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Variation and correlation in the timing of breeding of North Atlantic seabirds across multiple scales

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Abstract

1. Timing of breeding, an important driver of fitness in many populations, is widely studied in the context of global change, yet despite considerable efforts to identify environmental drivers of seabird nesting phenology, for most populations we lack evidence of strong drivers. Here we adopt an alternative approach, examining the degree to which different populations positively covary in their annual phenology to infer whether phenological responses to environmental drivers are likely to be (i) shared across species at a range of spatial scales, (ii) shared across populations of a species, or (iii) idiosyncratic to populations.

2. We combined 51 long-term datasets on breeding phenology spanning 50 years from nine seabird species across 29 North Atlantic sites and examined the extent to which different populations share early versus late breeding seasons depending on a hierarchy of spatial scales comprising breeding site, small-scale region, large-scale region and the whole North Atlantic.

3. In about a third of cases we found laying dates of populations of different species sharing the same breeding site or small-scale breeding region were positively correlated, which is consistent with the hypothesis that they share phenological responses to the same environmental conditions. In comparison we found no evidence for positive phenological covariation among populations across species aggregated at larger spatial scales.

4. In general we found little evidence for positive phenological covariation between populations of a single species, and in many instances the inter-year variation specific to a population was substantial, consistent with each population responding idiosyncratically to local environmental conditions. Black-legged kittiwake (*Rissa tridactyla*) was the exception, with populations exhibiting positive covariation in laying dates that decayed with the distance between breeding sites, suggesting that populations may be responding to a similar driver.

5. Our approach sheds light on the potential factors that may drive phenology in our study species, thus furthering our understanding of the scales at which different seabirds interact with interannual variation in their environment. We also identify additional systems and phenological questions to which our inferential approach could be applied.

Introduction

Predicting how organisms will respond to changing climate presents one of the greatest global challenges for ecologists. Some of the key responses that have been observed are changes in timing of seasonally recurring events (Parmesan & Yohe, 2003), which are often sensitive to environmental conditions, most notably temperature (Cohen, Lajeunesse, & Rohr, 2018; Thackeray et al., 2016). Timing of reproduction in relation to the timing of resource availability is expected to affect fitness, with mistiming expected to be detrimental (Varpe, 2017; Visser & Both, 2005). In order to respond to fluctuating environments, an individual may maximise its fitness if it can adjust timing of breeding to coincide with suitable conditions by responding to environmental drivers that cue the future arrival of a favourable environment (McNamara, Barta, Klaassen, & Bauer, 2011). Breeding phenology may be adjusted in response to one or multiple environmental cues and/or constraints, such as temperature (Chambers, Cullen, Coutin, & Dann, 2009), photoperiod (Dawson, King, Bentley, & Ball, 2001), wintering conditions (Dobson, Becker, Arnaud, Bouwhuis, & Charmantier, 2017), or resource availability, potentially mediated by body condition in the pre-breeding season (Daunt et al., 2014; Love, Gilchrist, Descamps, Semeniuk, & Bêty, 2010). The extent to which these different environmental drivers combine or interact to elicit a phenological response may differ between species and regions, hampering our ability to make general predictions regarding population responses to environmental change (Cohen et al., 2018; Thackeray, 2016; van de Pol et al., 2016).

Determining the conditions that drive phenological responses and the spatiotemporal scales at which they act requires both long-term data on phenology and fine-scale data on candidate environmental variables, and often involves comparison of environmental sensitivities across

a range of time-windows (van de Pol et al., 2016). While identifying a set of candidate environmental conditions and spatial scales is relatively straightforward for ectotherms that respond directly to temperature (Visser & Both, 2005) and species that are rooted/sessile or have small year-round ranges (Lindestad, Wheat, Nylin, & Gotthard, 2018), species at higher trophic levels and that are wide-ranging present a much greater challenge. For instance, wide-ranging species may respond to cues or conditions in the area where they breed (Frederiksen et al., 2004), at their wintering areas (Dobson et al., 2017; Szostek, Bouwhuis, & Becker, 2015), or both (Harrison, Blount, Inger, Norris, & Bearhop, 2011).

Identifying environmental drivers of phenology has proven especially challenging for seabirds. Globally, seabirds on average show no phenological trend over time or with spring sea surface temperature (Descamps et al., 2019; Keogan et al., 2018), in stark contrast to the pronounced phenological responses over time and with respect to temperature in the preceding months found in extra-tropical terrestrial systems (Thackeray et al. 2012; 2016; Cohen et al. 2018). The fact that some seabird populations exhibit substantial year to year variation in the timing of breeding (Burr et al., 2016; Keogan et al., 2018; Youngflesh et al., 2018), is consistent with populations responding to variation in their environment. Timing of breeding may be determined by climate or diet-related drivers, immediately prior to breeding or as carry-over effects from preceding months, either at breeding or winter grounds. However, the nature of the environmental drivers, when they occur and where they occur remains to be established. Most seabirds occupy higher trophic levels, and the breeding ranges of many species span large spatial gradients in environmental conditions. They can forage at great distances from the breeding site during the breeding season, and have some of the longest migrations known in the animal kingdom (Egevang et al., 2010). Although many seabird species winter far from their colonies, many also spend time at the breeding site before egg laying commences, such

that conditions at both breeding (Frederiksen et al., 2004; Love et al., 2010) and wintering grounds (Dobson et al., 2017; Szostek et al., 2015) may affect breeding phenology.

Identifying the environmental conditions that drive the phenology of each seabird population is critical because timing of breeding is strongly correlated with productivity, with earlier years more successful than later years (Durant et al. 2007; Ramirez et al. 2016; Keogan et al, 2020). However, the combination of an extensive set of potential environmental drivers and the short duration for the average time series (Keogan et al. 2018) makes this identification a huge challenge. As an alternative, we seek to identify the extent to which different seabird populations exhibit similar phenological responses to shared environmental drivers, which we predict should manifest in positively correlated phenological time series. This approach has the potential to greatly reduce the set of candidate environmental variables (see hypothetical scenarios and deductions in Figure 1).
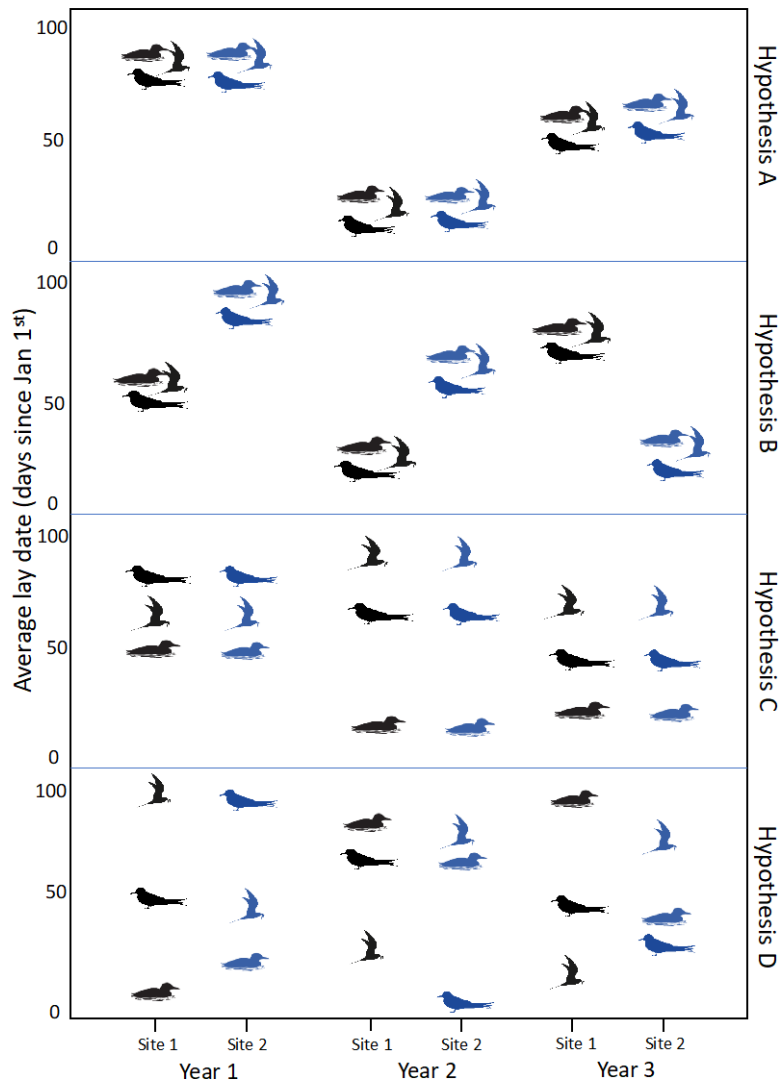
Figure 1. Schematic representation of interannual (co)variation in phenology across populations of four seabird species at two sites. Below we represent four hypotheses A-D. A. *Cross-species spatial effect*: A positive correlation in the phenological time series across all populations may arise if populations respond similarly to a shared environmental variable. B. *Cross-species site effect*: A positive correlation across populations of different species at a site (but not between sites) may arise if populations respond similarly to local environmental conditions which are uncorrelated between sites. C. *Species spatial effect*: A positive correlation across sites (but not species) may arise if environmental drivers of phenology are shared across sites, but the nature of the drivers or responses to them are species-specific. D. *Idiosyncratic population effect* Interannual variation in phenology but no correlation across sites or species may arise if each population responds to a different driver or idiosyncratically to the same local driver.

In this study, we aimed to identify the extent to which 51 populations (defined as a species breeding at a particular site) of nine seabird species breeding in the North Atlantic show positively correlated timing of breeding across years. We test four hypotheses. 1. *Cross-species spatial effect*: Phenology covaries positively across time for populations of all species found in the same geographic region during breeding or wintering season (defined at three spatial scales from the entire North Atlantic down to small-scale regions where breeding populations were < 120 km apart). Evidence for this would indicate that species and populations share a phenological response to a driver or drivers that show correlated interannual change across the geographic region. 2. *Cross-species site effect:* Phenology covaries positively across time for populations of different species at a site (but not between sites). Evidence for this would indicate that these populations are responding similarly to local environmental conditions that are uncorrelated between sites. 3. *Species spatial effect*: Phenology covaries positively across all populations of a species in either the North Atlantic or that share a breeding or wintering region. Evidence for this would indicate that populations of a species share a phenological response to a driver or drivers that show correlated interannual change across the focal spatial scale. *4. Idiosyncratic population effect*: The phenology of a population does not positively covary with other populations in the same region or of the same species. Evidence for this would indicate that populations of different species are responding to different drivers or idiosyncratically to the same local environmental drivers. In *lieu* of identifying the environmental drivers themselves, we can use estimates of positive correlations between phenological time series to deduce the likely attributes of environmental drivers and direct future examination.

Materials and Methods

Data collection

We compiled phenological data (annual average breeding times) on nine North Atlantic seabird species for which multiple populations have been studied (black-legged kittiwake (*Rissa tridactyla*), common tern (*Sterna hirundo*), roseate tern (*Sterna dougallii*), Arctic tern (*Sterna paradisaea*), European shag (*Phalacrocorax aristotelis*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*), common guillemot (*Uria aalge*), and Brünnich's guillemot (*Uria lomvia*)). At the time the study was conducted, no ethical approval was required from the host institutions of authors in order to undertake the analyses of first-party and third-party data. A study population was defined as a species breeding at a particular site. For each study population, annual data on breeding phenology during the period from 1968 to 2017 were selected in the following order of preference: median lay date (n = 24 populations); mean lay date (n = 5); median hatch date (n =6); mean hatch date (n = 12); first hatch date of the study population (n = 4), in units of ordinal days. Our rationale for this order of preferences was threefold. First, we preferred median to mean values as this measure is less sensitive to whether the distribution of breeding date is normal. Second, we preferred average dates over first dates as the former will be less sensitive to interannual variation in sample size. Third, lay date is preferred over hatch date since it includes all study nests whereas hatch dates excludes those that failed during incubation, which may show bias with respect to timing of breeding. We used only one measure of phenology for each population, and where only hatch date was available, we back-calculated lay date using information on the average incubation period (Sources in Table S1). All time series were a minimum of eight years, although the years did not need to be consecutive.

In addition to breeding site, we consider three larger spatial-scales: (i) North Atlantic: Includes all populations. (ii) Large Marine Ecosystem (LME): Populations were assigned to one of

eleven breeding LMEs to assess covariance at a smaller spatial scale (Figure 2a, Table 1). The wintering LMEs of individuals for each population was determined from available published tracking data. If tracking studies suggested a population may overwinter in several locations, the area where the highest proportion of birds from a population spent the winter was used to define that population's wintering ground. Across all populations, eleven potential wintering grounds were identified in total (Figure 2b, Table 1, see Table S1 for sources). As this was a population level analysis, we assumed that the individuals in a population shared a wintering region. We identified wintering region in different ways depending on the tracking data available for a population. For most populations information came from published papers (cited in Table S1), which identified the most common locations used overwinter for each species. For 11 Norwegian and two Scottish breeding populations, we used information from seatrack.seapop.no/map/, which presents wintering distributions from multiple years in kernel distribution maps. Based on visual inspection of the maps we assigned a wintering distribution as the location where highest percentage of individuals within a population spent the winter across all years available. (iii) Small-scale region: comprised of breeding sites that were < 120 km apart. We chose 120 km based on average foraging ranges during the breeding season of the study species, which are generally markedly less than this value (Thaxter et al., 2012). This classification allowed us to estimate the average positive covariance between populations within a small-scale region. In addition, for each time series we collated information on the latitude and longitude of the breeding site, and categorised sites as being either east ($< 35°$ W) or west ($> 35°$ W) coast of the North Atlantic Ocean.
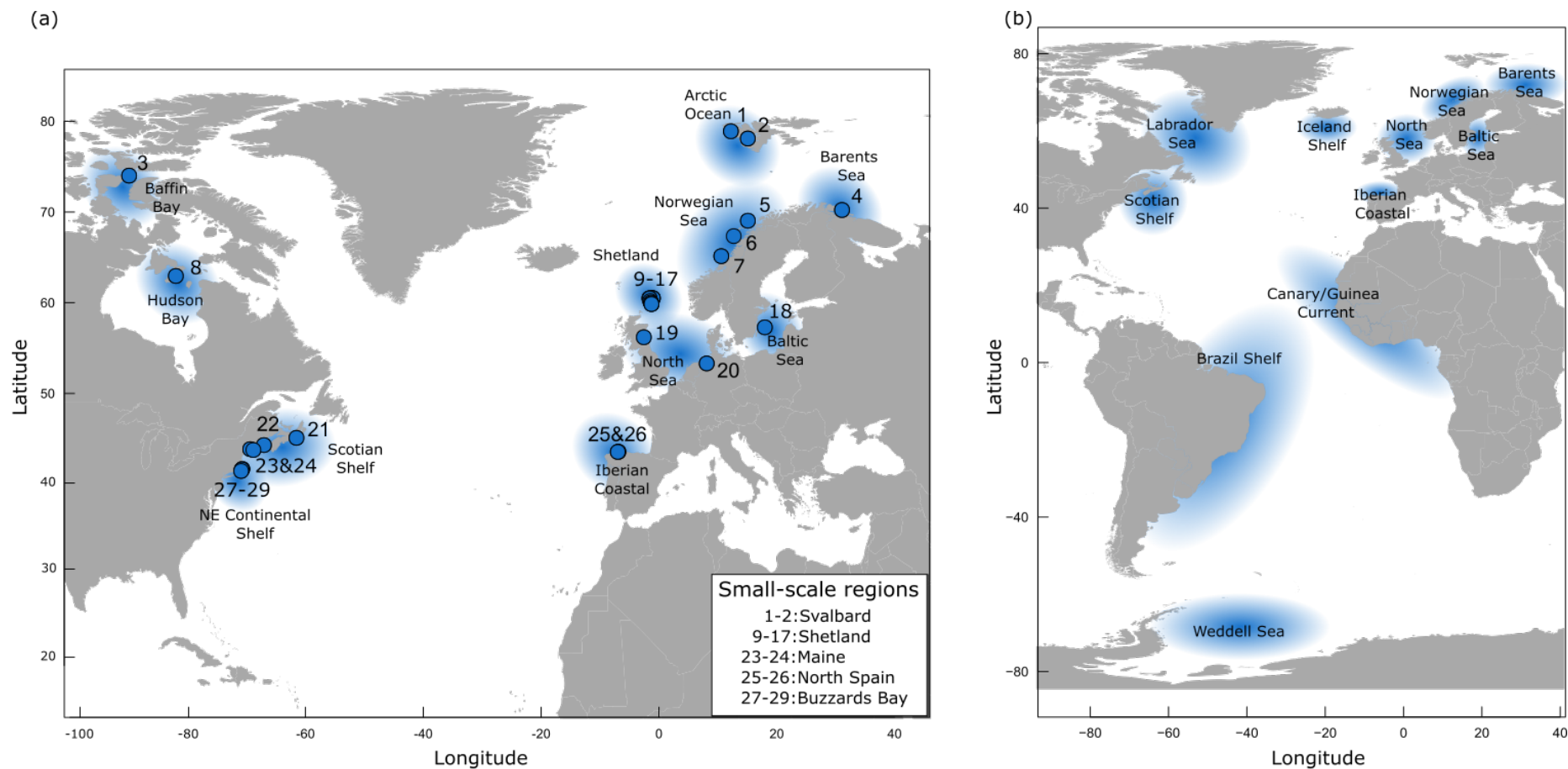
Figure 2. Map of sites in the North Atlantic included in the analyses. a) during the breeding season. Blue shading represents the Large Marine Ecosystem (LMEs) classification. Numbers correspond to the breeding sites named in Table 1, numbered in order of decreasing latitude. Only LMEs and small-scale regions (sites <120km apart) in which data for more than one site were available were included in the analysis of the annual covariance. b) during winter. Wintering LMEs represent the location where highest percentage of individuals within a population spend the winter. For further information, sources and site coordinates see Table S1.

Table 1. List of breeding sites and species included in the analyses in order of decreasing latitude, with breeding and wintering regions indicated. Site numbers on the left correspond to those in Figure 2a. Species are as follows: KI = black-legged kittiwake, CT = common tern, RT = roseate tern, AT = Arctic tern, SH = European shag, RA = razorbill, AP = Atlantic puffin, CG = common guillemot, BG = Brünnich's guillemot, with numbers in parenthesis indicating the number of populations of each species included in the analyses. Multiple wintering LMES listed in a single row appear in the same order as the species' listed at each breeding site. A term was only included in the analysis of annual covariance when data for more than one population were available.

#	AP (6)	RA (3)	CG (4)	BG (2)	SH (6)	KI (16)	AT (3)	CT (7)	RT (4)	Breeding site	Breeding small-scale region	Breeding LMES	Wintering LMES
1						x				Kongsfjorden	**Svalbard**	(Arctic Ocean)	**Labrador Sea**
2						x				Grumantbyen	**Svalbard**	(Arctic Ocean)	**Labrador Sea**
3			x			x				**Prince Leopold Island**	(Prince Leopold Island)	(Baffin Bay)	**Labrador Sea**
4	x	x	x			x				**Hornøya**	(Hornøya)	(Barents Sea)	**Barents Sea** / **Norwegian Sea** / **Barents Sea** / **Labrador Sea**
5	x					x				**Anda**	(Anda)	**Norwegian Sea**	**Iceland Shelf** / **Labrador Sea**
6	x				x	x				**Røst**	(Røst)	**Norwegian Sea**	**Iceland Shelf** / **Norwegian Sea** / **Labrador Sea**
7	x				x					**Sklinna**	(Sklinna)	**Norwegian Sea**	**Iceland Shelf** / **Norwegian Sea**
8				x						Coats Island	(Coats Island)	(Hudson Bay)	**Labrador Sea**
9						x				Burravoe	**Shetland**	**North Sea**	**Labrador Sea**
10						x				Esha Ness	**Shetland**	**North Sea**	**Labrador Sea**
11						x				Westerwick	**Shetland**	**North Sea**	**Labrador Sea**
12						x				Ramna Geo	**Shetland**	**North Sea**	**Labrador Sea**
13						x				Kettla Ness	**Shetland**	**North Sea**	**Labrador Sea**
14						x				No Ness	**Shetland**	**North Sea**	**Labrador Sea**
15						x				Troswick Ness	**Shetland**	**North Sea**	**Labrador Sea**
16						x				Compass Head	**Shetland**	**North Sea**	**Labrador Sea**
17		x		x		x				**Sumburgh Head**	**Shetland**	**North Sea**	**North Sea** / **North Sea** / **Labrador Sea**
18			x							Stora Karlsö	(Stora Karlsö)	(Baltic Sea)	Baltic Sea
19	x	x	x		x	x				**Isle of May**	(Isle of May)	**North Sea**	**North Sea** / **North Sea** / **North Sea** / **North Sea** / **Labrador Sea**

							Site	Region	Shelf	Current/Sea
20					x		Banter See	(Banter See)	**North Sea**	**Canary or Guinea Current**
21				x	x	x	**Country Island**	(Country Island)	**Scotian Shelf**	(Weddell Sea) / **Brazil Shelf** / **Brazil Shelf**
22	x	x		x	x		**Machias Seal Island**	(Machias Seal Island)	**Scotian Shelf**	**Gulf of Maine** / Unknown / (Weddell Sea) / **Brazil Shelf**
23					x		Eastern Egg Rock	**Maine**	**Scotian Shelf***	**Brazil Shelf**
24				x			Matinicus Rock	**Maine**	**Scotian Shelf***	(Weddell Sea)
25			x				A Forcada	**North Spain**	(Iberian Coastal)	**Iberian Coastal**
26			x				As Pantorgas	**North Spain**	(Iberian Coastal	
27					x	x	**Bird Island**	**Buzzards Bay**	(North East U.S Shelf)	**Brazil Shelf**
28					x	x	**Ram Island**	**Buzzards Bay**	(North East U.S Shelf)	**Brazil Shelf**
29					x	x	**Penikese Island**	**Buzzards Bay**	(North East U.S Shelf)	**Brazil Shelf**

Terms in bold represent effects for which year (co)variance was estimated. Terms in brackets represent effects which are confounded because the same combination of populations is grouped at another spatial scale, see main text for details. Confounded terms were not included in the model unless specified in the main text. Underlined terms were not included in estimates of site year (co)variance, in either one or both of the breeding and wintering models, as data for only one population available and covariance could therefore not be estimated. *Usually classed as North East U.S. Shelf but grouped here as Scotian Shelf.

Table 2. Hypotheses and how they relate to the structure of random terms used to capture year (co)variances (σ^2) for groupings of populations in the analyses. We use the among year variance for a grouping of populations as an estimate of the among year covariance between populations in the group. B indicates terms included in the breeding model, W indicates terms included in the wintering model.

Hypothesis and Description	Year (co)variance structure (where levels are unspecified see table 1 for levels that variances correspond to)	Model
1.1 Cross-species spatial effect (North Atlantic scale): Characterises the among-year variance in the mean annual average phenology means or medians across all populations breeding in the North Atlantic. Provides an estimate of the magnitude of a shared response to a trans North Atlantic driver.	$\mathbf{V}_{\text{global}} = \sigma^2_{\text{global}}$	B, W
1.2 Cross-species spatial effect (Breeding LMEs scale): Characterises among-year variance in the average phenology of all populations in the breeding Large Marine Ecosystem. This accounts for populations sharing a phenological response to a common broad scale regional driver during the summer.	$\mathbf{V}_{\text{breeding LMES}} = \begin{bmatrix} \sigma^2_{1,1} & 0 & 0 \\ 0 & \sigma^2_{2,2} & 0 \\ 0 & 0 & \sigma^2_{3,3} \end{bmatrix}$ Where $1-3$ correspond to different breeding LMEs	B
1.3 Cross-species spatial effect (Winter LME scale): Characterises among-year variance in the average phenology of all populations that share the same winter LME. This accounts for populations sharing a phenological response to a common regional driver during the winter.	$\mathbf{V}_{\text{wintering LMES}} = \begin{bmatrix} \sigma^2_{1,1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma^2_{8,8} \end{bmatrix}$ Where $1-8$ correspond to different wintering LMEs	W
1.4 Cross-species spatial effect (small-scale, i.e breeding colonies within 120km): Characterises among year variance in the average phenology of all populations found in the same local area. This accounts for a shared phenological response to small-scale regional conditions.	$\mathbf{V}_{\text{local}} = \begin{bmatrix} \sigma^2_{1,1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma^2_{12,12} \end{bmatrix}$ Where $1-5$ correspond to different small-scale regions.	B
2 Cross-species site effect: Characterises among year variance in the average phenology of all populations found at the same breeding site. This accounts for a shared phenological response to very local conditions.	$\mathbf{V}_{\text{site}} = \begin{bmatrix} \sigma^2_{1,1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma^2_{12,12} \end{bmatrix}$ Where $1-12$ correspond to different breeding sites.	B
3.1 Species spatial effect (North Atlantic scale): Characterises among year variance in the average phenology of all populations that belong to the same species. This accounts for the potential for species to share a phenological response to a spatially consistent driver.	$\mathbf{V}_{\text{species}} = \begin{bmatrix} \sigma^2_{1,1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma^2_{9,9} \end{bmatrix}$ Where $1-9$ correspond to different species	B,W
3.2 Species spatial effect (Winter LME scale): Characterises among year variance in the average phenology of all populations of the same species that share the same wintering LME. This accounts for populations of the same species sharing a phenological response to a common driver encountered in the same wintering LME	$\mathbf{V}_{\text{species wintering}} = \begin{bmatrix} \sigma^2_{1,1} & \dots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \dots & \sigma^2_{4,4} \end{bmatrix}$ Where 1 = Northern North Sea European shag, 2 = Northern North Sea Common guillemot, 3 = Brazil Shelf Roseate tern, 4 = Brazil Shelf Common tern	W

3.3 Species spatial effect (breeding colonies within 120km): Characterises among year variance in the average phenology of all populations within a small-scale region that belong to the same species. This takes into account the potential for members of a single species to share a phenological response to conditions at breeding sites within 120km.

$$\mathbf{V}_{\mathrm{p}} = \begin{bmatrix} \sigma_{1,1}^2 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & \sigma_{3,3}^2 \end{bmatrix}$$

B,W

Where 1 = Shetland Black-legged kittiwake, 2 = Buzzards Bay Roseate tern, 3 = Buzzards Bay Common tern

4. *Idiosyncratic population effect:* Allows for the residual among year variance to be heterogeneous across all populations. High residual variance implies that phenology is largely determined by a driver and/or response that is idiosyncratic to the population.

$$\mathbf{V}_{\mathrm{population}} = \begin{bmatrix} \sigma_{1,1}^2 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & \sigma_{51,51}^2 \end{bmatrix}$$

B,W

Where 1-51 correspond to different populations

Statistical Analyses

We used the *MCMCglmm* package (Hadfield, 2010) in R (v 3.5.1; R Core Team 2018), to fit linear mixed-effect models in a Bayesian framework. In these models, the Gaussian response variable was the yearly breeding phenology of each population. Random effects were used to (i) control for differences in mean/median timing among populations and (ii) identify the sources of positive covariance in phenology among populations (see Table 2 for full list of terms used). Estimating the unstructured 51 x 51 covariance matrix for annual timing among all populations was unfeasible given the number of observations we had. While methods to capture the major aspects of this among population covariance exist (Warton et al., 2015), our approach reduced the dimensionality of the problem by only estimating positive among year (co)variances where we hypothesised *a priori* they may exist and assuming other covariances = 0 (see Appendix 1). We used separate models to distinguish the positive (co)variance among populations that share breeding LMES (core model) versus wintering LMES (wintering model). An additional core model (fixed effects model) included latitude and the continental coast of the breeding site (east or west Atlantic Ocean) as fixed effects to account for broad geographic trends in the long-term mean/median phenology of populations.

We used random terms in two ways. First, we controlled for variation in the multi-year mean/median phenology of the time series' in each group by including species, LMES (breeding or wintering), small-scale region (groups of sites that are < 120 km apart), species within small-scale region, site, and population (site:species) as random terms. The year random term estimated the overall between-year (co)variance in timing of breeding across all populations. Secondly, we allowed the among-year variance to be heterogeneous across spatial and taxonomic groupings of populations (Table 2). For example, heterogenous year variance structure was applied at the species level to nine species groupings, which estimates a 9x9

matrix of among year (co)variance, where the annual variance of each species is along the diagonal and the dimensionality of the problem is reduced by fixing the off-diagonals (covariances between species) at zero. The year variance estimated for a species is equivalent to the among-year covariance among populations of that species (Figure 1, Table 2, see Appendix 1 for further explanation). For each of the year variances estimated for a grouping of populations, a high value indicated positive covariance among associated time series, such that populations within the grouping had similar patterns of early or late breeding years (Figure 1a,b,c). Conversely, low covariance indicated no tendency for shared early or late breeding events among the population time series within a grouping (Figure 1d). We only allowed for heterogeneity in year variance where data were available for two or more populations in each grouping. We also allowed the among-year residual variance to be heterogeneous across populations. For all random terms, effects were drawn from a normal distribution with mean = 0 and with the variance estimated from the data. As the sample sizes on which annual population averages varied among populations and years this introduced heterogeneity in the measurement error across observations. To control for measurement error we allowed for a slope of $\sqrt{1/n}$ (where n = annual sample size for a population) to vary across observations.

Given the five alternative random terms in the core model, the combination of populations was sometimes the same for more than one spatial scale. For example, both populations of European shag in North Spain were located < 120 km apart and were therefore included in the same small-scale region, and this same combination was found in the breeding LMEs, Iberian coastal. Where an identical set of populations were grouped by more than one random effect, only the level in which populations were in closest proximity (i.e., site, then small-scale region, then LME) was included. In such cases, the spatial-scale at which positive covariance arise cannot be distinguished and we highlight such cases in the results.

In the wintering model (Table 2), we tested for positive covariance among populations that share a wintering LMES. Year, species, population, and heterogeneous year variances across species and populations were retained as random terms from the core model. We also retained the species small-scale regional effect to control for similar responses of adjacent populations of the same species (e.g., nine populations of kittiwakes from Shetland) that may travel to the same wintering LMES. In addition to estimating positive covariance in phenology among all populations wintering in the same LMES, we also estimated the species-specific positive covariance among populations across years.

All models were run for 1,200,000 iterations, discarding the first 100,000 as burn-in and sampling every 100th iteration. For the residual priors we used an inverse-Wishart distribution. To improve mixing, for the remaining variance random terms we adopted parameter-expanded priors (Gelman, Van Dyk, Huang, & Boscardin, 2008), which give a scaled F distribution with numerator and denominator degrees of freedom = 1 and scale parameter = 1000 (Gelman, 2006). Trace plots of posterior distributions were examined to assess autocorrelation and model convergence. Statistical significance of fixed effects was inferred where 95% credible intervals (CIs) did not span zero. As variance estimates are bounded at zero, we infer that a random term is significant where visual inspection of posterior showed that the 2.5% CI was removed from zero.

The method we employed assumes that between grouping covariances are zero and that all non-zero covariances are positive. In appendix 2 we outline *post hoc* tests designed to assess model adequacy. To examine how properties of the data (effect size, replication, number of overlapping years, etc.) affected the accuracy and power of our approach for estimating

(co)variances, we conducted simulations of phenology based on the original data structure of the core model (Appendix 2). Simulations revealed that our method for estimating population covariance had good power to detect a (co)variance of 40 and moderate power to detect a (co)variance of 20. Power to detect a non-zero covariance was reduced when time series were short and care should be taken in interpreting covariance estimates with very broad credible intervals, as this may reflect low power rather than a true absence of a covariance.

Results

Phenological time series

The full dataset of 1041 phenological observations (annual means or medians) spanned 50 years and 51 populations across nine species and 29 breeding sites, with more recent years represented by more time-series than earlier years (Figure S1, Table S1). From visual inspection of population time series from the same species (Figure 3) or site (Figure 4) there were some instances where population responses appeared to be correlated (e.g., Black-legged kittiwake, Ram Island) and other instances where the time series appeared to be entirely uncorrelated (e.g., European shag).

Large-scale geographic trends

All model parameter estimates correspond to those obtained from the core breeding model unless the wintering model is specified. Average lay date was delayed with latitude ($b = 1.782$ days lat^{-1}, 95% CI = 0.879, 2.678), and, controlling for latitude, laying in the west Atlantic was 38 days later (95% CI = 16.119, 58.164) than the east Atlantic.
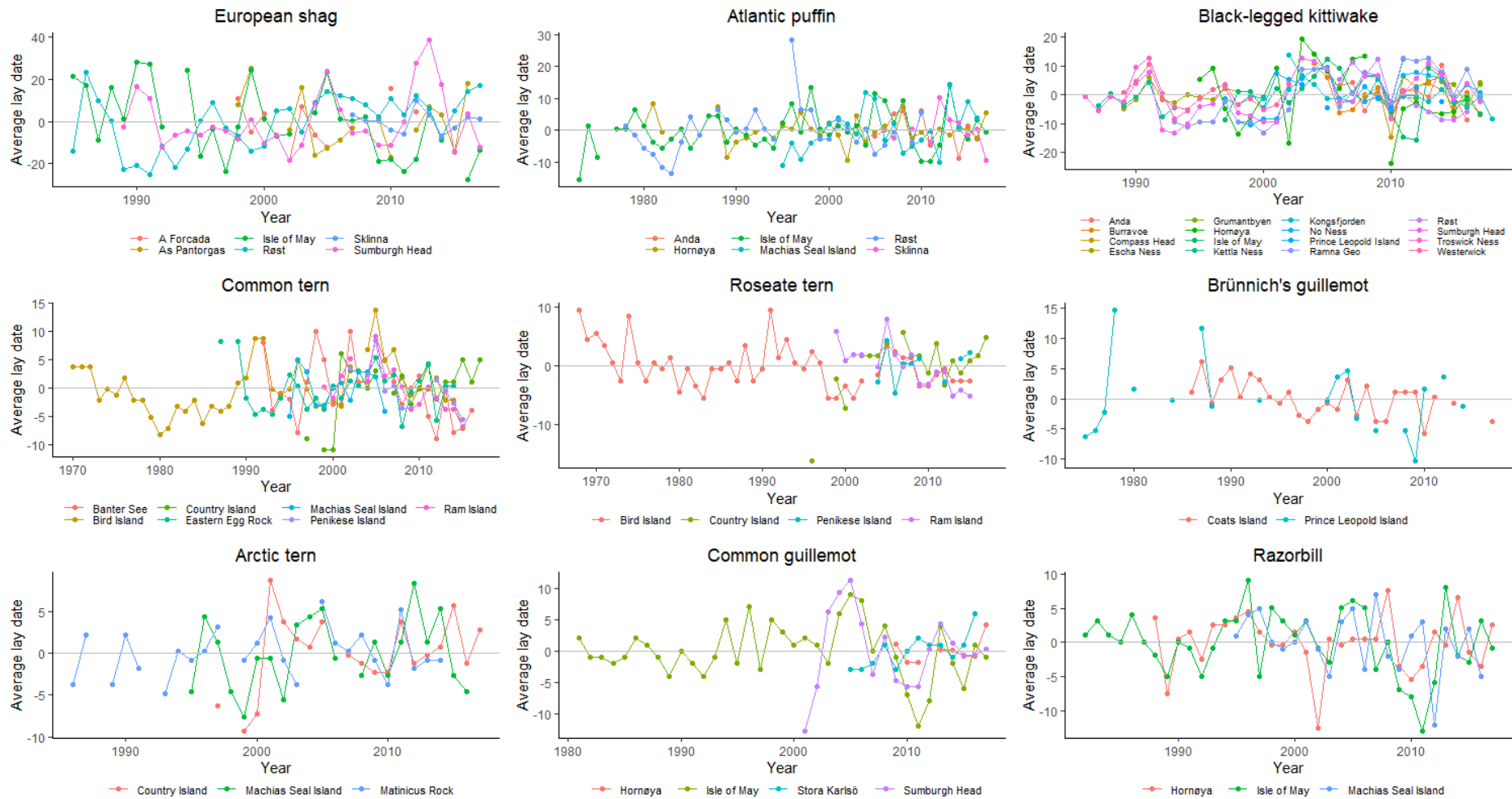
Figure 3. Annual lay dates of populations of all species included in the analysis. The grey line represents the line of central tendency of laying for each species.

Figure 4. Annual lay dates of populations at twelve sites for which more than one time series was available for analysis. The grey line represents the central tendency of laying at each site.

Cross-species spatial and site effects

To test whether the phenology of populations in the North Atlantic Ocean basin varies in a similar way from year to year we tested for covariance in timing between years across all time series'. Variance (in units of days^2) of the *cross-species spatial effect* at the North Atlantic scale was very low ($\sigma^2 = 0.173$, 95% CI = 0.000, 1.077, years = 49) in comparison to the average interannual variance in lay date shown by each population (Table S2), indicating that for North Atlantic seabirds in general, early and late years were not shared across all of the populations.

To assess *cross-species spatial effects* (LMEs scale) we estimated among year phenological covariance between populations sharing similar breeding or wintering LMEs. We detected no statistically significant cross-species covariance of populations that share a breeding LME region (Figure 5e, Tables S2, S3), although in the Norwegian Sea and the North Sea the credible intervals were wide. In the wintering model, significant covariance was found only for populations in the North Sea ($\sigma^2 = 18.236$, 95% CI = 10.014, 29.438, time series = 6, Figure S3b, Table S4), with the estimated variance corresponding to the shared phenological effects being in the range of ± 8.3 days in 95% of years. The posteriors for inter-year variance in phenology for populations that wintered in three additional LMEs (Gulf of Maine, Iceland Shelf and Barents Sea) were somewhat removed from zero, although the 2.5% CI was approximately 0. In the case of populations that winter on the Iceland Shelf, the posterior median for the among-year variance was large, but there was high uncertainty in the variance estimate (Figure S3b).

We estimated *cross-species spatial effects* for five small scale regions (each made up of sites within 120 km) and found among-year variance to be quite high in North Spain, Shetland and Svalbard, but only estimated well for Shetland ($\sigma^2 = 32.688$, 95% CI = 14.502, 59.032, time

series = 11, Figure 5c, Table S2). Of the 29 breeding sites, 12 held more than one species, allowing estimation of *cross-species site effects* (Figure 4 and 5b), with among year variance significant for only three sites: Country Island, Hornøya, and Prince Leopold Island. For these sites the 95% limits for the expected annual deviations are in the range ± 10.5 days, ± 7.1 days and ± 9.2 days, respectively. The peaks of the posterior distribution for inter-year variance for five additional sites (Bird Island, Isle of May, Machias Seal Island, Ram Island and Sumburgh Head) were removed from 0, but the 2.5% CI was approximately 0 (Figure 5b).

Species effects

We tested for among year phenological covariance between populations of the same species to test the hypothesis that there are environmental conditions that drive species-specific responses. The *species spatial effect (North Atlantic scale)* was only significant for black-legged kittiwakes ($\sigma^2 = 10.723$, 95% CI = 2.927, 22.228, time series = 16, Figure 5a, Table S2). Under a normal distribution with mean = 0 and variance = 10.723, the shared annual deviations in timings were expected to lie in the range ± 6.4 days in 95% of years. All other species covariance effects were small with the 97.5% quantile of the posterior for seven of the species < 6 (Table S2). For three species we estimated *species spatial effects* within small scale regions. We found a suggestion of positive covariance for common terns at Buzzards Bay (Figures 5d & S4c, Tables S2, S3), whereas for Roseate terns in this small-scale region the covariance was low. For kittiwakes across Shetland covariance was poorly estimated, making it unclear whether there is a species-specific response to a small-scale driver, in addition to the North Atlantic scale species effects and small-scale (Shetland) cross species effects that this species will be affected by. We found no evidence that breeding phenology of populations of the same species within a wintering region covaried (Figure S3d, Table S4), although for Roseate terns

at Brazil Shelf and Common guillemots at the Northern North Sea credible intervals were very broad.

Idiosyncratic population effects

Residual annual variance was significant for all of the 51 populations (Table S2) and varied substantially among species (Table 3), being particularly pronounced in European shags. Averaged across populations, the residual term explained substantially more of the annual (co)variance than any other term.
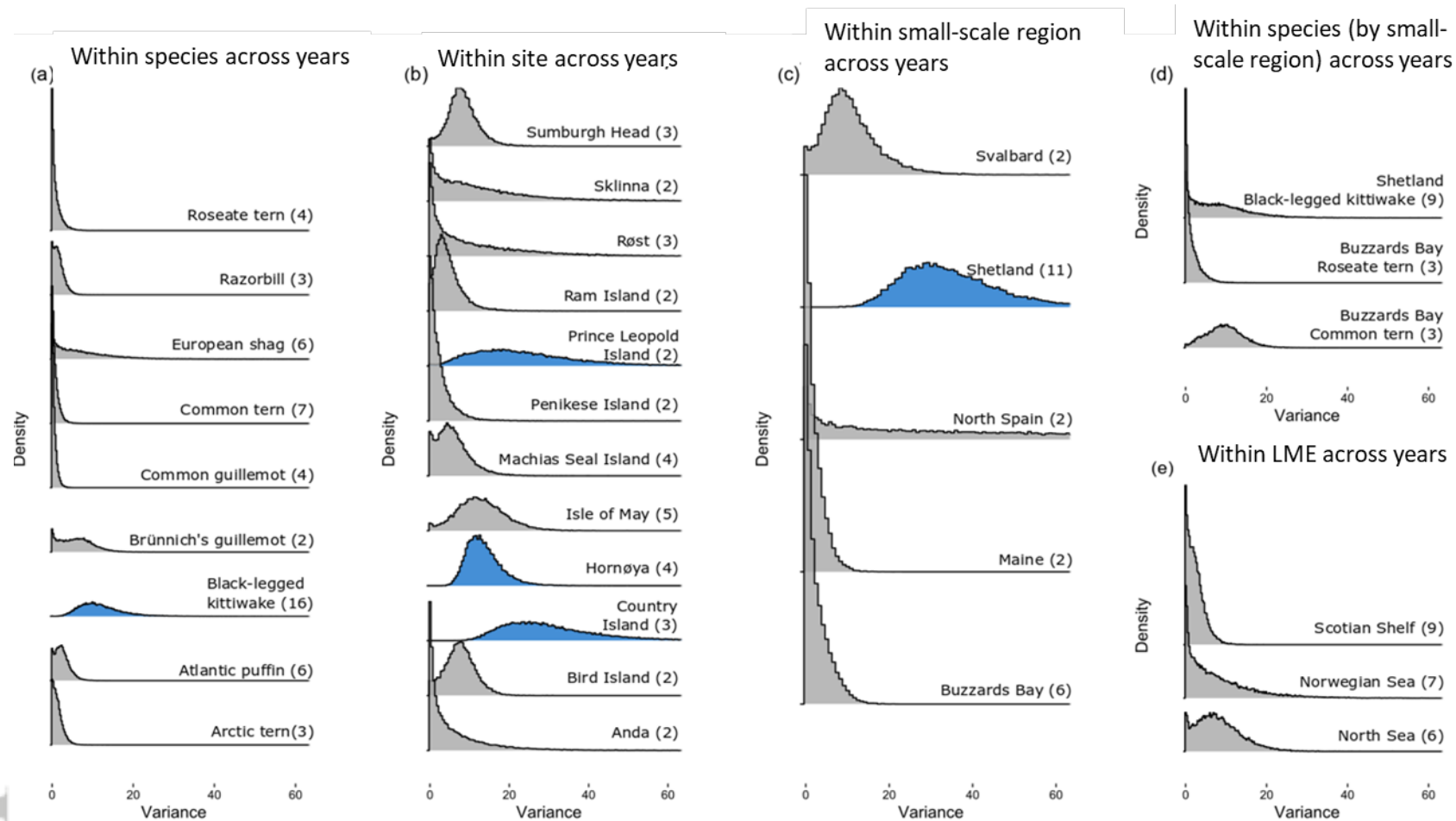
Figure 5. (Co)variance in timing of breeding of seabird populations across years during the breeding season. Plotted from the posterior distribution of the core random-effects model, representing shared variance across years according to (a) species, (b) site, (c) small-scale region (< 120 km apart), (d) species within small-scale region (i.e. populations of the same species within a group of nearby sites), and (e) Large Marine Ecosystem. On the y axes labels, values in parenthesis indicate the number of populations associated with each term. For interpretation, narrower histograms indicate a posterior distribution that has been estimated with higher precision (i.e. a tighter credible interval), and histograms with a centre of mass further removed from zero represent more posterior support for a positive (co)variance. Groups for which significant positive covariance was estimated (i.e. where 2.5% credible interval was removed from 0) are shaded in blue.

Table 3. Median residual variance for the nine species included in the analysis in order of decreasing variance. Residual variance is calculated from the core random effects model, and species are placed in order from highest to lowest values. Numbers in brackets indicate 95% credible intervals for the species medians. 95% range in days corresponds to the 0.025 and 0.975 quantiles of a normal distribution of mean = 0 and σ calculated from the residual variance.

Species	Median among-year residual variance	95% range in days
European shag	143.31 (45.55 – 278.17)	± 23.46 days
Atlantic puffin	25.12 (4.63 – 54.67)	± 9.82 days
Black-legged kittiwake	18.83 (3.59 - 41.92)	± 8.50 days
Razorbill	7.72 (1.24 - 15.07)	± 5.45 days
Brünnich's guillemot	7.38 (0.00 – 20.65)	± 5.33 days
Roseate tern	7.08 (0.00 – 17.48)	± 5.21 days
Common tern	5.31 (1.34 – 12.40)	± 4.52 days
Arctic tern	5.05 (1.05 – 11.03)	± 4.40 days
Common guillemot	4.65 (0.55 – 12.27)	± 4.23 days

Model diagnostics

The model which allowed for negative covariance between two populations at a single local site (Anda) estimated a non-significant negative covariance between populations at this site (Appendix 2: Table S6). Allowing for this negative correlation led to no substantial changes to other (co)variance parameters that these populations contributed to (Appendix 2, compare Tables S2&3 with S6).

For four species with data for > 5 populations (Black-legged kittiwake, common tern, Atlantic puffin, European shag) we compared pairwise correlations estimated from the raw data against those from the posterior distribution of the core random effects model as a diagnostic of the performance of the mixed-model approach. The model-based estimates corresponded well with estimates from pairwise correlations using the raw data and captured a spatial decay in pairwise correlations (Appendix 2, Figure S4). While estimates obtained via both approaches converged on zero as distance increased, a minor difference was that those from the model were always positive, whereas those estimated pairwise from the data were both positive and negative. Intraspecific pairwise Pearson's correlations of annual phenology between populations of black-legged kittiwakes, Atlantic puffins, and European shags all decreased with increased

distance (black-legged kittiwake: Mantel statistic [between distance and 1-correlation] r = 0.515, p = 0.004; Atlantic puffin: r = 0.803, p = 0.025; European shag: r = 0.526, p = 0.006. Appendix 2, Table S7, Figure S4).

The *a posteriori* quantile-quantile plot for pairwise population correlations revealed an excellent correspondence between empirical and model-based quantiles (Appendix 2, Figure S5). Model-based *a posteriori* simulations yielded a similar frequency of negative pairwise correlations between populations to that which we observe, indicating that the observed frequency of negative phenological correlations is consistent with what we would expect to observe by chance in the absence of any true negative covariances.

Discussion

Timing of breeding is often used as an indicator of response to environmental change, yet for many species the drivers of phenology and the spatiotemporal scale at which they operate remain unclear. We collated phenology from a diverse group of North Atlantic seabird populations and examined to what extent populations share early versus late breeding seasons between sites, species, breeding and wintering regions. We found no evidence that across species all populations in the North Sea collectively breed early or late, suggesting that if there is a common driver of phenology in the North Atlantic, such as sea surface temperature or North Atlantic Oscillation, it either does not exhibit correlated annual variation across this region and/or does not elicit a consistent response across populations. However, we did identify a pronounced difference in the median timings between the east and west Atlantic, with phenology more than a month later in the west. One potential explanation is that this may be due to differences in the temperature of the currents passing each coast (southward flowing Labrador Current being cold in comparison with the warmer and northward flowing Gulf

Stream) which leads to more pronounced seasonality in water temperature in the west for a given latitude (Mackas et al., 2012).

We also found no evidence for cross-species shared phenological responses for populations in the same breeding LMEs, and the same was true for most wintering LMEs (the exception being the North Sea). Primary productivity (Behrenfeld et al., 2006) and abundance of prey (Frederiksen et al., 2005) vary in their temporal availability at spatial scales smaller than the LME categorisation used in this study, such that although they occupy the same general ocean basin, the scale, magnitude and direction of any adjustment in timing of breeding in response to the environment may differ across sites within it. Furthermore, bathymetry, tides and currents are all important for prey distributions and aggregations, and thereby for seabird foraging (Amélineau, Grémillet, Bonnet, Bot, & Fort, 2016; Christensen-Dalsgaard, May, & Lorentsen, 2018; Vihtakari et al., 2018), and may vary considerably within small areas (Sankaranarayanan, 2007). At smaller spatial scales we found evidence for cross-species shared responses within about a third of small-scale regions and sites. Positive covariance in phenology at a local scale may be driven by several factors, such as local habitat or weather conditions (Porlier, Charmantier, Bourgault, Perret, & Blondel, 2012); abundance and phenology of prey (Frederiksen et al., 2005); inter- (Schoener, 1974) and intra-specific competition for food (Lewis, Sherratt, Hamer, & Wanless, 2001), social interaction – which has been implicated as an influence on intraspecific annual variation (Youngflesh et al. 2018), but might also arise between species – or a combination of effects. Small-scale physical features potentially cause subtle differences in conditions at each site despite site proximity, which could result in the observed differences in covariance between sites.

In terms of species effects, we detected significant positive covariance responses across populations of only one species, the black-legged kittiwake, with timing of breeding in populations from both sides of the Atlantic and spanning almost all of the breeding range tending to vary in tandem by ±6 days. In the North Atlantic, the majority of kittiwakes from most populations winter in the Labrador Sea, and one explanation for the covariance in phenological response is that they experience similar conditions during this period (Bogdanova et al., 2017; Frederiksen et al., 2012). It is plausible that water temperature over the winter, via its effect on resources, may determine when kittiwakes return to waters around their colonies, with carry-over effects on timing of breeding. Although there was significant among-year covariance in laying dates of kittiwakes across breeding sites, this only explained an average of 27.1% of the total among-year variance experienced by each population (min. = 11.97% [Hornøya], max. = 78.18% [Prince Leopold Island]), and correlations in lay date decreased with distance between sites. As kittiwakes are restricted to foraging on the water's surface, this may make them more responsive to environmental effects on local conditions than other species that can dive (Furness & Tasker, 2000). It is evident that kittiwakes may therefore be sensitive to environmental conditions across multiple spatial scales (Frederiksen et al., 2004).

With the exception of the black-legged kittiwake, we found no shared variance across populations of the same species, which implies that they do not respond similarly to a spatially consistent driver. A consequence of the low amount of regional synchrony for all species other than the kittiwake is that species may be somewhat buffered by a spatial portfolio effect (Schindler, Armstrong, & Reed, 2015). For instance, if extreme weather negatively impacts a population at one stage of the breeding season, a population at a different stage of reproduction elsewhere may experience less severe effects, thereby promoting stability at higher aggregate levels such as multiple populations of species at the regional or meta-population level

(Schindler et al., 2015). This may benefit the resilience of North Atlantic seabird species (Bogdanova et al., 2017; Fayet et al., 2017) in the face of wide-scale perturbations (Schindler et al., 2015) expected under future climate scenarios (Stocker et al., 2013).

We found that residual variance for European shags (i.e., between-year variance in lay date within a population, after all other terms have been taken into account) greatly exceeded the levels estimated for other species in the analysis (Table 3). European shags are partial migratory whereby a proportion of the population remain resident at the breeding colonies throughout the year, and most migrant individuals make shorter-distance movements than the other study species (Grist et al., 2014; Moe et al. 2021), so may be more sensitive to local conditions, such as abundance of forage fish (Lorentsen, Anker-Nilssen, Erikstad, & Røv, 2015) and have an unusually high capacity to adjust laying dates accordingly. While auk populations in our analysis do remain in the North Atlantic over winter and spring, many migrate to a variety of different areas (Fayet et al., 2017; Frederiksen et al., 2016), although it should be noted that synchronised survival in Atlantic puffin has been attributed to an overlap in non-breeding grounds of some Norwegian populations used in this analysis (Reiertsen et al., 2021). This suggests that the conditions driving auk phenology are unlikely to be consistent for all populations. Finally, the tern species included in this analysis (common, roseate and Arctic) are all long-distance migrants, and individuals from the same or different breeding sites may take alternative migration routes, at different times, and to different destinations (Becker et al., 2016; Egevang et al., 2010; Mostello, Nisbet, Oswald, & Fox, 2014; Nisbet, Arnold, Oswald, Pyle, & Pattern, 2017), potentially experiencing different conditions. Further research comparing laying dates of tracked individuals known to have similar migration strategies would therefore elucidate the extent to which phenology covaries between individuals within and across colonies (Grecian et al., 2016).

We restricted our analysis to include datasets of eight or more years in duration, but in some instances the time series overlap was low, reducing our ability to infer precise covariances. Our simulations (appendix 2) revealed that where time series are short and with limited overlap our power to detect a variance of 20 could fall below 0.8. Whilst the posterior median for year (co)variance was < 20 for 29 of 33 terms in our core model (Table S2), in 22 of these cases the 2.5% CI was removed from zero (i.e., variance was significant) or the upper 97.5% CI was < 20 (i.e., we can infer variance was low). Nonetheless there were cases where our CIs were broad and we anticipate that repeating these analyses in the future will improve precision thereby allowing additional insights to be gleaned. While our model structure did not allow for negative covariance between phenological time series, when we compared pairwise estimates of phenological correlations expected under our model to those obtained from raw data we found a good correspondence between the two (Figure S5). On this basis we infer that observed negative covariances are consistent with what one would expect to observe by chance when sample sizes are small, and the true covariance is close to zero. Finally, our analysis considered the effects of conditions at the breeding and main wintering grounds, but did not take into account pre-breeding, post-breeding, staging and migration routes. More detailed tracking information would allow future analyses to take this into account.

For many plant and animal taxa great strides have been made in identifying the aspects of the environment that give rise to temporal or spatial variation in phenology (e.g., Cohen et al. 2018; Thackeray et al. 2016), often finding that temperature in the two months or so preceding phenology has an important role. There may be other groups that are similar to seabirds in that identification of drivers of phenology is more challenging, perhaps due to environmental drivers influencing condition over a much longer period – as appears to be the case in red deer

(Stopher, Bento, Clutton-Brock, Pemberton, & Kruuk, 2014). In such cases and where data exist for multiple populations we anticipate our alternative approach will be useful. A second potential application of among year population phenology covariance estimation is to the study of communities. While many studies focus on individual species, a small number of studies have started to examine how phenological shifts influence synchrony and interactions at the level of the community (CaraDonna, Iler, & Inouye, 2014). We propose that the among population year covariance in phenology could be used to arrive at a measure of cohesiveness of the phenological response across a community that could be compared among sites or trophic levels. For instance, one measure of phenological cohesiveness at a site could be calculated as the *shared year variance* divided by *the mean of the total annual variances estimated across species (i.e., where total annual variance for a species = the shared year variance plus the annual variance unique to the species)*, giving a value that varies between 0 = no cohesiveness and 1 = perfect cohesiveness. In the case of seabirds this value would tend to be very low, whereas if it were applied to the leaf out phenology of temperate trees we would expect to see a much higher value (Roberts, Tansey, Smithers, & Phillimore, 2015).

Phenology is widely used as a measure of species' response to environmental change, yet for higher trophic level species, particularly those that are highly mobile, the drivers are often poorly understood. We estimated covariance of average lay date across multiple populations of seabirds, to identify the scale at which drivers of phenology operate in this group of highly mobile top predators. For many populations, the majority of annual variance in breeding time was at the site level, highlighting the importance of local conditions in driving phenology for some species in this taxonomic group. Should broad-scale perturbations cause conditions to deteriorate rapidly across a large region, we conclude that the near absence of regional phenological covariance, apart from black-legged kittiwakes, may allow for increased

resilience at the meta-population scale via phenological portfolio effects. Further research combining individual tracking and phenology data could reveal drivers operating at additional spatial, temporal and biological scales, for example conditions experienced by individuals or populations on migration routes, stop-overs, or during autumn or spring periods. Identifying the multiple scales at which phenology is driven will allow us to further understand how organisms respond to fluctuating conditions, and how they may continue to do so in the future.

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Conflict of interest
The authors declare no conflict of interest.

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