Journal of Ornithology

# Changes in spring migration: explaining differences between species

--Manuscript Draft--

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| **Manuscript Number:** | JORN-D-25-00296 |
| **Full Title:** | Changes in spring migration: explaining differences between species |
| **Article Type:** | Short Communication |
| **Keywords:** | arrival data; climate change; migration; phenology; variation across species |
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| **Order of Authors Secondary Information:** | |
| **Funding Information:** | |
| **Abstract:** | Advances in spring migration due to climate change are well known for many bird species. Recently, Hirschauer and Stanik (2023) reported changes in spring migration over the last 180 years. There is a huge variability across the considered 57 species, from an advance of 104 days to an arrival delayed by eight days. We apply statistical models to explain this variability. A stepwise backward selection leads to a model with three significant explanatory variables: migration (long-distant vs. short-distant migrants), diet and long-term trend. These three variables together can explain 60% of the observed variation. The model can also predict the strength of phenological adjustment. Thus, we highlight the need for analyses across species and their life history strategies and ecological features in order to investigate avian phenology changes. |

# Changes in spring migration: explaining differences between species

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Abstract: Advances in spring migration due to climate change are well known for many bird species. Recently, Hirschauer and Stanik (2023) reported changes in spring migration over the last 180 years. There is a huge variability across the considered 57 species, from an advance of 104 days to an arrival delayed by eight days. We apply statistical models to explain this variability. A stepwise backward selection leads to a model with three significant explanatory variables: migration (long-distant vs. short-distant migrants), diet and long-term trend. These three variables together can explain 60% of the observed variation. The model can also predict the strength of phenological adjustment. Thus, we highlight the need for analyses across species and their life history strategies and ecological features in order to investigate avian phenology changes.

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## Introduction

Climate change affects the world's flora and fauna. Studies on migratory birds have shown earlier arrival in breeding areas and earlier nesting (Butler 2003, Tryjanowski et al. 2005, Sparks et al. 2007, Romano et al. 2022). However, the response to climate change strongly varies between species (Butler 2003, Andreasson et al. 2023, Romano et al. 2022).

Recently, Hirschauer and Stanik (2023) investigated long-term changes in arrival dates of migrant bird species between an historical period (1842-1865) and a current period (2002-2022) for the same area in Germany (Kassel, Hesse). Data from both periods are available for 57 species. The median first arrival date was earlier in the current period for most species, with a difference of up to 104 days. However, four species arrive later than in the historical period, with a maximum difference of eight days. Thus, the species show a huge variability in the difference between the arrival dates: the difference ranges from -104 to 8 days with a median of -19 (interquartile range: -54 to -7). The response to climate change depends on life history strategies and ecological features of species. Here, we analyse the data presented by Hirschauer and Stanik (2023) to explain the variation across species.

Hirschauer and Stanik (2023) mention, without further statistical analysis, that in the subset of species with a difference of -10 or less days there are predominantly long-distant migrants. Indeed, a weaker advance in long-distant migrants was also observed by Tryjanowski et al. (2005) and confirmed in the meta-analysis presented by Romano et al. (2022). Romano et al. (2022) also showed influences of body size and diet diversity. Moreover, Tryjanowski et al. (2005) found that early species advance their arrival date more, and that species with a decreasing population change less. Tryjanowski and Sparks (2001) observed a negative correlation between earlier arrival dates and increased populations for the Red-backed Shrike (*Lanius collurio*). However, population declines may mask trends in arrival dates (Sparks et al. 2007).

## Methods

The historical and current median arrival dates are presented by Hirschauer and Stanik (2023) in their table 1. We corrected one obvious printing error in that table: the historical median arrival day of the Icterine Warbler (*Hippolais icterina*) is 134 (and not 105) according to the figures 1 and 2 of Hirschauer and Stanik (2023).

In order to explain differences in the magnitude of advancement between species we consider the following traits:

- Long-distant migrants (yes, no)
- Body size
- Diet (insectivorous [i.e. only or mainly insects or other invertebrates], granivorous, carnivorous, omnivorous)
- Diet diversity (broad, narrow; as in Kamp et al. 2021)
- Median historical first arrival date (according to Hirschauer and Stanik, 2023)
- Log-term trend in population size (negative, constant, positive)
- Population size (abundant, common, less common; as in Kamp et al. 2021)
- Habitat (forest, wetlands etc.; as in Kamp et al. 2021)

Species trait data are sourced from Fünfstock and Weiß (2018) as well as Kamp et al. (2021, Table S1). Moreover, long-term trends reported by Gerlach et al. (2025) are used; these trends span species-specific time periods from about 1860-1910 to 2022, and are therefore close to the time periods considered by Hirschauer and Stanik (2023). Gerlach et al. (2025) do not present a trend for the Redwing (*Turdus iliacus*). However, according to migration data from the Italian Alps (Franzoi et al. 2021) “constant” is used as the trend for the Redwing.

First, we separately analyse the different traits using simple linear regressions for continuous variables and one-way analyses of variance for categorical variables, respectively, with the difference in arrival times as dependent variable. All traits with a p-value less than 0.10 are included in a multivariable analysis of covariance model. Based on this multivariable model a stepwise backward selection (Sparks and Tryjanowski 2010) is performed, at each step the variable with the largest p-value is excluded from the model as long as this p-value is larger than 0.10.

Since 45 (79%) of the considered 57 species are insectivorous, we pool the other categories for our main analysis. However, in an additional sensitivity analysis, the four different diet categories are used.

All analyses are performed in SAS version 9.4 (SAS Institute Inc., Cary, NC), and the conventional significance level of 5% is applied.

## Results

In the univariable models the following variables are significant: distance ($p < 0.0001$), body size ($p = 0.0150$), diet ($p < 0.0001$), diet diversity ($p = 0.0173$), historical first arrival date ($p = 0.0006$), and long-term trend ($p < 0.0001$). These variables and population size ($p = 0.0771$) are included in the multivariable model. Habitat ($p = 0.3345$) is clearly not significant and not included in further analyses. In the stepwise backward selection the variables body size, population size, diet diversity, and first arrival date are removed as non-significant. Thus, the resulting model is a three-way analysis of variance model including three categorical variables. All three variables, i.e., distance, diet, and trend, are significant, see Table 1. The final model has a coefficient of determination of $R^2 = 60.4\%$. We checked for interactions between the three remaining variables, but all three possible interactions between two of the remaining variables are not significant.

Based on the final model (see Table 1) the contributions of the different variables on the arrival dates can be estimated, see Table 2. Short-distant migrants prepone their migration 22.54 days more than long-distance migrants. Insectivorous birds migrate 20.92 days later than non-insectivorous species. Species with a negative trend migrate 22.12 days later than species with a positive trend. Species with a constant trend are in between with a difference of 17.00 days to species with a positive trend.

Sensitivity analyses can demonstrate the robustness of statistical results if conclusions do not differ between the main analysis and additional sensitivity analyses. As mentioned above, we repeated the analysis with four diet categories. In this case, the same variables are removed from the model and the three variables distance, diet, and trend, are significant, similar to the main analysis (see supplementary material).

According to Fünfstock and Weiß (2018) we classify the Eurasian Wryneck (*Jynx torquilla*) as a long-distant migrant. However, Kamp et al. (2021) classify this species as a short-distant migrant. Indeed, van Wijk et al. (2013) found that some Central European populations are short-distant migrants. Therefore, in an additional sensitivity analysis the Eurasian Wryneck is classified as a short-distant migrant. The results are very similar (see supplementary material).

As mentioned above, Gerlach et al. (2025) do not report a trend for the Redwing. Therefore, we repeated the analysis without the Redwing. Again, the results are very similar (see supplementary material).

## Discussion

We can explain 60% of the variation across species in the data from Hirschauer and Stanik (2023) by three significant factors: distance, diet, and trend. The result that short-distant migrants adapt more to climate change and prepone migration more is consistent with other studies (see e.g. Butler et al. 2003, Tryjanowski et al. 2005, Gilroy et al. 2016, Romano et al.

2022). Short-distant migrants may have more plasticity and can better rely on meteorological cues indicating conditions further north (Butler et al. 2003, Tryjanowski et al. 2005).

The influence of the diet is not surprising since weather conditions and the availability of food are related especially for insectivorous species. Moreover, in some cases food abundance may have a more important influence on migration than weather (Dale 2024).

Another finding is the result that the long-term trend influences the migration date: species with a positive trend prepone migration most. Sparks et al. (2007) also found that declining species advance least. One might argue that this is a detection bias because species with a positive trend are easier to detect due to the enlarged population size. However, the population size is not significant in our analysis. Species with a negative trend such as the Common Starling (*Sturnus vulgaris*) are still abundant and easy to detect. Some other species with a negative trend live in human settlements and are easy to detect: White Stork (*Ciconia ciconia*), Northern House Martin (*Delichon urbicum*) and Barn Swallow (*Hirundo rustica*). Therefore, the effect could be real. However, our statistical analysis cannot detect the direction of causation. The need to arrive early in the breeding area to occupy the best territories is less important when a population is declining. Thus, declining species might advance their migration less. However, migratory diversity is lower in case of long-distance migration, and therefore, short-distant migrants might be more resilient, their migratory diversity facilitates responses to environmental change (Gilroy et al. 2016). This effect can explain the negative trend in long-distant migrants: they cannot easily prepone their migration and suffer more from climate change.

Our analysis has limitations, it is based on one region only, observer in the two time periods differ, and the analysis is based on not more than 57 species. Nevertheless, our statistical model can predict the strength of phenological adjustment, and it highlights the need for statistical analyses across species and their traits in order to detect avian phenology changes caused by climate change.

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Table 1: Results of the stepwise backward selection: removed and retained variables and related F tests with degrees of freedom and p-values

| Variable | F value | Degrees of freedom | p-value |
|---|---|---|---|
| Body size | 0.03 | 1, 47 | 0.8606 |
| | | Removed from the model in step 1 | |
| Population size | 0.27 | 2, 48 | 0.7647 |
| | | Removed from the model in step 2 | |
| Diet diversity | 1.06 | 1, 50 | 0.3073 |
| | | Removed from the model in step 3 | |
| Median historical first arrival date | 2.59 | 1, 51 | 0.1134 |
| | | Removed from the model in step 4 | |
| Distance | 14.17 | 1, 52 | 0.0004 |
| Diet | 10.58 | 1, 52 | 0.0020 |
| Long-term trend | 4.74 | 2, 52 | 0.0128 |

Table 2: Estimated model parameters and standard errors for the three-way analysis of variance with the variables distance, diet and trend

| | Estimated effect (in days) | Standard error |
|---|---|---|
| Intercept | -28.91 | 7.34 |
| Long-distance migrant | 0 (reference category) | |
| Short-distance migrant | -22.54 | 5.99 |
| Food: insectivorous | 0 (reference category) | |
| not insectivorous | -20.92 | 6.43 |
| Trend: positive | 0 (reference category) | |
| constant | 17.00 | 7.16 |
| negative | 22.12 | 7.27 |

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