# Global phenological insensitivity to shifting ocean temperatures among seabirds

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## Abstract

Reproductive timing in many taxa plays a key role in determining breeding productivity[1] and is often sensitive to climatic conditions[2]. Current climate change may alter timing of breeding at different rates across trophic levels, potentially resulting in temporal mismatch between the resource requirements of predators, and their prey[3]. 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 consumers[4]. However, the disconnection between studies of ecological change in marine systems makes it difficult to detect general patterns of timing of reproduction[5]. 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 resources[2].

The effects of rising global temperatures are having a profound impact on terrestrial and aquatic biota, including species abundance, distributions, behaviours, and interactions[6]. 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 advancing over time across a suite of terrestrial, freshwater and marine ecosystems[3,2]. As timing of breeding affects the abiotic conditions and biotic interactions to which parents and their offspring are exposed[7], breeding phenology is expected to play a key role in mediating the relationship between environmental temperature and fitness[1].

Globally, many species at higher trophic levels have poor conservation status[8]. Current evidence indicates that the phenology of species occupying higher trophic levels is less responsive to environmental change than that of primary producers and consumers[3,2,4], making them particularly susceptible to trophic mismatch and the associated negative demographic consequences[3,9]. However, previous studies which have combined estimates of phenological sensitivity (i.e. phenological change over time or in response to temperature) of multiple high trophic-level species to global change[3,2,9–13] have typically included few species or focused primarily on mean responses within taxa, trophic levels, or regions. Moreover, most earlier multi-species analyses have ignored sampling error in estimates of phenological sensitivity[9,11–14] (but see [2] for an alternative approach) or sources of statistical non-independence, such as phylogeny (but see [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 (e.g. body size, feeding ecology, migration strategy), biogeography (e.g. 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 ~20g to ~30kg, 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 deteriorating[18]. Seabirds exhibit considerable interspecific variation in feeding strategies, with breeding season foraging ranges varying from <10 to >1000 km and foraging depths from <1 m to 100s of metres deep. Outside the breeding season, some species remain close to their colony while others undertake the longest migrations known in the animal kingdom[19].

Studies of seabird breeding phenology have reported a variety of different trends over time[20]. 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 populations[21], of which the effects on higher trophic level organisms can be compared at global scales. Therefore, changes in temperature driven by climate change could be critical, generating a mismatch with prey availability (see further discussion below)[22]. Directional SST changes and fluctuations have been recorded in the waters surrounding many seabird breeding sites (Figure 1a, b, Supplementary Figure 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 variation in reproductive phenology (reviewed in [13]). However, using large-scale proxies instead of data on specific climate drivers (e.g. SST) may lead to spurious and simplistic assumptions of climate-ecology dynamics[23]. Furthermore, proxies at this scale are not amenable to global analyses, since regional proxies are not equivalent or comparable in a single analysis[23]. Thus, variation in the sensitivity in timing of breeding across species and regions remains unclear (but see [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 variance potentially indicative of phenological sensitivity to one or more unspecified environmental drivers.

We applied a phylogenetic mixed model meta-analysis to a global dataset comprising 209 phenological time series of breeding dates obtained from 145 seabird populations (Figure 1c. Median number of years/time-series = 18; min = 5; max = 48. Median sample size/year /time-series = 72; min = 6; max = 936), covering 61 species from five main orders. These taxonomic groups exhibit a wide variety of life-history, migration and foraging strategies, and are distributed from equator to 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 average[24]. Here, we (i) characterised latitudinal trends in the mean and between-year variance of seabird breeding phenology (laying and hatching dates), (ii) estimated the mean sensitivity of breeding phenology over time and in relation to SST in the waters around the sampled colonies, and (iii) identified predictors (body size, biogeography, phylogeny) of inter- and intra-specific variation around the mean response (mean, variance and both sensitivity measures) of each species/population (for specific predictions see Table 1 & 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, Figure 2a, b), which concurs 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 length[27].

Overall, the between-year variance in lay date among populations in our dataset 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 1573 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 meta-data) indicated that resident species were more variable than migrants (Supplementary Table 2, Figure 3b). This result is in accordance with results for terrestrial birds[28] 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 find that between-year variance in laying date was 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 the phylogenetic effects, the most threatened order[18], 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 cue[29]. In contrast, we find 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 season[30].

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, Figure 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 birds[3] (mean = -0.19 days yr$^{-1}$), terrestrial and marine vertebrates[3] (terrestrial mean = ~-0.25 days yr$^{-1}$, marine mean = ~-0.35 days yr$^{-1}$) or global estimates of marine species in general[9] (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 datasets (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 factors[31]. 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 $^{\circ}$C$^{-1}$, 95% CI: -4.896 – 4.482, $n$ = 108, Figure 3b, Supplementary Table

5). The average response is much shallower than the average response of lay date to air temperature reported for 27 UK terrestrial birds (mean = -3.8 days °$C^{-1}$ (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 °$C^{-1}$ (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 meta-data 1). In contrast, the most positive BLUP was 7.32 days °$C^{-1}$ (95% CI: 4.96 – 9.73) at Southeast Farallon Island, California, which is located in a highly variable upwelling zone, where inter-annual variance in SST is higher than average (Figure 1b, Supplementary meta-data), a condition that might select for plasticity. So, although on average, seabirds appear to be unresponsive to SST, we cannot rule out the possibility 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 meta-data), 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 mismatch[33]. 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 [22]). Differing rates of phenological response between seabirds and their food resources[9] 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 success[34] or population dynamics[35]. 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 sampling 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.

**Supplementary Information** is linked to the online version of the paper at www.nature.com/nature.

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## Author Contributions

KK, SL, ABP, SW, FD and RP conceived the study and wrote the manuscript. KK coordinated the study, compiled the dataset and wrote the first draft of the manuscript. KK conducted the statistical analyses under the guidance of ABP and with advice from SL and CAW. All others provided data and comments on later drafts of the manuscript.

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**Figure 1. SST trends and map of study sites included in the analyses.** a) Across year temporal changes in mean Sea Surface Temperature (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 dataset 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 spans 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 annual phenological central tendency.

**Figure 2. Mean and between-year variance in phenology separated by hemisphere. a)** represents the 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)** represents the between-year standard deviation in mean timing for residents (represented by 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 800g, in a region where there is no major upwelling system. The non-linearity in the plot is due to back calculation from the log scale.

**Figure 3*. Funnel plots of phenological trends in relation to year and sea surface temperature.* a)** represents year and **b)** represents sea surface temperature. 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% credible intervals (dashed red) from the basic model (Tables S3a, S5a).

**Table 1.** Predictions of the effect of life history and environmental variables on phenology from the four key models. Predictions in bold indicate they are supported by the model.

| **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 & short-distance migrants** | **because they may be more sensitive to conditions at the breeding site[28].** |
| | 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 temperatures[37].** |
| | in birds which feed at the surface | as they may be more sensitive to the timing at which lower trophic level prey are available[38]. |
| | at high latitudes | because polar systems are experiencing warming faster than other areas[41]. |
| **Sea Surface Temperature 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]. |
| | in residents & 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]. |
| | in birds which feed at the surface | as they are predicted to be more sensitive to the timing at which lower trophic level prey are available[38]. |
| | at high latitudes | as polar systems are experiencing warming faster than other areas[41]. |

## 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 (i.e. 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 which breed asynchronously or subannually (i.e. many tropical species[19]). 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 suitability of time series' are given 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 the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, a resource which provides interpolated *in situ* and satellite SST data on a one-degree grid[42].

For each time series we characterised the biogeography at the colony it 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 & Thurman (2014). These zones correspond to latitudinal bands of similar sea surface temperature and are categorized by levels of precipitation, wind and water temperature[43]. We combined hemisphere, ocean and global climate zone to identify 15 Biogeographic Regions (e.g. North Atlantic Temperate; South Pacific Subpolar etc.). Finally, we used the Longhurst Biogeographical Provinces to determine whether each location was situated within an Eastern Boundary (upwelling) zone[44]. These are areas of high productivity within the marine environment, and are also highly variable across seasons, years and decades[40,45].

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 online resources: www.audubon.org, www.birdlife.org, nzbirdsonline.org.nz, www.bird-research.jp and www.npolar.no (Supplementary meta-data). Feeding strategy was categorised either as surface feeder (feeding <1 metre below the surface), diver (feeding >1 metre below the surface), or kleptoparasite/predator (part-time marine foragers). Species which 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 metre 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 meta-data), 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 seabirds[50]. 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 which spend the winter outside the sector in which they breed were categorised together as "migrants", and those which 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, Southern Ocean-Indian sector.

We took into account phylogenetic relationships among species using 100 samples of the pseudo-posterior species tree[51] using the Hackett *et al.* (2008) backbone[52].

**Statistics** We used the *MCMCglmm* package[53] in R (v 3.2.2; R Core Team 2015), to fit Bayesian generalised linear mixed-effects models (GLMMs). We adopted a random effects meta-analytic (REMA) approach, estimating both fixed and random effects, while taking 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, though not every random variable was included in each model (see Tables S1-S5). The model was of the form

$$y_i = \mu + \beta x_i + \alpha_{f[i]} + s_{f[i]} + b_{g[i]} + l_{h[i]} + p_{j[i]} + e_i + m_i \qquad \text{eq. 1.}$$

where $y$ is the phenological response variable of each time series $i$, $\mu$ represents the global mean response (intercept), and $\beta x_i$ 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 history[16] 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 meta-data) 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) ($p_{j[i]}$), 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 (i.e. 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 $p_{j[i]}$ 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 on 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, below).

We calculated phylogenetic signal[16,54] in our response variables ($H^2$), i.e. the tendency of closely related species to resemble each other more than distantly related species, from $\sigma_a^2$ (the phylogenetic variance), and $\sigma_s^2$ (the species variance)

$$H^2 = \frac{\sigma_a^2}{(\sigma_a^2 + \sigma_s^2)} \qquad \text{eq. 2.}$$

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

(1) Multi-year mean phenology: we estimated the mean phenology (e.g. 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 non-linear 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.

*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 (Figure 2, 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 (i.e. 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).

(2) Between-year variance in phenology: the response variable (eq. 3) was based on the natural log of the between-year standard deviation ($s$) of each population ($\ln \sigma$), taking into account

the number of years (*n*). The sampling variance of this measure was quantified as ($s^2_{\ln \sigma}$) as in eq. 4[55]:

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

$$s^2_{\ln \hat{\sigma}} = \frac{1}{2(n-1)} \quad \text{eq. 4.}$$

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.

(3) 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 Generalised Least Squares (GLS) in nlme[56], 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 effects: 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 basis and hemispheres in our model.

*Post hoc test:* our primary ecological fixed effects model categorised 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 systems[58]. To consider these species we re-categorised 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.

(4) Phenological response to SST:  for each time series we averaged monthly temperature data from the local grid cell for the pre-breeding period (three, two 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 online resources: www.audubon.org, www.birdlife.org, nzbirdsonline.org.nz, www.bird-research.jp and www.npolar.no (Supplementary meta-data). Where incubation period was reported as a range, we calculated the central value; this method was used for 70 time series (Supplementary meta-data).

For each colony we calculated the reaction norms and associated standard errors of phenological response to SST (days $^{o}C^{-1}$) 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 meta-data). We compared among pre-breeding on the basis of 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 (2 month mean $\Delta$AIC = 0.02, 1 month mean $\Delta$AIC = 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 (3) above, predicting that timing of laying would be more sensitive to pre-breeding SST in species with smaller body mass, which 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 uncertainties[59]. 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 dataset 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 ($e_i$) the variance would be heterogeneous, with each phenophase varying independently of the other four (eq. S1). We used the idh() variance structure function in the MCMCglmm package[53]. This is consistent with phenophases being uncorrelated at the residual level (i.e. covariance = 0) but at the other random effects the correlation between phenophases is assumed to be 1.

$$\boldsymbol{V}_{e_i} = \begin{bmatrix} V_{1,1} & 0 & 0 & 0 & 0 \\ 0 & V_{2,2} & 0 & 0 & 0 \\ 0 & 0 & V_{3,3} & 0 & 0 \\ 0 & 0 & 0 & V_{4,4} & 0 \\ 0 & 0 & 0 & 0 & V_{5,5} \end{bmatrix} \quad \text{eq. S1}$$

These assumptions can be relaxed for each random effect and the covariance between phenophase can be estimated. We used the us() variance structure function (eq. S2), where *V* = variance, *C* = covariance and $e_i$ = random effect.

$$\boldsymbol{V}_{e_i} = \begin{bmatrix} V_{1,1} & C_{1,2} & C_{1,3} & C_{1,4} & C_{1,5} \\ C_{1,2} & V_{2,2} & C_{2,3} & C_{2,4} & C_{2,5} \\ C_{1,3} & C_{2,3} & V_{3,3} & C_{3,4} & C_{3,5} \\ C_{1,4} & C_{2,4} & C_{3,4} & V_{4,4} & C_{4,5} \\ C_{1,5} & C_{2,5} & C_{3,5} & C_{4,5} & V_{5,5} \end{bmatrix} \quad \text{eq. S2}$$

Allowing slopes of phenophases to covary for every random effect may result in a more informative estimate of phylogenetic signal (i.e. 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 dataset 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 (eq. S2) into a 2 x 2 grid (eq. S3).

$$\boldsymbol{V_{R.E}} = \begin{bmatrix} V_{lay,lay} & C_{lay,hatch} \\ C_{lay,hatch} & V_{hatch,hatch} \end{bmatrix} \text{ eq. S3}$$

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, 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 files 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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Figure 1

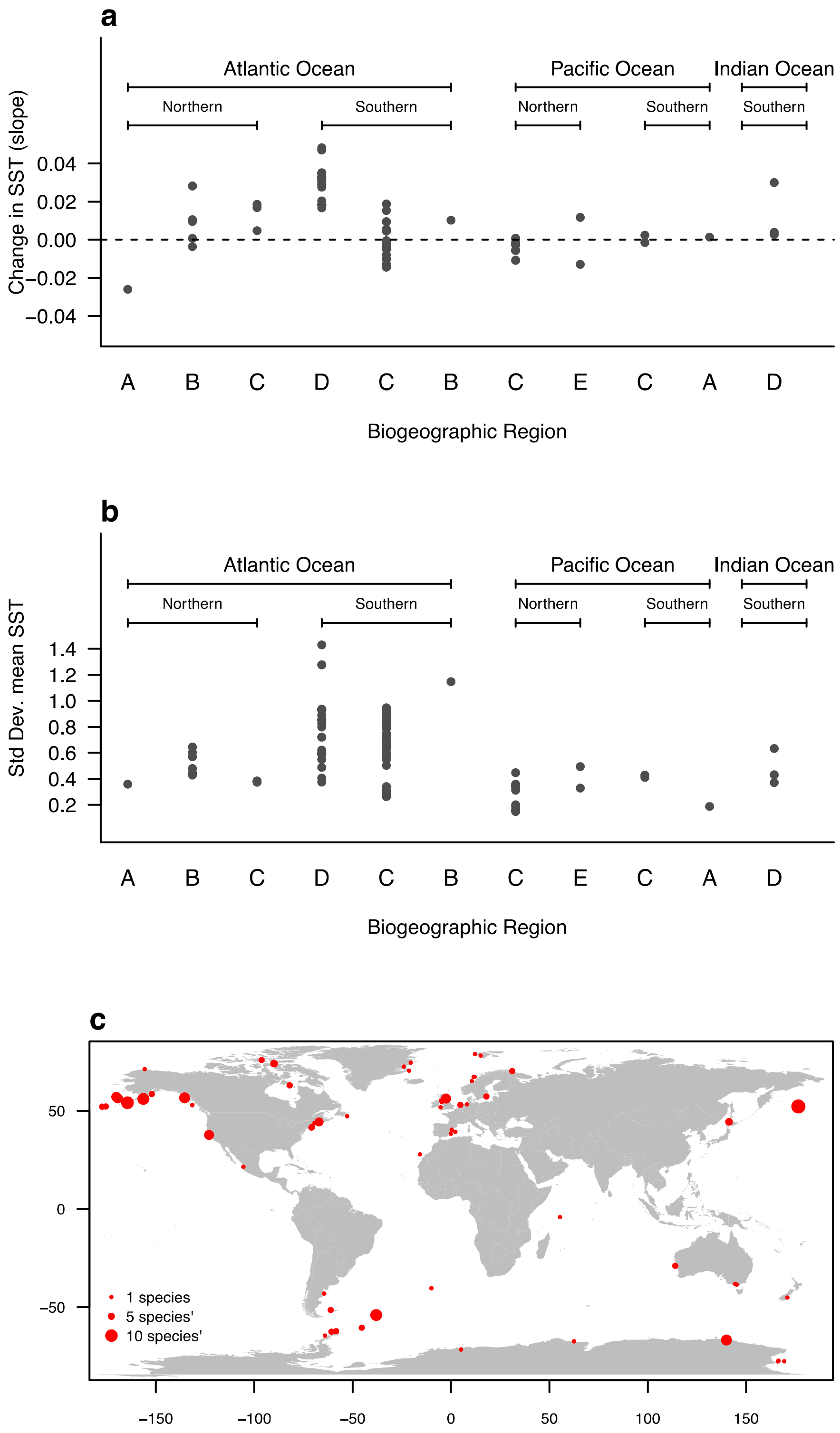

a
Atlantic Ocean
Pacific Ocean
Indian Ocean
Northern
Southern
Northern
Southern
Southern
Change in SST (slope)
0.04
0.02
0.00
−0.02
−0.04
A
B
C
D
C
B
C
E
C
A
D
Biogeographic Region
b
Atlantic Ocean
Pacific Ocean
Indian Ocean
Northern
Southern
Northern
Southern
Southern
Std Dev. mean SST
1.4
1.2
1.0
0.8
0.6
0.4
0.2
A
B
C
D
C
B
C
E
C
A
D
Biogeographic Region
c
50
0
−50
● 1 species
● 5 species'
● 10 species'
−150
−100
−50
0
50
100
150

Figure 2

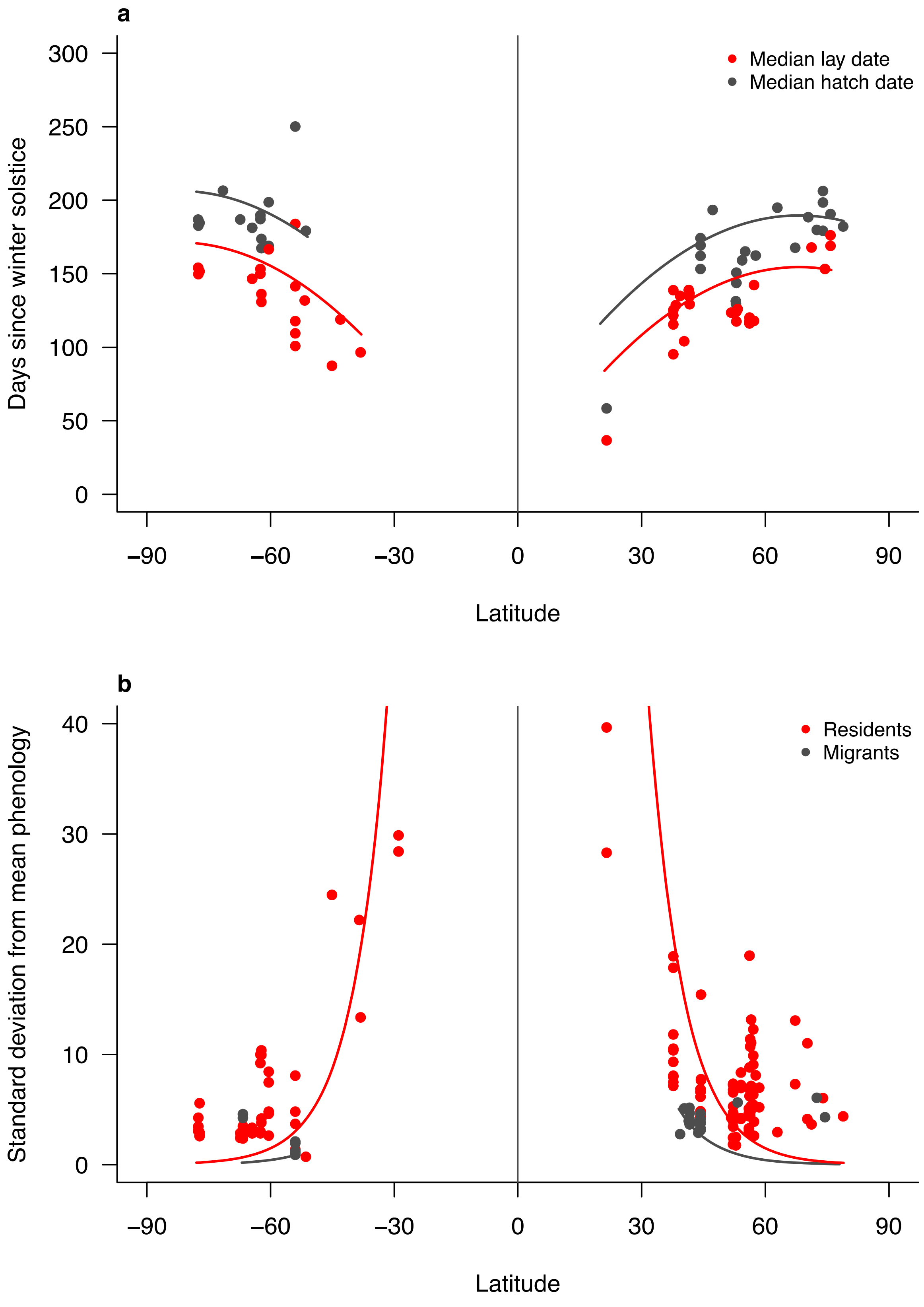
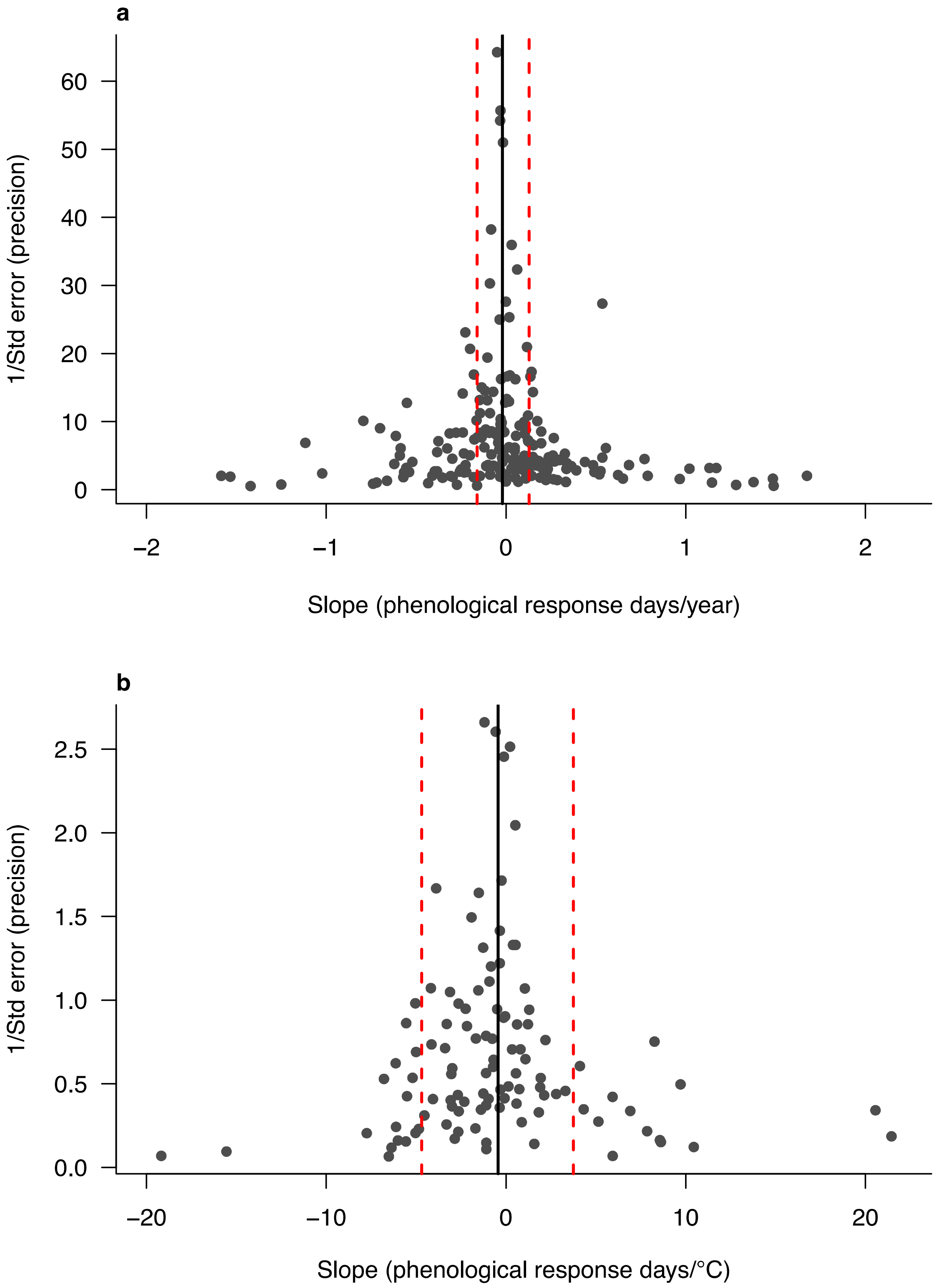

a
Median lay date
Median hatch date
Days since winter solstice
300
250
200
150
100
50
0
−90
−60
−30
0
30
60
90
Latitude
b
Residents
Migrants
Standard deviation from mean phenology
40
30
20
10
0
−90
−60
−30
0
30
60
90
Latitude

Figure 3


a
1/Std error (precision)
60
50
40
30
20
10
0
−2
−1
0
1
2
Slope (phenological response days/year)
b
1/Std error (precision)
2.5
2.0
1.5
1.0
0.5
0.0
−20
−10
0
10
20
Slope (phenological response days/°C)

Supplementary materials