

# 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 productivity<sup>1</sup>, and is often sensitive to climatic conditions<sup>2</sup>. 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 prey<sup>3</sup>. 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<sup>4</sup>. However, the disconnection between studies of ecological change in marine systems makes it difficult to detect general changes in the timing of reproduction<sup>5</sup>. 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  $\text{yr}^{-1}$ ) or in response to sea surface temperature (SST) ( $-0.272$  days  $^{\circ}\text{C}^{-1}$ ) 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<sup>2</sup>.**

The effects of rising global temperatures are having a profound impact on terrestrial and aquatic biota, influencing species abundance, distributions, behaviours and interactions<sup>6</sup>. 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<sup>2,3</sup>. As the timing of breeding affects the abiotic conditions and biotic interactions to which parents and their offspring are exposed<sup>7</sup>, breeding phenology is expected to play a key role in mediating the relationship between environmental temperature and fitness<sup>1</sup>.

Globally, many species at higher trophic levels have poor conservation status<sup>8</sup>. 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<sup>2,4</sup>, making them particularly susceptible to trophic mismatch and the associated negative demographic consequences<sup>3,9</sup>. 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<sup>2,3,9–13</sup> 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

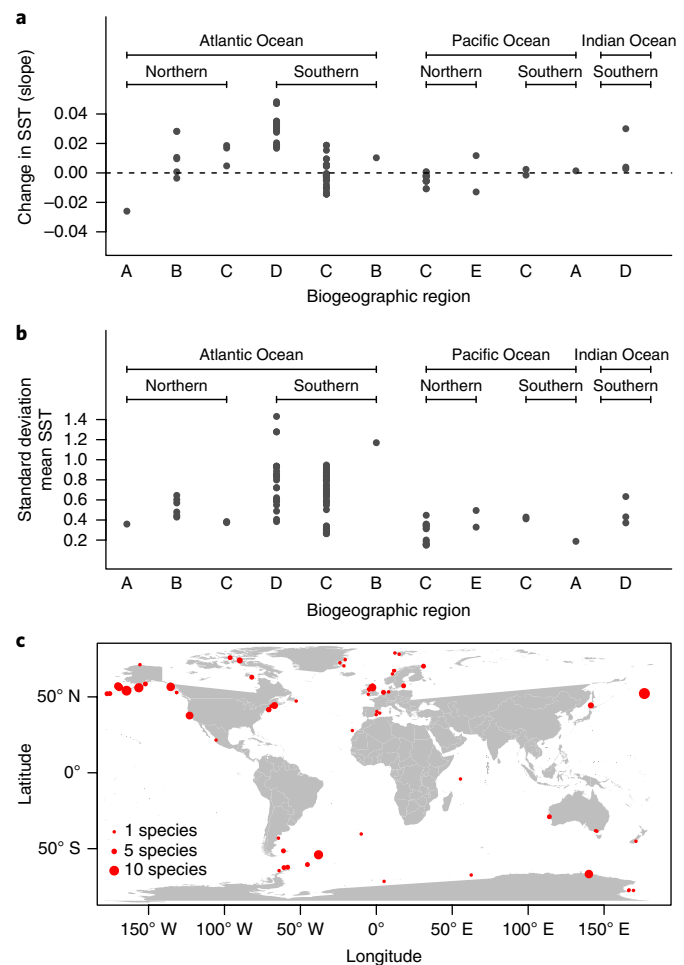
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estimates of phenological sensitivity<sup>9,11–14</sup> (but see ref. <sup>2</sup> for an alternative approach) or sources of statistical non-independence, such as phylogeny (but see ref. <sup>15</sup>). As such, it is not clear whether the variation 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<sup>16,17</sup>, 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 deteriorating<sup>18</sup>. 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 kingdom<sup>19</sup>.

Studies of seabird breeding phenology have reported a variety of different trends over time<sup>20</sup>. 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<sup>21</sup>. Changes in temperature driven by climate change could be critical, generating a mismatch with prey availability (see further discussion in the following)<sup>22</sup>. 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. <sup>13</sup>). 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 dynamics<sup>23</sup>. Furthermore, proxies at this scale are not amenable to global analyses, because regional proxies are not equivalent or comparable in a single analysis<sup>23</sup>. Thus, variation in the sensitivity in timing of breeding across species and regions remains unclear (but see ref. <sup>17</sup>). 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 average<sup>24</sup>. 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
<b>Mean phenology</b>		
Phenology will be later:	<b>at high latitudes</b>	<b>due to stronger photoperiodic cues at high latitudes<sup>25,26</sup>.</b>
<b>Between-year variance</b>		
Higher between-year variance will be observed in:	smaller birds	as they are more sensitive to environmental change <sup>37</sup> .
	<b>residents and short-distance migrants</b>	<b>because they may be more sensitive to conditions at the breeding site<sup>28</sup>.</b>
	surface feeders	which are more constrained in the water column, meaning that they can only exploit prey near the water surface <sup>38</sup> .
	<b>populations in upwelling zones</b>	<b>due to high variation in productivity in these areas<sup>39,40</sup>.</b>
<b>Temporal trends</b>		
A steeper negative slope will be observed in:	<b>birds with smaller body size</b>	<b>to avoid incurring fitness costs of thermoregulation when breeding at higher temperatures<sup>37</sup>.</b>
	birds that feed at the surface	as they may be more sensitive to the timing at which lower-trophic-level prey are available <sup>38</sup> .
	high latitudes	because polar systems are experiencing warming faster than other areas <sup>41</sup> .
<b>SST trends</b>		
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 <sup>37</sup> .
	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 <sup>28</sup> .
	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 <sup>38</sup> .
	high latitudes	as polar systems are experiencing warming faster than other areas <sup>41</sup> .

Predictions in bold indicate they are supported by the model.

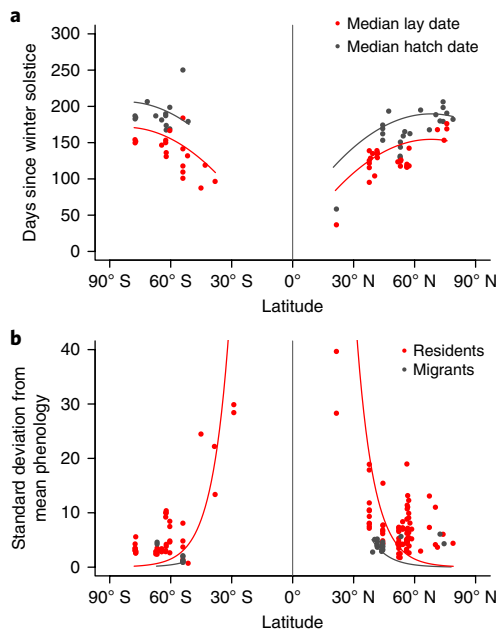
measures) of each species/population (for specific predictions see Table 1 and Methods).

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<sup>25,26</sup>. 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<sup>27</sup>.

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 birds<sup>28</sup> 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 order<sup>18</sup>, Procellariiformes, particularly giant petrels and fulmars (Procellariidae) and albatrosses (Diomedidae), stood out as least variable in timing of breeding. This response is consistent with a strong reliance on photoperiod as a cue<sup>29</sup>. 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 season<sup>30</sup>.

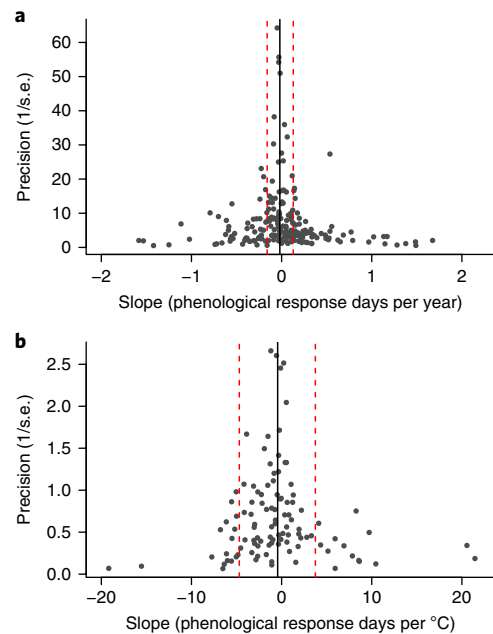
On average, seabirds showed no tendency to advance or delay breeding phenology over time ( $-0.020$  days yr<sup>-1</sup>, 95% CI:  $-0.160$ – $0.129$ ,  $n=209$ , Fig. 3a). This is in agreement with previous studies of this species group<sup>9,20</sup>, but the overall slope was much less steep than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



**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  $\text{lat}^{-1}$ , 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 general<sup>9</sup> (mean =  $\sim -0.4$  days  $\text{yr}^{-1}$ ). 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<sup>11,20</sup>. 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<sup>31</sup>. 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)<sup>32</sup>. 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  $0.6^{\circ}\text{C}$  decade<sup>-1</sup> 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 mismatch<sup>33</sup>. 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. <sup>22</sup>). Differing rates of phenological response between seabirds and their food resources<sup>9</sup> 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<sup>17,22</sup>, and whether it has an impact on breeding success<sup>34</sup> or population dynamics<sup>35</sup>. 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<sup>22,36</sup>.

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 species<sup>19</sup>). 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 grid<sup>42</sup>.

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 Thurman<sup>43</sup>. These zones correspond to latitudinal bands of similar SST and are categorized by levels of precipitation, wind and water temperature<sup>43</sup>. 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) zone<sup>44</sup>. These are areas of high productivity within the marine environment, and are also highly variable across seasons, years and decades<sup>39,45</sup>.

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](http://www.audubon.org), [www.birdlife.org](http://www.birdlife.org), [nzbirdsonline.org.nz](http://nzbirdsonline.org.nz), [www.bird-research.jp](http://www.bird-research.jp) and [www.npolar.no](http://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<sup>46–48</sup>. 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<sup>37,49</sup>. Furthermore, body mass can be used as a proxy for trophic level, which is difficult to classify explicitly in seabirds<sup>50</sup>. 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 tree<sup>51</sup> using the Hackett et al. backbone<sup>52</sup>.

**Statistics.** We used the *MCMCglmm* package<sup>53</sup> 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 of regression using short time series into account<sup>16,24</sup>.

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  $i$ ,  $\mu$  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<sup>16</sup> 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<sup>16,54</sup> in our response variables ( $H^2$ ), that is, 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)

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

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<sup>-1</sup>, 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)<sup>55</sup>:

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

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

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 nlme<sup>56</sup>, fitting an autoregressive model of order 1, AR(1)<sup>57</sup>, 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 systems<sup>38</sup>. 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](http://www.audubon.org), [www.birdlife.org](http://www.birdlife.org), [nzbirdsonline.org.nz](http://nzbirdsonline.org.nz), [www.bird-research.jp](http://www.bird-research.jp) and [www.npolar.no](http://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<sup>-1</sup>) 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 uncertainties<sup>39</sup>. 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 ( $e_i$ ) 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 package<sup>43</sup>. 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.

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

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](http://www.birdtree.org).

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# Global phenological insensitivity to shifting ocean temperatures among seabirds

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### Global phenological insensitivity to shifting ocean temperatures among seabirds

Supplementary Table 1. Model coefficients from (a) basic and (b-d) post hoc models of mean phenology. Geographical predictors include hemisphere (Northern and Southern) and latitude (absolute and quadratic). Metric of breeding phenology (mean and median lay date; first, mean and median hatch date), was included as a fixed effect in basic and *post hoc* models.

Model	Coefficient	Posterior mean	95% credibility interval		P MCMC
a) Basic model	Intercept*	35.371	-25.101	95.678	0.241
	Mean hatch date	8.457	3.689	13.117	0.001
	Mean lay date	-27.016	-33.709	-20.180	0.000
	Median hatch date	6.795	2.983	10.697	0.002
	Median lay date	-28.329	-33.654	-22.972	0.000
	Latitude (quadratic)	-0.032	-0.049	-0.015	0.001
	Latitude (absolute)	4.329	2.398	6.241	0.0001
	Southern hemisphere	120.637	73.909	166.783	0.00003
	Latitude (absolute):Southern hemisphere	0.905	0.073	1.728	0.031
	<u>Random effect predictors</u>	Variance			
	Phylogeny	553.878	0.000	1985.423	
	Species	223.551	0.000	434.854	
	Location	83.389	18.307	158.199	
	Biogeographic region	136.453	0.000	403.637	
	Species: Location	41.850	13.342	77.160	
	Residual (first hatch date)	60.083	13.463	111.463	
	Residual (mean hatch date)	16.942	0.002	34.120	
	Residual (mean lay date)	178.496	71.855	327.412	
	Residual (median hatch date)	5.394	0.001	25.904	
	Residual (median lay date)	97.176	43.720	170.987	
		Posterior mean			
	Phylogenetic signal	0.505	0.007	1.000	

**Post hoc**

<b>Model</b>	<b>Coefficient</b>	<b>Posterior mean</b>	<b>95% credibility interval</b>		<b>P MCMC</b>
b) Quadratic latitude, no mid-latitude points		123.738	35.546	211.160	0.006
	First hatch date <sup>1</sup>				
	Mean hatch date <sup>1</sup>	132.603	45.624	221.969	0.004
	Mean lay date <sup>1</sup>	96.180	9.384	183.820	0.030
	Median hatch date <sup>1</sup>	131.239	45.427	220.837	0.004
	Median lay date <sup>1</sup>	95.157	6.537	181.427	0.032
	Latitude (quadratic)	-0.003	-0.031	0.024	0.820
	Latitude (absolute)	1.166	-1.888	4.290	0.452
	Southern hemisphere	141.908	86.601	197.525	0.00002
	Latitude (absolute):Southern hemisphere	0.412	-0.535	1.373	0.391
	<u>Random effect predictors</u>	Variance			
	Phylogeny	302.339	0.000	1388.247	
	Species	226.916	0.000	394.899	
	Location	66.887	6.228	133.799	
	Biogeographic region	159.806	0.0002	426.548	
	Species: Location	42.664	12.643	78.908	
	Residual (first hatch date)	84.847	15.913	197.423	
	Residual (mean hatch date)	24.761	0.002	108.557	
	Residual (mean lay date)	146.904	0.001	256.179	
	Residual (median hatch date)	9.372	0.001	75.978	
	Residual (median lay date)	84.597	0.002	145.589	
<b>Model</b>	<b>Coefficient</b>	<b>Posterior mean</b>	<b>95% credibility interval</b>		<b>P MCMC</b>
c) Linear latitude, no mid-latitude points		132.519	97.215	169.119	0.000
	First hatch date <sup>1</sup>				



Mean hatch date <sup>1</sup>	141.362	105.880	178.108	0.000
Mean lay date <sup>1</sup>	104.831	69.112	141.057	0.000
Median hatch date <sup>1</sup>	140.000	103.986	175.791	0.000
Median lay date <sup>1</sup>	103.848	68.435	139.795	0.000
Latitude (absolute)	0.826	0.325	1.305	0.002
Southern hemisphere	142.742	87.619	197.358	0.00001
Latitude (absolute):Southern hemisphere	0.394	-0.562	1.327	0.407

<u>Random effect predictors</u>	Variance			
Phylogeny	297.721	0.000	1301.674	
Species	224.508	0.000	391.651	
Location	63.660	0.000	123.435	
Biogeographic region	151.255	0.00001	406.669	
Species: Location	43.816	13.713	81.165	
Residual (first hatch date)	85.088	17.335	198.668	
Residual (mean hatch date)	24.859	0.002	108.327	
Residual (mean lay date)	146.023	0.002	253.837	
Residual (median hatch date)	9.234	0.001	75.934	
Residual (median lay date)	83.993	0.003	143.869	

<b>Model</b>	<b>Coefficient</b>	<b>Posterior mean</b>	<b>95% credibility interval</b>		<b>P MCMC</b>
d) Allowing phenological slopes to differ					
	Intercept*	16.993	-44.767	80.697	0.595
	Mean hatch date <sup>1</sup>	29.342	1.484	56.029	0.023
	Mean lay date <sup>1</sup>	-36.284	-64.389	-8.059	0.014
	Median hatch date <sup>1</sup>	-5.090	-24.131	13.847	0.572
	Median lay date <sup>1</sup>	-36.107	-60.892	-11.104	0.006
	Latitude (quadratic)	-0.036	-0.053	-0.018	0.001
	Latitude (absolute)	4.924	2.977	6.849	0.0004

Southern hemisphere	166.267	142.578	188.847	0.000
Mean hatch date:Latitude (absolute)	-0.273	-0.680	0.149	0.165
Mean lay date:Latitude (absolute)	0.168	-0.321	0.655	0.488
Median hatch date:Latitude (absolute)	0.200	-0.118	0.516	0.195
Median lay date:Latitude (absolute)	0.148	-0.265	0.574	0.479
<u>Random effect predictors</u>	Variance			
Phylogeny	573.132	0.000	1974.454	
Species	214.419	0.000	421.344	
Location	100.425	26.131	188.128	
Biogeographic region	133.857	0.000	448.081	
Species: Location	45.986	17.190	81.992	
Residual (first hatch date)	61.733	18.258	119.835	
Residual (mean hatch date)	8.475	0.001	21.240	
Residual (mean lay date)	156.140	55.567	325.111	
Residual (median hatch date)	6.929	0.001	23.594	
Residual (median lay date)	98.544	44.337	184.984	

\*Intercept represents i) first hatch date, ii) zero degrees latitude, iii) Northern hemisphere. <sup>1</sup> Phenological measures represented by i) zero degrees latitude, ii) Northern hemisphere.

Supplementary Table 2. Model coefficients from (a) basic and (b) ecological models of between-year variance ( $\ln \sigma$ ). Upwelling zone is the environmental predictor. Geographical predictor represented by latitude (absolute and quadratic). Life history predictors include foraging strategy (surface feeder, kleptoparasite/generalist, pursuit diver), migration strategy (resident or migrant) and body mass in grams (natural log). Metric of breeding phenology (mean and median lay date; first, mean and median hatch date), mean year of each study (centred on the overall mean of all studies), were included as fixed effects in the ecological model. Random effects included phylogeny, species, location, biogeographic region, species:location interaction (population), and residual).

Model	Coefficient	Posterior mean	95% credibility interval		P MCMC
a) Basic model	Intercept	1.787	0.999	2.575	0.0002
	<u>Random effect predictors</u>	Variance			
	Phylogeny	0.492	0.031	1.185	
	Species	0.057	0.000	0.147	
	Location	0.056	0.000	0.114	
	Biogeographic region	0.036	0.000	0.070	
	Species: Location	0.537	0.000	1.257	
	Residual (first hatch date)	0.021	0.0002	0.064	
	Residual (mean hatch date)	0.010	0.0002	0.034	
	Residual (mean lay date)	0.035	0.0002	0.097	
	Residual (median hatch date)	0.041	0.001	0.088	
	Residual (median lay date)	0.034	0.0002	0.084	
		Posterior mean			
	Phylogenetic signal	0.842	0.508	1.000	
Model	Coefficient	Posterior mean	95% credibility interval		P MCMC
b) Ecological model	First hatch date <sup>1</sup>	3.556	1.955	5.153	0.0001
	Mean hatch date <sup>1</sup>	3.625	2.020	5.234	0.00005
	Mean lay date <sup>1</sup>	3.539	1.937	5.109	0.0001
	Median hatch date <sup>1</sup>	3.596	1.977	5.173	0.00005
	Median lay date <sup>1</sup>	3.663	2.041	5.233	0.00004
	Latitude (absolute)	-0.059	-0.108	-0.013	0.012

Latitude (quadratic)	0.000	0.000	0.001	0.075
Mean year	-0.012	-0.028	0.003	0.120
Upwelling	0.219	-0.348	0.798	0.446
Body mass (g) (log)	-0.083	-0.238	0.070	0.284
Kleptoparasite/generalist	0.892	0.201	1.584	0.013
Pursuit diver	-0.061	-0.616	0.486	0.838
Resident	0.627	0.262	0.997	0.001
<u>Random effect predictors</u>	Variance			
Phylogeny	0.531	0.121	1.020	
Species	0.023	0.000	0.073	
Location	0.059	0.000	0.118	
Biogeographic region	0.023	0.000	0.054	
Species: Location	0.170	0.000	0.500	
Residual (first hatch date)	0.018	0.0002	0.058	
Residual (mean hatch date)	0.017	0.0002	0.051	
Residual (mean lay date)	0.032	0.0002	0.086	
Residual (median hatch date)	0.044	0.001	0.093	
Residual (median lay date)	0.027	0.0002	0.072	

<sup>1</sup> Phenological measures represented by i) zero degrees latitude, ii) mean year (2003), iii) no upwelling zone, iv) zero gram body mass, v) surface feeder, vi) migrant.



Supplementary Table 3. Model coefficients from (a) basic, (b) ecological and (c) post hoc models of temporal trends (days yr<sup>-1</sup>). Environmental predictor measured as climate zone (equatorial, tropical, subtropical, temperate, subpolar, polar). Geographical predictors include ocean basin (Arctic, Atlantic, Indian, Pacific, Southern), hemisphere (Northern and Southern) and latitude (absolute). Life history predictors include foraging strategy (surface feeder, kleptoparasite/generalist, pursuit diver) and body mass in grams (natural log). Metric of breeding phenology (mean and median lay date; first, mean and median hatch date), mean year of each study (centred on the overall mean of all studies), were included as fixed effects in ecological and *post hoc* models.

Model	Coefficient	Posterior mean	95% credibility interval		P MCMC
a) Basic model	Intercept	-0.020	-0.160	0.129	0.295
	<u>Random effect predictors</u>	Variance			
	Phylogeny	0.012	0.000	0.042	
	Species	0.005	0.000	0.020	
	Location	0.019	0.000	0.051	
	Biogeographic region	0.007	0.000	0.025	
	Species:Location	0.034	0.004	0.063	
	Residual (first hatch date)	0.003	0.0002	0.011	
	Residual (mean hatch date)	0.018	0.0002	0.050	
	Residual (mean lay date)	0.005	0.0001	0.019	
	Residual (median hatch date)	0.003	0.0002	0.010	
	Residual (median lay date)	0.005	0.0002	0.018	
		Posterior mean			
	Phylogenetic signal	0.589	0.012	1.000	
Model	Coefficient	Posterior mean	95% credibility interval		P MCMC
b) Ecological model	First hatch date <sup>1</sup>	-0.060	-0.654	0.523	0.843
	Mean hatch date <sup>1</sup>	-0.086	-0.689	0.525	0.776
	Mean lay date <sup>1</sup>	-0.104	-0.701	0.478	0.723
	Median hatch date <sup>1</sup>	-0.048	-0.639	0.550	0.875
	Median lay date <sup>1</sup>	-0.063	-0.649	0.522	0.830
	Mean year	0.009	-0.002	0.021	0.107

Body mass (g) (log)	0.070	0.003	0.136	0.039
Kleptoparasite/predator	0.317	-0.012	0.643	0.058
Pursuit diver	0.120	-0.033	0.269	0.116
Latitude (absolute)	-0.008	-0.016	0.000	0.066
Southern hemisphere	-0.852	-1.667	-0.022	0.042
Indian Ocean	0.085	-0.326	0.515	0.704
Pacific Ocean	-0.096	-0.344	0.150	0.366
Latitude (absolute):Southern hemisphere	0.013	-0.001	0.026	0.059

<u>Random effect predictors</u>	Variance			
Phylogeny	0.006	0.000	0.024	
Species	0.003	0.000	0.011	
Location	0.009	0.000	0.032	
Biogeographic region	0.016	0.000	0.067	
Species:Location	0.039	0.016	0.064	
Residual (first hatch date)	0.006	0.000	0.018	
Residual (mean hatch date)	0.011	0.000	0.033	
Residual (mean lay date)	0.005	0.000	0.017	
Residual (median hatch date)	0.004	0.000	0.012	
Residual (median lay date)	0.006	0.000	0.022	

## Post hoc

Model	Coefficient	Posterior mean	95% credibility interval	P MCMC
c) Five oceans model	First hatch date <sup>2</sup>	-0.362	-0.826 0.078	0.106
	Mean hatch date <sup>2</sup>	-0.404	-0.871 0.043	0.075
	Mean lay date <sup>2</sup>	-0.404	-0.860 0.050	0.074
	Median hatch date <sup>2</sup>	-0.357	-0.811 0.093	0.111
	Median lay date <sup>2</sup>	-0.356	-0.807 0.095	0.110
	Mean year	0.007	-0.004 0.018	0.216
	Body mass (g) (log)	0.042	-0.021 0.105	0.186

Kleptoparasite/predator	0.205	-0.128	0.532	0.221
Pursuit diver	0.133	-0.021	0.284	0.087
Arctic Ocean	-0.338	-0.706	0.033	0.073
Indian Ocean	0.281	-0.465	1.045	0.462
Pacific Ocean	-0.060	-0.350	0.241	0.625
Southern Ocean	0.047	-0.209	0.310	0.727
<u>Random effect predictors</u>	Variance			
Phylogeny	0.007	0.000	0.029	
Species	0.004	0.000	0.014	
Location	0.012	0.000	0.037	
Biogeographic region	0.013	0.000	0.051	
Species: Location	0.037	0.012	0.062	
Residual (first hatch date)	1.000	1.000	1.000	
Residual (mean hatch date)	0.005	0.000	0.016	
Residual (mean lay date)	0.013	0.000	0.037	
Residual (median hatch date)	0.004	0.000	0.014	
Residual (median lay date)	0.004	0.000	0.012	

<sup>1</sup> Phenological measures represented by i) mean year (2003), ii) zero gram body mass, iii) surface feeder, iv) zero degrees latitude, v) Northern hemisphere, vi) Atlantic Ocean. <sup>2</sup> Phenological measures represented by i) mean year (2003), ii) zero gram body mass, iii) surface feeder, iv) Atlantic Ocean.

Supplementary Table 4. Estimation of the variance contributed by sampling error in the temporal slope model. Variance was estimated separately for each phenophase under a model with the intercept as a fixed effect a residual random term with a) and without b) a term for sampling error variance. The contribution of sampling error as a proportion of the total residual variance ( $\sigma_e^2$ ) was calculated as  $1 - \sigma_{e\text{ mev}}^2 / \sigma_{e\text{ no mev}}^2$ , where mev = model that accounts for sampling error variance and no mev = model that ignores sampling error variance.

Phenophase	Model accounting for sampling error			Model not accounting for sampling error			Percentage of variance accounted for by sampling error alone		
	Variance	95% Credible Interval		Variance	95% Credible Interval		Mean	95% Credible Interval	
Median hatch date	0.047	0.018	0.090	0.140	0.080	0.210	66.08	57.33	77.74
Mean hatch date	0.059	0.027	0.094	0.262	0.179	0.357	77.63	73.76	84.65
Median lay date	0.038	0.007	0.080	0.218	0.136	0.314	82.42	74.60	95.13
Mean lay date	0.095	0.024	0.181	1.139	0.637	1.771	91.68	89.77	96.24
First hatch date	0.003	0.000	0.011	0.085	0.042	0.134	96.23	91.54	100.00
<b>Mean % variance across all phenophases</b>							82.81	77.40	90.75



Supplementary Table 5. Model coefficients from (a) basic and (b) ecological models of SST trends (days °C<sup>-1</sup>), excluding sites where sea ice was recorded. Environmental predictors measured as climate zone (equatorial, tropical, subtropical, temperate, subpolar, polar). Geographical predictors include ocean basin (Arctic, Atlantic, Indian, Pacific, Southern), hemisphere (Northern and Southern) and latitude (absolute). Life history predictors include foraging strategy (surface feeder, kleptoparasite/generalist, pursuit diver), migration strategy (resident, migrant) and body mass in grams (natural log). Metric of breeding phenology (mean and median lay date; first, mean and median hatch date), was included as a fixed effect in basic and ecological models.

Model	Coefficient	Posterior mean	95% credibility interval		P MCMC
a) Basic model	Intercept	-0.272	-4.896	4.482	0.866
	<u>Random effects predictors</u>	Variance			
	Phylogeny	12.960	0.000	28.940	
	Species	0.653	0.000	2.633	
	Site	5.620	2.111	10.052	
	Biogeographic Region	15.178	0.000	54.667	
	Residual	0.179	0.0001	0.832	
		Posterior mean			
	Phylogenetic signal	0.978	0.627	1.000	
Model	Coefficient	Posterior mean	95% credibility interval		P MCMC
b) Ecological model	First hatch date	4.708	-7.168	17.661	0.438
	Mean hatch date	-0.088	-15.295	12.536	0.960
	Median hatch date	2.600	-10.194	16.344	0.737
	Mean lay date	1.549	-12.127	13.544	0.850
	Median lay date	3.605	-8.535	16.062	0.567
	Centred mean year	0.070	-0.124	0.301	0.519
	Body mass (g) (log)	0.196	-1.115	1.511	0.758
	Kleptoparasite/predator	0.380	-9.868	9.510	0.937
	Pursuit diver	-1.342	-5.339	2.046	0.450
	Latitude (absolute)	-0.081	-0.242	0.076	0.308
	Southern hemisphere	8.540	-25.029	40.644	0.638

Indian Ocean	-5.124	-26.804	22.228	0.687
Pacific Ocean	4.908	-1.206	10.321	0.094
Resident	-0.648	-3.174	1.918	0.600
Latitude (absolute):Southern hemisphere	-0.188	-0.777	0.443	0.577

Random effects predictors

	Variance		
Phylogeny	17.451	0.000	40.934
Species	1.191	0.000	4.913
Site	3.976	0.636	8.277
Biogeographic region	25.262	0.000	92.398
Residual	0.193	0.0001	0.917

<sup>1</sup> Phenological measures represented by i) mean year (2003), ii) zero gram body mass, iii) surface feeder, iv) zero degrees latitude, v) Northern hemisphere, vi) Atlantic Ocean, vii) migrant.

Supplementary Table 6. Coefficients from basic model of variance trends, relaxing the assumption that random effects are perfectly correlated across measures.

<b>Coefficient</b>	<b>Posterior mean</b>	<b>95% credibility interval</b>		<b>P MCMC</b>
Hatch date	1.580	0.843	2.328	0.000
Lay date	1.892	0.918	2.819	0.001
<b>Random effect predictors</b>				
	(co)Variance			
Phylogeny (hatch,hatch)	0.514	0.054	1.072	
Phylogeny (lay,hatch)	0.429	-0.015	1.033	
Phylogeny (lay,lay)	0.679	0.020	1.600	
Species (hatch,hatch)	0.040	0.000	0.118	
Species (lay,hatch)	0.026	-0.021	0.107	
Species (lay,lay)	0.079	0.000	0.215	
Location (hatch,hatch)	0.050	0.000	0.111	
Location (lay,hatch)	0.009	-0.018	0.050	
Location (lay,lay)	0.017	0.000	0.065	
Biogeographic Region (hatch,hatch)	0.135	0.000	0.458	
Biogeographic Region (lay,hatch)	0.135	-0.159	0.556	
Biogeographic Region (lay,lay)	0.717	0.030	1.717	
Species:Location (hatch,hatch)	0.032	0.000	0.070	
Species:Location (lay,hatch)	0.005	-0.016	0.033	
Species:Location (lay,lay)	0.013	0.000	0.049	
Residual (first hatch date)	0.024	0.000	0.073	
Residual (mean hatch date)	0.015	0.000	0.049	
Residual (mean lay date)	0.040	0.000	0.115	
Residual (median hatch date)	0.050	0.000	0.110	
Residual (median lay date)	0.041	0.000	0.105	
<b>Phylogenetic signal</b>				
	<b>Posterior mean</b>			

Lay date	0.904	0.471	1
Hatch date	0.945	0.631	1

Supplementary Table 7. Coefficients from basic model of temporal trends (days yr<sup>-1</sup>), relaxing the assumption that random effects are perfectly correlated across measures.

<b>Coefficient</b>	<b>Posterior mean</b>	<b>95% credibility interval</b>		<b>P MCMC</b>
Hatch date	0.017	-0.156	0.199	0.841
Lay date	-0.051	-0.321	0.225	0.659
<b>Random effect predictors</b>				
	(co)Variance			
Phylogeny (hatch,hatch)	0.020	0.000	0.069	
Phylogeny (lay,hatch)	-0.003	-0.036	0.023	
Phylogeny (lay,lay)	0.035	0.000	0.137	
Species (hatch,hatch)	0.007	0.000	0.024	
Species (lay,hatch)	0.001	-0.008	0.011	
Species (lay,lay)	0.011	0.000	0.041	
Location (hatch,hatch)	0.011	0.000	0.033	
Location (lay,hatch)	0.008	-0.012	0.040	
Location (lay,lay)	0.057	0.000	0.146	
Biogeographic Region (hatch,hatch)	0.007	0.000	0.027	
Biogeographic Region (lay,hatch)	0.001	-0.014	0.019	
Biogeographic Region (lay,lay)	0.034	0.000	0.130	
Species:Location (hatch,hatch)	0.030	0.000	0.054	
Species:Location (lay,hatch)	0.017	-0.007	0.048	
Species:Location (lay,lay)	0.040	0.000	0.098	
Residual (first hatch date)	0.004	0.000	0.013	
Residual (mean hatch date)	0.009	0.000	0.036	
Residual (mean lay date)	0.005	0.000	0.016	
Residual (median hatch date)	0.004	0.000	0.013	
Residual (median lay date)	0.004	0.000	0.012	
<b>Phylogenetic signal</b>				
	<b>Posterior mean</b>			

Lay date	0.753	0.017	1
Hatch date	0.750	0.018	1

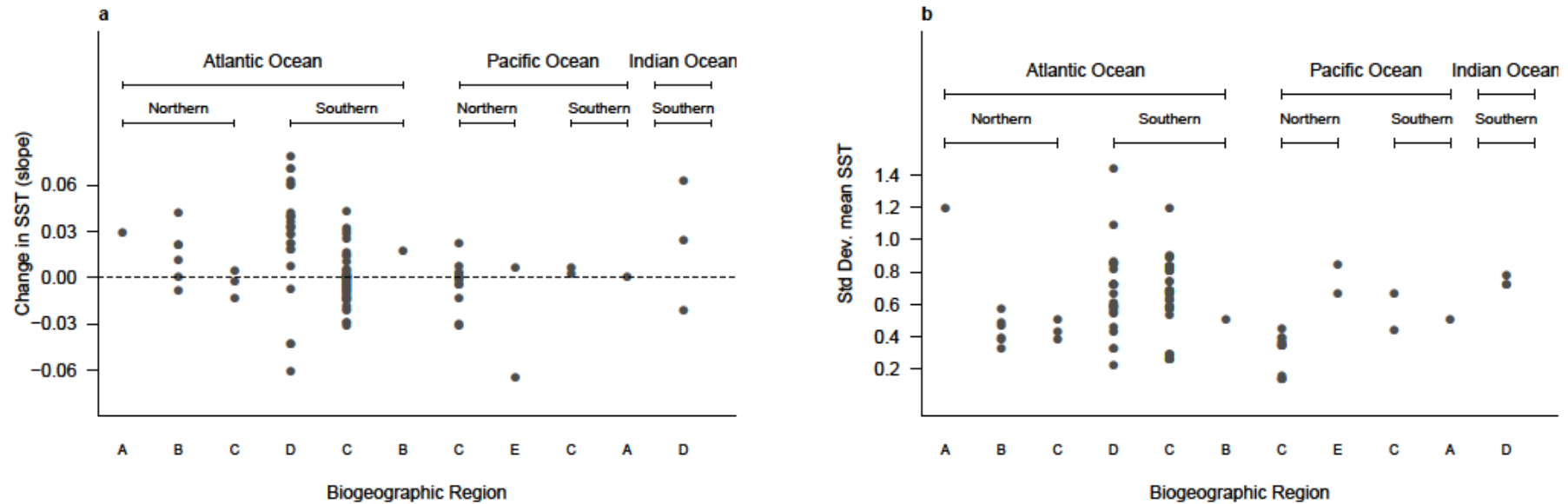
Supplementary Table 8. Coefficients from basic model of SST trends (days °C<sup>-1</sup>), relaxing the assumption that random effects are perfectly correlated across measures.

<b>Coefficient</b>	<b>Posterior mean</b>	<b>95% credibility interval</b>		<b>P MCMC</b>
Hatch date	-1.956	-6.723	2.641	0.344
Lay date	1.136	-3.906	6.261	0.632
<u>Random effect predictors</u>	(co)Variance			
Phylogeny (hatch,hatch)	11.137	0.000	27.504	
Phylogeny (lay,hatch)	4.187	-4.598	17.857	
Phylogeny (lay,lay)	10.415	0.000	36.077	
Species (hatch,hatch)	1.238	0.000	4.717	
Species (lay,hatch)	0.073	-1.221	1.609	
Species (lay,lay)	1.264	0.000	5.433	
Location (hatch,hatch)	0.796	0.000	2.672	
Location (lay,hatch)	0.183	-2.586	3.074	
Location (lay,lay)	8.823	0.000	21.504	
Biogeographic Region (hatch,hatch)	14.747	0.000	52.511	
Biogeographic Region (lay,hatch)	-0.137	-20.901	20.221	
Biogeographic Region (lay,lay)	24.619	0.000	73.847	
Residual	0.341	0.0001	1.415	
<b>Phylogenetic signal</b>	<b>Posterior mean</b>			
Lay date	0.929	0.063	1	
Hatch date	0.949	0.203	1	

Supplementary Table 9. Number of time series received, assessed for eligibility, and included in the review, with reasons for exclusions at each stage (see PRISMA checklist).

# of time series received:	<b>263</b>
Were they spring/summer breeders? Removed if <b>no</b>	-2
Was the study $\geq 5$ years in length? Removed if <b>no</b>	-1
Were the data collected annually throughout the breeding season? Removed if <b>no</b>	-4
Was the mean sample size $\geq 5$ individuals? Removed if <b>no</b>	-2
Was the phenophase arrival, fledge or first lay date? Removed if <b>yes</b>	-45
# of time series used in mean phenology, variance in phenology and temporal phenology models	<b>209</b>
Was the study $\geq 10$ years in length? Removed if <b>no</b>	-90
Did the study contain sea ice? Removed if <b>yes</b>	-11
# of time series used in SST model	<b>108</b>
Were metadata available for each fixed and random effect used in model? Removed if <b>no</b>	-1
Any analysis with migration strategy included	<b>208, 107</b>





Supplementary Figure 1. SST trends of study sites included in the analysis. 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 during the study period 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.

# Supplementary methods

Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
Antarctica	Adelie Land	Adelie Land	Antarctic skua	<i>Catharacta maccormicki</i>	66°70' S	140°00' E	Direct nest observation; precision ± 1 day
Antarctica	Adélie Land	Adélie Land	Cape petrel	<i>Daption capense</i>	66°70' S	140°00' E	Direct nest observation; precision ± 1 day
Antarctica	Adélie Land	Adélie Land	Southern fulmar	<i>Fulmarus glacialisoides</i>	66°70' S	140°00' E	Direct nest observation; precision ± 1 day
Antarctica	Adélie Land	Adélie Land	Wilson's storm petrel	<i>Oceanites oceanicus</i>	66°70' S	140°00' E	Direct nest observation; precision ± 1 day
Antarctica	Adélie Land	Adélie Land	Snow petrel	<i>Pagodroma nivea</i>	66°70' S	140°00' E	Direct nest observation; precision ± 1 day
Antarctica	Adélie Land	Adélie Land	Adélie penguin	<i>Pygoscelis adeliae</i>	66°70' S	140°00' E	Direct nest observation; precision ± 1 day
Antarctica	East Antarctica	Béchervaise Island	Adélie penguin	<i>Pygoscelis adeliae</i>	67°35' S	62°49' E	Direct nest observation; precision ± 1 day
Antarctica	Palmer Archipelago	Humble Island	Adélie penguin	<i>Pygoscelis adeliae</i>	64°46' S	64°06' W	Direct nest observation; precision ± 1 day
Antarctica	Peninsula	Cape Shirreff	Chinstrap penguin	<i>Pygoscelis antarctica</i>	62°28' S	60°46' W	Direct nest observation; precision ± 1 day
Antarctica	Peninsula	Cape Shirreff	Gentoo penguin	<i>Pygoscelis papua</i>	62°28' S	60°46' W	Direct nest observation; precision ± 1 day
Antarctica	Dronning Maud Land	Svarthamaren	Antarctic petrel	<i>Thalassoica antarctica</i>	71°53' S	5°10' E	Direct nest observation; precision +/- 1 day
Antarctica	Peninsula	Copacabana	Adélie penguin	<i>Pygoscelis adeliae</i>	62°10' S	58°30' W	Direct nest observation; precision ± 1 day
Antarctica	Peninsula	Copacabana	Gentoo penguin	<i>Pygoscelis papua</i>	62°10' S	58°30' W	Direct nest observation; precision ± 1 day
Antarctica	Ross Island	Cape Bird	Adélie penguin	<i>Pygoscelis adeliae</i>	77°22' S	166°47' E	Direct nest observation & chick hatch dates; precision ± 6 days
Antarctica	Ross Island	Cape Crozier	Adélie penguin	<i>Pygoscelis adeliae</i>	77°52' S	169°38' E	Direct nest observation & chick hatch dates; precision ± 6 days
Antarctica	Ross Island	Cape Royds	Adélie penguin	<i>Pygoscelis adeliae</i>	77°57' S	166°18' E	Direct nest observation & chick hatch dates; precision ± 2 days

Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
Argentina	Patagonia	Punta León	Imperial shag	<i>Phalacrocorax atriceps</i>	43°06' S	64°46' W	Direct nest observation; precision ± 5 days
Australia	Victoria	Phillip Island	Little penguin	<i>Eudiptula minor</i>	38°29' S	145°14' E	Direct nest observation; precision ± 2 days
Australia	Victoria	Pope's Eye	Australasian gannet	<i>Morus serrator</i>	38°16' S	144°41' E	Direct nest observation; precision ± 7 days
Australia	Western Australia	Pelsaert Island	Brown noddy	<i>Anous stolidus</i>	28°56' S	113°58' E	Estimate from egg density; precision ± 3 days
Australia	Western Australia	Pelsaert Island	Lesser noddy	<i>Anous tenuirostris melanops</i>	28°56' S	113°58' E	Estimate from egg density; precision ± 3 days
Canada	New Brunswick	Machias Seal Island	Razorbill	<i>Alca torda</i>	44°30' N	67°06' W	Direct nest observation; precision ± 5 days
Canada	New Brunswick	Machias Seal Island	Atlantic puffin	<i>Fratercula arctica</i>	44°30' N	67°06' W	Direct nest observation; precision ± 5 days
Canada	New Brunswick	Machias Seal Island	Common tern	<i>Sterna hirundo</i>	44°30' N	67°06' W	Direct nest observation; precision ± 1 day
Canada	New Brunswick	Machias Seal Island	Arctic tern	<i>Sterna paradisaea</i>	44°30' N	67°06' W	Direct nest observation; precision ± 1 day
Canada	Nunavut	Coats Island	Thick-billed murre	<i>Uria lomvia</i>	62°95' N	82°02' W	Direct nest observation; precision ± 2 days
Canada	Nunavut	Coats Island	Glaucous gull	<i>Larus hyperboreus</i>	62°95' N	82°02' W	Direct nest observation; precision ± 3 days
Canada	Nunavut	Prince Leopold Island	Glaucous gull	<i>Larus hyperboreus</i>	74°01' N	89°94' W	Direct nest observation; precision ± 3 days
Canada	Newfoundland	Gull Island	Leach's storm petrel	<i>Oceanodroma leucorhoa</i>	47°25' N	52°77' W	Estimate from chick wing length
Canada	Nunavut	Prince Leopold Island	Black-legged kittiwake	<i>Rissa tridactyla</i>	74°01' N	89°94' W	Direct nest observation; precision ± 2 days but sometimes missed due to bad weather.
Canada	Nunavut	Nasaruvaalik	Arctic tern	<i>Sterna paradisaea</i>	75°49' N	96°18' W	Direct nest observation; precision ± 1 day
Canada	British Columbia	Limestone Island	Ancient murrelet	<i>Synthliboramphus antiquus</i>	52°89' N	131°52' W	Chicks caught in funnels upon leaving burrows at night (1-2 days after hatching); sampled every night.

Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
Canada	Nunavut	Prince Leopold Island	Thick-billed murre	<i>Uria lomvia</i>	74°01' N	89°94' W	Direct nest observation; precision $\pm$ 2 days but sometimes missed due to bad weather.
Canada	Nunavut	Nasaruvaalik	Sabine's gull	<i>Xema sabini</i>	75°49' N	96°18' W	Direct nest observation; precision $\pm$ 1 day
Canada	British Columbia	Reef Island	Ancient murrelet	<i>Synthliboramphus antiquus</i>	52°87' N	131°51' W	Chicks caught in funnels upon leaving burrows at night (1-2 days after hatching); sampled every night.
Falkland/Malvinas Islands	South Atlantic	New Island	Black-browed albatross	<i>Thalassarche melanophris</i>	51°71' S	61°31' W	Direct nest observation; precision $\pm$ 1 day
Falkland/Malvinas Islands	South Atlantic	New Island	Southern rockhopper penguin	<i>Eudyptes chrysocome (chrysocome)</i>	51°71' S	61°31' W	Direct nest observation; precision $\pm$ 1 day
Germany	Niedersachsen	Banter See	Common tern	<i>Sterna hirundo</i>	53°30' N	08°06' E	Direct nest observation; nests checked every Monday, Wednesday and Friday
Greenland	North East	Karupelv Valley	Long-tailed skua	<i>Stercorarius longicaudus</i>	72°50' N	24°00' W	Direct nest observation; precision $\pm$ 2 days
Greenland	East Greenland	Ukaleqarteq / Kap Höegh	Little auk	<i>Alle alle</i>	70°44' N	21°35' W	Direct nest observation; precision $\pm$ 1 day (Checked every 2 to 3 days)
Greenland	North East	Zackenbergl	Long-tailed skua	<i>Stercorarius longicaudus</i>	74°28' N	20°34' W	Direct nest observation; precision $\pm$ 1 days
Japan	Hokkaido	Teuri Island	Rhinoceros auklet	<i>Cerorhinca monocerata</i>	44°25' N	141°19' E	Direct nest observation; nests checked every 5 days
Japan	Hokkaido	Teuri Island	Black-tailed gull	<i>Larus crassirostris</i>	44°25' N	141°19' E	Direct nest observation; nests checked every 5 days
Japan	Hokkaido	Teuri Island	Japanese cormorant	<i>Phalacrocorax capillatus</i>	44°25' N	141°19' E	Direct nest observation; nests checked every 5 days
México	Pacífico	Isla Isabel	Blue-footed booby	<i>Sula nebouxii</i>	21°50' N	105°50' W	Direct nest observation; precision $\pm$ 3 days. Lay date estimated from hatching dates or sizes of chicks.
New Zealand	Otago	Oamaru	Little penguin	<i>Eudyptula minor</i>	45°07' S	170°58' E	Direct nest observation; precision $\pm$ 5 days
Norway	Mainland	Anda	Black-legged kittiwake	<i>Rissa tridactyla</i>	69°04' N	15°10' E	Direct nest observation; precision $\pm$ 3 days

Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
Norway	Svalbard	Grumantbyen	Black-legged kittiwake	<i>Rissa tridactyla</i>	78°10' N	15°09' E	Direct nest observation; precision ± 10 days
Norway	Mainland	Hornøya	Black-legged kittiwake	<i>Rissa tridactyla</i>	70°23' N	31°09' E	Direct nest observation; precision ± 2 days
Norway	Nordland	Kårøysundet	Black-legged kittiwake	<i>Rissa tridactyla</i>	67°30' N	12°03' E	Method either: visual inspection, egg density loss function or chick head and bill length compared to chicks of known ages in same colony. Nests checked every 3-6 days.
Norway	Mainland	Anda	Atlantic puffin	<i>Fratercula arctica</i>	69°04' N	15°10' E	Direct nest observation; precision ± 3 days
Norway	Nordland	Hernyken	Atlantic Puffin	<i>Fratercula arctica</i>	67°26' N	11°52' E	Direct nest observation; precision ± 3 days
Norway	Mainland	Hornøya	Atlantic puffin	<i>Fratercula arctica</i>	70°22' N	31°08' E	Estimate from chick wing length
Norway	Mainland	Sklinna	Atlantic puffin	<i>Fratercula arctica</i>	65°13' N	10°58' E	Head and bill length growth curve
Norway	Mainland	Ellefsnyken	European shag	<i>Phalacrocorax aristotelis</i>	67°27' N	11°55' E	Direct nest observation; see reference for detailed methods
Norway	Svalbard	Kongsfjorden	Black-legged kittiwake	<i>Rissa tridactyla</i>	79°01' N	12°25' E	Direct nest observation & chick hatch dates from incubator; precision ± 2 days
Seychelles	Granitic Sechelles	Aride	Roseate tern	<i>Sterna dougallii</i>	40°10' S	55°04' E	Direct nest observation; precision ± 3 days. Lay date back-calculated from hatch date, subtracting incubation period of 22 days from first hatched chick in each clutch.
Spain	Balearic Is.	Pantaleu	Scopoli shearwater	<i>Calonectris diomedea</i>	30°34' N	2°21' E	Direct nest observation; precision ± 2 days
Spain	Valencia	Benidorm	European storm petrel	<i>Hydrobates pelagicus</i>	38°30' N	0°70' W	Direct nest observation; precision ± 7 days. Lay date was estimated from observed hatch date, or from interval sensing between two visits.
Spain	Catalonia	Ebro Delta	Audouin's gull	<i>Larus audouinii</i>	40°34' N	0°39' E	Direct nest observation; precision ± 1 day

Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
Spain	Canary Is	Veneguera	Cory's shearwater	<i>Calonectris borealis</i>	39°58' N	15°79' W	Arrival date from GLS data; precision ± 1 day
Sweden	Götaland	Stora Karlsö	Razorbill	<i>Alca torda torda</i>	57°28' N	17°97' W	Direct nest observation; precision ± 6 days
Sweden	Götaland	Stora Karlsö	Common guillemot	<i>Uria aalge aalge</i>	57°28' N	17°97' W	Direct nest observation; precision ± 3 days
The Netherlands	Noord-Holland	Kelderhuispolder	European herring gull	<i>Larus argentatus</i>	53°00' N	4°72' E	Direct nest observation; precision ± 1 day
The Netherlands	Noord-Holland	Kelderhuispolder	Lesser black-backed gull	<i>Larus fuscus</i>	53°00' N	4°72' E	Direct nest observation; precision ± 1 day
Tristan da Cunha	South Atlantic	Gough Island	Atlantic yellow-nosed albatross	<i>Thalassarche chlororhynchos</i>	40°32' S	9°94' W	Direct nest observation; precision ± 1 day
United Kingdom	Scotland	Isle of May	Black-legged kittiwake	<i>Rissa tridactyla</i>	56°11' N	2°33' W	Direct nest observation; nests checked daily
United Kingdom	Scotland	Isle of May	Common guillemot	<i>Uria aalge</i>	56°11' N	2°33' W	Direct nest observation; nests checked daily
United Kingdom	Scotland	Isle of May	Razorbill	<i>Alca torda</i>	56°11' N	2°33' W	Direct nest observation; nests checked daily
United Kingdom	Scotland	Isle of May	Atlantic Puffin	<i>Fratercula arctica</i>	56°11' N	2°33' W	First egg dates back calculated from daily checks of colony evidence of adults bringing chicks back to burrows. Median egg dates back calculated from wing and bill measurements of chicks (mean of 30 individuals/year).
United Kingdom	Scotland	Isle of May	European shag	<i>Phalacrocorax aristotelis</i>	56°11' N	2°33' W	Chicks were ringed at a mean age of 20-25 days during all years (800 pairs). Subset of nests (100 pairs) were checked weekly to ascertain lay date in some years.
United Kingdom	Wales	Skomer Island	Common guillemot	<i>Uria aalge</i>	51°74' N	5°29' W	Direct nest observation; precision ± 1 day
United Kingdom	Scotland	Ailsa Craig	Northern gannet	<i>Morus bassanus</i>	55°25' N	5°13' W	Direct nest observation; nests checked once per season. Young gannets aged and hatch date back calculated.

Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
United Kingdom	Scotland	Scar Rocks	Northern gannet	<i>Morus bassanus</i>	54°75' N	4°67' W	Direct nest observation; nests checked once per season. Young gannets aged and hatch date back calculated.
United Kingdom	Scotland	Troup Head	Northern gannet	<i>Morus bassanus</i>	57°70' N	2°30' W	Direct nest observation; nests checked once per season. Young gannets aged and hatch date back calculated.
United Kingdom OT	South Atlantic	Bird Island (South Georgia)	Southern giant petrel	<i>Macronectes giganteus</i>	54°00' S	38°03' W	Direct nest observation; precision ± 2 days
United Kingdom OT	South Atlantic	Bird Island (South Georgia)	Northern giant petrel	<i>Macronectes halli</i>	54°00' S	38°03' W	Direct nest observation; precision ± 2 days
United Kingdom OT	South Atlantic	Bird Island (South Georgia)	Wandering albatross	<i>Diomedea exulans</i>	54°00' S	38°03' W	Direct nest observation; precision ± 1 day
United Kingdom OT	South Atlantic	Bird Island (South Georgia)	Macaroni penguin	<i>Eudyptes chrysolophus</i>	54°00' S	38°03' W	Direct nest observation; precision ± 1 day
United Kingdom OT	Sub-Antarctic	Signy Island	Adélie penguin	<i>Pygoscelis adeliae</i>	60°45' S	45°36' W	Direct nest observation; precision ± 2 days
United Kingdom OT	Sub-Antarctic	Signy Island	Chinstrap penguin	<i>Pygoscelis antarctica</i>	60°45' S	45°36' W	Direct nest observation; precision ± 2 days
United Kingdom OT	South Atlantic	Bird Island (South Georgia)	Gentoo penguin	<i>Pygoscelis papua</i>	54°00' S	38°03' W	Direct nest observation; precision ± 2 days
United Kingdom OT	South Atlantic	Bird Island (South Georgia)	Grey-headed albatross	<i>Thalassarche chrysostoma</i>	54°00' S	38°03' W	Direct nest observation; precision ± 1 day
United Kingdom OT	South Atlantic	Bird Island (South Georgia)	Black-browed albatross	<i>Thalassarche melanophris</i>	54°00' S	38°03' W	Direct nest observation; precision ± 1 day
United States	California	South East Farallon Islands	Pigeon guillemot	<i>Cepphus columba</i>	37°42' N	123°00' W	Direct nest observation; precision ± 5 days
United States	California	South East Farallon Islands	Brandt's cormorant	<i>Phalacrocorax penicillatus</i>	37°42' N	123°00' W	Direct nest observation; precision ± 5 days
United States	California	South East Farallon Islands	Cassin's auklet	<i>Ptychoramphus aleuticus</i>	37°42' N	123°00' W	Direct nest observation; precision ± 5 days
United States	Alaska	Kasatochi	Crested auklet	<i>Aethia cristatella</i>	52°11' N	175°31' W	Direct nest observation; precision ± 4 days
United States	Alaska	Kiska	Crested auklet	<i>Aethia cristatella</i>	52°08' N	177°36' E	Direct nest observation; precision ± 4 days



Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
United States	Alaska	Kasatochi	Least auklet	<i>Aethia pusilla</i>	52°11' N	175°31' W	Direct nest observation; precision ± 4 days
United States	Alaska	Kiska	Least auklet	<i>Aethia pusilla</i>	52°08' N	177°36' E	Direct nest observation; precision ± 4 days
United States	Alaska	Buldir	Crested auklet	<i>Aethia cristatella</i>	52°21' N	176°56' E	Direct nest observation; precision ± 2 days
United States	Alaska	Buldir	Parakeet auklet	<i>Aethia psittacula</i>	52°21' N	176°56' E	Direct nest observation; precision ± 2 days
United States	Alaska	Chowiet	Parakeet auklet	<i>Aethia psittacula</i>	56°03' N	156°42' W	Direct nest observation; precision ± 2 days
United States	Alaska	Buldir	Least auklet	<i>Aethia pusilla</i>	52°21' N	176°56' E	Direct nest observation; precision ± 2 days
United States	Alaska	St. George	Least auklet	<i>Aethia pusilla</i>	56°35' N	169°35' W	Direct nest observation; precision ± 2 days
United States	Alaska	Buldir	Whiskered auklet	<i>Aethia pygmaea</i>	52°21' N	176°56' E	Direct nest observation; precision ± 2 days
United States	Alaska	St. Lazaria	Rhinoceros auklet	<i>Cerorhinca monocerata</i>	56°59' N	135°42' W	Direct nest observation; precision ± 2 days
United States	Alaska	Aiktak	Tufted puffin	<i>Fratercula cirrhata</i>	54°11' N	164°49' W	Direct nest observation; precision ± 4 days
United States	Alaska	Buldir	Tufted puffin	<i>Fratercula cirrhata</i>	52°21' N	176°56' E	Direct nest observation; precision ± 4 days
United States	Alaska	Chowiet	Tufted puffin	<i>Fratercula cirrhata</i>	56°03' N	156°42' W	Direct nest observation; precision ± 4 days
United States	Alaska	Aiktak	Horned puffin	<i>Fratercula corniculata</i>	54°11' N	164°49' W	Direct nest observation; precision ± 2 days
United States	Alaska	Buldir	Horned puffin	<i>Fratercula corniculata</i>	52°21' N	176°56' E	Direct nest observation; precision ± 2 days
United States	Alaska	Chowiet	Horned puffin	<i>Fratercula corniculata</i>	56°03' N	156°42' W	Direct nest observation; precision ± 2 days
United States	Alaska	Aiktak	Glaucous-winged gull	<i>Larus glaucescens</i>	54°11' N	164°49' W	Direct nest observation; precision ± 4 days
United States	Alaska	Buldir	Glaucous-winged gull	<i>Larus glaucescens</i>	52°21' N	176°56' E	Direct nest observation; precision ± 4 days
United States	Alaska	Chowiet	Glaucous-winged gull	<i>Larus glaucescens</i>	56°03' N	156°42' W	Direct nest observation; precision ± 4 days

Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
United States	Alaska	St. Lazaria	Glaucous-winged gull	<i>Larus glaucescens</i>	56°59' N	135°42' W	Direct nest observation; precision ± 4 days
United States	Alaska	Aiktak	Fork-tailed storm petrel	<i>Oceanodroma furcata</i>	54°11' N	164°49' W	Direct nest observation; precision ± 7 days
United States	Alaska	St. Lazaria	Fork-tailed storm petrel	<i>Oceanodroma furcata</i>	56°59' N	135°42' W	Direct nest observation; precision ± 7 days
United States	Alaska	Aiktak	Leach's storm petrel	<i>Oceanodroma leucorhoa</i>	54°11' N	164°49' W	Direct nest observation; precision ± 7 days
United States	Alaska	St. Lazaria	Leach's storm petrel	<i>Oceanodroma leucorhoa</i>	56°59' N	135°42' W	Direct nest observation; precision ± 7 days
United States	Alaska	St. Paul	Red-faced cormorant	<i>Phalacrocorax urile</i>	57°10' N	170°15' W	Direct nest observation; precision ± 2 days
United States	Alaska	Buldir	Red-legged kittiwake	<i>Rissa brevirostris</i>	52°21' N	176°56' E	Direct nest observation; precision ± 2 days
United States	Alaska	St. George	Red-legged kittiwake	<i>Rissa brevirostris</i>	56°35' N	169°35' W	Direct nest observation; precision ± 2 days
United States	Alaska	St. Paul	Red-legged kittiwake	<i>Rissa brevirostris</i>	57°10' N	170°15' W	Direct nest observation; precision ± 2 days
United States	Alaska	Buldir	Black-legged kittiwake	<i>Rissa tridactyla</i>	52°21' N	176°56' E	Direct nest observation; precision ± 2 days
United States	Alaska	Chowiet	Black-legged kittiwake	<i>Rissa tridactyla</i>	56°03' N	156°42' W	Direct nest observation; precision ± 2 days
United States	Alaska	East Amatuli	Black-legged kittiwake	<i>Rissa tridactyla</i>	58°55' N	152°10' W	Direct nest observation; precision ± 2 days
United States	Alaska	St. George	Black-legged kittiwake	<i>Rissa tridactyla</i>	56°35' N	169°35' W	Direct nest observation; precision ± 2 days
United States	Alaska	St. Paul	Black-legged kittiwake	<i>Rissa tridactyla</i>	57°10' N	170°15' W	Direct nest observation; precision ± 2 days
United States	Alaska	Aiktak	Ancient murrelet	<i>Synthliboramphus antiquus</i>	54°11' N	164°49' W	Direct nest observation; precision ± 4 days
United States	Alaska	Aiktak	Common guillemot	<i>Uria aalge</i>	54°11' N	164°49' W	Direct nest observation; precision ± 2 days

Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
United States	Alaska	Chowiet	Common guillemot	<i>Uria aalge</i>	56°03' N	156°42' W	Direct nest observation; precision ± 2 days
United States	Alaska	East Amatuli	Common guillemot	<i>Uria aalge</i>	58°55' N	152°10' W	Direct nest observation; precision ± 2 days
United States	Alaska	St. George	Common guillemot	<i>Uria aalge</i>	56°35' N	169°35' W	Direct nest observation; precision ± 2 days
United States	Alaska	St. Lazaria	Common guillemot	<i>Uria aalge</i>	56°59' N	135°42' W	Direct nest observation; precision ± 2 days
United States	Alaska	St. Paul	Common guillemot	<i>Uria aalge</i>	57°10' N	170°15' W	Direct nest observation; precision ± 2 days
United States	Alaska	Aiktak	Thick-billed murre	<i>Uria lomvia</i>	54°11' N	164°49' W	Direct nest observation; precision ± 2 days
United States	Alaska	Buldir	Thick-billed murre	<i>Uria lomvia</i>	52°21' N	176°56' E	Direct nest observation; precision ± 2 days
United States	Alaska	Chowiet	Thick-billed murre	<i>Uria lomvia</i>	56°03' N	156°42' W	Direct nest observation; precision ± 2 days
United States	Alaska	St. George	Thick-billed murre	<i>Uria lomvia</i>	56°35' N	169°35' W	Direct nest observation; precision ± 2 days
United States	Alaska	St. Lazaria	Thick-billed murre	<i>Uria lomvia</i>	56°59' N	135°42' W	Direct nest observation; precision ± 2 days
United States	Alaska	St. Paul	Thick-billed murre	<i>Uria lomvia</i>	57°10' N	170°15' W	Direct nest observation; precision ± 2 days
United States	California	South East Farallon Islands	Common guillemot	<i>Uria aalge</i>	37°42' N	123°00' W	Direct nest observation; precision ± 2 day
United States	Alaska	Cooper Island	Black guillemot	<i>Cepphus grylle</i>	71°24' N	155°68' W	Direct nest observation; precision ± 1 day
United States	California	South East Farallon Islands	Rhinoceros auklet	<i>Cerorhinca monocerata</i>	37°42' N	123°00' W	Direct nest observation; precision ± 5 days
United States	Massachusetts	Bird Island (Buzzards Bay)	Roseate tern	<i>Sterna dougallii</i>	41°67' N	70°72' W	Direct nest observation; precision ± 3 days
United States	Massachusetts	Penikese Island	Roseate tern	<i>Sterna dougallii</i>	41°45' N	70°92' W	Direct nest observation; precision ± 1 day
United States	Massachusetts	Ram Island	Roseate tern	<i>Sterna dougallii</i>	41°62' N	70°80' W	Direct nest observation & chick hatch dates;

Country	Region	Colony	Species	Latin	Latitude	Longitude	Sampling Techniques
United States	Massachusetts	Bird Island (Buzzards Bay)	Common tern	<i>Sterna hirundo</i>	41°67' N	70°72' W	precision ± 2 days Direct nest observation; precision ± 3 days
United States	Gulf of Maine	Eastern Egg Rock	Common tern	<i>Sterna hirundo</i>	43°85' N	69°38' W	Direct nest observation; precision ± 2 days
United States	Massachusetts	Penikese Island	Common tern	<i>Sterna hirundo</i>	41°45' N	70°92' W	Direct nest observation; precision ± 1 day
United States	Massachusetts	Ram Island	Common tern	<i>Sterna hirundo</i>	41°62' N	70°80' W	Direct nest observation & chick hatch dates; precision ± 2 days
United States	Gulf of Maine	Matinicus Rock	Arctic tern	<i>Sterna paradisaea</i>	43°76' N	68°85' W	Direct nest observation; precision ± 2 days

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## PRISMA 2009 Checklist

Global phenological insensitivity to shifting ocean temperatures among seabirds

Section/topic	#	Checklist item	Reported on page #
<b>TITLE</b>			
Title	1	Identify the report as a systematic review, meta-analysis, or both.	We do not identify it this way, though our title makes the meta-analysis aspect quite apparent.
<b>ABSTRACT</b>			
Structured summary	2	Provide a structured summary including, as applicable: background; objectives; data sources; study eligibility criteria, participants, and interventions; study appraisal and synthesis methods; results; limitations; conclusions and implications of key findings; systematic review registration number.	Yes
<b>INTRODUCTION</b>			
Rationale	3	Describe the rationale for the review in the context of what is already known.	Paragraph 4
Objectives	4	Provide an explicit statement of questions being addressed with reference to participants, interventions, comparisons, outcomes, and study design (PICOS).	Paragraph 5
<b>METHODS</b>			
Protocol and registration	5	Indicate if a review protocol exists, if and where it can be accessed (e.g., Web address), and, if available, provide registration information including registration number.	We did not pre-register. However, we do identify whether hypotheses are a priori or post hoc.
Eligibility criteria	6	Specify study characteristics (e.g., PICOS, length of follow-up) and report characteristics (e.g., years considered, language, publication status) used as criteria for eligibility, giving rationale.	Methods paragraph 2
Information sources	7	Describe all information sources (e.g., databases with dates of coverage, contact with study authors to identify additional studies) in the search and date last searched.	Methods paragraph 3 - 5
Search	8	Present full electronic search strategy for at least one database, including any limits used, such that it could be repeated.	NA



## PRISMA 2009 Checklist

Study selection	9	State the process for selecting studies (i.e., screening, eligibility, included in systematic review, and, if applicable, included in the meta-analysis).	Methods paragraphs 1 & 2
Data collection process	10	Describe method of data extraction from reports (e.g., piloted forms, independently, in duplicate) and any processes for obtaining and confirming data from investigators.	Methods paragraphs 1 & 5
Data items	11	List and define all variables for which data were sought (e.g., PICOS, funding sources) and any assumptions and simplifications made.	Methods paragraphs 2 – 5 & 15 - 17
Risk of bias in individual studies	12	Describe methods used for assessing risk of bias of individual studies (including specification of whether this was done at the study or outcome level), and how this information is to be used in any data synthesis.	Our approach of using raw data should not be susceptible to publication bias. Our funnel plots reveal no evidence of bias.
Summary measures	13	State the principal summary measures (e.g., risk ratio, difference in means).	Methods paragraph 1
Synthesis of results	14	Describe the methods of handling data and combining results of studies, if done, including measures of consistency (e.g., $I^2$ ) for each meta-analysis.	Methods statistics section

Section/topic	#	Checklist item	Reported on page #
Risk of bias across studies	15	Specify any assessment of risk of bias that may affect the cumulative evidence (e.g., publication bias, selective reporting within studies).	NA
Additional analyses	16	Describe methods of additional analyses (e.g., sensitivity or subgroup analyses, meta-regression), if done, indicating which were pre-specified.	Methods statistics section
<b>RESULTS</b>			
Study selection	17	Give numbers of studies screened, assessed for eligibility, and included in the review, with reasons for exclusions at each stage, ideally with a flow diagram.	Supplementary Table 9
Study characteristics	18	For each study, present characteristics for which data were extracted (e.g., study size, PICOS, follow-up period) and provide the citations.	Supplementary Tables 10 & 11
Risk of bias within studies	19	Present data on risk of bias of each study and, if available, any outcome level assessment (see item 12).	Not applicable given our method



## PRISMA 2009 Checklist

Results of individual studies	20	For all outcomes considered (benefits or harms), present, for each study: (a) simple summary data for each intervention group (b) effect estimates and confidence intervals, ideally with a forest plot.	We summarise the effects in a funnel plot.
Synthesis of results	21	Present results of each meta-analysis done, including confidence intervals and measures of consistency.	Paragraphs 6 – 9; Figures 2 & 3
Risk of bias across studies	22	Present results of any assessment of risk of bias across studies (see Item 15).	NA
Additional analysis	23	Give results of additional analyses, if done (e.g., sensitivity or subgroup analyses, meta-regression [see Item 16]).	Methods statistics section
<b>DISCUSSION</b>			
Summary of evidence	24	Summarize the main findings including the strength of evidence for each main outcome; consider their relevance to key groups (e.g., healthcare providers, users, and policy makers).	Paragraphs 6 - 11
Limitations	25	Discuss limitations at study and outcome level (e.g., risk of bias), and at review-level (e.g., incomplete retrieval of identified research, reporting bias).	These limitations are not really applicable. We do discuss the lack of studies at low latitudes.
Conclusions	26	Provide a general interpretation of the results in the context of other evidence, and implications for future research.	Paragraphs 10 & 11
<b>FUNDING</b>			
Funding	27	Describe sources of funding for the systematic review and other support (e.g., supply of data); role of funders for the systematic review.	See acknowledgements

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