# 1 Title

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

## 3 Running head

4 Climate change and autumn migration phenology

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#### 17 Abstract

18 Climate change has caused a clear and univocal trend towards advancement in spring 19 phenology. Changes in autumn phenology are much more diverse, with advancement, delays, 20 and 'no change' all occurring frequently. For migratory birds, patterns in autumn migration 21 phenology trends have been identified based on ecological and life-history traits. Explaining 22 interspecific variation has nevertheless been challenging, and the underlying mechanisms 23 have remained elusive. Radar studies on non-species-specific autumn migration intensity have 24 repeatedly suggested that there are strong links with weather. In long-term species-specific 25 studies, the variance in autumn migration phenology explained by weather has, nevertheless, 26 been rather low, or a relationship was even lacking entirely. We performed a spatially explicit 27 time-window analysis of weather effects on mean autumn passage of four trans-Saharan and 28 six intra-European passerines to gain insights into this apparent contradiction. We analysed 29 data from standardized daily captures at the Heligoland island constant-effort site (Germany), 30 in combination with gridded daily temperature, precipitation and wind data over a 55-year 31 period (1960–2014), across northern Europe. Weather variables at the breeding and stopover 32 grounds explained up to 80% of the species-specific interannual variability in autumn 33 passage. Overall, wind conditions were most important. For intra-European migrants, wind 34 was even twice as important as either temperature or precipitation, and the pattern also held in 35 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 36 37 contributions was completely reversed. Temperature and precipitation had strong trend 38 contributions, while wind conditions had only a minor impact because they did not show any 39 strong temporal trends. As such, understanding species-specific effects of climate on autumn 40 phenology not only provides unique insights into each species' ecology, but also how these 41 effects shape the observed interspecific heterogeneity in autumn phenological trends.

2

#### 42 Introduction

Every year, billions of animals migrate various distances across the Earth to increase their chances of survival and reproductive success (Bauer & Hoye, 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.

50 While the influence of climate on many aspects of spring phenology in animals and plants has 51 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 52 53 autumn phenology are still poorly understood (Walther et al., 2002; Renfrew et al., 2013; 54 Gallinat et al., 2015; Rivrud et al., 2016; Xu & Si, 2019). In general, spring (and summer) 55 activities and events have shown a rather clear advancement in response to recent climate 56 change across taxa (Menzel et al., 2006; Thackeray et al., 2010). The change in autumn 57 events and activities, however, is much less uniform, with advancements, no change, and 58 delays all being observed regularly (Lehikoinen et al., 2004; Menzel et al., 2006; Smith & 59 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 67 and climate has, amongst all animal groups, by far been studied most intensively in birds 68 (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; 69 70 Gordo, 2007; Bitterlin & Van Buskirk, 2014; Miles et al., 2017). Similarly to spring 71 migration, autumn migration nevertheless plays an essential, albeit different, role in the full 72 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 73 74 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 75 76 towards understanding the complete picture of the observed demographic changes in bird 77 populations.

78 Several hypotheses have been proposed (and sometimes also opposed) based on ecological 79 and life-history traits, to explain the observed differences between (and within) species in 80 temporal trends in avian autumn migration phenology, such as moulting strategy (Kovács et 81 al., 2011), (carry-over effects of) the timing of breeding (Lehikoinen et al., 2010; Stutchbury 82 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 83 84 distance (Gatter, 1992), and the ability for multiple broods (Jenni & Kéry, 2003; Van Buskirk 85 et al., 2009; Redlisiak et al., 2018). Some patterns are indeed present, e.g. (short-distance) 86 migrant birds both breeding and wintering within Europe seem to be delaying their autumn 87 migration in response to recent climate change, while (long-distance) trans-Saharan migrants 88 sometimes show advancements (Jenni & Kéry, 2003; Van Buskirk et al., 2009; but see the 89 meta-analysis by Bitterlin & Van Buskirk, 2014). The explained variation in trends has, 90 however, remained rather low and the mechanisms underlying many of the patterns rather 91 elusive (Knudsen et al., 2011; Gill et al., 2013; Bitterlin & Van Buskirk, 2014; Charmantier

92 & Gienapp, 2014; Chmura et al., 2019). To understand the patterns and causes of interspecific 93 differences in trends, it seems vital, however, to first understand the species-specific 94 (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 95 96 autumn migration, e.g. flight speed (Vansteelant et al., 2015), stopover transience and 97 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 98 99 previously proposed ecological or life-history traits to explain interspecific differences in 100 autumn migration trends, however, also refer to activities that have been suggested to be 101 dependent on climate, e.g. (timing of) moult (Cockburn et al., 2008), (carry-over effects of) 102 timing of breeding (Dunn & Winkler, 1999; Parmesan & Yohe, 2003; Gow et al., 2019), 103 breeding season length (Halupka & Halupka, 2017), and the prevalence of multiple brooding 104 (Husby et al., 2009). As such, interspecific differences in autumn phenology likely result from 105 a complex interplay of multiple mechanisms of which many can be linked to different 106 exposure and reactions to climate (Chmura et al., 2019).

107 Studies on the relationship between weather and avian autumn migration phenology have 108 been performed at three different levels of biological detail: migration intensity in general 109 using mostly radar, individual-specific migration using different tracking technologies, and 110 species-specific migration using mostly long-term count, observation, or ringing datasets. In 111 many cases, very strong links have been found between overall autumn migration intensity 112 and weather using radar technology (Erni et al., 2002; Van Belle et al., 2007; Nilsson et al., 113 2019). Extracting species-specific information using radar nevertheless remains notoriously 114 challenging (Schmaljohann et al., 2008; Hüppop et al., 2019). Recent technological 115 advancements in data acquisition with tracking devices are now providing ever-increasing 116 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).

124 With a systematic literature search (sensu Nakagawa et al., 2017; see Appendix S1 for a 125 description of the literature search and the resulting literature list, as well as a summary by 126 investigated weather variable types), we found 34 publications on the relationship between 127 long-term species-specific avian autumn migration phenology and climate (change). 128 Temperature has been investigated the most (28 out of 34 publications, i.e. 82%), followed by 129 the North Atlantic Oscillation (NAO) index (14/34, i.e. 41%), precipitation (10/34, i.e. 29%), 130 and wind-related variables (7/34, i.e. 21%). Of these, 57%, 43%, 60%, and 29% of the 131 publications reported finding relationships with temperature, the NAO index, precipitation, 132 and wind-derived variables, respectively. Next to possible biological reasons, however, we 133 identified a number of methodological limitations and statistical misconceptions that may 134 have contributed to the large diversity in these reported relationships. First, while it is weather 135 at the point of origin, i.e. breeding or stopover area, that is the critical determinant for 136 migration timing (Lack, 1960; Schmaljohann et al., 2017; Haest et al., 2018b), many studies 137 have used weather conditions at the location where the migration is measured. Second, even 138 though there are large uncertainties in the exact timing and duration of the influence of 139 weather on migration phenology (e.g. due to lag or indirect pathways) (Gordo, 2007; van de 140 Pol et al., 2016), most studies have made strong a priori assumptions on the time window of 141 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%).

149 Large uncertainties, if not complete knowledge gaps, hence remain on which weather 150 variables influence autumn migration phenology of which species, at which locations, and at 151 what time. We performed a spatially and temporally explicit analysis of weather data to 152 systematically examine the relationship between climate and avian autumn migration 153 phenology of ten passerine species at Heligoland (Germany) over a 55-year period (1960-154 2014). Similarly to Haest et al. (2018a) for spring migration phenology, we used as little as 155 possible a priori assumptions or hypotheses on the what, where and when of the weather 156 variables influencing autumn migration phenology. Instead, we took an exploratory data 157 analysis approach to see what the data can tell us about possible weather influences and 158 climate change effects on autumn migration phenology of birds.

#### 159 Materials and methods

#### 160 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).

168 We used yearly mean autumn passage dates (MAPD) over the period 1960-2014 as a measure 169 of autumn migration phenology (Table 1). To minimise potential bias due to the use of the 170 Gregorian calendar, we converted trapping dates to Winter Solstice-based dates (WSD) 171 instead of day-of-the-year (Sagarin, 2001). Yearly MAPD was calculated as the mean WSD 172 of all birds ringed between WSD 223 and 344, i.e. August 1 and November 30 approximately. 173 For convenience, we report dates throughout the paper as approximate Gregorian calendar 174 dates. We analysed MAPD data from ten passerines of which six mainly migrate to wintering 175 grounds within Europe or in the North of Africa, and four are trans-Saharan migrants (Table 176 1). The species in Table 1 are ordered by mean autumn passage date. We use this species 177 order, instead of according to phylogeny, in all tables throughout the manuscript to allow 178 comparison between species that are potentially subject to similar weather conditions prior to 179 or during their migration.

180 Birds of a certain species that are captured at Heligoland likely stem from different 181 populations (Dierschke et al., 2011). The measured MAPD for each species is, hence, 182 influenced by changes in the autumn phenology of each of these populations. This could 183 obscure the relationship between the measured MAPD and the influencing weather conditions 184 for each specific population. Different populations could, however, also be influenced by the 185 same weather conditions at a certain time and place, e.g. stopover areas or prior to crossing an 186 ecological barrier. Breeding or stopover areas of a species also might have changed over the 187 total analysed time period in response to climate change (Hitch & Leberg, 2007; Zuckerberg 188 et al., 2009). Yet if these areas are maintained for a long enough subset of the total analysed 189 time period, or the shifts are not over large distances compared to the spatial resolution of the 190 weather grids, it should be possible to link the observed MAPD to all of the different breeding 191 or stopover locations. As such, using migration passage data has both advantages and 192 disadvantages compared to breeding departure or winter area arrival data. Depending on the 193 species, both of these latter autumn migration phenology metrics are, however, often difficult 194 to estimate, particularly in passerine species.

**Table 1** Per-species overview of the average 5<sup>th</sup> and 95<sup>th</sup> percentile, and mean autumn passage date (MAPD) as Gregorian calendar date, standard deviation of MAPD (days), difference between the average 5<sup>th</sup> and 95<sup>th</sup> percentile (days), the total amount of ringed birds and the average number of birds ringed per vear. 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	Phylloscopus trochilus	10 Aug	25 Aug	15 Sep	3.89	36	12937	235
European Pied Flycatcher	Ficedula hypoleuca	11 Aug	27 Aug	18 Sep	5.35	38	9949	181
Garden Warbler	Sylvia borin	13 Aug	31 Aug	25 Sep	5.31	43	23090	420
Common Redstart	Phoenicurus phoenicurus	23 Aug	10 Sep	27 Sep	3.90	35	13613	248
European Robin	Erithacus rubecula	11 Sep	01 Oct	24 Oct	5.67	43	22086	402
Dunnock	Prunella modularis	17 Sep	03 Oct	20 Oct	5.98	33	9181	167
Song Thrush	Turdus philomelos	22 Sep	04 Oct	21 Oct	3.96	29	75734	1377
Common Chaffinch	Fringilla coelebs	22 Sep	12 Oct	11 Nov	7.57	50	25692	467
Redwing	Turdus iliacus	30 Sep	15 Oct	07 Nov	4.83	38	20914	380
Eurasian Blackbird	Turdus merula	08 Oct	27 Oct	20 Nov	5.02	43	53288	969

199

#### 200 *Climate data*

201 We acquired spatio-temporal data of air temperature, precipitation, and wind from the NCEP 202 Reanalysis I database (Kalnay et al., 1996; Kanamitsu et al., 2002) using the R package 203 RNCEP (Kemp et al., 2012). The spatial grid covered an area from roughly 48° to 72° N and 204 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 205 grid cell ranged from 1.875° to 3.75°, depending on the weather variable (Table 2). Ocean 206 207 grid cells were masked from the analysis. For each day and (land) grid cell, we derived four 208 variables from the NCEP database: mean daily air temperature, daily precipitation sum, mean 209 wind direction over 24 hours, and wind direction at midnight. We analysed both mean daily 210 winds and midnight winds, as most species in our analysis are known to mainly migrate 211 during the night, but others possibly migrate during both day and night (e.g. Dunnock). The 212 wind direction data were used to calculate the number of days for both winds originating from 213 and in the direction of Heligoland within any given time window, by counting every day with 214 a wind direction that fell between -45 and  $+45^{\circ}$  of the angle between Heligoland and the 215 centre of the grid cell under analysis. Depending on the location of the grid cell relative to 216 Heligoland, we then interpreted these to be head- or tailwinds. We chose to test both measures 217 for wind effects on migration as both hypotheses, i.e. headwinds delay migration and 218 tailwinds advance migration, represent different processes.

219 The usefulness of large-scale climate indices such as the North Atlantic Oscillation (NAO) 220 index, to explain biological processes has recently been strongly questioned (van de Pol et al., 221 2013; Mesquita et al., 2015; Haest et al., 2018a). As the NAO has nevertheless also been 222 frequently suggested to be related to autumn migration phenology (e.g. Calvert et al. (2009) 223 and Therrien et al. (2017); see Introduction and Appendix S1), we also performed a time 224 window analysis of daily NAO indices. The daily NAO data were downloaded from the 225 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). 226

Table 2 Properties and pre-processing of the weather data that were acquired from the NCEPReanalysis 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.

230 Next to the autumn migration phenology data at Heligoland, we also extracted ringing 231 recovery data, consisting of birds ringed at Heligoland and recovered elsewhere, as well as 232 birds ringed elsewhere and recovered on Heligoland. We extracted the locations and timing of 233 the ringing recoveries from during the breeding and (Heligoland) autumn migration period. 234 Depending on the species, the ring recoveries from the breeding period covered two or more 235 months between May and September. The ringing recoveries from the (Heligoland) autumn 236 migration period were two months long for all species and occurred between August and 237 November (Table S1 and Figure S1). Even though we only analysed MAPD data from 238 between 1960 and 2014, we included all of the recoveries since the start of the ringing 239 activities in Heligoland in 1909. We did so because the total number of ring recoveries for 240 certain species is already rather limited (Table S1). We used the ringing recovery data as a 241 qualitative means only to help interpret the likelihood of the location and timing of identified 242 weather signals.

243

#### 244 Avoiding spurious correlations due to shared trends

245 If two time series both contain a trend over time, it is likely that correlating the two series 246 without taking into account these shared trends will yield high, yet spurious, correlations 247 (Noriega & Ventosa-Santaulària, 2007; Haest et al., 2018a). To avoid such spurious 248 correlations due to the presence of trends alone, we determined whether a linear, quadratic, or 249 cubic trend over time was most appropriate for the MAPD time series of each species. To do 250 so, we compared the second-order Akaike Information Criterion (AICc) values (Burnham & 251 Anderson, 2002) for linear, quadratic, and cubic trend models. If a higher-order MAPD trend 252 model had an AICc value that was more than two units lower than the one from the previous 253 order model, we judged the higher-order model to be a better approximation of the trend over 254 time. We applied Augmented Dickey-Fuller tests (using the urca R package; Pfaff (2008)) to 255 verify that the chosen trends models had successfully reduced the MAPD time series to 256 stationarity. We checked for remaining autocorrelation in the residuals of the trend models 257 with a Durbin-Watson test up to lag two (using the the car R package; Fox & Weisberg 258 (2011)). The identified trend model for each species was used as the base model (for 259 comparison of reduction in AICc values by adding a weather variable) in the subsequent time 260 window analyses.

261

# 262 Finding the "weather variable – location – time window" combinations that influence 263 autumn migration phenology

264 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 265 266 spring migration phenology. In summary, the method breaks down into two main chunks of 267 analyses (Figure 1). First, a per grid cell search is performed of all possible time windows of 268 any length between two given dates, for each weather variable and over a spatial grid 269 covering a certain area of interest to the studied process. The time window analysis for each 270 pixel was done with the R package *climwin* (Bailey & van de Pol, 2016; van de Pol et al., 271 2016). The spatial grid covered all somewhat likely geographic breeding or autumn stopover 272 locations prior to Heligoland passage (see Climate data section). This first step ultimately 273 results in a per species "long-list" of all potential "weather variable – location – time window" 274 combinations, henceforth called candidate weather signals, that might possibly be influencing 275 MAPD. This "long-list" nevertheless still includes many spurious candidate weather signals 276 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 277

278 combination of variable importance methods in order to narrow down the candidates to a final 279 list of "weather variable - location - time window" combinations that most likely influence 280 autumn migration phenology. For more in-depth information on the methodology, we refer to 281 Haest et al. (2018a), in which each step is explained in detail, including explanations and 282 discussions on: (1) how spurious correlations are avoided; (2) choices for the maximum and 283 minimum time window length for each of the weather variable types; and (3) specific 284 (dis)advantages of each of the applied variable importance methods. Two small adjustments 285 were made to the second part of the overall analysis (right panel in Figure 1) to further 286 increase robustness of the methodology and to be able to more appropriately deal with a long 287 set of candidate weather signals (as occurred in this study). For ease of reference, we 288 summarized all of the settings and decision rules we used for the "weather variable – location 289 - time window" analysis, as well as the method adjustments compared to Haest *et al.* (2018a), 290 in Appendix S2.



291

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).

296 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):

$$\begin{array}{l} climate \ contributions \\ to \ trend \ in \ MAPD \end{array} = \sum_{i=1}^{n} \Big( \frac{\partial MAPD}{\partial Climate_{i}} \times \frac{dClimate_{i}}{dTime} \Big), \end{array}$$

302 where n is the total number of influencing weather variables for a given species. If a weather 303 variable has a strong effect on MAPD but it did not change strongly over the past five 304 decades, it will not contribute much to changes in MAPD over time. Similarly, a weather 305 variable may have a more moderate effect on MAPD but have a strong deterministic trend 306 over the studied period, and as such contribute greatly to the observed trend in MAPD. For 307 each species, we used the regression coefficients of a multiple linear regression between 308 MAPD and all of the identified final weather variables to estimate the various 309  $\partial MAPD/\partial Climate_i$ , and a simple linear regression between the respective weather variable 310 and time, i.e. years, to estimate  $dClimate_i/dTime$ . Standard errors were calculated 311 appropriately following error propagation rules (formula 3.18 in Taylor, 1997). Note that this 312 approach by definition ignores any other (non-climatic) factors that might possibly affect 313 changes in MAPD over time.

314

# 315 Assessing relative importance of the weather variable types in terms of effect and 316 temporal trend contributions

317 To get an idea about the relative overall importance of the three different weather variable 318 types, i.e. temperature, precipitation, and wind, on the interannual fluctuations in MAPD at 319 Heligoland across all species, we summed their respective mean relative variable importance 320 values. To compare the importance of each climate variable in terms of temporal trends in 321 MAPD over the past decades to the impact on interannual fluctuations in MAPD only, we 322 similarly also calculated the relative contributions of each weather variable type to the 323 temporal trends in MAPD as the sum of the absolute values of the trend contributions for each 324 climate variable, divided by the total sum of the trend contributions. We did this across all 325 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 326 327 differences in trend directions of TS (advance) and IE (delay) migrants.

#### 328 **Results**

#### 329 Trends in the mean autumn passage date time series

330 A linear trend was most appropriate to account for trends in the MAPD of eight of the ten 331 species (Table 3). Only for one trans-Saharan (Common Redstart) and one intra-European 332 (Dunnock) migrant species, the trend was better described by including a quadratic term, i.e. 333 trends were non-linear. The trends explained very little of the interannual variability in 334 MAPD ( $\mathbb{R}^2 \approx 0$  to 0.17). Intra-European migrants seem to be delaying autumn passage at 335 Heligoland over the last decades, while trans-Saharan migrants tend towards advancement. 336 The AICc of an intercept-only model, i.e. a null model without temporal trend, was more than 337 two values lower for Willow Warbler and European Pied Flycatcher, indicating (together with 338 the very low adjusted R<sup>2</sup>'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) trendover-time model, including the regression coefficients, their standard errors (SE) and the adjusted  $R^2$ 

of the selected best trend model.

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

346

#### 347 *From candidate weather signals to the most likely weather influences*

348 The spatio-temporal time window analysis initially resulted in a long-list of 306 candidate 349 weather signals across all ten species (12 to 46 candidates depending on the species; Table S4 350 and Figure S2 to Figure S7). From these signals, four were removed because the model 351 without accounting for trends had an AICc compared to an intercept-only model that was less 352 than two units lower. Subsequently, 119 candidate weather signals were removed from further 353 analysis due to collinearity with another candidate that showed a bigger  $\Delta AICc$  with an 354 intercept-only model. For five species that still had more than fifteen candidates left, we then 355 removed another 38 candidate signals based on the variable importance outcome using the 356 boruta method (Kursa & Rudnicki, 2010; Table S4). The final "long-list" of candidate 357 weather signals just prior to the variable importance analyses as such consisted of 145 358 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

360 that are very likely to be related to MAPD at Heligoland (Table S6).

361

#### 362 *Identified most influential "weather variable – location – time window" influences*

363 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 364 365 temperature, precipitation, head-, and tailwind signal for six, eight, five, and eight of the ten 366 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 367 368 between trans-Saharan and intra-European migrants in terms of location and time windows of 369 influence. The time window analysis of the daily NAO values resulted in a candidate signal 370 for Garden Warbler only (Appendix S3). A variable importance analysis in combination with 371 the final selected weather signals for Garden Warbler, however, showed that this NAO signal 372 did not hold any additional information.

373 Wind conditions seem to influence MAPD both at likely breeding and autumn stopover areas. 374 Temperature and precipitation influences were mainly located at likely breeding areas (6 out 375 of 7 for temperature, and 8 out of 9 for precipitation; Figure 2; see also Table S7 for 376 interpretations of the location and timing with respect to the species' lifecycles). One 377 precipitation (European Pied Flycatcher) and one temperature signal (Redwing) were located 378 at stopover areas close to and including Heligoland. Unambiguous identification of the 379 location of a signal as a breeding or stopover area, however, was not always evident, i.e. they 380 could sometimes be either of both.



381

# Garden Warbler

# Common Redstart

382 Figure 2 Per-species maps with the location and timing of the identified most important weather variables that 383 are likely to influence mean autumn passage date (MAPD) at Heligoland. Ellipses are approximations of the 384 likely areas of influences (see Appendix S2). T: temperature; P: precipitation; W: wind. Underlined wind signals 385 are midnight winds, non-underlined ones are based on 24h averages (see Methods). The wind arrows point in the 386 direction the wind is blowing (i.e. not originating). Dots and triangles indicate ring recoveries from breeding and 387 autumn migration months, respectively (see Table S1 and Figure S1). Greyscale heatmaps of these ring 388 recoveries were created using QGIS. The star marks the location of Heligoland. In the circular time window 389 figures, the grey background triangles represent the 5th and 95th percentile of all birds passing at Heligoland in 390 autumn across all years; the coloured rectangles represent the identified "best" time window or, for signals with 391 a window uncertainty >10%, the time window based on the medians for the time window opening and closing of 392 the 95% confidence interval of all time windows (see Figure S8 also).



394 Figure 2 (Continued)

396 The influences of wind on MAPD at Heligoland invariably occurred during the autumn 397 migration period. For four of the seven temperature signals, the best performing time window 398 occurred during the start and earlier half of the autumn migration period at Heligoland (Figure 399 2, Figure S8, and Table S7). One occurred towards the end of the migration period (Dunnock 400 in W Norway), one during spring migration (Eurasian Blackbird in S Finland - N Baltics), and 401 one during the spring migration and the breeding period (Common Redstart in C Sweden). 402 The timing of the identified best time windows for precipitation signals was highly variable. 403 Only two (European Pied Flycatcher in the Netherlands - Belgium - N Germany, and 404 Common Redstart in N Finland - NW Russia) occurred during the autumn migration period at 405 Heligoland. Five occurred between the end of spring migration and the end of the breeding 406 period (European Robin in E Finland, Song Thrush in W Russia, Common Chaffinch in N 407 Finland and in E Germany, and Eurasian Blackbird in N Norway). Two precipitation time 408 windows pointed towards even earlier periods in the year: during the start of migration at 409 Heligoland for Willow Warbler in the UK, and during a 3-month period prior to spring 410 migration at Heligoland for Garden Warbler in N Norway. Temporal autocorrelation caused 411 large uncertainties in the exact periods of influence for most temperature (6 out of 7) and 412 precipitation (7 of 9) signals, i.e. there were many different time windows at those locations 413 than performed similar, albeit slightly worse, in terms of AICc. Taking into account these 414 uncertainties, the periods of influence for temperature and precipitation potentially covered 415 much larger time windows. Timing of the wind influences was uncertain for only a few 416 signals, and to a much lesser extent.

417

#### 418 Weather variable types influencing autumn migration phenology

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

421 more important and frequent impact on MAPD at Heligoland, amounting to about half of the 422 total sum of the mean relative variable importance (Table 4). For intra-European migrant 423 species specifically, the same pattern seemed to hold, albeit perhaps with even more relative 424 emphasis on wind-related variables. For trans-Saharan migrants, the importance in function of 425 the weather variable types seemed more even, with each of the three weather variable types 426 amounting to about a third of the mean relative importance sum. In terms of wind, it was 427 mainly the occurrence of tailwinds that seemed to influence MAPD (Figure 2, 10 out of 16 428 wind signals). Frequency of headwinds seemed to influence the timing of MAPD much less (4 429 out of 16 wind signals). This suggests that in relation to wind, MAPD at Heligoland for these 430 ten species is mainly dependent on the relative occurrence of favourable winds to less 431 favourable winds, i.e. days with tailwinds, compared to days without tailwinds.

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

	Times se	electe	ed	Sum of t	he mea	n RelImp	Percentage o the	f the sun RelImp	of all of
Weather Variable	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%

435

#### 436 Explained variance in MAPD

437	Depending on the species, between 43% and 80% of the variance in MAPD was explained by
438	the model using all of the final identified weather signals (Table 5). On average across all
439	species, 62% of the variance was explained, with eight of the ten species having an adjusted
440	$R^2$ above 0.57. The similarity of the predictive $R^2$ values (calculated using leave-one-out) to

441 the adjusted  $R^2$  values furthermore confirms the robustness of the final identified weather

442 signals.

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

Species	Adjusted R <sup>2</sup>	Predictive R <sup>2</sup>
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

446

#### 447 Direction of the effect of the weather variables on MAPD

448 The effect of summer and autumn temperatures on MAPD was distinctly different for trans-449 Saharan and intra-European migrants (Figure S8 and Figure 3, Table S6 and Table S8): higher 450 temperatures lead to earlier passage at Heligoland for trans-Saharan birds, while they result in 451 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 452 453 identified signals were positively related to MAPD, i.e. increases in precipitation resulted in 454 later autumn passage at Heligoland. Common Redstart and Eurasian Blackbird showed 455 negative associations between precipitation and MAPD for areas in northern Scandinavia. 456 Common Chaffinch had a negatively related precipitation signal for eastern Germany. 457 Frequency of tailwinds was negatively associated with MAPD in six signals, and positively in 458 four cases. Frequency of headwinds was associated positively with MAPD in five signals (all 459 for intra-European species), and negatively in one (for a trans-Saharan species).

460

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

462 Contributions of weather variables' effects on MAPD to species-specific trends in MAPD at 463 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 464 465 (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, 466 467 both positive (delay in MAPD) and negative (MAPD advancement) trend contributions occur. 468 The contributions towards advancement in MAPD are, however, exclusively temperature and 469 precipitation signals. All wind signals push towards MAPD delay.

470 Across all species, the relative contributions of each climate variable to the trends in MAPD 471 (Table 7) remained largely similar to the relative weather variable importance for interannual 472 variations in MAPD (Table 4), i.e. wind has the strongest influence (41%), followed by 473 precipitation (30%) and temperature (29%). The same pattern largely remains for intra-474 European migrants, albeit perhaps with even more emphasis on wind (55%) compared to 475 precipitation (25%) and temperature (20%). For the trans-Saharan migrant species, the pattern 476 of weather variable importance is completely flipped, with temperature having the strongest 477 impact (48%) on the trends in MAPD, followed by precipitation (38%), and only then wind 478 and to a much lesser extent (14%).

479 **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.

			∂MAPD		dClimate			
			∂Climate		dTi	me	∂MAPD dClimate	
Species	Climate variable	ID	Coef.	SE	Coef.	SE	$\frac{1}{\partial Climate} \times \frac{1}{\partial Climate}$	SE
Willow	precipitation	1	0.11	0.03	-0.03	0.14	0.00	0.02
Warbler	tailwind in UK	27	0.48	0.12	0.00	0.03	0.00	0.01
European	temperature	3	-0.82	0.22	0.03	0.02	-0.03	0.02
Pied	tailwind in C Norway	27	-0.83	0.22	-0.02	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	-1.29	0.44	-0.03	0.02
Garden	precipitation	9	0.06	0.01	-0.46	0.25	-0.03	0.02
Warbler	temperature	2	-1.23	0.22	0.03	0.01	-0.04	0.02
	tailwind in SW Norway	20	-0.53	0.12	0.01	0.02	0.00	0.01
	headwind in the Baltic	16	-0.36	0.08	0.00	0.04	0.00	0.01
	states							
Common	temperature	2	-2.00	0.47	0.02	0.01	-0.04	0.02
Redstart	precipitation	6	-0.06	0.02	-0.38	0.20	0.02	0.01
European	tailwind in S and C	21	-0.66	0.14	-0.13	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	-0.78	0.40	-0.02	0.01	0.01	0.01
	headwind in	8	0.29	0.16	-0.02	0.04	0.00	0.01
	Norway/Sweden							
	tailwind in SW Norway	20	-0.19	0.10	-0.01	0.05	0.00	0.01
Song	precipitation	4	0.06	0.01	-0.01	0.33	0.00	0.02
Thrush	tailwind in S Norway	12	-0.36	0.06	-0.14	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	-0.05	0.02	-1.02	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	-0.10	0.03	-0.06	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	-0.58	0.22	-0.02	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

482

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%



486

487 Figure 3 Side-by-side comparison of the effect sizes of (a) climate on mean autumn passage dates 488 (MAPD) at Heligoland, (b) trends in climate variables, and (c) contributions of climate signals to 489 trends in MAPD, in function of the weather variable type and migration strategy. Dashed line bars 490 (95% confidence intervals) are signals from intra-European migrants, while full line bars represent 491 signals from trans-Saharan migrants. Head- and tailwind are interpretations of the wind signals based 492 on the location and wind direction (see Figure 2 and Table S6). WW: Willow Warbler, EPF: European 493 Pied Flycatcher, GW: Garden Warbler, CR: Common Redstart, ER: European Robin, D: Dunnock, 494 ST: Song Thrush, CC: Common Chaffinch, R: Redwing, and EB: Eurasian Blackbird. IDs are 495 identical to those in Table S6 and Figure S2 to Figure S8.

#### 496 **Discussion**

497 Which weather variable types influence interannual differences in avian autumn498 migration phenology?

499 Radar studies have repeatedly indicated strong relationships between non-species-specific 500 migration intensity and weather conditions (Erni et al., 2002; Van Belle et al., 2007; Nilsson 501 et al., 2019). Quantifying species-specific relationships between climate and autumn 502 migration phenology has, nevertheless, proven challenging. While it has long been recognised 503 that it is critical to use the right location and time of influence to assess the influence of 504 climate on migration timing (Lack, 1960; Shamoun-Baranes et al., 2006; Gordo, 2007), large 505 uncertainties in both space and time (due to a lack of sufficiently detailed data) have made it 506 methodologically challenging to identify these areas and times of influence (van de Pol et al., 507 2016; Haest et al., 2018b). Our study shows that an exploratory data analysis approach is able 508 to identify strong species-specific relationships between climate (change) and autumn 509 migration timing of ten passerine species at the island of Heligoland (Germany) by 510 specifically addressing the spatial and temporal uncertainties in the weather influences.

511 Across all ten species we studied, winds during the autumn migration period at both the likely 512 stopover and breeding grounds were the most frequent and important climate influence on 513 autumn migration timing (Table 4). Frequency of tailwinds had a bigger impact on migratory 514 progress at Heligoland than frequency of headwinds. Notwithstanding, we did also find 515 specific headwind frequency influences, including for one species (Dunnock) at roughly the 516 same location and time as a tailwind frequency influence. We, hence, did not only provide 517 further support for a "sit-and-wait-for-favourable-winds" strategy (Gauthreaux Jr. et al., 2005; 518 Delingat et al., 2008; Kemp et al., 2010; Eikenaar & Schmaljohann, 2015; Kölzsch et al., 519 2016; Nilsson et al., 2019), but also for a "sit-and-wait-to-avoid-unfavourable-winds" strategy 520 (see also Erni *et al.*, 2002), with "favourable winds" here defined as tailwinds and 521 "unfavourable winds" as headwinds, both independent of the wind speed (see Methods 522 section).

Depending on the species, temperature and precipitation at presumed breeding areas also 523 524 played important roles (Figure 2 and Table S6). The specific time windows of influence for 525 temperature and precipitation were much less certain than for wind conditions. For 526 temperature, the majority occurred just prior or during the autumn migration period at 527 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 528 529 earlier. This variability in the timing of the precipitation effects once more points towards the 530 complex amalgam of both direct and indirect (including time lagged, e.g. via food) effects 531 through which precipitation likely influences the timing of biological events. Across taxa and 532 biological events, similarly complex precipitation effects have been suggested for, e.g. plant 533 phenology (Peñuelas et al., 2004; Gordo & Sanz, 2010), insect migration and abundance 534 (Zipkin et al., 2012; Evans et al., 2019), avian spring migration and reproduction (Gordo et 535 al., 2005; Gordo, 2007; Haest et al., 2018b; Englert Duursma et al., 2019), and mammal 536 demography (Thibault et al., 2010; Campos et al., 2017).

537 Our results show how species-specific combinations of precipitation, temperature, tail- and 538 headwind influences at the breeding and stopover grounds (Figure 2) can explain between 539 50% and 80% of the interannual variation in autumn migration phenology (Table 5) in both 540 intra-European and trans-Saharan migrant bird species. Similar to previous studies on the 541 relationship between timing of (other) biological events and large-scale indices (van de Pol et 542 al., 2013; Chambers et al., 2014; Haest et al., 2018b), we found no support for any influence 543 of the North Atlantic Oscillation (index) on autumn migration phenology after more local 544 weather influences were taken into account.

545 It is important to note that the relative importance of the different weather variables might 546 only be representative for the studied species, geographical region, and populations, as the 547 influence of weather on bird migration phenology is species and context-dependent (Gordo, 548 2007; Calvert et al., 2009; Carey, 2009; Shaw, 2016; Haest et al., 2018b; Senner et al., 2018). 549 The larger relative importance of wind conditions at Heligoland might, for example, be 550 influenced by its geographic location at an ecological barrier, i.e. in the North Sea. For 551 migration across large land masses, wind might be less important as birds can, at any time, 552 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 553 554 obvious ecological barrier (Figure 2). Furthermore, strong wind influences on autumn 555 migration intensity (using radar) have recently also been shown across large parts of 556 (continental) Europe (Nilsson et al., 2019).

557

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

559 Our analysis provides a clear illustration of how species- or population-specific responses to 560 several climate (change) influences at the breeding and stopover grounds during and prior to 561 autumn migration, can bring about large interspecific variation in autumn migration 562 phenology trends (Figure 3, Table 6 and Table 7). The high variability in the time windows of 563 the climatic influences between and within both species and weather variable types, 564 furthermore illustrates that the climatic influences, next to direct effects on migration 565 departure and progress (Shamoun-Baranes et al., 2006; Calvert et al., 2009; Vansteelant et al., 566 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 567 568 differences in temporal trends in autumn migration phenology are very likely related to 569 differences in ecological and life-history traits (Jenni & Kéry, 2003; Bitterlin & Van Buskirk, 570 2014), but also suggest that these differences are related to different exposure and reactions to

571 climate during these prior life-history events (see also Chmura *et al.*, 2019).

572

#### 573 Long-distance versus short-distance migrants

574 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 575 576 this study; TS) versus the delay for short-distance (e.g. the intra-European migrants in this 577 study; IE) migrant bird species (Jenni & Kéry, 2003; Van Buskirk et al., 2009). Our results on 578 the effects and trend contribution of each weather variable (Figure 3 and Table 6) provide 579 some hints on the possible mechanisms through which climate (change) may be causing the 580 apparent distinction in autumn migration trends of IE (delay) and TS (advance) migrants. For 581 IE migrants, the climate contributions to MAPD trends (almost) unanimously pushed towards 582 a delay in autumn migration. Climate contributions for TS migrant species were more 583 heterogeneous, but particularly of interest is that contributions towards advancements were 584 exclusively temperature and precipitation effects, not wind effects. The contrast in 585 temperature trend contributions for IE and TS migrants seems to come about mainly due to 586 the different direction of the impact of temperature on MAPD, as most (6 of 7) of the 587 influencing temperatures have increased over past six decades. The contrast in precipitation 588 trend contributions, on the other hand, seems to be mainly due to decreasing precipitation 589 over time for TS migrants. As most of the precipitation influences had a delaying effect on 590 MAPD, i.e. a positive association, the decrease in precipitation over time translates in 591 advancing trend contributions for the TS migrants. Interestingly also, the overall large 592 importance of wind effects on interannual variation in MAPD (Table 4) is reflected in the 593 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 trendsover time in the influencing wind variables were largely lacking.

596 These observations, in combination with the weather variable type-specific locations and 597 timing (see Results section, Figure 2, Figure 3 and Table S7), fit with two previously 598 suggested hypotheses to explain the contrasting patterns in autumn migration phenology 599 trends between long- and short-distance migrants: (1) the optimal migration strategy (Jenni & 600 Kéry, 2003; Gordo, 2007), i.e. long-distance migrants depart earlier when they can to profit 601 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 602 603 effects of temperatures; and (2) the "sit-and-wait-for-favourable-winds" strategy strongly 604 affects interannual variability in migration timing of both long- and short-distance migrants 605 (Gauthreaux Jr. et al., 2005), but for the species in our study, strong contributions to long-606 term trends in migration timing only occurred for short-distance migrants because the wind 607 conditions that influence the long-distance migrants did not change in a specific direction. 608 Given that responses are highly species- and context-dependent, however, further studies are 609 needed on other species and locations to fully understand the mechanisms that drive 610 interspecific differences in autumn migration trends, including if there are indeed explicit 611 differences between long- and short-distance migrants.

612

#### 613 All aspects of climate (change) are important

614 Climate change involves much more than merely an increase in temperatures. The potential 615 role of altered precipitation, and especially of altered wind conditions, in the context of 616 climate change impacts on migration phenology has, nevertheless, typically received much 617 less attention (Gordo, 2007; Kemp *et al.*, 2010), with only 29% and 12% of species-specific 618 long-term studies investigating precipitation and wind, respectively (Appendix S1). Our study 619 shows how changes in both precipitation and wind conditions have already contributed to 620 trends in autumn migration phenology at Heligoland over the past decades (Figure 3, Table 6 621 and Table 7). A number of recent studies have also made projections on how future wind 622 conditions are likely to impact migration progress and timing (e.g. La Sorte & Fink, 2017; La 623 Sorte et al., 2018). Given the frequency and strength of precipitation and especially wind 624 effects on autumn migration phenology that we (Table 4) and other studies have found (e.g. 625 Calvert et al., 2009; Kemp et al., 2010; La Sorte et al., 2014; Laughlin et al., 2016), it appears 626 vital for future migration studies to investigate not only temperature, but also other climate 627 variables.

628

#### 629 Implications for (autumn) migration in other animal taxa

630 There are migrant species in many animal groups, but the link between migration and climate 631 (change) has been primarily studied in birds (Shaw, 2016). While the migration ecology of 632 any animal group, species, or population should be analysed within its own appropriate 633 ecological and geographical context, our results do provide some suggestive patterns for 634 migration in other animal taxa. Insect and bat migration timing, for example, are also highly 635 dependent on a mixture of temperature, precipitation, and wind conditions occurring prior or 636 during migration, through both direct and indirect effects (Wikelski et al., 2006; Bauer et al., 637 2011; Shaw, 2016; Pettit & O'Keefe, 2017). Similarly complex contributions towards 638 advancement and delays are hence to be expected and are likely also occurring already, 639 potentially causing ecological mismatches in multiple trophic interactions (Thackeray *et al.*, 640 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, 644 an explorative approach does not only seem appropriate, but furthermore also generates 645 hypotheses that can subsequently be tested using more confirmatory approaches. This applies 646 to bird migration, but perhaps even more so to the migrant species in any of the other animal 647 groups, as the link between climate (change) and migration has in most cases been studied 648 even less. As such, we encourage other researchers with similar time series data to follow a 649 similar approach in order to further unravel species- and population-specific responses of 650 autumn migration timing to climate change. By doing so, new patterns may arise at a meta-651 analysis level that could ultimately contribute towards understanding the observed 652 demographic changes in bird and other animal populations.

653

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#### 990 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.

994

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.

1000

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).

1005

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.

1009

1010 Figure S2 – Figure\_S2\_AICcR2SlopeMaps\_temperature.pdf: Per species  $\Delta$ AICc, adjusted R<sup>2</sup>,

1011 and regression coefficient maps of the identified best time windows for temperature.

1012

1013 Figure S3 – Figure\_S3\_AICcR2SlopeMaps\_precipitation.pdf: Per species  $\Delta$ AICc, adjusted

1014  $R^2$ , 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<sup>2</sup>, 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<sup>2</sup>, 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.

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1026 Figure S6 – Figure\_S6\_AICcR2SlopeMaps\_WindNight\_CFHelgo.pdf: Per species  $\Delta$ AICc, 1027 adjusted R<sup>2</sup>, and regression coefficient maps of the identified best time windows for the 1028 number of days with midnight winds coming from Heligoland.

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1030 Figure S7 - Figure\_S7\_AICcR2SlopeMaps\_WindNight\_GTHelgo.pdf: Per species  $\Delta$ AICc, 1031 adjusted R<sup>2</sup>, and regression coefficient maps of the identified best time windows for the 1032 number of days with midnight winds in the direction of Heligoland.

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Figure S8 – Figure\_S8\_OverviewSelectedTimeWindows.pdf: Per-species overview of the
time windows of the final selected weather variables in relation to the distribution of the birds
ringed at Heligoland across all years in both spring and autumn (violin plots).

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Table S1 – Table\_S1\_RingRecoveriesOverview.pdf: Per species overview of the months used
for visualizations in the manuscript and the number of recoveries for both the breeding period
and autumn migration ring recoveries.

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Table S2 – Table\_S2\_TimeTrend\_ADFtest.pdf: Per species overview of the Augmented
Dickey-Fuller test results for stationarity in the residuals of the mean autumn passage date
trend models (see Table 3).

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Table S3 – Table\_S3\_TimeTrend\_DurbinWatsonTest.pdf: Per species overview of the
Durbin-Watson test results for autocorrelation up to lag 2 in the residuals of the mean autumn
passage date trend models (see Table 3).

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1050 Table S4 - Table\_S4\_LongList\_CandidateWeatherPixels.pdf: Overview of the candidate 1051 weather signals selected from the  $\triangle$ AICc maps, including the identified time windows,  $\triangle$ AICc 1052 values compared to trend model (see Table 3) and an intercept-only model, probability Pc 1053 value that the  $\triangle$ 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 are 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.

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Table S5 – Table\_S5\_Shortlist\_OverviewRelativeVariableImportance.pdf – Overview of the relative variable importance of the candidate weather signals, calculated using three different methods: (1) the sum of the multi-model AICc weights across all the possible models with maximum four independent variables; (2) the boruta method; and (3) the game-theory-based LMG metric for variance decomposition in linear models. Effects represent the average conditional coefficient calculated over all possible models with a maximum of four independent variables. This table includes only the candidate weather signals that were not removed due to high collinearity with another better performing candidate signal, low performance compared to an intercept-only model, or because they were not in the top 15 of the variable reduction step using the boruta method (see Table S4).

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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.

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Table S7 – Table\_S7\_InterpretationLocationTimingFinallySelectedWeatherVariables.pdf –
Overview of the interpretation of the location and timing of each of the identified final
weather variables that are likely to affect mean autumn passage dates (MAPD) at Heligoland.

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.