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## Title

Weather at the winter and stopover areas determines spring migration onset, progress, and advancements in Afro-Palearctic migrant birds

## Authors

Birgen Haest<sup>1, 2, \*</sup>, Ommo Hüppop<sup>1</sup>, Franz Bairlein<sup>1</sup>

## Affiliations

<sup>1</sup> Institute of Avian Research ‘Vogelwarte Helgoland’, Wilhelmshaven, 26386, Germany

<sup>2</sup> Swiss Ornithological Institute, Sempach, CH-6204, Switzerland

\* Corresponding author: [birgen.haest@protonmail.com](mailto:birgen.haest@protonmail.com); +49 176 749 786 82

## ORCID

Birgen Haest: [0000-0002-8739-6460](https://orcid.org/0000-0002-8739-6460)

Ommo Hüppop: [0000-0001-7048-3747](https://orcid.org/0000-0001-7048-3747)

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## Author contributions

B.H., O.H., and F.B. conceptualized the study and contributed ideas. B.H. designed and conducted the analyses. B.H. wrote the paper, with contributions of O.H. and F.B.

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## Abstract

Climate change causes changes in the timing of life-cycle events across all trophic groups. Spring phenology has mostly advanced, but large, unexplained, variations are present between and within species. Each spring, migratory birds travel tens to tens of thousands of kilometers from their wintering to their breeding grounds. For most populations, large uncertainties remain on their exact locations outside the breeding area, and the time spent there or during migration. Assessing climate (change) effects on avian migration phenology has consequently been difficult due to spatial and temporal uncertainties in the weather potentially affecting migration timing. Here, we show for six trans-Saharan long-distance migrants that weather at the wintering and stopover grounds almost entirely ( $\approx 80\%$ ) explains inter-annual variation in spring migration phenology. Importantly, our spatiotemporal approach also allows for the systematic exclusion of influences at other locations and times. While increased spring temperatures did contribute strongly to the observed spring migration advancements over the 55-year study period, improvements in wind conditions, especially in the Maghreb and Mediterranean, have allowed even stronger advancements. Flexibility in spring migration timing of long-distance migrants to exogenous factors has been consistently underestimated due to mismatches in space, scale, time, and weather variable type.

## Significance Statement

Migratory birds show alarming declines across the globe, especially birds that migrate over long-distances. A limited ability to adjust spring arrival to climate change at the breeding grounds, especially compared to residents and shorter-distance migrants, is thought to be a major cause. Our results show that breeding area arrival of cross-continental migrant birds is nevertheless, similarly to short-distance migrants, largely driven by weather conditions at the wintering and stopover grounds. Additionally, our study indicates that not only temperature rise but also more favorable wind conditions have allowed birds to arrive earlier. A better understanding of climate change influences on the timing of biological phenomena is vital to understanding and ultimately battling the consequences of climate change on population demographics.

## Introduction

Ample evidence now exists that climate change is already impacting a broad range of organisms across all taxa, from plants to mammals, and across the globe (1–3). Migratory species are likely to be particularly vulnerable to climate change, as they presumably evolved to profit from spatiotemporally distinct, yet largely predictable, seasonal patterns of natural resource productivity (4, 5). Populations of long-distance, e.g. trans-Saharan, migratory bird species are currently declining considerably faster than those of resident or short-distance migrants (6, 7). Climate change has been repeatedly suggested to be one of the major causes of these (differences in) population declines (4, 6, 8, 9), yet the specific mechanisms through which this might be occurring are anything but clear (4, 6, 7, 10–12). A limited ability of long-distance migrants to adjust spring arrival to climate change at the breeding grounds has been suggested to be a major contributing factor (8, 13). If the distance between wintering and

breeding grounds is rather limited, spatiotemporal (auto-)correlations in the weather between the two areas render the conditions at the former to be a somewhat reliable cue to estimate appropriate arrival at the latter (14). For larger distances, these connections no longer hold, which, together with reduced seasonality in the tropics, has contributed to the hypothesis that long-distance migrants must rely primarily on endogenous rhythms for spring migration timing (15).

For a long time, it was indeed, and perhaps continues to be, thought that spring migration of long-distance migrants, especially the onset, relies primarily, or at the very least much more than for short-distance migrants, on endogenous rhythms (11, 15–18). Initially, this led to the suggestion that neither conditions at the wintering nor stopover areas *en route* to the breeding grounds have much influence on arrival at the breeding grounds (4, 13). Notwithstanding, strong advancements in spring migration timing of long-distance migratory birds have been repeatedly reported over the past two decades (11, 19–22). This has led to an ongoing debate with two somewhat opposing, albeit not necessarily mutually exclusive hypotheses. Some argue that given spring departure is under strong endogenous control and long-distance migrants have a limited ability to phenotypically adjust their advancement along the migration route, the advancement in arrival at the breeding ground is thus most likely to be caused by an evolutionary response in spring departure timing at the wintering grounds (19, 20, 23). Meanwhile, however, many studies have also been reporting on correlations between spring arrival (or passage) advancement of long-distance migrants and climate (change) at (approximate) wintering areas, but especially (potential) stopover areas along the migration route (11, 20, 21, 24). As a result, some suggest that phenotypic responses to weather along the migration route is the main mechanism of advancement for long-distance migrants, while spring departure from the wintering grounds changes little because it is under strong endogenous control (17, 18, 21). While mainly limited to a number of songbirds, the experimental evidence on internal clocks and the relevance of photoperiod as a trigger of migration are irrefutable (15, 25). Nonetheless, under laboratory conditions, endogenous rhythms often stray away rather far from one-year lifecycles, sometimes up to several months (15). Moreover, outside of experimental laboratory settings, environmental conditions encountered by individuals at the departure and stopover areas at the same date are different each year. Making the best decision, hence, inevitably entails some flexibility in the migratory response (25).

A major hurdle in investigating potential climate change effects on spring migration phenology, and consequently in further unraveling the exact mechanisms through which the observed advancements take place, has been the large uncertainties about where and when most individual migratory birds or populations exactly go to outside the breeding area, including which routes they take there (14, 25). One approach to deal with the spatial uncertainty has been to use large-scale climate indices, e.g. El Niño indices or the North Atlantic Oscillation index (21). Others have similarly used summary values of weather (or vegetation) conditions by averaging over (very) large areas, such as the entire Sahel region (20, 25) or the entire known wintering area of the species. The validity and biological meaning of the reported effects of such large-scale indices has recently, however, been strongly questioned (26). Many others resorted to using climatic conditions measured at the area of passage or arrival, even though these are not necessarily related to those where the birds are coming from and hence are more likely reacting to (14, 25). Next to these potential mismatches in space and scale, strong assumptions are generally also made on the timing, i.e. start and duration, of the climatic influence. The vast majority of studies use variables defined by months, e.g. monthly average temperature or monthly precipitation (14). Only sometimes, ad hoc periods are decided upon based on the species' ecology (21, 25), and although the exact timing of influences is in most migrant species and populations perhaps just as uncertain

as the locations, only very rarely an explicit time window search has been applied to determine the most likely time period of influence (14, 24).

Temperature has been repeatedly shown to be the most important exogenous factor impacting spring migration timing (11, 14, 25, 27), yet precipitation and wind effects have also been shown to have an effect (14, 28). For migratory herbivores, e.g. geese, primary productivity has been proposed to be a more likely cue or even better predictor of spring migration phenology. While it has been suggested that this green wave hypothesis could even be extended to insectivorous (or carnivorous) migrants (29, 30), it actually seems, even for herbivores, far from ubiquitously applicable (5).

In summary, the ongoing debate about the extent and mechanisms of climate change influences on spring migration phenology of long-distance migrants, has proven challenging due to the difficulties in identifying the appropriate location, time, scale, and type of possible weather influences. This resulted in most studies to resort to very rough spatial and temporal approximations or guesses of possible climatic influences. The inherent spatiotemporal inter- and auto-correlation of weather variables, however, strongly increases false positive probabilities for such approaches, further exacerbating the issue by resulting in many ‘significant’ yet biologically meaningless correlations (14). Not surprisingly then, reported effects of weather on spring migration timing have been strongly heterogeneous, and the current evidence on the location, time and types of climate change effects on spring migration phenology of long-distance migrants birds has remained largely anecdotal and often contradictory.

We use a recently developed spatiotemporally systematic method (14, 31) to overcome much of the challenges and uncertainties in matching the right location, time, and type of weather influences on spring migration phenology. The method consists of two main analyses parts. First, a per grid cell analysis is performed for each species of all possible time windows of any length between two given dates, for each weather variable and over a spatial grid covering the area of interest to the studied process. In other words, as few as possible assumptions are made on which weather variable influences spring migration in which location or during which timeframe. Instead, we search for the best performing time window for each grid cell and weather variable type (using the ‘*climwin*’ R package (32, 33)), by comparing AICc model values with a base model that consists of the temporal trend for that particular species. By applying the same procedure to a number of randomizations of the weather data, we then estimate the probability of obtaining a similar performing ‘best’ time window by chance only. Importantly, the method not only enables identifying the area, time, and type of the most likely weather influences for each species, but also excluding other areas, times, and types of weather that are very unlikely to be of any influence. For each species, this first step leads to a long-list of “weather variable – location – time window” combinations, henceforth called candidate weather signals, that might possibly be influencing the migration phenology at the location of observation. Due to spatiotemporal (auto-)correlation in the weather data, however, the long-list still contains many spurious candidate weather signals (14). In the second part of the analysis, the long-list of candidate weather signals for each species is then analyzed using an ensemble of variable importance methods to obtain a final list of the few most likely “weather variable – location – time window” influences on migration phenology.

We applied the method to the mean spring passage dates of six long-distance migrant species at the island of Helgoland (Germany) over the period 1960-2014 (Table S1 and Table S3), searching a spatial grid that covers all somewhat possible wintering or spring stopover locations prior to passage at Helgoland (see the Methods - Weather data section). As such, we first simultaneously determined the space, time window, and type of the most likely weather influences on the inter-annual variability in spring migration phenology (Table S8 to

Table S10). After determining the most influential weather influences for each of the six species, we then combined their effects on migration phenology with their change over time to assess the contribution of each climatic effect to the overall advancement in spring migration of the respective species (Table S12 and Table S13). A more detailed description of each step of the methodology is provided in the Materials and methods section. The code and data to replicate our results are available in a public repository (34).

## Results

We found that a mixture of wind, temperature, and precipitation effects at the winter and spring stopover grounds (Fig. 1), explains between 72% and 86% of the variance in spring migration phenology of long-distance migrants (Table 1). Predictive  $R^2$  (calculated using leave-one-year-out) were very similar to adjusted  $R^2$  (35) values, confirming robustness of the final identified weather signals. Repetitions of the analysis over 200 randomizations of each species' MSPD, furthermore, confirmed that such strong relationships (i.e. such high adjusted and predictive  $R^2$  values) are extremely unlikely (0%) to be obtained due to chance alone using our method (see Materials and Methods, Fig. S5 and Table S11). While we searched for weather influences over an area spanning from northern Scandinavia to Cameroon, and from Iceland and the Canary Islands to Poland, Greece, Libya, and Chad (see Materials and methods, Table S2, and Fig. S1 to Fig. S4), we only found weather influences at locations that are very likely winter or spring migration stopover locations (Fig. 1). The majority of the weather influences, especially in the case of winds, seem to typically be located just prior or after crossing an ecological barrier, such as the Sahara desert or the Mediterranean Sea (Fig. 2a). Additionally, temperature in central Europe, especially Germany, just prior to passage at Helgoland, seems to play an important role in fine-tuning migration progress over the last stretch of spring migration. An apparent lack of wind influences after crossing the Mediterranean strongly fits with the fact that from thereon birds are migrating almost exclusively over land. They can hence make a landing to rest or refuel at any time, rendering favorable wind conditions less important. Temperature conditions this far north along the route, however, are likely to indeed become much more informative and predictive about the conditions further north at the breeding grounds, indicating similar cue responses at these latitudes as observed in many short-distance migrants (14).

The time windows of the weather influences typically occurred from about one to two months before the start of their migration passage at Helgoland (across the whole study period) up to just prior or during the period of migration passage at Helgoland (Fig. 1). Most, if not all, of the time windows occurred just prior or during periods that birds are likely to be present at their winter and stopover locations, even though we allowed for time windows of any size between 1 and 365 days or 1 and 182 days, and starting up to 365 or 182 days prior to July 1 for temperature and precipitation, and wind, respectively. For some of the time windows, some uncertainty was present in the exact timing due to the inherent temporal autocorrelation of weather variables (Table S10).

Wind was the most influential weather type on inter-annual variability in spring migration phenology (44% of the overall weather type importance), but especially also in terms of causing the spring migration advancement (52%; Fig. 2; Table S13). Temperature had a similarly strong impact on inter-annual variability (41%), but this was somewhat reduced when assessing impacts on the temporal advancements in spring migration (36%). The role of precipitation was comparatively rather minor (around 15% in both cases). These results on the relative weather type importance strongly question whether the somewhat established hypothesis that temperature is the most important exogenous factor impacting spring

migration phenology (14, 18, 25, 27), actually holds for long-distance migrant birds in specific, or even in general.

For two of the six study species, rather strong linear temporal trends towards advancement still remained after accounting for the most influential weather signals (Garden Warbler:  $-0.09 \pm 0.02$  days/year or 47% of the original linear trend, and Willow Warbler:  $-0.12 \pm 0.03$  days/year or 41% of the original linear trend; Table S14). For two more species, moderate trends towards advancement remained (Common Whitethroat:  $-0.07 \pm 0.03$  days/year or 39% of the original linear trend, and Spotted Flycatcher:  $-0.05 \pm 0.02$  days/year or 31% of the original linear trend; Table S14). The adjustment of spring migration phenology to weather conditions at the wintering and stopover grounds was, hence, only sufficient to fully explain the observed trends in spring migration phenology for two of the six species (i.e. 33%; Common Redstart and European Pied Flycatcher).

## Discussion

As we did not work on individual birds, we cannot make any definite claims on whether the observed relationships between the weather variables and spring migration timing are due to phenotypic plasticity alone, or micro-evolutionary responses are also involved (10, 36). For each species, however, a high amount of the variation in migration phenology was explained by the weather conditions at only four or five winter or spring stopover areas (Table 1). This does seem to strongly suggest that phenotypic plasticity plays a key role in the recent advancements in spring migration phenology of long-distance migrants, including to a similar extent as for short-distance migrants (14). As such, while endogenous rhythms and photoperiod do play an irrefutable role in regulating spring migration (onset) in long-distance migrants (15), the rigidity in the real world, i.e. outside of laboratory settings, and relative importance compared to exogenous influences, i.e. conditions at the winter and stopover grounds, may have been consistently overestimated. Despite the high amount of explained variance in spring migration phenology by weather at the winter and spring stopover grounds across all six study species (Table 1), the observed advancements in spring migration were explained fully in only two (Table S14). Even if we were to attribute all of the explained variance in spring migration timing to phenotypic plasticity to weather at the wintering and stopover grounds, it would not suffice to fully explain the observed advancements. As such, again similar to observations in short-distance migrants (14), other adaptive processes such as micro-evolutionary processes (37, 38) or (winter or breeding) range changes (39) are, hence, likely also pushing towards advanced spring migration.

The locations (and relative effect sizes) of the weather influences, i.e. a combination of sub-Saharan likely wintering areas and Mediterranean and European spring stopover sites (Fig. 1 and Fig. 2), confirm that much, perhaps most, of the spring migration advancement in long-distance migrants occurs in response to weather along the migration route (17, 18, 21). Flexible responses to conditions at the wintering grounds, however, might also be very common: five out of the six species had at least one signal from a very likely wintering area. Depending on the species, their influence on the overall spring advancement may also play a substantial role, e.g. up to almost 50% for European Pied Flycatcher (Fig. 1; Table S10 and Table S12).

In summary, our results strongly suggest that there have been mismatches in space, time, scale, and weather variable type between the variables of influence and the variables used in analyses. This has led to a consistent underestimation of the flexibility of long-distance migrant birds in spring migration onset from the wintering areas, as well as adjustment of progress along the migration route. As such, the suggested negative impacts of climate change

on long-distance migrants' demographics due to their assumed inabilities of advancing spring departure from the wintering grounds (8, 13) has at least been based on false assumptions. While it is beyond doubt that climate change has already impacted the timing of several lifecycle events of migratory birds (1, 3, 4, 19, 26), strong evidence about how climate change is impacting migrant bird species demographics through changes in the timing of the migratory cycle, has yet to emerge (10). In fact, our results indicate that not only do, at least some, long-distance migrants strongly adjust their spring migration timing to prevailing weather conditions at the wintering and stopover locations, but also that favorable migratory conditions are now occurring more frequently (e.g. less days with headwind and more days with tailwinds, Fig. 1 and Table S12). Interestingly, a similar increase in favorable wind conditions has also been projected for future spring migration in North America over the current century (40). While many other potential pathways of climate change influences on bird population sizes have been suggested (4), current evidence still predominantly points towards (anthropogenic) land use change effects (6, 7).

## Materials and methods

### Spring migration passage data

The trapping garden on the island of Helgoland, Germany (54° 11' N, 07° 53' E; sometimes also spelled as Heligoland) is a constant-effort bird ringing site. Since 1960, comparable efforts and standardized methods are used with daily catches in the trapping garden throughout the whole year. Barely any landbirds breed on Helgoland, especially not long-distance migrants (21, 41, 42). Consequently, the birds used in this study to estimate spring migration phenology, are all birds in transit.

We analyzed data from six trans-Saharan, i.e. long-distance, migrants. We used yearly mean spring passage date (MSPD) over the period 1960–2014 as a measure of migration phenology (Table S1). To minimize potential bias due to the use of the Gregorian calendar, we converted trapping dates to Winter Solstice-based dates (WSD) instead of day-of-the-year (43), but report dates throughout the paper as the approximate Gregorian calendar date. Yearly MSPD was calculated as the mean of the winter solstice-based trapping date (WSD) of all birds between WSD 51 and 166, i.e. February 20 to June 14 approximately. To allow comparison between species that are potentially subject to similar weather conditions prior to or during their migration, the species in all the (supplementary) tables and figures in the paper are ordered by mean spring passage date.

Birds of a certain species that migrate through Helgoland stem from different breeding populations (44). As such, the measured MSPD at Helgoland will be influenced by changes in the spring phenology of each of these populations, which could potentially obscure the relation between the measured MSPD and the influencing weather conditions for each specific population. If the phenology of these different populations is, however, (a) related to changes in weather in their wintering or stopover areas, (b) the different populations show a relatively high winter and stopover-site fidelity, and (c) each population is represented by a sufficient amount of birds in the trappings, the fact that the observed MSPD is influenced by each of these populations should enable to link the observed MSPD to each of the different wintering or stopover sites (25). Birds from different wintering areas may also be influenced *en route* by the same weather conditions at a certain time and place, e.g. shared stopover areas or prior to crossing an ecological barrier. The wintering or stopover areas of a species also might have changed over the total analyzed time period (39, 45). Yet if these areas are maintained for a long enough subset of the total analyzed time period, or the shifts are not over large distances compared to the spatial resolution of the weather grids, it should be

possible to link the observed MSPD to all of the different wintering or stopover locations. As such, using migration passage data has both advantages and disadvantages compared to breeding area arrival data.

### **Weather data**

We used spatiotemporal data of air temperature, precipitation, and wind from the NCEP Reanalysis I database (46, 47), which we acquired using the R package *RNCEP* (34, 48). The spatial grid covered an area from roughly 2° to 74° N and 19° W to 24° E, ranging from northern Scandinavia in the North to Cameroon in the South, and from Iceland and the Canary Islands in the West to Poland, Greece, Libya, and Chad in the East. The spatial resolution of a grid cell ranged from 1.875° to 3.75°, depending on the weather variable (Table S2). Ocean grid cells were masked from the analysis. For each day and land grid cell, we derived three variables from the NCEP database: mean daily air temperature, daily precipitation sum, and wind direction at midnight (UTC). We analyzed midnight winds only, and not winds during the day, as all species in our study are known to mainly migrate during the night. In the time window analyses, the wind direction data were used to calculate the number of nights for both winds originating from and in the direction of Helgoland within any given time window, by counting every day with a wind direction that fell between -45 and +45° of the angle between Helgoland and the center of the grid cell under analysis. Depending on the location of the grid cell relative to Helgoland, we then interpreted these to be head- or tailwinds. We chose to test both measures for wind effects on migration as both hypotheses, i.e. headwinds delay migration and tailwinds advance migration, represent different processes.

### **Avoiding spurious correlations due to shared trends and temporal autocorrelation**

If two time series both show a temporal trend, correlating the two series without taking into account these shared trends will very often yield high, yet spurious, correlations (26, 49). Even after temporal trends are accounted for, any remaining autocorrelation in the time series may similarly produce spurious correlations (50). As such, we first determined whether a linear, quadratic, or cubic temporal trend was most appropriate for the MSPD time series of each species, by comparing the second-order Akaike Information Criterion (AICc) values (51) for linear, quadratic, and cubic trend models. If a quadratic or cubic temporal trend model had an AICc value that was more than two units lower than a linear trend model, we judged the higher-order model to be a better approximation of the trend over time. The identified trend model for each species was used as the base model (for comparison of reduction in AICc values by adding a weather variable) in the subsequent time window analyses. All species showed advancements in MSPD over the study period. Four of the six species had a linear trend, while for Willow Warbler and Common Whitethroat a quadratic and cubic trend, respectively, was most appropriate to account for trend (Table S3). We applied Augmented Dickey-Fuller tests (using the *urca* R package (52)) to verify that the chosen trends models had successfully reduced the MSPD time series to stationarity (Table S4). We checked and found no remaining autocorrelation in the residuals of the trend models with a Durbin-Watson test up to lag two (using the *car* R package (53); Table S5). The observed non-linearity of spring migration phenology in two of the six species could be occurring through various mechanisms, e.g. non-linear trends of influencing weather variables, or varying influences (in space and time) working in different proportions on different populations of the birds migrating through Helgoland. Future meta-analyses across many species, populations and time could provide insights into such potential underlying mechanisms.



## **Finding the “weather variable – location – time window” combinations that influence spring migration phenology**

To identify the most likely weather effects on the MSPD at Helgoland of each of the six study species, we applied a recently developed spatiotemporal methodology (14, 31), which involves a sequence of two main chunks of analysis. The first step consists of performing a time window analysis on each grid cell for each of the weather variables of interest (i.e. temperature, precipitation, number of days with tail- or headwind, Table S2) to find the best performing time window. We searched all time windows of any size larger than 14 days and up to 365 (temperature and precipitation) or 183 days (wind variables) in the past from the reference date 1 July (Table S6 and S7). We did this using the ‘*climwin*’ R package (32, 33) by calculating AICc model values for all time windows, and comparing them to the AICc of the predefined temporal trend model for that species (Table S3). The time window showing the biggest AICc reduction was identified as the best-performing time window. To subsequently estimate the probability of obtaining a similar performing best time window due to chance alone, we then repeat the time window analysis for a number of randomizations of the weather data. Ideally, one would do this for a large number of randomizations, e.g. a thousand or more, to accurately approximate the actual  $\Delta\text{AICc}$  distribution obtained by chance alone. Repeating such a high number of randomizations for multiple weather variables and over a large number of grid cells, however, quickly becomes an extremely resource-intensive task. As such, we used the alternative probability statistic  $P_c$  of the ‘*climwin*’ R package which was developed specifically for such situations (32, 33). Using as little as five randomizations, the  $P_c$  statistic already provides a reliable estimation of whether a similar performing best time window is likely to be obtained by chance.  $P_c$  ranges from 0 to 1, with values closer to 0 expressing a higher probability that such a strong relation is unlikely obtained by chance. Using simulated datasets with a sample size of 47, and a cut-off value of  $P_c < 0.5$  to decide on whether a signal is real, the false-positive and false-negative rate were both between 0.05 and 0.08 (32). To even further lower the amount of false positives, we lowered the  $P_c$  threshold to 0.3. Furthermore, our larger sample size (55 years compared to the 47 in the simulated datasets) also further decreased both false-positive and false-negative rates. In summary, in the first step the correlation of the identified best time window of a grid cell’s weather with MSPD was considered to be unlikely due to chance when its  $P_c$  statistic was lower than 0.3. The time window analyses were performed on a per-species, per-weather-variable, and per-grid-cell basis. For ease of reference, we summarized all of the settings and decision rules we used for the analyses in Table S6 and Table S7. Due to spatiotemporal autocorrelation, neighboring cells often had similar best-performing time windows with, sometimes only slightly, different  $\Delta\text{AICc}$  values. This often resulted in spatial gradients in the  $\Delta\text{AICc}$  maps we obtained for each weather variable. We chose to select as the candidate signals, the cells with the regional  $\Delta\text{AICc}$  maxima as the most representative of the potential relation between the weather variable for that area and the MSPD. This first step of the analysis resulted in an initial long-list of 310 candidate weather signals across all six species (38 to 67 candidates depending on the species; Table S8 and Fig. S1 to S4).

The second main part of the analysis consists of a combination of several feature filtering and variable importance algorithms to narrow down the long-list of candidates to those that are most likely to be the most influential on the MSPD of each species. In this part of the analysis, we no longer included the temporal trend variables. Spurious correlations due to trend only have already been checked for, and are hence no longer an issue at this stage. Instead, we now actually want to assess how strong the relationships are with MSPD without accounting for temporal trends. First, we checked whether the weather variable still showed a strong correlation with MSPD when not accounting for temporal trends. This led to the removal of 50 candidate signals because the model without accounting for trends had an AICc

compared to an intercept-only model that was less than two units lower. Next, we checked for collinearity among the remaining candidate signals. We removed 35 signals that had a Pearson correlation  $> 0.7$  with another candidate that had a bigger  $\Delta AICc$  with an intercept-only model. Subsequently, we removed 135 more signals using the *boruta* method (54) to reduce the maximum number of candidate signals per species to 15. Based on an ensemble variable importance analysis (51, 54–56) (Table S9), we ultimately extracted 26 signals across the six species that are very likely to be related to MSPD at Helgoland (Table S10, Fig. 1, and Fig. 2).

Even though we tailored our approach towards avoiding false positives, we cannot exclude them entirely (31). Even when no relationship whatsoever exists between MSPD and weather at any location and time window, we still might identify some in the time window analysis step (32). While the variable filtering in the second part of the analysis likely removes many, if not most, of these false positives, some might still remain, and may ultimately be designated as (relatively) important influences. This means that even in the absence of any relationship whatsoever between a biological response variable (i.e. MSPD in our case) and weather at any location and time, the approach might still end up with a number of false final weather variables by chance only. To estimate the probability of obtaining such a final list of (false) weather influences that show a relationship with MSPD that, due to chance only, is similarly strong as those we obtained for each species (Table 1), we repeated the full spatiotemporal analysis on 200 randomized versions of each species' MSPD. For each of these randomizations, we calculated the adjusted and predictive  $R^2$  values of both: (a) the model consisting of up to four variables identified as the most important influences, and (b) the best-performing model (in terms of  $AICc$ ). Using the distributions of all of the resulting adjusted and predictive  $R^2$  values across each species' randomizations (Table S11 and Fig. S5, we then estimated the probability of obtaining similarly performing final weather variables by chance only (i.e. 1 - the percentile of the  $R^2$  values of Table 1, in the  $R^2$  distributions of the randomizations).

### Contributions of each weather variable to the temporal trend in spring migration phenology of the species

The influence of a weather variable on inter-annual variability in spring migration phenology will only result in a push towards advancement (or delay) in the temporal trend of the migration phenology if the weather variable itself is also changing over time to a certain degree in a certain direction. To calculate the combined effect of (1) the change in MSPD in response to the weather variable and (2) the change in the weather variable over time, and, hence, the contribution of each of the final weather variables' influence to the temporal trend in MSPD, we used the chain rule (31, 57):

$$\text{climate contributions to trend in MSPD} = \sum_{i=1}^n \left( \frac{\partial MSPD}{\partial Climate_i} \times \frac{dClimate_i}{dTime} \right),$$

where  $n$  is the total number of influencing weather variables for a given species. We used the regression coefficients of a multiple linear regression between MSPD and all of the identified final weather variables for each of the species separately to estimate the various  $\partial MSPD / \partial Climate_i$ , and a simple linear regression between the respective weather variable and time, i.e. years, to estimate  $dClimate_i / dTime$ . Standard errors were calculated following error propagation rules (58). This approach by definition ignores any other (e.g. non-climatic) factors that might possibly affect changes in MSPD over time.

While weather variable effects on inter-annual variation in MSPD consist of a mix of positive and negative relationships, their contributions to the temporal trend in MSPD has been consistently towards advancements (Fig. 1 and Table S12). In other words, throughout the course of the 55-year study period, weather conditions favorable for migration progress have been occurring earlier (e.g. temperature) or more frequently (e.g. tailwinds), and conditions unfavorable for migration progress have been occurring less frequently (e.g. precipitation and headwinds).

### **Relative importance of the weather variable types in terms of effect and temporal trend contributions**

We calculated the relative overall importance across all species of the three different weather variable types, i.e. temperature, precipitation, and wind, on the inter-annual fluctuations in MSPD at Helgoland by summing their respective mean relative variable importance values. We, furthermore, also calculated the importance of each climate variable in terms of relative contributions to the temporal trends in MSPD over the past decades by summing the absolute values of the trend contributions for each climate variable, divided by the total sum of the trend contributions (Table S13).

### **Assessing remaining linear trends in MSPD after accounting for the identified weather signals**

After identifying the weather variables influencing and determining their effects on MSPD, we checked whether their combined effect completely explained the observed trends in MSPD. We did this by comparing the AICc of the model including all influencing weather variables for that species with the model that additionally included a linear temporal trend, i.e. a ‘year’ variable.

### **Data and code availability**

All R code and the phenology dataset, necessary to replicate the results of this study can be accessed at: <https://doi.org/10.5281/zenodo.3629178>.

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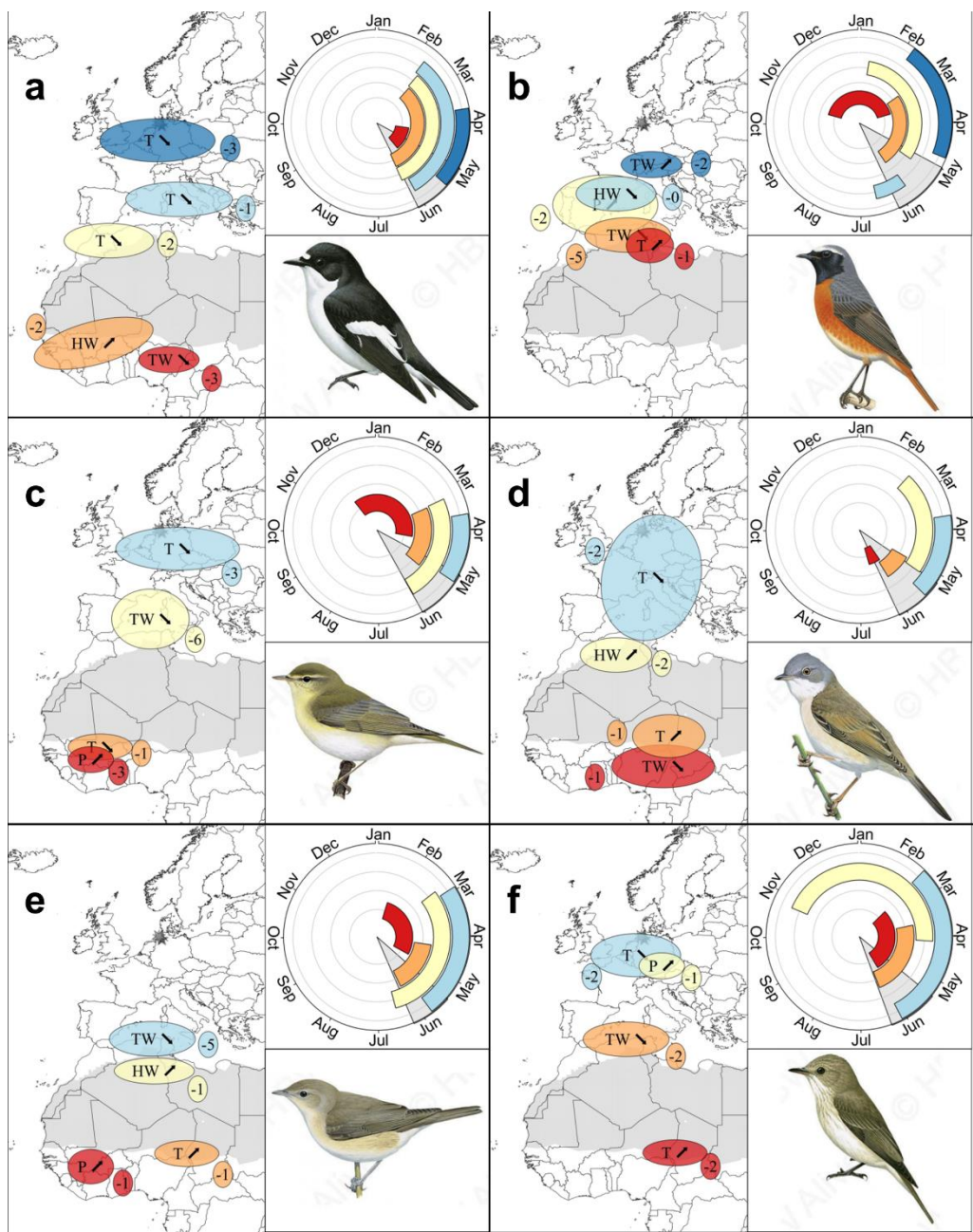
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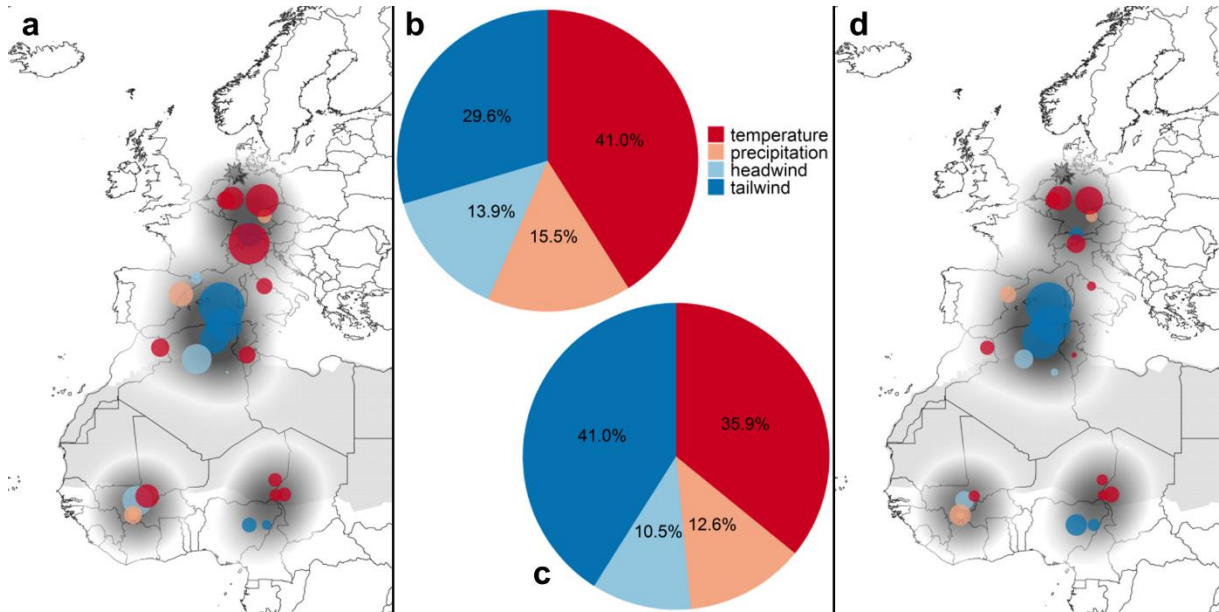
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**Fig. 1. Location, timing, and resulting change in spring phenology over the years 1960-2014 of the identified most important weather variables that are likely to influence mean spring passage at Helgoland for (a) European Pied Flycatcher, (b) Common Redstart, (c) Willow Warbler, (d) Common Whitethroat, (e) Garden Warbler, and (f) Spotted Flycatcher. Marked locations may represent smaller or larger areas of influence than what is marked in the map (see text). T: temperature; P: precipitation; HW: headwind; TW: tailwind. The grey background triangles in the upper right timing figures, represent the 5<sup>th</sup> and 95<sup>th</sup> percentile of all birds passing at Helgoland over the entire study period 1960-2014. The resulting change numbers in the maps are the number of days migration changed over the whole study period due to that weather influence, calculated using the chain rule (see Materials and Methods section, and Table S12). Helgoland is marked with a star. (Bird) Illustrations reproduced by permission of Lynx Edicions.**





**Fig. 2. Comparison of relative weather variable importance in terms of the effect on inter-annual variation of spring migration phenology (a, b), and their contributions to the advancement in spring passage over the study period 1960-2014 (c, d). (a)** Locations and relative effect sizes, based on the standardized regression coefficient using model averaging (see Methods), of the weather variables influences on **inter-annual variation** in mean spring passage dates; **(b)** Overall weather variable type importance across all species, in terms of explaining inter-annual variability in spring migration phenology; **(c)** Overall weather variable type importance across all species, in terms of contributions to the **long-term advancements** in spring migration passage; **(d)** Locations and relative sizes of the trend contributions of each weather variable to the advancement in spring migration passage. Point sizes in (a) and (d) are on a relative scale stretching from the respective overall minimum to the maximum across all species. The location of Helgoland is marked with a star.



## Tables

**Table 1 Explained variance in spring migration phenology and predictive performance using a linear model with all of the final identified weather signals for each species (see Fig. 1), but not the temporal trend variables (Table S3).** Adjusted  $R^2$  is defined as in (35). Predictive  $R^2$  was calculated leave-one-year-out.

Species	Adjusted $R^2$	Predictive $R^2$
European Pied Flycatcher	0.86	0.83
Common Redstart	0.76	0.71
Willow Warbler	0.80	0.78
Common Whitethroat	0.72	0.69
Garden Warbler	0.80	0.77
Spotted Flycatcher	0.76	0.73