Title

Autumn bird migration phenology: A potpourri of wind, precipitation, and temperature effects

Running head

Climate change and autumn migration phenology

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Abstract

Climate change has caused a clear and univocal trend towards advancement in spring phenology. Changes in autumn phenology are much more diverse, with advancement, delays, and ‘no change’ all occurring frequently. For migratory birds, patterns in autumn migration phenology trends have been identified based on ecological and life-history traits. Explaining interspecific variation has nevertheless been challenging, and the underlying mechanisms have remained elusive. Radar studies on non-species-specific autumn migration intensity have repeatedly suggested that there are strong links with weather. In long-term species-specific studies, the variance in autumn migration phenology explained by weather has, nevertheless, been rather low, or a relationship was even lacking entirely. We performed a spatially explicit time-window analysis of weather effects on mean autumn passage of four trans-Saharan and six intra-European passerines to gain insights into this apparent contradiction. We analysed data from standardized daily captures at the Heligoland island constant-effort site (Germany), in combination with gridded daily temperature, precipitation and wind data over a 55-year period (1960–2014), across northern Europe. Weather variables at the breeding and stopover grounds explained up to 80% of the species-specific interannual variability in autumn passage. Overall, wind conditions were most important. For intra-European migrants, wind was even twice as important as either temperature or precipitation, and the pattern also held in terms of relative contributions of each climate variable to the temporal trends in autumn phenology. For the trans-Saharan migrants, however, the pattern of relative trend contributions was completely reversed. Temperature and precipitation had strong trend contributions, while wind conditions had only a minor impact because they did not show any strong temporal trends. As such, understanding species-specific effects of climate on autumn phenology not only provides unique insights into each species’ ecology, but also how these effects shape the observed interspecific heterogeneity in autumn phenological trends.

Introduction

Every year, billions of animals migrate various distances across the Earth to increase their chances of survival and reproductive success (Bauer & Hoyer, 2014; Dokter *et al.*, 2018). Over the past decades, climate change has strongly influenced the timing of different aspects in the annual cycles and life stages of migratory animals (Parmesan & Yohe, 2003). These phenological changes could have consequences for their fitness and survival (Miller-Rushing *et al.*, 2010; Bairlein, 2016; Visser & Gienapp, 2019), which has resulted in further impetus to disentangle the specific relationships between weather and migration phenology.

While the influence of climate on many aspects of spring phenology in animals and plants has received a lot of attention, the relationship between climate and autumn phenology has been relatively neglected (Gallinat *et al.*, 2015). Consequently, the climatic factors controlling autumn phenology are still poorly understood (Walther *et al.*, 2002; Renfrew *et al.*, 2013; Gallinat *et al.*, 2015; Rivrud *et al.*, 2016; Xu & Si, 2019). In general, spring (and summer) activities and events have shown a rather clear advancement in response to recent climate change across taxa (Menzel *et al.*, 2006; Thackeray *et al.*, 2010). The change in autumn events and activities, however, is much less uniform, with advancements, no change, and delays all being observed regularly (Lehikoinen *et al.*, 2004; Menzel *et al.*, 2006; Smith & Paton, 2011; Chambers *et al.*, 2014).

For birds in specific, it is also generally accepted that spring migration has been advancing in response to recent climate change (Jonzén *et al.*, 2006; Knudsen *et al.*, 2011; Haest *et al.*, 2018a), and evidence has been accumulating that temperature is the most important climatic driver of spring migration phenology (Usui *et al.*, 2017; Haest *et al.*, 2018b; Van Doren & Horton, 2018). Notwithstanding, effects of weather and climate change are species- and likely even population-specific (Carey, 2009; Shaw, 2016; Haest *et al.*, 2018b), and weather factors other than temperature cannot be ignored (Haest *et al.*, 2018b). The link between migration

and climate has, amongst all animal groups, by far been studied most intensively in birds (Shaw, 2016). Yet, both the general patterns and the relationships with weather have again been investigated much less in autumn than in spring bird migration (Jenni & Kéry, 2003; Gordo, 2007; Bitterlin & Van Buskirk, 2014; Miles *et al.*, 2017). Similarly to spring migration, autumn migration nevertheless plays an essential, albeit different, role in the full annual cycle of birds. Mortality during autumn migration, for example, has been suggested to have strong demographic consequences (Klaassen *et al.*, 2014; Hewson *et al.*, 2016). An increased understanding of the relationship between autumn migration phenology and weather, as well as the potential impacts of climate change, is hence a vital piece of the puzzle towards understanding the complete picture of the observed demographic changes in bird populations.

Several hypotheses have been proposed (and sometimes also opposed) based on ecological and life-history traits, to explain the observed differences between (and within) species in temporal trends in avian autumn migration phenology, such as moulting strategy (Kovács *et al.*, 2011), (carry-over effects of) the timing of breeding (Lehikoinen *et al.*, 2010; Stutchbury *et al.*, 2011; Mitchell *et al.*, 2012; van Wijk *et al.*, 2017; McKinnon & Love, 2018), dietary guild (La Sorte *et al.*, 2015), average body size (Bitterlin & Van Buskirk, 2014), migration distance (Gatter, 1992), and the ability for multiple broods (Jenni & Kéry, 2003; Van Buskirk *et al.*, 2009; Redlisiak *et al.*, 2018). Some patterns are indeed present, e.g. (short-distance) migrant birds both breeding and wintering within Europe seem to be delaying their autumn migration in response to recent climate change, while (long-distance) trans-Saharan migrants sometimes show advancements (Jenni & Kéry, 2003; Van Buskirk *et al.*, 2009; but see the meta-analysis by Bitterlin & Van Buskirk, 2014). The explained variation in trends has, however, remained rather low and the mechanisms underlying many of the patterns rather elusive (Knudsen *et al.*, 2011; Gill *et al.*, 2013; Bitterlin & Van Buskirk, 2014; Charmantier

& Gienapp, 2014; Chmura *et al.*, 2019). To understand the patterns and causes of interspecific differences in trends, it seems vital, however, to first understand the species-specific (differences in) phenological responses to weather, and how these might be shaping the observed temporal trends. On the one hand, climatic effects on several specific aspects of autumn migration, e.g. flight speed (Vansteelant *et al.*, 2015), stopover transience and departure probability (Calvert *et al.*, 2009), and migration onset (Shamoun-Baranes *et al.*, 2006), are likely to influence overall migration timing and progress. In turn, many of the previously proposed ecological or life-history traits to explain interspecific differences in autumn migration trends, however, also refer to activities that have been suggested to be dependent on climate, e.g. (timing of) moult (Cockburn *et al.*, 2008), (carry-over effects of) timing of breeding (Dunn & Winkler, 1999; Parmesan & Yohe, 2003; Gow *et al.*, 2019), breeding season length (Halupka & Halupka, 2017), and the prevalence of multiple brooding (Husby *et al.*, 2009). As such, interspecific differences in autumn phenology likely result from a complex interplay of multiple mechanisms of which many can be linked to different exposure and reactions to climate (Chmura *et al.*, 2019).

Studies on the relationship between weather and avian autumn migration phenology have been performed at three different levels of biological detail: migration intensity in general using mostly radar, individual-specific migration using different tracking technologies, and species-specific migration using mostly long-term count, observation, or ringing datasets. In many cases, very strong links have been found between overall autumn migration intensity and weather using radar technology (Erni *et al.*, 2002; Van Belle *et al.*, 2007; Nilsson *et al.*, 2019). Extracting species-specific information using radar nevertheless remains notoriously challenging (Schmaljohann *et al.*, 2008; Hüppop *et al.*, 2019). Recent technological advancements in data acquisition with tracking devices are now providing ever-increasing information and insights into migratory behaviour of individuals, populations, and species that

have hitherto been difficult, if not impossible (Bridge *et al.*, 2011; Kays *et al.*, 2015; Wilmers *et al.*, 2015). At present, the potential for combining data for long-term insights, e.g. relationships with climate change, however, still remains limited due to the overall limited coverage in time, i.e. number of years, but also in number of individuals for each species or population (Bauer *et al.*, 2019). Already existing long-term species- or population-level migration datasets on the other hand do have the potential to provide species-specific insights into the relationship between avian autumn migration and climate (change).

With a systematic literature search (*sensu* Nakagawa *et al.*, 2017; see Appendix S1 for a description of the literature search and the resulting literature list, as well as a summary by investigated weather variable types), we found 34 publications on the relationship between long-term species-specific avian autumn migration phenology and climate (change). Temperature has been investigated the most (28 out of 34 publications, i.e. 82%), followed by the North Atlantic Oscillation (NAO) index (14/34, i.e. 41%), precipitation (10/34, i.e. 29%), and wind-related variables (7/34, i.e. 21%). Of these, 57%, 43%, 60%, and 29% of the publications reported finding relationships with temperature, the NAO index, precipitation, and wind-derived variables, respectively. Next to possible biological reasons, however, we identified a number of methodological limitations and statistical misconceptions that may have contributed to the large diversity in these reported relationships. First, while it is weather at the point of origin, i.e. breeding or stopover area, that is the critical determinant for migration timing (Lack, 1960; Schmaljohann *et al.*, 2017; Haest *et al.*, 2018b), many studies have used weather conditions at the location where the migration is measured. Second, even though there are large uncertainties in the exact timing and duration of the influence of weather on migration phenology (e.g. due to lag or indirect pathways) (Gordo, 2007; van de Pol *et al.*, 2016), most studies have made strong a priori assumptions on the time window of influence, e.g. using monthly averages. Third, in at least half of the studies that did report

finding relationships with autumn migration phenology, spurious correlations might have occurred due to (1) not accounting for shared trends; or (2) not accounting for multiple hypotheses testing (Appendix S1; Iler *et al.*, 2017; Haest *et al.*, 2018b, 2018a). Contrary to radar studies on general migration intensity, the amount of variance in species-specific migration phenology explained by weather variables has moreover been rather low (e.g. Gordo & Sanz, 2006: < 16%; Redlisiak *et al.*, 2018: $\approx$ 35%, but see Shamoun-Baranes *et al.*, 2006, for a notable exception for four soaring bird migrant species: > 54%). Large uncertainties, if not complete knowledge gaps, hence remain on which weather variables influence autumn migration phenology of which species, at which locations, and at what time. We performed a spatially and temporally explicit analysis of weather data to systematically examine the relationship between climate and avian autumn migration phenology of ten passerine species at Heligoland (Germany) over a 55-year period (1960–2014). Similarly to Haest *et al.* (2018a) for spring migration phenology, we used as little as possible a priori assumptions or hypotheses on the what, where and when of the weather variables influencing autumn migration phenology. Instead, we took an exploratory data analysis approach to see what the data can tell us about possible weather influences and climate change effects on autumn migration phenology of birds.

Materials and methods

Autumn migration passage data

For over a century now, migrant birds are being ringed on the island of Heligoland (54° 11' N, 07° 53' E; often also spelled Helgoland). Since 1960, comparable efforts and methods have been in place with daily catches in the trapping garden throughout the whole year, resulting in an unusual long-term dataset on migration phenology. Barely any landbirds breed on Heligoland, and with no other landmass being present in a radius of almost 50 km, few

birds reach the island during post-breeding dispersal (Hüppop & Hüppop, 2003, 2011; Hüppop & Winkel, 2006).

We used yearly mean autumn passage dates (MAPD) over the period 1960-2014 as a measure of autumn migration phenology (Table 1). To minimise 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 (Sagarin, 2001). Yearly MAPD was calculated as the mean WSD of all birds ringed between WSD 223 and 344, i.e. August 1 and November 30 approximately. For convenience, we report dates throughout the paper as approximate Gregorian calendar dates. We analysed MAPD data from ten passerines of which six mainly migrate to wintering grounds within Europe or in the North of Africa, and four are trans-Saharan migrants (Table 1). The species in Table 1 are ordered by mean autumn passage date. We use this species order, instead of according to phylogeny, in all tables throughout the manuscript to allow comparison between species that are potentially subject to similar weather conditions prior to or during their migration.

Birds of a certain species that are captured at Heligoland likely stem from different populations (Dierschke *et al.*, 2011). The measured MAPD for each species is, hence, influenced by changes in the autumn phenology of each of these populations. This could obscure the relationship between the measured MAPD and the influencing weather conditions for each specific population. Different populations could, however, also be influenced by the same weather conditions at a certain time and place, e.g. stopover areas or prior to crossing an ecological barrier. Breeding or stopover areas of a species also might have changed over the total analysed time period in response to climate change (Hitch & Leberg, 2007; Zuckerberg *et al.*, 2009). Yet if these areas are maintained for a long enough subset of the total analysed 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 MAPD to all of the different breeding

or stopover locations. As such, using migration passage data has both advantages and disadvantages compared to breeding departure or winter area arrival data. Depending on the species, both of these latter autumn migration phenology metrics are, however, often difficult to estimate, particularly in passerine species.

Table 1 Per-species overview of the average 5th and 95th percentile, and mean autumn passage date (MAPD) as Gregorian calendar date, standard deviation of MAPD (days), difference between the average 5th and 95th percentile (days), the total amount of ringed birds and the average number of birds ringed per year. Species are ordered by average MAPD.

Species name	Scientific name	Average 5th percentile	Average MAPD	Average 95th percentile	Standard deviation MAPD (days)	Difference 95th and 5th percentile (days)	Total birds ringed 1960-2014	Average birds / year
Willow Warbler	<i>Phylloscopus trochilus</i>	10 Aug	25 Aug	15 Sep	3.89	36	12937	235
European Pied Flycatcher	<i>Ficedula hypoleuca</i>	11 Aug	27 Aug	18 Sep	5.35	38	9949	181
Garden Warbler	<i>Sylvia borin</i>	13 Aug	31 Aug	25 Sep	5.31	43	23090	420
Common Redstart	<i>Phoenicurus phoenicurus</i>	23 Aug	10 Sep	27 Sep	3.90	35	13613	248
European Robin	<i>Erithacus rubecula</i>	11 Sep	01 Oct	24 Oct	5.67	43	22086	402
Dunnock	<i>Prunella modularis</i>	17 Sep	03 Oct	20 Oct	5.98	33	9181	167
Song Thrush	<i>Turdus philomelos</i>	22 Sep	04 Oct	21 Oct	3.96	29	75734	1377
Common Chaffinch	<i>Fringilla coelebs</i>	22 Sep	12 Oct	11 Nov	7.57	50	25692	467
Redwing	<i>Turdus iliacus</i>	30 Sep	15 Oct	07 Nov	4.83	38	20914	380
Eurasian Blackbird	<i>Turdus merula</i>	08 Oct	27 Oct	20 Nov	5.02	43	53288	969

Climate data

We acquired spatio-temporal data of air temperature, precipitation, and wind from the NCEP Reanalysis I database (Kalnay *et al.*, 1996; Kanamitsu *et al.*, 2002) using the R package *RNCEP* (Kemp *et al.*, 2012). The spatial grid covered an area from roughly 48° to 72° N and 29°W to 44° E, ranging from northern Scandinavia in the North to southern Germany in the South, and from Iceland in the West to western Russia in the East. The spatial resolution of a grid cell ranged from 1.875° to 3.75°, depending on the weather variable (Table 2). Ocean grid cells were masked from the analysis. For each day and (land) grid cell, we derived four variables from the NCEP database: mean daily air temperature, daily precipitation sum, mean wind direction over 24 hours, and wind direction at midnight. We analysed both mean daily

winds and midnight winds, as most species in our analysis are known to mainly migrate during the night, but others possibly migrate during both day and night (e.g. Dunnock). The wind direction data were used to calculate the number of days for both winds originating from and in the direction of Heligoland within any given time window, by counting every day with a wind direction that fell between -45 and $+45^\circ$ of the angle between Heligoland and the centre of the grid cell under analysis. Depending on the location of the grid cell relative to Heligoland, 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.

The usefulness of large-scale climate indices such as the North Atlantic Oscillation (NAO) index, to explain biological processes has recently been strongly questioned (van de Pol *et al.*, 2013; Mesquita *et al.*, 2015; Haest *et al.*, 2018a). As the NAO has nevertheless also been frequently suggested to be related to autumn migration phenology (e.g. Calvert *et al.* (2009) and Therrien *et al.* (2017); see Introduction and Appendix S1), we also performed a time window analysis of daily NAO indices. The daily NAO data were downloaded from the website of the Climate Prediction Center of the National Oceanic and Atmospheric Administration (<http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>).

Table 2 Properties and pre-processing of the weather data that were acquired from the NCEP Reanalysis I database

Weather variable	NCEP variable	Spatial Resolution (in degrees)	Number of analysed grid cells	Data pre-processing and comments
temperature	'air.2m'	1.875°	293	We calculated daily mean temperatures from the four 6-hour temperature values.
precipitation	'prate.sfc'	3.75°	84	Precipitation rate data were converted to mm/day. Spatial resolution is half that of the temperature data, because we took the mean over four grid cells.
wind direction	(East-West) 'uwnd' and (North-South) 'vwnd' at 925 hPa	2.5°	177	The 925 hPa pressure level roughly corresponds to 750 m altitude. The 6-hour interval values of the two wind components were used to calculate a mean daily wind direction, as well as the midnight wind direction using the values of midnight only.

Ring recovery data

Next to the autumn migration phenology data at Heligoland, we also extracted ringing recovery data, consisting of birds ringed at Heligoland and recovered elsewhere, as well as birds ringed elsewhere and recovered on Heligoland. We extracted the locations and timing of the ringing recoveries from during the breeding and (Heligoland) autumn migration period. Depending on the species, the ring recoveries from the breeding period covered two or more months between May and September. The ringing recoveries from the (Heligoland) autumn migration period were two months long for all species and occurred between August and November (Table S1 and Figure S1). Even though we only analysed MAPD data from between 1960 and 2014, we included all of the recoveries since the start of the ringing activities in Heligoland in 1909. We did so because the total number of ring recoveries for certain species is already rather limited (Table S1). We used the ringing recovery data as a qualitative means only to help interpret the likelihood of the location and timing of identified weather signals.

Avoiding spurious correlations due to shared trends

If two time series both contain a trend over time, it is likely that correlating the two series without taking into account these shared trends will yield high, yet spurious, correlations (Noriega & Ventosa-Santaulària, 2007; Haest *et al.*, 2018a). To avoid such spurious correlations due to the presence of trends alone, we determined whether a linear, quadratic, or cubic trend over time was most appropriate for the MAPD time series of each species. To do so, we compared the second-order Akaike Information Criterion (AICc) values (Burnham & Anderson, 2002) for linear, quadratic, and cubic trend models. If a higher-order MAPD trend model had an AICc value that was more than two units lower than the one from the previous

order model, we judged the higher-order model to be a better approximation of the trend over time. We applied Augmented Dickey-Fuller tests (using the *urca* R package; Pfaff (2008)) to verify that the chosen trends models had successfully reduced the MAPD time series to stationarity. We checked for remaining autocorrelation in the residuals of the trend models with a Durbin-Watson test up to lag two (using the *car* R package; Fox & Weisberg (2011)). 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.

Finding the “weather variable – location – time window” combinations that influence autumn migration phenology

To identify the weather variables that are most likely influencing the MAPD of each species at Heligoland, we applied a methodology similar to the one used in Haest *et al.* (2018a) for spring migration phenology. In summary, the method breaks down into two main chunks of analyses (Figure 1). First, a per grid cell search is performed of all possible time windows of any length between two given dates, for each weather variable and over a spatial grid covering a certain area of interest to the studied process. The time window analysis for each pixel was done with the R package *climwin* (Bailey & van de Pol, 2016; van de Pol *et al.*, 2016). The spatial grid covered all somewhat likely geographic breeding or autumn stopover locations prior to Heligoland passage (see Climate data section). This first step ultimately results in a per species “long-list” of all potential “weather variable – location – time window” combinations, henceforth called candidate weather signals, that might possibly be influencing MAPD. This “long-list” nevertheless still includes many spurious candidate weather signals due to spatio-temporal (auto-)correlations in the weather variables. In the second step (right panel of Figure 1), the “long-list” of candidate weather signals is further analysed using a

combination of variable importance methods in order to narrow down the candidates to a final list of “weather variable – location – time window” combinations that most likely influence autumn migration phenology. For more in-depth information on the methodology, we refer to Haest *et al.* (2018a), in which each step is explained in detail, including explanations and discussions on: (1) how spurious correlations are avoided; (2) choices for the maximum and minimum time window length for each of the weather variable types; and (3) specific (dis)advantages of each of the applied variable importance methods. Two small adjustments were made to the second part of the overall analysis (right panel in Figure 1) to further increase robustness of the methodology and to be able to more appropriately deal with a long set of candidate weather signals (as occurred in this study). For ease of reference, we summarized all of the settings and decision rules we used for the “weather variable – location – time window” analysis, as well as the method adjustments compared to Haest *et al.* (2018a), in Appendix S2.

Figure 1 Flow chart of the method to identify locations and time windows of the weather variables most likely affecting autumn migration phenology. Rectangles represent data input, rectangles with double vertical lines are data analyses, and parallelograms are results. Figure and method are slightly adjusted from Haest *et al.* (2018a).

Assessing contributions of each weather variable to each species' trend over time

To understand how the identified final weather variables have contributed to the observed trends in MAPD for each species and gain insights into the mechanisms that might be causing the observed differences in trends between species, we calculated the combined effect of (1) change in MAPD in response to the weather variable and (2) change in the weather variable over time, using the chain rule (McLean *et al.*, 2018):

$$\text{climate contributions to trend in MAPD} = \sum_{i=1}^n \left(\frac{\partial \text{MAPD}}{\partial \text{Climate}_i} \times \frac{d\text{Climate}_i}{d\text{Time}} \right),$$

where n is the total number of influencing weather variables for a given species. If a weather variable has a strong effect on MAPD but it did not change strongly over the past five decades, it will not contribute much to changes in MAPD over time. Similarly, a weather variable may have a more moderate effect on MAPD but have a strong deterministic trend over the studied period, and as such contribute greatly to the observed trend in MAPD. For each species, we used the regression coefficients of a multiple linear regression between MAPD and all of the identified final weather variables to estimate the various $\partial \text{MAPD} / \partial \text{Climate}_i$, and a simple linear regression between the respective weather variable and time, i.e. years, to estimate $d\text{Climate}_i / d\text{Time}$. Standard errors were calculated appropriately following error propagation rules (formula 3.18 in Taylor, 1997). Note that this approach by definition ignores any other (non-climatic) factors that might possibly affect changes in MAPD over time.

Assessing relative importance of the weather variable types in terms of effect and temporal trend contributions

To get an idea about the relative overall importance of the three different weather variable types, i.e. temperature, precipitation, and wind, on the interannual fluctuations in MAPD at Heligoland across all species, we summed their respective mean relative variable importance values. To compare the importance of each climate variable in terms of temporal trends in MAPD over the past decades to the impact on interannual fluctuations in MAPD only, we similarly also calculated the relative contributions of each weather variable type to the temporal trends in MAPD as the sum of the absolute values of the trend contributions for each climate variable, divided by the total sum of the trend contributions. We did this across all species, but also across each migration strategy (TS: trans-Saharan versus IE: intra-European migrants) to check for any possible patterns that might explain the frequently observed differences in trend directions of TS (advance) and IE (delay) migrants.

Results

Trends in the mean autumn passage date time series

A linear trend was most appropriate to account for trends in the MAPD of eight of the ten species (Table 3). Only for one trans-Saharan (Common Redstart) and one intra-European (Dunnock) migrant species, the trend was better described by including a quadratic term, i.e. trends were non-linear. The trends explained very little of the interannual variability in MAPD ($R^2 \approx 0$ to 0.17). Intra-European migrants seem to be delaying autumn passage at Heligoland over the last decades, while trans-Saharan migrants tend towards advancement. The AICc of an intercept-only model, i.e. a null model without temporal trend, was more than two values lower for Willow Warbler and European Pied Flycatcher, indicating (together with the very low adjusted R^2 's) that the MAPD of these species currently do not necessarily seem

to be changing strongly in a specific direction. Augmented Dickey–Fuller tests confirmed that all trend models successfully reduced the time series to stationarity (Table S2). No ‘significant’ autocorrelations were found in the detrended residuals using Durbin–Watson tests (Table S3).

Table 3 Per-species overview of the selection of the best mean autumn passage date (MAPD) trend-over-time model, including the regression coefficients, their standard errors (SE) and the adjusted R^2 of the selected best trend model.

Species name	Scientific name	Selected MAPD trend model	adj. R^2	Int.	SE	Trend coefficients			
						Lin.	SE	Quad.	SE
Willow Warbler	<i>Phylloscopus trochilus</i>	Linear	0.00	266.49	66.27	-0.01	0.03	-	-
European Pied Flycatcher	<i>Ficedula hypoleuca</i>	Linear	0.01	352.16	90.01	-0.05	0.05	-	-
Garden Warbler	<i>Sylvia borin</i>	Linear	0.08	459.99	85.85	-0.10	0.04	-	-
Common Redstart	<i>Phoenicurus phoenicurus</i>	Quadratic	0.17	263.71	0.48	-1.86	3.55	-12.81	3.55
European Robin	<i>Erithacus rubecula</i>	Linear	0.08	35.97	110.62	0.13	0.06	-	-
Dunnock	<i>Prunella modularis</i>	Quadratic	0.14	286.11	0.75	5.08	5.55	17.34	5.55
Song Thrush	<i>Turdus philomelos</i>	Linear	0.10	101.06	76.49	0.09	0.04	-	-
Common Chaffinch	<i>Fringilla coelebs</i>	Linear	0.14	-86.16	124.95	0.19	0.06	-	-
Redwing	<i>Turdus iliacus</i>	Linear	0.13	72.19	76.15	0.11	0.04	-	-
Eurasian Blackbird	<i>Turdus merula</i>	Linear	0.10	67.06	96.61	0.12	0.05	-	-

From candidate weather signals to the most likely weather influences

The spatio-temporal time window analysis initially resulted in a long-list of 306 candidate weather signals across all ten species (12 to 46 candidates depending on the species; Table S4 and Figure S2 to Figure S7). From these signals, four were removed because the model without accounting for trends had an AICc compared to an intercept-only model that was less than two units lower. Subsequently, 119 candidate weather signals were removed from further analysis due to collinearity with another candidate that showed a bigger $\Delta AICc$ with an intercept-only model. For five species that still had more than fifteen candidates left, we then removed another 38 candidate signals based on the variable importance outcome using the *boruta* method (Kursa & Rudnicki, 2010; Table S4). The final “long-list” of candidate weather signals just prior to the variable importance analyses as such consisted of 145 candidates across the ten species (Table S5). Based on the output of the variable importance

analysis (Table S5 and Appendix S2), we ultimately retrieved 32 signals across the ten species that are very likely to be related to MAPD at Heligoland (Table S6).

Identified most influential “weather variable – location – time window” influences

The final identified weather influences for each species consisted of two to five signals, depending on the species (Figure 2, Figure S8, and Table S6). There was at least one temperature, precipitation, head-, and tailwind signal for six, eight, five, and eight of the ten species, respectively. For three species (Garden Warbler, Dunnock, and Eurasian Blackbird), we found both tail- and headwind influences. We did not find any obviously distinct pattern between trans-Saharan and intra-European migrants in terms of location and time windows of influence. The time window analysis of the daily NAO values resulted in a candidate signal for Garden Warbler only (Appendix S3). A variable importance analysis in combination with the final selected weather signals for Garden Warbler, however, showed that this NAO signal did not hold any additional information.

Wind conditions seem to influence MAPD both at likely breeding and autumn stopover areas. Temperature and precipitation influences were mainly located at likely breeding areas (6 out of 7 for temperature, and 8 out of 9 for precipitation; Figure 2; see also Table S7 for interpretations of the location and timing with respect to the species’ lifecycles). One precipitation (European Pied Flycatcher) and one temperature signal (Redwing) were located at stopover areas close to and including Heligoland. Unambiguous identification of the location of a signal as a breeding or stopover area, however, was not always evident, i.e. they could sometimes be either of both.

Figure 2 Per-species maps with the location and timing of the identified most important weather variables that are likely to influence mean autumn passage date (MAPD) at Heligoland. Ellipses are approximations of the likely areas of influences (see Appendix S2). T: temperature; P: precipitation; W: wind. Underlined wind signals are midnight winds, non-underlined ones are based on 24h averages (see Methods). The wind arrows point in the direction the wind is blowing (i.e. not originating). Dots and triangles indicate ring recoveries from breeding and autumn migration months, respectively (see Table S1 and Figure S1). Greyscale heatmaps of these ring recoveries were created using QGIS. The star marks the location of Heligoland. In the circular time window figures, the grey background triangles represent the 5th and 95th percentile of all birds passing at Heligoland in autumn across all years; the coloured rectangles represent the identified “best” time window or, for signals with a window uncertainty >10%, the time window based on the medians for the time window opening and closing of the 95% confidence interval of all time windows (see Figure S8 also).

Figure 2 (Continued)

The influences of wind on MAPD at Heligoland invariably occurred during the autumn migration period. For four of the seven temperature signals, the best performing time window occurred during the start and earlier half of the autumn migration period at Heligoland (Figure 2, Figure S8, and Table S7). One occurred towards the end of the migration period (Dunnock in W Norway), one during spring migration (Eurasian Blackbird in S Finland - N Baltics), and one during the spring migration and the breeding period (Common Redstart in C Sweden). The timing of the identified best time windows for precipitation signals was highly variable. Only two (European Pied Flycatcher in the Netherlands – Belgium – N Germany, and Common Redstart in N Finland – NW Russia) occurred during the autumn migration period at Heligoland. Five occurred between the end of spring migration and the end of the breeding period (European Robin in E Finland, Song Thrush in W Russia, Common Chaffinch in N Finland and in E Germany, and Eurasian Blackbird in N Norway). Two precipitation time windows pointed towards even earlier periods in the year: during the start of migration at Heligoland for Willow Warbler in the UK, and during a 3-month period prior to spring migration at Heligoland for Garden Warbler in N Norway. Temporal autocorrelation caused large uncertainties in the exact periods of influence for most temperature (6 out of 7) and precipitation (7 of 9) signals, i.e. there were many different time windows at those locations than performed similar, albeit slightly worse, in terms of AICc. Taking into account these uncertainties, the periods of influence for temperature and precipitation potentially covered much larger time windows. Timing of the wind influences was uncertain for only a few signals, and to a much lesser extent.

Weather variable types influencing autumn migration phenology

While temperature and precipitation each amounted to about a quarter of the total sum of the mean relative variable importance across all species, wind variables clearly seem to have a

more important and frequent impact on MAPD at Heligoland, amounting to about half of the total sum of the mean relative variable importance (Table 4). For intra-European migrant species specifically, the same pattern seemed to hold, albeit perhaps with even more relative emphasis on wind-related variables. For trans-Saharan migrants, the importance in function of the weather variable types seemed more even, with each of the three weather variable types amounting to about a third of the mean relative importance sum. In terms of wind, it was mainly the occurrence of tailwinds that seemed to influence MAPD (Figure 2, 10 out of 16 wind signals). Frequency of headwinds seemed to influence the timing of MAPD much less (4 out of 16 wind signals). This suggests that in relation to wind, MAPD at Heligoland for these ten species is mainly dependent on the relative occurrence of favourable winds to less favourable winds, i.e. days with tailwinds, compared to days without tailwinds.

Table 4 Summary of the weather variable importance, based on the weather variable type (RelImp = relative variable importance). TS and IE represent trans-Saharan and intra-European migrant species.

Weather Variable	Times selected			Sum of the mean RelImp			Percentage of the sum of all of the RelImp		
	All species	TS	IE	All species	TS	IE	All species	TS	IE
Temperature	7	3	4	1.02	0.54	0.47	25%	32%	20%
Precipitation	9	4	5	1.15	0.54	0.61	28%	32%	26%
Wind (summed)	16	5	11	1.88	0.60	1.28	46%	36%	54%
Headwind	6	1	5	0.68	0.12	0.55	17%	7%	23%
Tailwind	10	4	6	1.20	0.47	0.73	30%	28%	31%

Explained variance in MAPD

Depending on the species, between 43% and 80% of the variance in MAPD was explained by the model using all of the final identified weather signals (Table 5). On average across all species, 62% of the variance was explained, with eight of the ten species having an adjusted R^2 above 0.57. The similarity of the predictive R^2 values (calculated using leave-one-out) to

the adjusted R^2 values furthermore confirms the robustness of the final identified weather signals.

Table 5 Explained variance in MAPD and predictive performance using a linear model with all of the final identified weather signals for each species (see Figure 2, Figure S8, and Table S6)

Species	Adjusted R^2	Predictive R^2
Willow Warbler	0.48	0.44
European Pied Flycatcher	0.67	0.62
Garden Warbler	0.80	0.77
Common Redstart	0.43	0.39
European Robin	0.57	0.51
Dunnock	0.61	0.57
Song Thrush	0.66	0.62
Common Chaffinch	0.63	0.58
Redwing	0.61	0.58
Eurasian Blackbird	0.72	0.67

Direction of the effect of the weather variables on MAPD

The effect of summer and autumn temperatures on MAPD was distinctly different for trans-Saharan and intra-European migrants (Figure S8 and Figure 3, Table S6 and Table S8): higher temperatures lead to earlier passage at Heligoland for trans-Saharan birds, while they result in delays for intra-European migrants. One spring (or early summer) temperature signal for Eurasian Blackbird was negatively related to MAPD. For precipitation, six out of the nine identified signals were positively related to MAPD, i.e. increases in precipitation resulted in later autumn passage at Heligoland. Common Redstart and Eurasian Blackbird showed negative associations between precipitation and MAPD for areas in northern Scandinavia. Common Chaffinch had a negatively related precipitation signal for eastern Germany. Frequency of tailwinds was negatively associated with MAPD in six signals, and positively in four cases. Frequency of headwinds was associated positively with MAPD in five signals (all for intra-European species), and negatively in one (for a trans-Saharan species).

Contributions of climatic influences and trends to the temporal trends in MAPD

Contributions of weather variables' effects on MAPD to species-specific trends in MAPD at Heligoland are a complex combination of both the strength and direction of both the (1) effects of weather variables on MAPD, and (2) trends over time in the weather variables (Figure 3 and Table 6). For intra-European migrants, all (twenty) weather influences have contributed towards a delay in MAPD, albeit to varying degrees. For trans-Saharan migrants, both positive (delay in MAPD) and negative (MAPD advancement) trend contributions occur. The contributions towards advancement in MAPD are, however, exclusively temperature and precipitation signals. All wind signals push towards MAPD delay.

Across all species, the relative contributions of each climate variable to the trends in MAPD (Table 7) remained largely similar to the relative weather variable importance for interannual variations in MAPD (Table 4), i.e. wind has the strongest influence (41%), followed by precipitation (30%) and temperature (29%). The same pattern largely remains for intra-European migrants, albeit perhaps with even more emphasis on wind (55%) compared to precipitation (25%) and temperature (20%). For the trans-Saharan migrant species, the pattern of weather variable importance is completely flipped, with temperature having the strongest impact (48%) on the trends in MAPD, followed by precipitation (38%), and only then wind and to a much lesser extent (14%).

Table 6 Contribution of the effect of each weather variable on mean autumn passage date (MAPD) to the overall trend in MAPD over the period 1960-2014. Negative values are in italics. IDs are identical to those in Table S6, and Figure S2 to Figure S8. Coef.: coefficient; SE: standard error.

Species	Climate variable	ID	$\partial MAPD$		$dClimate$		$\frac{\partial MAPD}{\partial Climate} \times$	$\frac{dClimate}{dTime}$	SE
			Coef.	SE	Coef.	SE			
Willow	precipitation	1	0.11	0.03	<i>-0.03</i>	0.14	<i>0.00</i>		0.02
Warbler	tailwind in UK	27	0.48	0.12	<i>0.00</i>	0.03	<i>0.00</i>		0.01
European	temperature	3	<i>-0.82</i>	0.22	0.03	0.02	<i>-0.03</i>		0.02
Pied	tailwind in C Norway	27	<i>-0.83</i>	0.22	<i>-0.02</i>	0.02	0.02		0.02
Flycatcher	tailwind in Ireland/UK	26	0.47	0.12	0.02	0.03	0.01		0.02
	precipitation	5	0.02	0.01	<i>-1.29</i>	0.44	<i>-0.03</i>		0.02
Garden	precipitation	9	0.06	0.01	<i>-0.46</i>	0.25	<i>-0.03</i>		0.02
Warbler	temperature	2	<i>-1.23</i>	0.22	0.03	0.01	<i>-0.04</i>		0.02
	tailwind in SW Norway	20	<i>-0.53</i>	0.12	0.01	0.02	<i>0.00</i>		0.01
	headwind in the Baltic states	16	<i>-0.36</i>	0.08	0.00	0.04	<i>0.00</i>		0.01
Common	temperature	2	<i>-2.00</i>	0.47	0.02	0.01	<i>-0.04</i>		0.02
Redstart	precipitation	6	<i>-0.06</i>	0.02	<i>-0.38</i>	0.20	0.02		0.01
European	tailwind in S and C	21	<i>-0.66</i>	0.14	<i>-0.13</i>	0.04	0.09		0.03
Robin	Norway								
	precipitation	9	0.07	0.02	0.70	0.38	0.05		0.03
Dunnock	temperature	1	1.17	0.62	0.03	0.01	0.03		0.02
	temperature	2	0.83	0.41	0.02	0.01	0.01		0.01
	tailwind in C Norway	12	<i>-0.78</i>	0.40	<i>-0.02</i>	0.01	0.01		0.01
	headwind in	8	0.29	0.16	<i>-0.02</i>	0.04	<i>0.00</i>		0.01
	Norway/Sweden								
	tailwind in SW Norway	20	<i>-0.19</i>	0.10	<i>-0.01</i>	0.05	0.00		0.01
Song	precipitation	4	0.06	0.01	<i>-0.01</i>	0.33	<i>0.00</i>		0.02
Thrush	tailwind in S Norway	12	<i>-0.36</i>	0.06	<i>-0.14</i>	0.06	0.05		0.02
Common	headwind in C Norway	29	1.03	0.22	0.02	0.03	0.02		0.03
Chaffinch	precipitation	11	0.11	0.02	0.04	0.24	0.00		0.03
	precipitation	9	<i>-0.05</i>	0.02	<i>-1.02</i>	0.33	0.06		0.02
Redwing	tailwind in S Sweden	11	0.41	0.10	0.02	0.04	0.01		0.01
	headwind in N France	7	0.60	0.11	0.01	0.03	0.01		0.02
	temperature	2	1.46	0.34	0.02	0.01	0.03		0.02
Eurasian	precipitation	8	<i>-0.10</i>	0.03	<i>-0.06</i>	0.14	0.01		0.01
Blackbird	tailwind in Poland/Baltics	29	0.59	0.19	0.02	0.02	0.01		0.01
	temperature	4	<i>-0.58</i>	0.22	<i>-0.02</i>	0.02	0.01		0.01
	headwind in C Norway	11	0.16	0.06	0.15	0.08	0.02		0.02
	headwind in W Germany	27	0.23	0.10	0.03	0.05	0.01		0.01

Table 7 Relative contributions of each climate variable to the trends in autumn migration phenology at Heligoland across all species and in function of the migration strategy. TS and IE stand for trans-Saharan migrants and intra-European migrants, respectively.

Climate variable	All species	TS	IE
temperature	29%	48%	20%
precipitation	30%	38%	25%
wind (summed)	41%	14%	55%
headwind	10%	0%	15%
tailwind	31%	14%	40%

Figure 3 Side-by-side comparison of the effect sizes of (a) climate on mean autumn passage dates (MAPD) at Heligoland, (b) trends in climate variables, and (c) contributions of climate signals to trends in MAPD, in function of the weather variable type and migration strategy. Dashed line bars (95% confidence intervals) are signals from intra-European migrants, while full line bars represent signals from trans-Saharan migrants. Head- and tailwind are interpretations of the wind signals based on the location and wind direction (see Figure 2 and Table S6). WW: Willow Warbler, EPF: European Pied Flycatcher, GW: Garden Warbler, CR: Common Redstart, ER: European Robin, D: Dunnock, ST: Song Thrush, CC: Common Chaffinch, R: Redwing, and EB: Eurasian Blackbird. IDs are identical to those in Table S6 and Figure S2 to Figure S8.

Discussion

Which weather variable types influence interannual differences in avian autumn migration phenology?

Radar studies have repeatedly indicated strong relationships between non-species-specific migration intensity and weather conditions (Erni *et al.*, 2002; Van Belle *et al.*, 2007; Nilsson *et al.*, 2019). Quantifying species-specific relationships between climate and autumn migration phenology has, nevertheless, proven challenging. While it has long been recognised that it is critical to use the right location and time of influence to assess the influence of climate on migration timing (Lack, 1960; Shamoun-Baranes *et al.*, 2006; Gordo, 2007), large uncertainties in both space and time (due to a lack of sufficiently detailed data) have made it methodologically challenging to identify these areas and times of influence (van de Pol *et al.*, 2016; Haest *et al.*, 2018b). Our study shows that an exploratory data analysis approach is able to identify strong species-specific relationships between climate (change) and autumn migration timing of ten passerine species at the island of Heligoland (Germany) by specifically addressing the spatial and temporal uncertainties in the weather influences.

Across all ten species we studied, winds during the autumn migration period at both the likely stopover and breeding grounds were the most frequent and important climate influence on autumn migration timing (Table 4). Frequency of tailwinds had a bigger impact on migratory progress at Heligoland than frequency of headwinds. Notwithstanding, we did also find specific headwind frequency influences, including for one species (Dunnock) at roughly the same location and time as a tailwind frequency influence. We, hence, did not only provide further support for a “sit-and-wait-for-favourable-winds” strategy (Gauthreaux Jr. *et al.*, 2005; Delingat *et al.*, 2008; Kemp *et al.*, 2010; Eikenaar & Schmaljohann, 2015; Kölzsch *et al.*, 2016; Nilsson *et al.*, 2019), but also for a “sit-and-wait-to-avoid-unfavourable-winds” strategy

(see also Erni *et al.*, 2002), with “favourable winds” here defined as tailwinds and “unfavourable winds” as headwinds, both independent of the wind speed (see Methods section).

Depending on the species, temperature and precipitation at presumed breeding areas also played important roles (Figure 2 and Table S6). The specific time windows of influence for temperature and precipitation were much less certain than for wind conditions. For temperature, the majority occurred just prior or during the autumn migration period at Heligoland. Timing of the precipitation influences was much more diverse, occurring during breeding periods, as well as autumn migration, but also during spring migration or even earlier. This variability in the timing of the precipitation effects once more points towards the complex amalgam of both direct and indirect (including time lagged, e.g. via food) effects through which precipitation likely influences the timing of biological events. Across taxa and biological events, similarly complex precipitation effects have been suggested for, e.g. plant phenology (Peñuelas *et al.*, 2004; Gordo & Sanz, 2010), insect migration and abundance (Zipkin *et al.*, 2012; Evans *et al.*, 2019), avian spring migration and reproduction (Gordo *et al.*, 2005; Gordo, 2007; Haest *et al.*, 2018b; Englert Duursma *et al.*, 2019), and mammal demography (Thibault *et al.*, 2010; Campos *et al.*, 2017).

Our results show how species-specific combinations of precipitation, temperature, tail- and headwind influences at the breeding and stopover grounds (Figure 2) can explain between 50% and 80% of the interannual variation in autumn migration phenology (Table 5) in both intra-European and trans-Saharan migrant bird species. Similar to previous studies on the relationship between timing of (other) biological events and large-scale indices (van de Pol *et al.*, 2013; Chambers *et al.*, 2014; Haest *et al.*, 2018b), we found no support for any influence of the North Atlantic Oscillation (index) on autumn migration phenology after more local weather influences were taken into account.

It is important to note that the relative importance of the different weather variables might only be representative for the studied species, geographical region, and populations, as the influence of weather on bird migration phenology is species and context-dependent (Gordo, 2007; Calvert *et al.*, 2009; Carey, 2009; Shaw, 2016; Haest *et al.*, 2018b; Senner *et al.*, 2018). The larger relative importance of wind conditions at Heligoland might, for example, be influenced by its geographic location at an ecological barrier, i.e. in the North Sea. For migration across large land masses, wind might be less important as birds can, at any time, land to rest or refuel (Bulte *et al.*, 2014; Shamoun-Baranes *et al.*, 2017). Nonetheless, some of the wind influences we found, were located far away from Heligoland and not always at any obvious ecological barrier (Figure 2). Furthermore, strong wind influences on autumn migration intensity (using radar) have recently also been shown across large parts of (continental) Europe (Nilsson *et al.*, 2019).

Why are trends in autumn phenology so variable, including opposite directions?

Our analysis provides a clear illustration of how species- or population-specific responses to several climate (change) influences at the breeding and stopover grounds during and prior to autumn migration, can bring about large interspecific variation in autumn migration phenology trends (Figure 3, Table 6 and Table 7). The high variability in the time windows of the climatic influences between and within both species and weather variable types, furthermore illustrates that the climatic influences, next to direct effects on migration departure and progress (Shamoun-Baranes *et al.*, 2006; Calvert *et al.*, 2009; Vansteelant *et al.*, 2015), likely also work through impacts on (and carry-over effects of) several life-history and ecological events prior to autumn migration. Our findings, hence, confirm that interspecific differences in temporal trends in autumn migration phenology are very likely related to differences in ecological and life-history traits (Jenni & Kéry, 2003; Bitterlin & Van Buskirk,

2014), but also suggest that these differences are related to different exposure and reactions to climate during these prior life-history events (see also Chmura *et al.*, 2019).

Long-distance versus short-distance migrants

One of the most frequent observed patterns in interspecific differences in autumn migration phenology trends, is the advancement for long-distance (e.g. the trans-Saharan migrants in this study; TS) versus the delay for short-distance (e.g. the intra-European migrants in this study; IE) migrant bird species (Jenni & Kéry, 2003; Van Buskirk *et al.*, 2009). Our results on the effects and trend contribution of each weather variable (Figure 3 and Table 6) provide some hints on the possible mechanisms through which climate (change) may be causing the apparent distinction in autumn migration trends of IE (delay) and TS (advance) migrants. For IE migrants, the climate contributions to MAPD trends (almost) unanimously pushed towards a delay in autumn migration. Climate contributions for TS migrant species were more heterogeneous, but particularly of interest is that contributions towards advancements were exclusively temperature and precipitation effects, not wind effects. The contrast in temperature trend contributions for IE and TS migrants seems to come about mainly due to the different direction of the impact of temperature on MAPD, as most (6 of 7) of the influencing temperatures have increased over past six decades. The contrast in precipitation trend contributions, on the other hand, seems to be mainly due to decreasing precipitation over time for TS migrants. As most of the precipitation influences had a delaying effect on MAPD, i.e. a positive association, the decrease in precipitation over time translates in advancing trend contributions for the TS migrants. Interestingly also, the overall large importance of wind effects on interannual variation in MAPD (Table 4) is reflected in the relative contributions to trends in MAPD for IE migrants (Table 7). For TS migrants,

however, the relative trend contributions of wind effects were strongly reduced because trends over time in the influencing wind variables were largely lacking. These observations, in combination with the weather variable type-specific locations and timing (see Results section, Figure 2, Figure 3 and Table S7), fit with two previously suggested hypotheses to explain the contrasting patterns in autumn migration phenology trends between long- and short-distance migrants: (1) the optimal migration strategy (Jenni & Kéry, 2003; Gordo, 2007), i.e. long-distance migrants depart earlier when they can to profit from resource peaks further along the migration route while short-distance migrants stay until deteriorating living conditions push the birds to move, seems to be reflected in the contrasting effects of temperatures; and (2) the “sit-and-wait-for-favourable-winds” strategy strongly affects interannual variability in migration timing of both long- and short-distance migrants (Gauthreaux Jr. *et al.*, 2005), but for the species in our study, strong contributions to long-term trends in migration timing only occurred for short-distance migrants because the wind conditions that influence the long-distance migrants did not change in a specific direction. Given that responses are highly species- and context-dependent, however, further studies are needed on other species and locations to fully understand the mechanisms that drive interspecific differences in autumn migration trends, including if there are indeed explicit differences between long- and short-distance migrants.

All aspects of climate (change) are important

Climate change involves much more than merely an increase in temperatures. The potential role of altered precipitation, and especially of altered wind conditions, in the context of climate change impacts on migration phenology has, nevertheless, typically received much less attention (Gordo, 2007; Kemp *et al.*, 2010), with only 29% and 12% of species-specific long-term studies investigating precipitation and wind, respectively (Appendix S1). Our study

shows how changes in both precipitation and wind conditions have already contributed to trends in autumn migration phenology at Heligoland over the past decades (Figure 3, Table 6 and Table 7). A number of recent studies have also made projections on how future wind conditions are likely to impact migration progress and timing (e.g. La Sorte & Fink, 2017; La Sorte *et al.*, 2018). Given the frequency and strength of precipitation and especially wind effects on autumn migration phenology that we (Table 4) and other studies have found (e.g. Calvert *et al.*, 2009; Kemp *et al.*, 2010; La Sorte *et al.*, 2014; Laughlin *et al.*, 2016), it appears vital for future migration studies to investigate not only temperature, but also other climate variables.

Implications for (autumn) migration in other animal taxa

There are migrant species in many animal groups, but the link between migration and climate (change) has been primarily studied in birds (Shaw, 2016). While the migration ecology of any animal group, species, or population should be analysed within its own appropriate ecological and geographical context, our results do provide some suggestive patterns for migration in other animal taxa. Insect and bat migration timing, for example, are also highly dependent on a mixture of temperature, precipitation, and wind conditions occurring prior or during migration, through both direct and indirect effects (Wikelski *et al.*, 2006; Bauer *et al.*, 2011; Shaw, 2016; Pettit & O’Keefe, 2017). Similarly complex contributions towards advancement and delays are hence to be expected and are likely also occurring already, potentially causing ecological mismatches in multiple trophic interactions (Thackeray *et al.*, 2010; Visser & Gienapp, 2019).

Arguably, one could dismiss our approach as being too exploratory. Given the current uncertainties, if not complete knowledge gaps, about which weather variables influence autumn migration phenology of which species at which locations and at what time, however,

an explorative approach does not only seem appropriate, but furthermore also generates hypotheses that can subsequently be tested using more confirmatory approaches. This applies to bird migration, but perhaps even more so to the migrant species in any of the other animal groups, as the link between climate (change) and migration has in most cases been studied even less. As such, we encourage other researchers with similar time series data to follow a similar approach in order to further unravel species- and population-specific responses of autumn migration timing to climate change. By doing so, new patterns may arise at a meta-analysis level that could ultimately contribute towards understanding the observed demographic changes in bird and other animal populations.

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References

- Bailey LD, van de Pol M (2016) climwin: An R Toolbox for Climate Window Analysis. *PLoS ONE*, **11**, e0167980. <http://doi.org/10.1371/journal.pone.0167980>.
- Bairlein F (2016) Migratory birds under threat. *Science*, **354**, 547–548. <http://doi.org/10.1126/science.aah6647>.
- Bauer S, Hoyer BJ (2014) Migratory Animals Couple Biodiversity and Ecosystem Functioning Worldwide. *Science*, **344**, 1242552–1242552. <http://doi.org/10.1126/science.1242552>.
- Bauer S, Nolet BA, Giske J, Chapman JW, Åkesson S, Hedenström A, Fryxell JM (2011) Cues and Decision Rules in Animal Migration. In: *Animal Migration: A synthesis* (eds Milner-Gulland EJ, Fryxell JM, Sinclair ARE), pp. 68–87. Oxford University Press.
- Bauer S, Shamoun-Baranes J, Nilsson C et al. (2019) The grand challenges of migration ecology that radar aeroecology can help answer. *Ecography*, **42**, 861–875. <http://doi.org/10.1111/ecog.04083>.
- Van Belle J, Shamoun-Baranes J, Van Loon E, Bouten W (2007) An operational model predicting autumn bird migration intensities for flight safety. *Journal of Applied*

- Ecology*, **44**, 864–874. <http://doi.org/10.1111/j.1365-2664.2007.01322.x>.
- Bitterlin L, Van Buskirk J (2014) Ecological and life history correlates of changes in avian migration timing in response to climate change. *Climate Research*, **61**, 109–121. <http://doi.org/10.3354/cr01238>.
- Bridge ES, Thorup K, Bowlin MS et al. (2011) Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. *BioScience*, **61**, 689–698. <http://doi.org/10.1525/bio.2011.61.9.7>.
- Bulte M, McLaren JD, Bairlein F, Bouten W, Schmaljohann H, Shamoun-Baranes J (2014) Can wheatears weather the Atlantic? Modeling nonstop trans-Atlantic flights of a small migratory songbird. *The Auk*, **131**, 363–370. <http://doi.org/10.1642/AUK-13-233.1>.
- Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach - 2nd edition*. Springer Science+Business Media LLC, 488 pp.
- Van Buskirk J, Mulvihill RS, Leberman RC (2009) Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Global Change Biology*, **15**, 760–771. <http://doi.org/10.1111/j.1365-2486.2008.01751.x>.
- Calvert AM, Taylor PD, Walde SJ (2009) Cross-scale environmental influences on migratory stopover behaviour. *Global Change Biology*, **15**, 744–759. <http://doi.org/10.1111/j.1365-2486.2008.01733.x>.
- Campos FA, Morris WF, Alberts SC et al. (2017) Does climate variability influence the demography of wild primates? Evidence from long-term life-history data in seven species. *Global Change Biology*, **23**, 4907–4921. <http://doi.org/10.1111/gcb.13754>.
- Carey C (2009) The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 3321–3330. <http://doi.org/10.1098/rstb.2009.0182>.
- Chambers LE, Beaumont LJ, Hudson IL (2014) Continental scale analysis of bird migration timing: influences of climate and life history traits—a generalized mixture model clustering and discriminant approach. *International Journal of Biometeorology*, **58**, 1147–1162. <http://doi.org/10.1007/s00484-013-0707-2>.
- Charmantier A, Gienapp P (2014) Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications*, **7**, 15–28. <http://doi.org/10.1111/eva.12126>.
- Chmura HE, Kharouba HM, Ashander J, Ehلمان SM, Rivest EB, Yang LH (2019) The mechanisms of phenology: the patterns and processes of phenological shifts. *Ecological Monographs*, **89**, e01337. <http://doi.org/10.1002/ecm.1337>.
- Cockburn A, Osmond HL, Double MC (2008) Swingin’ in the rain: condition dependence and sexual selection in a capricious world. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 605–612. <http://doi.org/10.1098/rspb.2007.0916>.
- Delingat J, Bairlein F, Hedenström A (2008) Obligatory barrier crossing and adaptive fuel management in migratory birds: The case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*). *Behavioral Ecology and Sociobiology*, **62**, 1069–1078. <http://doi.org/10.1007/s00265-007-0534-8>.
- Dierschke J, Dierschke V, Hüppop K, Hüppop O, Jachmann KF (2011) *Die Vogelwelt der Insel Helgoland*. Druckwerkstatt Schmittstrasse, 632 pp.
- Dokter AM, Farnsworth A, Fink D et al. (2018) Seasonal abundance and survival of North America’s migratory avifauna determined by weather radar. *Nature Ecology & Evolution*, **2**, 1603–1609. <http://doi.org/10.1038/s41559-018-0666-4>.
- Van Doren BM, Horton KG (2018) A continental system for forecasting bird migration. *Science*, **361**, 1115–1118. <http://doi.org/10.1126/science.aat7526>.
- Dunn PO, Winkler DW (1999) Climate change has affected the breeding date of tree

- swallows throughout North America. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **266**, 2487–2490.
- Eikenaar C, Schmaljohann H (2015) Wind conditions experienced during the day predict nocturnal restlessness in a migratory songbird. *Ibis*, **157**, 125–132. <http://doi.org/10.1111/ibi.12210>.
- Englert Duursma D, Gallagher R V., Griffith SC (2019) Variation in the timing of avian egg-laying in relation to climate. *Ecography*, **42**, 535–548. <http://doi.org/10.1111/ecog.03602>.
- Erni B, Liechti F, Underhill LG, Bruderer B (2002) Wind and rain govern the intensity of nocturnal bird migration in central Europe - a log-linear regression analysis. *Ardea*, **90**, 155–166.
- Evans TR, Salvatore D, van de Pol M, Musters CJM (2019) Adult firefly abundance is linked to weather during the larval stage in the previous year. *Ecological Entomology*, **44**, 265–273. <http://doi.org/10.1111/een.12702>.
- Fox J, Weisberg S (2011) *An {R} Companion to Applied Regression, Second Edition*. Thousand Oaks CA: Sage.
- Gallinat A, Primack RB, Wagner DL (2015) Autumn, the neglected season in climate change research. *Trends in Ecology and Evolution*, **30**, 169–176. <http://doi.org/10.1016/j.tree.2015.01.004>.
- Gatter W (1992) Zugzeiten und Zugmuster im Herbst: Einfluß des Treibhauseffekts auf den Vogelzug? *Journal of Ornithology*, **133**, 427–436. <http://doi.org/10.1007/BF01640470>.
- Gauthreaux Jr. SA, Michi JE, Belser CG (2005) The temporal and spatial structure of the atmosphere and its influence on bird migration strategies. In: *Birds of two worlds: the ecology and evolution of migration*, pp. 182–193. John Hopkins University Press Baltimore, MD.
- Gill JA, Alves JA, Sutherland WJ, Appleton GF, Potts PM, Gunnarsson TG (2013) Why is timing of bird migration advancing when individuals are not? *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132161. <http://doi.org/10.1098/rspb.2013.2161>.
- Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, **35**, 37–58. <http://doi.org/10.3354/cr00713>.
- Gordo O, Sanz JJ (2006) Climate change and bird phenology: a long-term study in the Iberian Peninsula. *Global Change Biology*, **12**, 1993–2004. <http://doi.org/10.1111/j.1365-2486.2006.01178.x>.
- Gordo O, Sanz JJ (2010) Impact of climate change on plant phenology in Mediterranean ecosystems. *Global Change Biology*, **16**, 1082–1106. <http://doi.org/10.1111/j.1365-2486.2009.02084.x>.
- Gordo O, Brotons L, Ferrer X, Comas P (2005) Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biology*, **11**, 12–21. <http://doi.org/10.1111/j.1365-2486.2004.00875.x>.
- Gow EA, Burke L, Winkler DW et al. (2019) A range-wide domino effect and resetting of the annual cycle in a migratory songbird. *Proceedings of the Royal Society B: Biological Sciences*, **286**, 20181916. <http://doi.org/10.1098/rspb.2018.1916>.
- Haest B, Hüppop O, Bairlein F (2018a) Challenging a 15-year-old claim: The North Atlantic Oscillation index as a predictor of spring migration phenology of birds. *Global Change Biology*, **24**, 1523–1537. <http://doi.org/10.1111/gcb.14023>.
- Haest B, Hüppop O, Bairlein F (2018b) The influence of weather on avian spring migration phenology: What, where and when? *Global Change Biology*, **24**, 5769–5788. <http://doi.org/10.1111/gcb.14450>.
- Halupka L, Halupka K (2017) The effect of climate change on the duration of avian breeding

- seasons: a meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20171710. <http://doi.org/10.1098/rspb.2017.1710>.
- Hewson CM, Thorup K, Pearce-Higgins JW, Atkinson PW (2016) Population decline is linked to migration route in the Common Cuckoo. *Nature Communications*, **7**, 12296. <http://doi.org/10.1038/ncomms12296>.
- Hitch AT, Leberg PL (2007) Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology*, **21**, 534–539. <http://doi.org/10.1111/j.1523-1739.2006.00609.x>.
- Hüppop O, Hüppop K (2003) North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 233–240. <http://doi.org/10.1098/rspb.2002.2236>.
- Hüppop O, Hüppop K (2011) Bird migration on Helgoland: the yield from 100 years of research. *Journal of Ornithology*, **152**, 25–40. <http://doi.org/10.1007/s10336-011-0705-2>.
- Hüppop O, Winkel W (2006) Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: the role of spatially different temperature changes along migration routes. *Journal of Ornithology*, **147**, 344–353. <http://doi.org/10.1007/s10336-005-0049-x>.
- Hüppop O, Ciach M, Diehl R, Reynolds DR, Stepanian PM, Menz MHM (2019) Perspectives and challenges for the use of radar in biological conservation. *Ecography*, **42**, 912–930. <http://doi.org/10.1111/ecog.04063>.
- Husby A, Kruuk LEB, Visser ME (2009) Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1845–1854. <http://doi.org/10.1098/rspb.2008.1937>.
- Iler AM, Inouye DW, Schmidt NM, Høye TT (2017) Detrending phenological time series improves climate-phenology analyses and reveals evidence of plasticity. *Ecology*, **98**, 647–655. <http://doi.org/10.1002/ecy.1690>.
- Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 1467–1471. <http://doi.org/10.1098/rspb.2003.2394>.
- Jonzén N, Lindén A, Ergon T et al. (2006) Rapid Advance of Spring Arrival Dates in Long-Distance Migratory Birds. *Science*, **312**, 1959–1961. <http://doi.org/10.1126/science.1126119>.
- Kalnay E, Kanamitsu M, Kistler R et al. (1996) The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society*, **77**, 437–471. [http://doi.org/10.1175/1520-0477\(1996\)077<0437:TNYRP>2.0.CO;2](http://doi.org/10.1175/1520-0477(1996)077<0437:TNYRP>2.0.CO;2).
- Kanamitsu M, Ebisuzaki W, Woollen J, Yang S-K, Hnilo JJ, Fiorino M, Potter GL (2002) NCEP–DOE AMIP-II Reanalysis (R-2). *Bulletin of the American Meteorological Society*, **83**, 1631–1643. [http://doi.org/10.1175/BAMS-83-11-1631\(2002\)083<1631:NAR>2.3.CO;2](http://doi.org/10.1175/BAMS-83-11-1631(2002)083<1631:NAR>2.3.CO;2).
- Kays R, Crofoot MC, Jetz W, Wikelski M (2015) Terrestrial animal tracking as an eye on life and planet. *Science*, **348**, aaa2478. <http://doi.org/10.1126/science.aaa2478>.
- Kemp MU, Shamoun-Baranes J, Van Gasteren H, Bouten W, van Loon E (2010) Can wind help explain seasonal differences in avian migration speed? *Journal of Avian Biology*, **41**, 672–677. <http://doi.org/10.1111/j.1600-048X.2010.05053.x>.
- Kemp MU, van Loon E, Shamoun-Baranes J, Bouten W (2012) RNCEP: Global weather and climate data at your fingertips. *Methods in Ecology and Evolution*, **3**, 65–70. <http://doi.org/10.1111/j.2041-210X.2011.00138.x>.

- Klaassen RHG, Hake M, Strandberg R et al. (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, **83**, 176–184. <http://doi.org/10.1111/1365-2656.12135>.
- Knudsen E, Lindén A, Both C et al. (2011) Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, **86**, 928–946. <http://doi.org/10.1111/j.1469-185X.2011.00179.x>.
- Kölzsch A, Müskens GJDM, Kruckenberg H, Glazov P, Weinzierl R, Nolet BA, Wikelski M (2016) Towards a new understanding of migration timing: slower spring than autumn migration in geese reflects different decision rules for stopover use and departure. *Oikos*, **125**, 1496–1507. <http://doi.org/10.1111/oik.03121>.
- Kovács S, Csörgö T, Harnos A, Fehérvári P, Nagy K (2011) Change in migration phenology and biometrics of two conspecific *Sylvia* species in Hungary. *Journal of Ornithology*, **152**, 365–373. <http://doi.org/10.1007/s10336-010-0596-7>.
- Kursa MB, Rudnicki WR (2010) Feature Selection with the Boruta Package. *Journal Of Statistical Software*, **36**, 1–13. <http://doi.org/Vol. 36, Issue 11, Sep 2010>.
- Lack D (1960) The Influence of Weather on Passerine Migration. *The Auk*, **77**, 171–209.
- Laughlin AJ, Sheldon DR, Winkler DW, Taylor CM (2016) Quantifying non-breeding season occupancy patterns and the timing and drivers of autumn migration for a migratory songbird using Doppler radar. *Ecography*, **39**, 1017–1024. <http://doi.org/10.1111/ecog.01988>.
- Lehikoinen E, Sparks TH, Žalakevičius M (2004) Arrival and Departure Dates. *Advances in Ecological Research*, **35**, 1–31. [http://doi.org/10.1016/S0065-2504\(04\)35001-4](http://doi.org/10.1016/S0065-2504(04)35001-4).
- Lehikoinen A, Saurola P, Byholm P, Lindén A, Valkama J (2010) Life history events of the Eurasian sparrowhawk *Accipiter nisus* in a changing climate. *Journal of Avian Biology*, **41**, 627–636. <http://doi.org/10.1111/j.1600-048X.2010.05080.x>.
- McKinnon EA, Love OP (2018) Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. *The Auk*, **135**, 834–856. <http://doi.org/10.1642/AUK-17-202.1>.
- McLean N, van der Jeugd HP, Van De Pol M (2018) High intra-specific variation in avian body condition responses to climate limits generalisation across species. *PLoS ONE*, **13**, 1–25. <http://doi.org/10.1371/journal.pone.0192401>.
- Menzel A, Sparks TH, Estrella N et al. (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969–1976. <http://doi.org/10.1111/j.1365-2486.2006.01193.x>.
- Mesquita M d. S, Erikstad KE, Sandvik H et al. (2015) There is more to climate than the North Atlantic Oscillation: a new perspective from climate dynamics to explain the variability in population growth rates of a long-lived seabird. *Frontiers in Ecology and Evolution*, **3**, 1–14. <http://doi.org/10.3389/fevo.2015.00043>.
- Miles WTS, Bolton M, Davis P et al. (2017) Quantifying full phenological event distributions reveals simultaneous advances, temporal stability and delays in spring and autumn migration timing in long-distance migratory birds. *Global Change Biology*, **23**, 1400–1414. <http://doi.org/10.1111/gcb.13486>.
- Miller-Rushing AJ, Høye TT, Inouye DW, Post E (2010) The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3177–3186. <http://doi.org/10.1098/rstb.2010.0148>.
- Mitchell GW, Newman AEM, Wikelski M, Ryan Norris D (2012) Timing of breeding carries over to influence migratory departure in a songbird: An automated radiotracking study. *Journal of Animal Ecology*, **81**, 1024–1033. <http://doi.org/10.1111/j.1365-2656.2012.01978.x>.
- Nakagawa S, Noble DWA, Senior AM, Lagisz M (2017) Meta-evaluation of meta-analysis:

- ten appraisal questions for biologists. *BMC Biology*, **15**, 18.
<http://doi.org/10.1186/s12915-017-0357-7>.
- Nilsson C, Dokter AM, Verlinden L et al. (2019) Revealing patterns of nocturnal migration using the European weather radar network. *Ecography*, **42**, 876–886.
<http://doi.org/10.1111/ecog.04003>.
- Noriega AE, Ventosa-Santaulària D (2007) Spurious regression and trending variables. *Oxford Bulletin of Economics and Statistics*, **69**, 439–444. <http://doi.org/10.1111/j.1468-0084.2007.00481.x>.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42. <http://doi.org/10.1038/nature01286>.
- Peñuelas J, Filella I, Zhang X et al. (2004) Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist*, **161**, 837–846.
<http://doi.org/10.1111/j.1469-8137.2003.01003.x>.
- Pettit JL, O’Keefe JM (2017) Day of year, temperature, wind, and precipitation predict timing of bat migration. *Journal of Mammalogy*, **98**, 1236–1248.
<http://doi.org/10.1093/jmammal/gyx054>.
- Pfaff B (2008) *Analysis of Integrated and Cointegrated Time Series with R. Second Edition*. Springer Science+Business Media LLC.
- van de Pol M, Brouwer L, Brooker LC et al. (2013) Problems with using large-scale oceanic climate indices to compare climatic sensitivities across populations and species. *Ecography*, **36**, 249–255. <http://doi.org/10.1111/j.1600-0587.2012.00143.x>.
- van de Pol M, Bailey LD, McLean N, Rijdsdijk L, Lawson CR, Brouwer L (2016) Identifying the best climatic predictors in ecology and evolution. *Methods in Ecology and Evolution*, **7**, 1246–1257. <http://doi.org/10.1111/2041-210X.12590>.
- Redlisiak M, Remisiewicz M, Nowakowski JK (2018) Long-term changes in migration timing of Song Thrush *Turdus philomelos* at the southern Baltic coast in response to temperatures on route and at breeding grounds. *International Journal of Biometeorology*, **62**, 1595–1605. <http://doi.org/10.1007/s00484-018-1559-6>.
- Renfrew RB, Kim D, Perlut N, Smith J, Fox JW, Marra PP (2013) Phenological matching across hemispheres in a long-distance migratory bird. *Diversity and Distributions*, **19**, 1008–1019. <http://doi.org/10.1111/ddi.12080>.
- Rivrud IM, Bischof R, Meisingset EL, Zimmermann B, Loe LE, Mysterud A (2016) Leave before it’s too late: Anthropogenic and environmental triggers of autumn migration in a hunted ungulate population. *Ecology*, **53**, 160. <http://doi.org/10.1890/15-1191>.
- Sagarin R (2001) False estimates of the advance of spring. *Nature*, **414**, 600.
<http://doi.org/10.1038/414600a>.
- Schmaljohann H, Liechti F, Bächler E, Steuri T, Bruderer B (2008) Quantification of bird migration by radar - A detection probability problem. *Ibis*, **150**, 342–355.
<http://doi.org/10.1111/j.1474-919X.2007.00797.x>.
- Schmaljohann H, Lisovski S, Bairlein F (2017) Flexible reaction norms to environmental variables along the migration route and the significance of stopover duration for total speed of migration in a songbird migrant. *Frontiers in Zoology*, **14**, 1–16.
<http://doi.org/10.1186/s12983-017-0203-3>.
- Senner NR, Stager M, Verhoeven MA, Cheviron ZA, Piersma T, Bouten W (2018) High-altitude shorebird migration in the absence of topographical barriers: avoiding high air temperatures and searching for profitable winds. *Proceedings of the Royal Society B: Biological Sciences*, **285**, 20180569. <http://doi.org/10.1098/rspb.2018.0569>.
- Shamoun-Baranes J, van Loon E, Alon D, Alpert P, Yom-Tov Y, Leshem Y (2006) Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? *Global Ecology and Biogeography*, **15**, 541–552.

- <http://doi.org/10.1111/j.1466-8238.2006.00261.x>.
- Shamoun-Baranes J, Liechti F, Vansteelant WMG (2017) Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *Journal of Comparative Physiology A*, **203**, 509–529. <http://doi.org/10.1007/s00359-017-1181-9>.
- Shaw AK (2016) Drivers of animal migration and implications in changing environments. *Evolutionary Ecology*, **30**, 991–1007. <http://doi.org/10.1007/s10682-016-9860-5>.
- Smith SB, Paton PWC (2011) Long-Term Shifts in Autumn Migration by Songbirds at a Coastal Eastern North American Stopover Site. *The Wilson Journal of Ornithology*, **123**, 557–566. <http://doi.org/10.1676/10-139.1>.
- La Sorte FA, Fink D (2017) Projected changes in prevailing winds for transatlantic migratory birds under global warming. *Journal of Animal Ecology*, **86**, 273–284. <http://doi.org/10.1111/1365-2656.12624>.
- La Sorte FA, Fink D, Hochachka WM et al. (2014) The role of atmospheric conditions in the seasonal dynamics of North American migration flyways. *Journal of Biogeography*, **41**, 1685–1696. <http://doi.org/10.1111/jbi.12328>.
- La Sorte FA, Hochachka WM, Farnsworth A et al. (2015) Migration timing and its determinants for nocturnal migratory birds during autumn migration. *Journal of Animal Ecology*, **84**, 1202–1212. <http://doi.org/10.1111/1365-2656.12376>.
- La Sorte FA, Horton KG, Nilsson C, Dokter AM (2019) Projected changes in wind assistance under climate change for nocturnally migrating bird populations. *Global Change Biology*, **25**, 589–601. <http://doi.org/10.1111/gcb.14531>.
- Stutchbury BJM, Gow EA, Done T, MacPherson M, Fox JW, Afanasyev V (2011) Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 131–137. <http://doi.org/10.1098/rspb.2010.1220>.
- Taylor JR (1997) *An introduction to error analysis, the study of uncertainties in physical measurements, Second Edition*. University Science Books, 346 pp.
- Thackeray SJ, Sparks TH, Frederiksen M et al. (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, **16**, 3304–3313. <http://doi.org/10.1111/j.1365-2486.2010.02165.x>.
- Therrien J-F, Lecomte N, Zgierski T et al. (2017) Long-term phenological shifts in migration and breeding-area residency in eastern North American raptors. *The Auk*, **134**, 871–881. <http://doi.org/10.1642/AUK-17-5.1>.
- Thibault KM, Ernest SKM, White EP, Brown JH, Goheen JR (2010) Long-term insights into the influence of precipitation on community dynamics in desert rodents. *Journal of Mammalogy*, **91**, 787–797. <http://doi.org/10.1644/09-mamm-s-142.1>.
- Usui T, Butchart SHM, Phillimore AB (2017) Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. *Journal of Animal Ecology*, **86**, 250–261. <http://doi.org/10.1111/1365-2656.12612>.
- Vansteelant WMG, Bouten W, Klaassen RHG et al. (2015) Regional and seasonal flight speeds of soaring migrants and the role of weather conditions at hourly and daily scales. *Journal of Avian Biology*, **46**, 25–39. <http://doi.org/10.1111/jav.00457>.
- Visser ME, Gienapp P (2019) Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution*, **12**. <http://doi.org/10.1038/s41559-019-0880-8>.
- Walther G-R, Post E, Convey P et al. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395. <http://doi.org/10.1038/416389a>.
- van Wijk RE, Schaub M, Bauer S (2017) Dependencies in the timing of activities weaken over the annual cycle in a long-distance migratory bird. *Behavioral Ecology and Sociobiology*, **71**, 73. <http://doi.org/10.1007/s00265-017-2305-5>.

- Wikelski M, Moskowitz D, Adelman JS, Cochran J, Wilcove DS, May ML (2006) Simple rules guide dragonfly migration. *Biology Letters*, **2**, 325–329. <http://doi.org/10.1098/rsbl.2006.0487>.
- Wilmer CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V (2015) The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology*, **96**, 1741–1753. <http://doi.org/10.1890/14-1401.1>.
- Xu F, Si Y (2019) The frost wave hypothesis: How the environment drives autumn departure of migratory waterfowl. *Ecological Indicators*, **101**, 1018–1025. <http://doi.org/10.1016/j.ecolind.2019.02.024>.
- Zipkin EF, Ries L, Reeves R, Regetz J, Oberhauser KS (2012) Tracking climate impacts on the migratory monarch butterfly. *Global Change Biology*, **18**, 3039–3049. <http://doi.org/10.1111/j.1365-2486.2012.02751.x>.
- Zuckerberg B, Woods AM, Porter WF (2009) Poleward shifts in breeding bird distributions in New York State. *Global Change Biology*, **15**, 1866–1883. <http://doi.org/10.1111/j.1365-2486.2009.01878.x>.

Supporting Information

Appendix S1 – Appendix_S1_LiteratureReview_AutumnMigrationClimate.pdf: Literature review of publications on species-specific relationships between avian autumn migration phenology and weather/climate.

Appendix S2 – Appendix_S2_WeatherSignalSearch_Settings.pdf: Overview of the settings and decision-rules used to obtain the final identified “weather variable – location – time window” combinations (Table S6) that most likely influence MAPD at Heligoland, and of how the ellipses were drawn for Figure 2 based on the intermediate results of Figure S2-S7 and Table S4.

Appendix S3 – AppendixS3_NAOAnalysis.pdf: Results of the North Atlantic Oscillation (NAO) time window analysis, and output of the variable importance analysis for Garden Warbler for the NAO in combination with the identified most influencing weather variables (see Table S6).

Figure S1 – Figure_S1_RingRecoveryMaps.pdf: Per species heatmaps and point data of the breeding (circles) and autumn migration (triangles) period ring recoveries (see Table S1). The location of Heligoland is marked by the star. The heatmaps were created using QGIS.

Figure S2 – Figure_S2_AICcR2SlopeMaps_temperature.pdf: Per species $\Delta AICc$, adjusted R^2 , and regression coefficient maps of the identified best time windows for temperature.

Figure S3 – Figure_S3_AICcR2SlopeMaps_precipitation.pdf: Per species $\Delta AICc$, adjusted R^2 , and regression coefficient maps of the identified best time windows for precipitation.

1015
1016 Figure S4 – Figure_S4_AICcR2SlopeMaps_WindDaysMean_CFHelgo.pdf: Per species
1017 $\Delta AICc$, adjusted R^2 , and regression coefficient maps of the identified best time windows for
1018 the number of days with wind (on average over the course of the whole day) coming from
1019 Heligoland.

1020
1021 Figure S5 – Figure_S5_AICcR2SlopeMaps_WindDaysMean_GTHelgo.pdf: Per species
1022 $\Delta AICc$, adjusted R^2 , and regression coefficient maps of the identified best time windows for
1023 the number of days with wind (on average over the course of the whole day) going in the
1024 direction of Heligoland.

1025
1026 Figure S6 – Figure_S6_AICcR2SlopeMaps_WindNight_CFHelgo.pdf: Per species $\Delta AICc$,
1027 adjusted R^2 , and regression coefficient maps of the identified best time windows for the
1028 number of days with midnight winds coming from Heligoland.

1029
1030 Figure S7 - Figure_S7_AICcR2SlopeMaps_WindNight_GTHelgo.pdf: Per species $\Delta AICc$,
1031 adjusted R^2 , and regression coefficient maps of the identified best time windows for the
1032 number of days with midnight winds in the direction of Heligoland.

1033
1034 Figure S8 – Figure_S8_OverviewSelectedTimeWindows.pdf: Per-species overview of the
1035 time windows of the final selected weather variables in relation to the distribution of the birds
1036 ringed at Heligoland across all years in both spring and autumn (violin plots).

1037

1038 Table S1 – Table_S1_RingRecoveriesOverview.pdf: Per species overview of the months used
1039 for visualizations in the manuscript and the number of recoveries for both the breeding period
1040 and autumn migration ring recoveries.

1041
1042 Table S2 – Table_S2_TimeTrend_ADFtest.pdf: Per species overview of the Augmented
1043 Dickey-Fuller test results for stationarity in the residuals of the mean autumn passage date
1044 trend models (see Table 3).

1045
1046 Table S3 – Table_S3_TimeTrend_DurbinWatsonTest.pdf: Per species overview of the
1047 Durbin-Watson test results for autocorrelation up to lag 2 in the residuals of the mean autumn
1048 passage date trend models (see Table 3).

1049
1050 Table S4 – Table_S4_LongList_CandidateWeatherPixels.pdf: Overview of the candidate
1051 weather signals selected from the $\Delta AICc$ maps, including the identified time windows, $\Delta AICc$
1052 values compared to trend model (see Table 3) and an intercept-only model, probability P_c
1053 value that the $\Delta AICc$ value was obtained by chance, locations of the identified grid cells, an
1054 ID value for comparison with the $\Delta AICc$ maps from Figures S2 to S7, and whether or not
1055 they were removed from further analysis due to collinearity with another candidate weather
1056 signal, a low $\Delta AICc$ compared to the intercept-only model, or because they were not in the
1057 top 15 of a variable importance analysis using the boruta method.

1058
1059 Table S5 – Table_S5_Shortlist_OverviewRelativeVariableImportance.pdf – Overview of the
1060 relative variable importance of the candidate weather signals, calculated using three different
1061 methods: (1) the sum of the multi-model $AICc$ weights across all the possible models with
1062 maximum four independent variables; (2) the boruta method; and (3) the game-theory-based

1063 LMG metric for variance decomposition in linear models. Effects represent the average
1064 conditional coefficient calculated over all possible models with a maximum of four
1065 independent variables. This table includes only the candidate weather signals that were not
1066 removed due to high collinearity with another better performing candidate signal, low
1067 performance compared to an intercept-only model, or because they were not in the top 15 of
1068 the variable reduction step using the boruta method (see Table S4).

1069

1070 Table S6 – Table_S6_OverviewFinallySelectedWeatherVariables.pdf – Overview of the
1071 identified final weather variables that are likely to affect mean autumn passage dates (MAPD)
1072 at Heligoland, including the identified time windows and locations.

1073

1074 Table S7 – Table_S7_InterpretationLocationTimingFinallySelectedWeatherVariables.pdf –
1075 Overview of the interpretation of the location and timing of each of the identified final
1076 weather variables that are likely to affect mean autumn passage dates (MAPD) at Heligoland.

1077

1078 Table S8 – Table_S8_SummaryDirectionWeatherSignals.pdf – Summary of the direction of
1079 the effects of the identified final weather variables on mean autumn passage dates at
1080 Heligoland.