Phenological trends in the pre- and post-breeding migration of long-distance migratory birds

Running Title: Phenological changes in bird migration

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Abstract

Phenological mismatch is often cited as a putative driver of population declines in long-distance migratory birds. The mechanisms and cues utilised to advance breeding ground arrival will impact the adaptability of species to further warming. Furthermore, timing of post-breeding migration potentially faces diverging selective pressures, with earlier onset of tropical dry seasons favouring migration advancement, whilst longer growing seasons in temperate areas could facilitate delayed departures. Despite this, few studies exist of migration phenology on the non-breeding grounds or on post-breeding passage. Here, we use first-arrival and last-departure dates of 20 species of trans-Saharan migratory birds from tropical non-breeding grounds (The Gambia), between 1964 and 2019. Additionally, we use first-arrival and last-departure dates, as well as median arrival and departure dates, at an entry/departure site to/from Europe (Gibraltar), between 1991 and 2018. We assess phenological trends in pre- and post-breeding migration, as well as individual species' durations of stay in breeding and non-breeding areas. Furthermore, we assess the extent to which inter-annual variation in these timings may be explained by meteorological and ecological variables.

We find significant advances in pre-breeding migration at both locations, whilst post-breeding migration is delayed. At Gibraltar, these trends do not differ between first/last and median dates of migration. The combination of these trends suggests substantial changes in the temporal usage of the two continents by migratory birds. Duration of stay (of species, not individuals) within Europe increased by 16 days, on average, over the 27-year monitoring period. By contrast, duration of species' stays on the non-breeding range declined by 63 days, on average, over the 56-year monitoring period. Taken together these changes suggest substantial, previously unreported alterations to annual routines in Afro-Palearctic migrants.

Keywords: phenological mismatch, avian migration, non-breeding, stopover site, The Gambia, Gibraltar, Sahel, NDVI, NAO index

Introduction

Long-distance migratory birds have evolved to take advantage of spatially-segregated, ephemeral resource peaks (Newton, 2008). This typically involves a pre-breeding migration from non-breeding locations at lower-latitude areas to mid- to high-latitude areas to breed. In order to time departure from the non-breeding grounds to coincide with resource peaks required for breeding, migrants must anticipate conditions on the breeding grounds, often from a different continent, or even hemisphere. It is likely that over long periods of selection, species have developed finely-tuned, endogenous circannual rhythms, triggering pre-breeding migration in response to increasing day-length (Helm et al., 2009; Marra et al., 2005). This may leave long-distance migrants vulnerable to uncoupling of day-length triggers on the non-breeding grounds and conditions on the breeding grounds.

Advancement in phenology is one of the most frequently documented biological responses to recent climate change, with events such as leaf bud-burst, insect emergence and bird breeding now occurring significantly earlier in the year in temperate regions than they did at the end of the last century (Burgess et al., 2018; Post et al., 2018). These advances exhibit significant spatial variation, due to the relationship between latitude and extent of warming and, therefore, the phenology of mid- to high-latitude areas has advanced more rapidly than those of the tropics (Post et al., 2018). The use of day-length as a departure cue should result in migratory populations arriving on breeding grounds at approximately the same time each year but substantially later than previously in phenological terms, leading to phenological mismatch (Saino et al., 2011; Taylor et al., 2016). Behavioural plasticity may, in some situations, permit a reduction in the time between arrival and breeding, enabling advances in laying date despite no change in arrival date (Newton, 2008). However, the severity of recent phenological shifts may have pushed some species to their physiological limits, with breeding date now constrained by the timing of arrival (Both & Visser, 2001). Perhaps as a consequence, advancements in breeding ground arrival are now well documented, as species attempt to adjust to these environmental changes (Gill et al., 2013; Jonzén et al., 2006; Newson et al., 2016). However, these advances in arrival may remain insufficient to track phenological shifts in, for example, prey availability on the breeding grounds, as evidence for phenological mismatch between migrants and their breeding habitats is plentiful (Burgess et al., 2018; Mayor et al., 2017; Møller et al., 2008; Saino et al., 2011).

The inability to track phenological advances on the breeding grounds has been frequently proposed as a putative cause of population declines of long-distance migrants (e.g. Jones & Cresswell, 2010). Mismatches are likely to lead to reduced food availability during the peak demand by chicks, ultimately leading to reduced productivity (Burgess et al., 2018). Additionally, migrants may be outcompeted by resident species that fill similar breeding niches, due to the residents' ability to better judge the onset of the breeding season (Wittwer et al., 2015). Such effects could impact long-distance migrants more than their short-distance counterparts, which winter closer to the breeding grounds and, therefore, may be more capable of anticipating breeding ground conditions (Møller et al., 2008). Given the certainty in further warming of mid- and high-latitudes, it is likely that the phenology of breeding habitats will continue to advance (Burgess et al., 2018). Thus, migrants will be required to continue to advance breeding ground arrival and breeding date, if they are to avoid further population declines.

The extent to which long-distance migratory species are capable of responding to phenological advances on the breeding ground will depend on the mechanisms by which they adjust breeding ground arrival date. Coppack and Both (2002) suggest adjustments to pre-breeding migration schedules, i.e. advancement of non-breeding ground departure or increased migration speed, as potential mechanisms. Perhaps the most parsimonious explanation for these adjustments is through selection for individuals that either utilise departure cues that are matched with advanced breeding ground phenology or which migrate more rapidly. These individuals would, therefore, migrate inherently earlier or faster than others within the population, though this relies on sufficient variation in endogenous migratory timing existing within migrant populations (Gill et al., 2013). Alternatively, individual plasticity may allow for year-to-year variation in migratory strategy. As such, migrants may make use of environmental cues, in addition to day length, to predict conditions on the breeding grounds (Saino et al., 2007; Saino & Ambrosini, 2008). If so, the ability of long-distance migrants to further advance breeding ground arrival date will be constrained by the level of correlation between these cues and the phenological state of the breeding grounds, which may be low given the high level of spatial heterogeneity expected in future climatic changes (Post et al., 2018).

The availability and extent of phenological data from Europe and North America mean that, to date, the vast majority of studies on migration and migration phenology are based on these regions. These studies have provided further insight into the pre-breeding migratory timings of Holarctic migrants, e.g. earlier stopover site arrival (Jonzén et al., 2006; Stervander et al., 2005) and increased migration speed following these stopovers (Marra et al., 2005; Tøttrup et al., 2008). However, this geographic bias of data has hitherto limited the study of similar trends in tropical and sub-tropical non-breeding areas and, as such, it remains unclear whether advances in breeding ground arrival are mirrored by advanced departures from the non-breeding grounds or by altered migration speed (though see Altwegg *et al.* (2012) and Bussière *et al.* (2015), which suggest advanced pre-breeding departure of a limited suite of migrants from South Africa). Many studies have found correlations between breeding ground/stopover site arrival date and non-breeding ground conditions. Such correlated conditions have included: rainfall (Gordo & Sanz, 2008; Saino et al., 2007), the normalized difference vegetation index (NDVI; Saino *et al.*, 2004; Gordo and Sanz, 2008; Balbontín *et al.*, 2009), temperature (Cotton, 2003; Gordo et al., 2005; Saino et al., 2007) and the North Atlantic Oscillation (NAO) index; the latter representing the difference between the normalised sea-level pressures at the Azores and Iceland, over the period December-March (Forchhammer et al., 2002; Hüppop & Hüppop, 2003; Jonzén et al., 2006). Together these studies suggest that migrants do make use of multiple environmental cues to anticipate conditions on the breeding grounds. Species tend to arrive on their breeding grounds earlier in years of high rainfall and higher NDVI on non-breeding grounds, potentially due to increased food availability enabling earlier and/or more rapid pre-migratory fattening and hence migration onset. Higher winter NAO index values, which tend to correlate with earlier, more productive springs in western Europe, were similarly associated with earlier breeding ground arrival, whereas responses to higher pre-departure temperatures on the non-breeding grounds are more varied (e.g. Gordo et al., 2005 cf. Saino et al., 2007). Whilst temperature could act as a direct cue to advance departure, it could also act via modulating food availability. However, whilst these variables appear to modulate breeding ground arrival, given that none of the studies mentioned above consider departure dates from non-breeding sites, it is unclear which aspect of pre-breeding migration they affect. In the Americas, increased tropical rainfall has been related to advanced departure of migrants from non-breeding areas, acting through increased food availability (Studds & Marra, 2011). This suggests that the ability to advance departure could be limited by the ability to advance fat-loading prior to leaving non-breeding areas. However, this evidence is limited to a single species in one area. Further studies incorporating timing of pre-breeding departures from non-breeding sites are necessary to better understand the mechanisms of advanced breeding ground arrival.

Whilst the study of pre-breeding departures from non-breeding grounds has received little attention, post-breeding departure timing is similarly neglected relative to breeding ground arrival phenology, even across Europe and North America. This may be due to less obvious and consistent phenological patterns during this period, potentially a result of less stringent time constraints on departure when compared to pre-breeding migration (Haest et al., 2019; La Sorte et al., 2015). In areas such as the Sahel in Africa, deteriorating conditions (in terms of NDVI and potentially food availability) over the north temperate late-summer to autumn period may place pressure on species to maintain current post-breeding migration phenology. In contrast, a lengthening growing season across mid- to high-latitudes over the last century, due to increased autumn temperatures, could permit long-distance migrants to extend their stay on the breeding grounds, perhaps even extending the breeding season (Menzel & Fabian, 1999; Walther et al., 2002). Those studies that have considered post-breeding migration of long-distance migrants have reflected this variation in potential selective pressures, with advancement (Jenni & Kéry, 2003), delay (Bitterlin & Van Buskirk, 2014; Kovács et al., 2011) and no trend (Van Buskirk et al., 2009) in departure from breeding grounds all reported. However, there are few studies of arrival phenology in non-breeding areas. Therefore, despite a lack of consensus in trends of post-breeding departures, migratory strategies of long-distance migrants away from these areas could have changed significantly. For example, species may increase migration speed in order to avoid hostile conditions on their migratory journey or utilise less-direct routes to take advantage of additional resources. Such factors, combined with the advance of pre-breeding migration, could result in substantial changes to the temporal partitioning of the annual cycle of long-distance migrants. Hence, there is a clear need to analyse trends in the timing of, not only pre-breeding, but also post-breeding migration to and from the non-breeding grounds.

Here, we use a novel dataset of departure and arrival dates of European-breeding migratory species to their African non-breeding range, and through a passage site on the boundary between Europe and Africa. We use these data, in combination with meteorological and ecological variables, to assess trends in departure and arrival dates at sites away from the breeding range, over a 28-56 year period. By studying phenology at these non-breeding localities, we aim to infer whether: (1) pre-breeding migration on the non-breeding grounds and/or at an intermediate migratory site has advanced, in line with those phenological changes observed on the breeding grounds, (2) the phenology of post-breeding migration has undergone any significant change at either site and (3) species are spending longer on European breeding grounds as a result of longer growing seasons and hence either altering the amount of time on the non-breeding range, or the speed of their migration to the non-breeding range.

Materials and methods

Study sites and species data

We extracted annual first-arrival and last-departure dates of trans-Saharan migratory bird species from two datasets, one from the northern edge of the sub-Saharan African non-breeding range and the other on the migratory route, on the Europe/Africa border. The first consisted of observations of 20 migratory passerine bird species (Table S1) recorded year-round by local ornithologists in The Gambia (**Fig. 1**), monitored between 1964 and 2019 (though discontinuously in some periods). We excluded a few observations of migrants remaining in The Gambia in June and July (the northern European breeding season), as these were likely to represent individuals that were unlikely to have migrated due to, for example, poor condition or injury. The second dataset consisted of daily bird ringing totals for 14 migratory passerine bird species from Gibraltar Bird Observatory (**Fig. 1**). Standardised ringing occurred daily at this site in spring and autumn, between 1991 and 2018. Exact start and end dates of ringing efforts varied between years (Table S2), due to the suitability of weather for ringing, but typically covered the periods February-May and August-November and, therefore, should encompass the earliest pre-breeding and latest post-breeding migration dates for all the migrant species we consider. The first record of a trapped individual of a species in the spring, and the last trapping record in autumn were extracted as the first and last observation for each year, respectively. Two migrant species (Eurasian Blackcap *Sylvia atricapilla* and Common Chiffchaff *Phylloscopus collybita*) for which we had arrival/departure dates in The Gambia were present year-round at Gibraltar (i.e. they had a small resident/overwintering population), so extracting first and last migration dates for these species at Gibraltar was not possible. A further four species (Northern Wheatear *Oenanthe oenanthe*, Western Olivaceous Warbler *Iduna opaca*, White Wagtail *Motacilla alba* and Yellow Wagtail *Motacilla flava*) that occurred in The Gambia were trapped very infrequently at Gibraltar, so were removed from the dataset (Table S1).

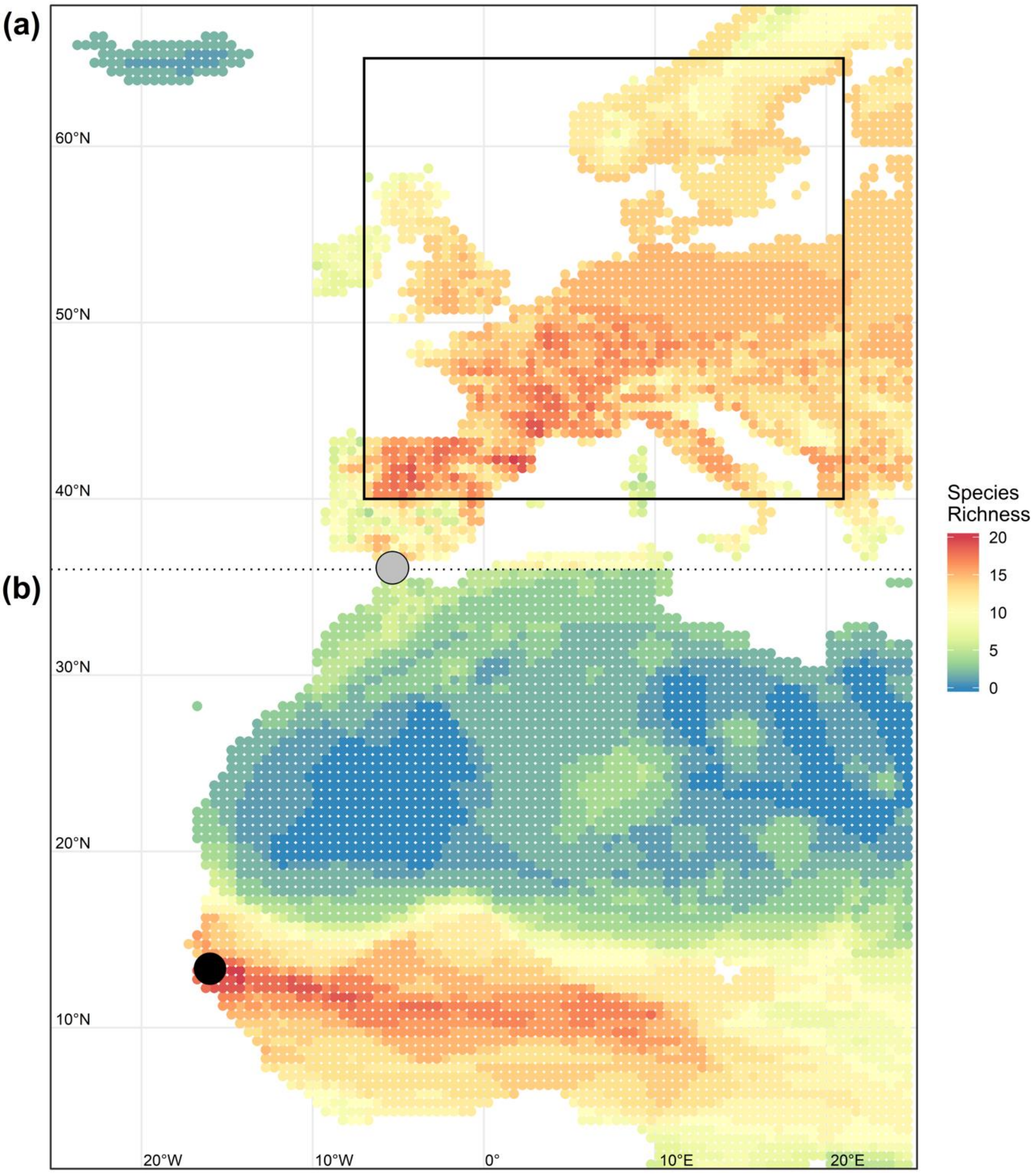

Figure 1. *Map of Africa and Europe, showing the study areas in The Gambia (black circle) and Gibraltar (grey circle). The box highlights the area defined as representing the core Western Europe breeding area for our study species, used when extracting meteorological variables. Shading represents, for the 20 study species:* ***(a)*** *Breeding species richness across Europe and* ***(b)*** *non-breeding species richness across North-West Africa (dotted line differentiates (a) and (b)). Gibraltar and The Gambia represent, in Europe and sub-Saharan*

Africa respectively, major first arrival and last departure locations for trans-Saharan migrants on the east-Atlantic flyway.

Migrants departing from The Gambia in Palearctic spring are likely to follow the east-Atlantic flyway (Fig. S1) into Europe and many may, therefore, be expected to utilise Gibraltar, situated at the narrowest passageway between Europe and Africa on this flyway, as a site to rest/refuel (BirdLife International, 2010). Therefore, when combined, these two datasets allow an analysis of long-term trends in timing of pre-breeding and post-breeding migration for a suite of common trans-Saharan migrants. Additionally, for years in which successive first arrival and last departure dates were available, we calculated durations of stay for individual species within Europe and in sub-Saharan Africa. It should be noted that duration of stay, as defined here, represents the time spent within a region by a species, i.e. from the first individual arriving to the last individual departing, and not the mean duration of individuals. Further, we assume that spring arrival and autumn departure dates from Gibraltar reflect the approximate duration of stay of the East Atlantic flyway populations of a species in Europe. Similarly, we assume that first post-breeding arrival and last pre-breeding departure from The Gambia reflects the approximate duration of stay of these populations within sub-Saharan Africa. This enabled an analysis of trends in duration of stay to assess whether the temporal partitioning of the annual cycle of migrants has changed over time.

The use of first and last dates to assess changes in phenology are susceptible to bias through changing observer effort and underlying population trends (Sparks et al., 2001; Tryjanowski & Sparks, 2001). For example, increasing observer effort could result in earlier arrival dates and later departure dates from a site. By contrast, declining populations could result in later apparent arrival and earlier apparent departure dates, a consequence of the reduced likelihood of detecting individuals from a smaller population. Observer effort remained similar throughout the study period in both locations, minimising the risk of the former situation. By contrast, populations of several long-distance migrants have declined in recent decades.

Hence, if we observed delayed arrival and advanced departures from our study sites, we could struggle to differentiate phenological change from recording bias. In fact, our results from Gibraltar demonstrated trends in migratory timings in the opposite direction to that which would be expected given recorded population declines, giving confidence that we detected real phenological changes, albeit perhaps slightly conservative give the declines of some species. Furthermore, whilst overall trends in migratory timings from The Gambia occurred in the directions we may predict through population changes, there was no correlation between individual species' migratory and population trends (Fig. S2). An additional consideration when using first and last recording dates is the tendency for first arriving individuals to advance their migration more rapidly than the bulk of the population (Lehikoinen et al., 2019; Sparks et al., 2007; Tøttrup et al., 2006). Therefore, trends observed in first and last individuals have the potential to be more extreme than that shown by the remainder of the population. The best available data for The Gambia do not permit extraction of median population phenological responses in the Sahelian non-breeding areas, though data for Gibraltar do permit median passage estimations. Hence, for Gibraltar, in addition to first arrival and last departure dates, we also extracted and analysed (see below) median passage dates for both pre- and post-breeding migration. We used daily ringing totals from Gibraltar for a species across a passage period to estimate the median passage date of all individuals. We extracted medians, rather than mean migration dates, as trapping effort was consistent throughout the ringing periods and not biased to, for example, weekends. We also estimated, for Europe, durations of stay for species in each year, based on these median passage dates. This enabled us to assess whether trends in, and drivers of, migratory timing differed between first/last and median passage at Gibraltar, a point part way through the migratory journey.

Meteorological and environmental data

Fortnightly NDVI values were obtained for the period 1982-2012 (the maximum period for which annual data were complete), for four areas on the east-Atlantic flyway: the Sahel, North

Africa, Gibraltar and Western Europe (**Figs. 1 & 2**). Data were downloaded from the Global Inventory Modelling and Mapping studies group (GIMMS; Tucker *et al.*, 2005). The Sahel was defined as the area 18°W-10°E and 14°-18°N immediately to the north of The Gambia, and North Africa as the area encompassing 10°-2°W and 30°-36°N (**Fig. 2)**; NDVI data were extracted for both regions. Both areas exhibit high NDVI seasonality (**Fig. 2**), where ephemeral resource peaks produce useful refuelling sites for migrants prior to/following the crossing of the Sahara. The eastern boundary of the Sahel was set at 10°E as we expect that individuals migrating further east than this would be less likely to follow the east-Atlantic flyway to/from western Europe. The southern and eastern boundaries of the North African region were selected to encompass the region of highest NDVI seasonality beyond Europe. Sahelian NDVI was highly correlated with Gambian NVDI (r_s>0.7). As we considered Sahelian NDVI as better representing overall sub-Saharan conditions, we used these data in models in preference to Gambian NDVI. In addition, species could utilise this wider Sahelian region as a final stopover site prior to crossing the Sahara, which could impact Gambian departure dates. We extracted site-specific NDVI data separately for Gibraltar given the possibility that migrants might decide whether to stop at this restricted passage site on the basis of NDVI in the local area, which was not strongly correlated with North African NDVI. We calculated Gibraltarian NDVI for the area 5.37°-5.34°W, and 36.1°-31.16°N. Finally, we calculated NDVI for Western Europe using the area 7°W-21°E, and 40°N-65°N. This area encompassed the highest breeding richness and the majority of range extents for populations of our 20 focal study species that were likely to use the East Atlantic migration flyway through Gibraltar (**Fig. 1**). The eastern boundary of the Western European region was set as we expect that individuals breeding further east would be less likely to migrate along the East-Atlantic flyway through both Gibraltar and The Gambia (BirdLife International, 2010).

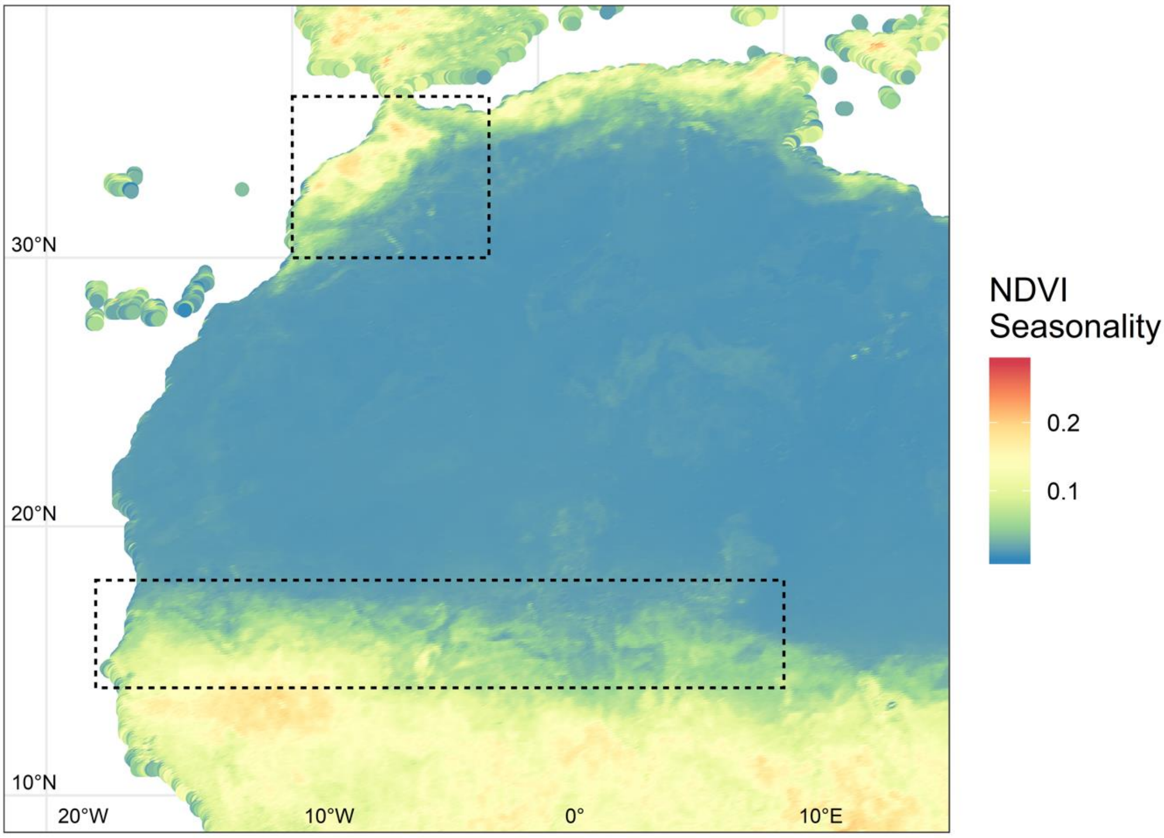

Figure 2. *NDVI seasonality (expressed as the mean standard deviation of annual NDVI over the period 1982-2012, derived from fortnightly records) of north-west Africa. The box highlights the area defined as North Africa (top) and the Sahel (bottom), used when extracting meteorological variables.*

For the Sahel, North Africa and Gibraltar regions, we calculated annual mean NDVI values separately for individual species, dependent upon their mean phenology. Mean NDVI was estimated for each species over the two months prior to mean departure and arrival dates (i.e. the mean date across all years of monitoring) in both The Gambia and Gibraltar. We hypothesise that NDVI will alter food availability, in turn impacting upon departure decisions and/or migration speed. For example, when exploring potential drivers of pre-breeding departure dates from The Gambia, mean Sahelian NDVI for the two months prior to species-specific mean departure date over the whole study period from The Gambia was calculated. Whereas, when exploring drivers of pre-breeding arrival dates at Gibraltar, mean Sahelian

NDVI for the two months prior to species-specific mean arrival date over the whole study period in Gibraltar was calculated. As large inter-specific variation in the timing of migration schedules exists, the mean arrival/departure dates and, therefore, NDVI values were calculated on a species-specific basis. For each species, we calculated the mean date of first/last recorded individual, across all years for which data were available, of all four migratory events: Gambian pre-breeding departure, Gibraltar pre-breeding arrival, Gibraltar post-breeding departure and Gambian post-breeding arrival (Table S3). Additionally, we calculated the mean dates of median arrival and departure at Gibraltar. The mean NDVI of the two months prior to these mean arrival/departure dates were then calculated for each species, for each year for The Sahel, North Africa and Gibraltar regions. This method ensured that the NDVI calculation period was fixed for each species enabling comparisons across years, whilst avoiding bias that might occur if its estimation window was altered each year in relation to a species annual phenology. Additionally, we calculated mean NDVI for August and September for each year across the western European region. The latter aimed to reflect post-breeding vegetation productivity in breeding areas, which could influence post-breeding departure dates through altered food availability. We did not calculate the mean NDVI of Europe in spring, as we included yearly winter NAO index values (see below), which correlates with productivity levels in Europe (Forchhammer et al., 2002).

NDVI was also used to identify the timing of the end of Sahelian growing season each year. To do so we fitted a smoothed function to fortnightly NDVI data over an annual cycle between March to February, following the methods of Mason *et al.* (2014). The period March to February was chosen to capture the start and end of the annual Sahelian NDVI cycle (Fig. S3). We calculated the maximum second derivative following an annual NDVI peak. This represented the point at which NDVI was declining most rapidly back to its dry season minima.

Monthly temperature data for the period 1960-2015 were downloaded from the Climatic Research Unit (CRU; Harris *et al.*, 2014), for the same four areas for which NDVI data were acquired, as well as for The Gambia. Unlike NDVI data, temperature data for The Gambia and the Sahel were not highly correlated ($r_s<0.7$). Mean temperature data were calculated in much the same way as NDVI. For The Gambia, the Sahel, North Africa and Gibraltar, we calculated yearly species-specific mean temperatures over the two months prior to their mean departure and arrival dates over the whole study period in both The Gambia and Gibraltar. For Western Europe, we calculated mean annual temperature across the August – September period.

Finally, monthly values of the North Atlantic Oscillation index for the period 1963-2019 were downloaded from CRU (Jones et al., 1997), representing the difference in normalised sea level pressure over the Azores and south-west Iceland. Yearly winter NAO index values were extracted from these data, taken as the cumulative NAO index over the months December to March, prior to pre-breeding migration (Hüppop & Hüppop, 2003).

Analyses of migration phenology

As migratory timings can be considered as species traits and, therefore, not phylogenetically independent, we used phylogenetic linear mixed models (PLMMs) to analyse both trends and drivers of inter-annual variation in migratory timings, at both The Gambia and Gibraltar. We fitted PLMMs with pre-breeding or post-breeding migration dates or durations of stay as a continuous response variable, depending on the specific analysis, using the R package MCMCglmm (Hadfield, 2010). The species ID and the phylogeny were included as random effects, the former to account for variability in the data caused by species-specific migration schedules. The phylogeny was built as a 50% majority-rule consensus tree (O'Reilly & Donoghue, 2018; Rubolini et al., 2015), using 1000 samples of the posterior distribution produced by Jetz et al. (2012). We used an uninformative, inverse Wishart distribution as a prior for both the random effects and residual variance. To fit the model, we ran an MCMC chain for at least 200,000 generations, recording model results every 1000 generations and ignoring the first 2000 generations as burn-in. We fitted each model four times and merged the four chains after verifying convergence using Gelman-Rubin diagnostics in the R-package coda (Plummer et al., 2006). We also visually inspected trace plots for each model to verify model convergence. We assessed the performance of each model by calculating conditional R^2 following the methods of Nakagawa & Schielzeth (2013). This multi-species approach was undertaken as we anticipated that individual species trends might be weak due to the paucity of data and the inherent variability likely in such data. This was confirmed in an exploratory data analysis, using linear models on individual species data (Figs. S4-6).

We first analysed trends in pre-breeding migration, post-breeding migration and duration of stay, fitting PLMMs, as previously described, with year as the sole continuous predictor variable in the models. Then, to identify drivers of inter-annual variation in pre-breeding and post-breeding migration timing, more complex models were fitted containing plausible combinations of potentially important meteorological and environmental predictors. Year was retained as a predictor variable in these models to minimise the likelihood of finding spurious relationships with climatic variables which were themselves correlated with year (Iler et al., 2017). For Gibraltar, we conducted these analyses twice, first on the dates from first/last individuals and second using median passage dates.

The combinations of meteorological/environmental variables included in models differed between analyses (**Table 1**), as the drivers of migration are likely to differ both spatially and temporally. To facilitate parameter exploration, we scaled each continuous predictor variable using *z*-transformations. Species with fewer than six years of data available for any individual analysis were removed from that analysis (Table S4). Sample sizes for models of the drivers of inter-annual variation in migratory timing were reduced in comparison to that of phenological trends in migration, as meteorological data were not available for the entire study period (**Table 2**).

Table 1. *Candidate meteorological variables included in the models to predict the timing of pre-breeding and post-breeding migration in the Gambia and Gibraltar.*

Location	**Model**	**Meteorological variable**
The Gambia	Pre-breeding departure	NAO Index
		Gambian temperature
		Sahelian NDVI
	Post-breeding arrival	European temperature
		European NDVI
		North African temperature
		North African NDVI
		Onset of Sahelian dry season
Gibraltar	Pre-breeding arrival	NAO Index
		Sahelian temperature
		Sahelian NDVI
		North African temperature
		North African NDVI
	Post-breeding departure	European temperature
		European NDVI
		Gibraltar temperature
		Gibraltar NDVI
		Onset of Sahelian dry season

Table 2. *Summary of datasets used to analyse trends in the timings of pre-breeding migration, post-breeding migration and duration of stay, as well as the drivers of inter-annual variation in the timings of pre-breeding and post-breeding migration. Datasets for first/last and median individuals at Gibraltar are identical, so are only included once here.*

Analysis	**Location**	**Event**	**Start Date**	**End Date**	**Nº of species**	**Total observation years**

Trend models	The Gambia	Pre-breeding departure	1965	2019	19	314
		Post-breeding arrival	1964	2018	19	333
		Duration of stay	1964	2018	13	150
	Gibraltar	Pre-breeding arrival	1992	2018	14	319
		Post-breeding departure	1991	2018	14	312
		Duration of stay	1992	2018	13	258
Drivers models	The Gambia	Pre-breeding departure	1988	2012	18	208
		Post-breeding arrival	1987	2012	16	197
	Gibraltar	Pre-breeding arrival	1992	2012	13	237
		Post-breeding departure	1991	2012	14	245

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Results

Trends in migratory timings

PLMMs were fitted separately to assess trends in first arrival and last departure dates of trans-Saharan migrants, at both The Gambia and Gibraltar. Models explained the trends in the timings of pre-breeding and post-breeding migration less well in The Gambia ($R^2 = 0.49$; $R^2 = 0.63$, respectively) than in Gibraltar ($R^2 = 0.84$; $R^2 = 0.82$, respectively), but performed well overall. Furthermore, we found significant trends in the timing of both of these events, at both locations (Table S5). Pre-breeding migration showed significant advancements at both locations, at rates of 0.44 days per year in The Gambia and 0.28 days per year in Gibraltar, between 1965-2019 and 1992-2018, respectively (**Fig. 3**). In contrast, post-breeding migration was significantly delayed at both locations, though at reduced rates compared to pre-breeding migration. Between 1964-2018 and 1991-2018, post-breeding migration was delayed by 0.24 days per year in The Gambia and 0.19 days per year in Gibraltar, respectively. Although both of these trends appear more pronounced in The Gambia, significant overlap of confidence intervals occurs with the Gibraltar model estimates (Table S5). PLMMs fitted to assess trends in median arrival and departure dates at Gibraltar also performed well ($R^2 = 0.7$; $R^2 = 0.68$ respectively), though slightly less well than the models of first arriving spring individuals and last departing autumn individuals. The temporal trends were again significant and had very similar slopes to those seen when analysing first arrivals and departures (**Fig. 3**) but with different intercepts, the latter as would be expected. Median pre-breeding migration date advanced by 0.27 days per year (cf. 0.28 days in first arrivals), whilst post-breeding migration was delayed by 0.22 days per year (cf. 0.19 days in last departures). Hence, overall, the advance in pre-breeding migration and the delay in post-breeding migration at Gibraltar were robust to whether we considered either the first arriving or last departing individuals versus the median passage in spring/autumn.

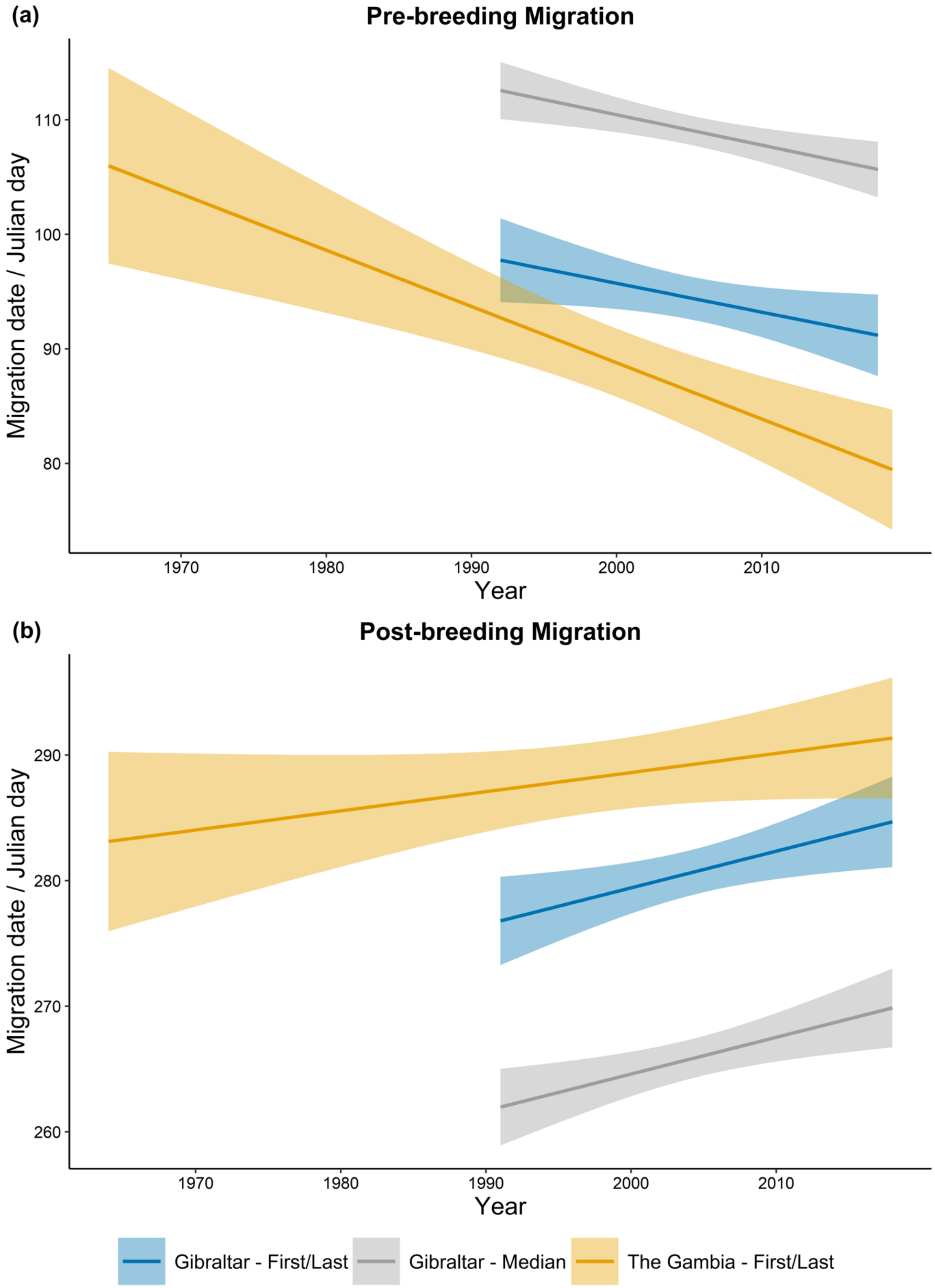

Figure 3. *Phenological trends in* ***(a)*** *pre-breeding and* ***(b)*** *post-breeding migration date at The Gambia and Gibraltar. Lines show the mean migration date across species, predicted by a linear model, with shaded regions displaying the 95% confidence intervals.*

PLMMs were also fitted to assess trends in duration of stay within sub-Saharan Africa and Europe, based on first arriving and last departing individuals. Whilst models performed similarly well in The Gambia and Gibraltar ($R^2 = 0.76$ and $R^2 = 0.79$, respectively), the trends in duration of stay differed markedly (**Fig. 4**). Due to delayed post-breeding arrival and advanced pre-breeding departure, trans-Saharan migrants following the east-Atlantic flyway spend significantly less time in sub-Saharan Africa now than in 1964. Over this period, duration of stay decreased by 1.15 days per year, equating to a total reduction in stay length of over 63 days. Whereas, in Europe, advancements in pre-breeding arrival of the first individuals and delays to post-breeding departure of the last individuals led to a significant increase in the duration of stay of migrant species (Table S5). Between 1992 and 2018, duration of stay in Europe increased by 0.59 days per year (i.e. an opposite change to that in sub-Saharan Africa but changing at half the rate *cf* sub-Saharan Africa), a total increase of over 16 days in just 27 years. Duration of stay within Europe was very similar when median passage times (as opposed to first/last individuals) were used (though model fit was slightly weaker: $R^2 = 0.67$; **Fig. 4**), with the median duration of stay increasing by 0.54 days per year. No significant difference existed in the rate of change of duration of stay in Europe between those calculated based on first/last dates through Gibraltar and those based upon median passage dates (Tables S5 & 6).

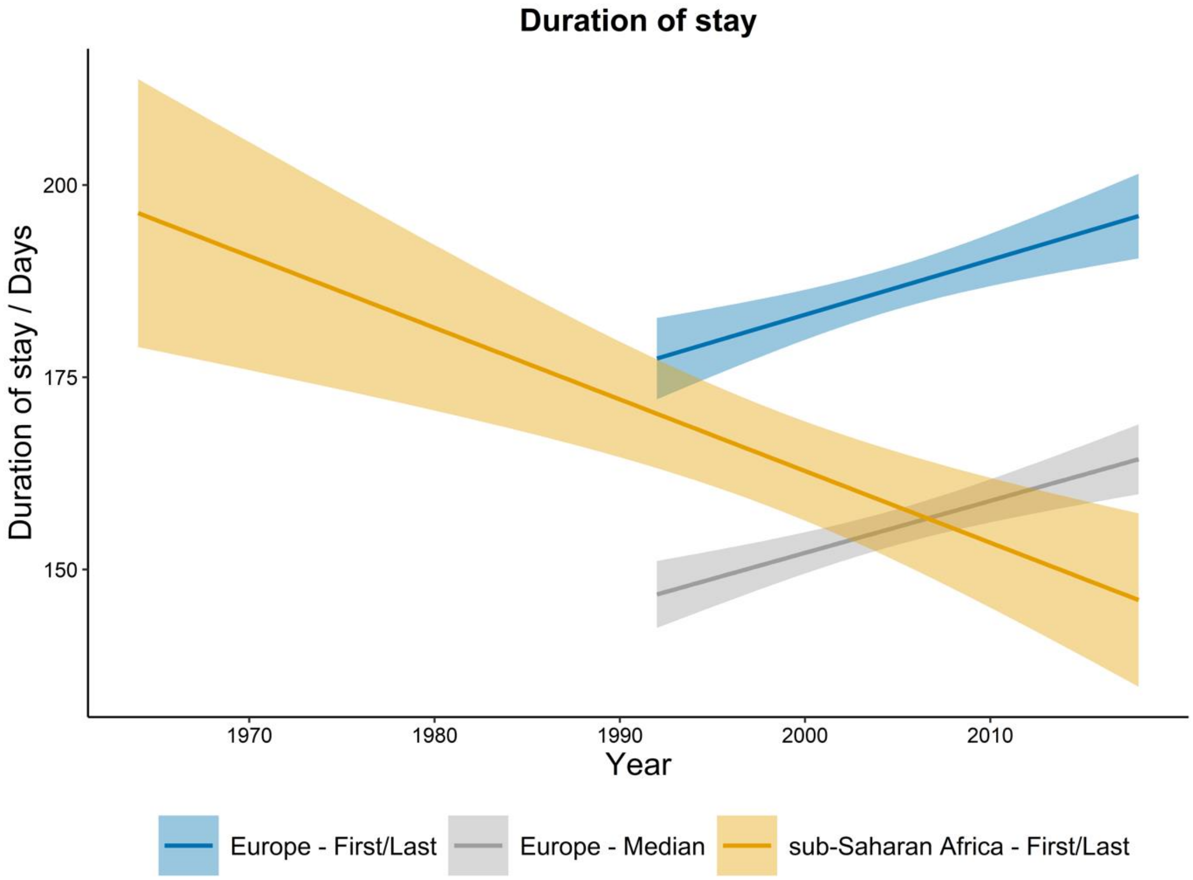

Figure 4. *Phenological trends in durations of stay within Europe and sub-Saharan Africa. Lines show the mean duration of stay across species, predicted by a linear model, with shaded regions displaying the 95% confidence intervals. Europe – First/Last trends are based on those individuals arriving first and departing last at Gibraltar. Whereas Europe – Median trends represents duration of stay based on median passage dates. Duration of stay in sub-Saharan Africa is based on first arrival and last departure dates in The Gambia.*

Drivers of arrival and departure trends

PLMMs were fitted separately to identify drivers of inter-annual variation in the timing of pre-breeding and post-breeding migration of trans-Saharan migrants, at both The Gambia and Gibraltar. For The Gambia, where data collection ran from 1964, the dataset to which these models were fitted was truncated in comparison the previous analyses (**Table 2**), as NDVI data were available only from 1982. As ringing data for Gibraltar were only available from

1991, there was no need to truncate this dataset. Potentially as a result of this reduced sample size, models explained variation in the timing of both pre-breeding and post-breeding migration of first/last individuals better for Gibraltar (R^2=0.79 and R^2=0.81, respectively) than for The Gambia (R^2=0.12 and R^2=0.5, respectively).

We found significant effects of meteorological variables on the timing of first/last pre-breeding migration dates at both The Gambia and Gibraltar, though the exact drivers differed between locations (**Fig. 5a & b**; Tables S7 & 8). Dates of last pre-breeding departure from The Gambia showed a significant negative relationship with pre-departure NDVI of the Sahel, with higher NDVI values resulting in earlier observed departure. Additionally, we a found a positive relationship, which bordered on significance, between pre-breeding departure dates and pre-departure temperatures of The Gambia. By contrast, dates of first pre-breeding arrivals at Gibraltar showed a significant positive relationship with the winter NAO index. We also found a positive relationship approaching significance between pre-breeding Gibraltarian arrival dates and North African NDVI. Negative relationships between year and pre-breeding migration were found at both locations.

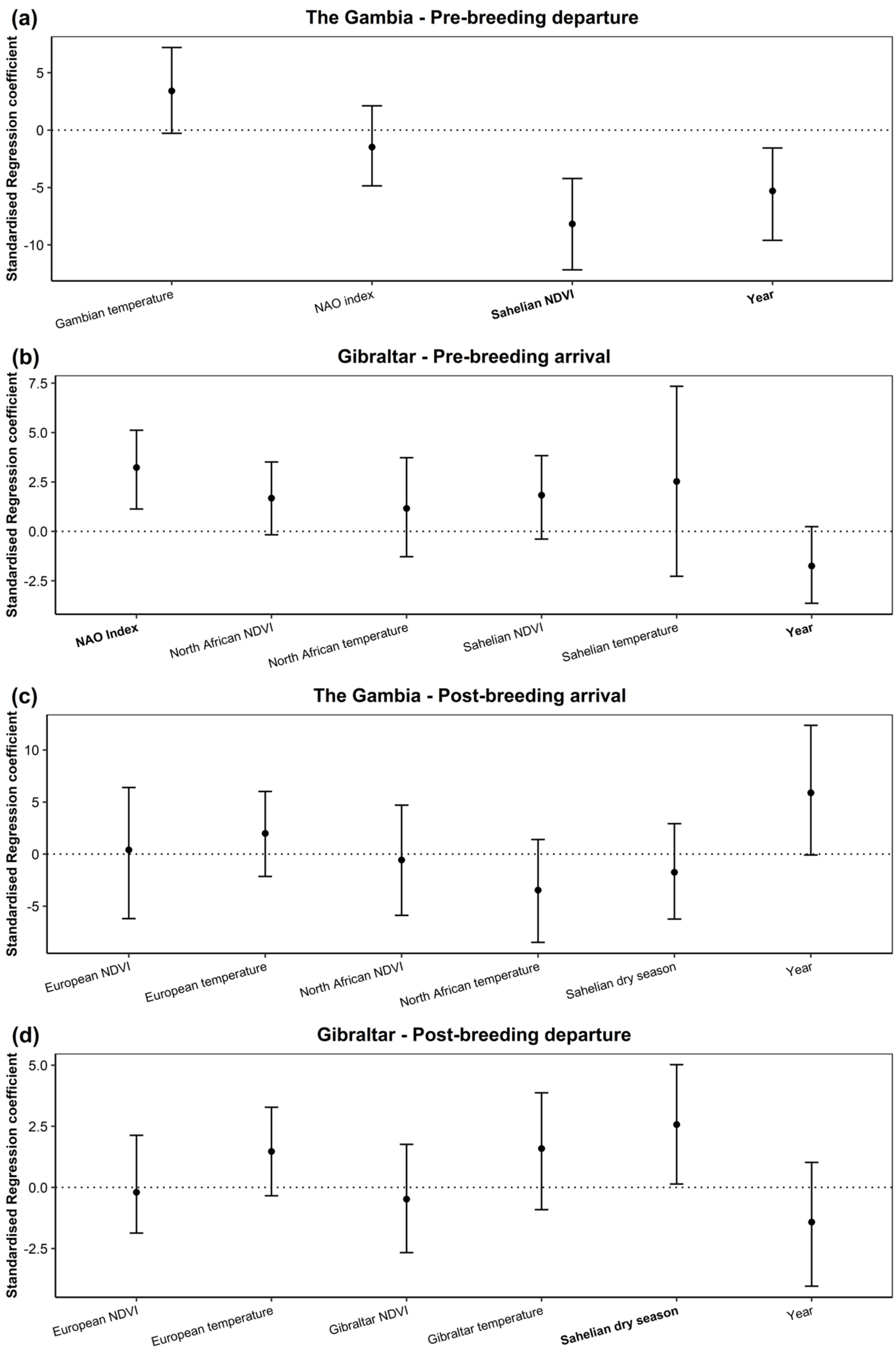
(a)
The Gambia - Pre-breeding departure
Standardised Regression coefficient
5
0
-5
-10
Gambian temperature
NAO index
Sahelian NDVI
Year
(b)
Gibraltar - Pre-breeding arrival
Standardised Regression coefficient
7.5
5.0
2.5
0.0
-2.5
NAO Index
North African NDVI
North African temperature
Sahelian NDVI
Sahelian temperature
Year
(c)
The Gambia - Post-breeding arrival
Standardised Regression coefficient
10
5
0
-5
European NDVI
European temperature
North African NDVI
North African temperature
Sahelian dry season
Year
(d)
Gibraltar - Post-breeding departure
Standardised Regression coefficient
5.0
2.5
0.0
-2.5
European NDVI
European temperature
Gibraltar NDVI
Gibraltar temperature
Sahelian dry season
Year

Figure 5. *Parameter coefficients from phylogenetic linear mixed models, used to assess the drivers of first and last pre-* ***(a,b)*** *and post-breeding* ***(c,d)*** *migration dates, in both The Gambia* ***(a,c)*** *and Gibraltar* ***(b,d)****. Error bars display 95% confidence intervals (CIs) around coefficients. Those CIs that overlap zero (dashed line) indicate non-significant effects, where p>0.05. Variables deemed significant using this approach are displayed in bold on the x-axes.*

Much like the models predicting pre-breeding migration, the relationships between the meteorological variables and first/last post-breeding migration dates varied between locations (**Fig. 5c & d**). We found no significant relationships between meteorological/ecological variables and dates of post-breeding arrival in The Gambia, although there was a weak negative relationship with pre-arrival NDVI of North Africa (Table S9). In contrast, dates of post-breeding departure from Gibraltar showed a significant positive relationship with the start date of the Sahelian dry season (which typically occurs in October), i.e. in years of earlier dry season onset, departure from Gibraltar was earlier. Additionally, although not significant at the p=0.05 level, dates of post-breeding departure from Gibraltar also showed a positive relationship with European autumn temperatures (Table S10).

The drivers of median migration dates at Gibraltar differed slightly from those of first/last dates (Fig S7). Median dates of pre-breeding arrival at Gibraltar showed a significant negative relationship with pre-arrival North African NDVI, in addition to a significant positive relationship with pre-arrival temperatures of the Sahel. Median post-breeding departure dates from Gibraltar were significantly negatively correlated with European autumn NDVI and pre-departure Gibraltarian NDVI. Additionally, year was retained as a significant driver in both models, showing a strong negative relationship with arrival dates and a strong positive relationship with departure date (Tables S11 & 12).

Discussion

Here, we have demonstrated advancements in the timing of pre-breeding migration of trans-Saharan migratory birds at both a tropical non-breeding area and an intermediate passage site. Additionally, we found delays to the timing of post-breeding migration of these same migrants at both locations. As a result of these contrasting trends, we observed substantial alterations to the temporal partitioning of the annual cycles of these species, at least in terms of when the first and last individuals of species arrive and depart from the regions. We also found that, at Gibraltar, the intermediate passage site, the trends of changing passage date over time did not differ significantly between first/last individuals and the median passage date, though clearly median passage dates differed from first and last arrival/departure dates. Here, we discuss these results, as well as our exploration of the factors identified as potential drivers of the observed trends. We go on to discuss the implications of our findings in relation to the potential impacts of continued climate change on the phenology and population trends of long-distance migrants.

Overall, we found that pre-breeding migration had advanced significantly, both in terms of departure from The Gambia and on passage at Gibraltar, the latter for both first and median dates of arrival. These findings are in line with phenological changes observed on the breeding grounds, with rates of advancement at Gibraltar most similar (0.28 days/year at Gibraltar cf. e.g. 0.26 days/year on the breeding grounds; Tøttrup et al., 2006). Additionally, despite being of greater mean magnitude, advancements in departure dates from The Gambia over time (0.44 days/year) overlapped significantly with those at Gibraltar, so could also be considered comparable to those on the breeding grounds. The similarity in rates of phenological change at our two study sites during pre-breeding migration are consistent with unaltered migratory speeds over time, though, without tracking individual birds, this cannot be proven. Hence, advances in arrival at Gibraltar are likely to have been driven, at least partially, by concurrent advances in departure from The Gambia (Ouwehand & Both, 2017), and it may even be the case that departures from Gambia have advanced more than at the intermediate passage site and on the breeding grounds.

The last departure of individuals of species from The Gambia, heading for the breeding grounds, occurred earlier in years of high pre-departure Sahelian NDVI, when resources were assumed to be more plentiful there. This is similar to findings in the Americas, which showed that departure from tropical non-breeding areas is facilitated by increased food availability (Studds & Marra, 2011). Thus, individuals are probably able to gain mass more rapidly and, therefore, depart at an earlier date. The median arrival of individuals at Gibraltar tended to occur later in years of high pre-arrival temperatures across the Sahel. These conditions are correlated with colder and, therefore, later European springs in which it may be costly to arrive early (Saino & Ambrosini, 2008). Alternatively, higher Sahelian temperatures may lead to more rapid declines in resources. This may limit pre-departure fattening rates, resulting in delayed departure from the Sahel and, therefore, arrival at Gibraltar. The median passage occurred earlier in years of higher North African NDVI, again potentially due to greater resource availability on refuelling stopovers. In contrast, timing of the first pre-breeding arrivals at Gibraltar was positively related to the winter NAO index, rather than temperature or NDVI variables. Hence, and in contrast to studies from the breeding grounds (Forchhammer et al., 2002; Hüppop & Hüppop, 2003; Jonzén et al., 2006), the earliest migrating individuals tended to arrive at Gibraltar later in years of strongly positive NAO, despite this correlating with typically wet and warm European springs. In such conditions, earlier arrival might have been expected to be advantageous. However, the more arid conditions across north-western Africa associated with these positive NAO conditions may limit food availability, forcing individuals to increase the length of resource replenishing stopovers (Jones et al., 2003). In fact, the NAO index showed a strong negative correlation with NDVI of the North African region prior to arrival (R_s = -0.61), which may explain why the drivers of first and median arrivals appear to differ. Additionally, local weather patterns across Africa resulting from these positive NAO conditions, e.g. stronger trade winds and more frequent Atlantic storms, could serve to "hold up" early migrating individuals across north-western Africa (George & Saunders, 2001; Jones et al., 2003). In order to account for these delays, migration speed may be increased following such pre-breeding stopovers, as has been observed in North America (Marra et al., 2005).

Year was a significant predictor of the latest pre-breeding migration departures in The Gambia and of subsequent median arrival dates at Gibraltar and approached significance for the first arriving individuals at Gibraltar (p=0.08), with both pre-breeding Gambian departure and Gibraltarian arrival dates becoming earlier in recent years. The retention of year, in addition to environmental variables in the models, suggests that an additional driver of these trends may have been excluded from the models. Perhaps more simply, there may be increasing selection over time for individuals that migrate earlier. It has been suggested that advances in the breeding ground arrival dates of long-distance migratory birds are driven not by plasticity in individual arrival date but rather by advanced arrival dates of progressive generations of new recruits (Gill et al., 2013). As development and miniaturization of tracking technology continues, testing such hypotheses for small passerine species may well become viable.

The ability to advance pre-breeding migration from their non-breeding grounds may render migrants more resilient to phenological advancements on the breeding grounds than previously thought, as individuals are not solely reliant on the ability to increase migration speed, which itself is likely to have morphological and physiological limits. However, notwithstanding uncertainty in future climatic predictions, declines in rainfall are forecast for some tropical regions, including the western Sahel (Biasutti, 2019). This may result in reduced productivity and, hence, fewer resources for refuelling in these areas. This could result in migrating birds needing longer to gain resources for migration, potentially constraining early departures from the non-breeding grounds (Marra et al., 2005). Alternatively, the changing distribution of resources could result in poleward shifts in non-breeding distributions, leading to shorter migrations for some species (La Sorte & Thompson, 2007). Such reduced migratory tendencies, and consequent fitness benefits have been observed recently in species such as White Stork in Europe (Cheng et al., 2019). However, for long-distance migrants whose breeding and non-breeding ranges are largely in different hemispheres, this could result in increased migration distances and, therefore, longer migratory durations (Howard et al., 2018).

In contrast to pre-breeding migration, we found that post-breeding migration occurred progressively later at both locations over time and for both median and last departure dates at Gibraltar. None of the meteorological or ecological variables included in our models were related to Gambian post-breeding arrival dates. However, last autumn departure from Gibraltar was positively correlated with the onset of the Sahelian dry season. Thus, individuals departed from southern Europe earlier in years when the Sahelian dry season occurred earlier, possibly to reach sub-Saharan Africa before Sahelian resources declined (Jenni & Kéry, 2003), though the cues that could lead to such a response are unknown. In contrast, median departure dates from Gibraltar showed a negative relationship with European autumn NDVI and, more locally, Gibraltarian NDVI. Higher NDVI values prior to departure may enable more rapid fat-loading, enabling earlier departure. This could suggest that drivers of post-breeding migration differ between individuals of the population on different migratory schedules. The latest migrating individuals, potentially from the most northerly parts of the breeding range, typically departed from Europe in October (Table S3). Therefore, our measure of European NDVI, which was calculated over August and September, may have little relevance to the timing of their departure. Instead, the senescence of resources in the Sahel, which typically begins in September and becomes more severe as the year progresses, may place a greater pressure on the migratory timing of these individuals (Jenni & Kéry, 2003). In contrast, median post-breeding departure typically occurred in September and individuals may be more able to take advantage of increased resources across Europe during this period, to depart more rapidly from the breeding grounds. These individuals, which may be from more centrally or southerly distributed breeding populations (and hence, start and finish breeding earlier), potentially migrate sufficiently early that the decline of resources in the Sahel is unlikely to impact their survival. Interestingly, year was retained as a significant predictor of median but not last departure dates at Gibraltar.

Due to the opposing trends in timing of pre- and post-breeding migration, population-level durations of stay of trans-Saharan migratory species changed significantly in both Europe and sub-Saharan Africa. Our models indicated that, on average, duration of stay (i.e. presence of any individuals of a species) within Europe, for populations passing Gibraltar, increased by over two weeks, across 27 years, whilst sub-Saharan Africa stay durations declined by over two months over the 55-year study period; the change in duration of stay at Gibraltar being consistent for both median passage and the timing of first arriving (spring) and last departing (autumn) individuals. Due to the population-level nature of our analyses, we are unable to assess changes in the time individuals spent in the North African region between Gambia and Gibraltar. Notwithstanding the fact that these results represent population-wide changes in phenology, they represent substantial, and previously undocumented, changes to the temporal-partitioning of the annual cycle of these long-distance migrants. These findings and their potential impacts, discussed below, highlight the need for increased focus on recording the phenology of post-breeding migration, as well as pre-breeding migration away from the breeding grounds.

Due to the inevitability of further rises in global temperatures, continued advancement of the spring phenologies of temperate ecosystems are likely (Vitasse et al., 2011). As such, pre-breeding migration is likely to continue to advance, unless individuals become limited by, for example, food availability. Furthermore, and counter to the suggestion of Jenni & Kéry (2003), we found that the timing of the Sahelian dry season has shown significant delays in recent times (Fig. S8). Currently, predictions of future rainfall across the Sahel vary among climatic models (Biasutti, 2019). However, if the recently observed delays to dry season onset continue, this could further reduce the necessity for some populations to depart from breeding grounds rapidly post-breeding. As a result, it is possible that species will further extend their annual duration of stay within Europe, at the expense of that within sub-Saharan Africa. This could result in the evolution of short-distance migratory strategies for some populations of these migrants, as has been observed in the Eurasian Blackcap, and predicted in selection experiments (Berthold et al., 1992; Pulido & Berthold, 2010). This is particularly interesting when considering the forecasts of increased migratory distance for long-distance Afro-Palearctic migrants, which are yet to account for the potential development of “short-stopping” (Doswald et al., 2009; Elmberg et al., 2014; Howard et al., 2018).

If it were to become climatically viable, shorter-distance (e.g. within the western Palearctic) migration would likely confer numerous benefits to populations that formerly undertook long-distance migrations. Firstly, shorter migration distances should result in reductions in both stopover number and migratory duration (Howard et al., 2018). Periods of migratory flight and stopover are both times of particularly high mortality, due to factors such as increased predation risk and unknown resource availability (Newton, 2008). Therefore, a reduction in migration distance should positively affect individual survival (Cheng et al., 2019). Additionally, shorter-distance migratory populations may be better able to anticipate breeding ground phenology, utilising better linked cues for timely pre-breeding departure (Both et al., 2010; Jonzén et al., 2006). Alongside reduced duration of pre-breeding migration, such populations should become less phenologically mismatched than long-distance migratory populations of the same species (Bearhop et al., 2005). However, such changes in migratory strategy would also have knock-on effects on temperate and tropical ecosystems. For example, an increase in avian richness in the Western Palearctic over the non-breeding period may increase competition for resources, with potential deleterious impacts upon resident and short-distance migratory species that spend the non-breeding season in this region. Conversely, through competitive release, a reduction in non-breeding species richness in tropical regions could benefit other species using the former non-breeding areas of migrants. However, as migrants are typically itinerant during the non-breeding season, due to the ephemeral nature of the resources they utilise, resident African species may be less capable of benefitting from any excess resource.

In conclusion, our findings provide new insight into the changing annual cycles of long-distance migrants under a period of recent rapid climate change. Long-distance migrants advanced pre-breeding departure from tropical non-breeding grounds aiding adaptation to rapid phenological advancement on breeding grounds. However, potential declines in productivity in these tropical areas may limit species' abilities to continue these advancements, due to the inability to further advance fat-loading prior to pre-breeding departure. An opposing trend in post-breeding migration meant that, at a population level, long-distance migrants now spend a markedly shorter period of time on the non-breeding grounds than they did in the latter part of the last century. Through continuation in these trends and selection for reduced migratory activity, we may see adoption of new migratory strategies in populations of these long-distance migratory species.

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