






RESEARCH ARTICLE

Among-species variation in six decades of changing migration timings explained through ecology, life-history and local migratory abundance

Vicki R. Dale¹  | Mark Bolton²  | Maria Dornelas³  | Anne E. Magurran³  | Roy Dennis^{2,4} | Roger Broad² | Nick J. Riddiford² | Paul V. Harvey² | Roger Riddington² | Deryk N. Shaw² | David Parnaby² | Jane M. Reid^{1,2,5} 

¹School of Biological Sciences, Zoology Building, University of Aberdeen, Aberdeen, UK

²Fair Isle Bird Observatory Trust, Fair Isle, Shetland, UK

³Centre for Biological Diversity, School of Biology, University of St Andrews, St Andrews, UK

⁴Roy Dennis Wildlife Foundation, Half Davoch Cottage, Forres, UK

⁵Centre for Biodiversity Dynamics, Department of Biology, NTNU, Trondheim, Norway

Correspondence

Vicki R. Dale, School of Biological Sciences, Zoology Building, University of Aberdeen, Aberdeen, UK.

Email: v.dale.19@abdn.ac.uk

Funding information

Natural Environment Research Council SUPER DTP

Abstract

Species exploiting seasonal environments must alter timings of key life-history events in response to large-scale climatic changes in order to maintain trophic synchrony with required resources. Yet, substantial among-species variation in long-term phenological changes has been observed. Advancing from simply describing such variation towards predicting future phenological responses requires studies that rigorously quantify and explain variation in the direction and magnitude of changing timings across diverse species in relation to key ecological and life-history variables. Accordingly, we fitted multi-quantile regressions to 59 years of multi-species data on spring and autumn bird migration timings through northern Scotland. We demonstrate substantial variation in changes in timings among 72 species, and tested whether such variation can be explained by species ecology, life-history and changes in local abundance. Consistent with predictions, species that advanced their migration timing in one or both seasons had more seasonally restricted diet types, fewer suitable breeding habitat types, shorter generation lengths and capability to produce multiple offspring broods per year. In contrast, species with less seasonally restricted diet types and that produce single annual offspring broods, showed no change. Meanwhile, contrary to prediction, long-distance and short-distance migrants advanced migration timings similarly. Changes in migration timing also varied with changes in local migratory abundance, such that species with increasing seasonal abundance apparently altered their migration timing, whilst species with decreasing abundance did not. Such patterns broadly concur with expectation given adaptive changes in migration timing. However, we demonstrate that similar patterns can be generated by numerical sampling given changing local abundances. Any apparent phenology-abundance relationships should, therefore, be carefully validated and interpreted. Overall, our results show that migrant bird species with differing ecologies and life-histories showed systematically differing phenological changes over six decades contextualised by large-scale environmental changes,

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Global Change Biology* published by John Wiley & Sons Ltd.

potentially facilitating future predictions and altering temporal dynamics of seasonal species co-occurrences.

KEYWORDS

climate change, EltonTraits, life-history, long-term data, migration timing, migratory bird, passage date, phenology, quantile regression, seasonality

1 | INTRODUCTION

Human actions have altered biotic and abiotic environments across the globe, driving recent decades of rapid climate and environmental changes that have caused dramatic and divergent changes in species' life-history schedules (i.e. phenologies, Menzel et al., 2006; Root et al., 2003; Thackeray et al., 2010), spatial distributions (Chen et al., 2011; Gillings et al., 2015; Parmesan & Yohe, 2003) and abundances (Martay et al., 2017). Now, a pressing challenge is to predict the impacts of continued large-scale environmental change on future responses of diverse species, which will in turn influence species interactions and population persistence (Urban et al., 2016).

Climate change currently constitutes a substantial component of environmental change, altering species phenology and threatening future species persistence (Bellard et al., 2012; Inouye, 2022; Post et al., 2018; Thomas et al., 2004). At mid-high latitudes, increasing temperatures are projected to drive increased durations of terrestrial primary production, due to observed advances in the onset of spring plant growth alongside predicted delays to autumn cessation (Gallinat et al., 2015; Menzel et al., 2006; Piao et al., 2019). Populations of species that depend on seasonal resources are predicted to decline if they cannot resynchronise their phenology with changing seasonal conditions ('match-mismatch hypothesis', Both et al., 2010; Burgess et al., 2018; Jones & Cresswell, 2010; Saino et al., 2011). In line with observed changes in spring plant phenology, diverse animal species have shifted timings of key life-history events and/or temporal space use over recent decades (birds: Newson et al., 2016; Rubolini et al., 2007; fish: Kovach et al., 2015; mammals: Bischof et al., 2012; Severson et al., 2021; global synthesis: Cohen et al., 2018; Renner & Zohner, 2018; Thackeray et al., 2016), commonly attributed to changing climatic conditions (Gordo, 2007). Analyses of avian migration have also reported positive correlations between changes in phenology and population size (Both et al., 2010; Møller et al., 2008; Visser & Both, 2005), as expected if failure to resynchronise results in trophic mismatches and demographic costs (Both et al., 2010; Burgess et al., 2018).

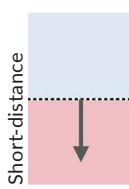
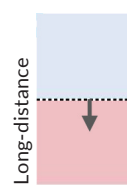
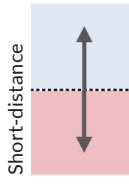
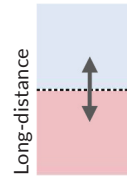


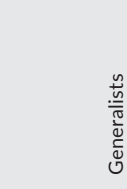
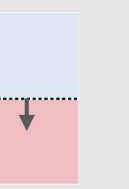
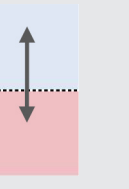
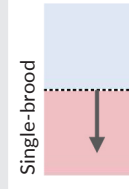
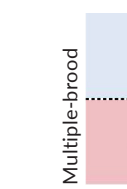

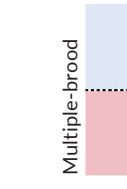
However, while such overarching generalisations have been drawn, the direction and magnitudes of observed phenological responses can vary substantially among species (Barrett, 2002; Hurlbert & Liang, 2012; Knudsen et al., 2007; Romano et al., 2023; Usui et al., 2017). Such variation could further complicate relationships between phenology and population dynamics by disrupting synchronies among species involved in successive temporally sensitive trophic and/or competitive interactions (e.g. Ahola et al., 2007;

Saino et al., 2009; Samplonius et al., 2018), generating unexpected population outcomes (Iler et al., 2021; Ockendon et al., 2014; Renner & Zohner, 2018; Thackeray et al., 2010; Visser & Both, 2005). Given this complexity, successfully predicting impacts of continued large-scale environmental change on population phenology and persistence within and among diverse species requires that we identify basic ecological and life-history attributes that predict observed variation in phenological responses (Knudsen et al., 2011; Salido et al., 2012).

Migration, defined as reversible seasonal movements between discrete breeding and non-breeding locations, is one critical life-history event where timings directly link periods of resource demand (e.g. reproduction) with spatially and temporally restricted resource abundance (Newton, 2008). Changes in migration timings, or lack of changes, could, therefore, severely disrupt trophic and/or competitive synchronies and substantially impact individual fitness and population outcomes. Migration has consequently been a focal point of efforts to identify key biological attributes explaining among-species variation in phenological responses over recent decades (Knudsen et al., 2011; Ockendon et al., 2014; Salido et al., 2012).

Trait-based analyses, which aim to identify common traits across species and populations that show similar responses, provide one route towards general prediction (Green et al., 2022; Urban et al., 2016). Such analyses can potentially identify types of species that need to respond to avoid trophic mismatches and/or that have capabilities to respond. Such understanding will facilitate effective transformation of observed variation in past phenological responses into predictions for future responses that can encompass wider ranges of species. Previous analyses of changing migration timings have focused on specific hypotheses relating to high-level ecological (e.g. diet, habitat use and/or specialism) and life-history traits (e.g. generation length, breeding duration, Table 1, Romano et al., 2023; Usui et al., 2017). Further, changes in population size have been hypothesised to affect, correlate with or result from species' phenological responses to changing seasonal conditions (Table 1, Chmura et al., 2019). However, most previous multi-species studies relied on meta-analyses of published estimates and/or data compilations from different systems (Bitterlin & van Buskirk, 2014; Møller et al., 2008; Romano et al., 2023; Usui et al., 2017). One resulting challenge is that pervasive methodological differences in how migration phenology is quantified contribute to apparent among-species variation (Knudsen et al., 2007). Perhaps unsurprisingly, such studies report mixed support for hypothesised effects of species ecology and

TABLE 1 Summary of focal explanatory variables, and predictions linking them to among-species variation in changing migration timing.

Explanatory variable	Predicted effect on changes in species spring phenology and rationale	Spring figures	Predicted effect on changes in species autumn phenology and rationale	Autumn figures	Description, data source and number of species included (spring/autumn)
Migration distance (factor)	<p>Prediction: Short-distance migrants will advance spring phenology more than long-distance migrants.</p> <p>Rationale: Greater spatial disconnect between breeding, passage and non-breeding sites (Bitterlin & van Buskirk, 2014; Both et al., 2006; Moussus et al., 2011; Usui et al., 2017). Stronger endogenous control over migration onset in long-distance migrants (Gwinner, 1996).</p>	<p>Short-distance</p>  <p>Long-distance</p> 	<p>Prediction direction: Short-distance migrants will change autumn phenology more than long-distance migrants. Direction of effects uncertain.</p> <p>Rationale: Same as spring</p>	<p>Short-distance</p>  <p>Long-distance</p> 	<p>Two categories, reflecting whether a species predominantly winters north (short-distance) or south (long-distance) of the Sahara Desert.</p> <p>Data Source: BirdLife International (2020) and BTO BirdFacts (Robinson, 2005)</p> <p>Species included: 64 63</p>
Diet (factor)	<p>Prediction: Habitat specialists, and species with more seasonally restricted diet types, will advance spring phenology more than generalists.</p> <p>Rationale: Specialists under stronger selection to advance their spring phenology with seasonal conditions than those with less seasonal requirements, since trophic synchrony will otherwise be rapidly lost ('match-mismatch hypothesis', Both et al., 2010)</p>	<p>Specialists</p>  <p>Generalists</p> 	<p>Prediction: Habitat specialists, and species with more seasonally restricted diet types, may advance autumn phenology whilst generalists may delay. However, the directions of effects are uncertain.</p> <p>Rationale: Migrants specialising on seasonal resources under strong selection to advance autumn phenology, since advances in phenology of resources will result in unfavourable conditions for breeding later in spring, assuming that food resource peaks are earlier but not more protracted. Meanwhile, generalist species more likely to benefit from predicted lengthening of seasonal growth periods as it may translate into lengthening suitable breeding conditions if food sources are available.</p>	<p>Specialists</p>  <p>Generalists</p> 	<p>Four categories, comprising invertebrate, plant-seed, omnivore, and vertebrate.</p> <p>Data Source: EltonTraits 1.0 (Wilman et al., 2014)</p> <p>Species included: 64 63</p>
Breeding habitat breadth (covariate)	<p>Prediction: Multi-brooded species will advance spring phenology more than single-brooded species.</p> <p>Rationale: Species capable of producing multiple offspring broods per year may benefit more from increasing the time spent at breeding sites, as they can increase reproductive output.</p>	<p>Single-brood</p>  <p>Multiple-brood</p> 	<p>Prediction: Multi-brooded species may delay autumn phenology whilst single-brooded species may advance.</p> <p>Rationale: Same as spring. There may be little benefit of remaining in breeding areas post-breeding.</p>	<p>Single-brood</p>  <p>Multiple-brood</p> 	<p>Total number of IUCN Level 1 habitat types suitable for breeding.</p> <p>Data Source: BirdLife International (2020)</p> <p>Species included: 62 62</p>
Brood number (factor)	<p>Prediction: Multi-brooded species will advance spring phenology more than single-brooded species.</p> <p>Rationale: Species capable of producing multiple offspring broods per year may benefit more from increasing the time spent at breeding sites, as they can increase reproductive output.</p>	<p>Single-brood</p>  <p>Multiple-brood</p> 	<p>Prediction: Multi-brooded species may delay autumn phenology whilst single-brooded species may advance.</p> <p>Rationale: Same as spring. There may be little benefit of remaining in breeding areas post-breeding.</p>	<p>Single-brood</p>  <p>Multiple-brood</p> 	<p>Two categories, reflecting whether a species produces a single offspring brood per year (not including replacement broods) or can produce multiple broods (both obligate and facultative multi-brood species).</p> <p>Data Source: BTO BirdFacts (Robinson, 2005)</p> <p>Species included: 63 62</p>

(Continues)

TABLE 1 (Continued)

Explanatory variable	Predicted effect on changes in species spring phenology and rationale	Spring figures	Predicted effect on changes in species autumn phenology and rationale	Autumn figures	Description, data source and number of species included (spring/autumn)
Generation length (covariate)	Prediction: Species with shorter generation lengths advancing spring phenology more than those with longer generation lengths. Rationale: Slower turnover in species with longer generation lengths imposes a limit on the rate at which migration timing can change due to micro-evolution and/or elimination of permanent environmental effects on individuals (Chmura et al., 2019; Gill et al., 2013).				Mean age of breeding adults. Data Source: BirdLife International (2020) Species included: 58/59
Change in local migratory abundance (β_{LMA}) (covariate)	Prediction: Populations of species advancing spring phenology will remain stable or increase in abundance, while populations of species that are not responding will decrease. Rationale: Changing migration timing could be adaptive, implying that local declines will follow from failure to adjust phenology (Both et al., 2006). However, similar patterns could potentially result from numerical sampling.				Proportional change in local migratory abundance on Fair Isle during the study period. Data Source: Fair Isle Migration Census Database Species included: 63/63

Note: Figures show the hypothesised direction(s) and magnitude of phenological change in spring and autumn, with red and blue indicating advances and delays in phenology, respectively. The number of species retained in analyses for each season, and data sources, are shown.

life-history on changes in migration timing (e.g. Bitterlin & van Buskirk, 2014; Romano et al., 2023; Usui et al., 2017), and limited support for associations between changes in phenology and population size (Both et al., 2010; Visser & Both, 2005, but see Møller et al., 2008). Such efforts have also focussed primarily on spring migration phenology. Relatively few studies have quantified changes in autumn migration timings (Gallinat et al., 2015; but see Romano et al., 2023). Even fewer have considered both seasons (but see Bitterlin & van Buskirk, 2014; Mills, 2005; Miles et al., 2017; van Buskirk et al., 2009), even though changing seasonality is predicted in both spring and autumn (Gallinat et al., 2015; Menzel et al., 2006). Predictions for effects of ecology and life-history on autumn phenology are consequently less well developed (Table 1), and an important first step is to quantify the degrees to which species' autumn migration timings are actually changing (Gallinat et al., 2015).

Progress in phenology research now requires that we rigorously and comparably quantify changes in spring and autumn migration phenology across diverse species with diverse ecological and life-history characteristics. Historically, phenological changes were quantified by monitoring changes in single metrics of phenological distributions, typically the mean or median date on which some event occurred. Now, it is clear that shapes of phenological distributions, and hence forms of within-population variation, can also change across years (Cadahía et al., 2017; Lehikoinen et al., 2019; Miles et al., 2017; van Buskirk et al., 2009). Multiple metrics describing these distributions (e.g. multiple quantiles) are consequently required to fully capture complex among-species variation in phenological change (Miles et al., 2017). However, such multi-metric approaches can generate misleading biases, because estimates of changes in different quantiles can be differentially sensitive to changes in the numbers of individuals whose migration timings are observed, which may to some degree reflect changes in population size and/or distribution. Consequently, changes in abundance have often been viewed as confounding nuisance variables in analyses of phenology, when in fact they are also points of biological interest (Miller-Rushing et al., 2008; but see Møller et al., 2008; Newson et al., 2016). Robust quantifications of multi-species relationships between changes in phenology and any measure of abundance, therefore, requires explicit estimation of the magnitudes of intrinsic sampling biases that can arise. Overall, advanced inferences on biological processes that influence species phenological responses to environmental change and population-level impacts now requires new analyses encompassing diverse species, multiple phenology metrics and both seasons and that consider systematic abundance biases in driving observed phenology patterns. This ambition requires long-term datasets where migration phenology has been recorded for diverse species using consistent field methods across several decades (Knudsen et al., 2007).

Such standardised multi-species data are most readily available from long-term single-site studies. Accordingly, we use 59 years of systematic observations from Fair Isle, Scotland, to quantify

among-species variation in changes in spring and autumn migration timings across 72 diverse bird species, using standardised multi-quantile analyses. We implement a trait-based phylogenetic comparative approach to test whether observed among-species variation in migration timings is explained by five focal ecological and life-history variables that are predicted to shape phenological responses to large-scale environmental change (namely migration distance, diet type, breeding habitat breadth, generation time and number of broods, summarised in Table 1). Further, we test the broad prediction that changes in local migratory abundance and phenology will be positively correlated across species, such that species whose migration timing is changing are remaining stable or increasing in abundance, while species whose migration timing is not changing are decreasing. Here, we explicitly examine whether any observed phenology-abundance associations can be explained solely by numerical sampling effects. Overall, our analyses reveal major ecological and life-history predictors of observed among-species variation in long-term phenological change, and also highlight core challenges of definitively linking changes in phenology and local abundance.

2 | MATERIALS AND METHODS

2.1 | Study system and species selection

Fair Isle (59°32' N, 0°28' W) lies between the Shetland and Orkney archipelagos in northern Scotland (Figure 1). It is an important migration passage site, used by diverse species on route to and from non-breeding areas in south-west Europe and Africa and breeding areas in Scandinavia and beyond. During spring and autumn migration seasons through 1955–2018, ornithological staff from Fair Isle Bird Observatory (FIBO) conducted daily surveys to count migrant birds following a standardised survey methodology (Supporting Information S1; Miles et al., 2017). In brief, Fair Isle is divided into three areas, and daily surveys are generally simultaneously carried out by three expert observers who each cover one area. Each observer spends a minimum of 3 hours walking routes within their area, maximising coverage of main areas of habitat used by migrant birds (Miles et al., 2017). Observers subsequently collate counts, excluding obvious duplicate sightings. Fair Isle is well suited for observational surveys because its relatively small size (7.68 km²) and predominantly open habitat facilitate extensive daily coverage with relatively high likelihood that birds present will be observed (Figure 1). The resulting database comprises estimates of the number of individuals of each species present on Fair Isle on each survey day. In all years, daily surveys were conducted during core survey periods designed to capture spring (start April–end June) and autumn (start August–end October) migrations. Surveys also extended into shoulder periods (March, July and November) in most years (Supporting Information S1). Since inspection suggested that data for 1955–1959 were not completely comparable with subsequent years, and data collection since 2019 has been disrupted, current analyses used data for 1960–2018 (i.e. 59 years).

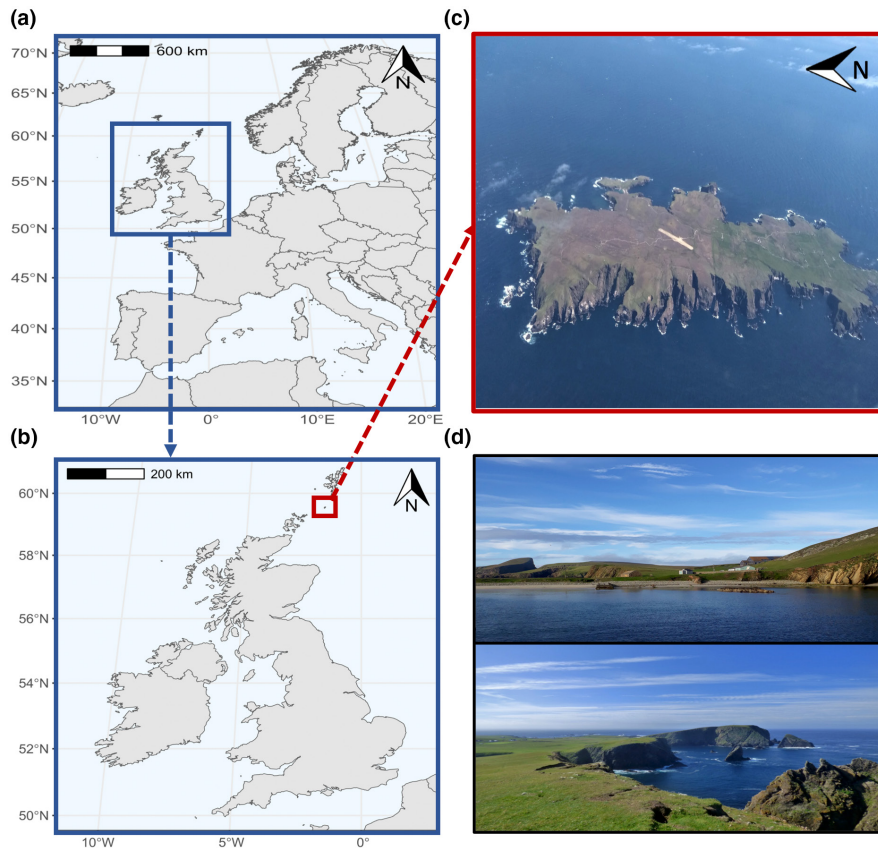


FIGURE 1 Maps showing the location of (a) UK within Europe and (b) Fair Isle within the UK, and images of (c) Fair Isle (taken from a western elevation) and (d) the open local grassland habitat. Map data are from R package ‘rnatuarearth’ (Massicotte & South, 2023). Photo credits: (c) Jill Andrews, (d) Sarah Fenn. Map lines do not necessarily depict accepted national boundaries.

To achieve the aim of quantifying changes in full distributions of species' migration timings, current analyses were restricted to species that occurred relatively frequently in spring and/or autumn. An initial list of 81 species was compiled, guided by published summaries of sighting frequencies on Fair Isle (Dymond, 1991). The few migrant species that also frequently bred on Fair Isle (e.g. Wheatear [*Oenanthe oenanthe*], Meadow Pipit [*Anthus pratensis*], Skylark [*Alauda arvensis*], Oystercatcher [*Haematopus ostralegus*]) were excluded because full distributions of migration passage dates were not distinguishable from observations of settled breeders. Groups whose taxonomic status changed during the study period were also excluded, since recorded totals were not comparable across all years (e.g. Redpolls, *Acanthis* sp.). Further species were then excluded in spring and/or autumn if they failed to meet four criteria: (i) Sightings occurred in >80% of years; (ii) Mean number of sightings per season-year >5; (iii) Most sightings occurred well within the core survey periods; and (iv) Spring and autumn migrations were temporally distinct, with few sightings through mid-summer. This process resulted in exclusion of differing sets of 17 species in spring and in autumn. The final dataset contained 72 species spanning 12 orders and 25 families, comprising 45 passerines (e.g. buntings, finches, hirundines, chats, warblers, corvids) and 27 non-passerines (e.g. sandpipers, rails, falcons, owls). Overall, 64 species were retained in each of the two seasons (spring and autumn), with 56 species included in both seasons and 16 species only included in one season (eight

in spring and eight in autumn). Full lists of species and exclusions are in [Supporting Information S2](#).

2.2 | Covariate data

We compiled data on the six focal ecological and life-history variables (Table 1) for all 72 species using standardised databases. Diet type was extracted from the EltonTraits 1.0 Database (Wilman et al., 2014), where species are assigned to one of five diet categories, comprising predominantly: (i) invertebrate, (ii) plant-seed, (iii) fruit-nectar, (iv) vertebrate, fish and/or scavenger (hereafter ‘vertebrate’) and (v) omnivore. No species included in our study had a predominantly fruit-nectar diet, leaving four diet types for analysis. Species classed as omnivores use multiple other categories, with no single category exceeding 50% of the diet, and hence explicitly represent diet generalists. Our ‘vertebrate’ group, which includes scavengers, can also be considered relatively generalist, with a less strongly seasonally restricted diet compared to the invertebrate and plant-seed groups.

Species were categorised as either long- or short-distance migrants reflecting whether they winter south or north of the Sahara Desert, respectively, based on species-level breeding and non-breeding range information (Table 1, BirdLife International, 2020; BTO BirdFacts, Robinson, 2005). This coarse two-level division is commonly applied in migration research (e.g. Jonzén et al., 2006). Since breeding and

non-breeding locations of passage populations are typically not known exactly, migration distances cannot be quantified more precisely.

Breeding habitat breadth was quantified as the total number of habitat types classed as 'suitable' or above for each species by BirdLife International (2020); higher values represent greater breadth. Habitat types were defined following the IUCN Habitats Classification Scheme (2012) at the broadest level (Level 1). Marine habitats were collapsed into a single category, leaving ten habitat types: forest, grassland, shrubland, wetland (inland), rock and/or cave, marine, artificial terrestrial, artificial aquatic, savannah & desert.

Species were categorised as single-brooded or multi-brooded depending on whether they are apparently limited to production of a single brood per season (not including replacement broods, BTO BirdFacts, Robinson, 2005). The multi-brooded group, therefore, comprises both obligate and facultative multi-brooded species. Generation length, defined as mean age (in years) of breeding adults, was extracted from BirdLife International (2020).

High-quality standardised data on changes in breeding population sizes for all focal species through the study period are not available at a relevant spatial scale. This is because Fair Isle is a passage site for populations travelling to and from diverse non-breeding and breeding grounds. Consequently, to examine the degree to which changes in migration timings were associated with changes in local migratory abundance, we computed a standardised measure of change as the slope of a linear regression of the total number of sightings of each species on Fair Isle in each season in each year on year (hereafter 'change in local migratory abundance', denoted β_{LMA} , Supporting Information S3). To ensure that estimates of β_{LMA} were robust, regressions were re-fitted after removing outliers with high leverage (defined as Cook's distance >0.5), which arose due to occasional unusually large migratory 'falls' of some species. Estimates were insensitive to outlier removal in most species. However, where outliers occurred near the start or end of the study period, removing them improved model fit, and corresponding estimates of β_{LMA} were retained. Estimates of β_{LMA} were then standardised to account for substantial among-species variation in mean abundances. Specifically, we divided each estimate by the species' season-specific mean number of sightings across years, giving β_{LMA} as a proportion of the species' mean local migratory abundance (Supporting Information S3).

Standardised data on the focal variables were not available for all species, or were not applicable (e.g. Cuckoo [*Cuculus canorus*] is a brood parasite and hence has no brood number). In such cases, variable values were defined as missing and species excluded from respective analyses (Table 1 shows final species sample sizes; further details in Supporting Information S2).

2.3 | Statistical analyses

Two-step quantile regression analyses were used to quantify changes in location and shape of sighting distributions across the selected

species in both seasons (Miles et al., 2017). First, seven metrics were extracted from the daily survey data for each species in each season-year. These comprised the ordinal spring and autumn days by which the 5th, 10th, 25th, 50th, 75th, 90th and 95th quantiles of each sighting distribution had occurred. This set of seven quantiles was selected to satisfactorily summarise changes across full sighting distributions (Supporting Information S4) and ensure consistency with previous analyses (Miles et al., 2017). Data collected in all core and shoulder survey periods were used. However, the few sightings between the end of June and mid-July were excluded. These often reflected occasional summering or breeding individuals, for example an occasional breeding pair of swallows (*Hirundo rustica*), rather than ongoing migration. Second, separate linear mixed models (LMMs) were fitted to estimates of each quantile metric in each season across all species, with year as a fixed linear covariate and random species effects on intercepts and slopes (Supporting Information S4). The fixed regression slopes on year quantify the overall mean change in migration timing across all species over the study period for each quantile. The random intercept and slope variances, respectively, quantify the among-species variance in migration timing at the study start, and in the change across years, for each quantile. The intercept-slope correlation quantifies the association between the original migration timing and the change in timing across species.

Effects of focal ecological and life-history variables (Table 1) on changes in migration timing, and associations with standardised β_{LMA} , were then quantified by additionally including each focal variable, and the two-way interaction with year, as fixed effects in the LMMs. Here, the interaction terms capture differences in the direction and/or magnitude of change in migration timing across years at different factor levels or covariate values. Estimates from LMMs excluding phylogeny were first used to quantify changes in migration timings across the species in our dataset. Then, to explicitly test hypotheses regarding the effects of our focal variables, we fitted additional models with random phylogeny effects, thereby controlling for shared evolutionary history (i.e. phylogenetic dependencies) between species (hereafter PLMMs).

Effects of each focal variable were modelled separately, in different univariate models. Proximately, this was necessary because not all variables were quantifiable for all species (Supporting Information S2, sample sizes in Table 1). Further, standard predictions (Table 1) do not specify interactions between explanatory variables. Additional analyses also showed that few variables were strongly correlated with, or nested within, each other (Supporting Information S5). This implies that effects of one focal variable cannot generally be strongly confounded with effects of other variables estimated independently. Indeed, multivariate models fitted to the subset of species for which all covariates were quantified returned similar results and conclusions as the main univariate models (Supporting Information S6). One exception, that the plant-seed and vertebrate diet groups were nested within the short-distance migrant group, is further dissected in Section 4.

Previous work highlighted that apparent differences in direction or rate of change in migration timing across quantiles could conceivably arise as an artefact of changing abundance across years, because extreme quantiles are more sensitive to sampling variance (Miller-Rushing et al., 2008). To avoid such artefacts, we did not quantify changes in the first and last sighting dates of each species in each season, which are known to poorly represent full sighting distributions (Goodenough et al., 2015). We additionally re-ran analyses weighting quantile values by the number of sightings in each season-year (W_i). This weighting (W_i) was designed to simultaneously control for systematic changes in abundance through the study period, and to reduce the relative influence of quantile estimates for years with fewer total sightings, which may be less precise. However, model estimates and hence conclusions remained similar irrespective of whether weightings were included (Supporting Information S7).

For analyses testing for associations between β_{LMA} and changes in migration timing, abundance changes remain an inferential concern. Here, β_{LMA} represents changes in local abundance over time, and hence changes in the numbers of individuals from which phenological changes were estimated. To test for resulting biases that might alter interpretations of estimated effects, we quantified effect sizes arising from purely random sampling of observation dates given observed changes in local migratory abundance in each season across years (Supporting Information S8). In brief, all sightings were pooled across all years for each species in each season, generating overall species and season-specific distributions of observation dates. Values were then randomly drawn (with replacement), with sample sizes for each species in each season-year equalling the total number of sightings of the focal species in each season-year in the real dataset, thereby replicating observed changes in local abundance. Further LMMs were then fitted to the randomly sampled datasets, thereby revealing null associations between β_{LMA} and changes in migration timing that simply reflect data structure due to changing local abundance. This process was repeated for 20 iterations. Results were highly consistent across iterations, meaning that further iterations were not required. Mean estimates and 95% confidence intervals (1.96 × standard deviation of pooled mean estimates) were calculated across the 20 replicates, allowing assessment of whether associations between β_{LMA} and migration timing estimated from the real data exceeded that which could arise solely due to sampling in the absence of any true association (Supporting Information S8). For reference, a diagram summarising our overall workflow is provided in Supporting Information S9.

2.4 | Implementation

Bayesian LMMs and PLMMs were fitted in package MCMCglmm (Hadfield, 2010) in R version 3.6.1 (R Core Team, 2019). Phylogenetic data from BirdTree (Jetz et al., 2012, www.birdtree.org, Supporting Information S10) were fitted using the 'ginverse' argument (Supporting Information S11 and S12). Inspection of standard diagnostic plots confirmed that model residuals were approximately

normally distributed with little evidence of directional changes in variance through the study period, and no overall evidence of major non-linearities. To facilitate parameter estimation and interpretation, β_{LMA} was z-score standardised across species within each season (i.e. mean-centred and divided by the standard deviation). Accordingly, values of zero denote stable local migratory abundance, while positive and negative values indicate increases and decreases, respectively.

For models estimating effects of fixed multi-level factors (Table 1), posterior mean slope estimates quantifying level-specific changes in migration timing per year were initially extracted from models without phylogenetic controls (LMMs) and are presented with 95% credible intervals (95% CIs). Significant directional changes in migration timings for species groups on Fair Isle were inferred if 95% CIs from LMMs did not include zero. For models estimating effects of fixed continuous covariates (Table 1), significant effects were similarly inferred if 95% CIs for covariate by year interaction terms did not include zero. We then used PLMMs to ascertain whether observed effects were still supported after controlling for phylogeny (shown by asterisks on results figures). To maintain consistency between plots of fixed factors and covariates and aid interpretation, effects of focal covariates (Table 1) were visualised by extracting posterior mean slope predictions from LMMs at selected covariate values. Autumn is depicted above spring so that the interval between seasons reflects the net change in time spent in breeding regions across years. We did not explicitly test for differences in changes in migration phenology between spring and autumn because different species were included in each season. All presented posterior mean slope estimates and 95% CIs represent changes in days per year for each factor level or covariate value. To facilitate biological understanding, we additionally comment on predicted changes in migration timings across 10 years (decades). Full details of model fitting, estimate extraction and pMCMC-values are provided in Supporting Information S11 and S12. All phenology and covariate data and code underlying our analyses are available in Dale et al. (2024).

3 | RESULTS

3.1 | Among-species variation in changes in migration timings

The initial LMMs quantified the forms and magnitudes of changes in migration timings across all 72 focal species over the last six decades (Figures 2 and 3). Overall, the 5th to 50th quantiles of the distributions of spring and autumn sighting dates, representing the first halves of the seasonal sighting distributions, on average advanced slightly (i.e. birds migrated earlier, Figure 3a,b). For example, the 5th quantile sighting date advanced by 0.85 and 0.71 days/decade in spring and autumn, respectively, while the 50th quantile (i.e. median) sighting date advanced by 0.53 days/decade in spring

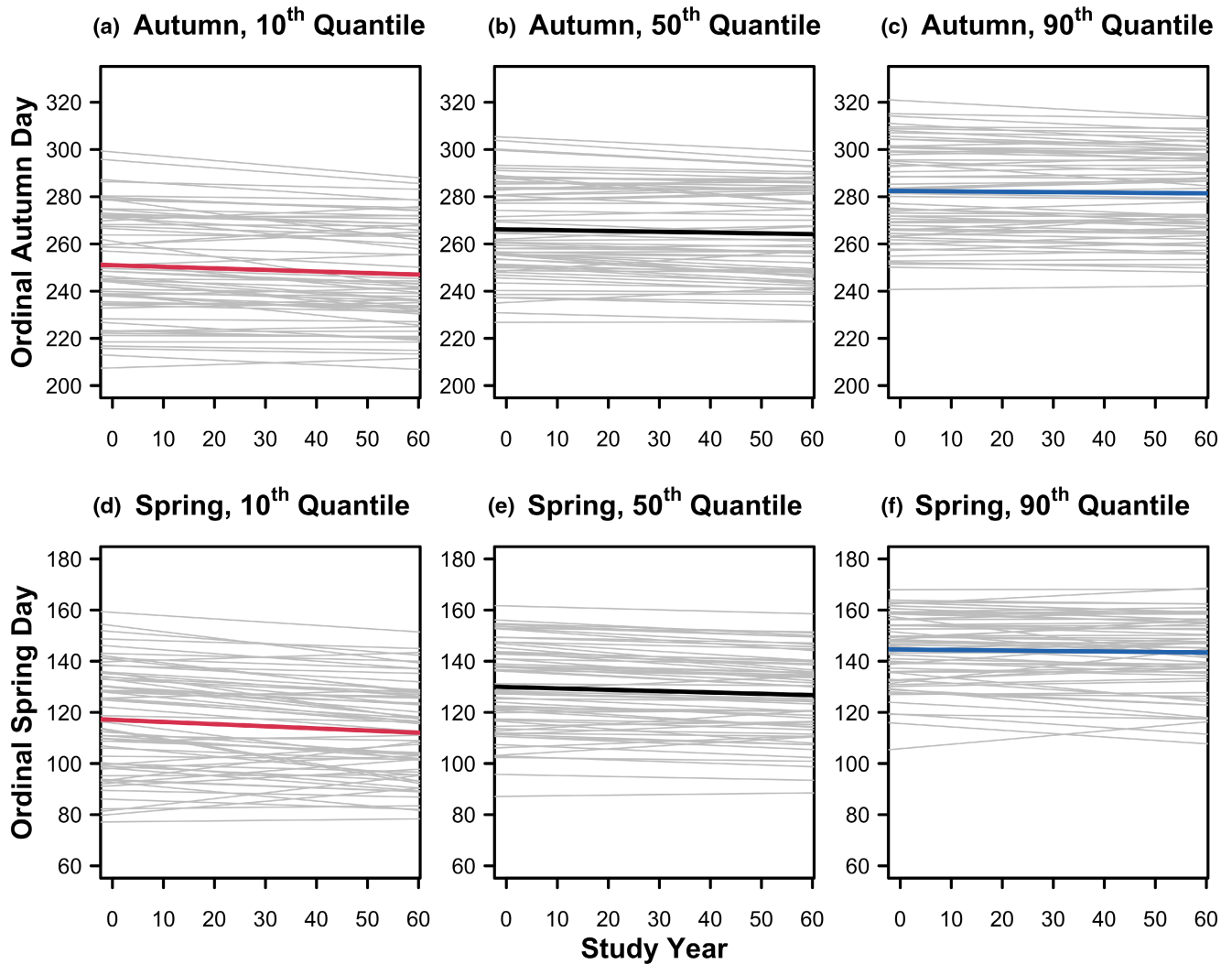


FIGURE 2 Illustrative examples of linear mixed models (LMMs) quantifying among-species variation in migration timings across the study period. Mean regression lines for the 10th (a, d red), 50th (b, e black) and 90th (c, f blue) quantiles of the sighting distributions on Fair Isle for 64 species in autumn (a–c) and spring (d–f) are shown. Thin grey lines represent regressions for individual species. Study years run 0–58 (representing 1960–2018). Ordinal days are counted from January 1st. Estimates are from LMMs without phylogeny.

and 0.35 days/decade in autumn. However, similar overall advances did not occur across the second halves of the seasonal sighting distributions, and effect sizes decreased towards zero across the 75th to 95th quantiles (Figure 3a,b). Together, these results imply that species' seasonal passage durations have extended over the last six decades.

These LMMs also demonstrated among-species variation in the intercept and slope of the regression of migration timing on year in all quantiles in both seasons (Figures 2 and 3; Supporting Information S11). There was greater variance in both intercept and slope in the earlier quantiles in both seasons (Figure 3a–f). Notably, the intercept-slope correlations were always negative, especially for early quantiles in spring (Figure 3g,h). Species that originally migrated through Fair Isle later within each season have, therefore, advanced their migration timing more than species that originally migrated earlier.

3.2 | Effects of ecological and life-history variables

Changes in migration timings did not differ markedly between long-distance and short-distance migrants for any quantiles in either spring or autumn (Figure 4). Long-distance migrants tended to show greater advances in the 5th to 25th quantiles of spring sighting dates than short-distance migrants (Figure 4b,d), but these differences were not strongly statistically supported. Advances for both distance groups were greater in these early quantiles than subsequently (Figure 4).

In contrast, changes in migration timings differed quite markedly between groups of species with different diet types (Figure 5). Specifically, spring sighting dates advanced for species with primarily invertebrate and plant-seed diets, but not for omnivores (Figure 5b,d,f). Meanwhile, the vertebrate diet group showed a notable delay (Figure 5h). Broadly similar patterns were evident in

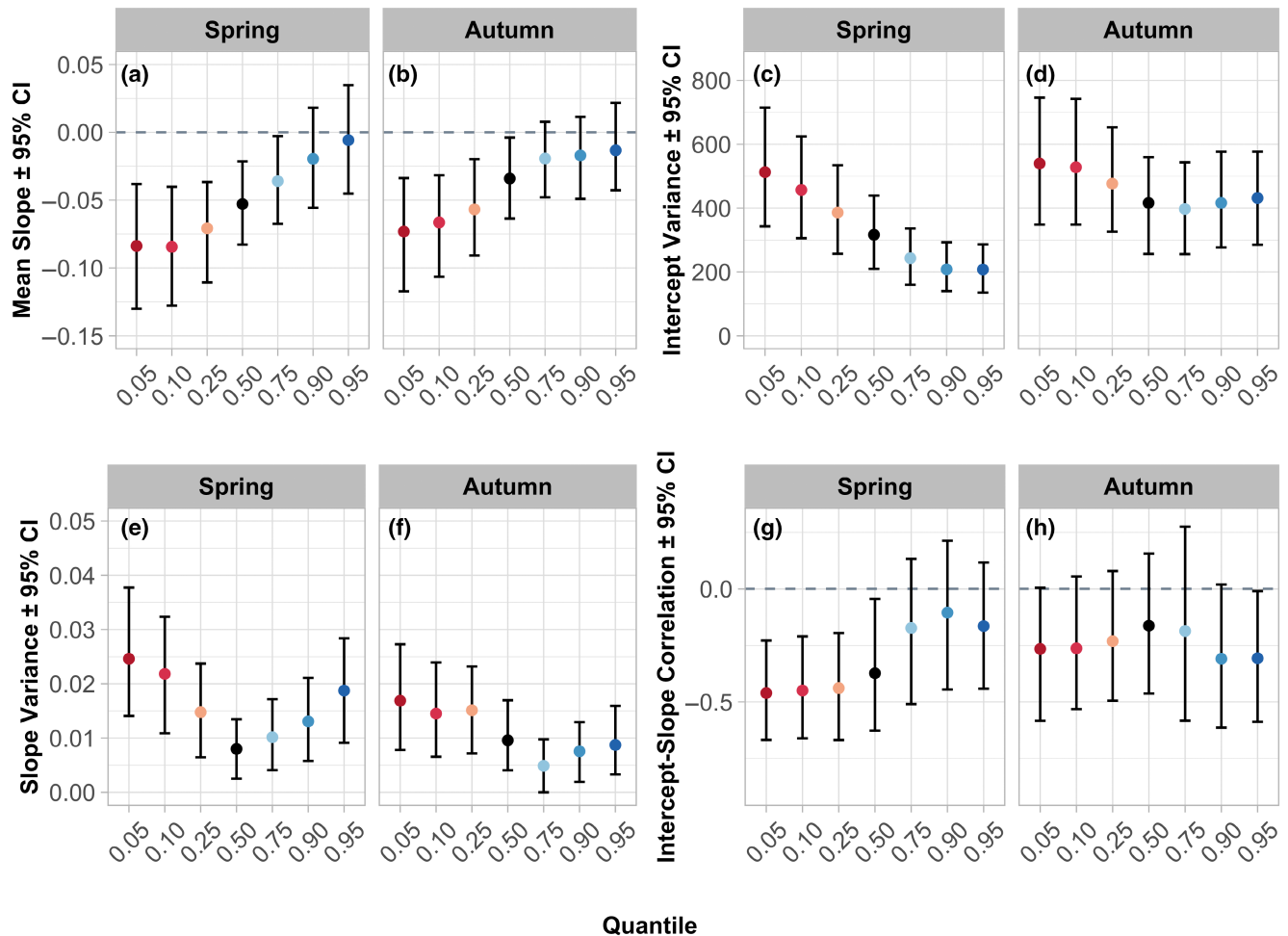


FIGURE 3 Posterior mean (a, b) slope (days/year), (c, d) intercept variance, (e, f) slope variance and (g, h) intercept-slope correlation for regressions of the 5th, 10th, 25th, 50th, 75th, 90th and 95th quantiles (coloured red to blue) of migrant sighting distributions on Fair Isle on year, in (a, c, e, g) spring and (b, d, f, h) autumn. 95% credible intervals are also shown. These slope and intercept estimates are from linear mixed models with fixed year effects only, without phylogeny, and together describe the among-species variation in trajectories of migration phenology across the study period. Note that the x-axis scale is not linear.

autumn, except that sighting dates for the vertebrate diet group tended to get earlier rather than later, and there was weaker overall evidence for among-group differences (Figure 5a,c,e,g). Across groups that showed changes in timings, predicted effect sizes were larger in spring. For example, posterior mean slope estimates for the 50th quantile ranged from -1.3 to $+1.1$ days/decade in spring and -0.8 to -0.2 days/decade in autumn (Figure 5). Estimates were also commonly larger for earlier quantiles, and decreased towards zero for later quantiles. This pattern is especially pronounced for the invertebrate diet group in both seasons (Figure 5c,d). Models controlling for phylogeny (PLMMs) further supported the effect of diet on changes in spring migration timing, showing differences between the vertebrate and omnivore diet groups for the 50th–95th quantiles.

Mean breeding habitat breadth values were 2.9 ± 1.2 SD (range 1–5) across species included in spring, and 2.8 ± 1.2 SD (range 1–7) in autumn. In spring, species with lower values (i.e. breeding habitat specialists) advanced their migration timing more than species

with higher values (i.e. breeding habitat generalists, Figure 6b,d). The PLMMs supported effects of habitat breadth on changes in migration timing for the 5th to 25th quantiles of spring sighting distributions (Figure 6b,d). However, no such effects were evident in autumn (Figure 6a,c). Here, advances in migration timing occurred across earlier quantiles, but not later quantiles, irrespective of habitat breadth.

Migration timings of single-brooded species have not, on average, changed for any quantile in either season (Figure 7a,b). In contrast, sighting dates for species capable of producing multiple offspring broods per year advanced across the 5th to 75th quantiles in both seasons, by 0.5–1.2 days/decade (Figure 7c,d). However, PLMMs only weakly supported the presence of a difference between the two groups for the 10th and 25th quantiles in spring (Figure 7d) and the 75th quantile in autumn.

Mean generation lengths were 5.4 ± 1.8 SD years (range 3.5–11.3) across species included in spring, and 5.5 ± 2.1 SD years (range 3.5–12.3) in autumn. In spring, species with shorter generation

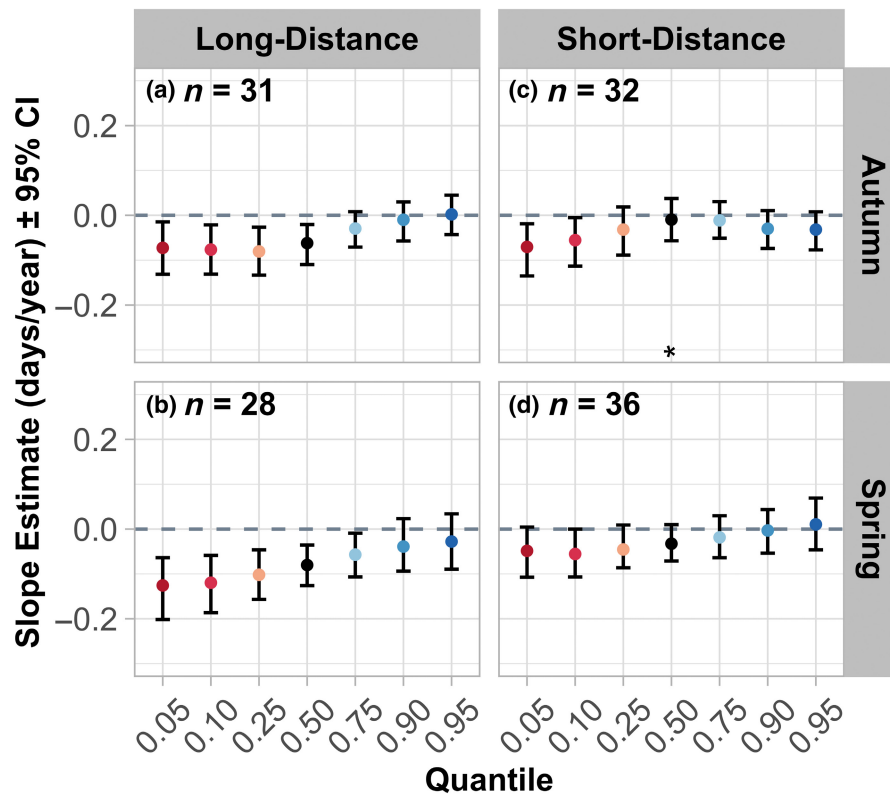


FIGURE 4 Posterior mean regression slopes (days/year, with 95% credible intervals) of the 5th, 10th, 25th, 50th, 75th, 90th and 95th quantiles (coloured red to blue) of sighting date distributions on year for (a, b) long-distance and (c, d) short-distance migrants in (a, c) autumn and (b, d) spring. Dashed lines emphasise zero (i.e. no change in timing). Numbers of species included in each group in each season are shown. Asterisks denote p -values ($*p < .05$; $**p < .01$; $***p < .001$) from phylogenetically controlled models (PLMMs) for the difference between each factor level and the leftmost level (here, long-distance migrants). An absence of asterisks correspondingly denotes no statistical support. Note that the x-axis scale is not linear.

lengths advanced their migration timings more than species with longer generation lengths (Figure 8b,d). The PLMMs supported effects of generation length on changes in migration timing for the 5th to 50th quantiles of spring sighting distributions (Figure 8f), but there was again no evidence of such effects in autumn (Figure 8a,c). Rather, autumn sighting dates got earlier across early quantiles, but not across later quantiles, largely independent of generation length (Figure 8a,c).

3.3 | Associations between changing phenology and changing local migratory abundance (β_{LMA})

Mean β_{LMA} , measured as the proportional change in local migratory abundance per year relative to the overall mean, was $0.00 \pm 0.02SD$ (range -0.05 to 0.04) in spring and $0.01 \pm 0.02SD$ (range -0.03 to 0.05) in autumn (Figure 9). The focal species, therefore, showed diverse local abundance trajectories, ranging from a 4.9% (95% CIs: 2.7%–7.1%) increase to a 4.6% (95% CIs: 2.6%–6.5%) decrease per year in spring or autumn. Overall, 95% CIs for 24 of 63 species in each season did not overlap zero,

indicating significant directional changes. Hence, given the observed among-species variation in changes in migration timings (Figure 3), there is considerable opportunity for associations between changes in timings and β_{LMA} .

In both seasons, changes in migration timing covaried with β_{LMA} , and the direction of effects varied across quantiles (Figure 10). Specifically, species with positive β_{LMA} (i.e. increasing local migratory abundance on Fair Isle) advanced their migration timing more than species with negative β_{LMA} (i.e. decreasing local migratory abundance) for the 5th to 25th quantiles in spring, but delayed more for the 90th and 95th quantiles (Figure 10b,d). Similar patterns were evident in autumn, but PLMMs only supported effects for the 90th and 95th quantiles (Figure 10g). Overall, this implies that passage time windows within each season have increased for species with increasing β_{LMA} , but tended to decrease for species with decreasing β_{LMA} .

However, although they differed from zero, estimated effect sizes for the interaction between year and β_{LMA} fell within the range of those generated with randomly resampled observation dates (Figure 10, full simulation results shown in Supporting Information S8). This implies that observed associations between changing migration timings and β_{LMA} arose because changing local

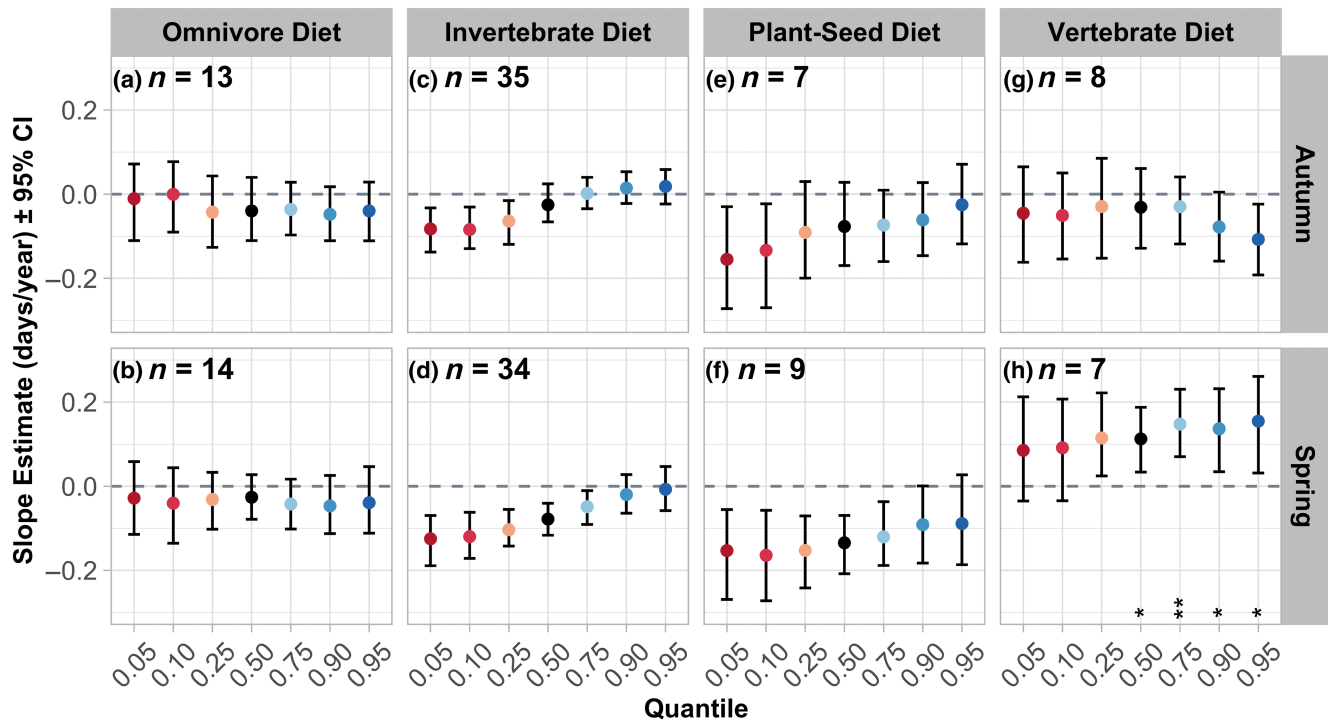


FIGURE 5 Posterior mean regression slopes (days/year, with 95% credible intervals) of the 5th, 10th, 25th, 50th, 75th, 90th and 95th quantiles (coloured red to blue) of sighting date distributions on year for species with (a, b) omnivore, (c, d) invertebrate, (e, f) plant-seed and (g, h) vertebrate diet types in (a, c, e, g) autumn and (b, d, f, h) spring. Asterisks denote p -values ($*p < .05$; $**p < .01$; $***p < .001$) from phylogenetically controlled models (PLMMs) for the difference between each factor level and the leftmost level (here, omnivores). An absence of asterisks correspondingly denotes no statistical support. Note that the x-axis scale is not linear.

abundances affected estimation of the quantile dates describing migration timings.

4 | DISCUSSION

Many species are showing directional long-term changes in migration timings, concurrent with rapid changes in large-scale seasonal climatic conditions (Knudsen et al., 2011). But, it is now clear that the direction and magnitude of such phenological changes varies substantially among species (Usui et al., 2017; van Buskirk et al., 2009). Identifying ecological, life-history and population parameters that explain, or covary with, observed variation in phenological changes is now required to facilitate the transition of phenology research from description to prediction (Knudsen et al., 2011; Salguero-Gómez et al., 2018). Our analyses of a 59-year multi-species dataset on bird migration timings support hypothesised effects of diet seasonality and habitat specialisation, and life-history traits such as generation length and annual reproductive capacity, on changes in migration phenology. However, they also revealed nuanced patterns of variation across quantiles within seasons, across seasons, and with trajectories of local seasonal migratory abundance. Overall, our results reveal how broad ecological and life-history categorisations can underlie complex variation in long-term phenological changes across a diverse set

of migrant bird species, manifested in the context of wider large-scale environmental changes.

4.1 | Effect of diet and habitat

Associations between species' breeding season ecology and changes in migration timing were evident, with greater advances in spring and autumn sighting dates of species with more seasonal diet types (invertebrate, plant-seed), and in spring sighting dates of species with narrower breeding habitat breadths. Meanwhile, omnivores, whose diets are presumably less seasonally constrained, did not advance in either season. These results broadly concur with expectations under the match-mismatch hypothesis (Table 1), which predicts that migrant species that specialise on highly seasonal diets (e.g. insects, plants, seeds) or habitats will be under stronger selection to track changes in seasonal conditions, since trophic synchrony will otherwise be rapidly lost (Both et al., 2010). Intensive breeding season research has proved that this conjecture holds for insectivorous migrant bird species, demonstrating a link between changing migration timing and breeding success (Both et al., 2006, 2010). Yet, multi-species studies and meta-analyses have so far found mixed support for associations between diet type or habitat breadth and changes in migration timings, including the predicted effects (Bitterlin & van Buskirk, 2014; La Sorte & Graham, 2021), no effect (Askeyev

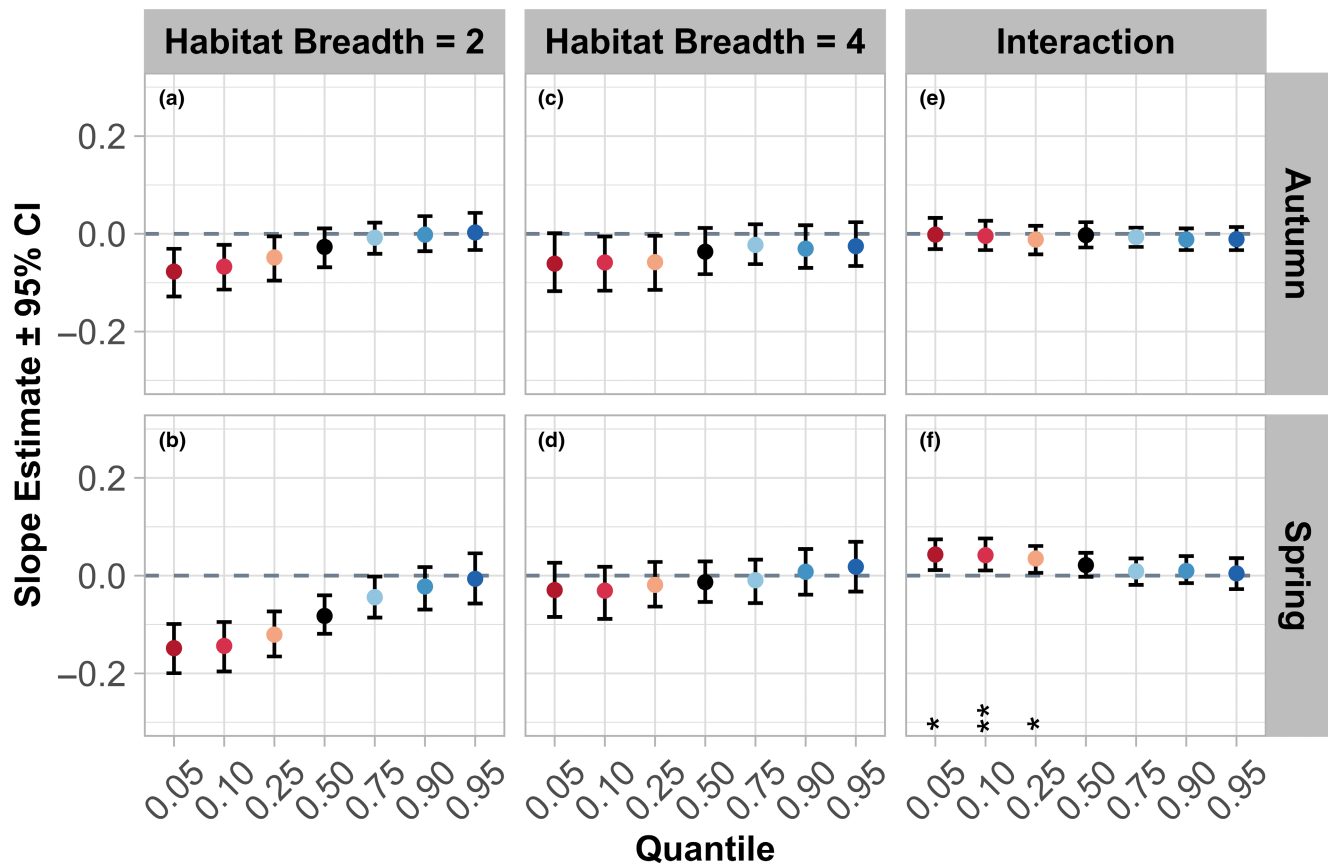


FIGURE 6 Posterior mean regression slopes (days/year, with 95% credible intervals) of the 5th, 10th, 25th, 50th, 75th, 90th and 95th quantiles (coloured red to blue) of sighting date distributions of migrants on year given relatively (a, b) low and (c, d) high habitat breadth values in (a, c) autumn and (b, d) spring. Breadth values of 2 and 4 are illustrative examples, representing approx. 25th and 75th quantiles of the covariate range in both seasons. Dashed lines emphasise zero (i.e. no change in timing). Interactions (e, f) represent the effect sizes estimated for the covariate (here, habitat breadth) by year interaction from phylogenetically controlled models (PLMMs) across quantiles and seasons. Asterisks denote associated p -values ($*p < .05$; $**p < .01$; $***p < .001$). An absence of asterisks correspondingly denotes no statistical support. Note that the x-axis scale is not linear.

et al., 2023; Usui et al., 2017) and even opposite effects (Romano et al., 2023; Végvári et al., 2010).

Both Végvári et al. (2010) and Romano et al. (2023) reported greater advances in spring migration timings of species with more generalist diet types, suggesting that greater diet flexibility could reduce constraints at passage sites. However, a recent meta-analysis of mean spring migration timings reported no effect of diet (Usui et al., 2017). Such contradictions could partly reflect different measures of diet and habitat breadth. Indeed, Usui et al. (2017) simply divided species into those with a predominantly invertebrate diet versus all others. In contrast, we defined four diet categories (Table 1). This makes conceptual sense because diet types other than invertebrate, such as plant-seed, are also highly seasonal and might consequently experience strong selection to adjust migration timing, while more generalist omnivores might not. Further, our analyses unexpectedly showed that spring migration timings for the defined vertebrate diet group (including scavengers) got notably later, by ~ 1.1 days/decade on average. Pooling all 'non-invertebrate' diet types into a single group would, therefore, obscure interesting and ecologically important opposing changes in migration timings.

Indeed, additional analyses demonstrate that we would have failed to reveal strong underlying associations between diet type and changing migration timing in both seasons if we had pooled diet groups in this way (Supporting Information S13). Future comparative studies on phenological changes should consequently strive for finer definitions and greater methodological consistency in quantifying species' ecological and life-history traits, as previously called for (Knudsen et al., 2007). Use of standardised trait databases, such as EltonTraits1.0 (Wilman et al., 2014), will facilitate such advances. Such future studies could then interrogate our interesting result that our 'vertebrate' diet group (i.e. raptors, piscivores and scavengers) have apparently delayed spring migration. Such analyses could include replication in other systems and stopover sites, and investigation of underlying ecological mechanisms.

4.2 | Effect of migration distance

Migration onset in long-distance migrants has been hypothesised to be relatively unresponsive to proximate conditions (Table 1). However,

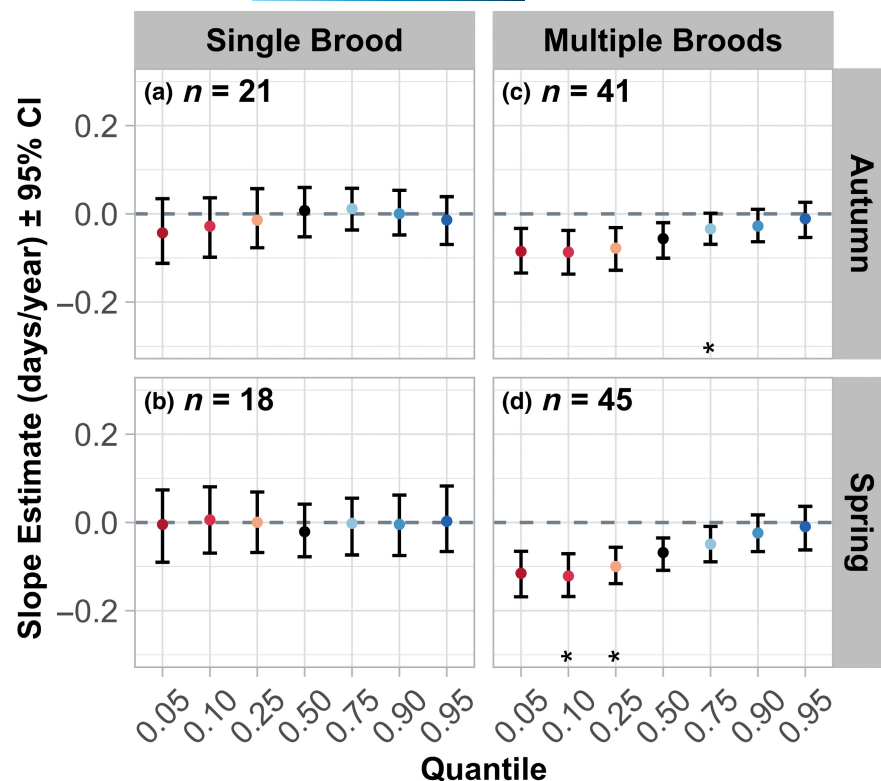


FIGURE 7 Posterior mean regression slopes (days/year, with 95% credible intervals) of the 5th, 10th, 25th, 50th, 75th, 90th and 95th quantiles (coloured red to blue) of sighting date distributions of migrants on year for (a, b) single-brooded and (c, d) multi-brooded species on Fair Isle in (a, c) autumn and (b, d) spring. Asterisks denote p -values ($*p < .05$; $**p < .01$; $***p < .001$) from phylogenetically controlled models (PLMMs) for the difference between each factor level and the leftmost level (here, single-brooded). An absence of asterisks correspondingly denotes no statistical support. Note that the x-axis scale is not linear.

our study showed no major difference in the change in migration timing between defined long-distance and short-distance migrants in either season; both groups showed some advance in early but not later quantiles. This further refutes the view that long-distance migrants are unable to adjust their migration timing (Gwinner, 1996; Jonzén et al., 2006; Végvári et al., 2010), and adds to already conflicting literature regarding relationships between migration distance and changing timing (reviewed by Knudsen et al., 2011). Several studies found greater advances in spring migration timing in short-distance versus long-distance migrants (Bitterlin & van Buskirk, 2014; Horton et al., 2019; Miller-Rushing et al., 2008; Romano et al., 2023; Usui et al., 2017), and greater delays in autumn (Jenni & Kéry, 2003; van Buskirk et al., 2009). However, some studies found no difference between the two groups (Hüppop & Hüppop, 2003; Zalakevicius et al., 2006), or even showed greater advances in long-distance migrants (Jonzén et al., 2006; Lawrence et al., 2022).

This lack of consensus could stem from multiple sources, but our study highlights potential effects of latitude and confounding nested variables such as diet type. First, since spring onset is advancing more rapidly at higher latitudes (Parmesan, 2007), populations migrating to northerly destinations, such as those moving through Fair Isle, might be under stronger selection to advance their migration timing. Indeed, other evidence of advancing timing in long-distance migrants has also come from high latitude Scandinavian populations (Hüppop & Hüppop, 2003; Jonzén et al., 2006). Such advances may be facilitated by increasing temperatures in Europe, improving migration conditions and allowing long-distance migrants to increase their rate of progress (Gordo, 2007; Marra et al., 2005). Data from multiple rather than single stopover sites, or continent-wide data

such as those increasingly available from large citizen science efforts (e.g. La Sorte & Graham, 2021; Robertson et al., 2024), will be required to quantify such effects.

Second, in our dataset, the plant-seed and vertebrate diet groups were nested within the short-distance migrant group (Supporting Information S5). Such nesting, combined with detected differences in changes in migration timing between different diet groups, implies that simply quantifying migration distance in a coarse dichotomous way risks confounding (or obscuring) effects of distance with effects of nested variables. In fact, with our dataset, changes in migration timing still did not differ between distance groups when models were re-run after excluding the nested plant-seed and vertebrate diet groups (thereby testing for distance effects solely within the invertebrate and omnivore groups). However, more detailed population-specific distance data are ideally required to fully test hypotheses regarding links between migration distance and changing timing without coarse categorisations, but such data are not yet generally available (but see Koleček et al., 2020).

4.3 | Effect of life-history

While species with shorter generation lengths, and multi-brooded species, have advanced their migration timing through Fair Isle in early spring quantiles, there was less evidence of such changes for species with longer generation lengths and single-brooded species. Effects of generation length on phenological changes have been postulated and tested for traits other than migration timing (Table 1). For example, Thackeray et al.'s (2010) meta-analysis reports

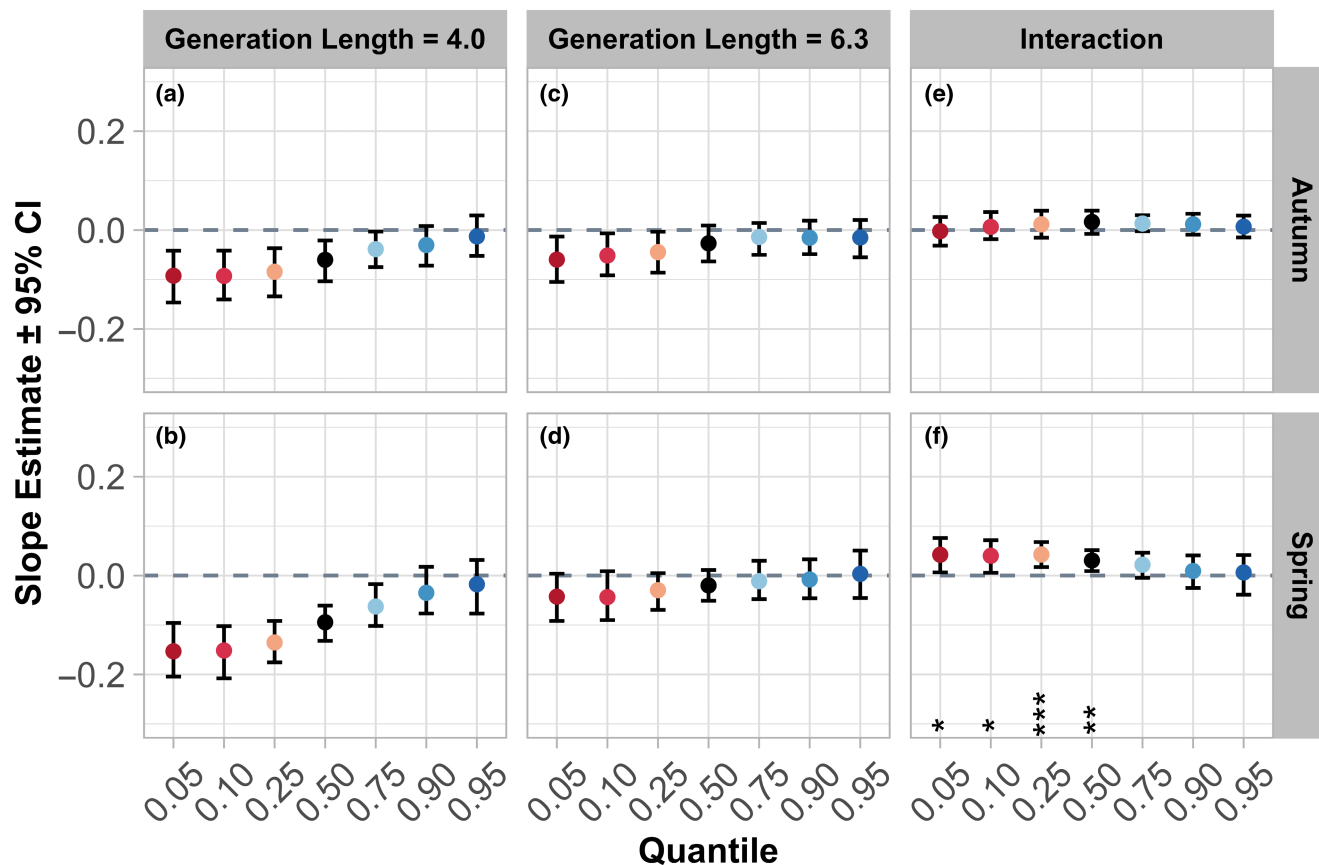


FIGURE 8 Posterior mean regression slopes (days/year, with 95% credible intervals) of the 5th, 10th, 25th, 50th, 75th, 90th and 95th quantiles (coloured red to blue) of sighting date distributions of migrants on year given (a, b) short and (c, d) longer generation lengths in (a, c) autumn and (b, d) spring. Generation length values of 4.0 and 6.3 are illustrative examples, representing approx. 25th and 75th quantiles of the covariate range in both seasons. Dashed lines emphasise zero (i.e. no change in timing). Interactions (e, f) represent the effect sizes estimated for the covariate (here, generation length) by year interaction from phylogenetically controlled models (PLMMs) across quantiles and seasons. Asterisks denote associated p -values (* $p < .05$; ** $p < .01$; *** $p < .001$). An absence of asterisks correspondingly denotes no statistical support. Note that the x-axis scale is not linear.

evidence of greater changes in phenology of diverse seasonal biological events for species with shorter generation lengths. However, such effects have rarely been quantified for migration timing, except for effects of population turnover in single species studies (e.g. Gill et al., 2013). Our observed effects of brood number on spring migration timing are broadly consistent with previous multi-species analyses (e.g. Møller et al., 2008; Végvári et al., 2010), and with the hypothesis that multi-brooded species might advance migration in spring to extend their breeding season and increase reproductive output (Table 1). This in turn implies that return autumn migrations might also be delayed (Jenni & Kéry, 2003). However, few previous studies on brood number have examined both seasons, or hence tested the dual predictions of advanced spring and delayed autumn migrations in multi-brood species, allowing extended reproduction (but see Bitterlin & van Buskirk, 2014; van Buskirk et al., 2009). Our analyses showed no evidence that multi-brooded species are now migrating later in autumn. Instead, in common with most of our analyses, the directions of changes in spring and autumn migration timings are similar. This is perhaps unsurprising given evidence that Scandinavian breeding populations are contracting their breeding

periods (Hällfors et al., 2020). Indeed, predicted extensions of late autumn growing periods in these systems (Gallinat et al., 2015) do not necessarily equate to protracted suitable breeding conditions for migrant populations.

4.4 | Associations between changing phenology and changing local migratory abundance

Our analyses revealed strong apparent associations between changing migration timings and changing local migratory abundances (β_{LMA}); species with stable or increasing local abundances are on average advancing their migration timings to much greater degrees. These patterns broadly concur with previous evidence that species that are changing their migration timing are increasing in abundance, whilst species that are not changing their timing are declining (Møller et al., 2008; Salido et al., 2012). Such observations are in turn broadly in line with wider expectations that adjusting migration timing will be adaptive, implying direct links between changing timing and population stability or growth (Both et al., 2006; Møller

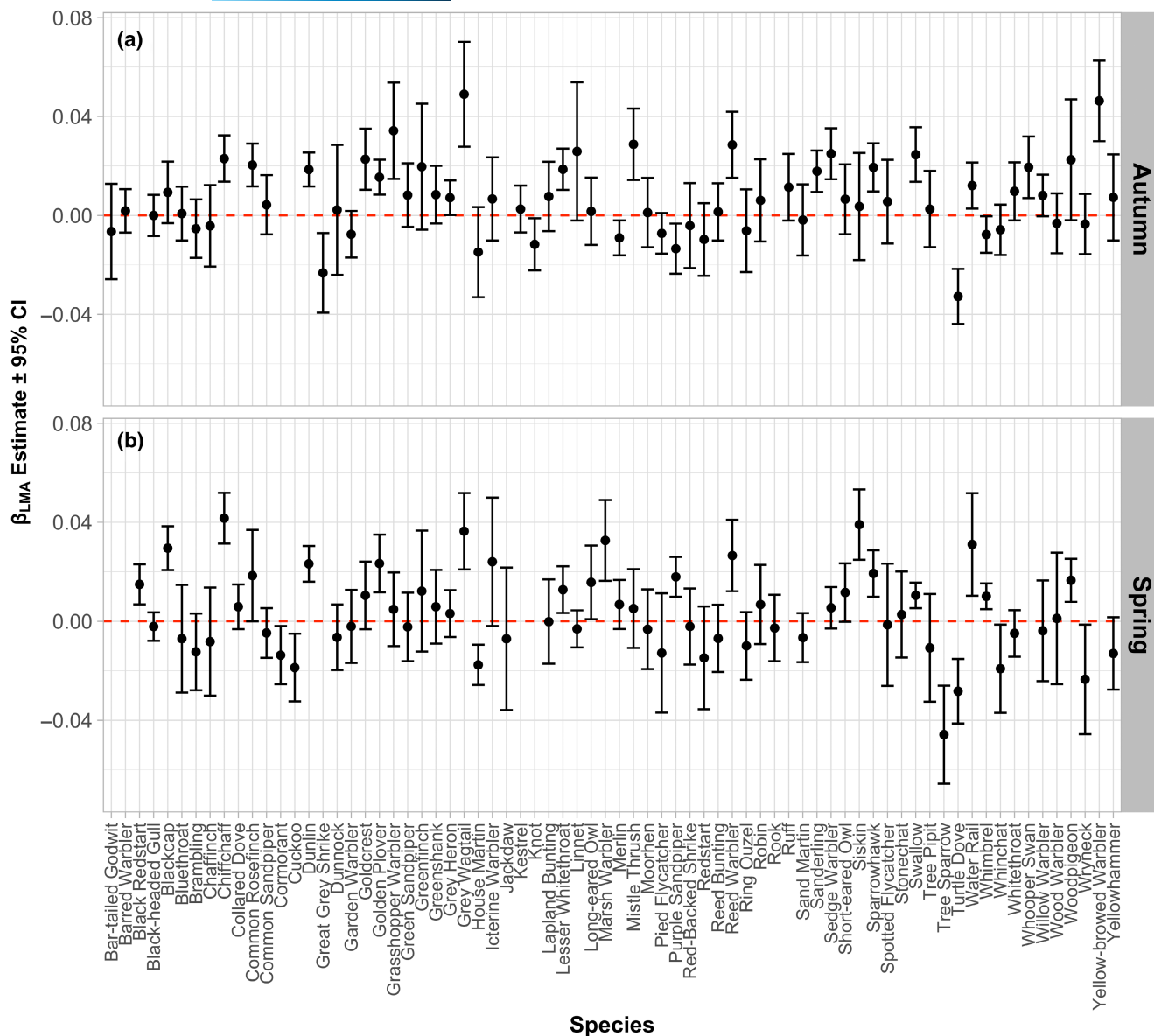


FIGURE 9 Estimated regression slopes for changes in (a) autumn and (b) spring standardised local migratory abundance (β_{LMA}) (sightings/year, with 95% confidence intervals) on year. Red dashed lines emphasise zero (i.e. no change in β_{LMA} across years). Positive and negative values denote increasing and decreasing β_{LMA} , respectively. Species are ordered alphabetically (left–right) according to common English names. Not all species are included in both seasons.

et al., 2008). However, the hypothesis that changing migration timing prevents population decline is very difficult to explicitly test, especially using large-scale observational data (such as is available for migratory bird assemblages).

First, standardised long-term data on breeding population sizes of multiple migrant species are rarely available. This challenge certainly applies in our case; exact breeding locations of populations migrating through Fair Isle are unknown, and presumably include remote geographical areas where breeding birds are not systematically surveyed. Our measure β_{LMA} will capture changing population sizes occurring at large spatial scales to some degree. Indeed, species with strongly negative β_{LMA} values in spring (≤ -0.02 , Figure 9) include UK Red Listed species that are known to have undergone substantial

large-scale population declines over recent decades (e.g. Cuckoo [*C. canorus*], Turtle Dove [*Streptopelia turtur*], Tree Sparrow [*P. montanus*] and Whinchat [*Saxicola rubetra*], Supporting Information S3). Further, species with strongly positive spring β_{LMA} values (≥ 0.02 , Figure 9) include species that have shown substantial population increases in UK and/or north-western Europe more widely (e.g. Blackcap [*Sylvia atricapilla*], Chiffchaff [*Phylloscopus collybita*], Reed Warbler [*Acrocephalus scirpaceus*], Siskin [*Carduelis spinus*]). However, β_{LMA} will of course also capture changing non-breeding and breeding distributions and migration routes of focal populations, which may independently affect migration timings (Anderson et al., 2023). β_{LMA} could also be affected by changing local stopover durations, although available data show no evidence of major long-term changes

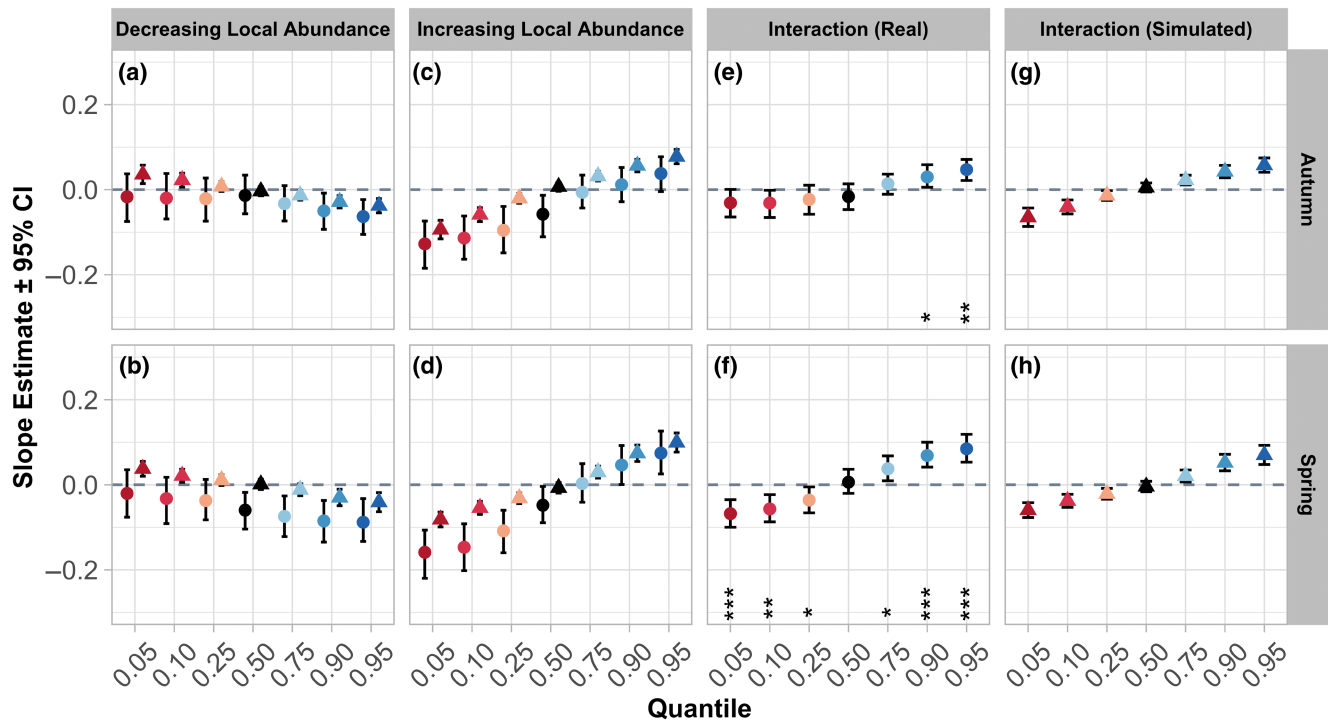


FIGURE 10 Posterior mean regression slopes (days/year, with 95% credible intervals) of the 5th, 10th, 25th, 50th, 75th, 90th and 95th quantiles (coloured red to blue) of sighting date distributions of migrants on year given illustrative values of β_{LMA} of (a, b) mean -1 standard deviation (negative, representing decreasing LMA), (c, d) mean $+1$ standard deviation (positive, representing increasing LMA), in (a, c) autumn and (b, d) spring. Circular points represent estimates from the real Fair Isle dataset, and triangular points represent estimates from randomly resampled dataset. Posterior mean effect sizes (with 95% credible intervals) for the β_{LMA} by year interactions across quantiles estimated from (e, f) phylogenetically controlled models (PLMMs) using the real Fair Isle dataset, and (g, h) from the randomly resampled dataset, in (e, g) autumn and (f, h) spring. Dashed lines emphasise zero (i.e. no change in timing). Asterisks denote associated p -values (* $p < .05$; ** $p < .01$; *** $p < .001$). An absence of asterisks correspondingly denotes no statistical support. Note that the x-axis scale is not linear.

in stopover durations on Fair Isle (Miles et al., 2017). Our substantial estimated associations between β_{LMA} and changing migration timings are also notable given the error implicit in β_{LMA} estimates, which will likely cause statistical underestimation of any true underlying effect sizes (i.e. statistical attenuation).

Second, irrespective of all challenges inherent in measuring population trends, our analyses reveal further general challenges of inferring any association between changing phenology and changing abundance that arise because changes in local abundance can directly affect the estimation of changes in phenology. This issue arises because, given a stationary distribution, estimation of outer quantile points depends on sample size. This sampling effect potentially biases estimates of any true biological association between changing phenology and changing abundance. Indeed, our simulations show that our estimated effect sizes did not exceed those that could be generated through random sampling from a stationary phenology distribution with changing abundances alone. Our results, therefore, reinforce that future analysts will need to carefully dissect overall relationships between changing phenology and any measure of changing abundance (e.g. Miller-Rushing et al., 2008), which can reflect combinations of numerical sampling and important biological effects. Further verification will require explicit tests of links between absence of change in migration timing and local abundance

declines for subsets of species where independent population census data are available (Iler et al., 2021; Newson et al., 2016). Such advances are required before any general conclusions on adaptive phenological changes can be drawn.

4.5 | Overall changes in migration timing and implications

Overall, the estimated magnitudes of changes in migration timing through Fair were often greater in spring than autumn, involving several quantiles and traits (e.g. most notably the vertebrate diet type). Such seasonal differences might be expected if migration timing is under stronger selection in spring, due to the need to synchronise reproduction with peak resource availability, or due to intraspecific competition for breeding territories and mates (Newton, 2008; e.g. Gordo et al., 2013; Velmala et al., 2015).

Changes in migration timing varied substantially among quantiles in both seasons, highlighting the value of multi-metric analyses for quantifying phenological responses (Knudsen et al., 2007; Miles et al., 2017). Predicted advances were typically greatest for early quantiles, and decreased towards zero across later quantiles. This ‘fan-shaped’ pattern signifies an overall increased duration of

passage through Fair Isle for many species during the 59-year study period. It concurs with previous analyses of 13 long-distance migrant species through Fair Isle (Miles et al., 2017), and with other studies on species breeding in the Northern Hemisphere (Bitterlin & van Buskirk, 2014; Lehikoinen et al., 2019; van Buskirk et al., 2009). Such patterns could reflect multiple processes, including within-season variation in selection, constraints on migration dates and/or changing compositions of migrants from different sub-populations with distinct breeding and/or non-breeding locations.

The strong negative intercept-slope correlations highlight a further general pattern, whereby species that originally migrated through Fair Isle relatively late in each season have advanced their migration timing more than species that originally migrated earlier. Such intercept-slope correlations are rarely reported in studies on migration phenology, but could reveal interesting forms of changing temporal assemblage structure with respect to key ecological variables (but see Stemkovski et al., 2022). For example, our analyses show that species with predominantly invertebrate diets were originally late spring migrants through Fair Isle and have advanced their migration timing, whilst species with vertebrate diets were originally early spring migrants and have got later (Supporting Information S11). Such opposing changes in timing will alter the degree of temporal overlap of different groups of migratory species, here presumably increasing spring overlaps between species with predominantly invertebrate versus vertebrate diet types. Our current analyses, therefore, highlight how species-specific variation in changing migration timings could alter key properties of the overall composite migrant assemblage, with dynamic knock-on consequences for species interactions and patterns of co-occurrence at non-breeding, passage and breeding grounds (Inouye, 2022).

AUTHOR CONTRIBUTIONS

Vicki R. Dale: Conceptualization; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Mark Bolton:** Conceptualization; supervision; writing – review and editing. **Maria Dornelas:** Conceptualization; supervision; writing – review and editing. **Anne E. Magurran:** Conceptualization; supervision; writing – review and editing. **Roy Dennis:** Data curation; methodology; resources. **Roger Broad:** Data curation; methodology; resources. **Nick J. Riddiford:** Data curation; methodology; resources. **Paul V. Harvey:** Data curation; methodology; resources. **Roger Riddington:** Data curation; methodology; resources. **Deryk N. Shaw:** Data curation; methodology; resources. **David Parnaby:** Data curation; methodology; resources. **Jane M. Reid:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; writing – review and editing.

ACKNOWLEDGEMENTS

We thank everyone who contributed to long-term data collection, in particular the late Peter Davis and Iain Robertson and numerous highly dedicated assistant wardens. We thank all Fair Isle residents for their long-term support, and W.T.S. Miles and I.J. Andrews for database construction and management. V.R.D was funded by a

UK NERC SUPER DTP PhD studentship supported by University of Aberdeen and Fair Isle Bird Observatory Trust.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data and R code that support the findings of this study are openly available in the Dryad Data Repository at <https://doi.org/10.5061/dryad.31zcrjdth> (Dale et al., 2024).

ORCID

Vicki R. Dale  <https://orcid.org/0000-0003-4155-909X>

Mark Bolton  <https://orcid.org/0000-0001-5605-687X>

Maria Dornelas  <https://orcid.org/0000-0003-2077-7055>

Anne E. Magurran  <https://orcid.org/0000-0002-0036-2795>

Jane M. Reid  <https://orcid.org/0000-0002-5007-7343>

REFERENCES

- Ahola, M. P., Laaksonen, T., Eeva, T., & Lehikoinen, E. (2007). Climate change can alter competitive relationships between resident and migratory birds. *Journal of Animal Ecology*, 76(6), 1045–1052. <https://doi.org/10.1111/j.1365-2656.2007.01294.x>
- Anderson, C. M., Fahrig, L., Rausch, J., Martin, J.-L., Daufresne, T., & Smith, P. A. (2023). Climate-related range shifts in Arctic-breeding shorebirds. *Ecology and Evolution*, 13, e9797. <https://doi.org/10.1002/ece3.9797>
- Askeyev, O., Askeyev, A., Askeyev, I., & Sparks, T. (2023). Significantly earlier spring migration in most bird species at the eastern limit of Europe. *Animals*, 13(19), 1–15. <https://doi.org/10.3390/ani13193031>
- Barrett, R. T. (2002). The phenology of spring bird migration to north Norway. *Bird Study*, 49(3), 270–277. <https://doi.org/10.1080/00063650209461275>
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4), 365–377. <https://doi.org/10.1111/j.1461-0248.2011.01736.x>
- BirdLife International. (2020). *IUCN Red List for birds*. Downloaded from: <http://www.birdlife.org> on September 1, 2020
- Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., van Moorter, B., & Mysterud, A. (2012). A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? *American Naturalist*, 180(4), 407–424. <https://doi.org/10.1086/667590>
- Bitterlin, L. R., & van Buskirk, J. (2014). Ecological and life history correlates of changes in avian migration timing in response to climate change. *Climate Research*, 61(2), 109–121. <https://doi.org/10.3354/cr01238>
- Both, C., Bouwhuis, S., Lessells, C. M., & Visser, M. E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, 441(1), 81–83. <https://doi.org/10.1038/nature04539>
- Both, C., van Turnhout, C. A. M., Bijlsma, R. G., Siepel, H., van Strien, A. J., & Foppen, R. P. B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B: Biological Sciences*, 277(1685), 1259–1266. <https://doi.org/10.1098/rspb.2009.1525>
- Burgess, M. D., Smith, K. W., Evans, K. L., Leech, D., Pearce-Higgins, J. W., Branston, C. J., Briggs, K., Clark, J. R., du Feu, C. R., Lewthwaite, K., Nager, R. G., Sheldon, B. C., Smith, J. A., Whytock, R. C., Willis,

- S. G., & Phillimore, A. B. (2018). Tritrophic phenological mismatch in space and time. *Nature Ecology & Evolution*, 2(6), 970–975. <https://doi.org/10.1038/s41559-018-0543-1>
- Cadahía, L., Labra, A., Knudsen, E., Nilsson, A., Lampe, H. M., Slagsvold, T., & Stenseth, N. C. (2017). Advancement of spring arrival in a long-term study of a passerine bird: Sex, age and environmental effects. *Oecologia*, 184(4), 917–929. <https://doi.org/10.1007/s00442-017-3922-4>
- Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045), 1024–1026. <https://doi.org/10.1126/science.1206432>
- Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B., & Yang, L. H. (2019). The mechanisms of phenology: The patterns and processes of phenological shifts. *Ecological Monographs*, 89(1), 1–22. <https://doi.org/10.1002/ecm.1337>
- Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, 8(3), 224–228. <https://doi.org/10.1038/s41558-018-0067-3>
- Dale, V. R., Bolton, M., Dornelas, M., Magurran, A., Dennis, R., Broad, R., Riddiford, N. J., Harvey, P. V., Riddington, R., Shaw, D. N., Parnaby, D., & Reid, J. M. (2024). *Data from: Among-species variation in six decades of changing migration timings explained through ecology, life-history and abundance [Dataset]*. Dryad Data Repository. <https://doi.org/10.5061/dryad.31zcrjdtth>
- Dymond, J. N. (1991). *The birds of Fair Isle*. Ritchie.
- Gallinat, A. S., Primack, R. B., & Wagner, D. L. (2015). Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, 30(3), 169–176. <https://doi.org/10.1016/j.tree.2015.01.004>
- Gill, J. A., Alves, J. A., Sutherland, W. J., Appleton, G. F., Potts, P. M., & Gunnarsson, T. G. (2013). Why is timing of bird migration advancing when individuals are not? *Proceedings of the Royal Society B: Biological Sciences*, 281(1774), 20132161. <https://doi.org/10.1098/rspb.2013.2161>
- Gillings, S., Balmer, D. E., & Fuller, R. J. (2015). Directionality of recent bird distribution shifts and climate change in Great Britain. *Global Change Biology*, 21(6), 2155–2168. <https://doi.org/10.1111/gcb.12823>
- Goodenough, A. E., Fairhurst, S. M., Morrison, J. B., Cade, M., Morgan, P. J., & Wood, M. J. (2015). Quantifying the robustness of first arrival dates as a measure of avian migratory phenology. *Ibis*, 157, 384–390. <https://doi.org/10.1111/ibi.12227>
- Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, 35(1–2), 37–58. <https://doi.org/10.3354/cr00713>
- Gordo, O., Tryjanowski, P., Kosicki, J. Z., & Fulin, M. (2013). Complex phenological changes and their consequences in the breeding success of a migratory bird, the white stork *Ciconia ciconia*. *Journal of Animal Ecology*, 82(5), 1072–1086. <https://doi.org/10.1111/1365-2656.12084>
- Green, S. J., Brookson, C. B., Hardy, N. A., & Crowder, L. B. (2022). Trait-based approaches to global change ecology: Moving from description to prediction. *Proceedings of the Royal Society B: Biological Sciences*, 289(1971), 20220071. <https://doi.org/10.1098/rspb.2022.0071>
- Gwinner, E. (1996). Circadian and circannual programmes in avian migration. *Journal of Experimental Biology*, 199(1), 39–48.
- Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22. <https://www.jstatsoft.org/v33/i02/>
- Hällfors, M. H., Antaõ, L. H., Itter, M., Lehikoinen, A., Lindholm, T., Roslin, T., & Saastamoinen, M. (2020). Shifts in timing and duration of breeding for 73 boreal bird species over four decades. *Proceedings of the National Academy of Sciences of the United States of America*, 117(31), 18557–18565. <https://doi.org/10.1073/pnas.1913579117>
- Horton, K. G., van Doren, B. M., la Sorte, F. A., Cohen, E. B., Clipp, H. L., Buler, J. J., Fink, D., Kelly, J. F., & Farnsworth, A. (2019). Holding steady: Little change in intensity or timing of bird migration over the Gulf of Mexico. *Global Change Biology*, 25(3), 1106–1118. <https://doi.org/10.1111/gcb.14540>
- Hüppop, O., & Hüppop, K. (2003). North Atlantic oscillation and timing of spring migration in birds. *Proceedings of the Royal Society B: Biological Sciences*, 270(1512), 233–240. <https://doi.org/10.1098/rspb.2002.2236>
- Hurlbert, A. H., & Liang, Z. (2012). Spatiotemporal variation in avian migration phenology: Citizen science reveals effects of climate change. *PLoS One*, 7(2), e31662. <https://doi.org/10.1371/journal.pone.0031662>
- Iler, A. M., Caradonna, P. J., Forrest, J. R. K., & Post, E. (2021). Demographic consequences of phenological shifts in response to climate change. *Annual Review of Ecology, Evolution, and Systematics*, 52, 221–245. <https://doi.org/10.1146/annurev-ecolsys-011921-032939>
- Inouye, D. W. (2022). Climate change and phenology. *Wiley Interdisciplinary Reviews: Climate Change*, 13(3), 1–17. <https://doi.org/10.1002/wcc.764>
- IUCN Habitats Classification Scheme. (2012). Version 3.1 (pp. 1–14).
- Jenni, L., & Kéry, M. (2003). Timing of autumn bird migration under climate change: Advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B: Biological Sciences*, 270(1523), 1467–1471. <https://doi.org/10.1098/rspb.2003.2394>
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491(7424), 444–448. <https://doi.org/10.1038/nature11631>
- Jones, T., & Cresswell, W. (2010). The phenology mismatch hypothesis: Are declines of migrant birds linked to uneven global climate change? *Journal of Animal Ecology*, 79(1), 98–108. <https://doi.org/10.1111/j.1365-2656.2009.01610.x>
- Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J. O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R., & Stenseth, N. C. (2006). Rapid advance of spring arrival dates in long-distance migratory birds. *Science*, 312(5782), 1959–1961. <https://doi.org/10.1126/science.1126119>
- Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P. P., Møller, A. P., Nilsson, A. L. K., Péron, G., ... Stenseth, N. C. (2011). Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, 86(4), 928–946. <https://doi.org/10.1111/j.1469-185X.2011.00179.x>
- Knudsen, E., Lindén, A., Ergon, T., Jonzén, N., Vik, J. O., Knape, J., Røer, J. E., & Stenseth, N. C. (2007). Characterizing bird migration phenology using data from standardized monitoring at bird observatories. *Climate Research*, 35(1–2), 59–77. <https://doi.org/10.3354/cr00714>
- Koleček, J., Adamík, P., & Reif, J. (2020). Shifts in migration phenology under climate change: Temperature vs. abundance effects in birds. *Climatic Change*, 159(2), 177–194. <https://doi.org/10.1007/s10584-020-02668-8>
- Kovach, R. P., Ellison, S. C., Pyare, S., & Tallmon, D. A. (2015). Temporal patterns in adult salmon migration timing across southeast Alaska. *Global Change Biology*, 21(5), 1821–1833. <https://doi.org/10.1111/gcb.12829>
- La Sorte, F. A., & Graham, C. H. (2021). Phenological synchronization of seasonal bird migration with vegetation greenness across dietary guilds. *Journal of Animal Ecology*, 90, 1–13. <https://doi.org/10.1111/1365-2656.13345>
- Lawrence, K. B., Barlow, C. R., Bensusan, K., Perez, C., & Willis, S. G. (2022). Phenological trends in the pre- and post-breeding migration of long-distance migratory birds. *Global Change Biology*, 28(2), 375–389. <https://doi.org/10.1111/gcb.15916>

- Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T. L., Dunn, E. H., Gregory, G., Karlsson, L., Kristiansen, V., Mackenzie, S., Newman, S., Røer, J. E., Sharpe, C., Sokolov, L. V., Steinholtz, Å., Stervander, M., Tirri, I. S., & Tjørnløv, R. S. (2019). Phenology of the avian spring migratory passage in Europe and North America: Asymmetric advancement in time and increase in duration. *Ecological Indicators*, 101, 985–991. <https://doi.org/10.1016/j.ecoli.2019.01.083>
- Marra, P. P., Francis, C. M., Mulvihill, R. S., & Moore, F. R. (2005). The influence of climate on the timing and rate of spring bird migration. *Oecologia*, 142(2), 307–315. <https://doi.org/10.1007/s00442-004-1725-x>
- Martay, B., Brewer, M. J., Elston, D. A., Bell, J. R., Harrington, R., Brereton, T. M., Barlow, K. E., Botham, M. S., & Pearce-Higgins, J. W. (2017). Impacts of climate change on national biodiversity population trends. *Ecography*, 40(10), 1139–1151. <https://doi.org/10.1111/ecog.02411>
- Massicotte, P., & South, A. (2023). *rnaturalearth: World map data from natural earth*. R package version 1.0.1. <https://CRAN.R-project.org/package=rnaturalearth>
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mäge, F., ... Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12(10), 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>
- Miles, W. T. S., Bolton, M., Davis, P., Dennis, R., Broad, R., Robertson, I., Riddiford, N. J., Harvey, P. V., Riddington, R., Shaw, D. N., Parnaby, D., & Reid, J. M. (2017). Quantifying full phenological event distributions reveals simultaneous advances, temporal stability and delays in spring and autumn migration timing in long-distance migratory birds. *Global Change Biology*, 23(4), 1400–1414. <https://doi.org/10.1111/gcb.13486>
- Miller-Rushing, A. J., Lloyd-Evans, T. L., Primack, R. B., & Satzinger, P. (2008). Bird migration times, climate change, and changing population sizes. *Global Change Biology*, 14(9), 1959–1972. <https://doi.org/10.1111/j.1365-2486.2008.01619.x>
- Mills, A. M. (2005). Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis*, 147(2), 259–269. <https://doi.org/10.1111/j.1474-919X.2005.00380.x>
- Møller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the United States of America*, 105(42), 16195–16200. <https://doi.org/10.1073/pnas.0803825105>
- Moussus, J. P., Clavel, J., Jiguet, F., & Julliard, R. (2011). Which are the phenologically flexible species? A case study with common passerine birds. *Oikos*, 120(7), 991–998. <https://doi.org/10.1111/j.1600-0706.2010.18955.x>
- Newson, S. E., Moran, N. J., Musgrove, A. J., Pearce-Higgins, J. W., Gillings, S., Atkinson, P. W., Miller, R., Grantham, M. J., & Baillie, S. R. (2016). Long-term changes in the migration phenology of UK breeding birds detected by large-scale citizen science recording schemes. *Ibis*, 158(3), 481–495. <https://doi.org/10.1111/ibi.12367>
- Newton, I. (2008). *The migration ecology of birds*. Elsevier Ltd.
- Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., Bertram, E., Bradbury, R. B., Bradley, C., Butchart, S. H. M., Doswald, N., Foden, W., Gill, D. J. C., Green, R. E., Sutherland, W. J., Tanner, E. V. J., & Pearce-Higgins, J. W. (2014). Mechanisms underpinning climatic impacts on natural populations: Altered species interactions are more important than direct effects. *Global Change Biology*, 20(7), 2221–2229. <https://doi.org/10.1111/gcb.12559>
- Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, 13(9), 1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change. *Nature*, 421, 37–42. <https://doi.org/10.1038/nature01286>
- Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, 25(6), 1922–1940. <https://doi.org/10.1111/gcb.14619>
- Post, E., Steinman, B. A., & Mann, M. E. (2018). Acceleration of phenological advance and warming with latitude over the past century. *Scientific Reports*, 8(1), 1–8. <https://doi.org/10.1038/s41598-018-22258-0>
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, 49(1), 165–182. <https://doi.org/10.1146/annurev-ecolsys-110617-062535>
- Robertson, E. P., La Sorte, F. A., Mays, J. D., Taillie, P. J., Robinson, O. J., Ansley, R. J., O'Connell, T. J., Davis, C. A., & Loss, S. R. (2024). Decoupling of bird migration from the changing phenology of spring green-up. *Proceedings of the National Academy of Sciences*, 121(12), e2308433121. <https://doi.org/10.1073/pnas.2308433121>
- Robinson, R. A. (2005). *BirdFacts: Profiles of birds occurring in Britain & Ireland (BTO research report 407)*. BTO. <http://www.bto.org/birdfacts>
- Romano, A., Garamszegi, L. Z., Rubolini, D., & Ambrosini, R. (2023). Temporal shifts in avian phenology across the circannual cycle in a rapidly changing climate: A global meta-analysis. *Ecological Monographs*, 93(1), 1–21. <https://doi.org/10.1002/ecm.1552>
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421(6918), 57–60. <https://doi.org/10.1038/nature01333>
- Rubolini, D., Møller, A. P., Rainio, K., & Lehikoinen, E. (2007). Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Climate Research*, 35(1–2), 135–146. <https://doi.org/10.3354/cr00720>
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K., Hüppop, O., Lehikoinen, A., Lehikoinen, E., Rainio, K., Romano, M., & Sokolov, L. (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences*, 278(1707), 835–842. <https://doi.org/10.1098/rspb.2010.1778>
- Saino, N., Rubolini, D., Lehikoinen, E., Sokolov, L. V., Bonisoli-Alquati, A., Ambrosini, R., Boncoraglio, G., & Møller, A. P. (2009). Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their hosts. *Biology Letters*, 5(4), 539–541. <https://doi.org/10.1098/rsbl.2009.0312>
- Salguero-Gómez, R., Violle, C., Gimenez, O., & Childs, D. (2018). Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. *Functional Ecology*, 32(6), 1424–1435. <https://doi.org/10.1111/1365-2435.13148>
- Salido, L., Purse, B. V., Marrs, R., Chamberlain, D. E., & Shultz, S. (2012). Flexibility in phenology and habitat use act as buffers to long-term population declines in UK passerines. *Ecography*, 35(7), 604–613. <https://doi.org/10.1111/j.1600-0587.2011.06797.x>
- Samplonius, J. M., Bartošová, L., Burgess, M. D., Bushuev, A. V., Eeva, T., Ivankina, E. V., Kerimov, A. B., Krams, I., Laaksonen, T., Mägi, M., Mänd, R., Potti, J., Török, J., Trnka, M., Visser, M. E., Zang, H., & Both, C. (2018). Phenological sensitivity to climate change is higher in resident than in migrant bird populations among European cavity

- breeders. *Global Change Biology*, 24(8), 3780–3790. <https://doi.org/10.1111/gcb.14160>
- Severson, J. P., Johnson, H. E., Arthur, S. M., Leacock, W. B., & Sutor, M. J. (2021). Spring phenology drives range shifts in a migratory Arctic ungulate with key implications for the future. *Global Change Biology*, 27(19), 4546–4563. <https://doi.org/10.1111/gcb.15682>
- Stemkovski, M., Bell, J. R., Ellwood, E. R., Inouye, B. D., Kobori, H., Lee, S. D., Lloyd-Evans, T., Primack, R. B., Templ, B., & Pearse, W. D. (2022). Disorder or a new order: How climate change affects phenological variability. *Ecology*, 104, e3846. <https://doi.org/10.1002/ecy.3846>
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241–245. <https://doi.org/10.1038/nature18608>
- Thackeray, S. J., Sparks, T. H., Frederiksen, M., Burthe, S., Bacon, P. J., Bell, J. R., Botham, M. S., Brereton, T. M., Bright, P. W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J. M., Harrington, R., Johns, D., Jones, I. D., Jones, J. T., Leech, D. I., ... Wanless, S. (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, 16(12), 3304–3313. <https://doi.org/10.1111/j.1365-2486.2010.02165.x>
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Biodiversity and Climate Change: Transforming the Biosphere*, 427, 145–148. <https://doi.org/10.2307/j.ctv8jnzv1.37>
- Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J. B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., de Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., ... Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, 353(6304), aad8466. <https://doi.org/10.1126/science.aad8466>
- Usui, T., Butchart, S. H. M., & Phillimore, A. B. (2017). Temporal shifts and temperature sensitivity of avian spring migratory phenology: A phylogenetic meta-analysis. *Journal of Animal Ecology*, 86(2), 250–261. <https://doi.org/10.1111/1365-2656.12612>
- van Buskirk, J., Mulvihill, R. S., & Leberman, R. C. (2009). Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Global Change Biology*, 15(3), 760–771. <https://doi.org/10.1111/j.1365-2486.2008.01751.x>
- Végyvári, Z., Bókony, V., Barta, Z., & Kovács, G. (2010). Life history predicts advancement of avian spring migration in response to climate change. *Global Change Biology*, 16(1), 1–11. <https://doi.org/10.1111/j.1365-2486.2009.01876.x>
- Velmala, W., Helle, S., Ahola, M. P., Klaassen, M., Lehikoinen, E., Rainio, K., Sirkiä, P. M., & Laaksonen, T. (2015). Natural selection for earlier male arrival to breeding grounds through direct and indirect effects in a migratory songbird. *Ecology and Evolution*, 5(6), 1205–1213. <https://doi.org/10.1002/ece3.1423>
- Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), 2561–2569. <https://doi.org/10.1098/rspb.2005.3356>
- Wilman, H., Belmaker, J., Simpson, J., de La Rosa, C., Rivadeneira, M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95(7), 2027. <https://doi.org/10.1890/13-1917.1>
- Zalakevicius, M., Bartkeviciene, G., Raudonikis, L., & Janulaitis, J. (2006). Spring arrival response to climate change in birds: A case study from eastern Europe. *Journal of Ornithology*, 147(2), 326–343. <https://doi.org/10.1007/s10336-005-0016-6>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Dale, V. R., Bolton, M., Dornelas, M., Magurran, A. E., Dennis, R., Broad, R., Riddiford, N. J., Harvey, P. V., Riddington, R., Shaw, D. N., Parnaby, D., & Reid, J. M. (2024). Among-species variation in six decades of changing migration timings explained through ecology, life-history and local migratory abundance. *Global Change Biology*, 30, e17400. <https://doi.org/10.1111/gcb.17400>