

## Article

# Between Summer and Spring: Temperatures Along Migration Routes and at Wintering Grounds Shape Spring Migration Timing in Dunnocks (*Prunella modularis*)

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## Abstract

Climate change shifts bird migration timing, but its influence on medium-distance migrants is understudied. We investigated how temperatures across Europe influence the dunnock's spring passage timing, using daily standardised ringing data from spring migration (26 March–16 May) at Hel Peninsula (N Poland, Baltic coast) over 1965–2025. We determined multi-year trends in the dates of the beginning (10% of passage = p10), median (p50), end (p90), and migration duration (MD = p90–p10) of dunnocks. We also tested the effects of temperatures, averaged for months of breeding (two parts: May–June, July–August), wintering (November–February), autumn (September–October) and spring (March–May) migrations, in four regions of Europe, on the dates of these percentiles during 1965–2025, using multiple linear regression. All phases of passage advanced by 5–8 days; MD remained stable over the 61 years. All phases were early with warm springs in central and southern Europe; p10 and p50 were delayed after warm winters. The p10 was early after warm summers in northern Europe. This shows that climate warming in Europe benefits dunnocks, but their decline across Europe suggests that habitat changes and extreme weather counteract these benefits. Understanding these trade-offs for medium-distance migrants is crucial for their conservation.

**Keywords:** spring phenology; spring migration; climate change; temperature increase; medium-distance migrant

## 1. Introduction

Global climate change, which has accelerated over recent decades, influences weather in the Northern Hemisphere [1,2]. These changes are leading to long-term increases in temperatures and changes in weather patterns [3,4], including more frequent extreme weather events, such as storms, strong winds, or droughts [5,6]. However, the intensity of these changes varies depending on latitude. In Europe, climate warming over the last few decades has been larger than the global average. This is most evident in Fennoscandia and southern Europe, where climate warming has been the greatest and has occurred at a faster rate than elsewhere [7,8]. Migratory birds breeding in Europe include long-distance migrants, which move to and from wintering grounds in Africa south of the Sahara, medium-distance migrants that reach the Mediterranean coast and northern

Academic Editor: Michael Wink

Received: 31 August 2026

Revised: 6 October 2026

Accepted: 13 October 2026

Published: 19 October 2026

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Africa, and short-distance migrants, which move a few hundred kilometres at most, and overwinter within Europe [9]. Movements of all these groups of migrants depend on weather conditions that influence them both directly and indirectly by affecting their environment [10,11]. The consequences of climate change for migratory birds can be positive or negative. The direct positive effect on birds' physiology can be reduced energy expenditure on thermoregulation [12] due to increased temperatures in early spring, autumn and winter. Increased temperatures may also help to reduce energy expenditure on egg incubation [13,14]. On the other hand, excessively high temperatures that cause heat stress can reduce survival and reproduction under climate change by increasing the energetic cost of thermoregulation, dehydration and overheating [12,15]. Negative effects of climate change also include increased frequency of storms, with heavy rain and strong winds, which prevent birds from migrating and foraging or prolong the time they require for these activities [16,17]. The indirect effects of climate change on birds include the positive influence of milder conditions in winter and spring, which facilitate early access to food sources and increase their availability [18–20]. However, for some feeding specialists, such changes in the timing of food availability may result in a mismatch between their arrival time at the breeding grounds and breeding and peak food availability [21,22]. Climate warming may also cause species' ranges to expand [23] or migration distances to shorten [24].

Spring phenology of many bird species in Europe has shifted earlier over recent decades [25–31]. Short- and medium-distance migrants generally show greater plasticity in responses to temperature than long-distance migrants, because they overwinter closer, at locations where annual temperature variation resembles that at the breeding sites. Such plasticity allows them to react to sudden changes in conditions quicker than long-distance migrants [28,32]. Responses of medium-distance migrants to changes in temperature and the range of their adaptability to these changes, and if and how they are similar to those of short- or long-distance migrants, are poorly understood [28,29,31].

To fill this knowledge gap, we set out to determine long-term trends and relationships to temperature in spring phenology of the dunnock, a model medium-distance migrant, on the southern Baltic coast. Such analyses have not yet been conducted for medium-distance migrants in the Baltic region. Most research on dunnocks' movements has focused on autumn migration [33], migration physiology or used counts of migrating individuals [34], but the phenology of its spring migration across Europe remains understudied [25–27]. The influence of climate change on dunnocks' spring migration timing has been studied only in the context of the influence of the North Atlantic Oscillation (NAO) [25,26]. To our knowledge, the relationship between temperature and changes in spring migration timing has not been investigated for this medium-distance migrant.

We focus on dunnock populations migrating in spring through the southern Baltic coast, which breed in northern and northeastern Europe, from wintering grounds in the Mediterranean region to breeding grounds in northern Eurasia (Figure 1A). These northern populations are considered short- or medium-distance migrants [25,27,31,35]. Using data from the Hel ringing station (N Poland, Baltic coast) during 1965–2025, we set out to determine long-term trends in spring phenology of dunnocks. We also aimed to determine the relationships between their spring phenology at the southern Baltic coast and temperature in the regions of Europe where they stay during subsequent life stages, over the past six decades, using our unique long-term dataset. Considering the shifts in migration timing in other species of short- and medium-distance migrants [28,29,31], and results of other studies on the dunnock [27,31], we expect that spring migration timing would shift earlier with the increase in temperatures in recent decades. Understanding the influence of climate warming on this species would contribute to its more efficient conservation.

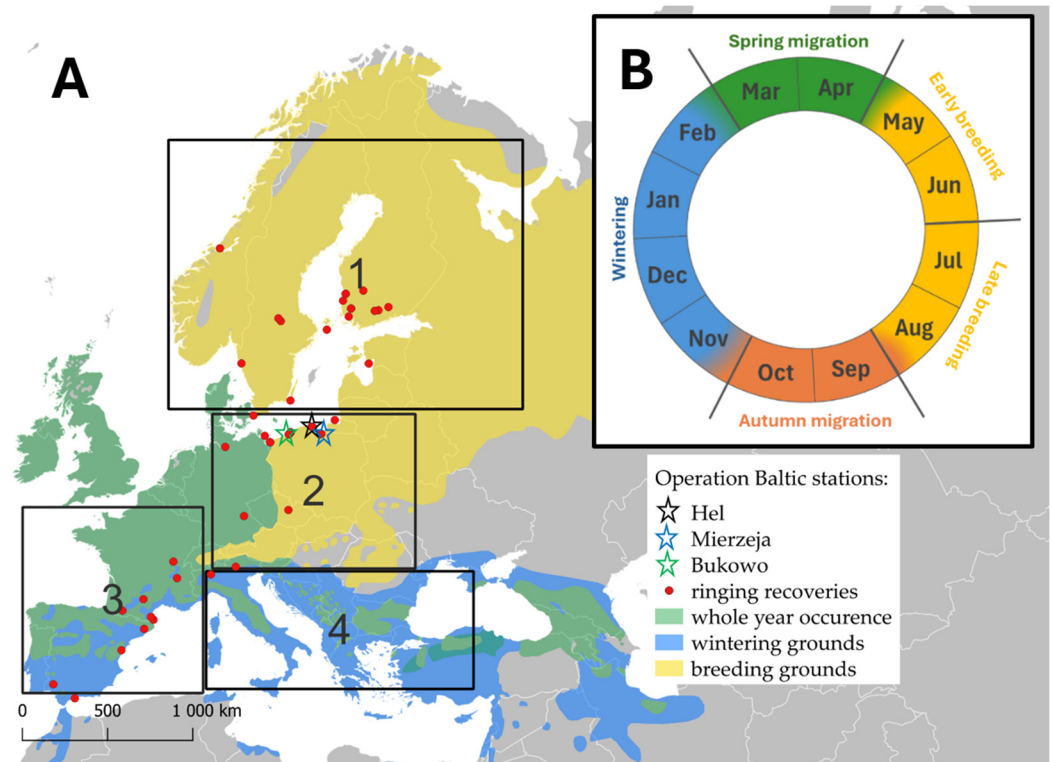


**Figure 1.** Geographical range of the dunnoek, location of the study site, and ringing recoveries of Dunnocks caught at the southern Baltic coast, and the annual cycle of dunnoek populations breeding in northern Europe. (A) The location of the Hel ringing station, where the analysed data were collected, and ringing recoveries of dunnocks caught there and at two further Operation Baltic stations, against the species range (map from BirdLife International 2025, modified). Areas 1–4 are the four regions within the dunnoek range, from which we used the temperature data. (B) The main life stages of the dunnoek we distinguished for analysis. Colour transitions indicate possible overlap between the life stages.

## 2. Materials and Methods

### 2.1. Study Species

The dunnoek is a small migratory passerine occurring in a limited area of Europe and the Middle East (Figure 1A) [36–39], inhabiting woodlands and young coniferous stands with dense undergrowth and bushes, including maquis or garrigues at the non-breeding grounds, as a ground-dwelling species [36,40,41]. In spring, their diet consists mainly of small invertebrates, particularly beetles (Coleoptera), spiders (Aranea), flies (Diptera) and ants (Formicidae), but in winter plant seeds predominate [36,39,40]. Various populations of dunnocks in Europe show different migratory patterns [42,43], from sedentary *hebridium* and *occidentalis* subspecies ranging from Ireland to western France [44] to obligatory short- and medium-distance migrant populations of the nominative subspecies breeding in central and northern Europe, respectively [36,39,45,46]. Our study focuses on northern populations originating from Fennoscandia, Baltic countries and north-western Russia, which winter in the Mediterranean region and migrate in spring from these wintering grounds via the southern Baltic coast to these northern breeding grounds [33,36,44–49] (Figure 1A). Spring and autumn migration routes of dunnocks across Europe are similar, according to ringing recoveries [50]. The annual cycle of these northern populations (Figure 1B) typically consists of a breeding season, which we divided into early breeding (May–June) and late breeding periods (July–August), when they lay one to two broods, and autumn migration to the south (September–October). This is followed by wintering (November–February) and spring migration to the north (March–April) [36,51–54].

## 2.2. Study Sites and Material

We used the dates on which dunnocks were caught during spring migration at the bird ringing station Hel (54.442 N, 18.334 E), situated on the Hel Peninsula in northern Poland (Figure 1A), which operates within the Operation Baltic research programme. Hel Peninsula is a spring stopover site for dunnocks during their migration to more northern and north-eastern breeding grounds (Figure 1A), but also a breeding area for local populations. Dunnocks were caught at Hel daily from 26 March to 16 May, which corresponds to the entire spring migration of this species on the southern Baltic coast in 1965–2025. During these 61 years, 2092 individuals were captured (Table S1). Birds were captured in mist nets located in coastal pine and mixed forest and bushes daily, from dawn to dusk. We used a constant number of 7-m and 12-m long mist nets throughout each spring season, but the number of mist nets ranged from 35 to 58 in various years. More details on the stations' routines are provided by [55]. Captured birds were ringed and aged. The age was determined based on contrasts in dunnocks' plumage and by the iris colour [54,56]. Each bird was classified into one of three age categories (immature, adult, and a fully grown bird of unknown age). Then, each individual was weighed, measured, and released, in accordance with the Operation Baltic protocol [55]. Capturing and ringing of birds were conducted with all the required permits issued by the General Directorate of Environmental Protection in Poland, with annual approvals of the Polish Bird Ringing Centre of the Polish Academy of Sciences and the Marine Office in Gdynia, as land managers.

## 2.3. Climate Variables and Data Selection

To determine the effects of temperature on the timing of dunnock spring passage, we used daily mean temperatures during 1965–2025 in four regions of Europe (Figure 1A). These regions were selected according to the locations of ringing recoveries of birds captured at the Operation Baltic field stations (Figure 1A, [49]) or elsewhere in the Baltic region [47,50] and defined by coordinates within the dunnock range in Europe. The temperature data were downloaded as daily mean temperatures within each region at a height of 2 m above ground from the ERA5 reanalysis based on the blended ECA&D dataset, from the Royal Netherlands Meteorological Institute (KNMI), by using the Climate Explorer tool <https://climexp.knmi.nl/> (accessed on 15 May 2025). Then, the daily mean temperatures were averaged to monthly mean temperatures. Monthly mean temperatures were averaged within two- or four-month periods (Table 1) corresponding to dunnocks' life stages (Figure 1B) in four regions (areas 1–4; Figure 1A) they visit at these life stages.

**Table 1.** Mean monthly temperature variables used in the analyses, averaged within two- or four-month periods in four regions (areas 1–4, Figure 1A) distinguished by provided area coordinates, the names of climate indices used in the text, and corresponding months.

| Description of Temperature Variable           | Area Coordinates                        | Symbol       | Variable Set | Months                       |
|-----------------------------------------------|-----------------------------------------|--------------|--------------|------------------------------|
| Mean temperature for northern Europe (area 1) | 55.737 S – 6.878 N, 4.581 W – 38.932 E  | T1May_Jun_1Y | green        | May–June                     |
|                                               |                                         | T1Jul_Aug_1Y | green        | July–August prior year       |
|                                               |                                         | T1Sep_Oct_1Y | blue         | September–October prior year |
| Mean temperature for central Europe (area 2)  | 46.034 S – 55.468 N, 8.825 W – 28.514 E | T2Mar_Apr    | green        | March–April                  |
|                                               |                                         | T2Sep_Oct_1Y | green        | September–October prior year |
|                                               |                                         | T2Nov_1Y_Feb | green        | November prior year–February |

|                                                   |                                         |              |      |                              |
|---------------------------------------------------|-----------------------------------------|--------------|------|------------------------------|
| Mean temperature for southwestern Europe (area 3) | 37.026 S – 50.010 N, –9.563 W – 7.931 E | T3Mar_Apr    | blue | March–April                  |
|                                                   |                                         | T3Sep_Oct_1Y | blue | September–October prior year |
|                                                   |                                         | T3Nov_1Y_Feb | blue | November prior year–February |
| Mean temperature for southern Europe (area 4)     | 37.344 S – 45.847 N, 8.230 W – 34.154 E | T4Sep_Oct_1Y | blue | September–October prior year |
|                                                   |                                         | T4Nov_1Y_Feb | blue | November prior year–February |

We used temperatures averaged for March–April along dunnocks' spring migration routes within area 2. For dunnocks' wintering in November–February, we averaged temperatures for November–December of the previous year and January–February of the same year as the analysed spring migration at the wintering grounds, in areas 3 and 4 where dunnocks stay at this time. For autumn migration routes, we averaged temperatures within area 2 for September–October of the year preceding the analysed spring migration. Finally, we averaged temperatures for the early breeding period (May–June) and late breeding period (July–August) of the previous year, from dunnocks' breeding area (area 1 in Figure 1A), where the studied populations stay in these months. In this way, we obtained 11 temperature variables for analyses (Table 1).

## 2.4. Statistical Analysis

### 2.4.1. Deriving Parameters of Migration Timing

We used daily numbers of dunnocks caught each spring, taking into account only the first capture date of each individual in a season. The few data gaps on days when mist nets were closed due to unfavourable weather conditions were filled in using the average number of birds caught at Hel on such days over the previous six years and the following six years, as in earlier studies [57–63]. Such gap days were at most three per season and occurred in 12 springs. We combined birds of all age categories to obtain sufficient samples for analyses in each spring (Table S1). Thus, we worked under the assumption that dunnocks of all age classes in spring were migrating to their breeding grounds. We excluded 11 years (1984–1994) when fewer than 10 dunnocks were caught; thus, we analysed data on 2038 dunnocks from 50 springs during 1965–2025 (Table S1). To show changes in spring migration timing, we used cumulative daily capture totals to calculate the dates on which 10%, 50% and 90% of all dunnocks caught each spring passed through Hel. We used these dates in subsequent years, expressed as the day number (1 January = Day 1), as the time series reflecting the timing of the first (p10), median (p50) and last (p90) phases of passage over 1965–2025, respectively, as in other studies [27,29,61–63]. We also estimated the migration duration (MD) as the difference in the dates of p10 and p90 of passage, hence the number of days when 80% of dunnocks passed each spring.

### 2.4.2. Determining Long-Term Trends in Parameters of Spring Migration Timing

To determine long-term patterns in the timing of the spring passage of the dunnock over 1965–2025, we used simple linear regression of these four migration parameters (p10, p50, p90, and MD) against the year number (YearN, with Year 1 = 1965), as in other studies [62,63].

### 2.4.3. Modelling Relationships Between Temperature Variables and the Dates of Each Phase of Spring Migration

Before conducting any multiple regression models, we checked whether any of the 11 temperature variables were correlated (Table S2) using Pearson's correlation with the

Bonferroni correction for numerous comparisons [64]. We avoided including strongly correlated variables with  $|r| > 0.70$  in the same model to reduce the risk of multicollinearity [65]. Two correlation coefficients exceeded the recommended threshold of  $|r| = 0.7$  (Table S2), so we divided the variables into two sets to separate these correlated variables in models to avoid the risk of multicollinearity [65,66]. We were aware that all temperature variables showed increasing trends and were correlated with the year; one of these correlations was  $|r| > 0.7$  (Table S2). However, we included the year number as an explanatory variable in these models to consider the effect of year when estimating the effects of the temperature variables on migration timing [28,67]. Before running multiple regression models, we standardised all explanatory variables, so that their mean was 0 and standard deviation was 1, as they were on different scales. Then, we used the year and each of the two sets of temperature variables, which we called “green” and “blue” sets for convenience, as explanatory variables in separate regression models. We ran two models (“green” and “blue”, each with the respective set of variables), for each of the three time series of the dates of the three phases of passage (p10, p50, and p90), which were used as response variables. Thus, in the first step, we ran six models, two for each of the three parameters of passage. We did not analyse MD, as it was derived from p10 and p90. To monitor the potential influence of including correlated variables on the results of our models, we closely monitored Variance Inflation Factors (VIF); if  $VIF < 10$ , the multicollinearity had no harmful effects [65,66]. For each of these six full models, we conducted the “all subsets regression” and selected the best model based on the model ranking according to the Akaike Information Criterion adjusted for small samples (AICc), with the package “MuMIn 1.43.17” [68] in R 4.5.1.

In the second step, we combined the variables selected in the first step in the two best models into one model using the “combined” set of temperature variables for each phase of passage, as in other studies [55,63]. Thus, we ran three “combined” multiple regression models, for the dates of each phase of passage (p10, p50, and p90) as subsequent response variables, and a combined set of temperature variables as explanatory variables (Table S3). We conducted the “all subsets regression” and chose the best model, with the lowest AICc, using model ranking by AICc (Table S4) as before. We further interpreted these “combined” final best models for each phase of passage. We calculated the adjusted coefficient of determination ( $AdjR^2$ ), which reflected the proportion of variation described by each best model. We assessed whether these final best models were not overfitted using the following three methods that are recommended by [67]: (1) examining diagnostic graphs to determine outliers and influential observations based on Cook’s distance [67]; (2) calculating the ratio of  $R^2$  to adjusted  $R^2$  ( $AdjR^2$ ), with values closer to 1 indicating good model fit; and (3) comparing  $AdjR^2$  with predictive  $R^2$  ( $predR^2$ ). Predictive  $R^2$  was calculated using a leave-one-out procedure, in which each observation was excluded in turn and the model’s ability to predict it was assessed. A small difference between  $AdjR^2$  and  $predR^2$  indicates model stability and low risk of overfitting. Method (1) was performed using an R script based on Crawley [69], while methods (2) and (3) used an R code written by Antonello Pareto [70]. Models that showed no evidence of overfitting across all three methods were further interpreted. These methods for model assessment follow earlier studies [61–63,71].

For these three best models, using the package “heplots 1.3–5”, we calculated partial correlation coefficients (pR), which we visualised as bars, to determine the strength and direction of the relationship between the response variable and one explanatory variable at a time, excluding the effects of the remaining variables [72]. A positive pR indicated that the analysed phase of migration occurred late with high temperatures, and a negative correlation indicated an early passage with high temperatures. The greater the total value of the estimate, the stronger the influence of the temperature on the migration timing. We

drew plots showing relationships between temperature variables from the best models and the dates of the three phases of passage with fitted regression lines, as well as the long-term trends in these dates, using the “ggplot2” package [73]. All analyses were conducted in R 4.5.1 [74].

### 3. Results

#### 3.1. Long-Term Trends in the Timing of Spring Migration

All three phases of the dunnock spring passage at Hel (p10, p50, and p90) shifted significantly earlier, but the migration duration (MD) remained stable at 29 days over 1965–2025 (Figure 2; Table S5). The first phase of passage (p10) shifted earlier by 4.8 days, the median (p50) by 8.3 days, and the last phase (p90) by 5.4 days during these 61 years (Figure 2; Table S5).

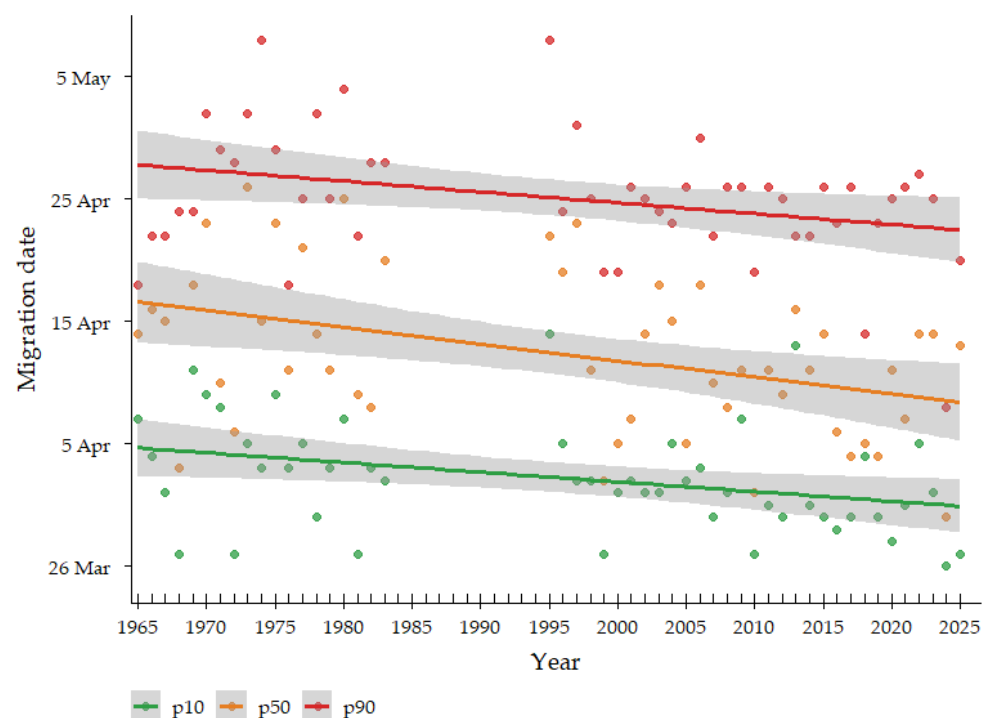


**Figure 2.** Multi-year trends in the timing of the three phases (p10, p50, p90) of spring passage of the dunnock at the Hel ringing station (N Poland) over 1965–2025. Circles are the dates when the respective percentiles of dunnocks were caught each year; lines show trends and grey areas show their confidence intervals for these percentiles. All trends were significant; the details of the regression are provided in Table S3 in the Supplementary Materials.

#### 3.2. The Effects of Temperature on the Timing of Subsequent Phases of Spring Migration

The partial “green” best models had three temperature explanatory variables for p10 and p90, and four explanatory variables, including the year, for p50 (Table S4, model ranking in Table S5). The “blue” best model had two explanatory variables for each phase of passage (Table S4, model ranking in Table S6). The “combined” final best models had three explanatory variables for p10 and p90, and one explanatory variable for p50 (Table 2, Figure 3, model ranking in Table S7).

**Table 2.** Effects of the temperature variables from the best “combined” models for three phases of spring migration (p10, p50, p90) of dunnoek at Hel in 1965–2025. AdjR<sup>2</sup> = adjusted coefficient of determination; Estimate = multiple regression coefficient; SE = its standard error; t, p = t-test and significance level; VIF = variance inflation factor; pR = Pearson’s partial correlation coefficient.

| Best "Combined" Models |                          |                   |                      |          |      |        |       |      |       |
|------------------------|--------------------------|-------------------|----------------------|----------|------|--------|-------|------|-------|
| Response Variable      | F Statistics             | AdjR <sup>2</sup> | Temperature Variable | Estimate | SE   | t      | p     | VIF  | pR    |
| p10                    | F <sub>3,46</sub> =13.36 | 43%               | (Intercept)          | 92.26    | 0.48 | 191.43 | 0.000 |      |       |
|                        |                          |                   | T_1_May_Jun_1Y       | −0.82    | 0.54 | −1.53  | 0.133 | 1.22 | −0.22 |
|                        |                          |                   | T_2_Mar_Apr          | −3.34    | 0.66 | −5.08  | 0.000 | 1.85 | −0.60 |
|                        |                          |                   | T_2_Nov_1Y_Feb       | 1.43     | 0.63 | 2.28   | 0.028 | 1.69 | 0.32  |
| p50                    | F <sub>2,47</sub> =15.98 | 29%               | (Intercept)          | 102.60   | 0.79 | 129.30 | 0.000 |      |       |
|                        |                          |                   | T_4_Mar_Apr          | −3.75    | 0.83 | −4.53  | 0.000 |      | −0.55 |
| p90                    | F <sub>3,46</sub> = 8.27 | 31%               | (Intercept)          | 115.25   | 0.63 | 181.68 | 0.000 |      |       |
|                        |                          |                   | T_2_Nov_1Y_Feb       | 1.38     | 0.77 | 1.80   | 0.079 | 1.44 | 0.26  |
|                        |                          |                   | T_2_Sep_Oct_1Y       | −1.76    | 0.70 | −2.53  | 0.015 | 1.33 | −0.35 |
|                        |                          |                   | T_4_Mar_Apr          | −2.48    | 0.85 | −2.93  | 0.005 | 1.65 | −0.40 |

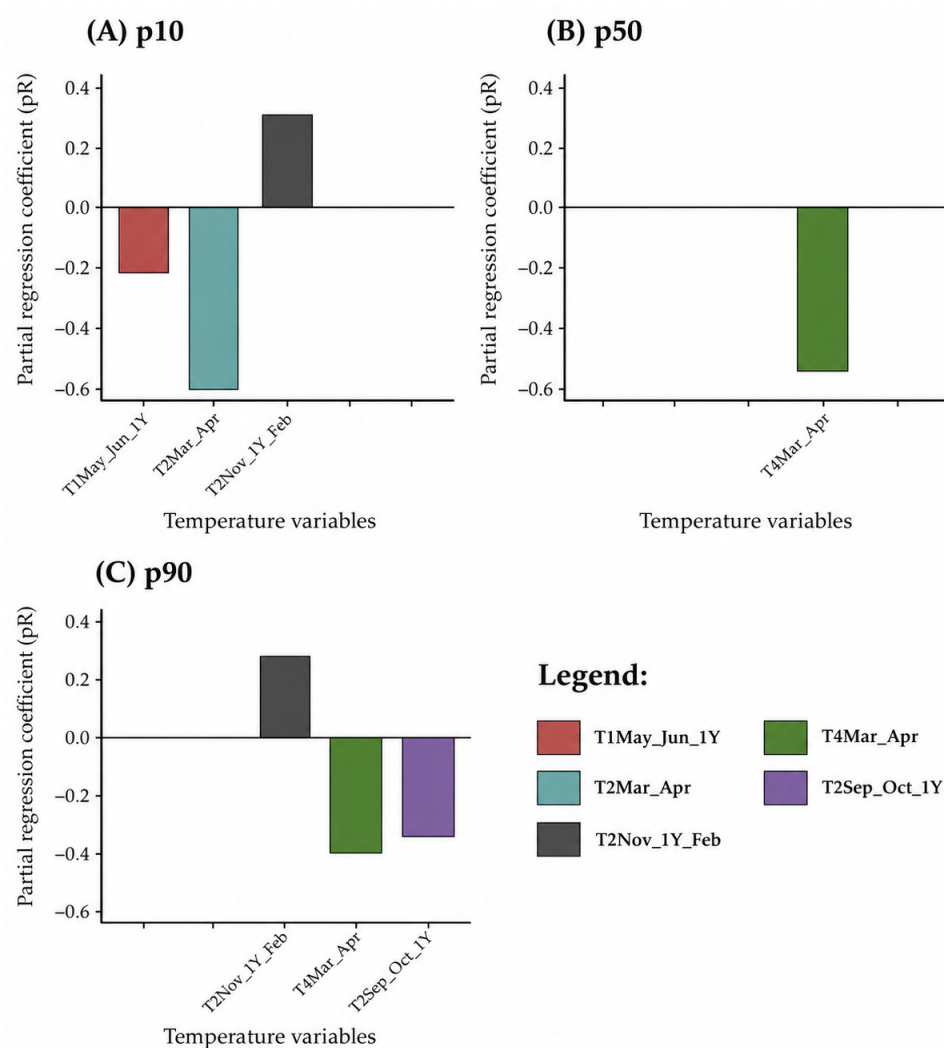


**Figure 3.** Partial correlation coefficients (pR) for the relationships between temperature variables derived from the “combined” best models and the three phases of passage at Hel ringing station

during 1965–2025. The negative value of  $pR$  indicates that the analysed phase of passage shifted earlier with higher temperature; the positive value represents the opposite. Further details on these models are in Table 2. Symbols of temperature variables are as in Table 1. (A) Results of the best model for the first phase of passage (p10); (B) results of the best model for the middle phase of passage (p50); (C) results of the best model for the last phase of passage (p90).

The diagnostics showed no overfitting in these best “combined” models (Table S8). None of the best partial and “combined” models but one (“green” partial model for p50) selected the Year (Table S4). For p50, consequently, the Year was included in the full “combined” model but was not chosen in the final best “combined” model (Table 2). In all best models, both partial and final, all VIFs were  $<3$  (Tables 2 and S4), which indicated a negligible bias in model results caused by multicollinearity.

The best “combined” model for the first phase of passage (p10) explained 43% of the variation in its timing with three temperature variables (Table 2, Figure 3A). The first phase of migration at Hel was early after warm May–June of the previous year (Figure 4B) at the breeding grounds in northern Europe (area 1 in Figure 1A), and with warm springs (Figure 4A) along migration routes in Central Europe (area 2 in Figure 1A).

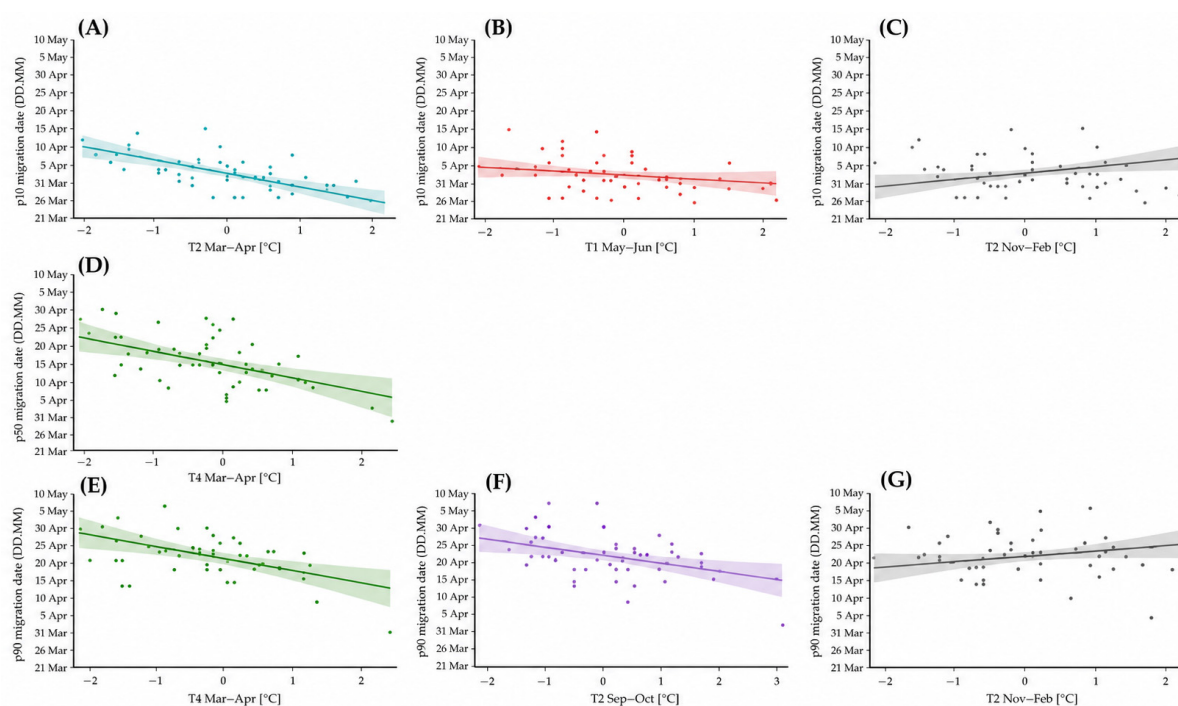


**Figure 4.** Relationships between the timing of each percentile (p10, p50, p90) of dunnocks’ spring migration at Hel in 1965–2025 and the temperature variables selected in the best “combined” models (Table 2). Points represent the dates of the respective percentiles of passage plotted against the values of the temperature variables in a given year. Regression lines show the trends, and shaded areas show their 95% confidence intervals. (A–C) The effects of the temperature variables and first (p10) phase of passage; (D) the effect of temperature variable and median (p50) of passage; (E–G) the effects of temperature variables on the end (p90) phase of passage.

The delay of the first phase of passage the following spring was related to warm winters (November–February) (Figure 4C) in central Europe (area 2 in Figure 1A). For the middle phase of passage (p50), the best “combined” model explained 29% of the variation in its timing at Hel (Table 2, Figure 3B) with spring temperatures (Figure 4D) at the wintering grounds in southwestern Europe (area 4 in Figure 1A). For the last phase of passage (p90), the best “combined” model explained 31% of the variation in its timing with three

temperature variables (Table 2, Figure 3C). This last phase of dunnoek passage at Hel was early after warm springs at wintering grounds in southwestern Europe (Table 2, Figures 3C and 4E), and after warm autumns in central Europe (Figure 4F) in the previous year. The delay in that last phase of spring migration was related to warm winters in central Europe (Figure 4G).

#### 4. Discussion

We found that dunnocks advanced their spring passage through the Baltic coast over 1965–2025. The first and last phases of passage (p10 and p90) shifted earlier by about 5 days, so the migration duration (MD) remained surprisingly stable over 61 years, contrary to our expectations that it would change, as at other sites. Interestingly, the median (p50) of passage shifted the most, by about 8 days. The annual variation in the timing of migration at Hel was associated with temperature variables, and all phases of passage were early during warm springs in central and southern Europe, as expected. The first phase of passage was early after warm winters in central Europe, but a similar relationship also occurred for the last phase, opposite to our expectations. The first phase of passage was also early after warm summers the previous year, suggesting a carry-over effect of the breeding success. We discuss our findings in the light of temperature increase during the last decades across the dunnoek range in Europe, including their breeding grounds, migration routes and wintering grounds.

##### *4.1. Multi-Year Trends in the Timing of Spring Passage in Comparison with Trends in Other Locations in Europe*

During the last six decades, all three stages of dunnoek spring passage at the Hel station shifted earlier, similarly to other short- and medium-distance migrants in Europe [25,26,28,29]. Our results correspond to those from the island of Christiansø situated in the Baltic Sea, where the dates of the first 5% of spring passage shifted earlier over 1976–1997 by 7.9 days [27], and at Blåvand bird observatory at the North Sea coast of Denmark, where analogous dates shifted earlier by 10.6 days over 1984–2021 [31]. Similarly to our results, the median of spring passage showed the greatest shift, by 11.6 days earlier, among all migration phases at Christiansø [27], but at Blåvand it shifted earlier only by 1.2 days [31]. The mean date of passage also shifted earlier by 5.3 days in Helgoland, Germany [25]. The last phase of dunnocks' passage also shifted earlier by 7 days at Christiansø [27], but not at Blåvand, where it was delayed [31]. A general trend to advance spring migration was also observed in dunnocks by Vähätalo et al. [26]. The differences between stations in the extent of the shift to earlier migration may result from differences in their locations (islands vs. seacoast) and varied proportions of individuals from different populations migrating through each station [75,76]. The source of these discrepancies might also be a different range of years and a longer time series of phenological data we analysed, as compared with other bird observatories [77].

Because both the first and last phases of dunnoek passage at Hel shifted similarly earlier, the migration duration (MD) did not change, oppositely to our expectations of prolonged passage due to a delayed end of migration, as at Blåvand [31]. This discrepancy between stations may be caused by varied proportions of birds from different age/sex groups passing through these sites, considering that birds of these groups may respond differently to temperatures, as in other species [62,78]. These differences can also originate from spatial variation in environmental conditions and varied influence of different cues on subsequent stages of migration. However, Cotton [79] reported parallel advances in both the start and end phases of passage in several other medium-distance migrants, resulting in little change in their passage duration, similarly to dunnocks at Hel.

The extended migration duration of dunnocks at Blåvand [31] may reflect a stronger asymmetry than at Hel in behavioural responses to climate change in birds forming different migration phases. In short-distance migrants, the timing of the first phase of migration (p10) is particularly responsive to conditions in the wintering areas and to large-scale climatic patterns, especially as it is often dominated by adult males, which compete for breeding territories [31]. In contrast, the timing of the last phase (p90) of passage may be related to environmental conditions and availability of the food base at stopover, or the timing of the species' breeding [80]. Thus, the stable migration duration at Hel does not necessarily contradict the general expectation of a prolonged passage under climate warming but rather suggests that the phenological response of migration may be site- and phase-specific [28,71,81–83].

Another reason for shifts to earlier passage of dunnocks through Hel may be increasingly favourable conditions associated with rising temperatures at their wintering sites and spring migration stopovers. These favourable conditions promote early food abundance and reduce thermoregulatory costs, allowing the birds to build up energy reserves more effectively, which enables them to migrate more quickly and efficiently [84,85]. Due to climate change over the last 60 years, including milder winters, some dunnocks have recently begun wintering in southern and western parts of Poland and in nearby countries [86,87]. Thus, we cannot exclude that some individuals wintering close to Hel might be captured at the beginning of the spring season, affecting shifts in the first phase of passage [75]. However, we reduced a possible bias caused by single individuals wintering nearby and occurring at Hel by using the dates for the first 10% of passage as the proxy for the beginning of passage, instead of First Arrival Dates, which are sensitive to exceptionally early individuals [88]. Moreover, dunnocks might be shortening their migration distance and wintering closer to their breeding grounds, as suggested for other migratory species [89,90]. Higher temperatures at breeding grounds result in greater food availability for insectivores, which may lead to birds' good physical condition at the end of breeding and faster preparation for migration. This, in turn, may benefit their fitness during autumn and winter months and ultimately early migration of the first birds the following spring. Increased autumn and winter temperatures may also provide a biological signal for birds to overwinter closer to breeding grounds, in southern Sweden or farther north in continental Europe, rather than in traditional wintering grounds [89,91]. This would lead to an early passage through Hel by dunnocks whose wintering and breeding grounds are nearby. The same effect may occur after warm autumns in central Europe. We suggest that the earlier spring passage of dunnocks at Hel over the last six decades may be explained by dunnocks' adaptation to increasing winter and spring temperatures in Europe, probably in combination with shortening of the dunnocks' migration distance.

#### 4.2. *The Effects of Temperature on the Timing of Subsequent Phases of Spring Passage*

Not selecting the year by any of the final “combined” best models suggested that its relationship to the timing of subsequent phases of dunnocks' passage was overtaken by the effects of temperature variables in these models. This showed that the temperature variables in these models, which were correlated with the year, explained the multi-year trends in all three phases (p10, p50, and p90) of passage better than the sequence of years.

##### 4.2.1. *The Effect of Temperatures in Spring*

All phases of spring migration of dunnocks through Hel were early with warm springs in central Europe and on the Apennine and Balkan Peninsulas, similar to phenological responses of other passerines to warm springs [28,29,92]. Analogous relationships to temperature have been shown especially among short- and medium-distance migrants [55,65,92,93]. Warm springs decrease birds' energy expenditure on thermoregulation [94].

High temperatures in spring promote earlier emergence of vegetation and small invertebrates like beetles (Coleoptera), spiders (Aranea), and ants (Formicidae), which are dunnocks' food [39,40,95]. This allows birds to forage more effectively at stopover sites along their migration routes in central Europe. During such conditions of effective foraging, the time spent by dunnocks at stopover sites in central Europe may be shorter than during cold springs [96–98], enabling the first birds to arrive at the southern Baltic coast early. Successful foraging improves birds' condition, increasing their fitness and survival [84,99–104], with carry-over effects on their next life stages, especially on breeding success [100,101,105–108]. Moreover, the timing of the initial phase of the passage (p10) at Hel was associated with temperatures in central Europe, while that of the median (p50) and end (q90) was related to temperatures in southern Europe. These differences may reflect the influence of environmental conditions encountered at different stages of migration. The association between p10 and temperatures in central Europe suggests that some early migrants pass through that region shortly before arriving at the southern Baltic coast; thus, conditions in central Europe might influence stopover duration and subsequent migration progress [109,110]. The absence of a significant correlation between p10 and temperature in the Iberian Peninsula, despite numerous ringing recoveries indicating dunnock movements between this area and the Baltic region, suggests that temperature in central Europe fine-tunes the timing of arrival at Hel [87]. In contrast, later migrants may follow different routes or originate from more distant wintering areas, including the Apennine and Balkan regions.

#### 4.2.2. The Effect of Temperatures in Winter

Warm winters in central Europe were related to delayed first (p10) and last (p90) phases of dunnocks' spring passage at Hel, in line with mild winter conditions generally being associated with earlier spring migration [62,63]. Analogous delays in the last phase of dunnock passage have also been reported in short-distance migrants, potentially reflecting carry-over effects of winter conditions on survival and the composition of the migrating population [62,63]. With winters becoming warmer and providing more favourable conditions during recent decades, the survival rate of both adult and immature birds may increase [10,16,111]. Their physical condition during spring migration would also be good because of a more accessible and abundant food supply during mild winters [16,112,113]. Favourable conditions allow more immature birds to survive winter and undertake spring migration. However, when immatures migrate from their wintering to breeding grounds for the first time, they have less experience, lower foraging efficiency, make more stops along the route, and usually migrate later in spring than adults [26,114]. Additionally, they may be more vulnerable to the direct effects of external variables such as temperature or rainfall [26,114]. Additionally, the young from late broods generally encounter deteriorating environmental conditions, like reduced food availability or bad weather [115,116] or are poor-quality individuals [117], which may affect the timing of departure from wintering grounds. Due to their lower experience and more frequent use of stopover sites than adults, an increased proportion of immatures that survived winter might delay the first and last phases of the spring passage on Hel. A similar view was held by Haest et al. [118], who found that the phenology of spring passage of short- and medium-distance migrants on Helgoland (Germany) was affected by winter and spring temperatures elsewhere across the non-breeding grounds. A similar delaying effect of warm winters at the wintering sites on the last phase of spring migration (p90) occurred in the song thrush at Hel [63].

#### 4.2.3. The Effect of Temperatures in Summer

Early first phase (q10) of the spring migration through Hel was related to warm summers during the early breeding season (May–June) at dunnocks' breeding grounds in north Europe, indicating carry-over effects of conditions at the breeding grounds on migration timing about 10 months later. Abundance of food during a warm summer means that adults are well-nourished and in good condition during the breeding season. Favourable conditions they encounter upon arriving at their breeding grounds enable them to secure a territory and begin breeding earlier [106,107,115,119]. Higher temperatures may be beneficial for egg incubation during the early breeding season, and promote earlier hatching and faster chick growth. However, this positive effect on offspring depends on temperatures remaining within the thermal tolerance range of the developing embryos [13,14]. An advanced beginning of spring migration might also be related to dunnocks' tendency to breed repeatedly [40,120,121]. Favourable conditions encourage adults to lay additional clutches during summer or repeat unsuccessful first broods [122]. Furthermore, good conditions promote early maturity of the young from first broods and the survival of immatures from all clutches [10,123,124]. Increased survival rates and good condition may have carry-over effects on later stages of the dunnock's life [107]. The fittest immatures from the first broods might survive winter well, similarly to well-nourished adults, and thus both groups might be able to migrate early through Hel the following spring at the beginning of the passage. Food abundance during warm summer also enables adults to rebuild their energy reserves depleted after breeding, and immatures to grow and fuel more quickly and depart for migration to the south early. Good nutrition affects not only migrants' condition but also the quality of their plumage [125]. Adult dunnocks undergo a complete post-breeding moult once a year, and immatures grow their first set of feathers in the nest and undergo partial post-juvenile moult at the breeding grounds in summer [126,127]. Thus, good weather conditions and abundant food in this period benefit their moult. Good-quality feathers influence subsequent stages of the life cycle as they are crucial for efficient migration, which may cause carry-over effects on the following spring passage, explaining our results [107,128,129].

#### 4.2.4. The Effect of Temperatures in Autumn

The last phase (p90) of dunnock's spring passage was early after warm autumns in central Europe the previous year, which might be associated with shortening of the species' migration routes over recent decades. Rising winter temperatures have contributed to northward shifts in wintering distributions of several European passerine species by reducing climatic constraints on overwintering at higher latitudes [130,131]. As a short- or medium-distance migrant, the dunnock has the potential to shift its wintering northwards in response to rising winter temperatures, as warmer conditions may benefit winter survival closer to the breeding grounds [36,89,132]. Dunnocks' overwintering has been reported in Poland, mostly in the southern part of the country, like the regions of Silesia [86] and central Poland near Warsaw [132], but also in northern Poland near the Hel Peninsula [133]. Reports of this species' overwintering also come from Denmark [134], Sweden [135] and Norway [136]. Warm autumns in central Europe might encourage a larger part of population to winter closer to breeding grounds than after cold autumns [75,89,90]. Rising temperatures associated with climate change can extend the seasonal activity period of many invertebrates, on which the dunnock feeds, by delaying their autumnal inactivity, diapause, and overwintering, thereby prolonging the availability of arthropod prey during late autumn [103,137]. Birds do not need to continue their migration to the south if the food supply and weather conditions are favourable closer to the breeding grounds, so they shorten the migration distance. A short distance to cross in spring may, in turn, promote early arrival of wrens on the southern Baltic coast.

#### 4.2.5. The Effect of Temperature on Population Size

The population size of the dunnock in Europe has decreased since the 1980s, according to the Pan-European Common Bird Monitoring Scheme [138,139]. These changes in numbers might be a result of ongoing climate change and extreme weather events. However, we suggest that increasing temperatures in Europe are not the main cause of the observed decline in dunnocks' population, because warm winters and springs seem to benefit this species by shorter migration distances, earlier spring passage and repeated broods. Alternative causes of the population decrease may be the simplification of forest structure in Scandinavia and the increasing proportion of deciduous forests in dunnocks' breeding areas [140–142], which suit the breeding biology of this species less than conifers [36]. Additionally, habitat changes, including intensive farming and most importantly, the degradation of the forest litter, may reduce food availability [140–142] and have a greater impact on the dunnock population size than climate warming.

### 5. Conclusions

We showed that temperatures in different regions of Europe, including those at the breeding grounds about 9–10 months earlier, had a carry-over effect on the timing of dunnocks' spring migration at Hel, which is a novel result for this species and for the group of medium-distance migrants in Europe. Thus, the temperature increase across Europe might explain the shift to earlier passage of dunnocks by about a week over 1965–2025. Our results suggest that rising temperatures in Europe benefit dunnocks, creating favourable conditions for foraging, early breeding and two clutches, which may have a carry-over effect on their next life stages. However, climate change also increases the frequency of severe weather events across Europe, probably partly overriding positive effects of higher temperatures. These single extreme events should be considered in future analyses, as they could bias data averaged over longer periods. However, the decline in dunnock numbers across Europe [138,139] suggests that unfavourable anthropogenic habitat changes and more frequent extreme weather events might counteract the positive effects of increasing temperatures on this species' numbers, which would require further research.

**Supplementary Materials:** The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/d18100640/s1>, Table S1. Numbers of dunnocks caught (n) in springs of subsequent years at Hel bird ringing station (N Poland). The years highlighted in grey were excluded from analyses because fewer than 10 dunnocks were caught. N analysed is the total number of analysed dunnocks, after excluding these years; Table S2. Pearson's correlation coefficients between the 11 climate indices in 1965–2025 used in regression models. Correlations significant after the Bonferroni correction are indicated with bold font. Green colour and frame indicate the set of temperature variables selected for "green" partial models; blue colour and frame indicate the set of temperature variables selected for "blue" partial models. Symbols of temperature variables as in Table 1. Table S3. Linear regression details for the multi-year trends in the timing of the first (p10), median (p50), and last (p90) phases of migration, and migration duration (MD) calculated as p90–p10. The table presents the estimate, standard error (SE), t-statistic, its level of significance (p) and coefficient of determination ( $R^2$ ). Coefficients of the regression line are:  $\alpha$ —intercept,  $\beta$ —slope coefficient. " $\beta \times \text{years}$ " is the estimated shift in migration timing (in days) during 1965–2025 (61 years). A negative value indicates an advance in the date of the analysed percentile over time; a positive value means the opposite; Table S4. Parameters of the best partial "green" and "blue" models. Table presents: Adj $R^2$ —adjusted coefficient of determination, F—best model statistics, Estimate—multiple regression coefficients, SE—standard error of the estimates, t, p—t-test and significance level of each estimate; VIF—variance inflation factor,  $R^2$ —partial determination coefficient for each estimate, pR—Pearson's partial correlation coefficient; Table S5. Model ranking of the partial

“green” multiple regression models for the dates of the first (p10), median (p50), and last (p90) phases of spring passage of the dunnoek at Hel in 1965–2025, used as response variables. Symbols of explanatory variables as 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), 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; Table S6. Model ranking of the partial “blue” multiple regression models for the dates of the first (p10), median (p50), and last (p90) phases of spring passage of the dunnoek at Hel in 1965–2025, used as response variables. Symbols of explanatory variables as 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), 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; Table S7. Model ranking of the final “combined” multiple regression models for the dates of the first (p10), median (p50), and last (p90) phases of spring passage of the dunnoek at Hel in 1965–2025, used as response variables. Symbols of explanatory variables as 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), 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; Table S8. Diagnostics for the best-fitted models for passage parameters (p10, p50, p90) of spring passage of dunnoek at Hel station in 1965–2025.  $R^2$ —multiple coefficient of determination,  $AdjR^2$ —adjusted coefficient of determination;  $AdjR^2/R^2$ —the ratio of these two coefficients of determination, the closer the ratio is to 1, the better the fit of the model to the data.  $AdjR^2 - predR^2$ —the closer this difference is to 0, the better the predictive value of the model, DW—Durbin–Watson statistics and its p value.

**Author Contributions:** Conceptualisation—Z.M. and M.R. Data collection—both authors. Methodology and software development—M.R. and Z.M. Formal analysis and visualisation of the results—Z.M. Supervision and funding acquisition—M.R. The original draft of the manuscript was prepared by Z.M. Z.M. and M.R. contributed to subsequent editing and responses to the reviews. All authors have read and agreed to the published 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 (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).

**Institutional Review Board Statement:** 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.

**Data Availability Statement:** Long-term ringing data are accessible via the Global Biodiversity Information Facility (GBIF) under “Ringing Data from the Bird Migration Research Station, University of Gdańsk” (Nowakowski J. 2017, Occurrence dataset <https://doi.org/10.15468/q5o88L> accessed via GBIF.org on 22 May 2025).

**Acknowledgments:** We are grateful to the thousands of volunteers 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 and Anna Woźnicka, for their extensive work in compiling and maintaining the databases.

**Conflicts of Interest:** The authors declare no conflicts of interest.

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