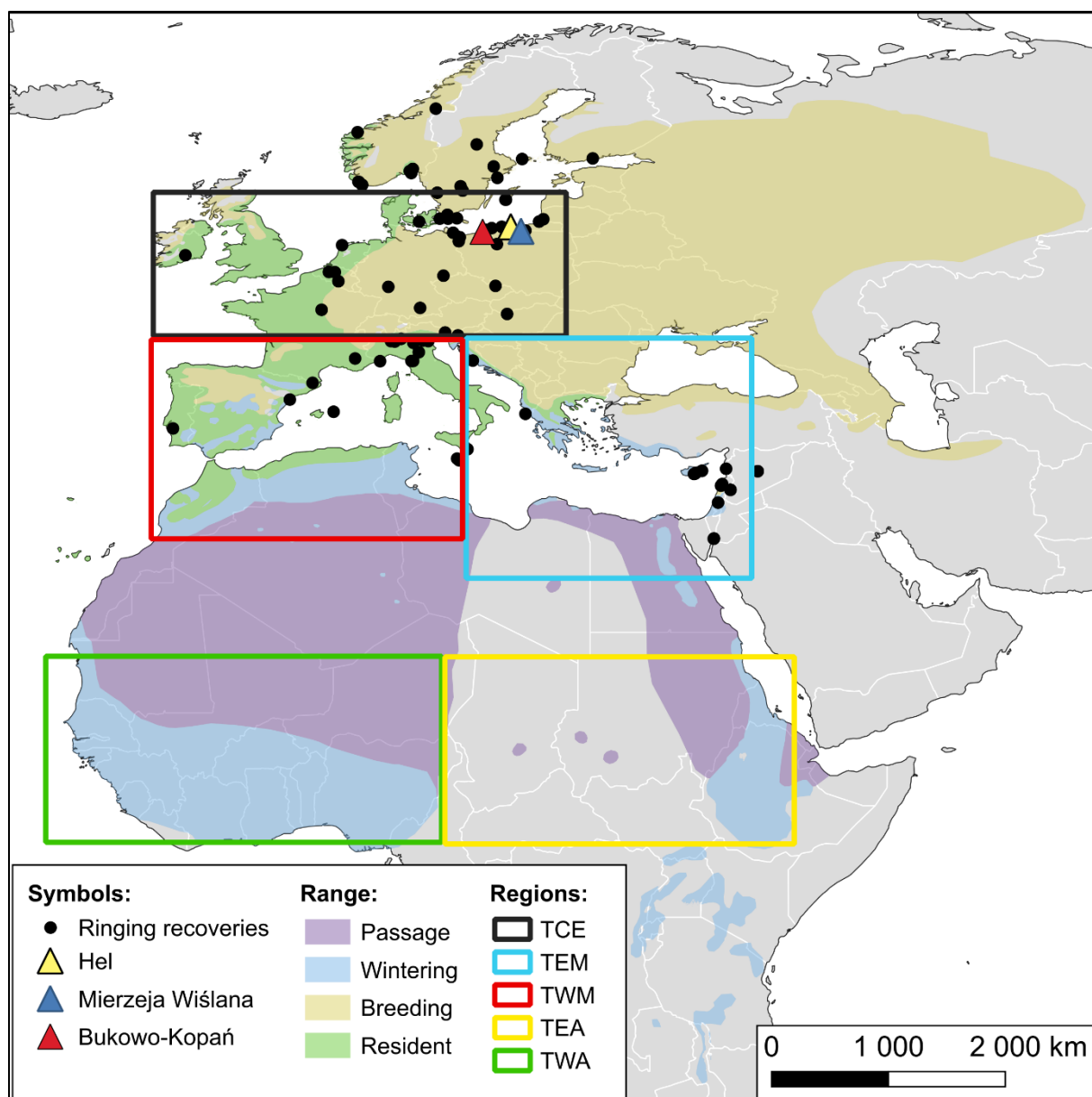


Fig. 1. Spatial context of the study. The map shows the locations of the Bukowo-Kopań ringing station ($54^{\circ}19'38''$ – $54^{\circ}27'54''$ N, $16^{\circ}13'33''$ – $16^{\circ}25'15''$ E), and two other stations of the Operation Baltic: Mierzeja Wiślana ($54^{\circ}21'57''$ N, $19^{\circ}23'30''$ E) and Hel ($54^{\circ}44'29''$ N, $18^{\circ}33'40''$ E), and ringing recoveries of Eurasian blackcaps caught at these stations during 1960–2025, against the species' range (BirdLife International and Handbook of the Birds of the World 2025). Rectangles indicate the geographic regions for which the temperature variables were analysed: Western Africa (TWA), Eastern Africa (TEA), Western Mediterranean (TWM), Eastern Mediterranean (TEM), and Central Europe (TCE).

2.2. Study Site and Methods of Catching Birds

Fieldwork was conducted at the Bukowo-Kopań ringing station (Baltic Sea coast, Poland) (Fig. 1), as part of the Operation Baltic research project. Blackcaps heading in spring to northern and northeastern breeding grounds use this area as a stopover site, and a local population also breeds around the station (Maciąg et al. 2017; Delmore et al. 2020). Following the Operation Baltic protocol (Busse and Meissner 2015), birds were caught in mist nets daily from dawn until dusk. The number of mist nets was constant within each spring, but varied annually (35-61 nets) (Table S1). Each caught bird was ringed, sexed and aged, and released after being measured. More details on the station's habitats and procedures were provided by Remisiewicz and Underhill (2022).

Our analysis used spring migration data collected between 26 March and 16 May in 1982–2025. Fieldwork was suspended during the springs of 2011 and 2020 due to logistical constraints; thus the dataset covered 42 spring seasons. To identify geographical regions used by the studied blackcap populations, we analysed a supplementary dataset of 105 ringing recoveries of blackcaps ringed at Bukowo-Kopań, and two other Operation Baltic stations (Hel and Mierzeja Wiślana) (Fig. 1) and recovered elsewhere, and of individuals ringed in other locations and recovered at these three stations, between 1960 and 2025. We mapped these ringing recoveries (Fig. 1) using QGIS v. 3.44.5 (QGIS Development Team 2025), against the blackcap geographical range (BirdLife International and Handbook of the Birds of the World 2025).

2.3. Temperature Variables

We used the mean regional tri-monthly temperatures to represent climatic conditions across the non-breeding areas and spring migration routes of the studied blackcap populations in Europe and Africa (Fig. 1). Daily mean temperatures from the ERA5 dataset (Hersbach et al. 2020) were downloaded using the KNMI Climate Explorer (Trouet and Van Oldenborgh 2013) for five regions: Western Africa (TWA), Eastern Africa (TEA), Western Mediterranean (TWM), Eastern Mediterranean (TEM), and Central Europe (TCE) (Table 1). We calculated seasonal means from these daily values for two periods: the wintering period (December–February; WIN) and spring migration (March–May; SPR).

Table 1. Temperature variables in areas we distinguished by coordinates within the Eurasian blackcaps' range (Fig. 1), used as explanatory variables in modelling the timing of the species' spring migration at Bukowo-Kopań in 1982–2025. Climate variables for winter (WIN) were averaged for December of the previous year and January – February of the year of the analysed spring passage; for spring (SPR) they were averaged for March – May of the analysed spring migration.

Climate index	Area coordinates	Abbreviation
Tri-monthly mean temperature for Eastern Africa	5°–20°N, 13°E–40°E	TEA_WIN TEA_SPR
Tri-monthly mean temperature for Western Africa	5°–20°N, -20°W–13°E	TWA_WIN TWA_SPR
Tri-monthly mean temperature for the Eastern Mediterranean	25°–45°N, 15°E–38°E	TEM_WIN TEM_SPR
Tri-monthly mean temperature for the Western Mediterranean	30°–45°N, 10°W–15°E	TWM_WIN TWM_SPR
Tri-monthly mean temperature for Central Europe	45°–58°N, 10°W–23°E	TCE_WIN TCE_SPR

We checked if these climate variables were correlated using Pearson's correlation coefficient, applying Benjamini and Hochberg's (1995) correction for multiple comparisons.

2.4. Methods of Data Analysis

2.4.1. Analysis of Multi-Year Trends in Regional Temperatures and Spring Migration Phenology

To check for long-term temperature changes in these regions, we evaluated multi-year trends in temperature variables for the whole study period (1982–2025), and in two sub-periods (1982–2004, 2005–2025) in which we analysed blackcap phenology, using simple linear regression. To test whether the rate of temperature change differed between the two study periods (1982–2004 and 2005–2025), we used linear regression models with the regional temperature as the response variable, and the year number (YearN, where Year 1=1982) as a continuous variable, and study period (PeriodN, where 0=1982–2004 and 1=2005–2025) as the

categorical variable, and their interactions, as explanatory variables. We applied the "all subsets" approach using the dredge function in the "MuMIn" package (Bartoń 2025), ranking models based on the Akaike Information Criterion corrected for small sample sizes (AICc).

For phenological analyses, we used only the first capture of each sexed individual within a season. We combined all age classes (adults, second-calendar-year birds, and full-grown birds) to ensure sufficient annual sample sizes (Table S1), and assuming that in spring all blackcaps were migrating to their breeding grounds. We excluded seasons where fewer than 5 birds of one sex were captured, thus, we finally analysed data from 38 spring seasons during 1982–2025, including 7257 blackcaps (2912 females, 4345 males).

First, to derive the measures of the migration timing for each sex, we calculated the dates at which 10% (p10), 50% (p50), and 90% (p90) of all males or females were ringed in each spring. We used these dates, expressed as the day of the year (1 January = Day 1), to reflect the timing of three phases of migration: the beginning (p10), the median (p50), and the end (p90) of passage (Tøttrup and Thorup 2008; Lehikoinen et al. 2019; Aharon-Rotman et al. 2021). To illustrate the sequence of passage for different sex (males, females) and age (adult and young birds) groups, we calculated their daily capture probabilities. For each day, this probability was expressed as the percentage of birds from four sex/age groups among all aged and sexed blackcaps. To visualise the changing proportions of these four groups during the migration season, we fitted locally estimated scatterplot smoothing (LOESS) curves to the daily percentages using the 'ggplot2' package (Wickham 2016). To estimate multi-year trends and test whether past and current responses of blackcaps to climate change differed, we divided our dataset into two sub-periods: 1982–2004 and 2005–2025. We used linear regression models for the dates of p10, p50, and p90 against the year (using YearN) to derive multi-year trends for the whole study period (1982–2025), and for two sub-periods (1982–2004, 2005–2025). To check for protandry and variations in multi-year trends, the full models included the year number (YearN), sex (SexN), the study period (PeriodN), and their interactions. We applied the "all subsets" approach using the AICc model ranking, as before.

2.4.2. Estimating the Effects of Temperatures on Spring Migration

To identify the effects of regional temperatures on migration timing, we ran multiple linear regression models where the time series of the dates of p10, p50, and p90 in 1982–2025 were response variables, as in earlier studies (Remisiewicz and Underhill 2022; Gołębiowski

and Remisiewicz 2026; Pinszke and Remisiewicz 2023, 2026). The explanatory variables included SexN as a categorical variable and the year and temperature variables (Table 1), which were treated as continuous variables and standardised before being included in the models. We were aware that all temperature variables exhibited multi-year trends and were thus correlated with the year, but we included the year as an explanatory variable in the models to control for its effect while estimating the effects of the temperature variables on the timing of passage (Frost 2019). Because correlations between winter TWA and TEA, and between spring TWA and TEA were stronger than the suggested threshold $r = |0.70|$ of potentially harmful multicollinearity (Dormann et al. 2013), we ran the partial “winter” and “spring” models for two sets of variables: one including TWA (without TEA), and the other including TEA (without TWA). Therefore, in the first stage, we ran 12 partial models: four models (for two seasons, each with two sets of variables) for each of the three phases of migration. For each partial model, we conducted model selection using the “all subsets” approach and model ranking by AICc, using the “MuMIn” package (Bartoń 2025), as before.

Next, for each migration phase, we selected the best partial models, with the lowest AICc. For each phase, from the two best partial “winter models” (for the two initial sets of “winter” variables), we used the one with the higher multiple coefficient of determination (R^2), which explained the larger proportion of variation, to indicate the temperature variables for the joint “winter and spring” models. Analogously, from the two best “spring” models for each migration phase, we used the one with higher R^2 to select the spring variables for the joint models.

We evaluated multicollinearity in the best partial and joint models using the Variance Inflation Factor (VIF). In all best models, VIF was < 4 , indicating no harmful multicollinearity (Dormann et al. 2013). To test for potential overfitting, we cross-validated the final models by inspecting diagnostic plots and comparing Adj R^2 to Predictive R^2 (pred R^2), calculated via Leave-One-Out Cross-Validation (Zuur et al. 2009). Minimal differences between Adj R^2 and pred R^2 confirmed model stability. First-order temporal autocorrelation in the model residuals was assessed using the Durbin-Watson test (Bence 1995) (Table S19). These methods of monitoring multicollinearity and stability of the final models follow other studies (Remisiewicz and Underhill 2020, 2025; Pinszke and Remisiewicz 2026).

The final “winter and spring” models provided estimates of the effect of the selected temperature variable on the dates of p10, p50, and p90 of the spring passage. We visualised

these relationships as scatter plots showing relationships of these variables to the dates of these phases of passage, and fitted linear regression lines, using the “ggplot2” package (Wickham 2016).

To investigate whether the relationships between migration timing and temperatures changed between 1982–2004 and 2005–2025, we ran models comparing the two periods. To maintain model consistency and avoid overparameterization, we included in these models only the phase-specific combinations of temperature variables selected in the final best "winter and spring" models for the relevant phase of passage. These models tested the interaction between the study period and each of the temperature variables (PeriodN: Temperature). These period-comparison models provided estimates of the effect of each temperature variable on the timing of the analysed phase of passage in the two sub-periods. We visualised these period-specific relationships as scatter plots with fitted linear regression lines using the “ggplot2” package (Wickham 2016). All statistical analyses were conducted in R 4.6.1 (R Core Team 2026).

3. Results

3.1. Long-Term Trends and Correlations in Regional Temperatures

Several winter and spring temperature variables were significantly correlated between the studied regions. The strongest positive correlations occurred between spring temperatures in Western Africa and Eastern Africa ($r = 0.82$), and winter temperatures in these two regions ($r = 0.71$) (Table S2). Several other regional winter and spring temperatures were strongly correlated ($0.70 > r > 0.60$). During the entire 44-year study period (1982–2025), the mean tri-monthly temperatures increased significantly across all five studied regions, by 1.3–2.3 °C in winter and by 1.4–2.1 °C in spring (Fig. 2a, b; Table S3).

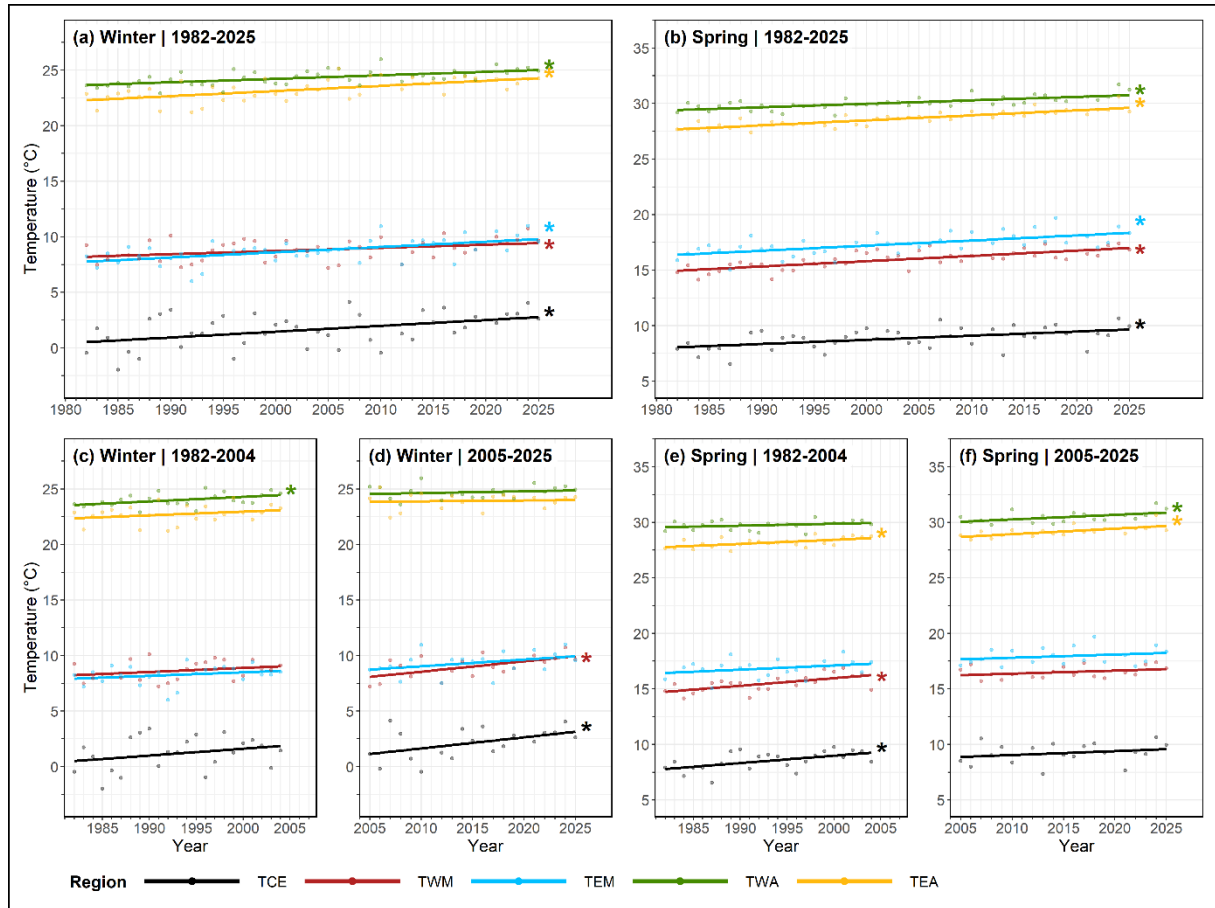


Fig. 2. Multi-year trends in mean tri-monthly temperatures during winter (December–February) and spring (March–May) months across the five studied regions for the entire study period (1982–2025), and for two sub-periods (1982–2004, 2005–2025). The panels show trends of temperatures for: (a) winter during 1982–2025, (b) spring during 1982–2025, (c) winter during 1982–2004, (d) winter during 2005–2025, (e) spring during 1982–2004, (f) spring during 2005–2025. Points represent the annual mean temperatures plotted against the corresponding year; lines show fitted linear regression; asterisks (*) indicate statistically significant trends. Colours of points and lines indicate geographical regions (symbols as in Fig. 1 and Table 1). Detailed parameters of regression are presented in Table S3.

Almost all regional temperatures showed increasing trends in the two sub-periods (Fig. 2b–f), but not all these trends were significant, likely due to the smaller number of years within each sub-period (Table S3). In 1982–2004, warming was significant for winter in Western Africa (TWA_WIN), and for spring in Central Europe (TCE_SPR), the Western Mediterranean (TWM_SPR) and Eastern Africa (TEA_SPR) (Fig. 2c, e). In contrast, during 2005–2025,

significant warming occurred for winter in Central Europe (TCE_WIN) and the Western Mediterranean (TWM_WIN), and for spring in Western Africa (TWA_SPR) and Eastern Africa (TEA_SPR) (Fig. 2d, f).

For most regions, the general warming had a similar rate in the two study periods, as indicated by results of model selection testing for differences between the study periods (Tables S4, S5). The exceptions were winter temperatures in the Western Mediterranean (TWM_WIN) and Eastern Africa (TEA_WIN). For the Western Mediterranean, the rate of warming differed between 1982–2004 and 2005–2025, as indicated by the inclusion of both the study period (PeriodN) and the continuous year effect (YearN) in the best model. For winter temperatures in Eastern Africa (TEA_WIN), the best model included the study period but excluded the continuous effect of the year. This indicates no gradual warming over the 44 years in this region, but a significant step-increase of average winter temperatures between the first and the second period.

3.2. Protandry and Sex-Specific Multi-Year Trends in the Timing of Spring Migration

Over 1982–2025, the first phase (p10) of spring passage shifted earlier by approximately 9 days for both sexes (Fig. 3a; Table S6). Protandry occurred only at this phase, with males migrating on average 2.2 days earlier than females. No interaction between the year and sex in the best model indicated that this degree of protandry occurred across all 44 years of study (Tables S7, S8). The median dates (p50) advanced by 9 days for males and 7 days for females, whereas the end of migration (p90) showed no significant trend. The dates of p50 and p90 did not differ between the sexes.

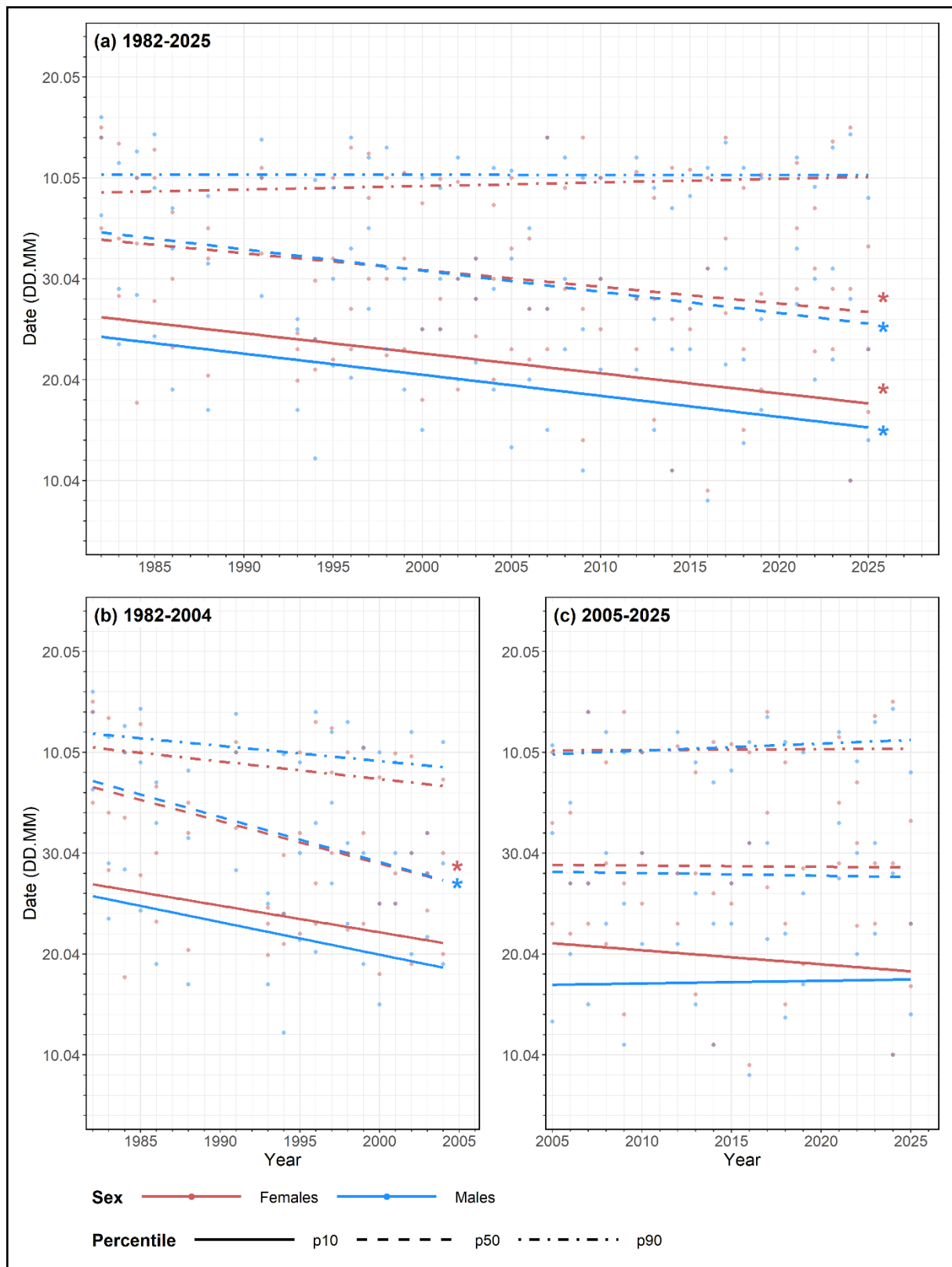


Fig. 3. Multi-year trends in the timing of the first (p10), middle (p50), and last (p90) phases of spring migration for male and female Eurasian blackcaps at Bukowo-Kopań. The panels show trends for (a) the entire study period (1982–2025), and for two sub-periods: (b) 1982–2004 and

(c) 2005–2025. Points represent the annual dates of the respective percentiles plotted against the corresponding year. Lines show fitted linear regression trends; asterisks (*) indicate statistically significant trends. The details of the regressions are presented in Table S6.

The multi-year trends in the dates of passage differed between 1982–2004 and 2005–2025. For the first phase of passage (p10), the dates showed a tendency to advance by approximately 7 days for males and 6 days for females during 1982–2004, although these shifts were only nearly significant (Fig. 3b). During 2005–2025, the beginning of passage showed no multi-year trends for both sexes (Fig. 3c). For the median phase (p50), the trends differed between the two periods, as supported by an interaction between the study period and the year in the best model (Table S8). The p50 dates advanced by 10 days for males and females during 1982–2004, but showed no multi-year trend over 2005–2025 (Fig. 3c). The dates of the end of passage (p90) showed no trends across both periods.

Throughout the migration season, young males dominated the passage. The proportion of adult males was highest only during the first phase of migration (p10) and then declined. In contrast, the proportion of young females increased towards the median phase (p50) and remained high, while adult females formed the smallest group across all phases (Fig. S1)

3.3. Effects of Temperature Variables on Spring Migration Timing

Partial “winter” best models with either TWA or TEA explained from 3% to 35% of the variation in the timing of the subsequent phases of spring migration. For the first phase of passage (p10), both partial “winter” models indicated early passage after warm winters in Central Europe (TCE_WIN). The best model for the set of variables with TWA had higher R^2 than the one with TEA. Thus, we used the temperature variables from that first model for the joint “winter and spring” model. For the median date of migration (p50), both “winter” models indicated an early median passage (p50) with warm winters in Central Europe (TCE_WIN) and with cold winters in the Western Mediterranean (TWM_WIN). For the last phase of passage (p90), both “winter” models indicated an early end of passage with cold winters in the Western Mediterranean (TWM_WIN).

Partial “spring” best models with either TWA or TEA explained from 0% to 43% of the variation in the timing of the three phases of passage (Tables S13-S16). For the first (p10) and

median (p50) phases, both “spring” models indicated early passage with high spring temperatures in Central Europe (TCE_SPR) and the Eastern Mediterranean (TEM_SPR). Because the models with TWA had a higher R^2 than those with TEA for both phases, we used the temperature variables from the models with TWA for the joint “winter and spring” models. Neither of the “spring” models for the last phase of passage (p90) selected any temperature or year variables.

The best joint “winter and spring” models explained 43%, 42% and 4.5% of the variation in the timing of the first (p10), median (p50) and last (p90) phases of passage, respectively (Table S17, S18). For both sexes, p10 was early with warm springs in Central Europe (TCE_SPR), the Eastern Mediterranean (TEM_SPR), and Eastern Africa (TEA_SPR) (Fig. 4, Table S19). The median phase (p50) for both sexes was early with warm springs in Central Europe (TCE_SPR) and the Eastern Mediterranean (TEM_SPR), and warm winters in the Western Mediterranean (TWM_WIN). The end of passage (p90), for both sexes, was late after warm winters in the Western Mediterranean (TWM_WIN).

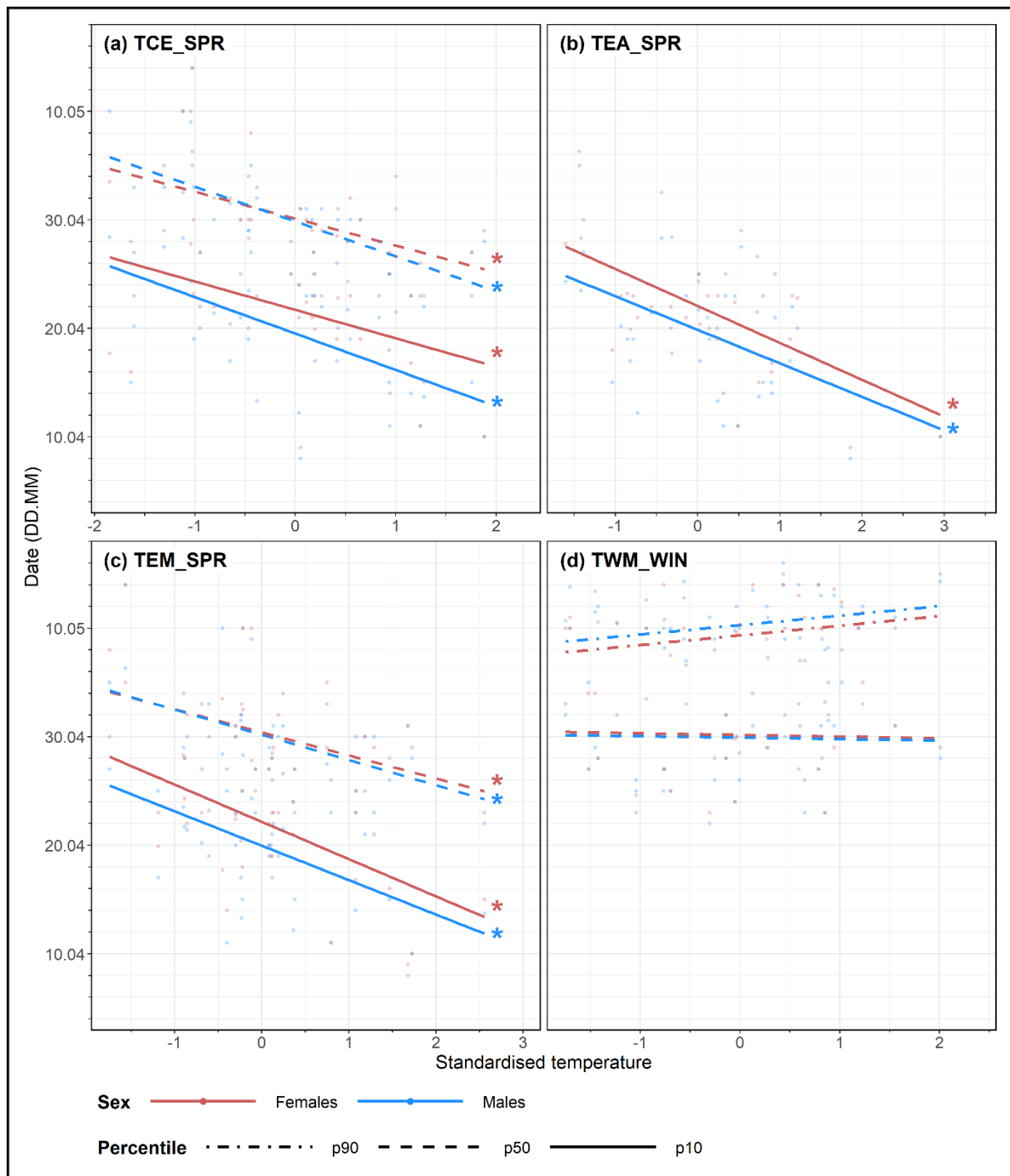


Fig. 4. Relationships between the timing of the percentiles (p10, p50, p90) of male and female Eurasian blackcaps' spring migration at Bukowo-Kopań in 1982–2025 and the regional temperature variables selected in the best “winter and spring” models (Table S14). Points represent the dates of the respective percentiles of passage plotted against the standardised temperature values in a given year. Linear regression lines show the modelled trends. The panels show the effects of: (a) spring temperatures in Central Europe (TCE_SPR) on p10 and p50; (b) spring temperatures in Eastern Africa (TEA_SPR) on p10; (c) spring temperatures in

the Eastern Mediterranean (TEM_SPR) on p10 and p50; and (d) winter temperatures in the Western Mediterranean (TWM_WIN) on p50 and p90. Asterisks (*) indicate statistically significant relationships.

Diagnostic tests confirmed the stability of the final “winter and spring” models (Table S20, Fig. S2). High ratios of Adj R^2 to R^2 and small discrepancies between the Adj R^2 and pred R^2 indicated that the models for p10 and p50 were not overfitted and had good predictive values. Visual inspection of diagnostic plots confirmed that the assumptions of the regression models were met, with no highly influential outliers. The Durbin-Watson test indicated positive autocorrelation in the residuals. Such autocorrelation is an expected and inherent feature of multi-decadal ecological time series, as successive years naturally share similar climatic patterns; nevertheless, the high stability of our models confirms the reliability of the identified climatic relationships.

3.4. Differences Between the Two Periods in Relationships to Temperatures

During 1982–2004, the median of passage (p50) was early with warm spring temperatures in Central Europe, but in 2005–2025, this relationship became weaker (Fig. 5a), as indicated by the interaction between the study period and the effect of Central European spring temperatures (TCE_SPR) (Table S21, Table S22). This was the only significant interaction between temperatures and the study period.

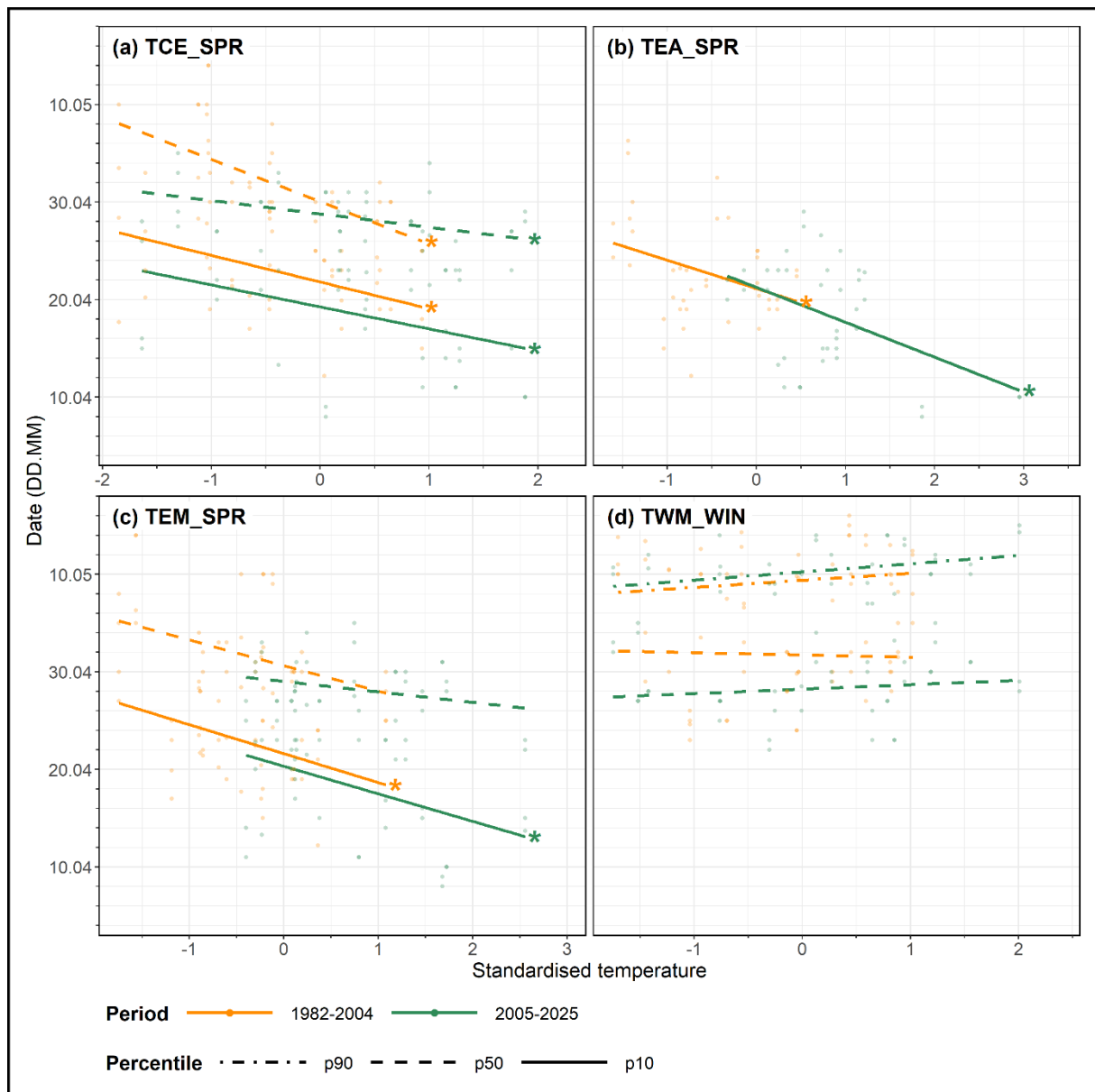


Fig. 5. Relationships between the timing of the selected percentiles (p10, p50, p90) of Eurasian blackcaps' spring migration at Bukowo-Kopań and the regional temperature variables, compared between the two study periods (1982–2004 and 2005–2025). Points represent the dates of the respective percentiles of passage plotted against the standardised temperature values in a given year. Linear regression lines show the modelled trends for each period. The panels show the period-specific effects of: (a) spring temperatures in Central Europe (TCE_SPR), (b) spring temperatures in Eastern Africa (TEA_SPR), (c) spring temperatures in the Eastern Mediterranean (TEM_SPR), and (d) winter temperatures in the Western Mediterranean (TWM_WIN). Asterisks (*) indicate statistically significant relationships within a given period.

In contrast, best models showed no interactions with the period for the effects of spring temperatures in Central Europe (TCE_SPR) and Eastern Africa (TEA_SPR) on p10 (Fig. 5a), spring temperatures in the Eastern Mediterranean (TEM_SPR) on p10 and p50, and winter temperatures in the Western Mediterranean (TWM_WIN) on p50 and p90. This indicates that the effects of these temperature variables on the dates of the respective phases of passage remained similar between 1982–2004 and 2005–2025.

4. Discussion

Our study demonstrated that both male and female blackcaps advanced their spring passage through the southern Baltic coast over 1982–2025 at similar rates. However, while the first cohorts of migrants kept shifting their passage earlier, retaining the two-day protandry at the beginning of passage over these 44 years, the migration timing for the remaining phases of migration stabilised during 2005–2025. Contrary to our expectations considering sex differences in migration strategy, the annual variation in the timing of passage of both sexes was similarly related to regional temperatures. The early and median phases of passage were early during warm springs in Central Europe and Eastern Africa, but the last phase was delayed after warm winters in the Western Mediterranean, in both sexes. We discuss these findings in the context of biological limits and temperature increase in the recent decades across blackcap wintering grounds and migration routes.

4.1. Protandry and the period-specific multi-year trends in spring migration timing

In our study, protandry was stable at the beginning of the spring passage (p10), with males arriving on average 2.2 days earlier than females during the entire 1982–2025 period. This overall advancement suggests that early spring passage with favourable temperature conditions provides fundamental advantages, similar for both sexes, such as a longer breeding season and the potential to raise multiple broods, as we discussed in our previous study (Pinszke and Remisiewicz 2026). This two-day difference remained stable in the two time periods and did not change whether the first phase of passage advanced during 1982–2004 or stabilised during 2005–2025. This suggests that the mating opportunity drives protandry regardless of climatic fluctuations, and both sexes likely use the same environmental cues, including encountered temperatures, to adjust their migration timing to current conditions, which allows them to shift their timing similarly and maintain the protandry.

In contrast, we found no protandry in the median (p50) and the end (p90) phases of passage in either period, suggesting that the pressure for early arrival of males fades as the season progresses. There was no protandry in the median of passage, even though its timing advanced by 10 days in both sexes during 1982–2004. This suggests that the time-minimising strategy might be used only by the earliest migrants, which are mostly adults and young males. While the median passage still includes adult males, the competition for the best territories is likely already lower. The late phase, however, consists mainly of young females and young males, which face less pressure to arrive early because young females do not establish territories and young males stand lower chances of securing prime breeding spots than adult males. Our findings regarding the constant degree of protandry align with studies from Helgoland and Christiansø (Rainio et al. 2007; Tøttrup and Thorup 2008). These studies covered 1976–1997, corresponding to our first study period, and also reported no changes in the degree of protandry in blackcaps. However, the lack of protandry in our median dates contrasts with data from Helgoland and Christiansø, where the median of passage was earlier in males (Rainio et al. 2007). This discrepancy might result from differences in the composition of populations passing through these stations, and some difference in the analysed years (Sparks and Tryjanowski 2005).

When examining the two periods, the first phase of migration (p10) showed an advancing tendency during 1982–2004, which, although not significant, corresponded to the pattern observed during 1976–1997 at Christiansø for both sexes (Tøttrup and Thorup 2008). This trend is in line with other studies that showed clear advancements from a corresponding timeframe. For example, the first capture dates of blackcaps advanced between 1959 and 2002 at the Curonian Spit of the Baltic Sea (Sokolov 2006), and the first arrival dates shifted earlier in the UK during 1982–2005 (Croxtton et al. 2005). Because those studies combined both sexes, the sample size might have been large enough to confirm a clear shift, while our data, separated by sex, showed only a tendency for advance. The recent lack of clear trends in the first phase of passage (p10) aligns with findings from a stopover site in Eilat, Israel, where male and female blackcaps showed no shifts in timing of the 30th percentile of passage between 2000 and 2017 (Aharon-Rotman et al. 2021).

The median of passage (p50) advanced by 10 days during the first period (1982–2004) in both sexes, matching the tendency observed at Christiansø (Tøttrup and Thorup 2008). Such a large shift, even though this phase consists mainly of less-competitive young birds (Fig. S1),

shows flexibility among all migrants, driven by a general response to changing weather and food availability along migration routes. From a broader historical perspective, the mean arrival dates of blackcaps in Central Europe are now 15 days earlier than a century ago (Bozó and Csörgő 2020), confirming their long-term adjustment to warmer springs. However, dividing our dataset into two periods revealed the limits of this phenological plasticity. During 2005–2025, the median (p50) showed no trends, indicating that the mean migration timing has stabilized. This recent stabilization aligns with findings from Eilat, along the Eastern flyway, where the median timing of passage remained unchanged between 2000 and 2017 (Aharon-Rotman et al. 2021), even though the overall warming trend continued. This result updates our previous assumption that blackcaps continuously shifted their timing over the last four decades (Pinszke and Remisiewicz 2026). Instead, once the core of migrants shifted their passage by 10 days in 1982–2004, the advance ceased, likely to prevent an ecological mismatch in arrivals and the food peak on the breeding grounds, regardless of the continuing warming trend.

Finally, the timing of the end of the passage (p90) remained similar across both study periods, which aligns with the stable dates of the 95th percentile of passage at Christiansø during 1976–1997 (Tøttrup and Thorup 2008), and of the 70th percentile of passage in Eilat during 2000–2017 (Aharon-Rotman et al. 2021). The late phase of passage (p90) at Bukowo-Kopań consisted mainly of young females and young males (Fig. S1), which face lower selective pressure for early arrival compared to adult males competing for prime territories (Dierschke et al. 2005; Neate-Clegg and Tingley 2023). Milder winters might also increase survival of weaker individuals, which then depart from wintering grounds later, migrate slower, and arrive at our stopover site later than fitter individuals, which might maintain the consistent end of the passage, despite its earlier beginning (Redlisiak et al. 2021).

4.2. Regional temperature effects on the early phase of spring migration

The first phase of migration (p10) of male and female blackcaps responded uniformly to spring temperature changes in different regions of non-breeding grounds, rather than one sex showing greater sensitivity to spring warming, as found, for example, in the song thrush (Redlisiak et al. 2021). We suggest that in the blackcap, both sexes share the same degree of phenological flexibility in adaptations to shifting weather patterns, because they equally benefit from an early spring arrival in terms of breeding success (Bearhop et al. 2005).

In our partial “winter” models, the timing of the first phase of passage was also earlier with warmer winters in Central Europe. This matches the establishment of new wintering areas in the British Isles by the blackcap (Berthold and Terrill 1988; Pulido and Berthold 2004; Kopiec and Ożarowska 2012). As an increasing number of blackcaps successfully overwinter closer to their breeding grounds, the timing of migrants becomes responsive to winter temperatures in the Mediterranean and Central Europe. Although this effect of winter temperatures was ultimately masked by that of spring temperatures in our final models, it indicated that the shift towards shorter migration influences the timing of the beginning of passage at stopover sites along the spring routes.

Although a recent study by Wynn et al. (2026) suggested that blackcaps breeding in eastern Europe have reduced their use of the historic eastern flyway, the timing of early blackcap passage (p10) at our station remained related to spring temperatures in Eastern Africa both in 1982–2004 and 2005–2025. Because these first cohorts of migrants still respond to environmental conditions in Eastern Africa, they likely continue to winter there. This continued use of the eastern flyway is supported by stable isotope analyses confirming that migrants arrive in Eilat directly from East African wintering areas (Aharon-Rotman et al. 2021). Therefore, while eastern breeders may have abandoned these grounds (Wynn et al. 2026), the northern-breeding long-distance populations of blackcaps passing the Baltic coast (Maciag et al. 2017; Spina et al. 2022) likely have not. In Eastern Africa, high spring temperatures accelerate vegetation drying, shortening the period of optimal food availability needed to accumulate fat before crossing the Sahara (Loske 1990; Thingstad et al. 2015; Aloni et al. 2019). To escape these deteriorating conditions, both sexes might be forced to initiate migration early, overriding other strategic differences (Maggini and Bairlein 2012; Aloni et al. 2019; Maggini et al. 2020). This uniform response to regional temperatures strongly argues against spatial sex segregation. If males wintered significantly closer to the breeding grounds than females (Cristol et al. 1999; Marra and Holmes 2001; Catry et al. 2006), we would expect sex-specific sensitivities to temperatures in different regions of non-breeding grounds. Instead, their identical responses suggest that early-migrating males and females share wintering ranges. A similar lack of spatial sex segregation was demonstrated using geolocators in another long-distance migrant between Western Africa and Europe, the northern wheatear (*Oenanthe oenanthe*) (Schmaljohann et al. 2016). Collectively, these findings support that protandry in many migrants is driven by earlier departure from shared wintering grounds rather than distinct wintering latitudes (Briedis et al. 2019; Pedersen et al. 2020).

Following departure from wintering grounds, the progress of early migrants is shaped by temperatures closer to their breeding grounds, as indicated by the consistent advancement of early passage at the Baltic coast during warm springs in the Eastern Mediterranean and Central Europe across both 1982–2004 and 2005–2025. The influence of Central European temperatures corresponds to the relationship of the first arrival dates of blackcap in Dorset, UK, to winter and spring temperatures in Central England (Croxtton et al. 2005). However, blackcaps arriving in the UK were also early with warmer spring temperatures in the Western Mediterranean, reflecting their use of the western flyway (Croxtton et al. 2005). In contrast, the earliest spring migrant blackcaps at our station showed no response to Western Mediterranean temperatures. While previous studies linked blackcaps' first arrivals at the Curonian Spit to spring temperatures in the Western Mediterranean (Sokolov 2006), those analyses did not account for conditions along the eastern flyway. Our geographically wider models across both flyways revealed that Eastern African and Eastern Mediterranean conditions were dominant in shaping early passage. This dominant eastern influence, coupled with the absence of western temperature effects, suggests that while our station captures mixed populations, the very first arrivals overwinter in the east and use the eastern flyway (Remisiewicz and Underhill 2022, 2025).

Migrants exhibit flexibility during their passage through Europe, adjusting their speed and advancing their arrival in northern Europe in response to environmental conditions en route (Tøttrup and Thorup 2008; Tøttrup et al. 2010). Warm spring promotes early development of vegetation and increases insect abundance, allowing both male and female birds to refuel efficiently and maintain a rapid pace of passage (Marra et al. 2005; Aloni et al. 2019; Amaral et al. 2025). The combination of early departure from Eastern African wintering areas with warm winters, and a faster passage through subsequent regions of Europe during warm springs, combined with increasing temperature trends in all these regions, likely explains the advancement of the first phase of blackcap spring migration at the Baltic coast.

4.3. Regional temperatures and ecological constraints as factors shaping the median and late passage

The median of blackcaps' passage at our station was strongly influenced by spring temperatures in Central Europe, where migration routes of blackcaps arriving in spring from all directions cross before reaching the southern Baltic coast. High spring temperatures in Central Europe advanced the median of blackcap migration, as warm weather promotes vegetation

growth and insect emergence along migration routes. This regional effect aligns with findings from the Curonian Spit, where the medians of blackcap passage were consistently early during warm springs in the Baltic region (Sokolov 2006). Although the migrating population initially advanced its median passage in response to warming Central European springs, the recent weakening of this relationship (2005–2025) despite continued regional warming suggests the birds have reached a biological threshold of advancing the spring passage. We suggest that blackcaps cannot advance their spring passage without facing severe ecological risks, such as arriving on the breeding grounds before sufficient food is available. This type of ecological mismatch, where birds breed too late to exploit the optimal food supply, has been shown in other migrants (Burgess et al. 2018). For example, in the Netherlands, pied flycatchers suffered severe population declines in areas where they could not advance their breeding sufficiently to align with earlier caterpillar peaks (Both et al. 2006). Although a flexible diet might initially buffer the effects of this mismatch for blackcaps, the limit to their phenological response suggests they could eventually face similar risks.

The timing of the last phase of blackcaps' migration remained stable across 1982–2025 and was related to different environmental conditions than the earlier phases. Specifically, both the median and late phases of passage were delayed following warm winters in the Western Mediterranean, contrasting with previous studies from the Curonian Spit (Sokolov 2006) and the UK (Croxtton et al. 2005) where warm conditions advanced blackcap passage. We suggest this contrasting response highlights a severe phenological mismatch on the stopover grounds, as warm winters in the Western Mediterranean region frequently cause vegetation to develop too early (Solakis-Tena et al. 2025), shifting peak insect abundance before late migrants arrive to refuel (Marra et al. 2005; Mayor et al. 2017; Maggini et al. 2020; Harvey et al. 2023). Because these late cohorts are dominated by young, inexperienced birds, they struggle to forage efficiently in such depleted environments (Wunderle 1991; Morel et al. 2024), forcing them to extend stopovers to accumulate sufficient fat (Yong et al. 1998). This struggle to refuel might also explain why late passage shows almost no relationship to other regional temperatures. Limited by their physical condition rather than adjusting to environmental cues, the migration timing of these birds is dictated by individual foraging success.

5. Conclusions

Across the 44-year study period, the early (p10) and median (p50) phases of spring passage advanced by 7 to 9 days for both sexes, a shift driven by rapid changes during 1982–

2004, followed by a stabilisation of timing during 2005–2025, whereas the end of migration (p90) remained unchanged. This recent stabilisation suggests that migrants have reached a threshold in their phenological flexibility, preventing a severe mismatch between arrival dates and the peak availability of food resources on the breeding grounds. Despite these temporal shifts, a 2.2-day protandry occurred only at the beginning of passage and remained stable over 44 years, suggesting that selective pressures preserve timing differences between sexes and their parallel responses to regional warming. While early migrants dynamically respond to favourable spring temperatures to arrive sooner, late migrants are delayed by harsh winter conditions in the Western Mediterranean, which explains no long-term trends in p90. Although current climate warming seemingly benefits blackcaps, driving their rapid population growth since the 1980s (PECBMS 2025), further temperature increases may exceed the species' limits of phenological changes and force shifts in their wintering and breeding ranges.

DECLARATIONS

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Effect of long-term temperature changes at non-breeding grounds on phenological shifts in spring migration timing of male and female blackcaps on the southern Baltic coast

Supplementary Materials: Figures S1-S2 and Tables S1-S23

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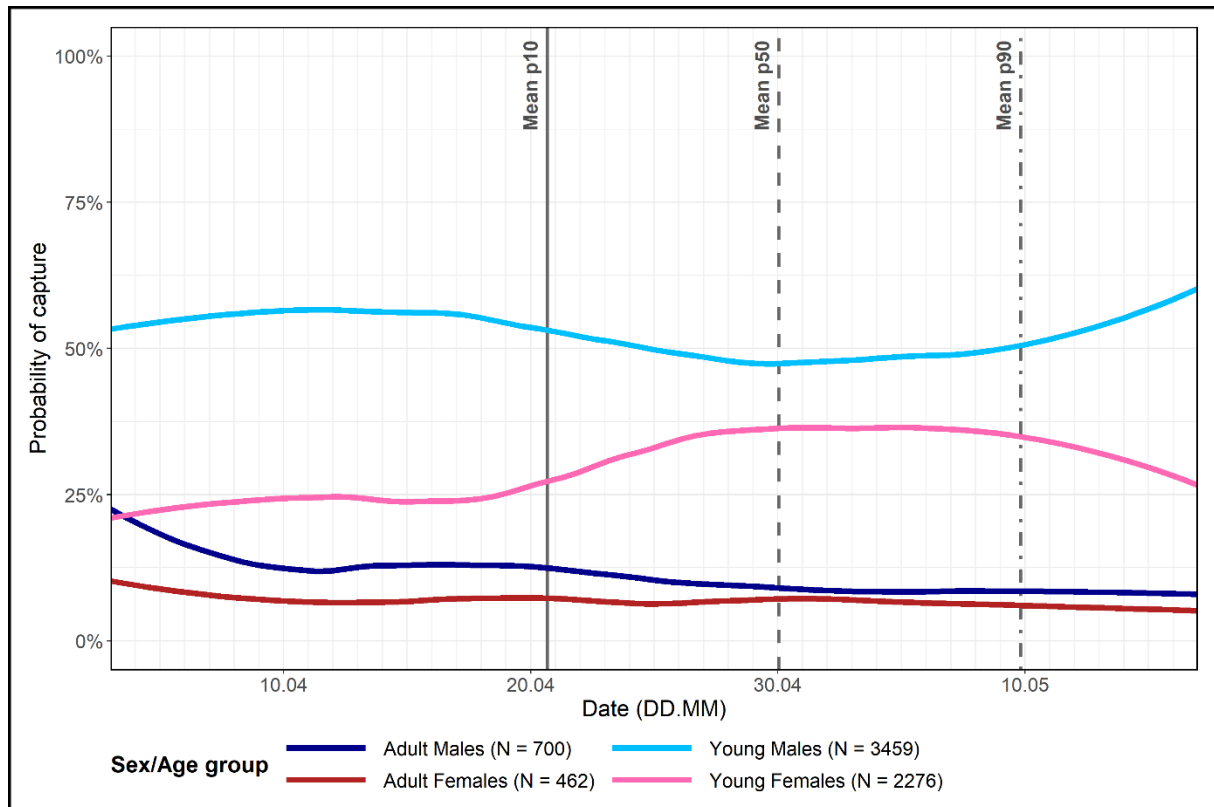


Figure S1. Daily capture probability of adult and young (second-calendar-year birds) male and female Eurasian blackcaps during spring migration at Bukowo-Kopań. Coloured smoothed (LOESS) curves show proportions of each sex/age group changing over the season. Vertical lines indicate the mean dates of the first (p10, solid line), median (p50, dashed line), and last (p90, dot-dash line) phases of passage calculated for all these age/sex groups combined.

(a)

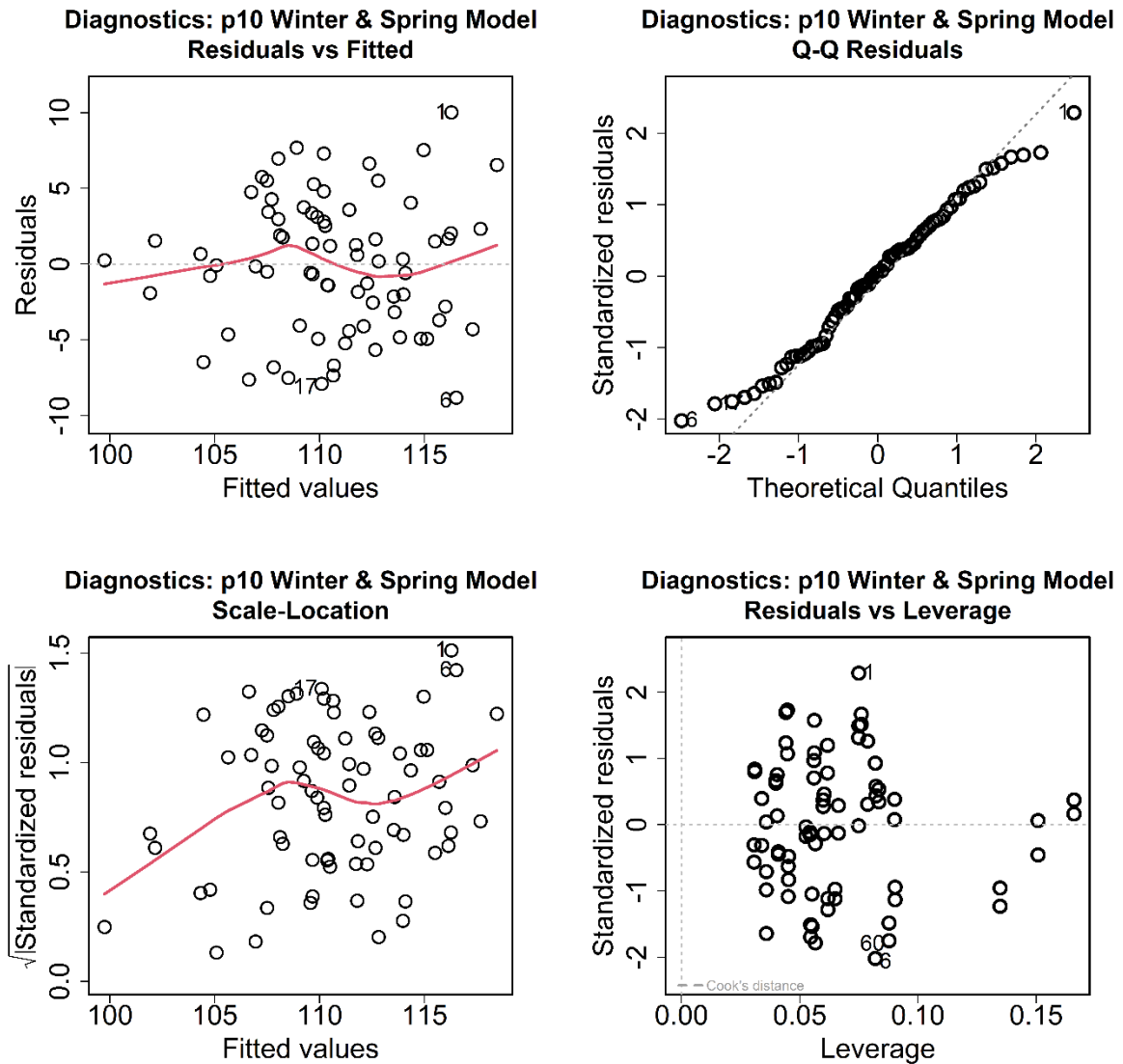


Figure S2. Diagnostic plots for the final best “winter and spring” linear regression models for the dates of the first (p10), median (p50), and last (p90) phases of spring migration. The plots present residuals versus fitted values, normal Q-Q plots, scale location plots, and residuals versus leverage to assess regression assumptions, including linearity, normality of residuals, and identification of highly influential data points (Cook's distance). (a) Diagnostic plots for the best model for p10; (b) Diagnostic plots for the best model for p50; (c) Diagnostic plots for the best model for p90.

(b)

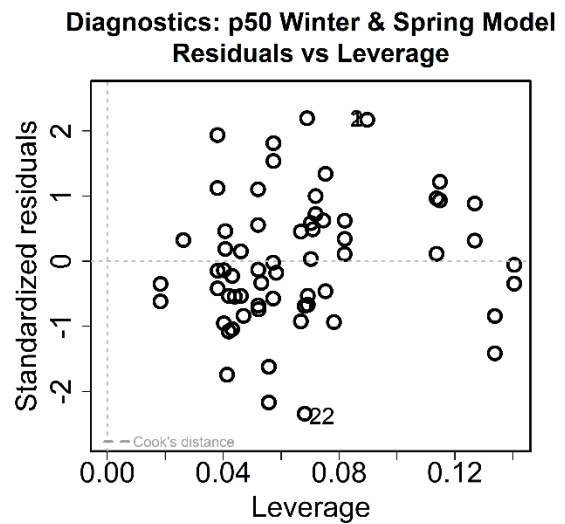
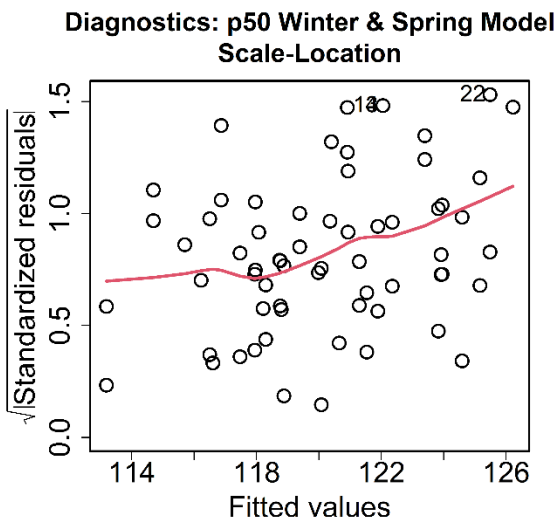
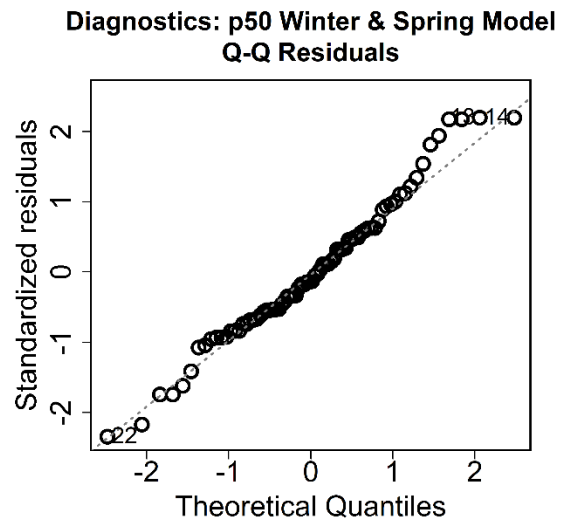
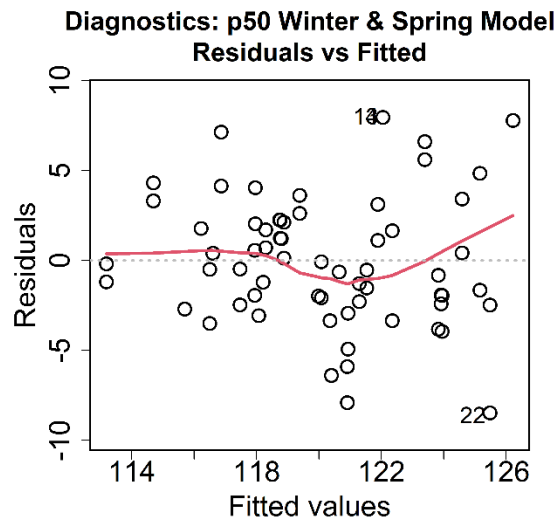


Figure S2. Continued

(c)

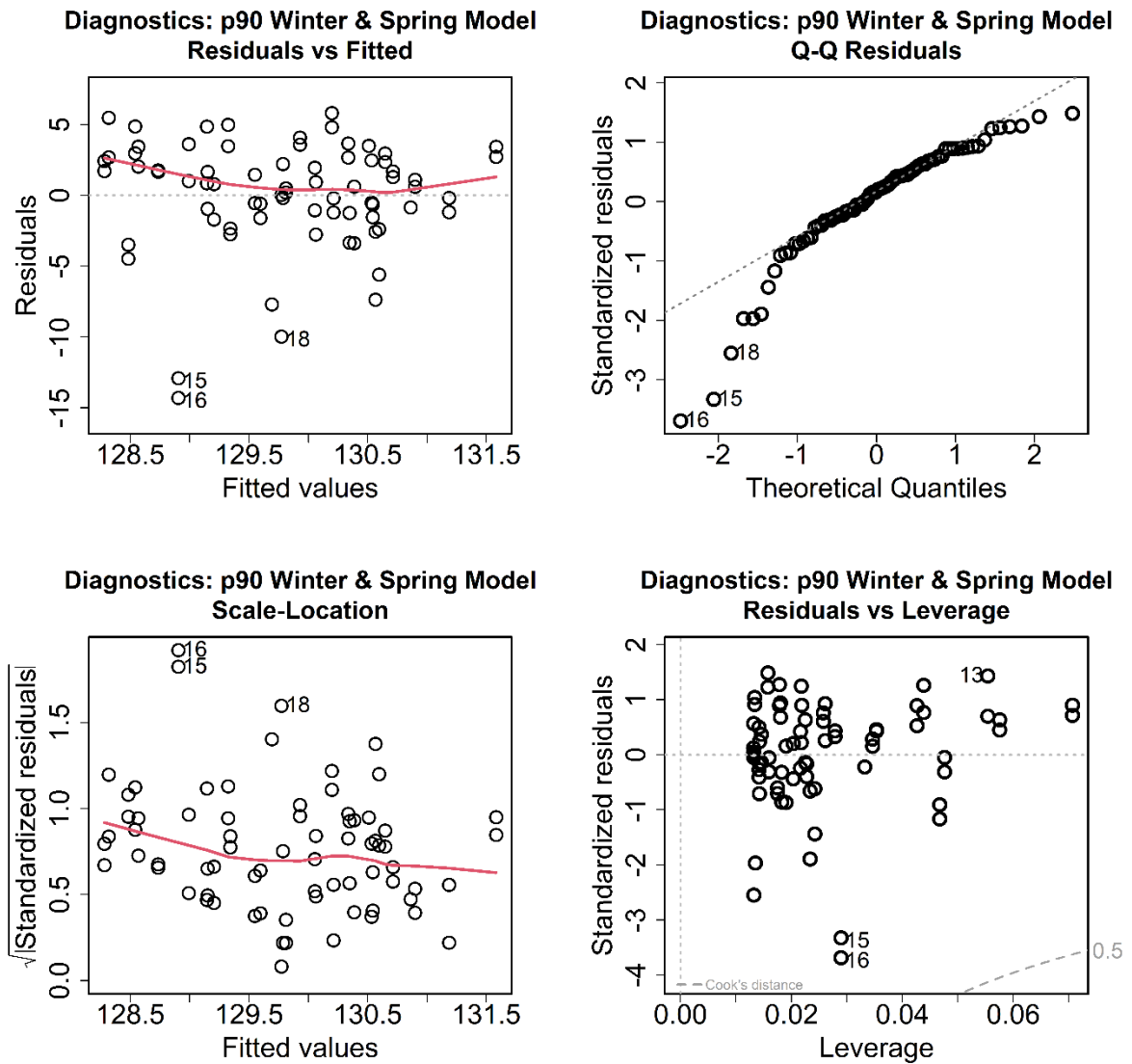


Figure S2. Continued

Table S1. Numbers of captured males, females, and all Eurasian blackcaps (*Sylvia atricapilla*) caught, and of the nets used during each spring migration season (26 March–16 May) at Bukowo-Kopań in subsequent years of the period 1982–2025. Grey fields – seasons which were excluded from analyses, because the station did not operate or fewer than 5 birds of one sex were caught. Total for analyses (bold font) indicates the numbers of individuals considered in the models.

Year	Females	Males	Total	N nets
1982	44	54	98	57
1983	34	46	80	57
1984	8	13	21	57
1985	5	8	13	42
1986	13	11	24	51
1987	3	5	8	50
1988	15	20	35	45
1989	3	8	11	45
1990	4	4	8	45
1991	6	22	28	45
1992	3	12	15	45
1993	8	11	19	37
1994	23	35	58	47
1995	17	18	35	47
1996	32	32	64	47
1997	47	62	109	47
1998	48	71	119	47
1999	56	77	133	47
2000	38	81	119	47
2001	72	110	182	47
2002	43	91	134	57
2003	54	88	142	51
2004	68	94	162	46
2005	124	154	278	50
2006	133	162	295	50
2007	89	119	208	50
2008	59	91	150	54
2009	124	143	267	50
2010	149	143	292	46
2011	0	0	0	0
2012	105	175	280	35
2013	162	273	435	44
2014	77	140	217	41
2015	73	119	192	48
2016	151	230	381	51
2017	77	126	203	52
2018	123	258	381	52
2019	128	225	353	53
2020	0	0	0	0
2021	156	196	352	46
2022	119	180	299	57
2023	145	165	310	47
2024	148	298	446	48
2025	139	204	343	61
Grand total	2925	4374	7299	
Total for analyses	2912	4345	7257	

Table S2. Pearson’s correlation coefficients between the winter and spring temperature variables in 1982–2025. Bold values indicate statistically significant correlations, after Benjamini-Hochberg correction for multiple comparisons with an accepted 5% level of false positives. Abbreviations of the temperature variables as in Table 1.

Variables	TCE	SPR	TWM	WIN	TWM	SPR	TEM	WIN	TEM	SPR	TWA	WIN	TWA	SPR	TEA	WIN	TEA	SPR
TCE_WIN		0.58		0.47		0.40		0.18		0.45		-0.08		0.36		-0.15		0.52
TCE_SPR				0.24		0.50		0.12		0.38		0.10		0.35		0.09		0.43
TWM_WIN						0.33		0.55		0.32		0.34		0.47		0.08		0.52
TWM_SPR								0.45		0.45		0.46		0.64		0.48		0.56
TEM_WIN										0.55		0.59		0.62		0.65		0.63
TEM_SPR												0.25		0.52		0.43		0.61
TWA_WIN														0.62		0.71		0.59
TWA_SPR																0.50		0.82
TEA_WIN																		0.51

Table S3. Linear regression parameters for the long-term trends in the mean tri-monthly temperatures during winter and spring in the five studied regions across the full period (1982–2025) and two sub-periods (1982–2004 and 2005–2025) (Figure 2). The table presents the intercept (α), slope coefficient (β), standard error (SE), t-value (t), significance level (p), R^2 and Adjusted R^2 . 'Change in period' is the estimated total shift in temperature ($^{\circ}\text{C}$) during the analysed period, calculated by multiplying the slope coefficient β by the number of years. A positive β value indicates an increase in temperature over time. Abbreviations of the temperature variables are provided in Table 1.

Period	Temperature variable	α	β	SE	t	p	R^2	Adj R^2	No of years	Change in period
1982-2025	TCE_WIN	-103.15	0.05	0.02	3.17	0.0030	0.20	0.18	44	2.3
	TWM_WIN	-48.17	0.03	0.01	2.68	0.0107	0.15	0.13		1.3
	TEM_WIN	-86.26	0.05	0.01	4.32	0.0001	0.32	0.30		2.1
	TWA_WIN	-39.01	0.03	0.01	4.66	<0.0001	0.35	0.34		1.4
	TEA_WIN	-69.45	0.05	0.01	4.87	<0.0001	0.37	0.36		2.0
	TCE_SPR	-65.78	0.04	0.01	3.75	0.0006	0.26	0.24		1.6
	TWM_SPR	-79.31	0.05	0.01	6.93	<0.0001	0.55	0.53		2.1
	TEM_SPR	-74.70	0.05	0.01	5.07	<0.0001	0.39	0.38		2.0
	TWA_SPR	-32.52	0.03	0.01	6.16	<0.0001	0.49	0.47		1.4
	TEA_SPR	-61.52	0.05	0.00	9.90	<0.0001	0.71	0.70		2.0
1982-2004	TCE_WIN	-121.29	0.06	0.05	1.33	0.1994	0.08	0.03	23	1.4
	TWM_WIN	-63.64	0.04	0.03	1.37	0.1847	0.08	0.04		0.8
	TEM_WIN	-54.82	0.03	0.03	1.19	0.2489	0.06	0.02		0.7
	TWA_WIN	-56.67	0.04	0.02	2.39	0.0262	0.21	0.18		0.9
	TEA_WIN	-43.62	0.03	0.03	1.30	0.2067	0.08	0.03		0.8
	TCE_SPR	-124.63	0.07	0.02	2.93	0.0080	0.29	0.26		1.5
	TWM_SPR	-121.16	0.07	0.02	3.67	0.0014	0.39	0.36		1.6
	TEM_SPR	-58.42	0.04	0.02	1.59	0.1268	0.11	0.07		0.9
	TWA_SPR	-4.97	0.02	0.01	1.41	0.1745	0.09	0.04		0.4
	TEA_SPR	-45.04	0.04	0.01	3.21	0.0042	0.33	0.30		0.8
2005-2025	TCE_WIN	-199.49	0.10	0.05	2.19	0.0430	0.22	0.17	21	2.1
	TWM_WIN	-179.60	0.09	0.03	3.03	0.0075	0.35	0.31		2.0
	TEM_WIN	-112.71	0.06	0.04	1.63	0.1215	0.14	0.08		1.3
	TWA_WIN	-7.57	0.02	0.02	0.72	0.4791	0.03	-0.03		0.3
	TEA_WIN	8.72	0.01	0.03	0.28	0.7826	0.01	-0.05		0.2
	TCE_SPR	-61.93	0.04	0.03	1.03	0.3180	0.06	0.00		0.7
	TWM_SPR	-39.02	0.03	0.02	1.43	0.1696	0.11	0.06		0.6
	TEM_SPR	-40.21	0.03	0.03	1.02	0.3207	0.06	0.00		0.6
	TWA_SPR	-52.70	0.04	0.02	2.49	0.0234	0.27	0.22		0.9
	TEA_SPR	-70.89	0.05	0.01	3.35	0.0038	0.40	0.36		1.0

Table S4. Model selection for the linear regression models for the regional temperature variables, used as response variables to test for changes in temperature trends between the two study periods. The explanatory variables in the full models included year number (YearN), study period (PeriodN), and their interaction. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), log-likelihood (logLik), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Parameters of the best models are presented in more detail in Table S5.

Temperature variable	(Intercept)	PeriodN	YearN	PeriodN:YearN	df	AICc	delta	weight
TCE_WIN	0.47		0.05		3	149.48	0.00	0.69
	0.25	-0.75	0.08		4	151.07	1.58	0.31
TWM_WIN	7.91	-0.94	0.06		4	111.35	0.00	0.41
	8.20	-2.36	0.04	0.06	5	111.80	0.45	0.33
	8.18		0.03		3	112.32	0.96	0.26
TEM_WIN	7.71		0.05		3	115.23	0.00	1.00
TWA_WIN	23.63		0.03		3	74.64	0.00	1.00
TEA_WIN	22.72	1.20			3	102.32	0.00	0.43
	22.25		0.05		3	103.09	0.77	0.29
	22.45	0.70	0.02		4	103.20	0.88	0.28
TCE_SPR	8.02		0.04		3	106.77	0.00	0.67
	7.88	-0.48	0.05		4	108.22	1.45	0.33
TWM_SPR	14.91		0.05		3	75.71	0.00	1.00
TEM_SPR	16.34		0.05		3	99.09	0.00	0.71
	16.44	0.35	0.03		4	100.91	1.82	0.29
TWA_SPR	29.38		0.03		3	50.21	0.00	1.00
TEA_SPR	27.63		0.05		3	41.09	0.00	1.00

Table S5. Parameters of the best linear regression models for the regional temperature variables used as response variables, selected based on the lowest AICc (Table S4). The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), significance level (p), and Variance Inflation Factor (VIF) for the intercept and explanatory variables selected in the best models, as well as the R² and Adjusted R² (Adj R²) for the entire model.

Temperature variable	Explanatory variable	Estimate	SE	t	p	VIF	R ²	Adj R ²
TCE_WIN	(Intercept)	0.47	0.42	1.12	0.2676		20.00%	18.00%
	YearN	0.05	0.02	3.17	0.0030			
TWM_WIN	(Intercept)	7.91	0.30	26.25	<0.0001		21.80%	17.80%
	PeriodN	-0.94	0.52	-1.82	0.0769	3.88		
	YearN	0.06	0.02	2.96	0.0052	3.88		
TEM_WIN	(Intercept)	7.71	0.28	27.69	<0.0001		31.80%	30.10%
	YearN	0.05	0.01	4.32	0.0001			
TWA_WIN	(Intercept)	23.63	0.17	137.57	<0.0001		35.20%	33.60%
	YearN	0.03	0.01	4.66	<0.0001			
TEA_WIN	(Intercept)	22.72	0.16	140.68	<0.0001		38.30%	36.80%
	PeriodN	1.20	0.24	4.99	<0.0001			
TCE_SPR	(Intercept)	8.02	0.25	31.86	<0.0001		26.00%	24.10%
	YearN	0.04	0.01	3.75	0.0006			
TWM_SPR	(Intercept)	14.91	0.17	85.69	<0.0001		54.50%	53.40%
	YearN	0.05	0.01	6.93	<0.0001			
TEM_SPR	(Intercept)	16.34	0.23	71.10	<0.0001		39.10%	37.60%
	YearN	0.05	0.01	5.07	<0.0001			
TWA_SPR	(Intercept)	29.38	0.13	228.84	<0.0001		48.70%	47.40%
	YearN	0.03	0.01	6.16	<0.0001			
TEA_SPR	(Intercept)	27.63	0.12	239.89	<0.0001		71.00%	70.30%
	YearN	0.05	0.00	9.90	<0.0001			

Table S6. Linear regression parameters for the long-term trends in the dates for the first (p10), median (p50), and last (p90) phases of spring migration of the Eurasian blackcaps at Bukowo-Kopań in the entire study period (1982–2025) and two sub-periods (1982–2004 and 2005–2025) (Figure 3). The table presents the intercept (a), slope coefficient (β), standard error (SE), t-value (t), significance level (p), R^2 and Adjusted R^2 . 'Change in period' is the estimated total shift in arrival timing (in days) during the analysed period, calculated by multiplying the slope coefficient by the number of years. A negative β value indicates an advance in the date of the analysed percentile over time.

Percentile	Period	Sex	a	β	SE	t	p	R^2	Adj R^2	No of years	Change in period
p10	1982-2025	Males	114.46	-0.21	0.07	-3.01	0.0050	20.10%	17.80%	44	-9.19
		Females	116.39	-0.20	0.07	-2.96	0.0050	19.50%	17.30%		-8.74
	1982-2004	Males	116.07	-0.32	0.17	-1.90	0.0750	17.50%	12.70%	23	-7.41
		Females	117.18	-0.26	0.15	-1.76	0.0970	15.40%	10.40%		-6.08
	2005-2025	Males	106.31	0.03	0.21	0.13	0.8990	0.10%	-5.80%	21	0.56
		Females	114.42	-0.14	0.22	-0.63	0.5340	2.30%	-3.40%		-2.92
p50	1982-2025	Males	124.82	-0.21	0.05	-3.90	<0.0001	29.70%	27.80%	44	-9.25
		Females	124.04	-0.17	0.06	-2.96	0.0050	19.50%	17.30%		-7.32
	1982-2004	Males	127.61	-0.45	0.15	-2.98	0.0080	34.30%	30.50%	23	-10.27
		Females	126.97	-0.42	0.16	-2.63	0.0180	28.90%	24.70%		-9.69
	2005-2025	Males	118.78	-0.03	0.12	-0.21	0.8330	0.30%	-5.60%	21	-0.55
		Females	119.14	-0.01	0.12	-0.11	0.9180	0.10%	-5.80%		-0.27
p90	1982-2025	Males	130.31	0.00	0.05	-0.01	0.9900	0.00%	-2.80%	44	-0.03
		Females	128.53	0.04	0.06	0.63	0.5340	1.10%	-1.70%		1.56
	1982-2004	Males	132.00	-0.15	0.15	-1.00	0.3340	5.50%	-0.10%	23	-3.46
		Females	130.65	-0.17	0.17	-1.04	0.3110	6.00%	0.50%		-3.99
	2005-2025	Males	128.15	0.07	0.09	0.76	0.4580	3.30%	-2.40%	21	1.47
		Females	129.96	0.01	0.12	0.07	0.9430	0.00%	-5.80%		0.19

Table S7. Model selection for the linear regression models for the dates of the first (p10), median (p50), and last (p90) phases of spring passage, used as response variables to test for changes in protandry. The explanatory variables in the full models included sex (SexN), year number (YearN), study period (PeriodN), and their interactions. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), log-likelihood (logLik), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Parameters of the best models are presented in more detail in Table S8.

Percentile	(Intercept)	PeriodN	SexN	YearN	PeriodN:SexN	PeriodN:YearN	SexN:YearN	df	AICc	delta	weight
p10	114.34		2.17	-0.20				4	472.75	0.00	0.63
	115.43			-0.20				3	473.84	1.09	0.37
p50	127.29	-8.33		-0.43		0.41		5	432.74	0.00	1.00
	129.83							2	429.60	0.00	0.25
	129.26	1.13						3	430.23	0.63	0.18
	130.30		-0.95					3	430.68	1.08	0.15
p90	130.21	2.70		-0.07				4	431.27	1.67	0.11
	131.33	-2.27		-0.16		0.20		5	431.35	1.75	0.11
	129.74	1.13	-0.95					4	431.35	1.75	0.11
	129.42			0.02				3	431.54	1.94	0.10

Table S8. Parameters of the best linear regression models for the dates of the first (p10), median (p50), and last (p90) phases of spring migration used as response variables, selected based on the lowest AICc (Table S7). The table presents the coefficient estimate (Estimate), its standard error (SE), t-value (t), significance level (p), and Variance Inflation Factor (VIF) for the intercept and explanatory variables selected in the best models, as well as the R² and Adjusted R² for the entire model.

Percentile	Explanatory variable	Estimate	SE	t	p	VIF	R ²	Adj R ²
p10	(Intercept)	114.34	1.41	81.34	<0.0001			
	SexN	2.17	1.20	1.81	0.0750	1.00	23%	20%
	YearN	-0.20	0.05	-4.24	0.0001	1.00		
p50	(Intercept)	127.29	1.34	95.07	<0.0001			
	PeriodN	-8.33	3.85	-2.16	0.0337	17.66	34%	31%
	YearN	-0.43	0.09	-4.71	<0.0001	6.32		
	PeriodN:YearN	0.41	0.14	2.98	0.0040	28.45		
p90	(Intercept)	129.83	0.46	282.86	<0.0001		0%	0%

Table S9. Model selection for the “winter” models of relationships including the TWA temperature variable (without TEA) between dates of the first (p10), median (p50), and last (p90) phases of spring migration of the Eurasian blackcap at Bukowo-Kopań and winter large-scale temperature variables, excluding the winter TEA variable, in 1982–2025. The candidate explanatory variables are listed in the table heading. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Bold digits indicate variables selected for the best partial “winter” model. Parameters of this best model are presented in more detail in Table S10. Abbreviations of the temperature variables are provided in Table 1.

Percentile	(Intercept)	SexN	TCE_WIN	TEM_WIN	TWA_WIN	TWM_WIN	YearSt	SexN:TCE_WIN	SexN:TEM_WIN	SexN:TWA_WIN	SexN:TWM_WIN	SexN:YearSt	df	AICc	delta	weight
p10	109.77	2.17	-2.36	-1.56		1.33	-1.18						7	467.95	0.00	0.15
	109.66	2.17	-1.88				-1.69						5	468.00	0.05	0.15
	109.74	2.17	-2.86	-2.10		1.38							6	468.02	0.07	0.15
	109.73	2.17	-1.89	-0.90			-1.23						6	468.75	0.80	0.10
	109.69	2.17	-2.40	-1.45									5	469.01	1.06	0.09
	110.75		-1.88				-1.69						4	469.34	1.40	0.08
	110.85		-2.36	-1.56		1.33	-1.18						6	469.39	1.44	0.07
	109.66	2.17	-2.11			0.66	-1.82						6	469.40	1.45	0.07
	110.82		-2.86	-2.10		1.38							5	469.41	1.46	0.07
	109.79	2.17	-1.96	-1.78	0.73	1.25	-1.64						8	469.74	1.79	0.06
p50	120.13		-1.68			1.44	-2.14						5	431.38	0.00	0.53
	120.13		-1.33		0.59	1.30	-2.59						6	432.94	1.56	0.24
	120.17		-1.76	-0.53		1.67	-1.92						6	433.04	1.67	0.23
p90	129.82					0.88							3	428.30	0.00	0.28
	129.74			0.78									3	429.21	0.91	0.18
	130.29	-0.95				0.88							4	429.39	1.09	0.16
	129.83												2	429.60	1.31	0.15
	129.78			0.41		0.66							4	430.02	1.72	0.12
	129.81		-0.34			1.03							4	430.12	1.82	0.11

Table S10. Parameters of the best “winter” linear regression models including the TWA temperature variable (without TEA) for the dates of the first (p10), median (p50), and last (p90) phases of spring migration and winter regional temperatures in 1982–2025. The best models had the lowest AICc (Table S9). The table presents the coefficient estimate (estimate), standard error (std.error), t-value (statistic), significance level (p), and Variance Inflation Factor (VIF) for the intercept and explanatory variables selected by the best model, as well as the R² and Adjusted R² for the entire model. Abbreviations of the temperature variables are provided in Table 1.

Percentile	Explanatory Variable	Estimate	SE	t	p	VIF	R ²	Adj R ²
p10	(Intercept)	109.77	0.81	136.28	<0.0001			
	SexN	2.17	1.13	1.91	0.0599	1.00		
	TCE_WIN	-2.36	0.75	-3.15	0.0024	1.55	33.80%	29.00%
	TEM_WIN	-1.56	0.81	-1.92	0.0595	1.76		
	TWM_WIN	1.33	0.76	1.74	0.0856	1.67		
	YearSt	-1.18	0.77	-1.53	0.1304	1.75		
p50	(Intercept)	120.13	0.46	263.76	<0.0001			
	TCE_WIN	-1.68	0.59	-2.85	0.0057	1.51	34.90%	32.10%
	TWM_WIN	1.44	0.54	2.66	0.0096	1.31		
	YearSt	-2.14	0.55	-3.86	0.0002	1.41		
p90	(Intercept)	129.82	0.45	287.43	<0.0001			
	TWM_WIN	0.88	0.47	1.86	0.0667		4.50%	3.20%

Table S11. Model selection for the “winter” models of relationships including the TEA temperature variable (without TWA) between dates of the first (p10), median (p50), and last (p90) phases of spring migration of the Eurasian blackcap at Bukowo-Kopań and winter large-scale temperature variables, excluding the winter TWA variable, in 1982–2025. The candidate explanatory variables are listed in the table heading. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Bold digits indicate variables selected for the best partial “winter” model. Parameters of this best model are presented in more detail in Table S12. Abbreviations of the temperature variables are provided in Table 1.

Percentile	(Intercept)	SexN	TCE_WIN	TEA_WIN	TEM_WIN	TWM_WIN	YearSt	SexN:TCE_WIN	SexN:TEA_WIN	SexN:TEM_WIN	SexN:TWM_WIN	SexN:YearSt	df	AICc	delta	weight
p10	109.80	2.17	-2.99	-1.84									5	465.32	0.00	0.68
	110.89		-2.99	-1.84									4	466.79	1.47	0.32
p50	120.13		-1.68			1.44	-2.14						5	431.38	0.00	0.70
	120.17		-1.76		-0.53	1.67	-1.92						6	433.04	1.67	0.30
p90	129.82					0.88							3	428.30	0.00	0.25
	129.74				0.78								3	429.21	0.91	0.16
	130.29	-0.95				0.88							4	429.39	1.09	0.15
	129.83												2	429.60	1.31	0.13
	129.78				0.41	0.66							4	430.02	1.72	0.11
	129.77			0.32		0.89							4	430.10	1.80	0.10
	129.81		-0.34			1.03							4	430.12	1.82	0.10

Table S12. Parameters of the best “winter” linear regression models including the TEA temperature variable (without TWA) for the dates of the first (p10), median (p50), and last (p90) phases of spring migration and winter regional temperatures in 1982–2025. The best models had the lowest AICc (Table S11). The table presents the coefficient estimate (Estimate), standard error (SE), t-value (t), significance level (p), and Variance Inflation Factor (VIF) for the intercept and explanatory variables selected by the best model, as well as the R² and Adjusted R² for the entire model. Abbreviations of the temperature variables are provided in Table 1.

Percentile	Explanatory variable	Estimate	SE	t	p	VIF	R ²	Adj R ²
p10	(Intercept)	109.80	0.81	136.05	<0.0001			
	SexN	2.17	1.13	1.91	0.0598	1.00	31.90%	29.00%
	TCE_WIN	-2.99	0.61	-4.95	<0.0001	1.02		
	TEA_WIN	-1.84	0.62	-2.96	0.0041	1.02		
p50	(Intercept)	120.13	0.46	263.76	<0.0001			
	TCE_WIN	-1.68	0.59	-2.85	0.0057	1.51	34.90%	32.10%
	TWM_WIN	1.44	0.54	2.66	0.0096	1.31		
	YearSt	-2.14	0.55	-3.86	0.0002	1.41		
p90	(Intercept)	129.82	0.45	287.43	<0.0001		4.50%	3.20%
	TWM_WIN	0.88	0.47	1.86	0.0667			

Table S13. Model selection for the “spring” models of relationships including the TWA temperature variable (without TEA) between dates of the first (p10), median (p50), and last (p90) phases of spring migration of the Eurasian blackcap at Bukowo-Kopań and spring large-scale temperature variables, excluding the spring TEA variable, in 1982–2025. The candidate explanatory variables are listed in the table heading. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Bold digits indicate variables selected for the best partial “spring” model. Parameters of this best model are presented in more detail in Table S14. Abbreviations of the temperature variables are provided in Table 1.

Percentile	(Intercept)	SexN	TCE_SPR	TEM_SPR	TWA_SPR	TWM_SPR	YearSt	SexN:TCE_SPR	SexN:TEM_SPR	SexN:TWA_SPR	SexN:TWM_SPR	SexN:YearSt	df	AICc	delta	weight
p10	109.82	2.17	-1.85	-1.85	-1.23								6	453.76	0.00	0.29
	109.81	2.17	-2.22	-1.96	-1.67	1.04							7	453.86	0.10	0.27
	109.84	2.17	-2.13	-2.54									5	454.54	0.77	0.19
	109.80	2.17	-2.08	-2.10	-1.56		0.81						7	455.25	1.49	0.14
	109.81	2.18	-2.22	-1.85	-1.23			0.74					7	455.71	1.95	0.11
p50	120.15		-2.38	-1.37									4	425.45	0.00	0.31
	120.14		-2.07	-1.13		-0.69							5	426.06	0.62	0.22
	120.15		-2.11	-0.99			-0.71						5	426.51	1.06	0.18
	120.08		-2.11				-1.29						4	426.86	1.41	0.15
	120.14		-2.27	-1.09	-0.51								5	426.99	1.55	0.14
p90	129.83												2	429.60	0.00	0.41
	130.30	-0.95											3	430.68	1.08	0.24
	129.78			0.40									3	431.12	1.52	0.19
	129.81						0.22						3	431.54	1.94	0.16

Table S14. Parameters of the best “spring” linear regression models including the TWA temperature variable (without TEA) for the dates of the first (p10), median (p50), and last (p90) phases of spring migration and spring regional temperatures in 1982–2025. The best models had the lowest AICc (Table S13). The table presents the coefficient estimate (Estimate), standard error (SE), t-value (t), significance level (p), and Variance Inflation Factor (VIF) for the intercept and explanatory variables selected by the best model, as well as the R² and Adjusted R² for the entire model. Abbreviations of the temperature variables are provided in Table 1.

Percentile	Explanatory variable	Estimate	SE	t	p	VIF	R ²	Adj R ²
p10	(Intercept)	109.82	0.74	148.24	<0.0001			
	SexN	2.17	1.04	2.08	0.0411	1.00		
	TCE_SPR	-1.85	0.61	-3.03	0.0034	1.23	43.30%	40.10%
	TEM_SPR	-1.85	0.72	-2.56	0.0125	1.62		
	TWA_SPR	-1.23	0.71	-1.73	0.0881	1.71		
p50	(Intercept)	120.15	0.44	270.38	<0.0001			
	TCE_SPR	-2.38	0.50	-4.81	<0.0001	1.14	37.90%	36.20%
	TEM_SPR	-1.37	0.51	-2.67	0.0094	1.14		
p90	(Intercept)	129.83	0.46	282.86	<0.0001		0.00%	0.00%

Table S15. Model selection for the “spring” models of relationships including the TEA temperature variable (without TWA) between dates of the first (p10), median (p50), and last (p90) phases of spring migration of the Eurasian blackcap at Bukowo-Kopań and spring large-scale temperature variables, excluding the spring TWA variable, in 1982–2025. The candidate explanatory variables are listed in the table heading. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Bold digits indicate variables selected for the best partial “spring” model. Parameters of this best model are presented in more detail in Table S16. Abbreviations of the temperature variables are provided in Table 1.

Percentile	(Intercept)	SexN	TCE_SPR	TEA_SPR	TEM_SPR	TWM_SPR	YearSt	SexN:TCE_SPR	SexN:TEA_SPR	SexN:TEM_SPR	SexN:TWM_SPR	SexN:YearSt	df	AICc	delta	weight
p10	109.87	2.17	-1.77	-1.27	-1.76								6	454.17	0.00	0.27
	109.88	2.17	-2.06	-2.24	-1.96		1.47						7	454.31	0.15	0.25
	109.84	2.17	-2.13		-2.54								5	454.54	0.37	0.23
	109.88	2.17	-2.04	-1.45	-1.88	0.69							7	455.45	1.28	0.14
	109.87	2.18	-2.14	-1.27	-1.76			0.74					7	456.12	1.95	0.10
p50	120.12		-2.17	1.58	-1.41		-1.71						6	425.32	0.00	0.25
	120.15		-2.38		-1.37								4	425.45	0.12	0.23
	120.14		-2.07		-1.13	-0.69							5	426.06	0.74	0.17
	120.15		-2.11		-0.99		-0.71						5	426.51	1.19	0.14
	120.08		-2.11				-1.29						4	426.86	1.53	0.12
	120.13		-2.51	0.45	-1.64								5	427.25	1.93	0.09
p90	129.83												2	429.60	0.00	0.34
	130.30	-0.95											3	430.68	1.08	0.20
	129.79			0.45									3	430.88	1.27	0.18
	129.78				0.40								3	431.12	1.52	0.16
	129.81						0.22						3	431.54	1.94	0.13

Table S16. Parameters of the best “spring” linear regression models including the TEA temperature variable (without TWA) for the dates of the first (p10), median (p50), and last (p90) phases) of spring migration and spring regional temperatures in 1982–2025. The best models had the lowest AICc (Table S15). The table presents the coefficient estimate (Estimate), standard error (SE), t-value (t), significance level (p), and Variance Inflation Factor (VIF) for the intercept and explanatory variables selected by the best model, as well as the R² and Adjusted R² for the entire model. Abbreviations of the temperature variables are provided in Table 1.

Percentile	Explanatory variable	Estimate	SE	t	p	VIF	R ²	Adj R ²
p10	(Intercept)	109.87	0.74	147.89	<0.0001			
	SexN	2.17	1.04	2.08	0.0416	1.00		
	TCE_SPR	-1.77	0.63	-2.82	0.0063	1.30	43.00%	39.80%
	TEA_SPR	-1.27	0.79	-1.61	0.1114	2.11		
	TEM_SPR	-1.76	0.78	-2.27	0.0264	1.85		
p50	(Intercept)	120.12	0.44	274.90	<0.0001			
	TCE_SPR	-2.17	0.55	-3.98	0.0002	1.43		
	TEA_SPR	1.58	0.86	1.84	0.0697	3.62	41.70%	38.40%
	TEM_SPR	-1.41	0.65	-2.17	0.0334	1.91		
	YearSt	-1.71	0.84	-2.03	0.0460	3.59		
p90	(Intercept)	129.83	0.46	282.86	<0.0001		0.00%	0.00%

Table S17. Model selection for the “winter and spring” models of relationships between the dates of the first (p10), median (p50), and last (p90) phase and the temperature variables selected in the best partial “winter” model including the TWA variable (Table S10) and the best partial “spring” model including the TEA variable (Table S16) in 1982–2025. The candidate explanatory variables are listed in the table heading. The table presents the coefficient estimates for the intercept and the explanatory variables selected in each model, followed by the model statistics: degrees of freedom (df), Akaike Information Criterion corrected for small sample sizes (AICc), the difference in AICc relative to the best model (delta AICc), and the Akaike weight (weight). The table presents the set of models with delta AICc < 2. Bold digits indicate variables selected for the final best “winter and spring” model. Parameters of this best model are presented in more detail in Table S18. Abbreviations of the temperature variables are provided in Table 1.

Percentile	(Intercept)	SexN	TCE_SPR	TCE_WIN	TEA_SPR	TEM_SPR	TEM_WIN	TWM_WIN	YearSt	df	AICc	delta	weight
p10	109.87	2.17	-1.77		-1.27	-1.76				6	454.17	0.00	0.21
	109.88	2.17	-2.06		-2.24	-1.96			1.47	7	454.31	0.15	0.19
	109.84	2.17	-2.13			-2.54				5	454.54	0.37	0.17
	109.90	2.17	-1.72		-1.67	-1.73		0.71		7	455.25	1.08	0.12
	109.91	2.17	-2.02		-2.70	-1.94		0.75	1.52	8	455.27	1.10	0.12
	109.81	2.17	-1.70	-0.86		-2.33				6	455.37	1.20	0.11
	109.85	2.17	-1.59	-0.49	-1.06	-1.77				7	456.16	1.99	0.08
p50	120.18		-2.08			-1.12		0.99	-1.02	6	424.60	0.00	0.12
	120.17		-2.46			-1.61		0.81		5	424.79	0.19	0.11
	120.11		-1.67	-1.08	1.55	-1.39		1.00	-1.81	8	424.92	0.32	0.11
	120.14		-2.05	-0.85		-1.49		1.08		6	425.22	0.63	0.09
	120.12		-2.17		1.58	-1.41			-1.71	6	425.32	0.72	0.09
	120.16		-1.74	-0.78		-1.04		1.22	-0.96	7	425.39	0.80	0.08
	120.15		-2.13		1.11	-1.39		0.77	-1.65	7	425.42	0.82	0.08
	120.15		-2.38			-1.37				4	425.45	0.85	0.08
	120.09		-2.09					0.90	-1.65	5	425.77	1.17	0.07
	120.07		-1.69	-0.89				1.17	-1.52	6	426.07	1.47	0.06
	120.09		-1.86	-0.77	1.99	-1.42			-1.83	7	426.20	1.60	0.06
	120.15		-2.11			-0.99			-0.71	5	426.51	1.91	0.05
p90	129.82							0.88		3	428.30	0.00	0.48
	130.29	-0.95						0.88		4	429.39	1.09	0.28
	129.83									2	429.60	1.31	0.25

Table S18. Parameters of the best “winter and spring” linear regression models for the dates of the first (p10), median (p50), and last (p90) and the temperature variables selected in the best partial “winter” model including the TWA variable and the best partial “spring” model including the TEA variable in 1982–2025. The best models had the lowest AICc (Table S17). The table presents the coefficient estimate (estimate), standard error (SE), t-value (t), significance level (p), and Variance Inflation Factor (VIF) for the intercept and explanatory variables selected by the best model, as well as the R² and Adjusted R² for the entire model. Abbreviations of the temperature variables are provided in Table 1.

Percentile	Explanatory variable	Estimate	SE	t	p	VIF	R ²	Adj R ²
p10	(Intercept)	109.87	0.74	147.89	<0.0001			
	SexN	2.17	1.04	2.08	0.0416	1.00		
	TCE_SPR	-1.77	0.63	-2.82	0.0063	1.30	43.00%	39.80%
	TEA_SPR	-1.27	0.79	-1.61	0.1114	2.11		
	TEM_SPR	-1.76	0.78	-2.27	0.0264	1.85		
p50	(Intercept)	120.18	0.43	276.39	<0.0001			
	TCE_SPR	-2.08	0.54	-3.83	0.0003	1.43		
	TEM_SPR	-1.12	0.61	-1.84	0.0702	1.69	42.20%	39.00%
	TWM_WIN	0.99	0.49	2.03	0.0466	1.19		
	YearSt	-1.02	0.66	-1.56	0.1239	2.22		
p90	(Intercept)	129.82	0.45	287.43	<0.0001			
	TWM_WIN	0.88	0.47	1.86	0.0667		4.50%	3.20%

Table S19. Simple linear regression parameters for the relationships between the dates of the first (p10), median (p50), and last (p90) phases of spring migration of male and female Eurasian blackcaps and the key temperature variables selected by the “winter and spring” models in 1982–2025 (Figure 4). The table presents the intercept (a), slope coefficient (β), standard error (SE), t-value (t), significance level (p), Adjusted R² (Adj R²).

Percentile	Variable	Sex	a	β	SE	t	p	Adj R ²
p10	TCE_SPR	Males	109.52	-3.35	0.86	-3.89	<0.0001	27.6%
		Females	111.71	-2.62	0.89	-2.94	0.0060	17.2%
	TEM_SPR	Males	109.96	-3.17	0.92	-3.44	0.0010	22.7%
		Females	112.16	-3.43	0.85	-4.05	<0.0001	29.4%
	TEA_SPR	Males	109.87	-3.09	0.87	-3.55	0.0010	23.9%
		Females	112.06	-3.40	0.79	-4.29	<0.0001	32.0%
p50	TCE_SPR	Males	119.85	-3.21	0.66	-4.85	<0.0001	37.9%
		Females	120.11	-2.48	0.72	-3.45	0.0010	22.8%
	TEM_SPR	Males	120.18	-2.32	0.79	-2.95	0.0060	17.2%
		Females	120.41	-2.13	0.78	-2.72	0.0100	14.8%
	TWM_WIN	Males	119.91	-0.13	0.84	-0.16	0.8750	-2.7%
		Females	120.16	-0.16	0.82	-0.19	0.8510	-2.7%
p90	TWM_WIN	Males	130.29	0.87	0.61	1.42	0.1640	2.7%
		Females	129.35	0.89	0.73	1.22	0.2300	1.3%

Table S20. Diagnostic tests for the final best “winter and spring” linear regression models for the dates of the first (p10), median (p50), and last (p90) of spring migration. The table presents the multiple coefficient of determination (R^2), adjusted R^2 , (Adj R^2) the ratio of Adj R^2 to R^2 , predictive R^2 (Pred R^2) calculated based on the Predicted Residual Error Sum of Squares (PRESS) to evaluate model overfitting, and the Durbin-Watson statistics (DW) along with its p-value (DW_p) to assess first-order autocorrelation in the residuals.

Percentile	R^2	Adj R^2	$R^2/\text{Adj } R^2$	Pred R^2	PRESS	DW	DW p	Adj R^2 - Pred R^2
p10	43.00%	39.80%	0.925	0.347	1686.2	1.251	<0.0001	0.0510
p50	42.20%	39.00%	0.923	0.335	1148.2	1.211	<0.0001	0.0550
p90	4.50%	3.20%	0.711	-0.007	1209	1.234	<0.0001	0.0390

Table S21. Model selection for the linear regression models testing the interaction between the key temperature variables and the study period (PeriodN) on the dates of the first (p10), median (p50), and last (p90). The table presents the set of models with delta AICc < 2. Parameters of this best model are presented in more detail in Table S22. Abbreviations of the temperature variables are provided in Table 1.

Percentile	Temperature Variable	(Intercept)	PeriodN	TCE_SPR	TEM_SPR	TEA_SPR	TWM_WIN	PeriodN:TCE_SPR	PeriodN:TEM_SPR	PeriodN:TEA_SPR	PeriodN:TWM_WIN	df	AICc	delta	weight
p10	TCE_SPR	111.92	-2.60	-2.44								4	467.57	0.00	1.00
	TEM_SPR	111.06			-3.30							3	466.16	0.00	0.67
		111.65	-1.29		-2.88							4	467.56	1.40	0.33
	TEA_SPR	110.97				-3.25						3	464.33	0.00	1.00
	TCE_SPR	120.05	-1.26	-4.33				2.97				5	423.80	0.00	1.00
p50		120.29			-2.22							3	444.13	0.00	0.45
	TEM_SPR	121.03	-1.60		-1.70							4	444.65	0.52	0.34
		120.64	-1.63		-2.62				1.55			5	445.62	1.49	0.21
	TWM_WIN	121.76	-3.46									3	448.69	0.00	1.00
		129.82					0.88					3	428.30	0.00	0.41
p90	TWM_WIN	129.83										2	429.60	1.31	0.22
		129.39	0.85				0.80					4	429.64	1.34	0.21
		129.26	1.13									3	430.23	1.94	0.16

Table S22. Parameters of the best linear regression models testing the interaction between the key temperature variables and the study period (PeriodN) on the dates of the first (p10), median (p50), and last (p90). The best models were selected based on the lowest AICc (Table S21). The table presents the coefficient estimate (Estimate), standard error (SE), t-value (t), significance level (p), and Variance Inflation Factor (VIF) for the intercept and explanatory variables, as well as the R² and Adjusted R² for the entire model.

Percentile	Temperature variable	Explanatory variable	Estimate	SE	t	p	VIF	R ²	Adj R ²
p10	TCE_SPR	(Intercept)	111.92	0.86	129.82	<0.0001			
		PeriodN	-2.60	1.26	-2.06	0.0434	1.19	27.70%	25.70%
		TCE_SPR	-2.44	0.67	-3.65	0.0005	1.19		
	TEM_SPR	(Intercept)	111.06	0.58	190.15	<0.0001		26.90%	25.90%
		TEM_SPR	-3.30	0.63	-5.22	<0.0001			
	TEA_SPR	(Intercept)	110.97	0.57	192.99	<0.0001		28.60%	27.70%
		TEA_SPR	-3.25	0.60	-5.45	<0.0001			
	TCE_SPR	(Intercept)	120.05	0.69	174.64	<0.0001			
		PeriodN	-1.26	0.95	-1.33	0.1886	1.20	41.00%	38.60%
		TCE_SPR	-4.33	0.80	-5.42	<0.0001	3.07		
		PeriodN:TCE_SPR	2.97	1.02	2.91	0.0048	2.76		
p50	TEM_SPR	(Intercept)	120.29	0.51	238.08	<0.0001		18.20%	17.10%
		TEM_SPR	-2.22	0.55	-4.06	0.0001			
	TWM_WIN	(Intercept)	121.76	0.73	166.71	<0.0001		13.20%	12.00%
		PeriodN	-3.46	1.03	-3.35	0.0013			
	TWM_WIN	(Intercept)	129.82	0.45	287.43	<0.0001		4.50%	3.20%
		TWM_WIN	0.88	0.47	1.86	0.0667			

Table S23. Simple linear regression parameters for the relationships between the dates of the first (p10), median (p50), and last (p90) of spring migration of male and female Eurasian blackcaps and the key temperature variables, partitioned by the two sub-periods: 1982–2004 and 2005–2025 (Figure 5). The table presents the intercept (α), slope coefficient (β), standard error (SE), t-value (t), significance level (p), R^2 and Adjusted R^2 .

Percentile	Temperature variable	Period	α	β	SE	t	p	R^2	Adj R^2
p10	TCE_SPR	1982-2004	111.81	-2.73	1.03	-2.64	0.0120	16.20%	13.90%
		2005-2025	109.26	-2.25	0.90	-2.52	0.0160	15.00%	12.60%
	TEM_SPR	1982-2004	111.62	-2.97	1.20	-2.47	0.0180	14.50%	12.10%
		2005-2025	110.32	-2.82	1.07	-2.64	0.0120	16.20%	13.90%
	TEA_SPR	1982-2004	111.14	-2.90	1.33	-2.19	0.0350	11.80%	9.30%
		2005-2025	111.26	-3.58	1.16	-3.09	0.0040	20.90%	18.70%
p50	TCE_SPR	1982-2004	120.05	-4.33	0.94	-4.60	<0.0001	37.00%	35.20%
		2005-2025	118.79	-1.37	0.50	-2.76	0.0090	17.40%	15.10%
	TEM_SPR	1982-2004	120.64	-2.62	1.29	-2.03	0.0500	10.20%	7.70%
		2005-2025	119.01	-1.07	0.63	-1.69	0.1000	7.40%	4.80%
	TWM_WIN	1982-2004	121.73	-0.23	1.09	-0.21	0.8330	0.10%	-2.60%
		2005-2025	118.22	0.45	0.50	0.91	0.3680	2.30%	-0.50%
p90	TWM_WIN	1982-2004	129.38	0.73	0.96	0.76	0.4530	1.60%	-1.20%
		2005-2025	130.24	0.84	0.42	1.99	0.0540	9.90%	7.40%

Gdańsk, 28.08.2026r.

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OŚWIADCZENIE

Oświadczam, że jestem główną i wiodącą autorką cyklu publikacji stanowiącego podstawę mojej rozprawy doktorskiej:

1. Pinszke A., Remisiewicz M. (2023). Long-term changes in autumn migration timing of Garden Warblers *Sylvia borin* at the southern Baltic coast in response to spring, summer and autumn temperatures. *The European Zoological Journal*, 90:1, 283-295, DOI: 10.1080/24750263.2023.219229
2. Pinszke A., Remisiewicz M. (2026). The Influence of Winter and Spring Large-Scale Climate Patterns on the Timing of Male and Female Blackcap Spring Passage at the Baltic Coast. *Biology* 15: 1518, DOI: 10.3390/biology15171518
3. Pinszke A., Remisiewicz M. (manuskrypt wysłany do czasopisma *Journal of Biometeorology*). Effect of long-term temperature changes at non-breeding grounds on phenological shifts in spring migration timing of male and female blackcaps on the southern Baltic coast.

Mój udział polegał na:

- współtworzeniu koncepcji badawczych wszystkich trzech publikacji,
- przygotowaniu, weryfikacji i integracji baz danych,
- przeprowadzeniu całości analiz statystycznych,
- opracowaniu wyników i przygotowaniu oprawy graficznej, w tym rycin oraz map,
- napisaniu pierwotnych wersji wszystkich trzech manuskryptów oraz wprowadzaniu merytorycznych poprawek autorskich,
- dostosowywaniu treści oraz tytułów prac do wymogów i profilu tematycznego docelowych czasopism naukowych.

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1. Pinszke A., Remisiewicz M. (2023). Long-term changes in autumn migration timing of Garden Warblers *Sylvia borin* at the southern Baltic coast in response to spring, summer and autumn temperatures. *The European Zoological Journal*, 90:1, 283-295, DOI: 10.1080/24750263.2023.219229
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