

Spatial variation in spring arrival patterns of Afro-Palearctic bird migration across Europe

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Running head: Arrival timing of Afro-Palearctic migrants

Aim: Geographical patterns of migrant species arrival have been little studied, despite their relevance to global change responses. Here, we quantify continent-wide inter-specific variation in spatio-temporal patterns of spring arrival of 30 common migrant bird species and relate these to species characteristics and environmental conditions.

Location: Europe

Time period: 2010-2019

Major taxa studied: Birds, 30 species

Methods: Using citizen science data from EuroBirdPortal, we modelled arrival phenology for 30 Afro-Palearctic migrant species across Europe to extract start and duration of species arrival at a 400 km square resolution. We related inter and intra-specific variation in arrival and duration to species characteristics and temperature at the start of the growing season (green-up) .

Results: Spatial variation in start of arrival times indicates it took on average 1.6 days for the leading migratory front to move northwards by 100 km (range: 0.6—2.5 days). There was a major gradient in arrival phenology, from species which arrived earlier, least synchronously, in colder temperatures and progressed slowly northwards to species which arrived later, most synchronously and in warmer temperatures, and advanced quickly through Europe. The slow progress of early arrivers suggests that temperature limits their northward advance; this group included Aerial Insectivores and species wintering north of the Sahel. For the late arrivers, which included species wintering further south, seasonal resource availability in Africa may delay their arrival into Europe.

Main conclusions: We found support for the green-wave hypothesis applying widely to migratory landbirds. Species arrival phenologies are linked to ecological differences between taxa, such as diet, and wintering location. Understanding these differences informs predictions of species' sensitivity to global change. Publishing these arrival phenologies will facilitate further research and have additional conservation benefits such as informing designation of hunting seasons. Our methods are applicable to any taxa with repeated occurrence data across large scales.

Key words: phenology, European-African migrants, bird migration, spring arrival, spatial variation, intraspecific and interspecific variation, EuroBirdPortal, citizen scientists, complete lists and casual records

1. Introduction

Timing of arrival on the breeding grounds for temperate-breeding migrants, or *spring arrival*, can have significant demographic consequences, affecting individual survival and productivity (Lerche-Jørgensen et al. 2018, Halupka et al. 2023). The optimal time for arrival involves trade-offs between various factors, including the availability of food (Lack 1950, Perrins 1970) and the survival of young (Drent 2006) and their parents (Lerche-Jørgensen et al. 2018). Optimal arrival timing will vary between and within species over space and time, depending upon, amongst other factors, diet, competition (Kokko 1999), and the time required to breed, seasonal changes in weather and local conditions (Winkler et al. 2014, Drent 2006, Bauer et al. 2020) and their cumulative impacts on individual fitness within a population. Recent climate change has significantly altered the phenology of many temperate plants and insects (Menzel et al. 2006, Wolkovich et al. 2014), frequently changing the time of peak food availability for migratory animals. The degree to which species have been able to shift their arrival phenology to compensate for this varies (Thackeray et al. 2016, Cohen et al. 2018, Youngflesh et al. 2021), potentially altering species interactions.

Data availability has constrained most existing studies of arrival phenology to focus on relatively small geographical areas (Thackeray et al. 2016, Newson et al. 2016), despite evidence of large-scale spatial variation in phenological metrics (Bell et al. 2019). Consequently, spatial variation in spring arrival, within and among species, and the possible causes of this variation remain understudied (Cohen et al. 2018). However, the growth in citizen science recording, especially for popular taxa like birds, and the development of a multitude of associated online recording and integrated storage portals (e.g., eBird, Sullivan et al. 2014, EuroBirdPortal (<https://eurobirdportal.org/ebp/en/>)), have meant that it is now possible to model arrival phenology for many species at a continental scale (Lehikoinen et al. 2019, Youngflesh et al. 2021, 2023).

Here, for the first time, we describe inter-specific spatial variation in species' spring migration across Europe. We focus on spring arrival timing due to its potential importance for life-time fitness, given the links between arrival times and peak food supply, productivity, individual condition and survival (Saino et al. 2011, Sander et al. 2021). Note, "arrival" here means arrival into locations in Europe but is not restricted to individuals arriving on their breeding grounds. Past phenology studies mostly use first arrival dates, despite first arrivals potentially demonstrating outlying behaviours. The recording of first arrivals is also inherently biased by species and site-level variation in observer effort and population size (Lehikoinen et al. 2019). Consequently, here, we model the entire arrival period, facilitating the derivation of metrics reflecting 'end of arrival' and 'duration of arrival' across species, as well as start of arrival. This enables a more robust analysis of spatial variation in arrival phenology within and between species.

We focus our attention on three key issues:

- 1) **Spatial variation in spring arrival.** Temperate zone-breeding migratory birds are expected to arrive on their breeding grounds later at higher latitudes given the later arrival of spring with latitude (Youngflesh et al. 2021). To date, whether and how this varies between species has not been systematically described. Here, we quantify variation within and between species for the start and duration of arrival and describe the rate of change in these variables with increasing latitude. We then use a Principal Component Analysis (PCA) analysis to identify common gradients in arrival phenology across species.
- 2) **Morphological and life history predictors of arrival times.** We test the extent to which inter-specific variation in spring arrival can be explained by four key traits: wintering zone, foraging guild, body size, and length of breeding season. Previous studies suggest that small-bodied migrants may arrive later at higher latitudes, as colder temperatures present higher metabolic challenges (Buckley et al. 2018), though the relationship between body size, starvation risk and predation risk is complex and varies with latitude, an animal's physiology and environment as well as temperature (McNamara et al. 2016). Migrants wintering further south may arrive later due to the longer travel distance (Usui et al. 2017) or because of seasonal food constraints in Africa (Davies et al. 2023). We expect that migrants with a primary food source that has a short seasonal peak may have more constrained local arrival windows (Both et al. 2010). By contrast, species with a longer breeding season may arrive earlier to ensure enough time for replacement or additional broods (Morrison et al. 2019).
- 3) **Arrival phenology associations with temperature and possible risk of resource limitation.** Given the importance of temperature in driving changes in phenology and the potential implications for populations (Thackeray et al. 2016), we test the extent to which migration phenologies relate to temperature. We expect that early arriving species with slow rates of movement northwards are more likely to be limited by cold temperatures than species which move more rapidly northward. We also quantify spatial variation in each species' arrival temperature relative to spatial variation in spring green-up temperature (i.e. temperature at start of spring as defined by emergence of spring vegetation, Smets et al. 2022), to identify species and latitudes where individuals may be most vulnerable to resource limitations (Marra et al. 2005), and assess the extent these species follow expectations from the green-wave hypothesis (Wang et al. 2019).

2. Methods

2.1 Avian occurrence data

Bird occurrence data came from EuroBirdPortal (EBP, <https://eurobirdportal.org/ebp/en/>), a European Bird Census Council (EBCC) project with 81 partner institutions covering 31 European countries, which collates and combines bird records into a single online dataset. The data are contributed at a daily resolution and, at least, at the 10km x 10km level using the European Economic Area 10 x 10km reference grid (<https://www.eea.europa.eu/en/datahub/datahubitem-view/3c362237-daa4-45e2-8c16-aaadfb1a003b>). Partners vary in their recording procedures and practices and data come, essentially, in two forms: complete lists (detection/non-detection data, where all birds seen or heard are recorded) and ad hoc casual records (presence-only data, where an unknown proportion of the species seen or heard are recorded) – see S1.

We analysed data recorded between 2010 and 2019 for the 30 species of Afro-Palaearctic migrant passerines, and near-passerines, currently included in the EBP database (Table S1). We used presence or absence of a species within a complete list or pseudo-complete list (see S1 & Table S2), rather than counts of individuals, as count data were not available for most records. As our focus is on spring phenology, we only used data collected from the 1st January to the 19th July (200 ordinal days). This broad date range was used as we did not want to influence start and end dates by using too narrow a window. The final dataset consisted of 2,047,685 complete lists and 1,315,678 pseudo-complete lists.

2.2 Modelling species-specific spatial variation in spring arrival

We modelled species arrival phenology across Europe using a Generalised Additive Modelling (GAM) framework with one model per species. In summary, we used binomial models with a logit link, in which the dependent variable was whether or not the species occurred in a complete list or pseudo-complete list (1 or 0) in relation to day of year, easting, northing and year (as a factor). Scheme and list type (complete or pseudo-complete) were included as control variables, and list length was used as a measure of effort (for details see S2).

We predicted phenology curves of daily species occurrence for every 100 km square unit from our fitted model, assuming “complete lists” with all variables at their mean values. For each species, we made arrival predictions for all 100 km squares up to the latitude of the most northerly part of a species breeding range, the latter derived from IUCN range polygon data (BirdLife International and Handbook of the Birds of the World 2020).

Next, we derived the start and end of arrival from the phenology curve, defining these events as occurring when a proportion of the maximal value was reached (following Youngflesh et al. 2021). To ensure the first peak in arrival date was always selected, we restricted the maximal peak to be a point

before 166 ordinal days (15th June). The start of spring arrival was the ordinal day when the phenology curve reached 10% of the maximal value (adjusted to account for higher baseline values in overwintering birds - see S2) and the end of arrival was the ordinal day when the phenology curve reached 90% of this value. We removed three squares across two species where the start of arrival and end of arrival were the same day, and 61 squares across 10 species where the start of arrival was earlier than day 31 (3.2%), as this most likely reflected overwintering birds and did not represent migratory timing. Duration of arrival was calculated as end of arrival minus start of arrival. The end of arrival was highly correlated with the start (PPMCC $r = 0.828$), so we have not included it here.

2.3 Exploring spatial and species variation in start and duration of spring arrival

2.3.1 Species variation in start of and duration of arrival with change in northing

To reduce spatial autocorrelation (due to the estimates for arrival all coming from the same model which included spatial smooths), and associated non-convergence issues in our models, we aggregated the 100 km square predictions for start and duration of arrival to a 400 x 400 km resolution (EPSG:3035), taking the mean predicted start and duration across the 16 100 km squares included in each. This also helped to reduce the influence of any extreme predictions to ensure the predictions better reflected the population mean. We modelled spatial variation in start and duration of arrival using northing, easting and species identity, including interactions between both northing and easting and species. Easting and northing were standardised and centred prior to modelling. We used a Generalised Linear Mixed Model (GLMM) with a Gaussian distribution and an identity link. Spatial plots of the model residuals showed spatial autocorrelation, so we also included a species-specific gaussian autocorrelation structure, which removed this (Equation 1).

Eq (1): $\text{response} \sim \text{species} + \text{northing}:\text{species} + \text{easting}:\text{species} + \text{gau}(\text{coords}+0|\text{species})$

In models of the start of arrival, the parameter estimate for the $\text{northing}:\text{species}$ interaction represents the change in start of arrival with increasing northing (higher latitudes) for each species, which can be considered a measure of the speed of the population movement northwards through Europe. For duration, the $\text{northing}:\text{species}$ interaction represents the species-specific variation in duration of arrival with northing.

2.3.2 Identifying common gradients in arrival phenology

Lastly, to identify and understand common gradients in phenology between species, we used a PCA of species-specific mean and standard errors for the start of, end of and duration of spring arrival and the

rate of change in each of these parameters with northing. All variables were scaled and centred prior to analysis.

2.4 Influence of species' traits on start and duration of spring arrival

To assess the influence of selected species' traits on arrival timing, we obtained data for four morphological or life history traits, previously linked to arrival phenology (Table 1). Trait values for each species are in Table S3 & Figure S1.

We used a GLMM with a gaussian distribution and an identity link to model start and duration of spring arrival against northing, easting and morphological/life history traits (Equation 2).

Eq(2): Dependent variable ~ easting+foraging category*northing+breeding season length
*northing+wintering region*northing+log(body mass)*northing+
(1+northing|species)+gau(coordinates+0|species).

We included interactions between each trait and northing to specifically quantify their impact on the effects of northing on spring arrival. We included a random effect of species, conditional on northing, allowing a different intercept for each species. We also included a species-specific spatial random effect, allowing different spatial correlation for each species. This addressed the pseudo-replication from having spatially explicit estimates for start and duration of arrival but not for species traits. We used the *emmeans* package (Lenth et al. 2023) to run posthoc tests to find which factor levels in the categorical variables were significantly different to each other.

2.5 Arrival phenology associations with temperature and potential for resource limitation

We assessed variation in the potential for resource limitation due to sub-optimal arrival timing (Marra et al. 2005) by determining how well arrival temperatures matched start of spring green-up temperatures. Mean temperature at arrival onset came from the E-OBS gridded dataset of mean daily temperatures at 0.1 degree lat-long resolution (Cornes et al. 2018). Temperature data for the years of the EBP data (2010-2019) were extracted for the whole of Europe. Average daily temperatures for each 0.1 degree grid, for each ordinal day, over the whole series of years were matched to each 400 km square to give the mean value for each square and day. From this, we derived mean spring temperature during a five-day window centred on the start of spring arrival (from here-on referred to as “start of arrival temperature”) for each species and 400 km square.

We extracted start-of-season (SOS, start of spring green-up from optical Sentinel-2, Smets et al. 2022) for the whole of Europe from 2017 (earliest available year) to 2019 (final year of our EBP data). We

matched this to temperature data by location and date and then averaged over all the SOS temperatures for each 400 km square to get an average start of spring temperature or “start of green-up temperature”. We fitted a GLMM with a gaussian distribution and an identity link to the relationship between start of arrival temperature and green-up temperature. Start of arrival temperature was the dependent variable and green-up temperature and species were the predictor variables. We included an interaction between start of spring arrival and species and a gaussian spatial autocorrelation term dependent on species as in Equation 1.

We explored the relationship between temperature and the first two principal components (PCs) from the PCA analysis using two linear regressions: start of arrival temperature (mean across Europe for each species) against PC1 and PC2 and the difference between start of arrival temperature and start green-up temperature against PC1 and PC2 (mean across Europe for each species).

All data were analysed in R version 3.6.3 (R core development team 2021), details of packages used are in S3.

Results

3.1 Exploring spatial and species variation in start and duration of spring arrival

3.1.1 Variation in start and duration of arrival across species

On average, as expected, birds arrive later at higher latitudes ($\beta = 1.6 \pm 0.02$ days per 100 km, $p < 0.001$), with arrival onset dates ranging from mid-February in the far south of Europe to early May in the far north (Figure 1a). Birds also arrive slightly later in the east than the west, though this effect is weaker ($\beta = 0.04 \pm 0.02$ d, $p < 0.05$).

Spatial variation in the duration of spring arrival (which includes passage and arrival on breeding grounds) follows a pattern similar to start of arrival, being shortest in the north ($\beta = -0.53 \pm 0.02$ d per 100 km, $p < 0.001$) and somewhat longer towards the west of Europe ($\beta = -0.05 \pm 0.02$ d, $p < 0.05$, Figure 1b). Generally, across species, duration of arrival is longer when spring arrival starts earlier (Figure 1).

Our full phenology traits dataset is available [here](#). For a more detailed breakdown of species differences in start and duration of arrival, see S4, Figure S2 and Figure S3.

3.1.2 Variation in start and duration of arrival with northing between species

The rate of change in start and duration of arrival differed significantly between species (Figure 2, Figure S4). Start of spring arrival was later at higher latitudes for all species. House Martin and Sedge Warbler had the highest rate of change (2.4 days per 100 km) in start of spring arrival with northing, indicative of a slow rate of progression of their migration front across Europe, contrasting with the rapid migration of Red-backed Shrike across Europe of 0.7 days per 100 km northing (Figure 2).

In general, spring arrival duration did not vary with latitude (20 species, Figure 2, Figure S4) but, for 9 species, arrival duration was longer at more southerly locations (possibly reflecting a longer passage period); for Blackcap, arrival duration was slightly shorter in the south than the north.

3.1.4 Identifying common gradients in arrival phenology

The first two principal components from the PCA explained 41.74% and 23.39% of the variation respectively (Figure 3). High values of PC1 (e.g. Red-backed Shrike, Marsh Warbler) translated to a later and more synchronous arrival, and a faster population movement northwards (Table S4). High values of PC2 (e.g. House Martin, Chiffchaff) translated to earlier and less synchronous arrival, a slower population movement northwards and larger changes in duration of arrival between northern and southern locations (Table S4). This effectively shows a gradient in arrival phenology between the late and fast arriving species and the early and slower arriving species.

3.2 Morphological or life history predictors of arrival times

Foraging guild, log(body mass) and wintering zone were all significantly correlated with arrival phenology (details in S5). In summary, Aerial Insectivores had a slower rate of movement northwards than Aerial Sallying species (Est = 21.3 ± 2.98 versus Est = 11.1 ± 1.94 , Tukey pairwise comparisons $p = 0.013$, Figure S5a) and duration of arrival for Aerial Insectivores was much longer than other foraging guilds at low northings and similar to the other foraging guilds at high northings (Est = -9.87 ± 2.61 , $p = 0.0002$, Figure S5d). Species from the north wintering zone (above Sahel) started arriving before species from the wintering zones further south (Tukey pairwise comparisons $p < 0.001$, Figure S5c) and had a longer duration of arrival, regardless of northing (Tukey pairwise comparisons $p < 0.001$ Figure S5e). Species from the humid and southern wintering zone had a faster rate of population movement northwards than species from the arid zone (Est = 13.0 ± 1.01 versus 18.2 ± 1.52 , Tukey pairwise comparisons $p = 0.022$, Figure S5c). Heavier species started arriving later (Est = 6.29 ± 1.92 , $p = 0.001$, Figure S5b) and showed a faster population movement northwards through Europe (Est = -1.79 ± 0.82 , $p = 0.028$, Figure S5b) compared to lighter species. Breeding season length was not significantly related to the start or duration of arrival or the change in either of these with northing ($p > 0.191$).

3.3 Arrival phenology associations with temperature and potential for resource limitation

Species arrive at colder temperatures at more northerly latitudes (Figure 4). Species with high PC1 loadings (later and faster arrivers) arrived at warmer temperatures (LM: Est = 0.664 ± 0.127 , $p < 0.001$). Species with high PC1 loadings arrived at temperatures closer to green-up temperatures (Est = 0.432 ± 0.109 , $p < 0.001$), whereas species with high PC2 loadings arrived at temperatures further from green-up temperatures (Est = -0.428 ± 0.145 , $p < 0.007$).

Arrival temperatures were broadly correlated with green-up temperatures across a species' range but, when looking across all 400 km squares, most species arrived in a narrower temperature window than green-up temperatures (Figure 4). For the vast majority of latitudes and species, individuals started to arrive at lower temperatures than the mean start of green-up temperature (Figure 4, Table S5, Figure S6). However, for Garden Warbler, Marsh Warbler, Sedge Warbler, and to a lesser extent Swift, start of arrival temperatures were warmer than green-up temperatures at the highest latitudes.

4. Discussion

For the first-time, we describe interspecific variation in the spring arrival of 30 Afro-Palaearctic migrant bird species across Europe. Birds arrived first in south-west Europe and last in north-east Europe, the duration of population arrival was shortest in the north-east at < 20 days; and longest in the south (> 40 days). Across all species it took, on average, 1.6 days for the leading migratory front to spread northwards by 100 km (range: 0.6 to 2.5 days). These general patterns varied between species, particularly in relation to foraging guild and wintering location. A gradient of opposing phenological traits was evident, from species which arrived early, at colder temperatures, but less synchronously and progressed slowly northward (which included mainly aerial foragers and species wintering north of the Sahel) to those which arrived later and more synchronously, at temperatures closer to green-up temperatures, and progressed faster northwards (which included heavier species which wintered in the humid and southern zone of Africa). By describing these continent-wide parameters of migration phenology, we hope to stimulate further research into the causes and implications of spatial variation in arrival phenology between and within species.

The mean rate of spring arrival advance of 1.6 days per 100 km northwards closely matches rates calculated by Briedis et al. (2020) based on tracking data from 564 individuals of 23 species (1.5 days per degree northwards). The south-west to north-east gradient in arrival dates (Figure 1) reflects the gradient of spring green-up (Briedis et al. 2020), which gives support to the green wave hypothesis applying to migratory passerines (Wang et al. 2019, Thorup et al. 2017), that species broadly track vegetation emergence on their spring migration. By comparing start of arrival temperature and green-up temperature we show that, broadly, species track vegetation emergence/green-up, arriving close to

the green-up temperature (Figure 4 & S6, Table S5). Between-species variability in speed of spread northwards and arrival temperatures suggests other factors will interact with temperature, including how closely a species' primary food source tracks green-up (Wang et al. 2019), how far north they winter (Youngflesh et al. 2021, 2023) and how sensitive their primary food sources is to temperature (Winkler et al. 2013). From our PCA we found that species which started arriving later also had a shorter duration of arrival, which suggests a driving selection pressure to arrive early enough to match peak food supply (Lack 1950, Perrins 1970) though, again, considerable inter and intra species variability is evident.

Two distinct, opposing phenological patterns are evident. These are (i) early and slow arriving species with a long arrival duration, and (ii) late and fast arriving species with a shorter arrival duration. Youngflesh et al. 2021 found a similar pattern of early arrivers travelling more slowly on the Neotropical flyway, overwintering further north and being more responsive to earlier spring. This suggests an advantage to species wintering closer to the breeding grounds and therefore being more able to detect and respond to European spring phenological cues than species wintering further away (Lehikoinen et al. 2004). Of all species included in this analysis, those wintering north of the Sahel were the earliest to start arriving (Figure S3 & Figure S5) and arrived in the coldest temperatures (Table S5). However, in our analysis, the Aerial Insectivores also had high loadings on the early and slow PCA gradient (Figure 3) and many of them winter further south. One important difference between strategies for Aerial Insectivores and north-wintering species is that Aerial Insectivores had longer arrival durations in the south only, whereas northern wintering species had longer arrival durations regardless of latitude. In general, this pattern seems to reflect a longer period of passage in the south for Aerial Insectivores due to an overall slower pace of advance northwards (passage birds could not be distinguished from those arriving on their breeding grounds). For species wintering north of the Sahel, the longer duration of arrival regardless of latitude suggests more intraspecies variability in arrival, possibly due to contrasting selection pressures between males, females and first year birds (Kokko 1999, Catry et al. 2005, Lerche-Jørgensen et al. 2018). The Aerial Insectivores rely on aerial insects whose activity will be strongly influenced by air temperature (Schifferli et al. 2014) and, therefore, the cost of high chick mortality for arriving too early (Shiple et al. 2020) is probably higher than for the species wintering north of the Sahel, who are all Aboreal Gleaning north wintering species. Late and fast arriving species exhibited a different migratory strategy, arriving at warmer temperatures closer to green-up temperature compared to the early and slow species. This is possibly due to seasonal environmental constraints in resource availability in Africa (Pedersen et al. 2020, Davies et al. 2023), as faster arrival was linked to wintering in the humid and southern zones and therefore required traversing more of Africa. Because they arrived in Europe later, there was a stronger pressure to rapidly progress through Europe to ensure arrival in time for peak food supply. Given the

relatively constant availability of aerial insects beyond the start of spring, Aerial Insectivores are likely to be relatively insensitive to mismatch (Martay et al. 2023).

The start of spring is advancing faster at higher latitudes (Post et al. 2018, Liu et al. 2019, Youngflesh et al. 2021) and species appear to be getting squeezed with green-up temperatures closer, or above arrival temperatures at higher latitudes (Figure 4). Some adaptation to this scenario is evident, with most of our studied species apparently adjusting their migratory journeys to arrive earlier at higher latitudes than would be expected based on arrival durations at lower latitudes (Figure 4, Figure S6). The two opposing migration strategies could influence the vulnerability of species to environmental change. The early and slow arrivers, which appear to be temperature-limited, would be expected to advance their arrival more in response to temperature rises from global warming than the late and fast arrivers. Physiological constraints will limit the potential of a species to advance further and arrive at even colder temperatures (McNamara et al. 2016) and individuals who do manage to advance their arrival timing sufficiently are at greater risk of storm or cold related mortality at higher latitudes (Newton 2007). On the other hand, the late and fast arrivers may be more vulnerable to resource limitations by arriving too late. Only four species (Garden, Sedge and Marsh Warblers and Swift) showed possible mismatch at higher latitudes by arriving after green-up temperatures.

We found mixed support for our expected morphological and life history predictors of arrival times. Contrary to expectations (Buckley et al. 2018), smaller bodied individuals tended to arrive earlier than larger species, although the latter showed more rapid rates of migration northwards. As expected, species wintering further south arrived later than those that winter north of the Sahel (Usui et al. 2017), although the north wintering species had a longer arrival duration. Although we didn't find simple differences between foraging guild and arrival time, Aerial Insectivores had the slowest rate of advance in arrival date across Europe, and a significantly longer arrival duration, particularly in the south, than other groups. Given the relatively extended period of aerial insect food availability during the summer (Martay et al. 2023), this partially supports the hypothesis that migrants with a seasonally constrained primary food source will be under greater pressure to arrive on their breeding grounds early (Both et al. 2010). More research is needed to understand the key drivers and associated effects of phenological mismatch, which are likely to be dependent on the details of changing predator-prey relationships (Kharouba & Wolkovid 2020, Samplonius et al. 2021).

Limitations

As with any study using semi-structured and unstructured data rather than a structured survey, there are limitations to trade off against the advantage of a much larger area of coverage. Firstly, coverage and data quality can vary between schemes, depending on how much complete lists are promoted. We compensated for this by creating pseudo-complete lists from casual records. Although these are not as

informative as complete lists, they can be reasonably robust if the density of the casual records is sufficient (Kéry et al. 2010). We could not explore yearly variation here due to poor coverage in the early years in some areas of Europe but both overall coverage and quality of the data collected by online bird portals in Europe have been steadily improving and, therefore, the EuroBirdPortal dataset does provide a good baseline for exploring future changes in spatial variation. As well as spatial differences in data quality there were inherent differences between species in the numbers of records. Some species will be recorded by birdwatchers less frequently than others, either because they are difficult to identify (e.g. Marsh Warbler), or they are nocturnal (e.g. Nightjar), or a species may be misidentified due song similarity (e.g. Garden Warbler and Blackcap) or visual similarity (e.g. Chiffchaff and Willow Warbler). Additionally, weather conditions and variation in habitat will also affect detectability (Morelli et al. 2022). Unfortunately, it was not possible for us estimate detectability here, as the vast majority of records did not have information on survey time or survey area, and no records had information on survey habitat, weather conditions and observer identity. Detection bias can potentially have a significant impact on predictions of abundance (Johnson et al. 2018), however, because we are concerned with the pattern in occurrence through the seasons and not absolute abundance or first arrival dates, any influence of detectability in these temporal patterns should be minimal. Additionally, the sheer volume of data we have (over 3 million records) will mean the effect of any one record is relatively small, and therefore, the influence of, for example, a less experienced observer or a misty day will be minimal.

It was not possible to separate locally breeding and passage individuals in the EBP data, and so our estimations of the duration of arrival will partly reflect passage, especially in southern regions. Therefore, inferences based on arrival duration need to be interpreted with this in mind but can still give us useful insights. For example, as discussed above, the discovery that arrival duration was longer in the south particularly for the early arriving Aerial Insectivores but not for early arriving north wintering species, points to different migration strategies for the two groups. Interestingly, for the majority (20 of 30 species), arrival duration did not change significantly with latitude, though whether this indicates minimal effects of passage birds or that the duration of arrival onto the breeding grounds is longer in the north we cannot determine from the EBP data. This is something which it would be useful and interesting to explore in future analyses, possibly using ringing data to quantify the proportion of passage and breeding birds for each day of spring.

Conclusion

Here, we present the first Europe-wide 400 km resolution database of arrival timings and rates of spread northwards for 30 species of African-Palaeartic migrant birds. We found support for the green-wave hypothesis applying widely to migratory landbirds, with our study species broadly tracking green-up; however, between-species variability in speed of spread northwards and arrival

temperatures suggests many other interacting factors. We identified four species which arrive after green-up temperatures are reached at high latitudes; these would be interesting candidates for further demographic study to assess potential vulnerability to resource limitation. There was a distinct gradient in phenology from early/slow arrivers to fast/late arrivers. These different migration strategies could affect vulnerability to global change, though the relationship may be confounded by many interacting associated factors (Franks et al. 2018, Martay et al. 2023). However, much of the current research does not account for spatial differences in arrival phenology across species and within species. Here, we have shown that, due to advances in citizen science, it is now possible to model phenology at a relatively fine scale throughout continents for a wide range of species, enabling a much fuller understanding of year-round phenological variation between and within species and the associated trade-offs and pressures that species face. This knowledge can help enhance understanding, helping to mitigate threats to migrant species, for example, by using the date of the start of spring migration for each European country to inform hunting legislation (Andreotti et al. 2023). Our approaches could be applied to other taxa where data are sufficient.

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Data accessibility statement: The bird occurrence data used in this paper (EBP data request id: BTO_03_2020) are available upon request from the EBP project (email: Gabriel Gargallo on anella@ornitologia.org and Verena Keller on verena.keller@vogelwarte.ch). EBP datasets related to specific requests are stored permanently in the EBP data repository to allow other researchers to replicate the analyses using the same dataset. The analysis code, predicted start and end dates of spring arrival at a 100 km square resolution and the phenology curves from which these were derived are available in Zenodo deposit [10.5281/zenodo.10949352](https://zenodo.org/record/10949352). The average temperature data is available from doi:10.1029/2017JD028200 and the spring green-up temperature data is available from <https://land.copernicus.eu/pan-european/biophysical-parameters/high-resolution-vegetation-phenology-and-productivity/vegetation-phenology-and-productivity>. The Birdlife polygons of species ranges are available from <http://datazone.birdlife.org/species/requestdis>

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Conflict of interest: The authors declare no conflict of interest.

Table 1. Morphological and life history traits.

Variable	Trait represented	Source	Reference
Log(body mass) (continuous)	Body size	Storchová, & Horak 2017	Usui et al. 2017
Foraging guild (categorical: Aerial Sallying, Aerial Insectivore, Aboreal Gleaning, Ground Forager and Foraging Generalist)	Diet and potential prey availability	Tobias & Pigot 2019	Bitterlin & Van Buskirk 2014
Wintering region (categorical: arid, humid & southern, north, for map see Figure S1)	A surrogate for migration distance, given the continental scale of our analysis (Ockendon et al 2012).	Hewson & Noble 2009, Vickery et al. 2014 updated to account for recent northwards shifts in wintering Chiffchaff and Blackcap.	Ockendon et al. 2012
Breeding season length (incubation + nestling + fledging x average number of broods) (continuous)	Breeding season length	Storchová & Horak 2017 (a brood size of 1 was inferred for the cuckoo)	Morrison et al. 2019

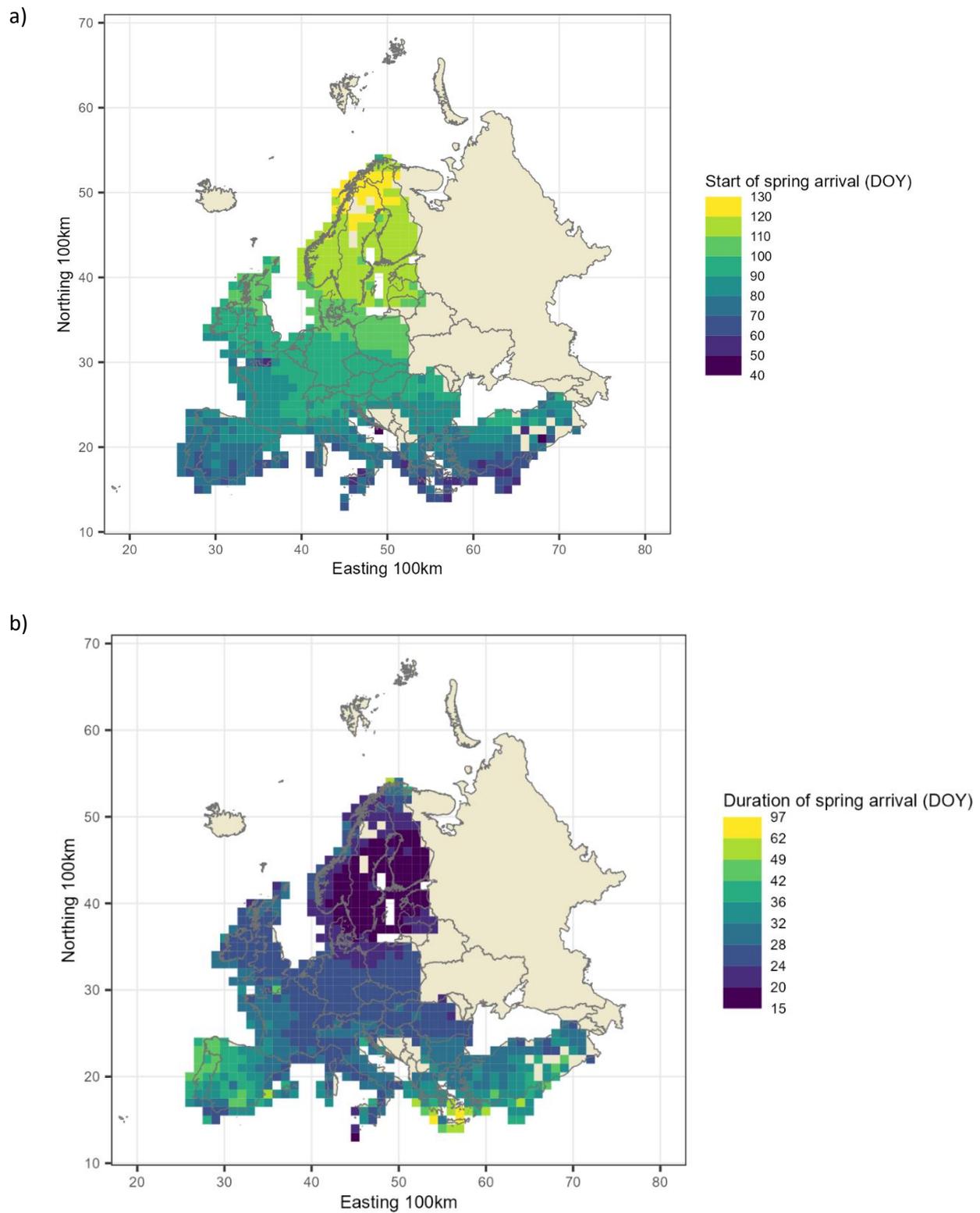


Figure 1. a) Start of arrival (day of year) and b) duration of arrival (days) averaged over all species at a 100 km square resolution. The axes are in units of 100 km, i.e. 50 is 50,000 km. Insufficient data were available from grey areas to model phenology.

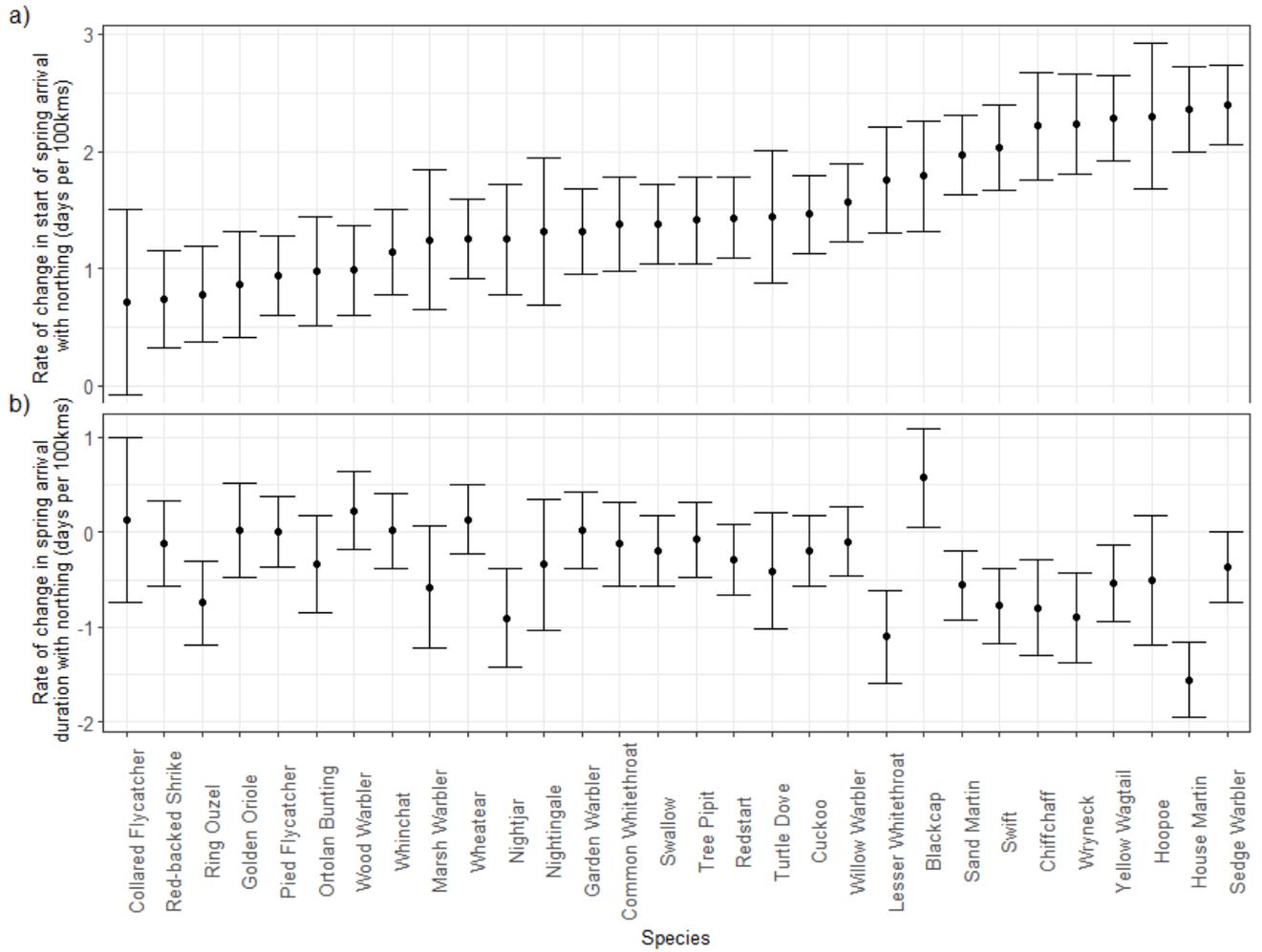


Figure 2. Species plot of rate of change in a) start of and b) duration of spring arrival (days) with a 100 km increase in northing. The bars are the 95% confidence intervals on the parameter estimate. Positive values indicate an increase in the dependent variable with increasing northing and negative values a decrease.

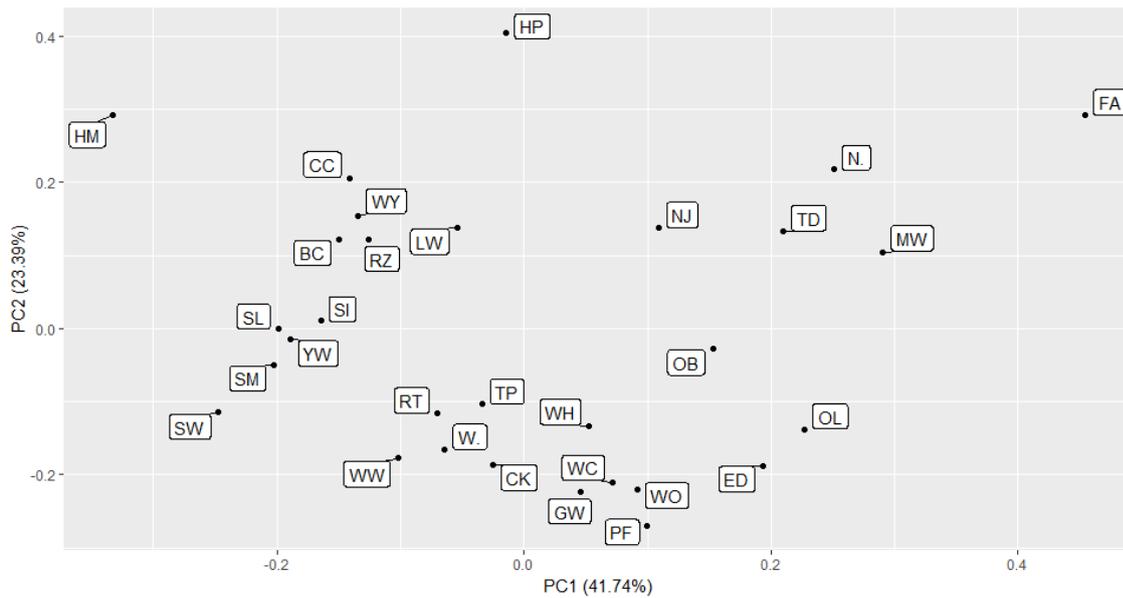


Figure 3. Biplot plot of PCA on start of, end of, duration of spring arrival, and the rate of change in each of these parameters with northing. High values of PC1 translated to a later and more synchronous arrival, and a faster population movement northwards. High values of PC2 translated to earlier and less synchronous arrival, a slower population movement northwards and larger changes in duration of arrival between northern and southern location (Table S4). Species' codes are explained in Table S2.

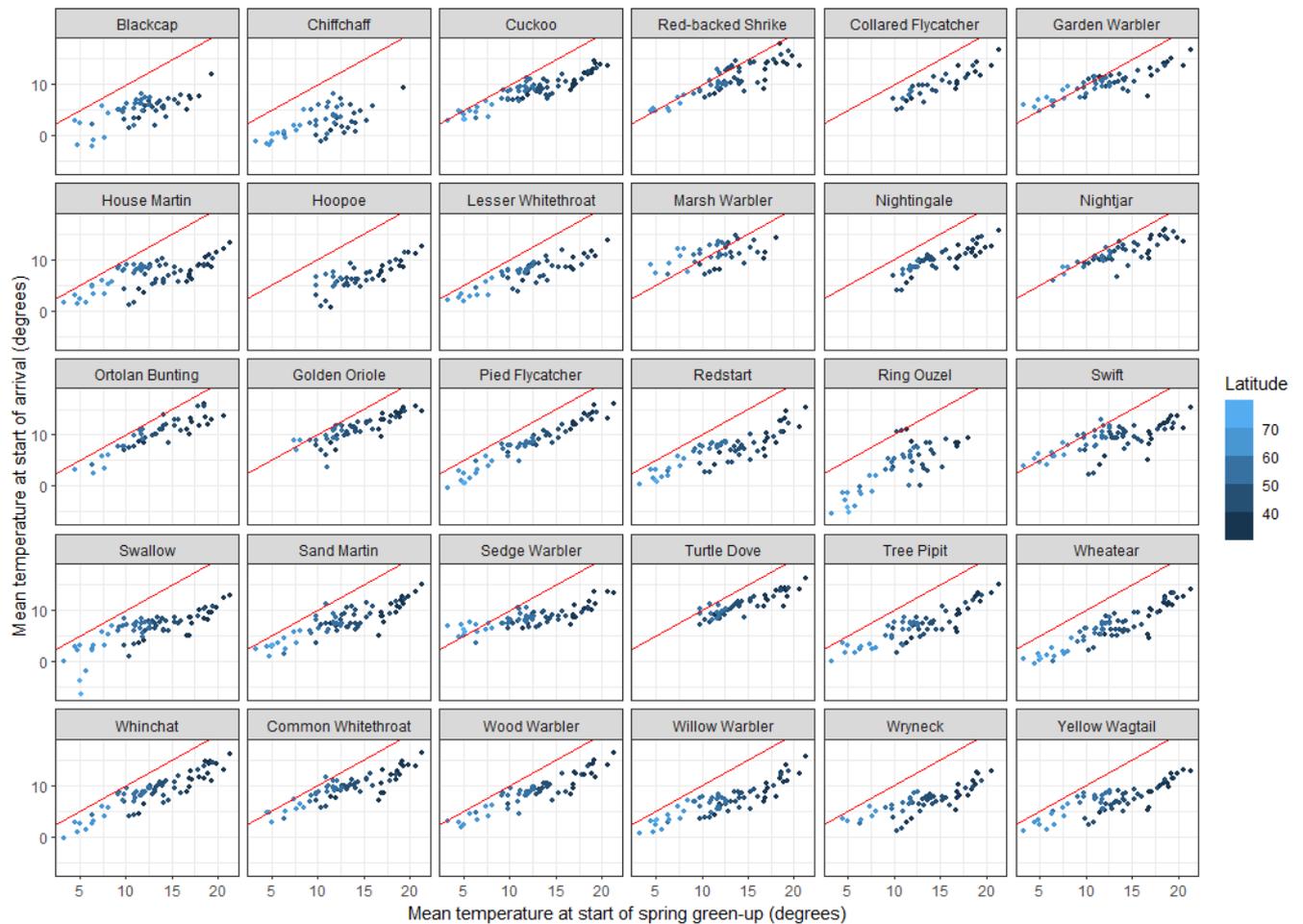


Figure 4. Spatially explicit 400 km square estimates of the temperature at the start of arrival against the temperature at the start of spring green-up for each species; the red line is the 1:1 line.

Supplementary Material

S1. Avian occurrence data

Table S1. The number of complete and pseudo-complete lists contributed by each portal

Table S2. The number of EBP occurrences for each species

S2. Modelling species-specific spatial variation in spring phenology

Table S3. Species specific morphological traits.

Figure S1. Map of wintering zones.

S3. Statistical software

S4. Variation in start and duration of arrival between species

Figure S2. Map of 400 km squares which have data for all species

Figure S3. The geographic variation in start and duration of spring arrival

Figure S4. Change in start and duration of spring arrival with increasing northing

Table S4. The loadings matrix for the first 2 principal component axes

S5. Morphological/life history predictors of arrival times

Figure S5: Significant relationships between start and duration of arrival with morphological traits

Table S5. Species specific relationships of mean arrival temperature against mean green-up temperature.

Figure S6. Temperature at start of spring arrival minus the green-up temperature against latitude

Supplementary material

S1. Avian occurrence data

EuroBirdPortal (EBP) partners vary in their recording procedures and practices, and data come, essentially, in two forms: complete lists and casual records. Complete lists are survey events in which all the birds seen or heard during a site visit are recorded, they can therefore be treated as detection/non-detection data. Casual records are *ad hoc* records where an unknown proportion of the species seen or heard are recorded and are therefore treated as presence-only data. Complete lists are each classified as separate survey events, it is possible to have several different complete lists for a particular 10 km square on a particular day. Casual records are aggregated for each 10 km square per day and treated here as *pseudo-lists* (Kery et al. 2010). We used *records total* as the measure of effort as it was available for the entire dataset. For complete lists, this is the total number of species in the list. For casual records, the records total is the number of different combinations of observer and species recorded in the given date and 10 km square.

Table S1. The number of complete and pseudo-complete lists contributed by each portal.

Portal	No. of complete lists and pseudo complete lists
Artportalen (https://artportalen.se/)	31,828
Artsobservasjoner (https://artsobservasjoner.no/)	143,763
Aves-Symfony (http://aves.vtaky.sk/en/zoology)	28,213
Birds.cz (https://birds.cz/avif/)	21,754
BirdTrack (https://app.bto.org/birdtrack/login/login.jsp)	1,058,308
Dabasdati (http://dabasdati.lv/)	22,450
DOFbasen (http://www.dofbasen.dk/)	129,898
eBird (https://ebird.org/)	373,439
Ornitho (https://data.bioloVISION.net/)	1,161,986
MAP (http://map.mme.hu/)	35,797
Observation.org (https://observation.org/)	65,996
OpenBirdMaps (http://www.openbirdmaps.ro/)	19,740
OrnitoData (http://pasaridinromania.sor.ro/ornitodata)	4,647
Plutof (https://plutof.ut.ee/)	10,536
SmartBirds (http://www.smartbirds.org/)	8,752
Sovon Live Atlas (https://www.liveatlas.nl/)	110,402
Tiira (http://tiira.fi/)	102,364
Trektellen (https://www.trektellen.org/)	33,490

Table S2. The number of EBP occurrences for the 30 species included in the analyses, along with abbreviated species codes.

English Name	Scientific Name	Species Code	Total number of species occurrences
Barn Swallow	<i>Hirundo rustica</i>	SL	855,692
Collared Flycatcher	<i>Ficedula albicollis</i>	FA	12,474
Common Chiffchaff	<i>Phylloscopus collybita</i>	CC	1,031,921
Common Cuckoo	<i>Cuculus canorus</i>	CK	364,635
Common Nightingale	<i>Luscinia megarhynchos</i>	N.	251,905
Common Redstart	<i>Phoenicurus phoenicurus</i>	RT	165,954
Common Sand Martin	<i>Riparia riparia</i>	SM	199,012
Common Swift	<i>Apus apus</i>	SI	468,838
Common Whitethroat	<i>Curucca communis</i>	WH	406,065
Eurasian Blackcap	<i>Sylvia atricapilla</i>	BC	1,010,368
Eurasian Golden Oriole	<i>Oriolus oriolus</i>	OL	145,059
Eurasian Hoopoe	<i>Upupa epops</i>	HP	128,117
Eurasian Wryneck	<i>Jynx torquilla</i>	WY	58,739
European Nightjar	<i>Caprimulgus europaeus</i>	NJ	16,086
European Pied Flycatcher	<i>Ficedula hypoleuca</i>	PF	88,095
European Turtle Dove	<i>Streptopelia turtur</i>	TD	110,219
Garden warbler	<i>Sylvia borin</i>	GW	204,368
Lesser whitethroat	<i>Curruca curruca</i>	LW	169,673
Marsh Warbler	<i>Acrocephalus palustris</i>	MW	83,004
Northern House Martin	<i>Delichon urbicum</i>	HM	425,543

Northern Wheatear	<i>Oenanthe Oenanthe</i>	W.	168,837
Ortolan Bunting	<i>Emberiza hortulana</i>	OB	14,986
Red-backed Shrike	<i>Lanius collurio</i>	ED	124,261
Ring Ouzel	<i>Turdus torquatus</i>	RZ	36,828
Sedge Warbler	<i>Acrocephalus schoenobaenus</i>	SW	177,579
Tree Pipit	<i>Anthus trivialis</i>	TP	164,572
Whinchat	<i>Saxicola rubetra</i>	WC	96,387
Willow Warbler	<i>Phylloscopus trochilus</i>	WW	428,842
Wood Warbler	<i>Phylloscopus sibilatrix</i>	WO	63,869
Yellow Wagtail	<i>Motacilla flava</i>	YW	177,511

S2. Modelling species-specific spatial variation in spring phenology

Modelling phenology

We modelled species phenology across the whole of Europe using one model per species. Specifically, we used binomial models with a logit link, in which the dependent variable was whether or not the species occurred in a complete list or pseudo-complete list (1 or 0).

The data were modelled using a Generalised Additive Modelling (GAM) framework to describe spatio-temporal variation and to maximise flexibility in relationships over the relatively large survey area. Given what we understand about how bird occurrence varies through spring, and with changes in latitude and longitude, we included an easting–northing (EPSG:3035) anisotropic 2D smooth (allowing bird occurrence to vary spatially), a smoothed 1D ordinal day term (allowing bird occurrence to vary depending on the time of year), and an interaction between the easting–northing smooth and the ordinal day smooth (allowing the relationship between bird occurrence and ordinal day to vary spatially) to create a 3D smooth.

To account for the variation in the recording procedures of the recording scheme used to collate the data we included recording scheme as a factor variable (Table A1). A factor was also included to denote whether a record came from a complete list or a pseudo-complete list.

For the UK, which had a large volume of complete lists relative to its geographical size, only complete lists were included. For other countries, we included all complete lists but only included pseudo-complete lists of casual records where the records total (sum of total number of unique species per observer, see S1) for the pseudo-complete list was greater than 15. We arrived at this value by testing the effect of using different cut-offs for inclusion of pseudo-complete lists based on the records total value (5, 10, 15, 20 or 25; > 75% of complete lists had a records total value of 25 or less). Our plots showed very similar phenology curves with overlapping confidence intervals for cut-offs of 15 and above. This value was also close to the mean number of species in complete lists (16.69). Thus, for these pseudo-complete lists, it is likely that most species of interest were recorded.

The only effort-related datum available for all records was *records total* (total number of species for a complete list and sum of total number of unique species per observer for a pseudo-complete list), so this was used as our metric of effort. Total number of species detected per list is considered to form an asymptotic relationship with the amount of time spent surveying, with a higher number of species/records indicating a greater total amount of time spent surveying (Kelling et al. 2015). This was included as a linear response variable in our binomial model, as it was assumed that the logit-linear relationship of the logit link would approximate the asymptotic curve.

We included year as a factor in a random effects smooth to account for any additional differences between years due, for example, to weather.

To account for variability in sampling effort between areas, as well as any residual spatial autocorrelation, we included a Markov random field (MRF) smooth. For these smooths the spatial neighbourhood structure of the 100 km squares is taken into account. The smooth acts to make neighbouring spatial units more similar than non-neighbouring spatial units so, in this case, neighbouring 100 km squares will be more similar to each other. The MRF smooth requires a parameter, k , the value of which controls the level of smoothing. Here, we needed the value of k to ensure sufficient smoothing to mask localised differences that do not help to explain the overall pattern of occurrence in Europe, without losing important spatial variation in occurrence. After testing several different values of k by visually assessing impacts on the predicted 100 km square phenology curves and how well they reflected the underlying raw data, we used $k = 600$, which is roughly 75% of the number of 100 km squares and gave a suitable level of smoothing to reflect the underlying data but avoided biases due to outliers in areas with small sample sizes. We trialled including an interaction between the MRF smooth and ordinal day but this did not provide as good an explanation of the spatial variation in phenology as was provided by a model without this term.

The final structure for each species-specific phenology model was:

Species occurrence ~ te(ordinal date, easting, northing, d=c(1,2)) + records total + recording scheme + datatype + s(100 km square MRF smooth) + s(1|year as a factor)

Determining spring arrival start and end dates from phenology curves

We used the GAM predict function (Wood et al. 2011) in R to produce, from our fitted model, phenology curves for every 100 km square unit. This involved estimating species occurrence (the probability of a species being recorded in a complete list/pseudo-complete list) for every ordinal day between 1 (1st January) and 200 (19th July) for each 100 km square. For each species, we made predictions for latitudes up to and including the breeding range (as determined by BirdLife species range polygons, BirdLife International and Handbook of the Birds of the World 2020). The random effect of year was excluded, the datatype was set to “complete list”, the records total to 15, and the recording scheme to *Global ornitholo*, the scheme from which the majority of the records came (though predictions were trialled with other partners, and this made no visible difference to the predicted phenology curves). The 100 km square was set to the 100 km square of interest for each prediction and the easting and northing to the centroids of the 100 km square of interest. We did not generate predictions for 100 km squares with fewer than 10 occurrences of a species, as the phenology curves were ill defined and unreliable for areas from which a species was mostly absent.

Next we derived the start and end of arrival from the phenology curve. We experimented with several ways of estimating these parameters: finding turning points, calculating second derivatives (Newson et al. 2016) and using a proportion of the maximal value (Youngflesh et al. 2021). We visually assessed the effectiveness of each method on a range of species and curve shapes. Using a proportion of the maximal value gave the most reliable and consistent results for a wide variety of curve shapes and magnitudes and so this is the method used here (see Zenodo deposit [10.5281/zenodo.10949352](https://zenodo.org/record/10949352) for maps of phenology curves for each species). In part of their range, some species showed a bimodal distribution that probably reflects the initial arrival followed by a drop off in detection during incubation and an increase in detection during nestling feeding. To ensure the first peak was always selected we restricted the maximum peak to be a point before 166 ordinal days (15th June). The start of spring arrival was the ordinal day when the phenology curve reached 10% of the maximal value (adjusted to account for higher baseline values in overwintering birds-see below) and the end of spring arrival was the ordinal day when the phenology curve reached 90% of this value.

Some species overwinter in part of Europe (e.g., Blackcap and Chiffchaff); therefore, the minimum occurrence value for these species is higher than zero. In these cases, taking the 10th percentile of the maximum value selected a date too early before the start of increasing occurrence that signifies arrival. Therefore, we subtracted the minimum predicted value from the maximum predicted value for all species and took the 10th percentile of that for the start of spring arrival. For species which do not overwinter, the minimum prediction was very close to zero and so made minimal difference to the estimate, but for species which overwinter, this approach allowed us to account for a higher minimum predicted value due to small numbers of over-wintering birds. Phenology predictions for 100 km squares with very low predicted occurrence for a species were unrealistic. Therefore, we filtered predictions for each species, removing 100 km squares where the maximum occurrence was less than 1% of the maximum occurrence for the species across all squares. We removed any squares where the start of arrival and end of arrival were the same day, as this was obviously implausible, or where the start of arrival was less than 31 days- as this was most likely due to the influence of overwintering birds and therefore did not represent migratory timing.

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Table S3. Species specific morphological traits. Body mass and breeding period (number of broods x incubation, nestling and fledging period) from Storchova & Horak 2017, foraging category from Tobias & Pigot 2019 (though we changed Aerial, Screener to Aerial Insectivore as this term is more widely understood) and wintering region from Hewson & Noble 2007 and Vickery et al. 2014, but updated to account for recent northwards shifts in wintering Chiffchaff and Blackcap.

Scientific name	Common name	Foraging category	Wintering zone	Body mass (g)	Breeding period
<i>Acrocephalus palustris</i>	Marsh Warbler	Arboreal Gleaning	humid&southern	12	24
<i>Acrocephalus schoenobaenus</i>	Sedge Warbler	Arboreal Gleaning	arid	11.9	28
<i>Anthus trivialis</i>	Tree Pipit	Ground Foraging	humid&southern	22.15	39
<i>Apus apus</i>	Common Swift	Aerial Insectivore	humid&southern	40	64
<i>Caprimulgus europaeus</i>	European Nightjar	Aerial Insectivore	humid&southern	71.5	52.5
<i>Cuculus canorus</i>	Common Cuckoo	Foraging Generalist	humid&southern	111	31
<i>Delichon urbicum</i>	Northern House-martin	Aerial Insectivore	humid&southern	19.5	63
<i>Emberiza hortulana</i>	Ortolan Bunting	Ground Foraging	arid	23.75	25
<i>Ficedula albicollis</i>	Collared Flycatcher	Aerial Sallying	humid&southern	13.95	30
<i>Ficedula hypoleuca</i>	European Pied Flycatcher	Foraging Generalist	humid&southern	13.2	30
<i>Hirundo rustica</i>	Barn Swallow	Aerial Insectivore	humid&southern	18.95	87.5
<i>Jynx torquilla</i>	Eurasian Wryneck	Ground Foraging	arid	40	33
<i>Lanius collurio</i>	Red-backed Shrike	Aerial Sallying	humid&southern	31.2	29
<i>Luscinia megarhynchos</i>	Common Nightingale	Foraging Generalist	humid&southern	20.15	36
<i>Motacilla flava</i>	Yellow Wagtail	Ground Foraging	arid	16.5	28
<i>Oenanthe Oenanthe</i>	Northern Wheatear	Aerial Sallying	arid	22.95	42
<i>Oriolus oriolus</i>	Eurasian Golden Oriole	Arboreal Gleaning	humid&southern	69.75	35
<i>Phoenicurus phoenicurus</i>	Common Redstart	Aerial Sallying	arid	15.7	56
<i>Phylloscopus collybita</i>	Chiffchaff	Arboreal Gleaning	north	7.7	58
<i>Phylloscopus sibilatrix</i>	Wood Warbler	Arboreal Gleaning	humid&southern	9.95	25
<i>Phylloscopus trochilus</i>	Willow Warbler	Arboreal Gleaning	humid&southern	9.1	26
<i>Riparia riparia</i>	Common Sand Martin	Aerial Insectivore	humid&southern	13.5	74
<i>Saxicola rubetra</i>	Whinchat	Aerial Sallying	humid&southern	16.6	31
<i>Streptopelia turtur</i>	European Turtle-dove	Ground Foraging	arid	144	90
<i>Sylvia atricapilla</i>	Eurasian Blackcap	Arboreal Gleaning	north	18.6	24
<i>Sylvia borin</i>	Garden Warbler	Arboreal Gleaning	humid&southern	18.7	22
<i>Sylvia communis</i>	Common Whitethroat	Arboreal Gleaning	arid	14.75	22
<i>Sylvia curruca</i>	Lesser Whitethroat	Arboreal Gleaning	arid	12.4	23
<i>Turdus torquatus</i>	Ring Ouzel	Arboreal Gleaning	north	108	42
<i>Upupa epops</i>	Eurasian Hoopoe	Ground Foraging	arid	65	44

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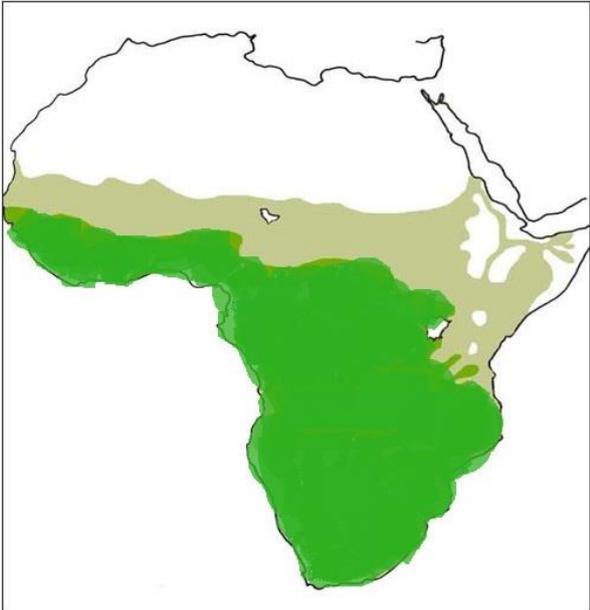
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Figure S1. Map of wintering zones. The green area is the humid and southern zone, the khaki area is the arid zone and the white area is the north zone.



1 **S3. Statistical software**

2 Due to the large volume of data, the JASMIN supercomputer
3 (<https://www.ceda.ac.uk/services/jasmin/>) was used to run the phenology modelling parts of the
4 analysis. For our initial phenology models, we used GAMs from the *mgcv* package (Wood
5 2011). For our models using the values derived from the phenology models (start and duration
6 of spring arrival), we used GLMMs fitted using the *glmmTMB* package (Brooks et al. 2017,
7 *version 1.1.3*). We used the *prcomp* from the *stats* package to run the PCA (R Core Team 2022)
8 and the *factoextra* package (Kassambara & Mundt 2020) to visualise the PCA. We extracted
9 start-of-season dates (start of spring green-up from optical Sentinel-2, Smets et al. 2022) and
10 corresponding temperatures (E-OBS gridded dataset of mean daily temperatures, Cornes et al.
11 2018) for the whole of Europe from 2017 (earliest available year) to 2019 (final year of our EBP
12 data) using the *exactextractr* package (Baston 2022).

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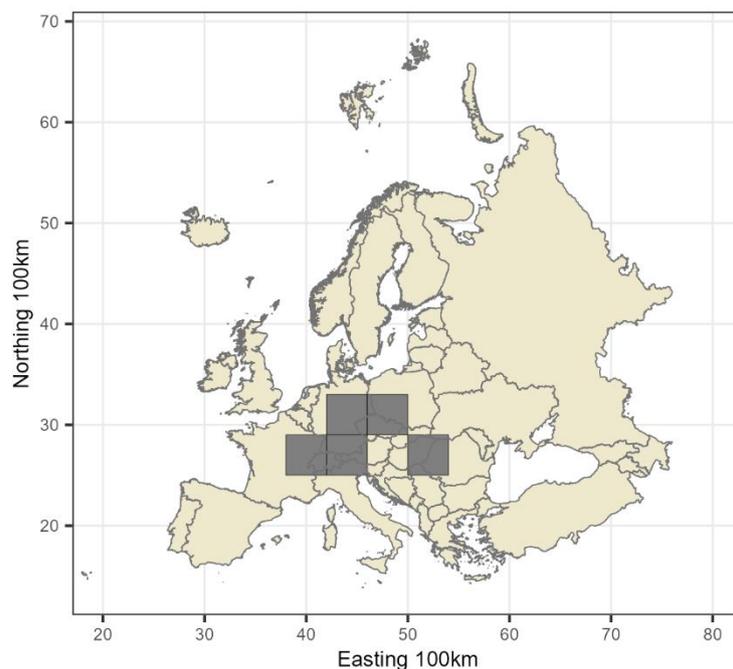
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37 **S4. Variation in start and duration of arrival between species**

38 To assist in comparing start and duration of arrival between species despite differing ranges we
39 used the models detailed in Equation 1, section 2.3, to predict arrival date for five 400 km
40 squares which all species occurred in (Figure S2) and averaged these to get the mean and
41 standard error.



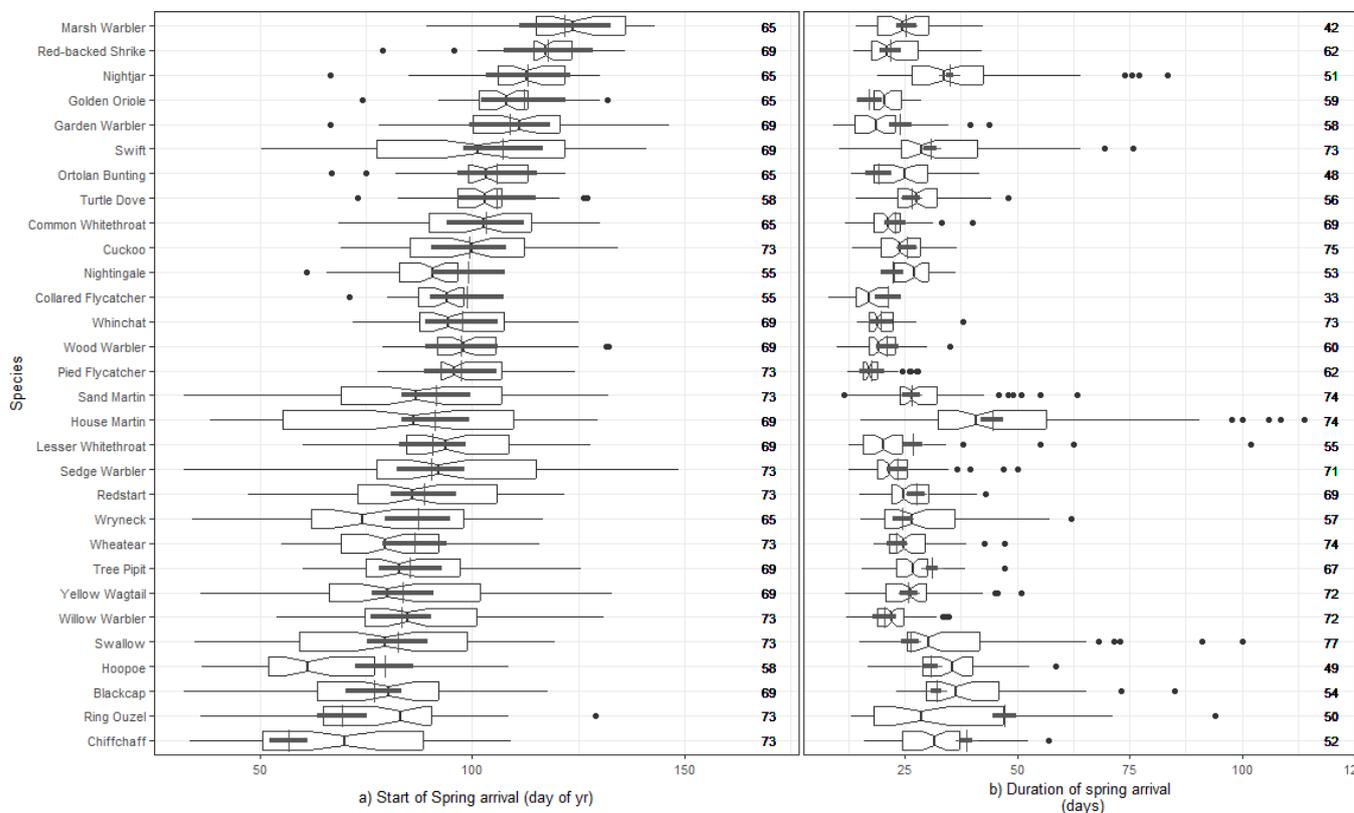
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43 **Figure S2.** Map of 400 km square which have data for all species. The axes are in units of 100 km, i.e. 50
44 is 50,000 km.

45 When accounting for differing species ranges (black bars on boxplots in Figure S3) Chiffchaff
46 and Ring Ouzel are the earliest to arrive (median arrival dates of 26th February \pm 2.3 days and
47 12th March \pm 3.1 days respectively) and Red-backed shrike and Marsh Warbler the latest
48 (median arrival dates of 28th April \pm 5.5 days and 2nd May \pm 5.3 days respectively). Collared
49 Flycatcher shows the least geographical variation in start of arrival dates (range = 33 days) and
50 Sedge Warbler shows the most (range = 117 days), for Collared Flycatcher, at least, this may be
51 influenced by the small sample size.

52 The duration of arrival is much less variable between species than the start of arrival, with
 53 median arrival durations across Europe ranging from 17 (for Pied and Collared Flycatcher) to
 54 41 (House Martin) days. Predicted durations, standardised to the average of five 400 km squares
 55 in which all species occur, ranged from 17 for Golden Oriole to 47 for Ring Ouzel. House
 56 Martin shows the largest spread in duration of spring arrival across Europe (99 days), while
 57 Golden Oriole show the smallest (14 days). As Golden Oriole has a sample size roughly
 58 comparable to the average across other species, we can discount sample size influence in this
 59 case.

60



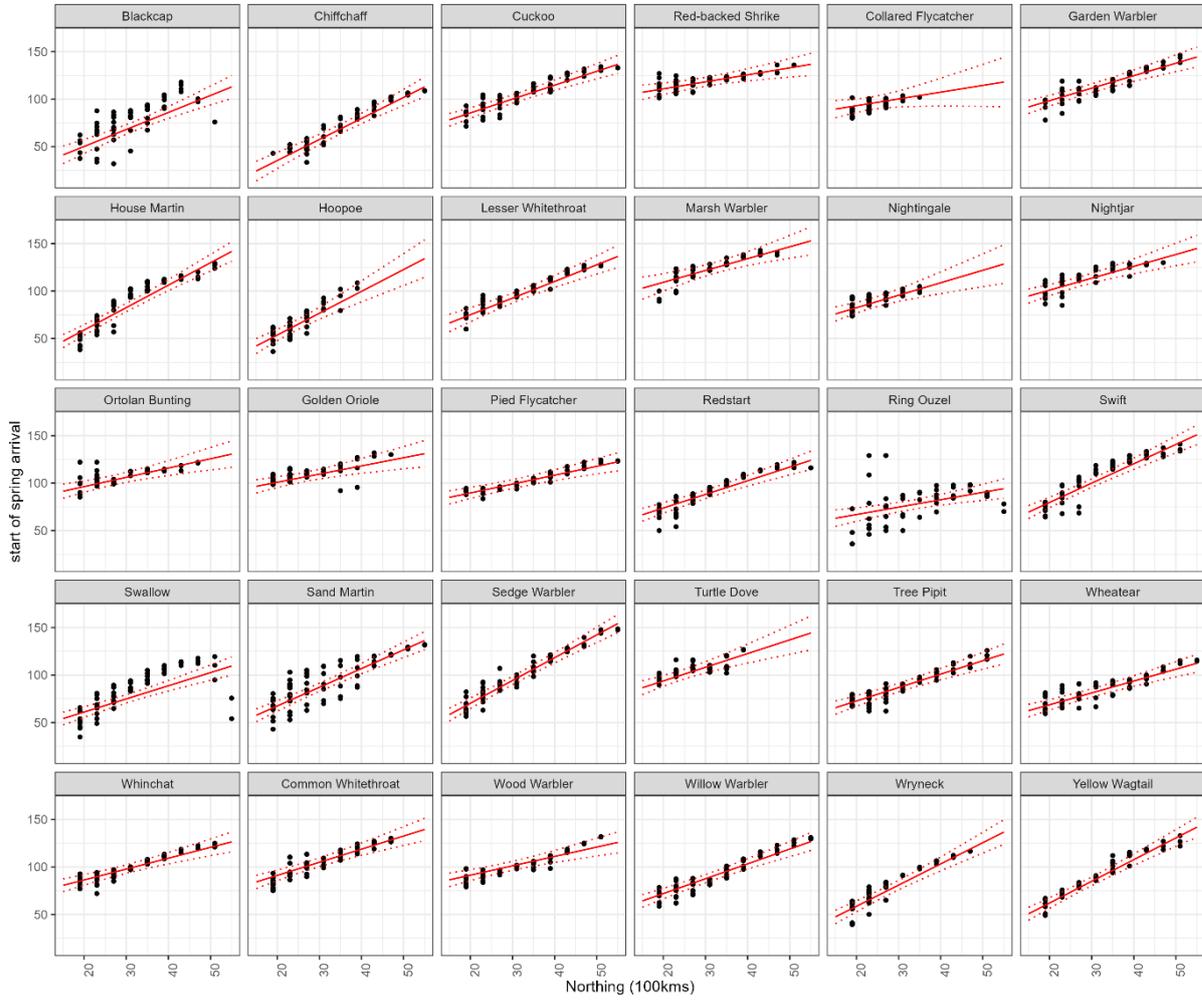
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62 **Figure S3.** The geographic variation across all 400 km square estimates in a) start of and b) duration of
 63 spring arrival, per species. The box shows the interquartile range, the central line the median, and the
 64 whiskers extend to the largest/smallest value within 1.5 times the IQR above/below the 75th/25th
 65 percentile, dots are points outside this range. The maximum latitude that we have enough data to produce
 66 a phenology plot for is shown to the right of the boxplots for each species in a) and sample sizes (number
 67 of 400 km squares with estimates) for each species are shown as numbers to the right of the boxplots in
 68 b). The black bars with a central line are the predicted mean and 95% confidence of intervals of the start,
 69 or duration of arrival averaged over the same five 400 km squares (shown in Figure S2) in which all
 70 species are present, to allow cross-species comparisons on the same range.

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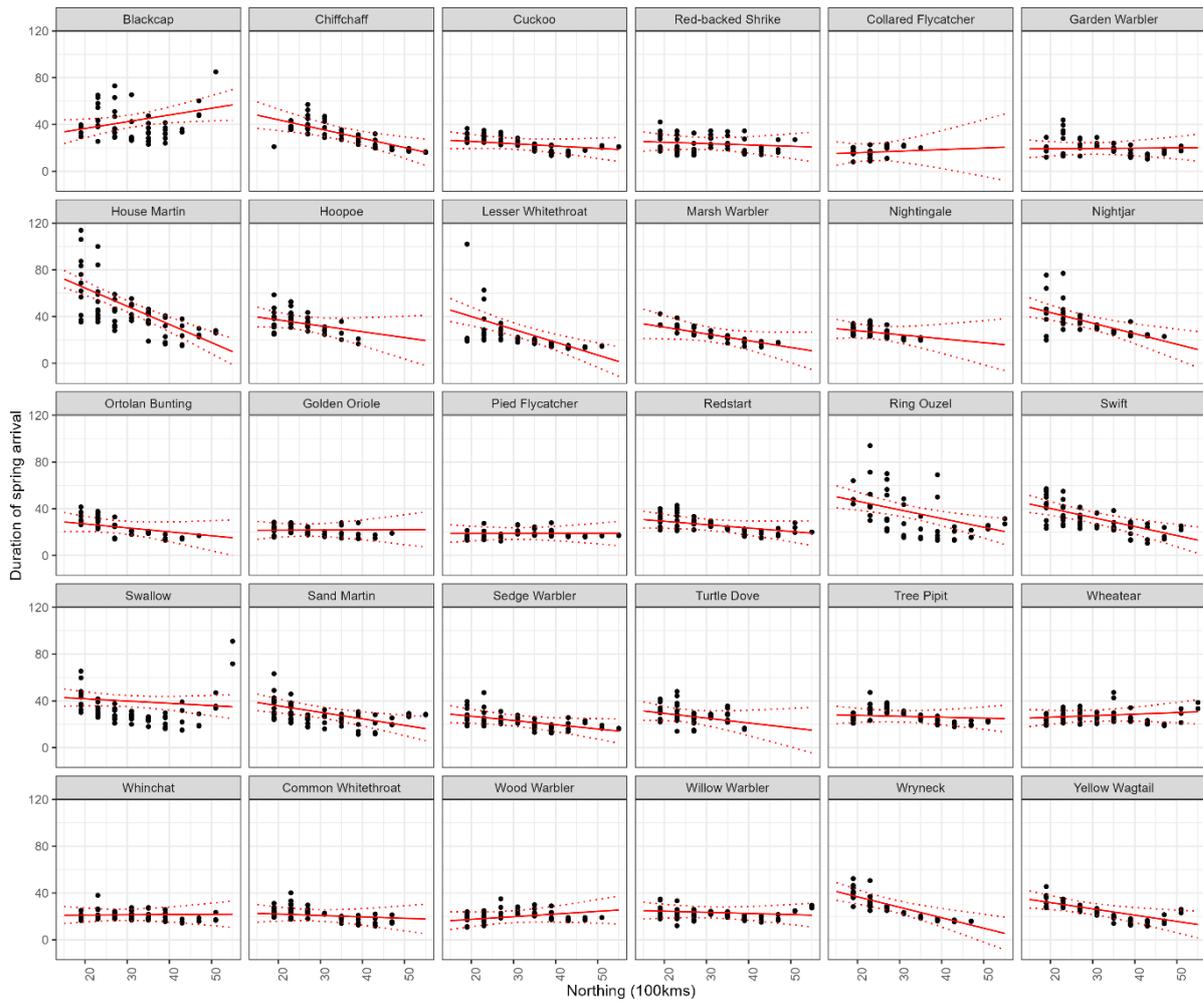
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73 a)



74

75 b)



76

77 **Figure S4.** Species plot of change in a) start of and b) duration of spring arrival with increasing northing.

78 The red line is the predicted effect from the model when easting is set to the mean value and the black
79 dots are the 400 km square estimates of the start and duration of arrival. The x-axis is in units of 100 km,
80 i.e. 50 is 50,000 km.

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88 **Table S4.** The loadings matrix for the first 2 principal component axes (scaled between -1 and +1).

Variables	PC1	PC2
Mean start of spring arrival	0.260	-0.268
Standard deviation in start of spring arrival	-0.423	0.089
Mean duration of spring arrival	-0.248	0.368
Standard deviation in duration of spring arrival	-0.247	0.313
Mean end of spring arrival	0.156	-0.097
Standard deviation in end of spring arrival	-0.395	-0.077
Mean rate of change in start of spring arrival with northing	-0.325	0.225
Standard error in rate of change in start of spring arrival with northing	0.304	0.414
Mean rate of change in duration of spring arrival with northing	0.169	-0.323
Standard error in rate of change in duration of spring arrival with northing	0.304	0.414
Mean rate of change in end of spring arrival with northing	-0.197	-0.052
Standard error in rate of change in end of spring arrival with northing	0.304	0.414

89

90

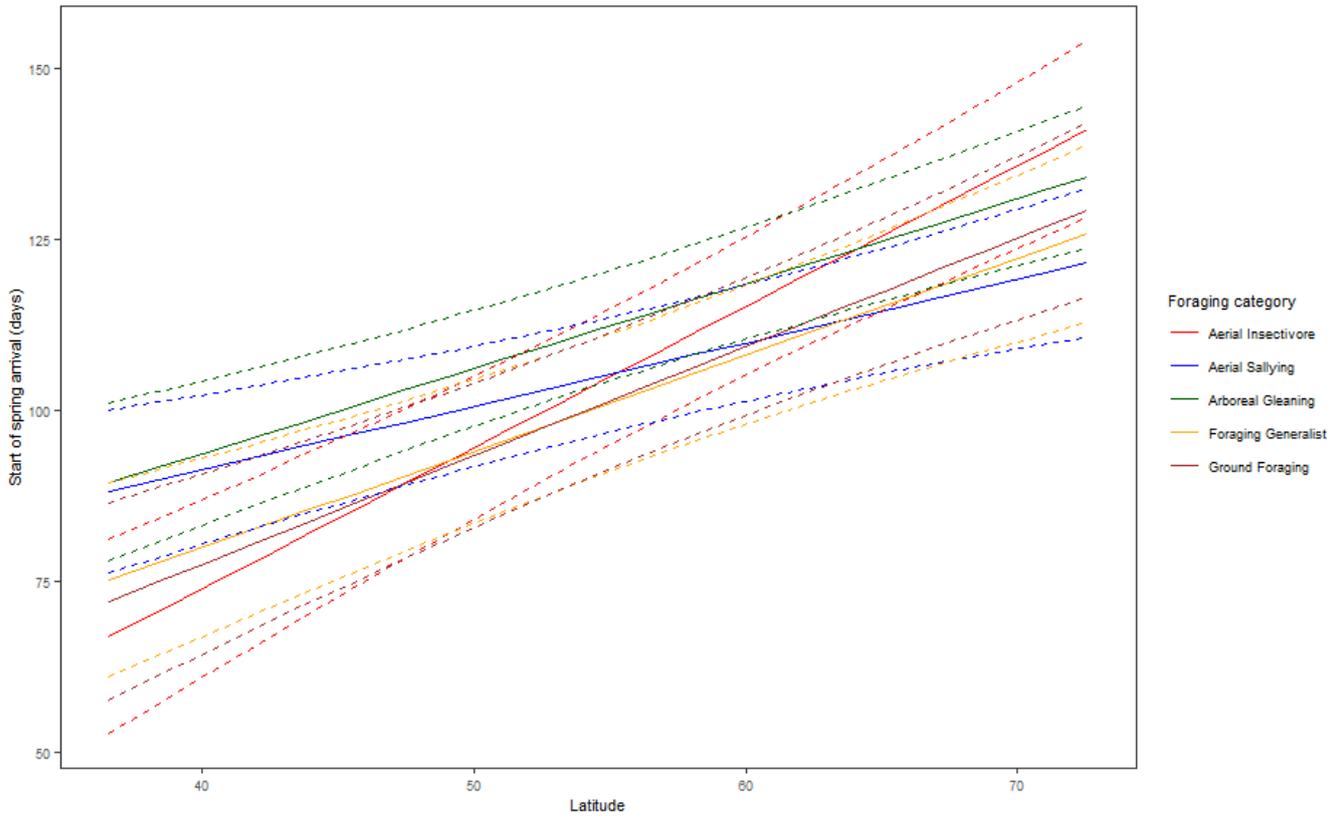
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92 **S5. Morphological/ life history predictors of arrival times**

93 Aerial insectivores had a significantly faster rate of change in start of spring arrival with
94 northing, which translates to a slower population movement northwards across Europe,
95 compared to Aerial Sallying species (Est = 21.3 ± 2.98 versus Est = 11.1 ± 1.94 , Tukey pairwise
96 comparisons $p = 0.013$, Figure S6a). Rate of change in the start of spring arrival with northing
97 also varied with log body mass, heavier species started arrival later (Est = 6.29 ± 1.92 , $p = 0.001$)
98 and showed faster population movement northwards through Europe (Est = -1.79 ± 0.82 , $p =$
99 0.028) compared to lighter birds (Figure S6b). Species from the “north” wintering zone (above
100 the Sahel), started arriving before species from the arid and humid and southern areas (Tukey
101 Pairwise comparisons $p = 0.001$ and $p < 0.001$ respectively, Figure S6c). Species from the
102 humid and southern wintering zone had a slower rate of change in arrival with northing (faster
103 population movement northwards) compared to species from the arid zone (Est = 13.0 ± 1.01
104 versus 18.2 ± 1.52 , Tukey pairwise comparisons $p = 0.022$, Figure S6c).

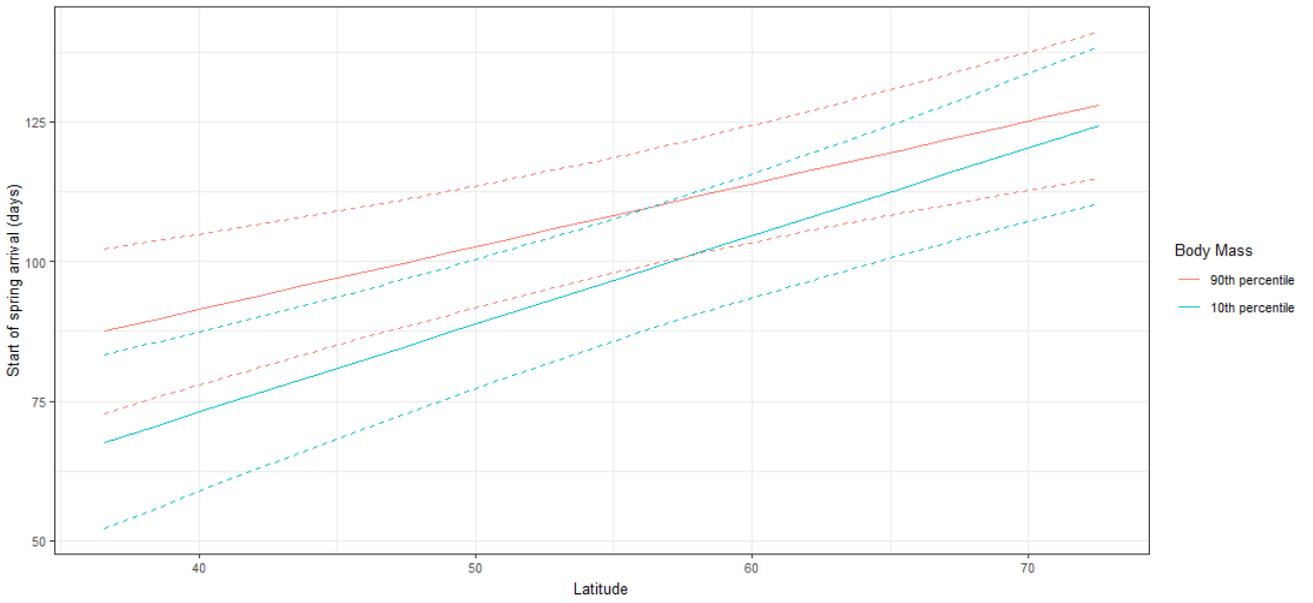
105 For Aerial Insectivores, duration of arrival was significantly different to all other foraging
106 categories (Tukey pairwise analysis $p < 0.0002$), with much longer durations than the other
107 foraging guilds at more southerly latitudes and similar durations to the other foraging guilds at
108 more northerly latitudes (Est = -9.87 ± 2.61 , $p = 0.0002$, Figure S6d). Arboreal Gleaners also
109 had longer durations of arrival at more southerly latitudes compared to northerly latitudes (Est =
110 -2.46 ± 1.17 , $p = 0.037$) but to a lesser extent. For all other foraging guilds duration did not vary
111 significantly with northing ($p > 0.053$). Species from the north wintering zone had a
112 significantly longer duration of arrival than other groups (Tukey pairwise comparisons $p <$
113 0.001 , Figure S6e) and duration was significantly longer at more southerly latitudes compared
114 to northerly latitudes for species wintering in arid (Est = -5.37 ± 1.31 , $p < 0.001$) and humid and
115 southern (Est = -2.03 ± 0.87 , $p = 0.020$) zones but change in duration with northing was not
116 significantly different between the 3 groups (Tukey pairwise comparisons $p > 0.114$).

117 a)



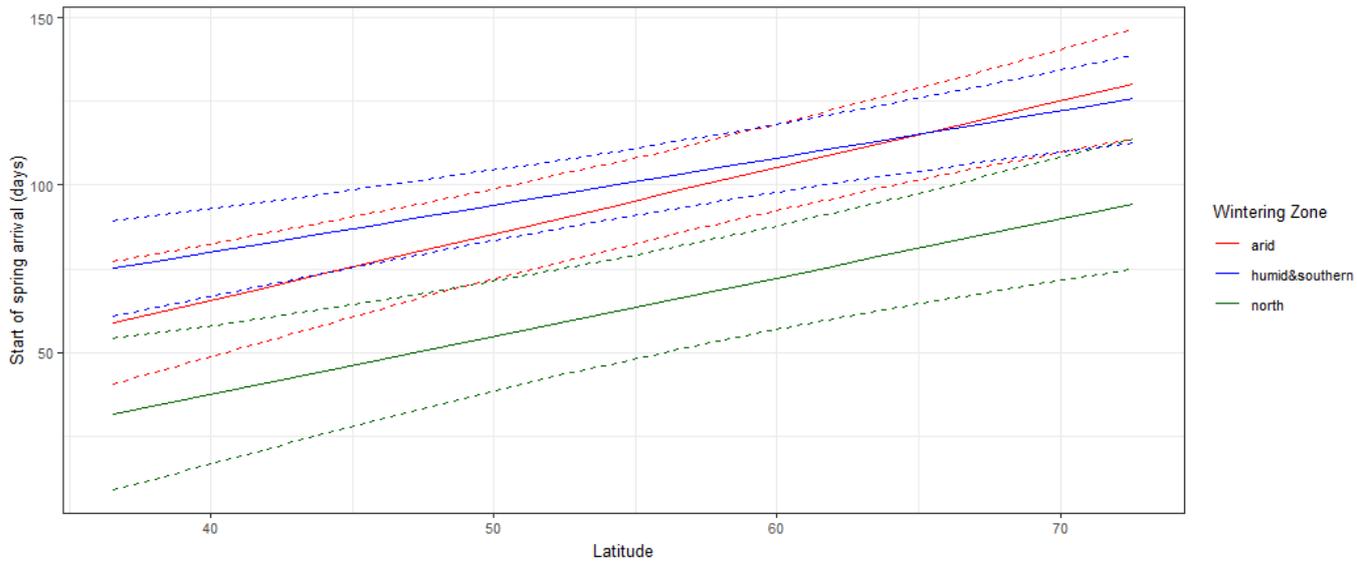
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119 b)



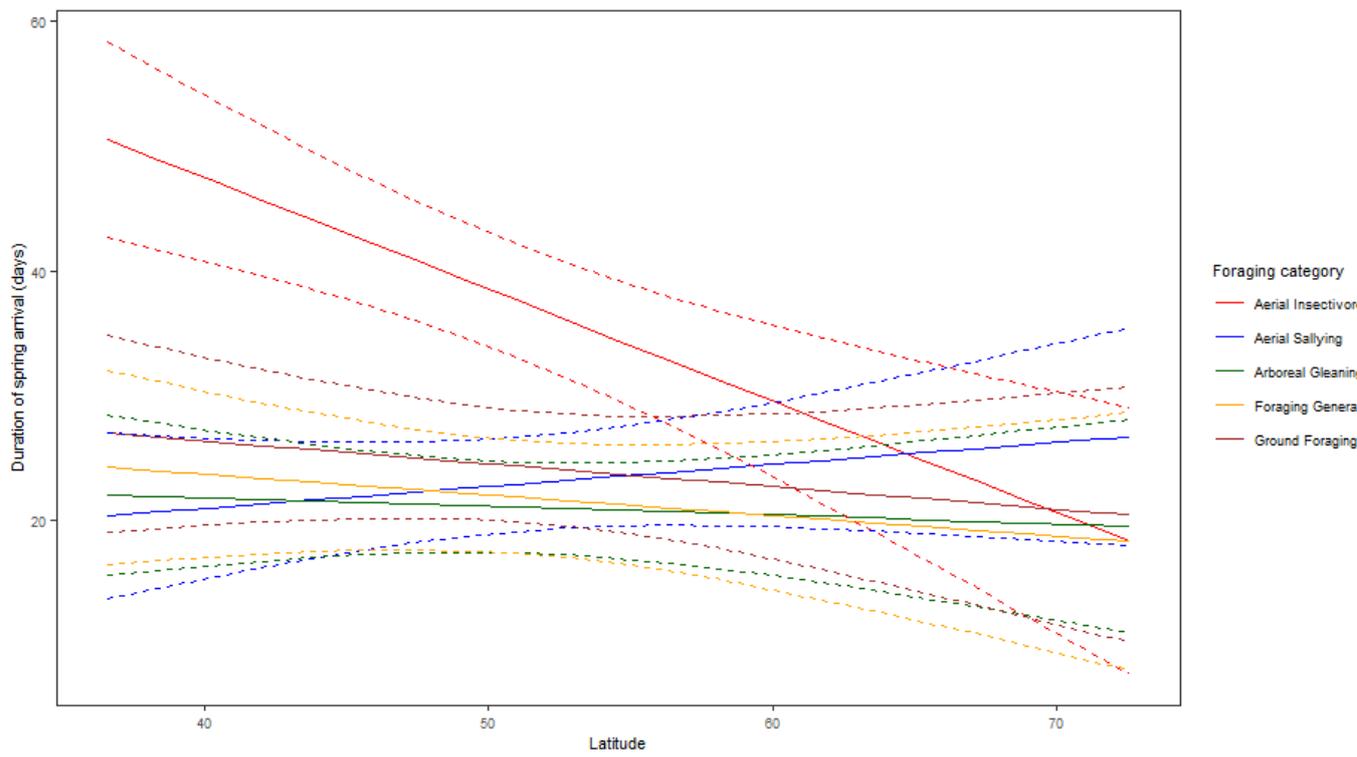
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121 c)



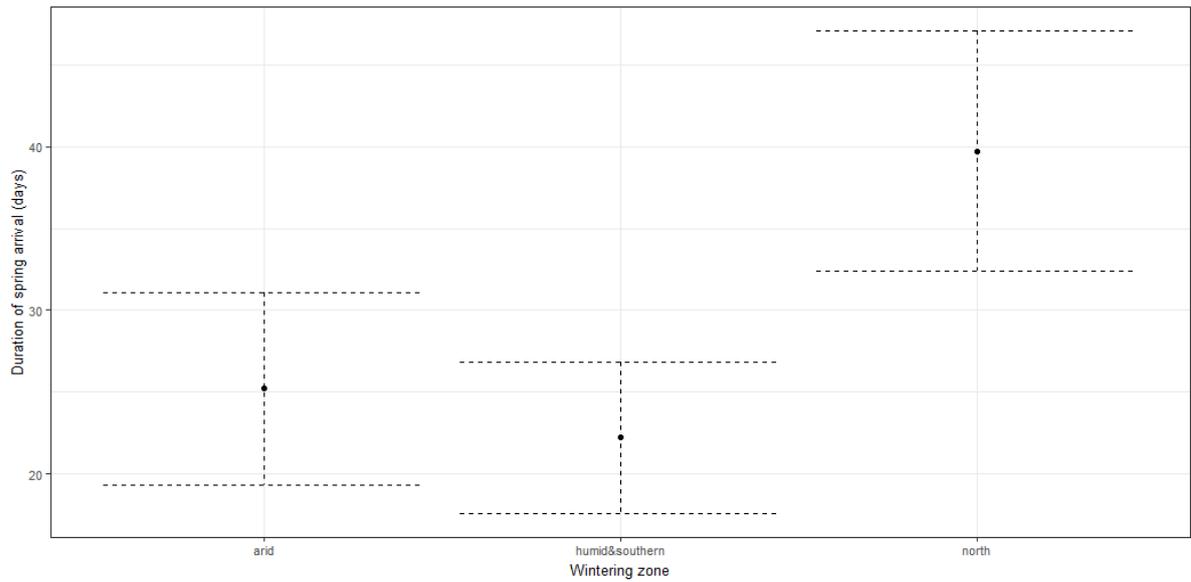
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123 d)



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125 e)



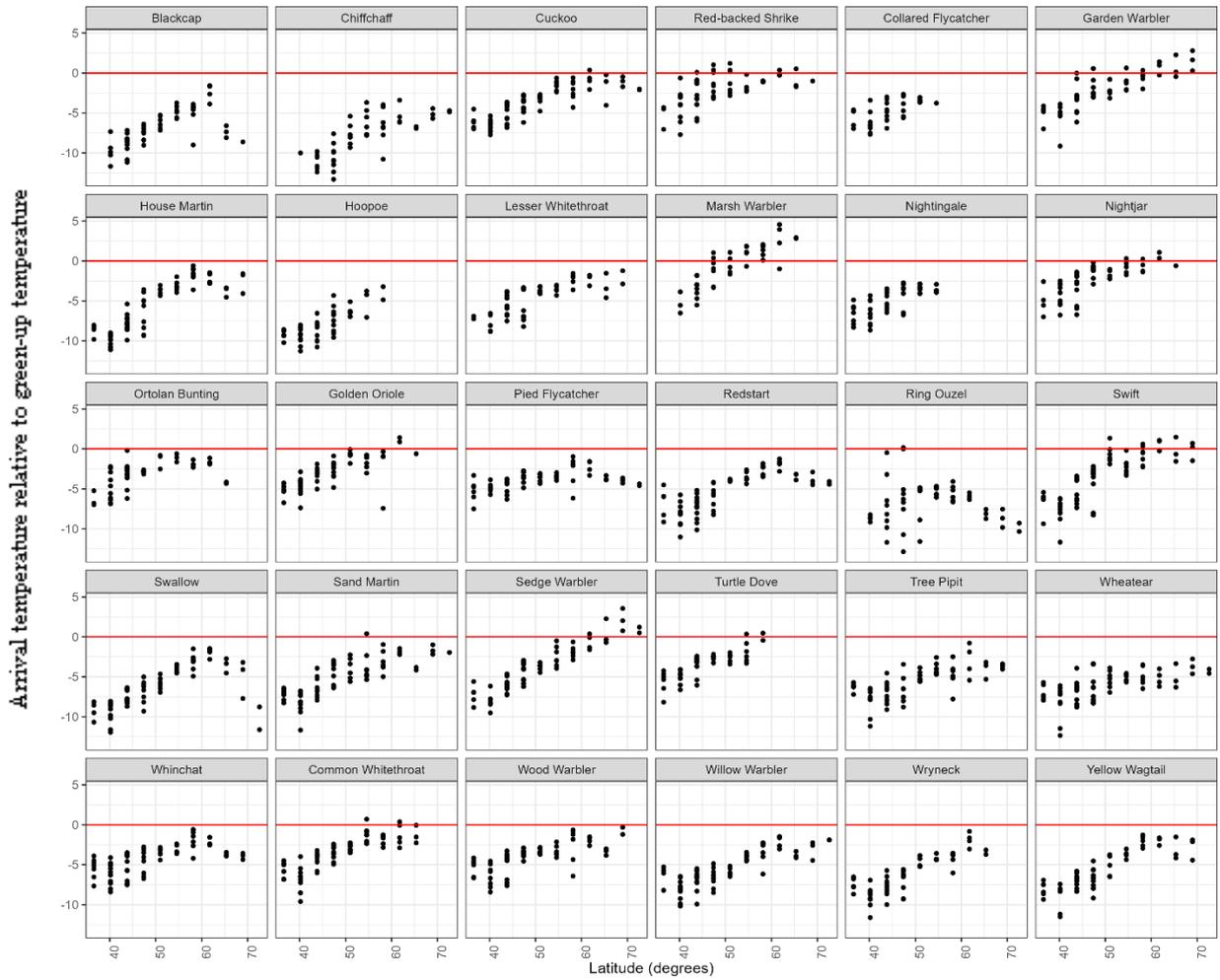
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127 **Figure S5:** Significant relationships between start of, and duration of, spring arrival with morphological
 128 and life history traits for 30 species of Afro-Palearctic migrant birds (the model uses northings but here
 129 we have transformed the axis to latitude for ease of interpretation). Values plotted are the predicted
 130 response from our model detailed in Equation 2 with all continuous variables at mean values and all
 131 discrete variables with modal values apart from the specific variable of interest presented in the plot.

132

133 **Table S5.** The intercept and gradient for species specific relationships of mean temperature on arrival
 134 against mean green-up temperature.

Species	Intercept (°C)	Gradient (°C)
Blackcap	-5.60 ± 1.24	0.84 ± 0.09
Ring Ouzel	-1.62 ± 1.72	1.04 ± 0.09
Chiffchaff	0.35 ± 1.71	0.74 ± 0.09
Swallow	1.10 ± 1.62	0.82 ± 0.07
Wheatear	1.22 ± 1.63	0.87 ± 0.07
Hoopoe	1.39 ± 2.00	0.74 ± 0.1
Tree Pipit	1.94 ± 1.65	0.85 ± 0.07
Collared Flycatcher	2.07 ± 2.15	0.92 ± 0.11
Redstart	2.16 ± 1.65	0.84 ± 0.08
Willow Warbler	2.59 ± 1.63	0.82 ± 0.07
Wryneck	2.76 ± 1.77	0.73 ± 0.09
Pied Flycatcher	2.83 ± 1.68	0.87 ± 0.08
Yellow Wagtail	2.91 ± 1.64	0.77 ± 0.07
Sand Martin	3.10 ± 1.62	0.84 ± 0.07
Whinchat	3.25 ± 1.64	0.84 ± 0.07
House Martin	3.52 ± 1.64	0.72 ± 0.07
Nightingale	3.53 ± 1.99	0.80 ± 0.1
Wood Warbler	4.14 ± 1.70	0.80 ± 0.08
Wheatear	4.32 ± 1.71	0.84 ± 0.08
Ortolan Bunting	4.54 ± 1.77	0.82 ± 0.08
Cuckoo	4.65 ± 1.63	0.78 ± 0.07
Lesser whitethroat	4.83 ± 1.67	0.66 ± 0.08
Golden Oriole	5.15 ± 1.83	0.80 ± 0.09
Red Shrike	5.63 ± 1.70	0.83 ± 0.08
Nightjar	6.12 ± 1.81	0.78 ± 0.09
Swift	6.17 ± 1.64	0.67 ± 0.07
Sedge warbler	7.09 ± 1.63	0.59 ± 0.07
Turtle Dove	7.18 ± 1.93	0.65 ± 0.09
Marsh Warbler	7.81 ± 1.88	0.73 ± 0.11
Garden warbler	8.02 ± 1.69	0.65 ± 0.08



135

136 **Figure S6.** The temperature at start of spring arrival minus the green-up temperature against latitude, the
 137 red line shows zero difference between green-up temperature and arrival temperature.

138

139



Citation on deposit: Border, J. A., Boersch-Supan, P. H., Pearce-Higgins, J. W., Hewson, C. M., Howard, C., Stephens, P. A., ...Baillie, S. R. (2024). Spatial variation in spring arrival patterns of Afro-Palaeartic bird migration across Europe. *Global Ecology and Biogeography*, Article e13850.

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