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Research Article

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Posted Date: November 13th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11180743/v1

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Additional Declarations: No competing interests reported.

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; Podhrázský 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 (Croxton 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).

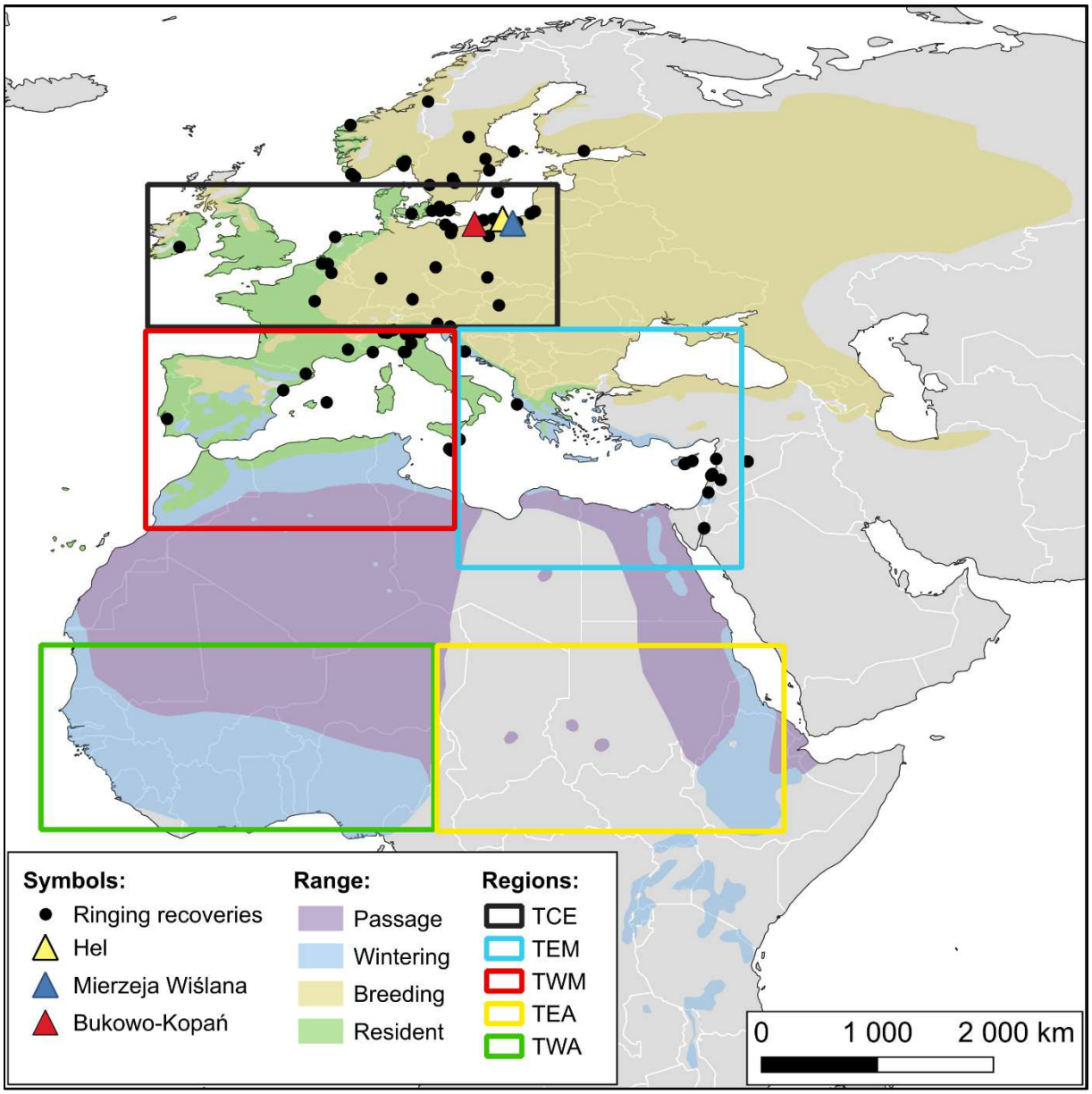


Fig. 1. Spatial context of the study. The map shows the locations of the Bukowo-Kopań ringing station (54°19′38″–54°27′54″ N, 16°13′33″–16°25′15″ E), and two other stations of the Operation Baltic: Mierzeja Wiślana (54°21′57″ N, 19°23′30″ E) and Hel (54°44′29″ N, 18°33′40″ E), and ringing recoveries 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; Gołębiewski 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 (predR^2), calculated via

Leave-One-Out Cross-Validation (Zuur et al. 2009). Minimal differences between Adj R^2 and predR^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).

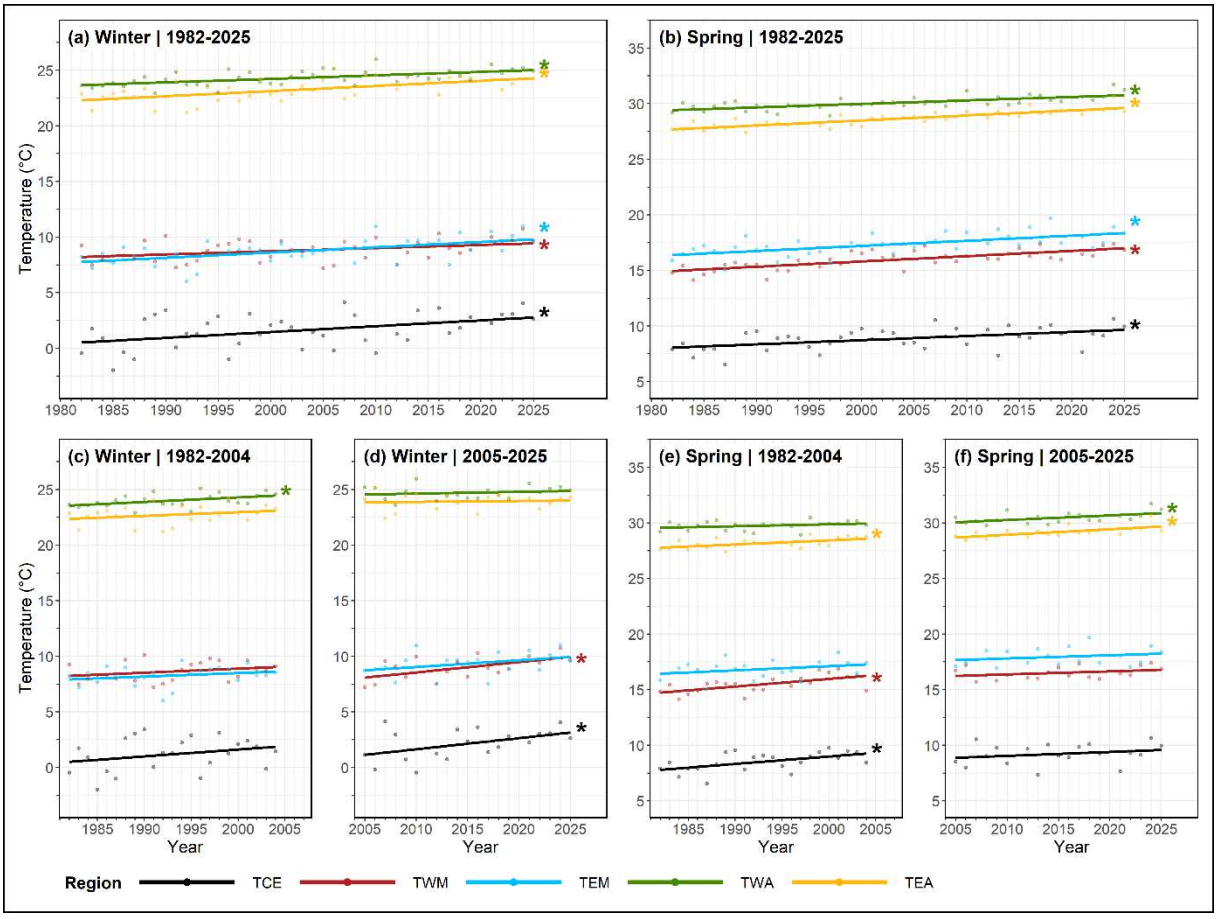


Fig. 2. Multi-year trends in mean tri-monthly temperatures during winter (December–February) and spring (March–May) months across the five studied regions for the entire study period (1982–2025), and for two sub-periods (1982–2004, 2005–2025). The panels show trends of temperatures for: (a) winter during 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.

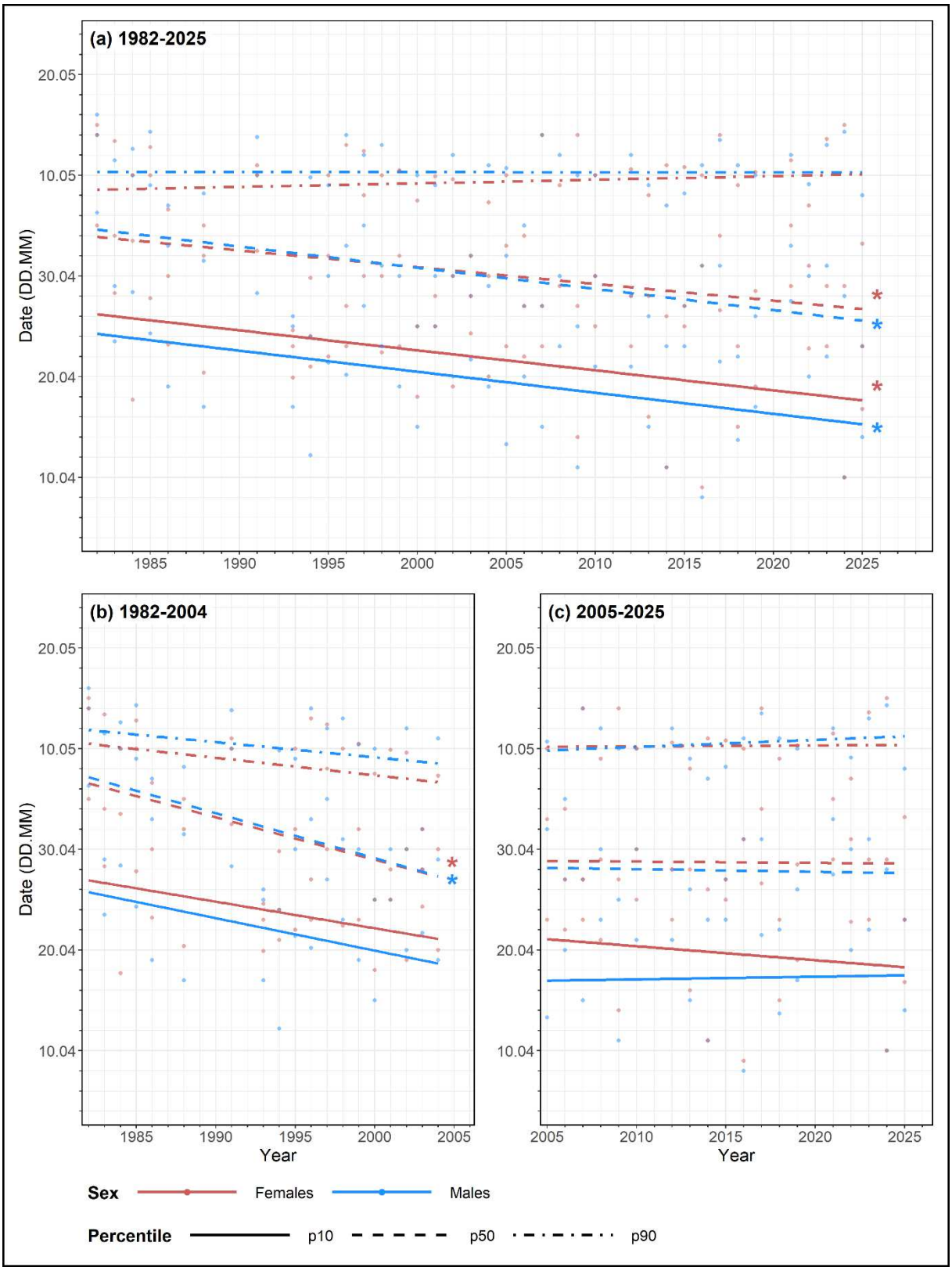


Fig. 3. Multi-year trends in the timing of the first (p10), middle (p50), and last (p90) phases of spring migration for male and female Eurasian blackcaps at Bukowo-Kopań. The panels show trends for (a) the entire study period (1982–2025), and for two sub-periods: (b) 1982–2004

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)

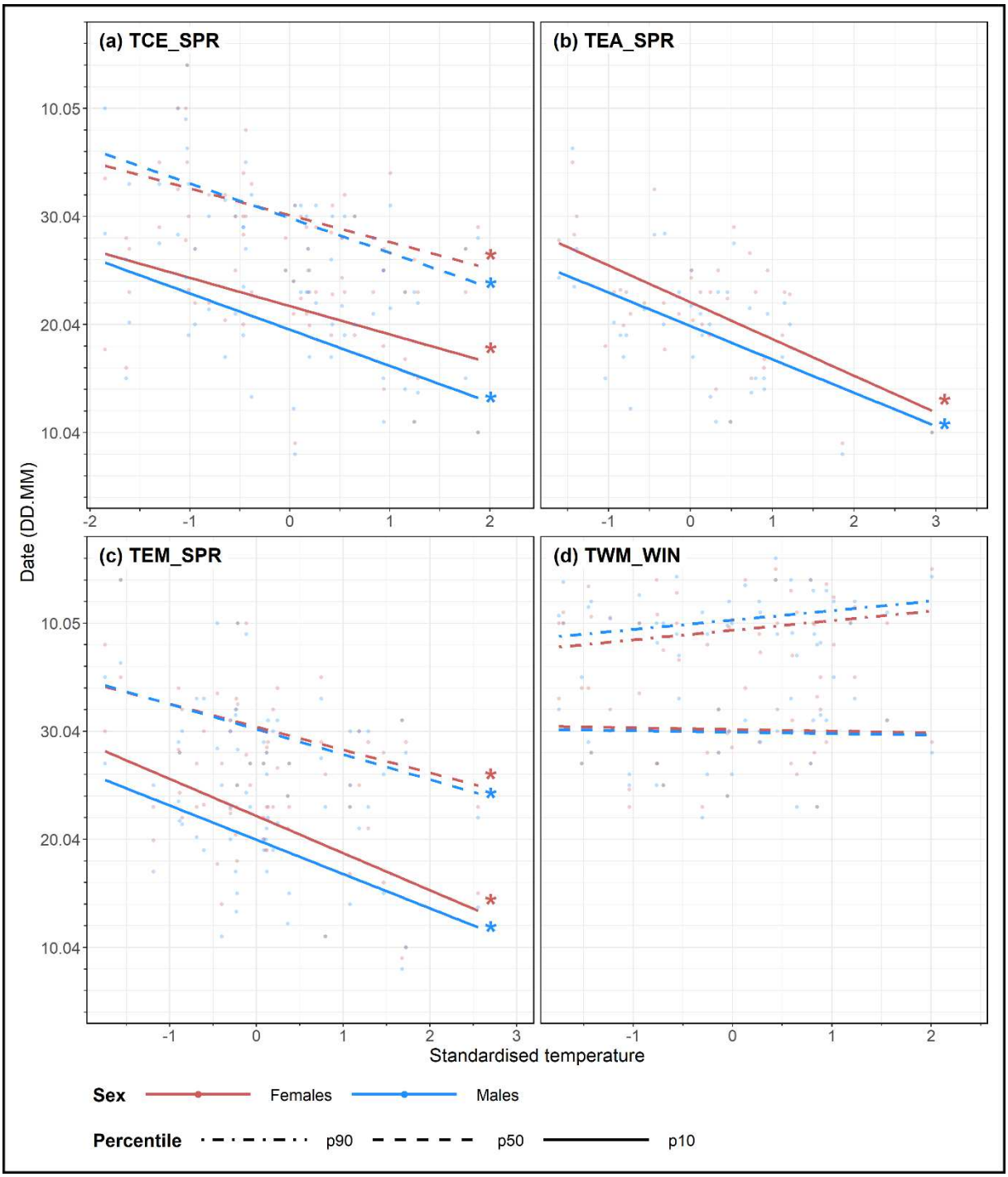
3.3. Effects of Temperature Variables on Spring Migration Timing

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).



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377 **Fig. 4.** Relationships between the timing of the percentiles (p10, p50, p90) of male and
378 female Eurasian blackcaps' spring migration at Bukowo-Kopań in 1982–2025 and the
379 regional temperature variables selected in the best "winter and spring" models (Table S14).
380 Points represent the dates of the respective percentiles of passage plotted against the
381 standardised temperature values in a given year. Linear regression lines show the modelled
382 trends. The panels show the effects of: (a) spring temperatures in Central Europe (TCE_SPR)
383 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.

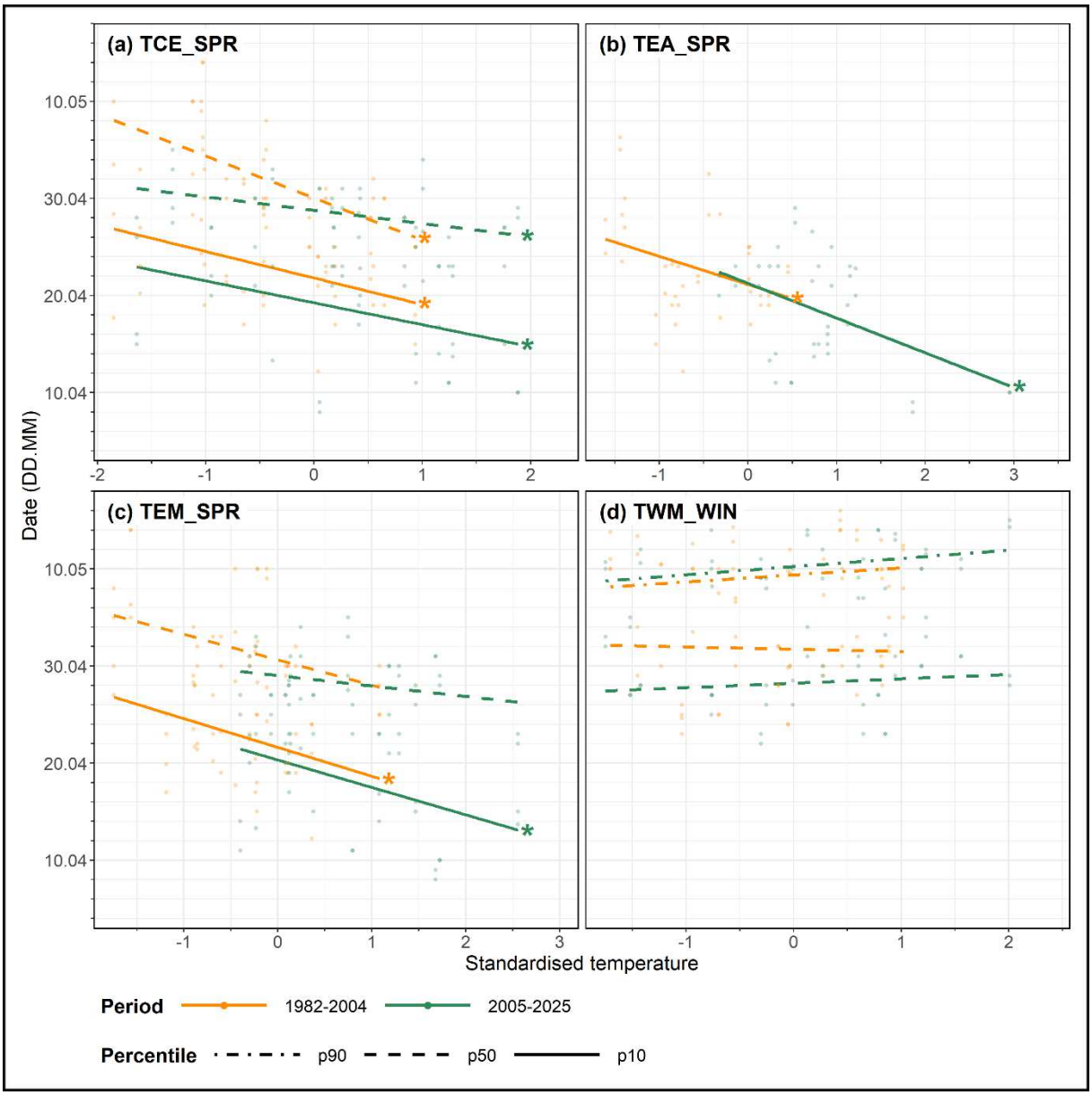


Fig. 5. Relationships between the timing of the selected percentiles (p10, p50, p90) of Eurasian blackcaps' spring migration at Bukowo-Kopań and the regional temperature variables, compared between the two study periods (1982–2004 and 2005–2025). Points represent the dates of the respective percentiles 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 (Croxton 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 (Maciąg 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 (Croxton 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 (Croxton 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 (Croxton 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

Author Contributions: Conceptualisation – AP and MR. Data collection – AP and MR. Methodology and software development – AP and MR. Formal analysis and visualisation of the results – AP. Supervision and funding acquisition – MR. The original draft of the manuscript was prepared by AP, and both authors contributed to subsequent editing and responses to the reviews. Both authors have reviewed and approved the final version of the manuscript.

Funding: This research was supported by the Bird Migration Research Station, University of Gdańsk, through Special Research Facility grants (SPUB) provided by the Polish Ministry of Science and Higher Education (including SPUB No. 203733/E-335/SPUB/2016/4 for 2016–2018, SPUB No. 38/E-335/SPUB/2019 for 2019–2021 and SPUB No. 74/566668/SPUB/SP/2023 for 2023–2025).

Data Availability: Long-term ringing data of the Operation Baltic project are accessible via the Global Biodiversity Information Facility (GBIF) as: Nowakowski J (2017). Ringing Data from the Bird Migration Research Station, University of Gdańsk. University of Gdańsk. Occurrence dataset https://doi.org/10.15468/q5o88l accessed via GBIF.org on 2026-09-27.

Conflicts of Interest: The authors declare they have no financial or non-financial competing interests that are directly relevant to the content of this article.

Consent to Participate declaration: not applicable.

Ethics Approval and Field Permissions: All birds were trapped and ringed under the official permits issued by the Polish Ringing Centre. Field studies at all Operation Baltic stations were conducted in accordance with national ethical guidelines and environmental regulations and relevant permits from land managers.

Acknowledgments

We are grateful to the thousands of citizen scientists who participated in Operation Baltic over the past four decades; their dedicated fieldwork made this study possible. We thank the staff of the Bird Migration Research Station, especially Jarosław K. Nowakowski,

Krzysztof Stępniewski, Wioletta Wójcik, Justyna Szulc and Anna Woźnicka, for their extensive work in compiling and maintaining the databases. ERA5 temperature data (Hersbach et al. 2020) were provided by KNMI Climate Explorer (Trouet and Van Oldenborgh 2013) (accessed on 10 August 2026).

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