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Global phenological insensitivity to shifting ocean temperatures among seabirds

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Reproductive timing in many taxa plays a key role in determining breeding productivity¹, and is often sensitive to climatic conditions². Current climate change may alter the timing of breeding at different rates across trophic levels, potentially resulting in temporal mismatch between the resource requirements of predators and their prey³. This is of particular concern for higher-trophic-level organisms, whose longer generation times confer a lower rate of evolutionary rescue than primary producers or consumers⁴. However, the disconnection between studies of ecological change in marine systems makes it difficult to detect general changes in the timing of reproduction⁵. Here, we use a comprehensive meta-analysis of 209 phenological time series from 145 breeding populations to show that, on average, seabird populations worldwide have not adjusted their breeding seasons over time (-0.020 days yr⁻¹) or in response to sea surface temperature (SST) (-0.272 days °C⁻¹) between 1952 and 2015. However, marked between-year variation in timing observed in resident species and some Pelecaniformes and Suliformes (cormorants, gannets and boobies) may imply that timing, in some cases, is affected by unmeasured environmental conditions. This limited temperature-mediated plasticity of reproductive timing in seabirds potentially makes these top predators highly vulnerable to future mismatch with lower-trophic-level resources².

The effects of rising global temperatures are having a profound impact on terrestrial and aquatic biota, influencing species abundance, distributions, behaviours and interactions⁶. Changes in phenology—the timing of seasonally recurring life-history events—are one of the most apparent responses to rising global temperatures. At higher latitudes, many spring and early summer events are occurring earlier over time across a suite of terrestrial, freshwater and marine ecosystems^{2,3}. As the timing of breeding affects the abiotic conditions and biotic interactions to which parents and their offspring are exposed⁷, breeding phenology is expected to play a key role in mediating the relationship between environmental temperature and fitness¹.

Globally, many species at higher trophic levels have poor conservation status⁸. Current evidence indicates that the phenology of species occupying higher trophic levels is less responsive to environmental change than that of primary producers and consumers²⁻⁴, making them particularly susceptible to trophic mismatch and the associated negative demographic consequences^{3,9}. However, previous studies that have combined estimates of phenological sensitivity (that is, phenological change over time or in response to temperature) of multiple high-trophic-level species to global change^{2,3,9-13} have typically included only a few species or have focused primarily on mean responses within taxa, trophic levels or regions. Moreover, most earlier multi-species analyses have ignored sampling error in

A full list of affiliations appears at the end of the paper.

estimates of phenological sensitivity^{9,11–14} (but see ref. ² for an alternative approach) or sources of statistical non-independence, such as phylogeny (but see ref. ¹⁵). As such, it is not clear whether the variation in rates of phenological sensitivity reported in the literature is simply the result of the sampling error variance that is characteristic of regression using short time series^{16,17}, or represents true variation. If true variation in phenological sensitivity exists, this may arise where the strength of plasticity covaries with attributes of particular species (for example, body size, feeding ecology or migration strategy), biogeography (for example, upwelling, latitude, hemisphere or ocean basin) or an interaction between two or more of these effects. Testing the influence of these variables on variation in phenological sensitivity at a global scale across multiple populations will help to ascertain general patterns and highlight those taxa and regions most likely to be vulnerable to climate change.

Seabirds are one of the best-studied groups of higher-trophic-level organisms, and are considered here to include species from the orders Sphenisciformes, Procellariiformes, Suliformes, Pelecaniformes and Charadriiformes. Found throughout the world's oceans, they range in size from ~20 g to ~30 kg, and generally exhibit long generation times and slow, inflexible life histories. They are more threatened than any other comparable avian group, with the conservation status of many species rapidly deteriorating¹⁸. Seabirds exhibit considerable interspecific variation in feeding strategies, with breeding season foraging ranges varying from <10 to >1,000 km and foraging depths from <1 m to 100s of metres. Outside the breeding season, some species remain close to their colony while others undertake the longest migrations known in the animal kingdom¹⁹.

Studies of seabird breeding phenology have reported a variety of different trends over time²⁰. Among the local environmental drivers of phenology that have been identified, sea surface temperature (SST) is widely reported to correlate with the distribution, abundance and phenology of both local and migratory prey populations²¹. Changes in temperature driven by climate change could be critical, generating a mismatch with prey availability (see further discussion in the following)²². Directional SST changes and fluctuations have been recorded in the waters surrounding many seabird breeding sites (Fig. 1a,b and Supplementary Fig. 1), with both metrics of change varying geographically. Large-scale climatic variables, such as the North Atlantic Oscillation and the Southern Oscillation Index may also explain annual variations in reproductive phenology (reviewed in ref. ¹³). However, using large-scale proxies instead of data on specific climate drivers (for example, SST) may lead to spurious and simplistic assumptions of climate–ecology dynamics²³. Furthermore, proxies at this scale are not amenable to global analyses, because regional proxies are not equivalent or comparable in a single analysis²³. Thus, variation in the sensitivity in timing of breeding across species and regions remains unclear (but see ref. ¹⁷). Due to their trophic position, global distribution and the numerous long-term studies available, seabirds constitute a tractable and powerful group for a global meta-analysis of breeding phenology. Such an analysis allows us to not only make general inferences about the degree to which breeding phenology has changed both over time and in relation to SST, but also about the life history traits underpinning variation in phenological responsiveness (Table 1). Finally, it allows us to examine predictors of between-year phenological variation, with high between-year variance potentially indicative of phenological sensitivity to one or more unspecified environmental drivers.

We applied a phylogenetic mixed model meta-analysis to a global data set comprising 209 phenological time series of breeding dates obtained from 145 seabird populations (Fig. 1c; median number of years per time-series = 18, min = 5, max = 48; median sample size per year per time-series = 72, min = 6, max = 936), covering 61 species from five main orders. These taxonomic groups exhibit

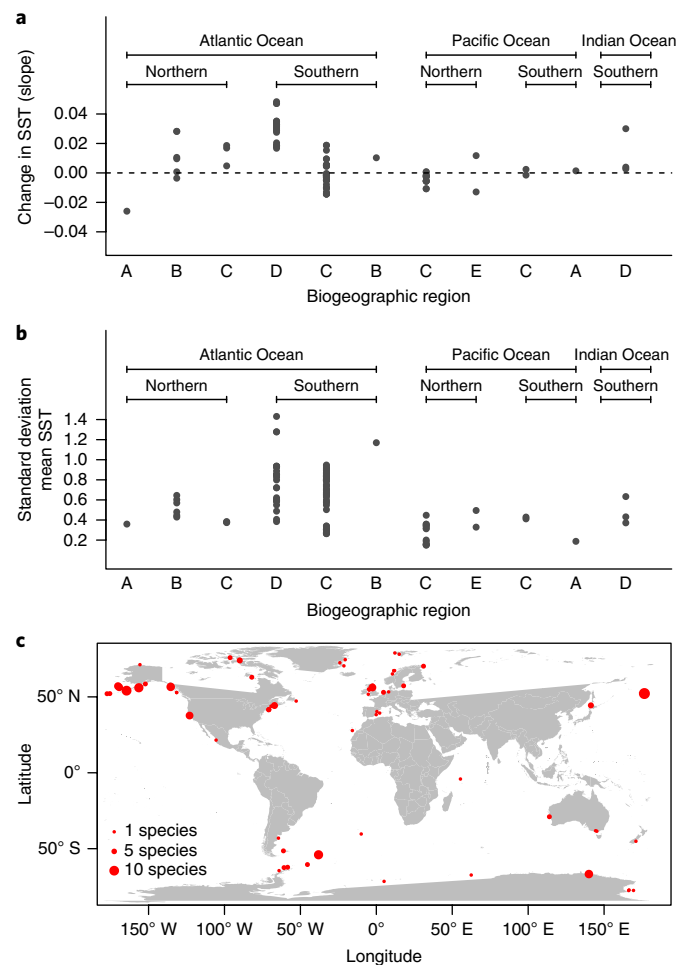


Fig. 1 | SST trends and map of study sites included in the analyses. a, Across-year temporal changes in mean SST in the three months prior to breeding across all biogeographic regions, represented by slopes between 1982 (when SST time series began) and 2015 for each site. Each point represents a slope, with positive slopes indicating warming and negative slopes indicating cooling. **b**, Standard deviation from the mean SST at each site during the same study period. A = polar, B = subpolar, C = temperate, D = subtropical, E = tropical. **c**, The full data set comprises 209 time series from 61 seabird species and across 64 locations, collected between 1952 and 2015. The data include slopes for 32 genera, 9 families and 5 orders (Sphenisciformes (6), Procellariiformes (15), Suliformes (3), Pelecaniformes (5), Charadriiformes (32)) and span all seven continents. The underrepresentation of tropical time series is due to a combination of a paucity of long-term data for these regions and the asynchronous nature of breeding in many tropical species, which diminishes the informativeness of measuring the annual phenological central tendency.

a wide variety of life-history, migration and foraging strategies, and are distributed from the equator to the poles across all principal oceanographic regimes. Meta-analyses provide a robust approach for identifying average effect sizes across studies, and for identifying predictors of variation around the average²⁴. Here, we (1) characterized latitudinal trends in the mean and between-year variance of seabird breeding phenology (laying and hatching dates), (2) estimated the mean sensitivity of breeding phenology over time and in relation to SST in the waters around the sampled colonies, and (3) identified predictors (body size, foraging and migration strategy, biogeography and phylogeny) of inter- and intraspecific variation around the mean response (mean, variance and both sensitivity

Table 1 | Predictions of the effect of life history and environmental variables on phenology from the four key models

Prediction		Reason
Mean phenology		
Phenology will be later:	at high latitudes	due to stronger photoperiodic cues at high latitudes^{25,26}.
Between-year variance		
Higher between-year variance will be observed in:	smaller birds	as they are more sensitive to environmental change ³⁷ .
	residents and short-distance migrants	because they may be more sensitive to conditions at the breeding site²⁸.
	surface feeders	which are more constrained in the water column, meaning that they can only exploit prey near the water surface ³⁸ .
	populations in upwelling zones	due to high variation in productivity in these areas^{39,40}.
Temporal trends		
A steeper negative slope will be observed in:	birds with smaller body size	to avoid incurring fitness costs of thermoregulation when breeding at higher temperatures³⁷.
	birds that feed at the surface	as they may be more sensitive to the timing at which lower-trophic-level prey are available ³⁸ .
	high latitudes	because polar systems are experiencing warming faster than other areas ⁴¹ .
SST trends		
A steeper negative slope will be observed in:	birds with smaller body size	to avoid incurring fitness costs of thermoregulation when breeding at higher temperatures ³⁷ .
	residents and short-distance migrants	as they are likely to respond to conditions at the breeding site more readily than species which overwinter in different basins ²⁸ .
	birds that feed at the surface	as they are predicted to be more sensitive to the timing at which lower-trophic-level prey are available ³⁸ .
	high latitudes	as polar systems are experiencing warming faster than other areas ⁴¹ .

Predictions in bold indicate they are supported by the model.

measures) of each species/population (for specific predictions see Table 1 and Methods).

With increasing latitude, we found that breeding occurred later in the calendar year and that between-year variance in phenology decreased (Supplementary Table 1 and Fig. 2a,b), which agrees with earlier results obtained from regional studies^{25,26}. The low variance at high latitudes may arise due to the shortened period of favourable conditions and the strong seasonal cue that photoperiod provides, whereas the much greater variance at lower latitudes may relate to the reduction of seasonality and the relatively weaker cue from day length²⁷.

Overall, the between-year variance in lay date among populations in our data set ranged from <1 in the black-browed albatross (*Thalassarche melanophris*) at New Island, Falklands, consistent with 95% of annual means occurring within a three-day period, to 1,573 in the blue-footed booby (*Sula nebouxii*) at Isla Isabel, Mexico, consistent with 95% of annual means occurring within a five-month period. Examination of life-history traits potentially explaining this variation (Supplementary metadata) indicated that resident species were more variable than migrants (Supplementary Table 2 and Fig. 3b). This result is in accordance with results for terrestrial birds²⁸ and may arise if the laying dates of resident species are more sensitive to local foraging conditions

as a cue to initiate breeding in anticipation of the timing of future resources. Controlling for biogeographic trends, we found that between-year variance in laying date is highly phylogenetically conserved ($H^2=0.84$, 95% credible interval (CI): 0.508–1, $n=208$, Supplementary Table 2). From inspection of the best linear unbiased predictors (BLUPs) for phylogenetic effects, the most threatened order¹⁸, Procellariiformes, particularly giant petrels and fulmars (Procellariidae) and albatrosses (Diomedeidae), stood out as least variable in timing of breeding. This response is consistent with a strong reliance on photoperiod as a cue²⁹. In contrast, we found that Pelecaniformes and Suliformes (cormorants, gannets and boobies) vary substantially among years in timing of breeding, suggesting that these species may adjust egg laying in relation to some aspect of the local environment (weather, oceanographic conditions or food availability) in the lead-up to the breeding season³⁰.

On average, seabirds showed no tendency to advance or delay breeding phenology over time (-0.020 days yr⁻¹, 95% CI: -0.160 – 0.129 , $n=209$, Fig. 3a). This is in agreement with previous studies of this species group^{9,20}, but the overall slope was much less steep than those from similar analyses of UK birds³ (mean = -0.19 days yr⁻¹), terrestrial and marine vertebrates³ (terrestrial mean = ~ -0.25 days yr⁻¹, marine mean = ~ -0.35 days yr⁻¹)

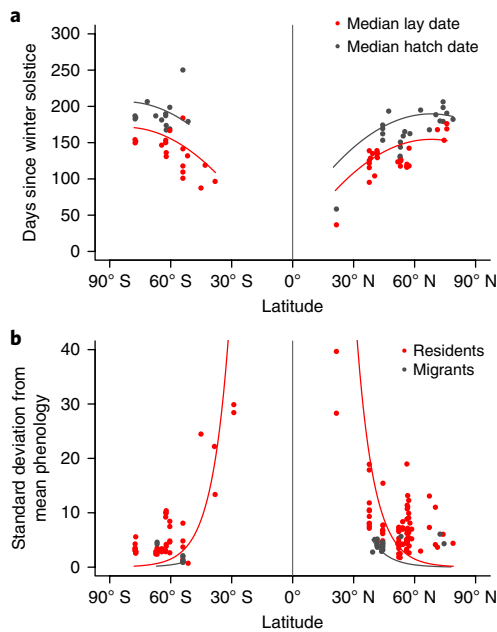


Fig. 2 | Mean and between-year variance in phenology separated by hemisphere. **a**, Differences in latitudinal gradient between Northern and Southern Hemispheres, where each data point (grey or red) represents the median timing of breeding of a population. Lines (grey = lay date, red = hatch date) represent the delay in phenology approaching the poles in days lat^{-1} , and were estimated using values from Supplementary Table 1. **b**, Between-year standard deviation in mean timing for residents (red dots) and migrants (grey dots). Lines are plotted from the ecological model and represent the median lay date in the mean year of study of an average surface-feeding resident bird, weighing 800 g, in a region where there is no major upwelling system. Nonlinearity in the plot is due to back calculation from the log scale.

or global estimates of marine species in general⁹ (mean = ~ -0.4 days yr^{-1}). We found limited evidence for true variation around the mean response (Supplementary Table 3), with 83% of the variation in raw slope estimates of phenology over time attributable to sampling error arising from linear regressions based on small data sets (Supplementary Table 4). Of the remaining true variation, we found that the mean slope estimates did not differ significantly among oceans (Supplementary Table 3). This result runs counter to previous studies of seabird breeding phenology, which have reported variation in long-term trends among biogeographic realms^{11,20}. However, we found some evidence that temporal response may vary among species at shared breeding sites (Supplementary Table 3), although sampling covariance between the different phenological measures is likely to inflate this variance estimate. Among-population variation makes it difficult to predict which species and sites will be most phenologically responsive to changing environments, as it implies that the degree of environmental sensitivity in seabird breeding may be determined by a combination of intrinsic and extrinsic factors³¹. Of the environmental or life-history variables we considered, body mass was the only significant positive predictor of the temporal trend (Supplementary Table 3), with larger-bodied species responding at a slower rate over time than smaller species, in accordance with our predictions (Table 1).

Globally, we found no evidence that seabirds as a group have shifted their laying date in relation to SST in waters around the breeding site in the three months preceding egg laying (mean = -0.272 days $^{\circ}\text{C}^{-1}$, 95% CI: -4.896 – 4.482 , $n = 108$, Fig. 3b, Supplementary Table 5). The average response is much shallower

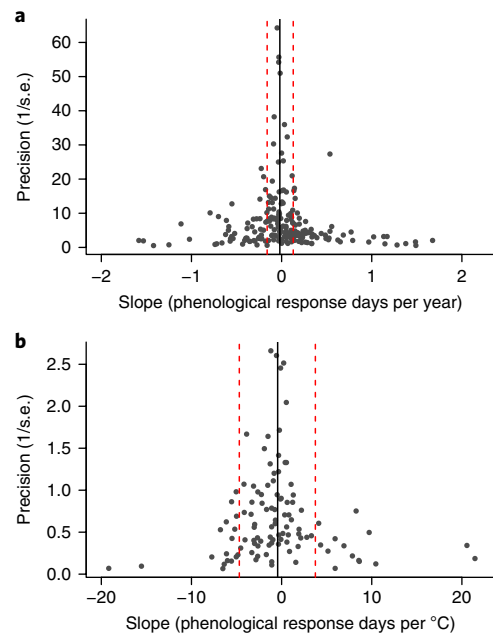


Fig. 3 | Funnel plots of phenological trends in relation to year and SST. **a, b**, Funnel plots in relation to year (**a**) and SST (**b**). Each point represents a slope estimate from the meta-analysis, with negative slopes indicating an advance and positive slopes indicating a delay, in phenological trends. Positioning of each point on the y axis indicates the precision (1/s.e.) of the estimate. Thus, points with higher precision are expected to converge on the true average response. Lines represent the posterior for the average response or intercept (black) and its 95% CI (dashed red) from the basic model (Supplementary Tables 3a and 5a). s.e., standard error.

than the average response of lay date to air temperature reported for 27 UK terrestrial birds (mean = -3.8 days $^{\circ}\text{C}^{-1}$ (air temperature))³². In broad agreement with the temporal analysis we found no evidence that true variation in the slope of the covariation with SST is predicted by phylogeny, species, biogeographic region or life-history traits. We did, however, find significant variation in slopes among sites, and the lowest BLUP was -2.96 days $^{\circ}\text{C}^{-1}$ (95% CI: -6.00 – 0.13) at Skomer Island, Wales, where SST in the focal time period has increased significantly by 0.6°C decade⁻¹ since 1982 (Supplementary metadata 1). In contrast, the most positive BLUP was 7.32 days $^{\circ}\text{C}^{-1}$ (95% CI: 4.96 – 9.73) at Southeast Farallon Island, California, which is located in a highly variable upwelling zone, where interannual variance in SST is higher than average (Fig. 1b and Supplementary metadata), a condition that might select for plasticity. So, although, on average, seabirds appear to be unresponsive to SST, we cannot rule out the possibility that some populations are temperature-sensitive in either direction.

That we could detect no trend in seabird phenology over time or in relation to SST (Supplementary metadata) suggests that if lower trophic levels are shifting in parallel with changing SST, seabirds, in general, may be at risk from increasing levels of trophic mismatch³³. To date, there are very few studies that have reported the slope of the phenology of poikilothermic seabird prey and lower trophic levels in relation to SST (but see ref. ²²). Differing rates of phenological response between seabirds and their food resources⁹ may leave them short of critical prey during the breeding season under future climate regimes. However, there is limited and mixed evidence on the frequency of climate-induced mismatch^{17,22}, and whether it has an impact on breeding success³⁴ or population dynamics³⁵. Alternatively, any negative fitness consequences of trophic asynchrony may be ameliorated by the ability

of some species to alter their behaviour, for example by switching prey or adjusting foraging effort^{22,36}.

Our study represents the most statistically rigorous and spatially representative meta-analysis to date of the reproductive phenology of a group of upper-trophic-level predators, seabirds. Contrary to previous assertions, we find that once sampling error has been taken into account, in most cases the phenology of seabirds shows no trend over time and appears to be largely insensitive to changing SST. While certain populations may be responding, most of the among-species variation in estimates of phenological sensitivity can be attributed to slope estimation error. Overall, this inflexibility in breeding phenology in relation to temperature may leave seabirds vulnerable to trophic mismatch arising from shifts in timing of their prey.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at <https://doi.org/10.1038/s41558-018-0115-z>.

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Author contributions

K.K., S.L., A.B.P., S.W., E.D. and R.P. conceived the study and wrote the manuscript. K.K. coordinated the study, compiled the data set and wrote the first draft of the manuscript. K.K. conducted the statistical analyses under the guidance of A.B.P. and with advice from S.L. and C.A.W. All others provided data and comments on later drafts of the manuscript.

Competing interests

The authors declare no competing interests.

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Methods

Data collection. To prevent an effect of publication bias and to ensure that positive, negative and neutral phenological trends were included, we used only raw time series (see PRISMA checklist). For each time series we used consistent methods to calculate slopes (that is, rate of phenological change), between-year variance and, crucially, standard error. Raw phenological data were compiled from a variety of sources between October 2015 and October 2016. We contacted 120+ known seabird researchers and owners of time series to request annual data on seabird breeding phenology and life history. Furthermore, requests were made via Twitter and at the World Seabird Conference in Cape Town (October 2015); the Pacific Seabird Group Annual Meeting in Oahu (February 2016); The Seabird Group conference in Edinburgh (September 2016); and the International Albatross and Petrel Conference in Barcelona (September 2016).

Data. Annual data on breeding phenology during the period 1952 and 2015 were the median or mean date of laying or the median, mean or first date of hatching of the study population, in units of ordinal days. Population was defined as an individual species at a breeding site. We only considered populations that breed seasonally during spring and summer (austral and boreal) months, as measures of phenological central tendency are not informative for species that breed asynchronously or subannually (that is, many tropical species¹⁹). Time series were required to be a minimum of five years for the temporal analysis and ten years for the analysis of SST, although the years did not need to be consecutive. Details of criteria used to choose the suitability of time series are provided in Supplementary Table 9, and the field methods used to collect each time series are outlined in the Supplementary Methods.

Monthly means of NOAA optimum interpolation (OI) sea surface temperature (SST) V2 for the period 1982–2015 were obtained from NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, a resource that provides interpolated in situ and satellite SST data on a one-degree grid⁴².

For each time series we characterized the biogeography where the colony was located. We collated information on the location (latitude and longitude) and hemisphere of each population, and for our primary fixed-effects model we assigned each location to one of the three main oceans: Atlantic, Pacific or Indian. Global climate zones (Equatorial, Tropical, Subtropical, Temperate, Subpolar or Polar) were identified using the classification from Trujillo and Thurman⁴³. These zones correspond to latitudinal bands of similar SST and are categorized by levels of precipitation, wind and water temperature⁴³. We combined hemisphere, ocean and global climate zone to identify 15 biogeographic regions (for example, North Atlantic Temperate, South Pacific Subpolar). Finally, we used the Longhurst Biogeographical Provinces to determine whether each location was situated within an Eastern Boundary (upwelling) zone⁴⁴. These are areas of high productivity within the marine environment, and are also highly variable across seasons, years and decades^{39,45}.

We collated data on several aspects of the ecology and life history of each species that may affect the phenological slope (with year or temperature), mean or between-year variance. These data were provided by authors and supplemented using the following online resources: www.audubon.org, www.birdlife.org, nzbirdsonline.org.nz, www.bird-research.jp and www.npolar.no (Supplementary metadata). Feeding strategy was categorized either as surface feeder (feeding < 1 m below the surface), diver (feeding > 1 m below the surface) or kleptoparasite/predator (part-time marine foragers). Species that seek out prey by diving under water may be able to exploit a wider range of prey than those constrained to feeding on the surface (< 1 m depth), thus reducing the necessity to adjust breeding phenology to buffer mismatch^{46–48}. We also compiled data on average body mass of every species (Supplementary metadata), as small-bodied seabird species are predicted to be more sensitive to temperature change due to the higher cost of thermoregulation^{37,49}. Furthermore, body mass can be used as a proxy for trophic level, which is difficult to classify explicitly in seabirds⁵⁰. We used log body mass in analyses. The migration strategy of individuals from each population was assigned based on the behaviour of the majority (>80%) of individuals. Long-distance trans-equatorial migrants, and species that spend the winter outside the sector in which they breed were categorized together as 'migrants', and those that remain in the same ocean sector throughout the year were classified as 'residents'. Sectors were defined as North Atlantic, Mediterranean, South Atlantic, Southern Ocean-Atlantic sector, North Pacific, South Pacific, Southern Ocean-Pacific sector, Indian and Southern Ocean-Indian sector.

We took into account phylogenetic relationships among species using 100 samples of the pseudo-posterior species tree⁵¹ using the Hackett et al. backbone⁵².

Statistics. We used the *MCMCglmm* package⁵³ in R (v 3.2.2), to fit Bayesian generalized linear mixed-effects models (GLMMs). We adopted a random effects meta-analytic (REMA) approach, estimating both fixed and random effects, while taking the sampling error characteristic or regression using short time series into account^{16,24}.

We included cross-classified random effects to account for and estimate sources of variance, although not every random variable was included in each model (Supplementary Tables 1–5). The model was of the form

$$y_i = \mu + \beta x_i + \alpha_{f[i]} + s_{f[i]} + b_{g[i]} + l_{h[i]} + p_{f[i]} + e_i + m_i \quad (1)$$

where y is the phenological response variable of each time series i , μ represents the global mean response (intercept), and βx_i the fixed effects. For each response variable we also included a null model with the intercept as the sole fixed effect, as this allowed us to infer which random terms captured most of the variance.

$\alpha_{f[i]}$ is the effect of phylogenetic non-independence due to shared evolutionary history¹⁶ for the f th species. $s_{f[i]}$ is the non-phylogenetic species-specific effect for the f th species. Spatial variation was accounted for via two terms, g th biogeographic region ($b_{g[i]}$) (see Supplementary metadata) and h th site ($l_{h[i]}$). In certain analyses we included multiple measures/traits for a time series and in these cases we could fit the interaction between site and species (population) ($p_{f[i]}$), which provided us with an estimate of intraspecific geographic variation that is unique to each (j th) population. In these cases the residual term (e_i) captures variation within a site and species (population), and we allowed this variance to be heterogeneous across different phenophases (that is, median lay date, mean lay date, first hatch date, median hatch date, mean hatch date). In other analyses only a single measure/trait was included and in such instances $p_{f[i]}$ was not estimable. In this case the residual term captured variance both due to intraspecific geographic variation that is unique to each species and differences among phenological measures/traits. Our response variables were themselves estimates that have error associated with them and we incorporated sampling error variances as m_i , which means that the analyses were weighted. For the sampling error term, the among-observation variance was set to 1, and for all other random terms the variance was estimated. The specification of these models assumed that random effects for different measures were perfectly correlated. To test whether this impacted our estimation of phylogenetic signal we then relaxed this assumption and estimated the covariance between random effects for measures of laying and hatching phenology (Variance structure of models section).

We calculated phylogenetic signal^{16,54} in our response variables (H^2), that is, the tendency of closely related species to resemble each other more than distantly related species, from σ_a^2 (the phylogenetic variance) and σ_s^2 (the species variance)

$$H^2 = \frac{\sigma_a^2}{(\sigma_a^2 + \sigma_s^2)} \quad (2)$$

We considered the following four response variables and clearly identify where analyses are post hoc rather than a priori.

Multi-year mean phenology. We estimated the mean phenology (for example, average laying date overall) across all years for each time series. Measurement variance in the mean was quantified as the squared standard error. To examine latitudinal trends in mean date we included both absolute latitude and its quadratic term (to test both linear and nonlinear effects); hemisphere; and the interaction between latitude and hemisphere as fixed effects. Additional fixed effects were trait (laying and hatching date) and phenological measurement (mean, median, first date). See Table 1 for predictions.

In post hoc tests, mean phenology is delayed as latitude increases in both hemispheres, with a significant quadratic term, such that the slope appears to reach an asymptote toward the poles (Fig. 2 and Supplementary Table 1). However, seabirds at low latitudes are underrepresented in this study. When we removed three low-latitude data points, there was no support for the quadratic relationship (Supplementary Table 1) but the positive linear relationship between latitude and breeding phenology remained (posterior mean = 0.81 days lat⁻¹, 95% CI: 0.33–1.29, $n = 206$, Supplementary Table 1). The intercepts of each measure of phenology (that is, mean laying date, first hatching date) differed significantly, although a test including the interaction between latitude and phenological measure revealed no difference in their latitudinal slopes (Supplementary Table 1).

Between-year variance in phenology. The response variable (equation (3)) was based on the natural log of the between-year standard deviation (s) of each population ($\ln s$), taking into account the number of years (n). The sampling variance of this measure was quantified as ($s_{\ln s}^2$) as in equation (4)⁵⁵:

$$\ln \hat{\sigma} = \ln s + \frac{1}{2(n-1)} \quad (3)$$

$$s_{\ln s}^2 = \frac{1}{2(n-1)} \quad (4)$$

The model included phenological trait and measure, latitude and its quadratic term, hemisphere, presence or absence of upwelling and, to test for decadal patterns, the mean year of each time series as fixed effects. We included body mass, foraging and migration strategies in the same model to investigate the effects of life-history traits on between-year variance. See Table 1 for predictions.

Temporal trend in phenology. We estimated the linear slope (and standard error) of phenological change over time for each measure (median, mean, first date) and trait (laying or hatching date) of a population using generalized least squares (GLS) in nlme⁵⁶, fitting an autoregressive model of order 1, AR(1)⁵⁷, to take into

account temporal autocorrelation in each individual time series. We used these slope estimates in a meta-analysis, and included the squared standard error of the slope to weight the analysis. We included three types of fixed effect: methodology (trait, measure, mean year of time series), life history and ecology (body mass and foraging strategies) and biogeography (ocean basin, hemisphere, latitude). See Table 1 for predictions. We did not make predictions about which ocean basins or hemisphere might show the steepest slopes, but allowed the response to differ among ocean basin and hemispheres in our model.

Our primary ecological fixed-effects model categorized locations into one of the three main ocean basins (Atlantic, Indian, Pacific), and included the interaction between latitude and hemisphere as an additional parameter. This approach considered the life histories of wide-ranging polar species, which may have large foraging ranges. Yet many species forage near to the colony, or may have evolved alongside the unique oceanographic features of polar systems³⁸. In a post hoc test, we considered these species by re-categorizing ocean basins into five discrete water bodies (Arctic, Atlantic, Indian, Pacific, Southern) and ran our ecological model again, replacing the three ocean variable with five oceans, and removing the interaction between latitude and hemisphere.

Phenological response to SST. For each time series we averaged monthly temperature data from the local grid cell for the pre-breeding period (three months, two months and one month prior to laying, including the month in which laying began) each year. In some cases sea ice cover meant that an average temperature was not estimable and affected time series were excluded from this analysis. We restricted this analysis to laying dates only, representing each population with a single time series in declining order of preference of measurements: median, mean and first date. In populations for which we only had data on timing of hatching, we back-calculated lay dates using information on the duration of incubation period and average number of eggs. These data were provided by authors and supplemented using the following online resources: www.audubon.org, www.birdlife.org, nzbirdsonline.org.nz, www.bird-research.jp and www.npolar.no (Supplementary metadata). Where the incubation period was reported as a range, we calculated the central value; this method was used for 70 time series (Supplementary metadata).

For each colony we calculated the slope and associated standard errors of the phenological response to SST (days °C⁻¹) using the GLS methods as described for the temporal trends, but retaining year as an additional predictor, in order to de-trend the data and allow us to consider the effects of SST independently of time (Supplementary metadata). We compared among pre-breeding on the basis of the Akaike information criterion (AIC) and found very little difference, as expected given the overlap between time periods and month-to-month temporal autocorrelation is SST. Across time series the three-month period had the lowest mean AIC (two-month mean ΔAIC = 0.02, one-month mean ΔAIC = 0.50) and for consistency we used this time period in subsequent analyses.

We then passed the slopes of phenology regressed on three-month SST into a meta-analysis, with the squared standard error of the slope included for weighting. We tested similar predictions as in analysis (3) above, predicting that timing of laying would be more sensitive to pre-breeding SST in species with smaller body mass, that feed on the surface, or that remain in the same ocean basin over winter. Measure, trait and mean year of study were also included as fixed effects.

All models were run for 30,000 iterations on each phylogenetic tree sample, discarding the first 10,000 as burn-in, and sampling every 10th iteration. We repeated this process over 100 phylogenetic trees, and the pooled posterior distributions take into account both model and phylogenetic uncertainties³⁹. Parameter-expanded priors were used for all random effects except the residual, which followed an inverse Wishart distribution. Plots of the mean and variance of the posterior distribution were examined to assess autocorrelation in the posterior samples. Statistical significance of fixed effects was inferred where 95% credible intervals did not span zero.

Variance structure of models. Our data set contains five phenophases: median lay date (1), mean lay date (2), first hatch date (3), median hatch date (4) and mean hatch date (5). The core models (with the exception of temperature) run under the assumption that within the residual term (ϵ_i) the variance would be heterogeneous, with each phenophase varying independently of the other four (equation (5)). We used the `idh()` variance structure function in the MCMCglmm package³³. This is consistent with phenophases being uncorrelated at the residual level (that is, covariance = 0) but at the other random effects the correlation between phenophases is assumed to be 1.

$$V_{\epsilon_i} = \begin{bmatrix} V_{1,1} & 0 & 0 & 0 & 0 \\ 0 & V_{2,2} & 0 & 0 & 0 \\ 0 & 0 & V_{3,3} & 0 & 0 \\ 0 & 0 & 0 & V_{4,4} & 0 \\ 0 & 0 & 0 & 0 & V_{5,5} \end{bmatrix} \quad (5)$$

These assumptions can be relaxed for each random effect and the covariance between phenophase can be estimated. We used the `us()` variance structure function (equation (6)), where V is variance, C is covariance and RE is random effect:

$$V_{RE} = \begin{bmatrix} V_{1,1} & C_{1,2} & C_{1,3} & C_{1,4} & C_{1,5} \\ C_{1,2} & V_{2,2} & C_{2,3} & C_{2,4} & C_{2,5} \\ C_{1,3} & C_{2,3} & V_{3,3} & C_{3,4} & C_{3,5} \\ C_{1,4} & C_{2,4} & C_{3,4} & V_{4,4} & C_{4,5} \\ C_{1,5} & C_{2,5} & C_{3,5} & C_{4,5} & V_{5,5} \end{bmatrix} \quad (6)$$

Allowing slopes of phenophases to covary for every random effect may result in a more informative estimate of phylogenetic signal (that is, perhaps signal is observed at one stage of reproduction but not another), but requires a large amount of data at each level to confidently estimate multiple (co)variances. As our data set was not large enough to run models with fully unstructured (co)variance, we only estimate the covariance between lay and hatch dates. We restructured the covariance matrix for each random effect (equation (6)) into a 2 × 2 grid (equation (7)):

$$V_{RE} = \begin{bmatrix} V_{lay,lay} & C_{lay,hatch} \\ C_{lay,hatch} & V_{hatch,hatch} \end{bmatrix} \quad (7)$$

Thus, three slopes (lay date, hatch date and the covariance between the two) were estimated for each random effect (phylogeny; species; biogeographic region; location and species:location). We ran the three key models (between-year variance, temporal and SST) using this error structure to assess whether any of our key insights were sensitive to the assumption that lay and hatch dates are perfectly correlated.

When the assumption of perfect correlation between the two measures was relaxed, we found that phylogenetic signal remained significant for the variance and SST models (Supplementary Tables 6 and 8). We also found some evidence for phylogenetic signal in the temporal model (Supplementary Table 7). These results are in agreement with the key findings of our core models.

Data availability. The authors declare that all biological data generated and analysed in this study are available within the article, its Supplementary Information and in the following repository: <https://github.com/katkeogan/seabird-metaanalysis>. The NOAA optimum interpolation (OI) sea surface temperature (SST) V2 data that the support the findings of this study are available from NOAA/OAR/ESRL Physical Sciences Division, <http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html>. The phylogenetic trees generated and analysed in this study were obtained from BirdTree, www.birdtree.org.

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