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Global phenological insensitivity to shifting ocean temperatures among seabirds

Katharine Keogan^{1*}, Francis Daunt², Sarah Wanless², Richard A. Phillips³, Craig A. Walling¹, Philippa Agnew⁴, David G. Ainley⁵, Tycho Anker-Nilssen⁶, Grant Ballard⁷, Robert T. Barrett⁸, Kerry J. Barton⁹, Claus Bech¹⁰, Peter Becker¹¹, Per-Arvid Berglund¹², Tim Birkhead¹³, Loïc Bollache^{14,15}, Alexander L. Bond^{16,17}, Sandra Bouwhuis¹¹, Russell W. Bradley⁷, Zofia M. Burr¹⁸, Kees Camphuysen¹⁹, Paulo Catry²⁰, Andre Chiaradia²¹, Signe Christensen-Dalsgaard⁶, Richard Cuthbert¹⁶, Nina Dehnhard²², Sébastien Descamps²³, Tony Diamond²⁴, George Divoky²⁵, Hugh Drummond²⁶, Katie M. Dugger²⁷, Michael J. Dunn³, Louise Emmerson²⁸, Kjell Einar Erikstad^{23,29}, Jérôme Fort³⁰, William Fraser³¹, Anthony Gaston³², Meritxell Genovart³³, Olivier Gilg^{14,34}, Jacob González-Solís³⁵, José Pedro Granadeiro³⁶, David Gremillet^{37,38}, Jannik Hansen³⁹, Sveinn A. Hanssen⁶, Mike Harris², April Hedd⁴⁰, Jefferson Hinke⁴¹, José Manuel Igual³³, Jaime Jahncke⁷, Ian Jones⁴², Peter J. Kappes⁴³, Johannes Lang^{14,44}, Magdalene Langset⁶, Amélie Lescroël³⁷, Svein-Håkon Lorentsen⁶, Phil O'B. Lyver⁴⁵, Mark Mallory⁴⁶, Børge Moe⁶, William A. Montevecchi⁴⁷, David Monticelli⁴⁸, Carolyn Mostello⁴⁹, Mark Newell², Lisa Nicholson⁵⁰, Ian Nisbet⁵¹, Olof Olsson⁵², Daniel Oro³³, Vivian Pattison⁵³, Maud Poisbleau²², Tanya Pyk⁵⁴, Flavio Quintana⁵⁵, Jaime Ramos⁴⁸, Raúl Ramos³⁵, Tone Kirstin Reiertsen²³, Cristina Rodríguez²⁶, Peter Ryan⁵⁶, Ana Sanz-Aguilar³³, Niels M. Schmidt⁵⁷, Paula Shannon⁵⁸, Benoît Sittler^{14,59}, Colin Southwell²⁸, Christopher Surman⁵⁰, Walter S. Svagej⁶⁰, Wayne Trivelpiece⁶¹, Pete Warzybok⁷, Yutaka Watanuki⁶², Henri Weimerskirch⁶³, Peter R. Wilson⁶⁴, Andrew G. Wood³, Albert B. Phillimore^{1†}, Sue Lewis^{1,2†}

*Corresponding author

† These authors contributed equally to this work.

¹ Institute of Evolutionary Biology, University of Edinburgh, Ashworth Laboratories, Charlotte Auerbach Road, EH9 3FL, United Kingdom

² Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, United Kingdom

³ British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, Cambridgeshire CB3 0ET, United Kingdom

⁴ Oamaru Blue Penguin Colony, Waterfront Road, Oamaru 9400, New Zealand

⁵ HT Harvey and Associates, 983 University Avenue, Building D, Los Gatos, CA 95032 USA

⁶ Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgard, 7034 Trondheim, Norway

⁷ Point Blue Conservation Science, 3820 Cypress Drive, Suite 11, Petaluma, CA 94954, USA

⁸ Department of Natural Sciences, Tromsø University Museum, PO Box 6050 Langnes, NO-9037 Tromsø, Norway

⁹ Landcare Research, Private Bag 6, Nelson, New Zealand

¹⁰ Department of Biology, Norwegian University of Science and Technology, Norway

¹¹ Institute of Avian Research, An der Vogelwarte 21, 26386 Wilhelmshaven, Germany

¹² Institute of Marine Research, Department of Aquatic Resources, Swedish University of Agricultural Sciences, Sweden

¹³ Department of Animal and Plant Sciences, University of Sheffield, United Kingdom

¹⁴ Groupe de Recherche en Ecologie Arctique, 16 rue de Vernet, F-21440 Francheville, France

¹⁵ Laboratoire Chrono-environnement, Université de Bourgogne France Comté, F-25000 Besançon, France

¹⁶ RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, United Kingdom

¹⁷ Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, A1B 3X9 Canada

¹⁸ The University Centre in Svalbard, NO-9171 Longyearbyen, Norway

49 ¹⁹ Department of Coastal Systems, Royal Netherlands Institute for Sea Research P.O. Box 59, 1790
50 AB Den Burg, Texel & Utrecht University, Utrecht, Netherlands

51 ²⁰ MARE – Marine and Environmental Sciences Centre, ISPA – Instituto Universitário, Rua Jardim
52 do Tabaco 34, 1149-041 Lisbon, Portugal

53 ²¹ Phillip Island Nature Parks, PO Box 97 Cowes, Victoria 3922, Australia

54 ²² Department of Biology, Behavioural Ecology and Ecophysiology Group, University of Antwerp,
55 Campus Drie Eiken, Universiteitsplein 1, 2610 Antwerp (Wilrijk), Belgium

56 ²³ Norwegian Polar Institute (FRAM), High North Research Centre for Climate and the Environment,
57 Tromsø, Norway

58 ²⁴ University of New Brunswick, Fredericton N.B. E3B 5A3, Canada

59 ²⁵ Friends of Cooper Island, 652 32nd Avenue E, Seattle, WA 98112, USA

60 ²⁶ Instituto de Ecología, Universidad Nacional Autónoma de México, A.P. 70-275, 04510 DF, Mexico

61 ²⁷ U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit. Department of
62 Fisheries and Wildlife, 104 Nash Hall, Corvallis, OR, USA

63 ²⁸ Australian Antarctic Division, Channel Highway, Kingston, 7050, Tasmania, Australia

64 ²⁹ Centre for Conservation Biology, Department of Biology, Norwegian University of Science and
65 Technology, Trondheim, Norway.

66 ³⁰ Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS-Université de La Rochelle, La
67 Rochelle, France

68 ³¹ Polar Oceans Research Group, Sheridan, MT 59749 USA

69 ³² Environment Canada, National Wildlife Research Centre, Carleton University,
70 Ottawa, Ontario K1A 0H3, Canada.

71 ³³ Population Ecology Group, IMEDEA (CSIC-UIB), Esporles, Spain

72 ³⁴ Laboratoire Biogéosciences, UMR CNRS 6282, Université de Bourgogne Franche Comté, Dijon,
73 France

74 ³⁵ Departament de Biologia Animal, Universitat de Barcelona, Av Diagonal 643, Barcelona 08028,
75 Spain

76 ³⁶ CESAM, Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa,
77 Campo Grande, 1749-016 Lisbon, Portugal

78 ³⁷ Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS - Université de Montpellier -
79 Université Paul-Valéry Montpellier - EPHE, Montpellier, France

80 ³⁸ FitzPatrick Institute, DST-NRF Centre of Excellence at the University of Cape Town, Rondebosch
81 7701, South Africa

82 ³⁹ Department of Bioscience, Aarhus University, Denmark

83 ⁴⁰ Wildlife Research Division, Science and Technology Branch, Environment Canada

84 ⁴¹ Antarctic Ecosystem Research Division, National Marine Fisheries Service, National Oceanic and
85 Atmospheric Administration, La Jolla, USA

86 ⁴² Department of Biology, Memorial University. St. John's, Newfoundland and Labrador, A1B 3X9,
87 Canada

88 ⁴³ Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, 104
89 Nash Hall, Corvallis, OR, USA

90 ⁴⁴ Working Group for Wildlife Biology, Justus Liebig University Giessen, Leihgesterner Weg 217, D-
91 35392 Giessen, Germany

92 ⁴⁵ Landcare Research, PO Box 6940, Lincoln, 7640, New Zealand

93 ⁴⁶ Biology, Acadia University, Wolfville, Nova Scotia, Canada, B4P2R6

94 ⁴⁷ Department of Psychology, Biology and Ocean Sciences, Memorial University of Newfoundland

95 ⁴⁸ MARE – Marine and Environmental Sciences Centre, Department of Life Sciences, University of
96 Coimbra, 3004-517 Coimbra, Portugal

- 97 ⁴⁹ Massachusetts Division of Fisheries and Wildlife, 1 Rabbit Hill Road, Westborough, MA 01581,
98 USA
- 99 ⁵⁰ Halfmoon Biosciences, 45 Heather Road, Ocean Beach, WA 6333, Australia
- 100 ⁵¹ I. C. T. Nisbet & Company, 150 Alder Lane, North Falmouth, MA 02556, USA
- 101 ⁵² Stockholm Resilience Centre, Stockholm University, 106 91 Stockholm, Sweden
- 102 ⁵³ Laskeek Bay Conservation Society, 3207 Wharf Way, Queen Charlotte, BC V0T 1S0, Canada
- 103 ⁵⁴ Deakin Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin
104 University, 221 Burwood Hwy, Burwood, VIC 3125, Australia
- 105 ⁵⁵ Instituto de Biología de Organismos Marinos (IBIOMAR-CONICET), Boulevard Brown 2915,
106 Puerto Madryn (U9120ACD), Chubut, Argentina
- 107 ⁵⁶ Percy FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of
108 Cape Town, Rondebosch 7701, South Africa
- 109 ⁵⁷ Arctic Research Centre, Department of Bioscience, Aarhus University, Denmark
- 110 ⁵⁸ National Audubon Society Seabird Restoration Program, 12 Audubon Road, Bremen, ME 04551,
111 USA
- 112 ⁵⁹ Chair Nature Protection and Landscape Ecology, University of Freiburg, Tennebacher Straße 4, D-
113 79106 Freiburg, Germany
- 114 ⁶⁰ Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata-
115 CONICET, Deán Funes 3250, Mar del Plata (B7602AYJ), Buenos Aires, Argentina
- 116 ⁶¹ 5959 Shoreline Highway, Bolinas, California 94929, USA
- 117 ⁶² Graduate School of Fisheries Sciences, Hokkaido University, Minato-cho 3-1-1, Hakodate, 041-
118 8611, Japan
- 119 ⁶³ CEBC, Centre National de la Recherche Scientifique (CNRS), 405 Route de Prissé la Charrière,
120 79360 Villiers-en-Bois, France
- 121 ⁶⁴ Landcare Research, Tamaki Campus, Auckland, New Zealand

1 **Abstract**

2
3 The timing of reproduction plays a key role in determining productivity¹, and is influenced by
4 climatic conditions and seasonal peaks in abundance of prey species². Current patterns of
5 climate change may alter timing of breeding at different rates across trophic levels, resulting in
6 trophic mismatch³. This is of particular concern for higher trophic level organisms, whose
7 longer generation times confer a lower capacity for plastic responses or evolutionary rescue
8 than the primary producers and consumers on which they depend^{4,5}. However, studies of
9 ecological change in marine systems have been largely disconnected, making general patterns
10 difficult to detect⁶. Here, we present a comprehensive global meta-analysis of upper trophic
11 level predator phenology, based on 211 phenological time series from 147 breeding populations
12 representing all the major families of a well-studied group, seabirds. We show that overall,
13 between 1952 and 2015, seabird populations worldwide have not adjusted their breeding
14 phenology over time (-0.020 days yr⁻¹) or in parallel with rising sea surface temperatures (SST)
15 (-0.272 days °C⁻¹). Between-year variance in breeding phenology of individual populations
16 decreases towards the poles and is phylogenetically conserved. Marked inter-year variation
17 observed in some taxa, including resident species and some Pelecaniformes and Suliformes
18 (cormorants, gannets and boobies), may imply that other unmeasured environmental conditions
19 are affecting breeding phenology. This global study highlights very limited temperature-
20 mediated plasticity or micro-evolution in the timing of seabird reproduction in response to
21 anthropogenic change in SST, which may make these highly vulnerable top predators
22 susceptible to future trophic mismatch³.

1 The effects of rising global temperatures are having a profound impact on terrestrial
2 and aquatic biota, including species abundance, distributions, behaviours, and interactions⁷.
3 Changes in phenology - the timing of seasonally recurring life history events - are one of the
4 most apparent responses to rising global temperatures; at higher latitudes many spring and early
5 summer events are advancing over time across a suite of terrestrial, freshwater and marine
6 ecosystems^{2,3}. As timing of breeding affects the abiotic conditions and biotic interactions to
7 which parents and their offspring are exposed⁸, breeding phenology is expected to play a key
8 role in mediating the relationship between environmental temperature and fitness¹.

9 Globally, many species at higher trophic levels have poor conservation status⁹. Current
10 evidence indicates that the phenology of species occupying higher trophic levels is less
11 responsive to environmental change than that of primary producers and consumers^{2,3}, making
12 them particularly susceptible to trophic mismatch and the associated negative demographic
13 consequences^{2,10}. However, previous studies which have combined estimates of phenological
14 sensitivity (i.e. phenological change over time or in response to temperature) of multiple high
15 trophic-level species to global change^{2,3,10-14} have typically included few species and/or
16 focused primarily on mean responses within taxa, trophic levels, or regions. Moreover, most
17 earlier multi-species analyses have ignored the inherent uncertainty in estimates of
18 phenological sensitivity^{10,12-15} (but see ³ for an alternative approach) and/or sources of
19 statistical non-independence, such as phylogeny (but see ¹⁶). As such, it is not clear whether
20 the variation in rates of phenological sensitivity reported in the literature is simply the result of
21 estimation error inherent to regression using short time series^{17,18}, or represents true variation.
22 If phenological sensitivity exists, this true variation may be driven by attributes of particular
23 species (e.g. body size, feeding ecology, migration strategy), biogeography (e.g. upwelling,
24 latitude, hemisphere or ocean basin), or an interaction between two or more of these effects.
25 Testing the ability of these variables to predict variation in phenological sensitivity at a global

26 scale across multiple populations will help to ascertain general patterns and highlight those
27 taxa and regions most likely to be more- or less- vulnerable to climate change.

28 One of the best-studied groups of higher trophic level organisms is that of seabirds,
29 defined here as including species from the Orders Sphenisciformes, Procellariiformes,
30 Suliformes, Pelecaniformes and Charadriiformes. Found throughout the world's oceans, they
31 range in size from ~20g to ~30kg, and generally exhibit long generation times and slow,
32 inflexible life histories. They are more threatened than any other comparable avian group, with
33 a rapidly deteriorating global conservation status¹⁹. Some are prey specialists, feeding
34 exclusively on zooplankton, fish or cephalopods, while others remain generalist, feeding in a
35 variety of habitats²⁰. Seabirds exhibit considerable interspecific variation in feeding strategies,
36 with breeding season foraging ranges varying from <10 to >1000 km and species feeding at
37 water depths that range from <1 metre below the ocean surface to several hundred metres deep.
38 Outside the breeding season individuals of some species remain close to their breeding site
39 while others undertake the longest migrations known in the animal kingdom²⁰.

40 Studies of seabird breeding phenology have reported a variety of different trends over
41 time²¹. Among the local environmental drivers of phenology that have been identified, sea
42 surface temperature (SST) provides a proxy of the distribution, abundance and phenology of
43 both local and migratory prey populations²², of which the effect on higher trophic level
44 organisms can be compared at global scales. Therefore, changes in temperature owing to
45 climate change could be critical, playing into a mismatch with prey availability (see further
46 discussion below)²³. Large-scale climatic variables, such as the North Atlantic Oscillation and
47 the Southern Oscillation Index, have also been examined to explain annual variation in
48 reproductive phenology (reviewed in ¹⁴). The marine regions highly impacted by climatic
49 changes coincide with highest seabird biodiversity²⁴. However, using large-scale proxies in
50 lieu of finer-scale climate data (e.g. local SST) may lead to spurious and simplistic assumptions

51 of climate-ecology dynamics. Furthermore, proxies at this scale are not amenable to global
52 analyses, since regional proxies are not equivalent or comparable in a single analysis²⁵. Thus,
53 variation in the sensitivity in timing of breeding across species and regions remains unclear
54 (but see ¹⁸). Due to their trophic position, global distribution and the numerous long-term
55 studies to which they have been subjected, seabirds present a tractable and powerful group for
56 a global meta-analysis of breeding phenology. Such an analysis allows us to not only make
57 general inferences about the degree to which breeding phenology has changed both over time
58 and in relation to SST, but also about the life history traits underpinning variation in
59 phenological responsiveness (Table 1). Finally, it allows us to examine predictors of inter-year
60 phenological variation, with high variance potentially indicative of phenological sensitivity to
61 one or more unspecified environmental drivers.

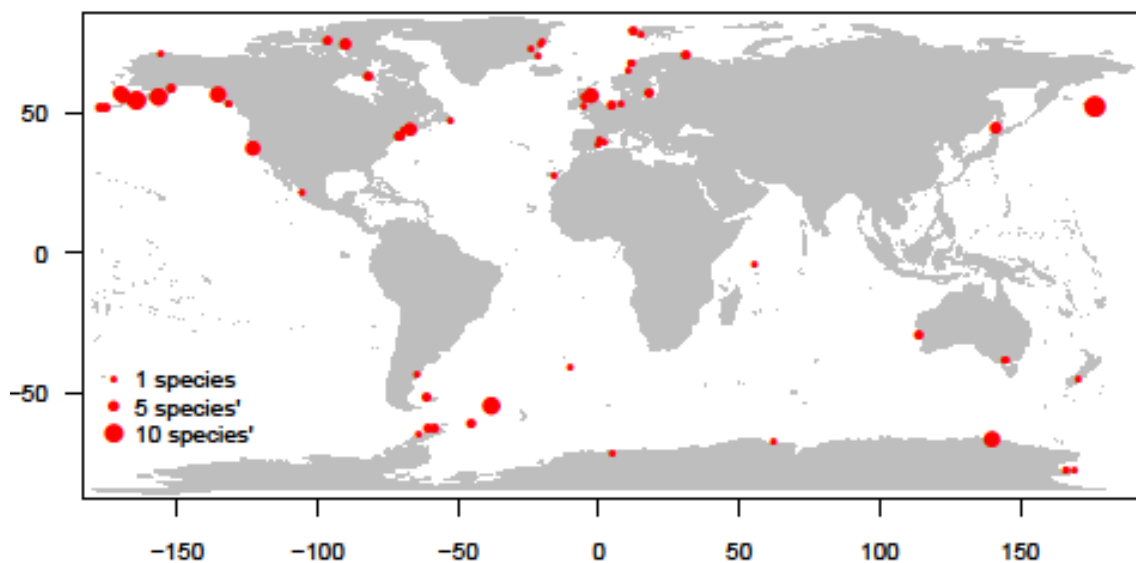
Table 1. Predictions of the effect of life history and environmental variables on phenology from the four key models. Black = supported by model; red = unsupported by model; grey = not included. For full predictions see Supplementary Table 11)

| | | Life history variables | | | Environmental variables | |
|----------------|---------------------|------------------------|--|--|-------------------------|-----------------------|
| Model name | Prediction | Body Size | Migration Strategy (Residents, short- & long-distance migrants) | Feeding strategy (Surface, diver, generalist) | Latitude | Upwelling (yes/no) |
| Mean Phenology | Later phenology | NA | NA | NA | High | NA |
| Variance | Most variable group | Smaller birds | Residents & short-distance | Surface feeders | NA | Yes |
| Temporal | Steeper slope | Smaller birds | NA | Surface feeders | High | NA |
| SST | Steeper slope | Smaller birds | Residents & short-distance | Surface feeders | High | NA |

62

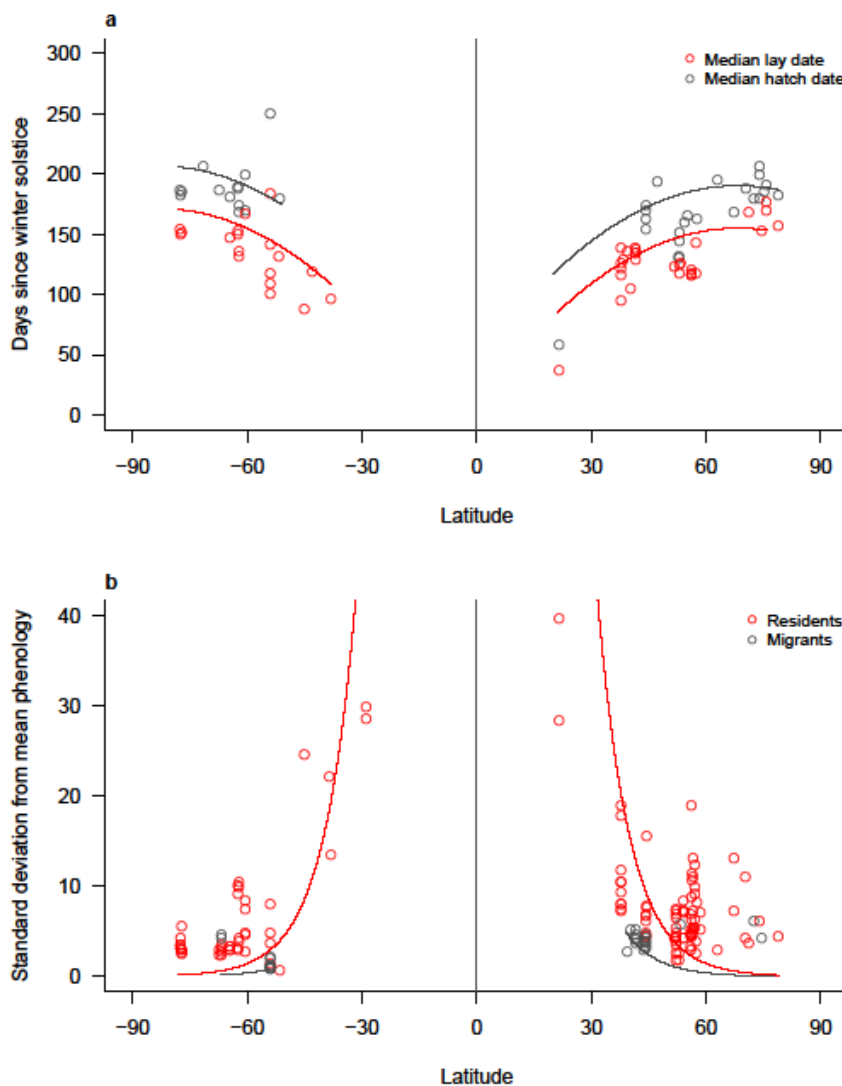
63 We applied a phylogenetic mixed model meta-analysis to a global dataset comprising
64 211 phenological time series of breeding dates obtained in 147 seabird populations (Fig. 1),
65 covering 62 species from five main orders. These taxonomic groups exhibit a wide variety of
66 life histories, migration and foraging strategies, distributed from equator to poles across all
67 principal oceanographic regimes. Meta-analyses provide a robust approach for identifying

68 average effect sizes across studies, and for identifying predictors of variation around the
69 average²⁶. Here, we (i) characterised latitudinal trends in the mean and between-year variance
70 of seabird breeding phenology (laying and hatching dates), (ii) estimated the mean sensitivity
71 of breeding phenology over time and in relation to SST in the waters around the sampled
72 colonies, and (iii) identified predictors of inter- and intra-specific variation around the mean
73 response (mean, variance and both sensitivity measures) of each species/population (body size,
74 biogeography, phylogeny; for specific predictions see Table 1 & Methods).



75 **Figure 1. Map of study sites included in the analyses.** The full dataset comprises 211 time series from 62 seabird
76 species and across 65 locations, collected between 1952 and 2015. The data include slopes for 32 genera, 9 families, and 5
77 orders (Sphenisciformes (6), Procellariiformes (15), Suliformes (3), Pelecaniformes (5), Charadriiformes (33)) and spans all
78 seven continents.

79
80 With increasing latitude, we found that breeding occurred later in the calendar year and
81 that between-year variance in phenology decreased (Table S1, Fig. 2a, b), which concurs with
82 earlier results obtained from regional studies^{27,28}. The low variance at high latitudes may arise
83 due to the shortened period of favourable conditions and the strong seasonal cue that
84 photoperiod provides, whereas the much greater variance at lower latitudes may relate to the
85 reduction of seasonality and the relatively weaker cue from day length²⁹.



109 **Figure 2. a) Mean and b) between-year variance in phenology separated by hemisphere.** a) represents the differences in
 110 latitudinal gradient between Northern and Southern Hemispheres, where each data point (grey or red) represents the median
 111 timing of breeding of a population. Lines (grey = lay date, red = hatch date) represent the delay in phenology approaching
 112 the poles in days lat^{-1} , and were estimated using values from Table S1a. b) represents the between-year standard deviation in
 113 mean timing for residents (represented by red dots) and migrants (grey dots). Lines are plotted from the ecological model
 114 and represent the median lay date in the mean year of study of an average surface feeding resident bird, weighing 800g, in a
 115 region where there is no major upwelling system. The quadratic of absolute latitude reflects the tendency for slopes to be less
 116 steep with increasing latitude, but is non-significant (Table S2b).

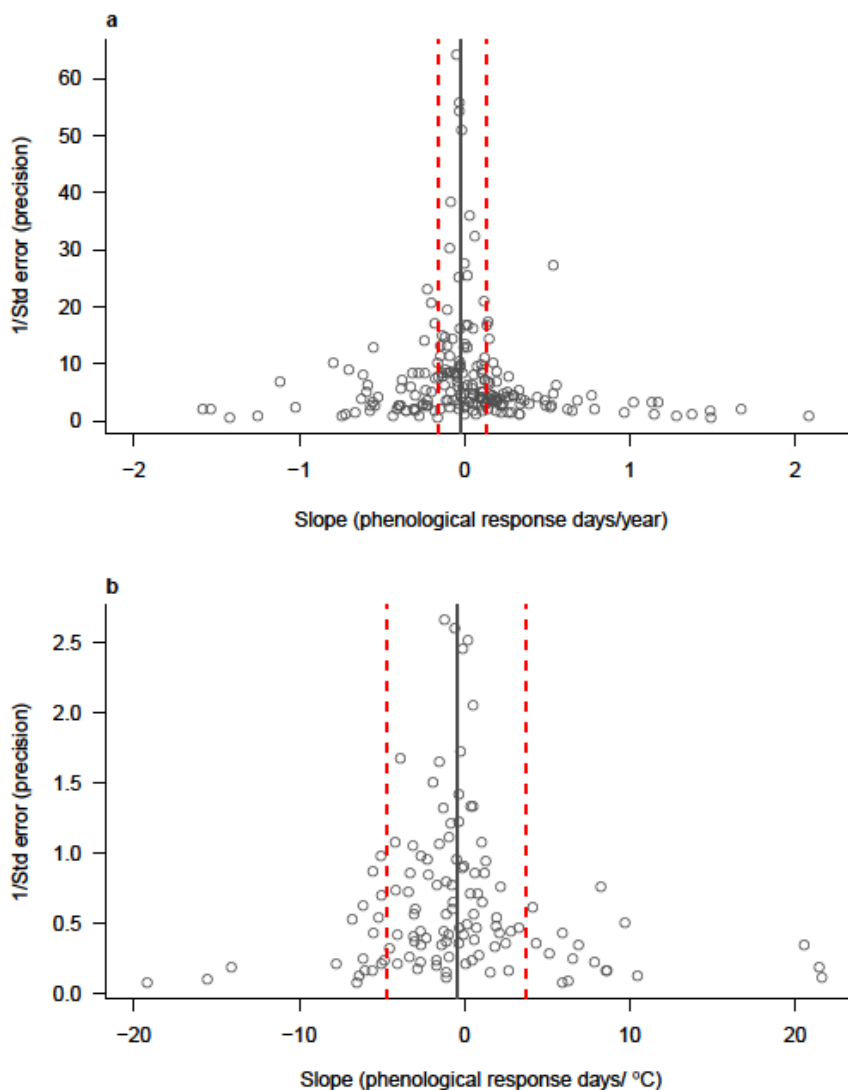
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118 Overall, the between-year variance in lay date among populations in our dataset ranged
 119 from < 1 in the black-browed albatross (*Thalassarche melanophris*) at New Island,
 120 Falklands/Malvinas, consistent with 95% of annual means occurring within a three-day period,
 121 to 1573 in the blue-footed booby (*Sula nebouxii*) at Isla Isabel, Mexico, consistent with 95%

122 of annual means occurring within a five-month period. Examination of life history traits
123 potentially explaining this variation (Table S7) indicated that resident species were more
124 variable than migrants (Table S2b, Fig 2b). This result is in accord with findings for terrestrial
125 birds³⁰ and may arise if the laying dates of resident species are more sensitive to local foraging
126 conditions, either as a cue to initiate breeding in anticipation of the timing of future resources,
127 or as a constraint on egg-production when conditions are poor³¹. Between-year variance in
128 laying date was highly phylogenetically conserved ($H^2 = 0.84$, 95% Credible Interval [CI]:
129 $0.505 - 1$, $n = 210$, Table S2a.). From inspection of the best linear unbiased predictors (BLUPs)
130 for the phylogenetic effects, the most threatened Order¹⁹, Procellariiformes, particularly giant
131 petrels and fulmars (Procellariidae), and albatrosses (Diomedeidae), stood out as least variable
132 in its timing of breeding. This response is consistent with a strong reliance on photoperiod as
133 a cue³². In contrast, we find that Pelecaniformes and Suliformes (cormorants, gannets and
134 boobies) vary substantially in inter-annual timing of breeding, suggesting that these species
135 may adjust egg laying in relation to some aspect of the local environment (weather,
136 oceanographic conditions or food availability) in the lead-up to the breeding season³³.

137 On average, seabirds showed no tendency to advance or delay breeding phenology over
138 time (-0.02 days yr⁻¹, 95% CI: $-0.161 - 0.128$, $n = 211$, Fig. 3a), in agreement with previous
139 studies^{10,21}. However, we found limited evidence for true variation around the mean response
140 (Table S3a), with 87% of the variation in raw slope estimates of phenology over time
141 attributable to estimation error arising from linear regressions based on small datasets (Table
142 S4a, b). Of the remaining true variation, we found that the mean slope estimates did not differ
143 significantly among oceans (Table S3b, c, Fig S1). This result runs counter to previous studies
144 of seabird breeding phenology, which have reported variation in long-term trends among
145 biogeographic realms^{12,21}. However, we found some evidence that temporal response may vary
146 among species at common breeding sites (Table S3a-c). Such variation makes it difficult to

147 predict which species and sites will be most phenologically responsive to changing SST, as it
148 implies that the degree of environmental sensitivity in seabird breeding may be determined by
149 a combination of intrinsic and extrinsic factors³⁴. Of the environmental or life history variables
150 we considered, body mass was the only significant positive predictor of the temporal trend
151 (Table S3b, c), with larger-bodied species responding at a slower rate over time than smaller
152 species, in accordance with our predictions (Table 1).



194 **Figure 3. Phenological trends in relation to year (a) and sea surface temperature (b).** Funnel plots of precision (1/S.E.)
195 against slope. Lines represent the posterior for the average response or intercept (black) and its 95% credible intervals (dashed
196 red) from the basic model.

197

198

199 Globally we found no evidence that seabirds as a group have shifted their laying date
200 in relation to SST at the breeding site in the three months preceding egg-laying (mean = -0.272
201 days °C⁻¹, 95% CI: -4.896 – 4.482, $n = 108$, Fig. 3b, Table S5a). As in the analysis of temporal
202 trends, we found no evidence that true variation in the slope of the covariation with SST is
203 predicted by phylogeny, species, biogeographic regions, or life history traits. We did, however,
204 find significant variation in slopes among sites, and the extreme BLUPs range from -2.96 days
205 °C⁻¹ (95% CI: -6.00 – 0.13) at Skomer Island, Wales to 7.32 days °C⁻¹ (95% CI: 4.96 – 9.73) at
206 Southeast Farallon Island, California, which is located in a highly variable upwelling zone,
207 where SST effects on breeding phenology, as in other upwelling systems, are known to be
208 closely correlated³⁵. So, whilst on average, seabirds appear to be unresponsive to SST, we
209 cannot rule out the possibility some populations are temperature sensitive in either direction.

210 That we could detect no trend in seabird phenology over time or in relation to rising
211 SST (Table S7), suggests that if lower trophic levels are shifting in parallel with changing SST,
212 seabirds, in general, may be at risk from increasing levels of trophic mismatch³⁶. To date, there
213 are very few studies that have reported the slope of the phenology of cold-blooded seabird prey
214 and lower trophic levels in relation to SST (but see²³). Differing rates of phenological response
215 between seabirds and their food resources¹⁰ may leave them short of critical prey during the
216 breeding season under future climate regimes. However, there is limited and mixed evidence
217 on the frequency of climate-induced mismatch^{18,23}, and whether it has an impact on breeding
218 success³⁷ or population dynamics³⁸. Alternatively, any negative fitness consequences of trophic
219 asynchrony may be ameliorated by the ability of some species to alter their behaviour, e.g. by
220 switching prey or adjusting foraging effort^{23,39}.

221 Our study represents the most statistically rigorous and spatially representative meta-
222 analysis to date of the reproductive phenology of a group of upper trophic-level predators,
223 seabirds. Despite what has been written earlier in the literature, we find that once measurement

224 error has been taken into account, in most cases the phenology of seabirds appears to be
225 insensitive to changing SST, and shows no trend over time. While certain populations may be
226 responding, the variation in estimates of phenological sensitivity among most species may be
227 attributable to estimation error. 45% of global seabird species are declining, primarily due to a
228 variety of anthropogenic influences¹⁹, and this study sends a message that many seabird species
229 at high trophic levels may also struggle to adjust their behaviour or evolve to cope with the
230 unprecedented speed of current environmental change.

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1 **Methods**

2 **Data** Annual data on breeding phenology during the period 1952 and 2015 were the median or
3 mean date of laying or the median, mean or first date of hatching of the study population, in
4 units of ordinal days. Population was defined as an individual species at a breeding site. We
5 only considered populations that breed seasonally during spring and summer (austral and
6 boreal) months, as measures of phenological central tendency are not informative for species
7 which breed asynchronously. Time series' were required to be a minimum of five years for the
8 temporal analysis and ten years for the analysis of SST, although the years did not need to be
9 consecutive. Details of field methods used to collect each time series are given in the Table S6.

10 Monthly means of NOAA Optimum Interpolation (OI) Sea Surface Temperature (SST)
11 V2 for the period 1982 – 2015 were obtained from the NOAA/OAR/ESRL PSD, Boulder,
12 Colorado, USA, (<http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html>), a
13 resource which provides interpolated *in situ* and satellite SST data on a one-degree grid¹.

14 For each time series we characterised the biogeography at the colony it was located.
15 We collated information on the location (latitude and longitude) and hemisphere of each
16 population, and for our primary fixed effects model we assigned each location to one of the
17 three main oceans: Atlantic, Pacific or Indian. Global climate zones (Equatorial, Tropical,
18 Subtropical, Temperate, Subpolar or Polar) were identified using the classification from
19 Trujillo & Thurman (2014). These zones correspond to latitudinal bands of similar sea surface
20 temperature and are categorized by levels of precipitation, wind and water temperature². We
21 combined hemisphere, ocean and global climate zone to identify 15 Biogeographic Regions
22 (e.g. North Atlantic Temperate; South Pacific Subpolar etc.). Finally, we used the Longhurst
23 Biogeographical Provinces to determine whether each location was situated within an Eastern

24 Boundary (upwelling) zone³. These are areas of high productivity within the marine
25 environment, and are also highly variable across seasons, years and decades^{4,5}.

26 We collated data on several aspects of the ecology and life history of each species that
27 may affect the phenological slope (with year or temperature), mean or between-year variance.
28 These data were provided by authors and supplemented using online resources:
29 www.audubon.org, www.birdlife.org, nzbirdsonline.org.nz, www.bird-research.jp and
30 www.npolar.no (Table S7). Feeding strategy was categorised either as surface feeder (feeding
31 <1 metre below the surface), diver (feeding >1 metre below the surface), or
32 kleptoparasite/predator (part-time marine foragers). Species which seek out prey by diving
33 under water may be able to exploit a wider range of prey than those constrained to feeding on
34 the surface (<1 metre depth), thus reducing the necessity to adjust breeding phenology to buffer
35 mismatch⁶⁻⁸. We also compiled data on average body mass of every species (Table S7), as
36 small-bodied seabird species are predicted to be more sensitive to temperature change due to
37 the higher cost of thermoregulation^{9,10}. Furthermore, body mass can be used as a proxy for
38 trophic level, which is difficult to classify explicitly in seabirds¹¹. We used log body mass in
39 analyses. The migration strategy of individuals from each population was assigned based on
40 the behaviour of the majority (>80%) of individuals. Long distance trans-equatorial migrants,
41 and species which spend the winter outside the sector in which they breed were categorised
42 together as “migrants”, and those which remain in the same ocean sector throughout the year
43 were classified as “residents”. Sectors were defined as North Atlantic, Mediterranean, South
44 Atlantic, Southern Ocean-Atlantic sector, North Pacific, South Pacific, Southern Ocean-Pacific
45 sector, Indian, Southern Ocean-Indian sector.

46 We took into account phylogenetic relationships among species using 100 samples of
47 the pseudo-posterior species tree (www.birdtree.org)¹² using the Hackett *et al.* (2008)
48 backbone.

49 **Statistics** We used the *MCMCglmm* package¹³ in R (v 3.2.2; R Core Team 2015), to fit
50 Bayesian generalised linear mixed-effects models (GLMMs). We adopted a random effects
51 meta-analytic (REMA) approach, estimating both fixed and random effects, while taking
52 measurement error into account^{14,15}.

53 We included cross-classified random effects to account for and estimate sources of
54 variance, though not every random variable was included in each model (see Tables S1-S5).
55 The model was of the form

$$56 \quad y_i = \mu + \beta x_i + \alpha_{f[i]} + s_{f[i]} + b_{g[i]} + l_{h[i]} + p_{j[i]} + e_i + m_i \quad \text{eq. 1.}$$

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

61 $\alpha_{f[i]}$ is the effect of phylogenetic non-independence due to shared evolutionary
62 history¹⁴ for the f th species. $s_{f[i]}$ is the non-phylogenetic species-specific effect for the f th
63 species. Spatial variation was accounted for via two terms, g th biogeographic region ($b_{g[i]}$)
64 (see Table S7) and h th site ($l_{h[i]}$). In certain analyses we included multiple measures/traits for
65 a time series and in these cases we could fit the interaction between site and species
66 (population) ($p_{j[i]}$), which provided us with an estimate of intraspecific geographic variation
67 that is unique to each (j th) population. In these cases the residual term (e_i) captures variation
68 within a site and species (population), and we allowed this variance to be heterogeneous across
69 different phenophases (i.e. median lay date, mean lay date, first hatch date, median hatch date,
70 mean hatch date). In other analyses only a single measure/trait was included and in such
71 instances $p_{j[i]}$ was not estimable. In this case the residual term captured variance both due to
72 intraspecific geographic variation that is unique to each species and differences among

73 phenological measures/traits. Our response variables were themselves estimates that have error
74 associated with them and we incorporated measurement error variances as m_i , which means
75 that the analyses were weighted. For the measurement error term, the among-observation
76 variance was set to 1, and for all other random terms the variance was estimated. The
77 specification of these models assumed that random effects for different measures were
78 perfectly correlated. To test whether this impacted on our estimation of phylogenetic signal we
79 then relaxed this assumption and estimated the covariance between random effects for
80 measures of laying and hatching phenology (See Supplementary Methods and Results).

81 We calculated phylogenetic signal^{14,16} in our response variables (H^2), i.e. the tendency
82 of closely related species to resemble each other more than distantly related species, from σ_a^2
83 (the phylogenetic variance), and σ_s^2 (the species variance)

$$84 \quad H^2 = \frac{\sigma_a^2}{(\sigma_a^2 + \sigma_s^2)} \quad \text{eq. 2.}$$

85

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

88 (1) Multi-year mean phenology: we estimated the mean phenology (e.g. average laying date
89 overall) across all years for each time series. Measurement variance in the mean was quantified
90 as the squared standard error. To examine latitudinal trends in mean date we included both
91 absolute latitude and its quadratic term (to test both linear and non-linear effects); hemisphere;
92 and the interaction between latitude and hemisphere as fixed effects. Additional fixed effects
93 were trait (laying and hatching date) and phenological measurement (mean, median, first date).
94 See Table 1 and Supplementary Table 11 for predictions.

95 *Post hoc tests*: mean phenology is delayed as latitude increases in both hemispheres, with a
96 significant quadratic term, such that the slope appears to reach an asymptote toward the poles
97 (Fig. 2, Table S1a). However, seabirds at low latitudes are underrepresented in this study. When
98 we removed three low latitude data points, there was no support for the quadratic relationship
99 (Table S1b) but the positive linear relationship between latitude and breeding phenology
100 remained (posterior mean = 0.81 days.lat⁻¹, 95% CI: 0.33 – 1.29, $n = 206$, Table S1c). The
101 intercepts of each measure of phenology (i.e. mean laying date, first hatching date) differed
102 significantly, although a test including the interaction between latitude and phenological
103 measure revealed no difference in their latitudinal slopes (Table S1d).

104

105 (2) Between-year variance in phenology: the response variable (eq. 3) was based on the natural
106 log of the between-year standard deviation (s), taking into account the number of years (n). The
107 sampling variance of this measure was quantified as ($s^2_{\ln \sigma}$) as in eq. 4¹⁷:

108
$$\ln \hat{\sigma} = \ln s + \frac{1}{2(n-1)} \quad \text{eq. 3.}$$

109
$$s^2_{\ln \hat{\sigma}} = \frac{1}{2(n-1)} \quad \text{eq. 4.}$$

110

111 The model included phenological trait and measure, latitude and its quadratic term, hemisphere,
112 presence or absence of upwelling and, to test for decadal patterns, the mean year of each time
113 series as fixed effects. We included body mass, foraging and migration strategies in the same
114 model to investigate the effects of life history traits on between-year variance. See Table 1 and
115 Supplementary Table 11 for predictions.

116

117 (3) Temporal trend in phenology: we estimated the linear slope (and standard error) of
118 phenological change over time for each measure (median, mean, first date) and trait (laying or
119 hatching date) of a population using Generalised Least Squares (GLS) in nlme¹⁸, fitting an
120 autoregressive model of order 1, AR(1)¹⁹, to take into account temporal autocorrelation in each
121 individual time series. We used these slope estimates in a meta-analysis, and included the
122 squared standard error of the slope to weight the analysis. We included three types of fixed
123 effects: methodology (trait, measure, mean year of time series), life history and ecology (body
124 mass and foraging strategies), and biogeography (ocean basin, hemisphere, latitude). See Table
125 1 and Supplementary Table 11 for predictions. We did not make predictions about which ocean
126 basins or hemisphere might show the steepest slopes, but allowed the response to differ among
127 ocean basins and hemispheres in our model.

128 *Post hoc test:* our primary ecological fixed effects model categorised locations into one of the
129 three main ocean basins (Atlantic, Indian, Pacific), and included the interaction between
130 latitude and hemisphere as an additional parameter. This approach considered the life histories
131 of wide-ranging polar species which may have large foraging ranges. Yet many species forage
132 near to the colony, or may have evolved alongside the unique oceanographic features of polar
133 systems²⁰. To consider these species we re-categorised ocean basins into five discrete water
134 bodies (Arctic, Atlantic, Indian, Pacific, Southern) and ran our ecological model again,
135 replacing the three ocean variable with five oceans, and removing the interaction between
136 latitude and hemisphere.

137

138 (4) Phenological response to SST: for each time series we averaged monthly temperature data
139 from the local grid cell for the pre-breeding period (three months prior to laying, including the
140 month in which laying began) each year. This temperature variable was selected for ease of

141 estimation across all taxa. In some cases sea ice cover meant that an average temperature was
142 not estimable and affected time series' were excluded from this analysis. We restricted this
143 analysis to laying dates only, representing each population with a single time series in declining
144 order of preference of measurements: median, mean and first date. In populations for which we
145 only had data on timing of hatching, we back-calculated lay dates using information on the
146 duration of incubation period and average number of eggs. These data were provided by authors
147 and supplemented using online resources: www.audubon.org, www.birdlife.org,
148 nzbirdsonline.org.nz, www.bird-research.jp and www.npolar.no (Table S7). Where incubation
149 period was reported as a range, we calculated the central value; this method was used for 70
150 time series (Table S7).

151 For each colony we calculated the reaction norms and associated standard errors of
152 phenological response to SST (days °C⁻¹) using the GLS methods as described for the temporal
153 trends, but retaining year as an additional predictor, in order to de-trend the data and allow us
154 to consider the effects of SST independently of time (Table S7). We then fed the phenology on
155 SST slopes into a meta-analysis, with the squared standard error of the slope included for
156 weighting. We tested similar predictions as in (3) above, predicting that timing of laying would
157 be more sensitive to pre-breeding SST in species with smaller body mass, which feed on the
158 surface, or that remain in the same ocean basin over winter. Measure, trait and mean year of
159 study were also included as fixed effects.

160 All models were run for 30,000 iterations on each phylogenetic tree sample, discarding
161 the first 10,000 as burn-in and sampling every 10th iteration. We repeated this process over 100
162 phylogenetic trees and the pooled posterior distributions take into account both model and
163 phylogenetic uncertainties²¹. Parameter-expanded priors were used for all random effects
164 except the residual, which followed an inverse Wishart distribution. Plots of the mean and
165 variance of the posterior distribution were examined to assess autocorrelation in the posterior

166 samples. Statistical significance of fixed effects was inferred where 95% credible intervals did
167 not span zero.

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54 KK, SL, ABP, SW, FD and RP conceived the study and wrote the manuscript. KK coordinated
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60 Correspondence and requests for materials should be addressed to K.K. (k.keogan@ed.ac.uk).