

Global phenological insensitivity to shifting ocean temperatures among seabirds

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120 **Abstract**

121

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

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

146 Globally, many species at higher trophic levels have poor conservation status⁸. Current
147 evidence indicates that the phenology of species occupying higher trophic levels is less
148 responsive to environmental change than that of primary producers and consumers^{3,2,4}, making
149 them particularly susceptible to trophic mismatch and the associated negative demographic
150 consequences^{3,9}. However, previous studies which have combined estimates of phenological
151 sensitivity (i.e. phenological change over time or in response to temperature) of multiple high
152 trophic-level species to global change^{3,2,9-13} have typically included few species or focused
153 primarily on mean responses within taxa, trophic levels, or regions. Moreover, most earlier
154 multi-species analyses have ignored sampling error in estimates of phenological sensitivity^{9,11-}
155 ¹⁴ (but see ² for an alternative approach) or sources of statistical non-independence, such as
156 phylogeny (but see ¹⁵). As such, it is not clear whether the variation in rates of phenological
157 sensitivity reported in the literature is simply the result of the sampling error variance that is
158 characteristic of regression using short time series^{16,17}, or represents true variation. If true
159 variation in phenological sensitivity exists, this may arise where the strength of plasticity
160 covaries with attributes of particular species (e.g. body size, feeding ecology, migration
161 strategy), biogeography (e.g. upwelling, latitude, hemisphere or ocean basin), or an interaction
162 between two or more of these effects. Testing the influence of these variables on variation in

163 phenological sensitivity at a global scale across multiple populations will help to ascertain
164 general patterns and highlight those taxa and regions most likely to be vulnerable to climate
165 change.

166 Seabirds are one of the best-studied groups of higher trophic level organisms, and are
167 considered here to include species from the orders Sphenisciformes, Procellariiformes,
168 Suliformes, Pelecaniformes and Charadriiformes. Found throughout the world's oceans, they
169 range in size from ~20g to ~30kg, and generally exhibit long generation times and slow,
170 inflexible life histories. They are more threatened than any other comparable avian group, with
171 the conservation status of many species rapidly deteriorating¹⁸. Seabirds exhibit considerable
172 interspecific variation in feeding strategies, with breeding season foraging ranges varying from
173 <10 to >1000 km and foraging depths from <1 m to 100s of metres deep. Outside the breeding
174 season, some species remain close to their colony while others undertake the longest migrations
175 known in the animal kingdom¹⁹.

176 Studies of seabird breeding phenology have reported a variety of different trends over
177 time²⁰. Among the local environmental drivers of phenology that have been identified, sea
178 surface temperature (SST) is widely reported to correlate with the distribution, abundance and
179 phenology of both local and migratory prey populations²¹, of which the effects on higher
180 trophic level organisms can be compared at global scales. Therefore, changes in temperature
181 driven by climate change could be critical, generating a mismatch with prey availability (see
182 further discussion below)²². Directional SST changes and fluctuations have been recorded in
183 the waters surrounding many seabird breeding sites (Figure 1a, b, Supplementary Figure 1),
184 with both metrics of change varying geographically. Large-scale climatic variables, such as the
185 North Atlantic Oscillation and the Southern Oscillation Index may also explain annual
186 variation in reproductive phenology (reviewed in ¹³). However, using large-scale proxies
187 instead of data on specific climate drivers (e.g. SST) may lead to spurious and simplistic

188 assumptions of climate-ecology dynamics²³. Furthermore, proxies at this scale are not
189 amenable to global analyses, since regional proxies are not equivalent or comparable in a single
190 analysis²³. Thus, variation in the sensitivity in timing of breeding across species and regions
191 remains unclear (but see ¹⁷). Due to their trophic position, global distribution and the numerous
192 long-term studies available, seabirds constitute a tractable and powerful group for a global
193 meta-analysis of breeding phenology. Such an analysis allows us to not only make general
194 inferences about the degree to which breeding phenology has changed both over time and in
195 relation to SST, but also about the life history traits underpinning variation in phenological
196 responsiveness (Table 1). Finally, it allows us to examine predictors of between-year
197 phenological variation, with high variance potentially indicative of phenological sensitivity to
198 one or more unspecified environmental drivers.

199 We applied a phylogenetic mixed model meta-analysis to a global dataset comprising
200 209 phenological time series of breeding dates obtained from 145 seabird populations (Figure
201 1c. Median number of years/time-series = 18; min = 5; max = 48. Median sample size/year
202 /time-series = 72; min = 6; max = 936), covering 61 species from five main orders. These
203 taxonomic groups exhibit a wide variety of life-history, migration and foraging strategies, and
204 are distributed from equator to poles across all principal oceanographic regimes. Meta-analyses
205 provide a robust approach for identifying average effect sizes across studies, and for identifying
206 predictors of variation around the average²⁴. Here, we (i) characterised latitudinal trends in the
207 mean and between-year variance of seabird breeding phenology (laying and hatching dates),
208 (ii) estimated the mean sensitivity of breeding phenology over time and in relation to SST in
209 the waters around the sampled colonies, and (iii) identified predictors (body size,
210 biogeography, phylogeny) of inter- and intra-specific variation around the mean response
211 (mean, variance and both sensitivity measures) of each species/population (for specific
212 predictions see Table 1 & Methods).

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

219 Overall, the between-year variance in lay date among populations in our dataset ranged
220 from < 1 in the black-browed albatross (*Thalassarche melanophris*) at New Island, Falklands,
221 consistent with 95% of annual means occurring within a three-day period, to 1573 in the blue-
222 footed booby (*Sula nebouxii*) at Isla Isabel, Mexico, consistent with 95% of annual means
223 occurring within a five-month period. Examination of life history traits potentially explaining
224 this variation (Supplementary meta-data) indicated that resident species were more variable
225 than migrants (Supplementary Table 2, Figure 3b). This result is in accordance with results for
226 terrestrial birds²⁸ and may arise if the laying dates of resident species are more sensitive to local
227 foraging conditions as a cue to initiate breeding in anticipation of the timing of future resources.
228 Controlling for biogeographic trends, we find that between-year variance in laying date was
229 highly phylogenetically conserved ($H^2 = 0.84$, 95% Credible Interval [CI]: 0.508 – 1, $n = 208$,
230 Supplementary Table 2). From inspection of the best linear unbiased predictors (BLUPs) for
231 the phylogenetic effects, the most threatened order¹⁸, Procellariiformes, particularly giant
232 petrels and fulmars (Procellariidae), and albatrosses (Diomedeidae), stood out as least variable
233 in timing of breeding. This response is consistent with a strong reliance on photoperiod as a
234 cue²⁹. In contrast, we find that Pelecaniformes and Suliformes (cormorants, gannets and
235 boobies) vary substantially among years in timing of breeding, suggesting that these species
236 may adjust egg laying in relation to some aspect of the local environment (weather,
237 oceanographic conditions or food availability) in the lead-up to the breeding season³⁰.

238 On average, seabirds showed no tendency to advance or delay breeding phenology over
239 time (-0.020 days yr^{-1} , 95% CI: $-0.160 - 0.129$, $n = 209$, Figure 3a). This is in agreement with
240 previous studies of this species group^{9,20}, but the overall slope was much less steep than those
241 from similar analyses of UK birds³ (mean = -0.19 days yr^{-1}), terrestrial and marine vertebrates³
242 (terrestrial mean = ~ -0.25 days yr^{-1} , marine mean = ~ -0.35 days yr^{-1}) or global estimates of
243 marine species in general⁹ (mean = ~ -0.4 days yr^{-1}). We found limited evidence for true
244 variation around the mean response (Supplementary Table 3), with 83% of the variation in raw
245 slope estimates of phenology over time attributable to sampling error arising from linear
246 regressions based on small datasets (Supplementary Table 4). Of the remaining true variation,
247 we found that the mean slope estimates did not differ significantly among oceans
248 (Supplementary Table 3). This result runs counter to previous studies of seabird breeding
249 phenology, which have reported variation in long-term trends among biogeographic
250 realms^{11,20}. However, we found some evidence that temporal response may vary among species
251 at shared breeding sites (Supplementary Table 3), although sampling covariance between the
252 different phenological measures is likely to inflate this variance estimate. Among-population
253 variation makes it difficult to predict which species and sites will be most phenologically
254 responsive to changing environments, as it implies that the degree of environmental sensitivity
255 in seabird breeding may be determined by a combination of intrinsic and extrinsic factors³¹. Of
256 the environmental or life history variables we considered, body mass was the only significant
257 positive predictor of the temporal trend (Supplementary Table 3), with larger-bodied species
258 responding at a slower rate over time than smaller species, in accordance with our predictions
259 (Table 1).

260 Globally we found no evidence that seabirds as a group have shifted their laying date
261 in relation to SST in waters around the breeding site in the three months preceding egg laying
262 (mean = -0.272 days $^{\circ}\text{C}^{-1}$, 95% CI: $-4.896 - 4.482$, $n = 108$, Figure 3b, Supplementary Table

263 5). The average response is much shallower than the average response of lay date to air
264 temperature reported for 27 UK terrestrial birds (mean = $-3.8 \text{ days } ^\circ\text{C}^{-1}$ (air temperature))³². In
265 broad agreement with the temporal analysis we found no evidence that true variation in the
266 slope of the covariation with SST is predicted by phylogeny, species, biogeographic region, or
267 life-history traits. We did, however, find significant variation in slopes among sites, and the
268 lowest BLUP was $-2.96 \text{ days } ^\circ\text{C}^{-1}$ (95% CI: $-6.00 - 0.13$) at Skomer Island, Wales, where SST
269 in the focal time period has increased significantly by $0.6^\circ\text{C decade}^{-1}$ since 1982
270 (Supplementary meta-data 1). In contrast, the most positive BLUP was $7.32 \text{ days } ^\circ\text{C}^{-1}$ (95% CI:
271 $4.96 - 9.73$) at Southeast Farallon Island, California, which is located in a highly variable
272 upwelling zone, where inter-annual variance in SST is higher than average (Figure 1b,
273 Supplementary meta-data), a condition that might select for plasticity. So, although on average,
274 seabirds appear to be unresponsive to SST, we cannot rule out the possibility some populations
275 are temperature-sensitive in either direction.

276 That we could detect no trend in seabird phenology over time or in relation to SST
277 (Supplementary meta-data), suggests that if lower trophic levels are shifting in parallel with
278 changing SST, seabirds, in general, may be at risk from increasing levels of trophic mismatch³³.
279 To date, there are very few studies that have reported the slope of the phenology of
280 poikilothermic seabird prey and lower trophic levels in relation to SST (but see ²²). Differing
281 rates of phenological response between seabirds and their food resources⁹ may leave them short
282 of critical prey during the breeding season under future climate regimes. However, there is
283 limited and mixed evidence on the frequency of climate-induced mismatch^{17,22}, and whether it
284 has an impact on breeding success³⁴ or population dynamics³⁵. Alternatively, any negative
285 fitness consequences of trophic asynchrony may be ameliorated by the ability of some species
286 to alter their behaviour, for example by switching prey or adjusting foraging effort^{22,36}.

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

295

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

298 Correspondence and requests for materials should be addressed to KK (k.keogan@ed.ac.uk).

299 **Acknowledgements**

300 The work presented here could not have been carried out without the long-term data collection
301 by field workers at all sites. Many thanks to the staff of the Alaska Maritime National Wildlife
302 Refuge; Department of Fisheries; DPaW; Environment Canada; Natural Resources Canada;
303 New Bedford Harbor Trustee Council; Oamaru Blue Penguin Colony; Phillip Island Nature
304 Parks; Government of Greenland (Ministry of Domestic Affairs, Nature and Environment) in
305 Nuuk; Island Conservation Society for permission to work on Aride Island, Seychelles; Aage
306 V Jensen Charity Foundation; The Norwegian Environment Agency (and its predecessors), the
307 SEAPOP programme (www.seapop.no) and its key institutions: The Norwegian Institute for
308 Nature Research, The Norwegian Polar Institute and Tromsø University Museum; South
309 African National Antarctic Programme; US Fish and Wildlife Service; Government of Tristan
310 da Cunha; the British Antarctic Survey. Specific thanks go to Bill Sydeman, Shae Surman, Mal

311 McCrae, Bill Fogg, Murray Davidson, Pia Boschetti, Teresa Catry, Patricia Pedro, Laurent
312 Demongin, Marcel Eens, Petra Quillfeldt, Brigitte Sabard, Jérôme Moreau, Eric Buchel,
313 Vladimir Gilg, Vadim Heuacker, Ann Harding, Françoise Amélineau, Julien Nezan, Knowles
314 Kerry, Judy Clarke, Akiko Kato, Tomohiro Deguchi, Motohiro Ito, Peter Dann, Leanne
315 Renwick, Paula Wasiak, Agustina Gómez-Laich, Paula Giudicci, Luciana Gallo, Sabrina
316 Harris, Dave Houston, Peter Menkhorst, F. I. Norman, Chantelle M. Burke, Noelle Laite, Peter
317 Mallam, Paul M. Regular, Heather Renner, Nora Rojek, Marc Romano, Leslie Slater, Tim
318 Birkhead, Jarrod Hadfield, Anthony Gaston and three anonymous reviewers for their helpful
319 comments.

320 KK was supported by a Principal's Career Development Scholarship from the University of
321 Edinburgh. ABP was funded by NERC fellowship (Ne/I020598/1). SL was funded by a NERC
322 fellowship (NE/E012906/1) and by NERC National Capability. FD and SW were funded by
323 CEH and JNCC. ND and MP were supported with post-doctoral fellowship grants by the
324 Research Fund - Flanders FWO (1265414N & 12Q6915N to ND) and (1.2.619.10.N.00 &
325 1.5.020.11.N.00 to MP). FQ was funded by the National Research Council of Argentina
326 (CONICET): PIP 5387/05, PIP 11420100100186 and PIP 11220130100268, Ministerio de
327 Ciencia, Tecnología e Innovación Productiva Argentina: PICT 04-20343, PICT 13-1229 and
328 Wildlife Conservation Society research grant (ARG_5AR03). PC and JPG were funded by
329 FCT – Portugal through UID/MAR/04292/2013 granted to MARE and Falkland Islands
330 Government. WAM and AH supported by NSERC (Discovery Grant [WAM] and PDF [AH]),
331 Environment Canada, and Memorial University of Newfoundland. AWD is funded by
332 NSERC, Environment Canada, and the New Brunswick Wildlife Council, by agreement with
333 Canadian Wildlife Service (Atlantic Region). RAP, MJD and AGW work as part of British
334 Antarctic Survey Polar Science for Planet Earth Programme (Ecosystems component), funded
335 by the Natural Environment Research Council. TMP was funded by BirdLife Australia, Deakin

336 University, Department of Conservation and Natural Resources, and Holsworth Wildlife
337 Research Fund. The Banter See common tern study was performed under the license of the city
338 of Wilhelmshaven and supported by the Deutsche Forschungsgemeinschaft (BE 916/3 to 9).
339 Data from Béchervaise Island were collected following protocols approved by the Australian
340 Antarctic Animal Ethics Committee and supported through the Australian Antarctic program
341 through Australian Antarctic Science projects 2205, 2722 and 4087. The field work in Norway
342 and Svalbard was an integrated part of the SEAPOP programme, with financial support from
343 the Norwegian Environment Agency, Ministry of Climate and Environment, Ministry of
344 Petroleum and Energy and the Norwegian Oil and Gas Association. The French Polar Institute
345 funded the field work at Hochstetter (IPEV; program “1036 Interactions”), and Ukaleqarteq
346 (program “388”). DGA, GB, KMD, PJK and AL were supported by U.S. National Science
347 Foundation grants OPP 9526865, 9814882, 0125608, 0944411 and 0440643 with logistical
348 support from the U.S. Antarctic Program. POL and PRW were supported by New Zealand’s
349 Ministry of Business, Innovation and Employment Grants C09X0510 and C01X1001, with
350 logistical support from N.Z. Antarctic Programme.

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352 KK, SL, ABP, SW, FD and RP conceived the study and wrote the manuscript. KK coordinated
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355 provided data and comments on later drafts of the manuscript.

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357 www.nature.com/reprints. The authors declare no competing financial interests.

358 **Competing Financial Interests statement** The authors declare no competing financial
359 interests.

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441

442 **Figure 1. SST trends and map of study sites included in the analyses.** a) Across
443 year temporal changes in mean Sea Surface Temperature (SST) in the three months
444 prior to breeding across all biogeographic regions represented by slopes between
445 1982 (when SST time series' began) and 2015 for each site. Each point represents a
446 slope, with positive slopes indicating warming and negative slopes indicating cooling.
447 b) Standard deviation from the mean SST at each site during the same study period.
448 A = Polar, B = Subpolar, C = Temperate, D = Subtropical, E = Tropical. c) The full
449 dataset comprises 209 time series from 61 seabird species and across 64 locations,
450 collected between 1952 and 2015. The data include slopes for 32 genera, 9 families,
451 and 5 orders (Sphenisciformes (6), Procellariiformes (15), Suliformes (3),
452 Pelecaniformes (5), Charadriiformes (32)) and spans all seven continents. The
453 underrepresentation of tropical time series is due to a combination of a paucity of
454 long-term data for these regions and the asynchronous nature of breeding in many
455 tropical species, which diminishes the informativeness of measuring annual
456 phenological central tendency.

457

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

469

470 **Figure 3. Funnel plots of phenological trends in relation to year and sea surface**
471 **temperature.** a) represents year and b) represents sea surface temperature. Each
472 point represents a slope estimate from the meta-analysis, with negative slopes
473 indicating an advance and positive slopes indicating a delay, in phenological trends.
474 Positioning of each point on the y-axis indicates the precision ($1/\text{S.E.}$) of the estimate.
475 Thus, points with higher precision are expected to converge on the true average
476 response. Lines represent the posterior for the average response or intercept (black)
477 and its 95% credible intervals (dashed red) from the basic model (Tables S3a, S5a).

478

479

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482

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

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

486

487 **Methods**

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

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

509 Monthly means of NOAA Optimum Interpolation (OI) Sea Surface Temperature (SST)
510 V2 for the period 1982 – 2015 were obtained from the NOAA/OAR/ESRL PSD, Boulder,

511 Colorado, USA, a resource which provides interpolated *in situ* and satellite SST data on a one-
512 degree grid⁴².

513 For each time series we characterised the biogeography at the colony it was located.
514 We collated information on the location (latitude and longitude) and hemisphere of each
515 population, and for our primary fixed effects model we assigned each location to one of the
516 three main oceans: Atlantic, Pacific or Indian. Global climate zones (Equatorial, Tropical,
517 Subtropical, Temperate, Subpolar or Polar) were identified using the classification from
518 Trujillo & Thurman (2014). These zones correspond to latitudinal bands of similar sea surface
519 temperature and are categorized by levels of precipitation, wind and water temperature⁴³. We
520 combined hemisphere, ocean and global climate zone to identify 15 Biogeographic Regions
521 (e.g. North Atlantic Temperate; South Pacific Subpolar etc.). Finally, we used the Longhurst
522 Biogeographical Provinces to determine whether each location was situated within an Eastern
523 Boundary (upwelling) zone⁴⁴. These are areas of high productivity within the marine
524 environment, and are also highly variable across seasons, years and decades^{40,45}.

525 We collated data on several aspects of the ecology and life history of each species that
526 may affect the phenological slope (with year or temperature), mean or between-year variance.
527 These data were provided by authors and supplemented using online resources:
528 www.audubon.org, www.birdlife.org, nzbirdsonline.org.nz, www.bird-research.jp and
529 www.npolar.no (Supplementary meta-data). Feeding strategy was categorised either as surface
530 feeder (feeding <1 metre below the surface), diver (feeding >1 metre below the surface), or
531 kleptoparasite/predator (part-time marine foragers). Species which seek out prey by diving
532 under water may be able to exploit a wider range of prey than those constrained to feeding on
533 the surface (<1 metre depth), thus reducing the necessity to adjust breeding phenology to buffer
534 mismatch⁴⁶⁻⁴⁸. We also compiled data on average body mass of every species (Supplementary
535 meta-data), as small-bodied seabird species are predicted to be more sensitive to temperature

536 change due to the higher cost of thermoregulation^{37,49}. Furthermore, body mass can be used as
537 a proxy for trophic level, which is difficult to classify explicitly in seabirds⁵⁰. We used log
538 body mass in analyses. The migration strategy of individuals from each population was
539 assigned based on the behaviour of the majority (>80%) of individuals. Long distance trans-
540 equatorial migrants, and species which spend the winter outside the sector in which they breed
541 were categorised together as “migrants”, and those which remain in the same ocean sector
542 throughout the year were classified as “residents”. Sectors were defined as North Atlantic,
543 Mediterranean, South Atlantic, Southern Ocean-Atlantic sector, North Pacific, South Pacific,
544 Southern Ocean-Pacific sector, Indian, Southern Ocean-Indian sector.

545 We took into account phylogenetic relationships among species using 100 samples of
546 the pseudo-posterior species tree⁵¹ using the Hackett *et al.* (2008) backbone⁵².

547 **Statistics** We used the *MCMCglmm* package⁵³ in R (v 3.2.2; R Core Team 2015), to fit
548 Bayesian generalised linear mixed-effects models (GLMMs). We adopted a random effects
549 meta-analytic (REMA) approach, estimating both fixed and random effects, while taking
550 sampling error characteristic or regression using short time series into account^{16,24}.

551 We included cross-classified random effects to account for and estimate sources of
552 variance, though not every random variable was included in each model (see Tables S1-S5).

553 The model was of the form

$$554 \quad y_i = \mu + \beta x_i + \alpha_{f[i]} + s_{f[i]} + b_{g[i]} + l_{h[i]} + p_{j[i]} + e_i + m_i \quad \text{eq. 1.}$$

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

559 $\alpha_{f[i]}$ is the effect of phylogenetic non-independence due to shared evolutionary
 560 history¹⁶ for the f th species. $s_{f[i]}$ is the non-phylogenetic species-specific effect for the f th
 561 species. Spatial variation was accounted for via two terms, g th biogeographic region ($b_{g[i]}$)
 562 (see Supplementary meta-data) and h th site ($l_{h[i]}$). In certain analyses we included multiple
 563 measures/traits for a time series and in these cases we could fit the interaction between site and
 564 species (population) ($p_{j[i]}$), which provided us with an estimate of intraspecific geographic
 565 variation that is unique to each (j th) population. In these cases the residual term (e_i) captures
 566 variation within a site and species (population), and we allowed this variance to be
 567 heterogeneous across different phenophases (i.e. median lay date, mean lay date, first hatch
 568 date, median hatch date, mean hatch date). In other analyses only a single measure/trait was
 569 included and in such instances $p_{j[i]}$ was not estimable. In this case the residual term captured
 570 variance both due to intraspecific geographic variation that is unique to each species and
 571 differences among phenological measures/traits. Our response variables were themselves
 572 estimates that have error associated with them and we incorporated sampling error variances
 573 as m_i , which means that the analyses were weighted. For the sampling error term, the among-
 574 observation variance was set to 1, and for all other random terms the variance was estimated.
 575 The specification of these models assumed that random effects for different measures were
 576 perfectly correlated. To test whether this impacted on our estimation of phylogenetic signal we
 577 then relaxed this assumption and estimated the covariance between random effects for
 578 measures of laying and hatching phenology (Variance Structure of Models section, below).

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

582
$$H^2 = \frac{\sigma_a^2}{(\sigma_a^2 + \sigma_s^2)} \quad \text{eq. 2.}$$

583

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

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

593 *Post hoc tests*: mean phenology is delayed as latitude increases in both hemispheres, with a
594 significant quadratic term, such that the slope appears to reach an asymptote toward the poles
595 (Figure 2, Supplementary Table 1). However, seabirds at low latitudes are underrepresented in
596 this study. When we removed three low latitude data points, there was no support for the
597 quadratic relationship (Supplementary Table 1) but the positive linear relationship between
598 latitude and breeding phenology remained (posterior mean = 0.81 days.lat⁻¹, 95% CI: 0.33 –
599 1.29, $n = 206$, Supplementary Table 1). The intercepts of each measure of phenology (i.e. mean
600 laying date, first hatching date) differed significantly, although a test including the interaction
601 between latitude and phenological measure revealed no difference in their latitudinal slopes
602 (Supplementary Table 1).

603

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

606 the number of years (n). The sampling variance of this measure was quantified as ($s^2_{\ln \sigma}$) as in
607 eq. 4⁵⁵:

$$608 \quad \ln \hat{\sigma} = \ln s + \frac{1}{2(n-1)} \quad \text{eq. 3.}$$

$$609 \quad s^2_{\ln \hat{\sigma}} = \frac{1}{2(n-1)} \quad \text{eq. 4.}$$

610

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

616

617 (3) Temporal trend in phenology: we estimated the linear slope (and standard error) of
618 phenological change over time for each measure (median, mean, first date) and trait (laying or
619 hatching date) of a population using Generalised Least Squares (GLS) in nlme⁵⁶, fitting an
620 autoregressive model of order 1, AR(1)⁵⁷, to take into account temporal autocorrelation in each
621 individual time series. We used these slope estimates in a meta-analysis, and included the
622 squared standard error of the slope to weight the analysis. We included three types of fixed
623 effects: methodology (trait, measure, mean year of time series), life history and ecology (body
624 mass and foraging strategies), and biogeography (ocean basin, hemisphere, latitude). See Table
625 1 for predictions. We did not make predictions about which ocean basins or hemisphere might
626 show the steepest slopes, but allowed the response to differ among ocean basis and hemispheres
627 in our model.

628 *Post hoc test:* our primary ecological fixed effects model categorised locations into one of the
629 three main ocean basins (Atlantic, Indian, Pacific), and included the interaction between
630 latitude and hemisphere as an additional parameter. This approach considered the life histories
631 of wide-ranging polar species which may have large foraging ranges. Yet many species forage
632 near to the colony, or may have evolved alongside the unique oceanographic features of polar
633 systems⁵⁸. To consider these species we re-categorised ocean basins into five discrete water
634 bodies (Arctic, Atlantic, Indian, Pacific, Southern) and ran our ecological model again,
635 replacing the three ocean variable with five oceans, and removing the interaction between
636 latitude and hemisphere.

637

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

651 For each colony we calculated the reaction norms and associated standard errors of
652 phenological response to SST (days °C⁻¹) using the GLS methods as described for the temporal
653 trends, but retaining year as an additional predictor, in order to de-trend the data and allow us
654 to consider the effects of SST independently of time (Supplementary meta-data). We compared
655 among pre-breeding on the basis of AIC and found very little difference, as expected given the
656 overlap between time periods and month-to-month temporal autocorrelation is SST. Across
657 time series the three-month period had the lowest mean AIC (2 month mean $\Delta AIC = 0.02$, 1
658 month mean $\Delta AIC = 0.50$) and for consistency we used this time period in subsequent analyses.

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

665 All models were run for 30,000 iterations on each phylogenetic tree sample, discarding
666 the first 10,000 as burn-in and sampling every 10th iteration. We repeated this process over 100
667 phylogenetic trees and the pooled posterior distributions take into account both model and
668 phylogenetic uncertainties⁵⁹. Parameter-expanded priors were used for all random effects
669 except the residual, which followed an inverse Wishart distribution. Plots of the mean and
670 variance of the posterior distribution were examined to assess autocorrelation in the posterior
671 samples. Statistical significance of fixed effects was inferred where 95% credible intervals did
672 not span zero.

673 **Variance Structure of Models:**

674 Our dataset contains five phenophases: median lay date (1), mean lay date (2), first hatch date
675 (3), median hatch date (4) and mean hatch date (5). The core models (with the exception of
676 temperature) run under the assumption that within the residual term (e_i) the variance would
677 be heterogeneous, with each phenophase varying independently of the other four (eq. S1).
678 We used the `idh()` variance structure function in the `MCMCglmm` package⁵³. This is
679 consistent with phenophases being uncorrelated at the residual level (i.e. covariance = 0) but
680 at the other random effects the correlation between phenophases is assumed to be 1.

681

$$682 \quad \mathbf{V}_{e_i} = \begin{bmatrix} V_{1,1} & 0 & 0 & 0 & 0 \\ 0 & V_{2,2} & 0 & 0 & 0 \\ 0 & 0 & V_{3,3} & 0 & 0 \\ 0 & 0 & 0 & V_{4,4} & 0 \\ 0 & 0 & 0 & 0 & V_{5,5} \end{bmatrix} \quad \text{eq. S1}$$

683

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

687

$$688 \quad \mathbf{V}_{e_i} = \begin{bmatrix} V_{1,1} & C_{1,2} & C_{1,3} & C_{1,4} & C_{1,5} \\ C_{1,2} & V_{2,2} & C_{2,3} & C_{2,4} & C_{2,5} \\ C_{1,3} & C_{2,3} & V_{3,3} & C_{3,4} & C_{3,5} \\ C_{1,4} & C_{2,4} & C_{3,4} & V_{4,4} & C_{4,5} \\ C_{1,5} & C_{2,5} & C_{3,5} & C_{4,5} & V_{5,5} \end{bmatrix} \quad \text{eq. S2}$$

689

690 Allowing slopes of phenophases to covary for every random effect may result in a more
691 informative estimate of phylogenetic signal (i.e. perhaps signal is observed at one stage of

692 reproduction but not another), but requires a large amount of data at each level to confidently
693 estimate multiple (co)variances. As our dataset was not large enough to run models with fully
694 unstructured (co)variance, we only estimate the covariance between lay and hatch dates. We
695 restructured the covariance matrix for each random effect (eq. S2) into a 2 x 2 grid (eq. S3).

696

$$697 \quad \mathbf{V}_{RE} = \begin{bmatrix} V_{lay,lay} & C_{lay,hatch} \\ C_{lay,hatch} & V_{hatch,hatch} \end{bmatrix} \text{ eq. S3}$$

698

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

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

709 **Data availability** The authors declare that all biological data generated and analysed in this
710 study are available within the article, its supplementary information files and in the following
711 repository: <https://github.com/katkeogan/seabird-metaanalysis>. The NOAA Optimum
712 Interpolation (OI) Sea Surface Temperature (SST) V2 data that support the findings of this
713 study are available from NOAA/OAR/ESRL Physical Sciences Division,

714 <http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html>. The phylogenetic trees
715 generated and analysed in this study were obtained from BirdTree, www.birdtree.org.

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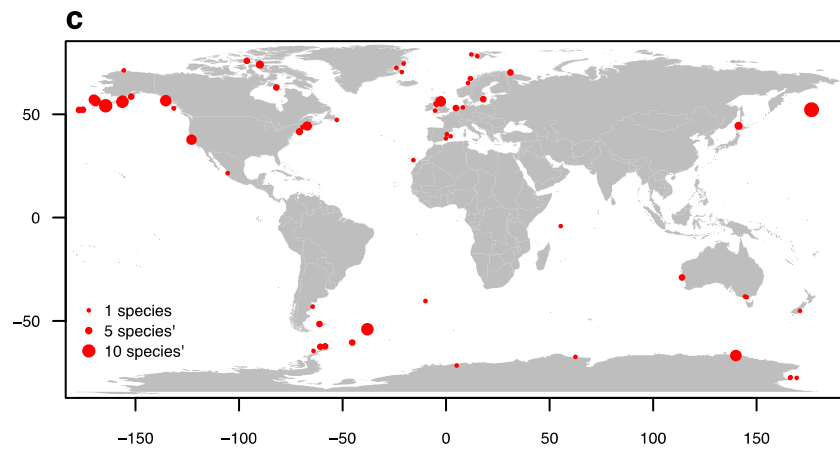
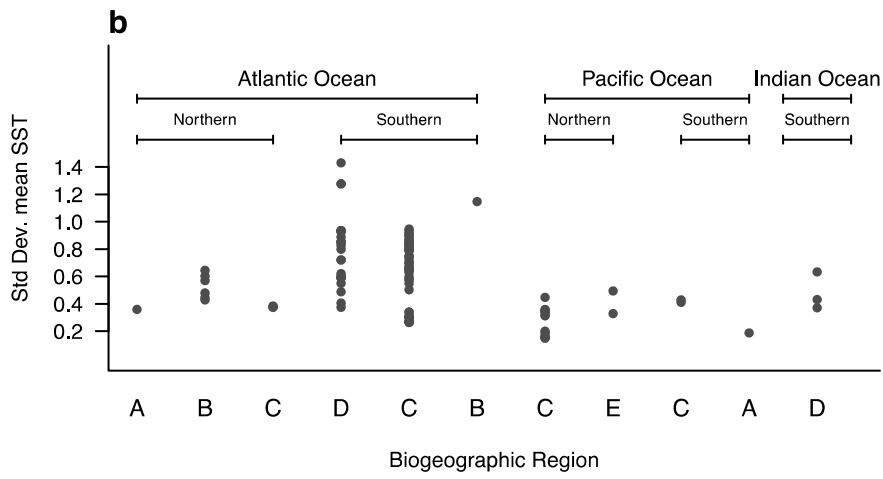
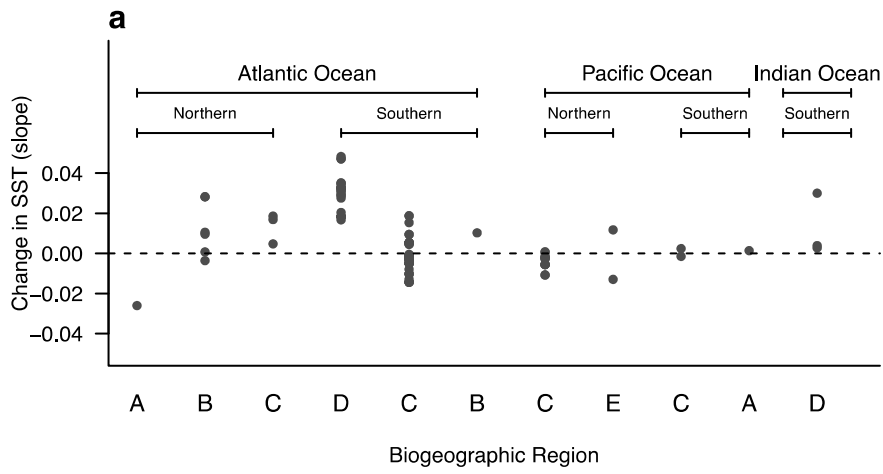
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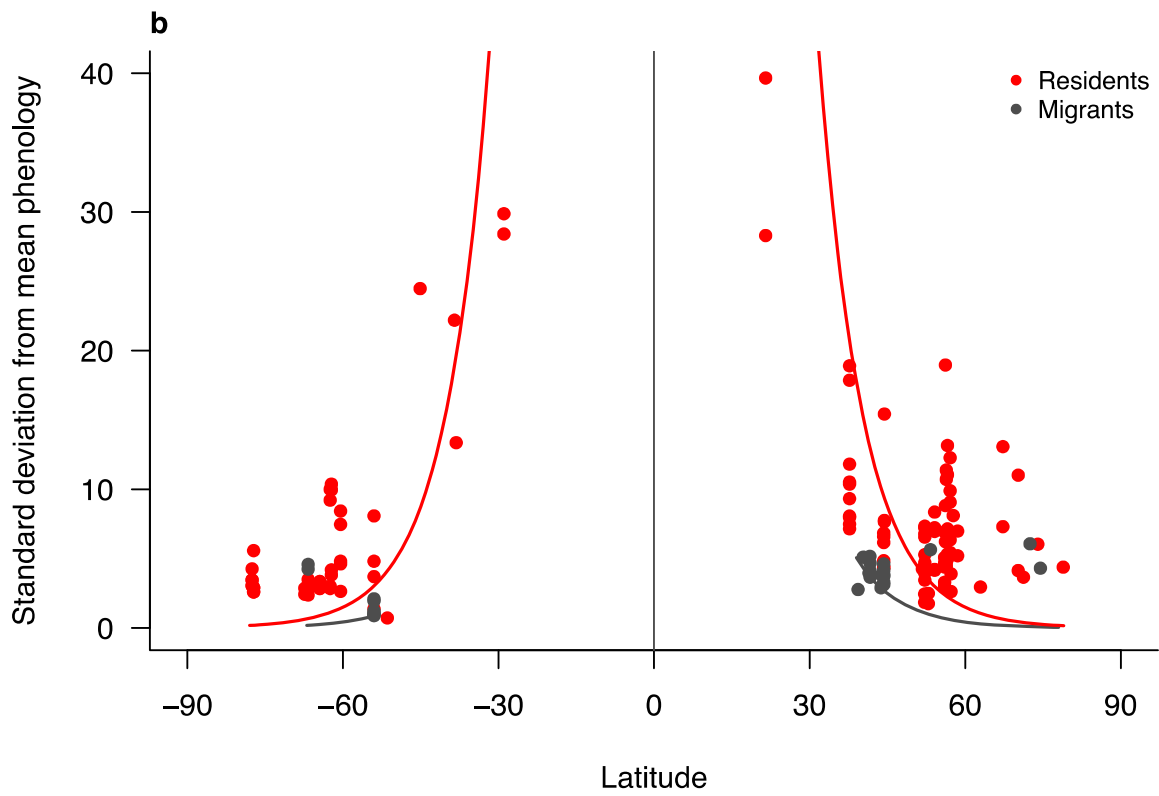
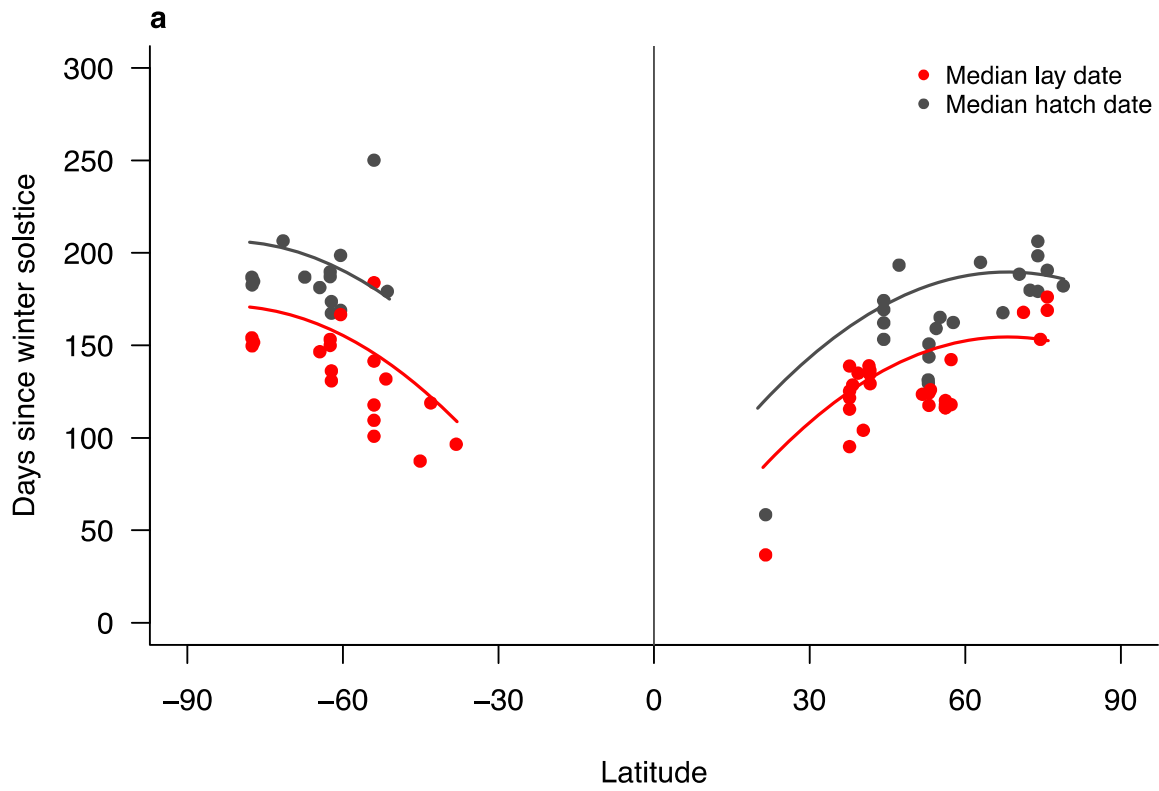
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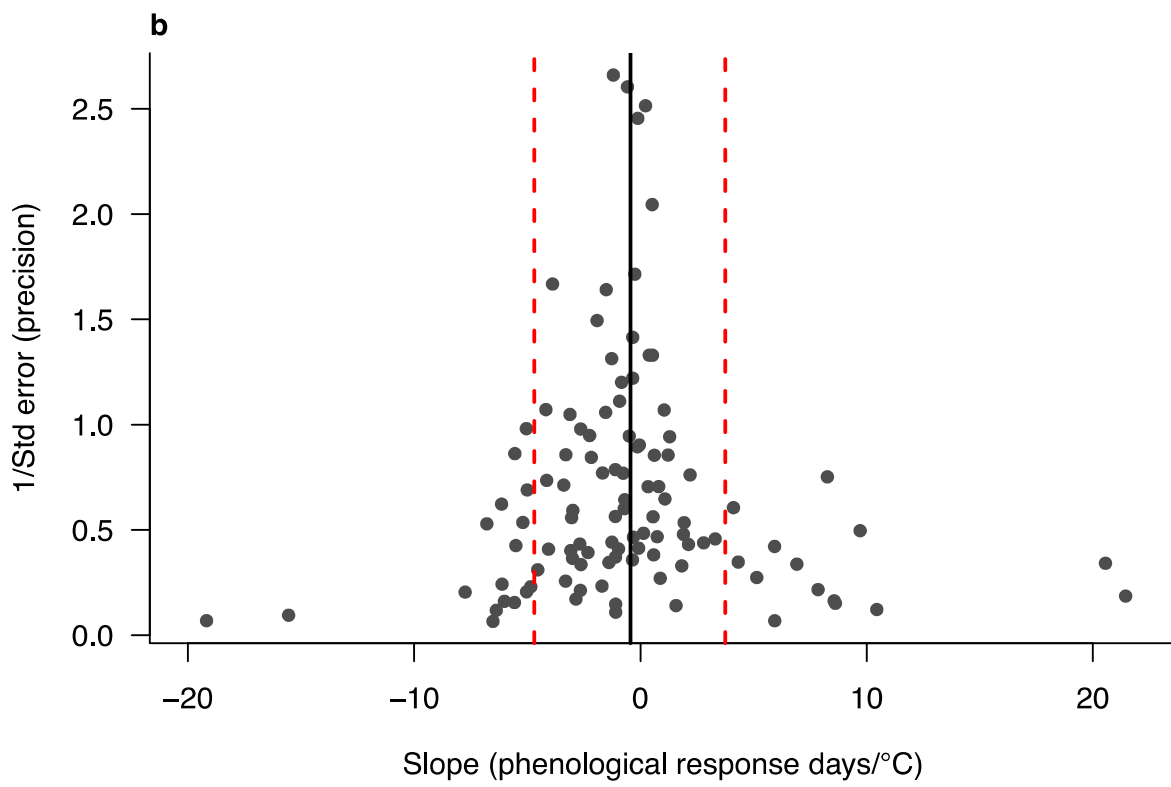
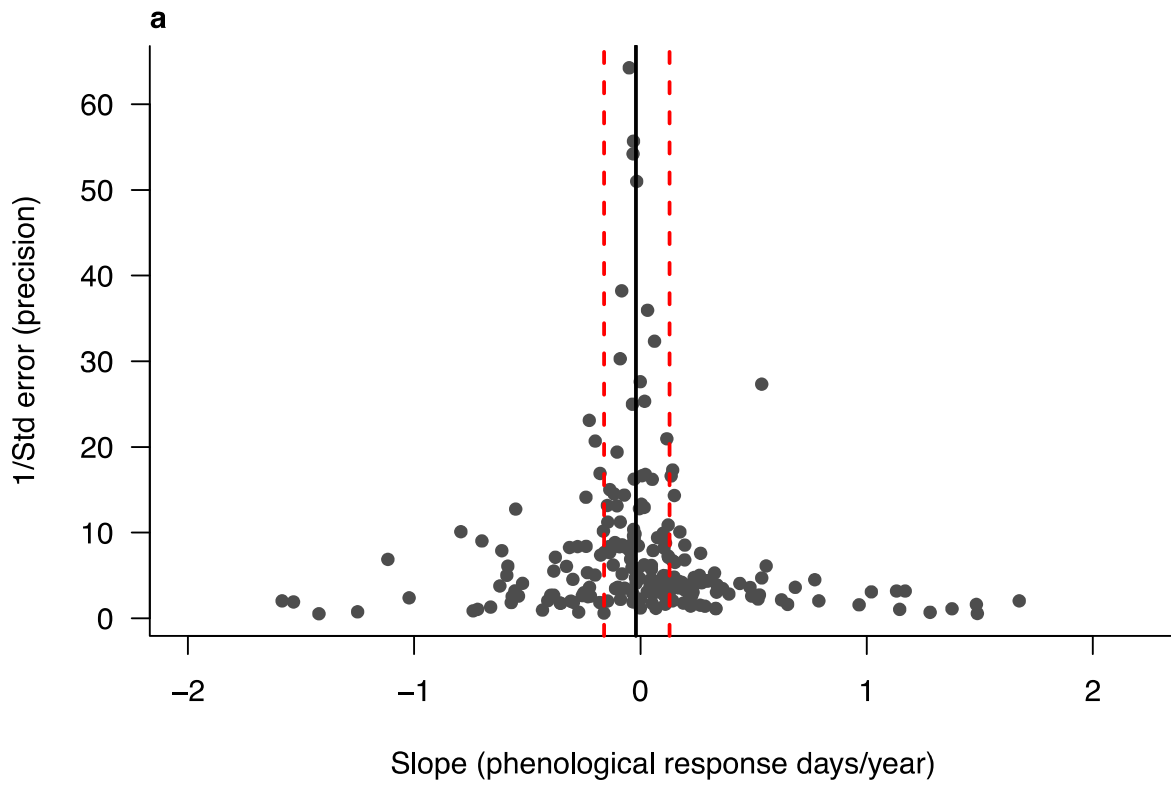
767 Figure 1



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776 Supplementary materials

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