Title: The collapse of environmental predictability erodes reproductive success in a Tropical seabird

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Abstract (121/125)

Climate change can alter not only when seasonal events occur on average, but also how predictable they are from year to year. Many long-lived seabirds show a paradox: breeding dates remain stable even as populations decline. Using two decades of data from Blue-footed Boobies (*Sula nebouxii*), we tested whether loss of environmental predictability could reduce reproductive success even when mean timing remained stable. Mean timing of the winter–spring phytoplankton bloom and mean breeding mismatch showed no clear trend, but year-to-year variability in bloom timing increased markedly. Mismatch relative to bloom onset became more variable, and both expected nest success and its consistency declined. These results show that predictability loss can erode synchrony and demography even when mean timing appears unchanged

Main text:

Climate change is shifting the seasonal timing of biological events across ecosystems, from flowering and migration to the onset of reproduction (*1*, *2*). Most research has focused on whether seasonal events occur earlier or later on average, yet many long-lived seabirds show a striking paradox: mean breeding dates often remain stable even as sea-surface temperatures warm and populations decline (*3*–*5*). This is unexpected because reproductive success in seasonal breeders depends on aligning offspring demand with seasonal peaks in food availability (*6*, *7*). The paradox suggests that climate impacts may be missed when attention focuses only on changes in mean timing. We propose that climate change can erode demography not only by shifting when seasonal resources occur, but also by reducing how predictable those resources are from year to year.

Changes in climatic variability, not just changes in mean conditions, may disrupt the cues organisms use for critical decisions. Reproductive timing depends on environmental signals whose value lies in how consistently they forecast the future food window from year to year (*8*). In seabirds, breeding decisions often rely on oceanographic conditions such as sea surface temperature and upwelling intensity, yet their relationships to local prey availability can be indirect, lagged, and regionally variable (*11*, *12*). If these cue-resource relationships become noisier, environment predictability declines, weakening the link between the conditions experienced when breeding decisions are made and the food window that chicks ultimately encounter. More broadly, this highlights a limitation in how phenological change is typically assessed; most studies test for directional shifts in mean timing (*13*), even though climate change can also alter year-to-year variance in seasonal dynamics (*14*, *15*). That variance matters because it affects how reliably conditions at the time of decision predict later resource availability. When predictability declines, breeding synchrony can erode even if mean timing appears stable, consistent with the idea of "phenological disorder", in which seasonal dynamics become less predictable than simply earlier or later (*16*).

Here, we test whether loss of environmental predictability can explain demographic decline in blue-footed boobies (*Sula nebouxii*) breeding on Isla Isabel, Mexico (Fig. S1). In this system, reproductive success depends on a seasonal pulse of ocean productivity, associated with a winter–spring phytoplankton bloom (*17*), which regulates the availability of small pelagic fish that support the marine food web (*18*, *19*). Using satellite-derived chlorophyll-a time series together with two decades of individual-based breeding records (>8,000 attempts), we evaluate three predictions (Fig. 1): (i) bloom timing becomes less predictable through time, as shown by increasing interannual variability, (ii) breeding synchrony erodes as mismatch becomes more variable, even if mean mismatch does not shift directionally, and (iii) reduced synchrony translates into lower reproductive success. We also test whether sensitivity to this environmental instability varies with age (*20*, *21*).

The timing of seabird breeding is closely tied to seasonal ocean productivity. In our system, we expect boobies to begin laying near bloom onset so that incubation and chick rearing overlap with the seasonal rise in prey availability and the period of highest offspring energy demand (Fig. 1A). A key question, however, is how predictable bloom timing remains from year to year (Fig. 1B). Our conceptual model proposes that if year-to-year variability in bloom timing increases, breeding synchrony will weaken and reproductive success will decline even if mean bloom timing does not shift (Fig. 1C–D). We therefore analyzed bloom timing, phenological mismatch, and nest success using location–scale models that estimate effects on both means and variability (*22*), combining chlorophyll-a time series with two decades of individual-based breeding records to test whether increasing bloom variability was associated with reduced synchrony and lower reproductive success (Fig. 1D).

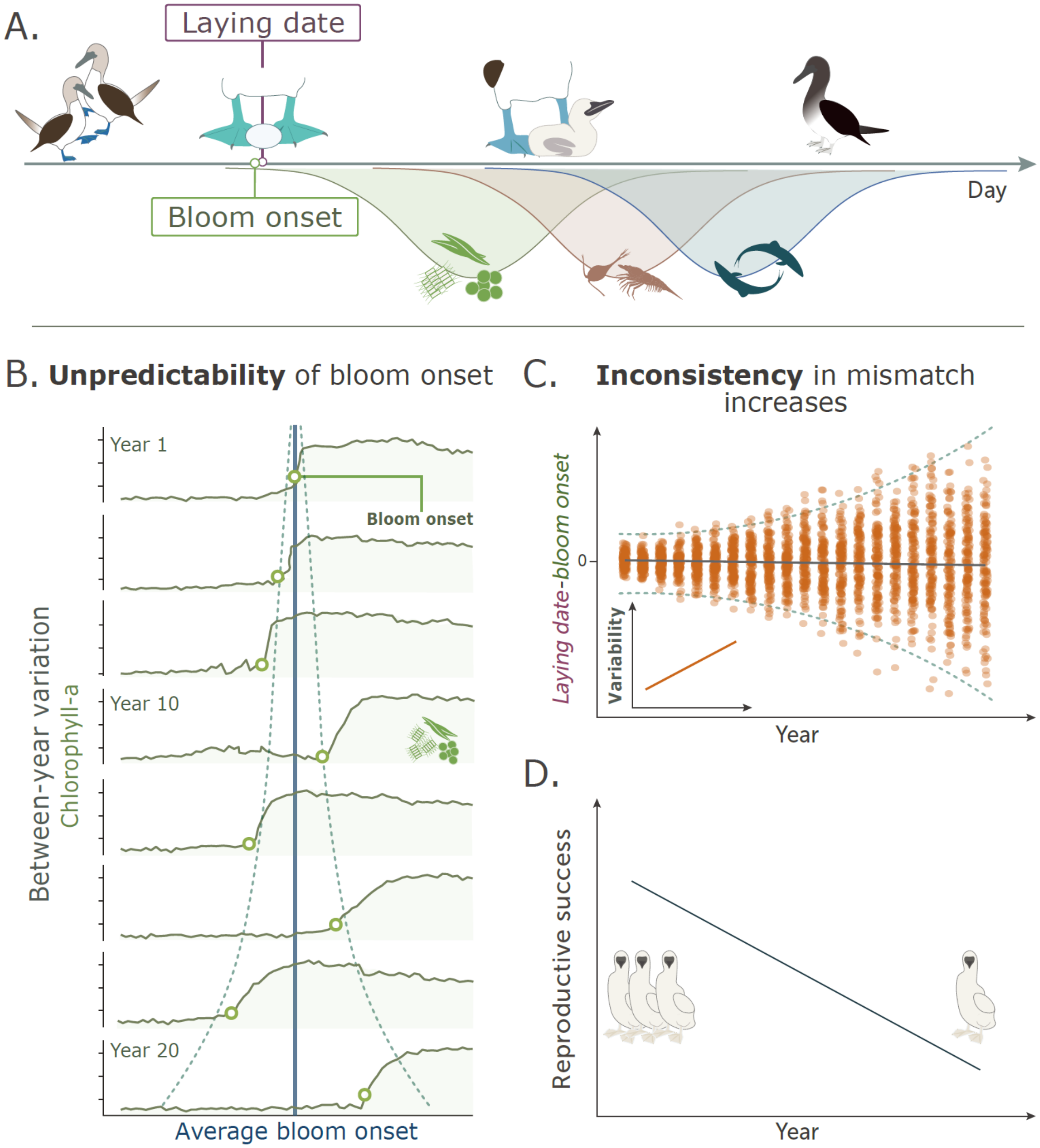

Figure 1. Conceptual model linking bloom predictability, breeding synchrony, and reproductive success. (**A**) Expected alignment between the breeding cycle and seasonal productivity: laying begins near bloom onset, and incubation and chick rearing occur as prey availability increases and offspring energy demand rises. (B) Bloom timing may vary among years; greater year-to-year dispersion would increase environmental unpredictability (σ). (C) Breeding timing may also vary among years; greater dispersion in phenological mismatch (laying date − bloom onset) reduce breeding synchrony by increasing year-to-year inconsistency in the alignment between reproduction and the resource pulse (σ). (D) We predict that reduced synchrony will lower

reproductive success over time and increase the inconsistency of reproductive outcomes through time.

Apparent stable bloom timing with declining predictability

Over the 21-year study period (2003-2023), mean (μ) timing of the winter-spring chlorophyll-a bloom showed no significant directional trend ($\beta_{\mathrm{time}(\mu)} = 0.532$; 95% credible interval = [-0.382, 1.469]). On average, bloom onset occurred approximately seven days after the boreal winter solstice (Fig. 2A). In contrast, year-to-year variability in bloom timing increased by about 12% per year (95% CI: ~5–20%; log-scale $\beta_{\mathrm{time}(\sigma)} = 0.114$, 95% CI = [0.048, 0.184]; Fig. 2B), implying an approximately tenfold increase in dispersion across the full study period and indicating declining predictability.

Increasing variability in breeding synchrony

Across 8,378 female breeding attempts, the mean mismatch between laying date and bloom onset showed no significant directional trend over time ($\beta_{\mathrm{time}(\mu)} = -1.967$, 95% CI = [-5.367, 1.399]; Fig. 2C). Variability in mismatch, however, increased steadily. The standard deviation of mismatch, interpreted here as a measure of inconsistency in breeding timing, increased by approximately 2.3% per year ($\beta_{\mathrm{time}(\sigma)} = 0.023$, 95% CI = [0.018, 0.028]; Fig. 2D), indicating that mismatch became more dispersed from year to year.

Individuals differed in both their mean mismatch and their inconsistency. The correlation between individual-level mean mismatch and variability was strongly and significantly positive ($\rho_{\mathrm{femaleID}(\mu,\sigma)} = 0.805$; 95% CI = [0.711, 0.891]), indicating that individuals with larger average mismatches also showed greater year-to-year variation in mismatch. After accounting for temporal change in both the mean and variability of mismatch, the extent of mismatch showed a significant quadratic association with age, decreasing early in life and then tending to increase at older ages ($\beta_{\mathrm{age}^{2}(\mu)} = 0.334$, 95% CI = [0.291, 0.377]; Fig. 3A) Individual age trajectories differed among birds, as shown by a significantly large positive correlation between individual-specific age effects and mismatch ($\rho_{(\mathrm{femaleID},\ \mathrm{age})} = 0.454$, 95% CI = [0.180, 0.729]). Consistency in mismatch also varied with age, declining at younger ages and tending to increase again later in life ($\beta_{\mathrm{age}^{2}(\sigma)} = 0.003$, 95% CI = [0.001, 0.004]; Fig. 3B).

Declining reproductive success and consistency

We next asked whether erosion of breeding synchrony translated into declines in reproductive success and its consistency. To analyze reproductive outcomes, we used ordinal models in which success was defined by the number of chicks fledged from a nest (hereafter nest success). In these models, we evaluated how phenological mismatch and time affected both mean reproductive success (location parameter, μ) and the consistency of reproductive outcomes. We interpret the scale parameter (ζ) as consistency in reproductive outcomes: higher values indicate more consistent outcomes, with clearer separation among fledging categories, whereas lower values indicate more variable outcomes.

Mean expected nest success showed a significant quadratic relationship with phenological mismatch ($\beta_{\mathrm{mismatch}^2(\mu)}$ = -0.0003, 95% CI = [-0.0007, -0.0001]; Fig. 3C), indicating that reproductive success was highest when breeding was closely matched to bloom onset and declined as breeding occurred further from that window. Predicted outcome probabilities showed that matched breeding increased the likelihood of fledging one or two chicks, whereas severe mismatch shifted outcomes toward lower fledging success; this decline was asymmetric, with especially poor outcomes among very late breeders. Nest success also became less consistent as mismatch increased, as indicated by a decline in the scale parameter ($\beta_{\mathrm{mismatch}(\zeta)}$ = -0.001, 95% CI = [-0.002, -0.000]), showing that reproductive outcomes became more variable with increasing mismatch.

Mean expected nest success significantly declined over time ($\beta_{\mathrm{time}(\mu)}$ = -0.419, 95% CI = [-1.073, -0.034]; Fig. 2E). Based on posterior-predicted outcome probabilities, expected fledging output was 54.3% lower in the last study year than in the first (holding other predictors at their centered values). At the same time, nest success became less consistent, as indicated by a decline in the scale parameter ($\beta_{\mathrm{time}(\zeta)}$ = -0.015, 95% CI = [-0.020, -0.009]; Fig. 2F). Mean expected success also varied with age, following a significant quadratic pattern across the lifespan, with lower values at younger and older ages ($\beta_{\mathrm{age}^2(\mu)}$ = -0.075, 95% CI = [-0.156, -0.031]; Fig. 3D).

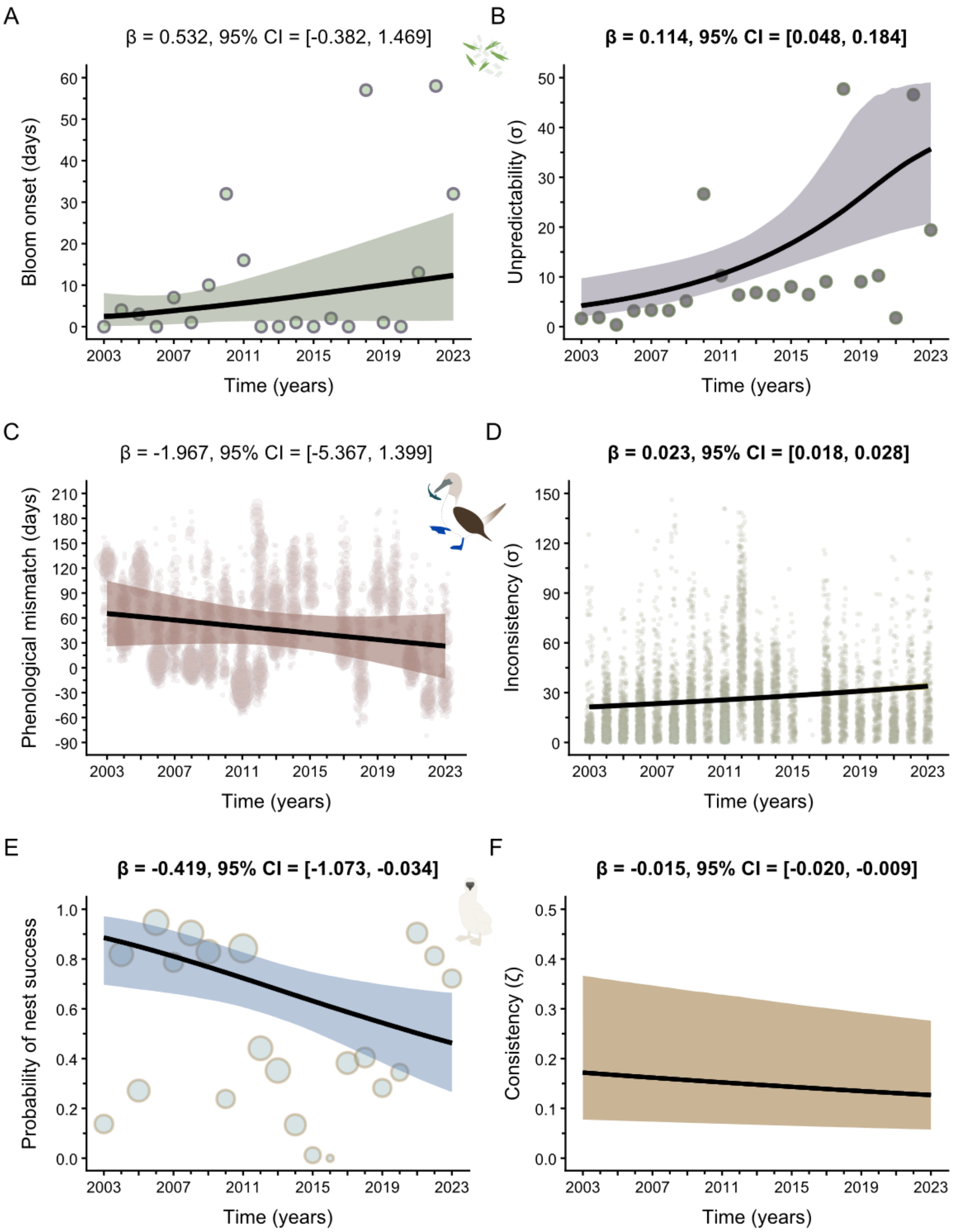

Figure 2 Temporal changes in bloom timing, phenological mismatch, and nest success in female Blue-footed Boobies (2003–2023). (**A**) Mean timing of the winter–spring chlorophyll-a bloom showed no directional change over time, whereas (**B**) year-to-year variability increased, indicating declining environmental predictability (increasing standard deviation, σ; higher dispersion). Points in (A–B) are annual estimates (one point per year). (C) Mean phenological mismatch between laying date and bloom onset remained stable, while (D)) variability in mismatch increased, indicating declining breeding synchrony, i.e., breeding consistency. Points in (C–D) represent individual breeding attempts; point size is proportional to sample size in (C), and uniform in (D). (E) Mean expected nest success declined over time; points show yearly binned values with size proportional to the number of breeding attempts in that year. (F) Nest success consistency also

declined, indicated by a decrease in the precision parameter (also known as the discrimination parameter, ζ). Panel (F) does not show raw points because precision (ζ) is a model-based scale parameter for ordinal outcomes rather than a directly observed quantity. Solid lines show posterior means and shaded bands show 95% credible intervals. Intervals in (D) are narrow and closely overlap the posterior mean. Subtitles report slope estimates (β) with 95% credible intervals (bold indicates intervals excluding zero).

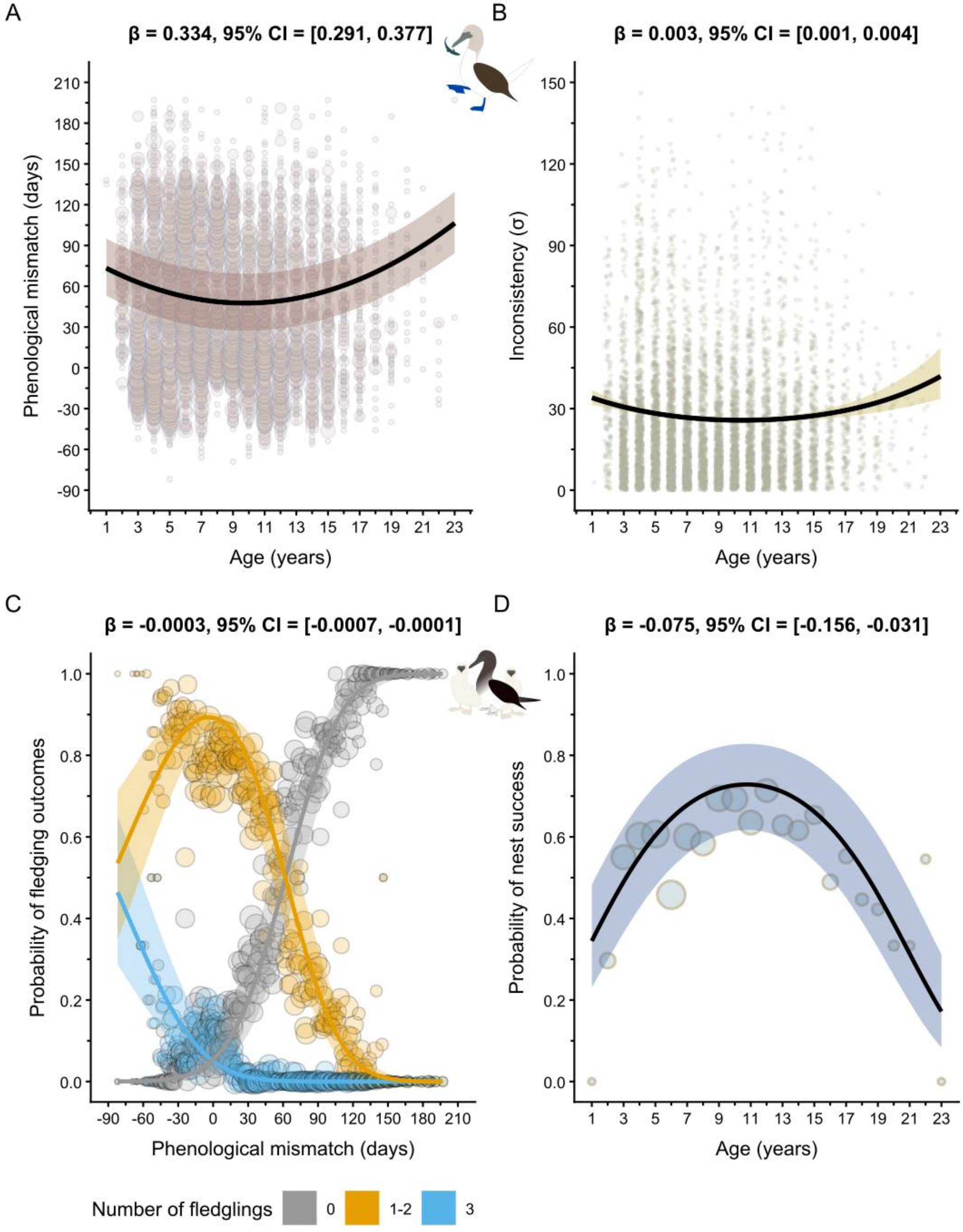

Figure 3. Age-related patterns in phenological mismatch and reproductive performance in female Blue-footed Boobies. (**A**) Mean phenological mismatch declined through early adulthood, reached a minimum near age 9, and increased at older ages. Points show raw observations (size proportional to the number of breeding attempts per age). (B) Variability in phenological mismatch (σ), changed non-linearly with age, indicating increasing breeding consistency through early

adulthood followed by declining consistency later in life. (C) Predicted probabilities of fledging outcomes (0, 1–2, or 3 fledglings) varied non-linearly with phenological mismatch: success was highest near synchrony (mismatch = 0) and declined with increasing mismatch as failure became more likely. The probability of producing three fledglings declined with increasing mismatch, whereas the probability of producing one to two fledglings followed a unimodal pattern, peaking near zero mismatch. (D) Mean expected nest success varied with age, peaking in midlife and declining at younger and older ages. Point size is proportional to the number of observations contributing to each value (age or mismatch). Lines show the population-level posterior mean with 95% credible intervals. Subtitles report model slope estimates (β) with 95% credible intervals (bold indicates intervals excluding zero).

Environmental unpredictability as a driver of demographic change

Our results show that demographic decline in this population is associated with a loss of environmental predictability, rather than with a directional shift in timing. The central prediction of our hypothetical model (Fig. 1) was supported: neither the mean timing of the winter–spring phytoplankton bloom (Fig. 2A) nor the mean mismatch between laying date and bloom onset (Fig. 2C) showed a significant directional shift over the study period. However, this apparent stability masks a substantial and significant change in the structure of variation. Interannual variability in bloom timing increased markedly (Fig. 2B), and this increase was mirrored by rising variability in phenological mismatch between breeding and the resource pulse (Fig. 2D). As a result, synchrony weakened even though average timing remained unchanged, and reproductive performance declined and became less consistent (Fig. 2E–F).

Beyond mean shifts: a broader pattern of phenological disruption

A growing body of evidence suggests that climate change is altering not only when seasonal events occur on average, but also how predictable their timing is from year to year (*14*). In our system, mean timing remained stable while variance increased in both the resource pulse and breeding responses (Fig. 2A–D), demonstrating that synchrony can erode even without directional shifts in mean phenology (*12*). This pattern is consistent with phenological disorder (*16*), in which seasonal processes become less reliable rather than simply earlier or later. Although phenological research has often emphasized directional advances in mean timing, particularly in temperate systems (*1*, *2*, *10*), global analyses now indicate that climate forcing is also amplifying variability in the timing of primary productivity across latitudes, including marine systems (*23*). Under these conditions, predictability becomes a limiting factor for maintaining synchrony with resource peaks. Evidence for this broader decline in seasonal reliability spans taxa from flowering plants to vertebrates (*23–25*), suggesting that declining predictability may be a widespread but under-detected dimension of climate change.

Constraints on phenological adjustment

In this system, successful breeding requires initiating reproduction well before the peak in primary productivity so that chick-rearing coincides with high prey availability (Fig. 1). One possible response to increased variability would be to advance breeding dates, reducing the risk of missing early resource peaks. However, our results show that this strategy is constrained. Reproductive success followed a significant non-linear relationship with phenological mismatch: success was highest near low mismatch and declined as mismatch increased, while the probability of the highest fledging outcome dropped sharply away from the optimal window (Fig. 3D). When the bloom occurred very early, maintaining synchrony would have required birds to initiate breeding during periods of low seasonal productivity (Fig. S2). In addition, early breeding would expose incubation and early chick-rearing to adverse conditions associated with the end of the hurricane season (*26*, *27*). Together, these constraints likely limit how far breeding can advance, even as environmental variability increases.

Individual variation in sensitivity to declining predictability

Responses to declining predictability were not uniform across individuals. Both phenological mismatch and reproductive success showed strong and significant age-related patterns, with improvement early in life and decline later (Fig. 3A, C), consistent with experience-related improvement and senescence documented in long-lived species (*28*, *29*). Individuals also differed in their mismatch trajectories across age (Fig. 3A), suggesting that the capacity to maintain synchrony under increasingly variable conditions is shaped by more than age alone. One possibility is that cumulative environmental experience contributes to this heterogeneity, as ageing trajectories can be modified by environmental history (*20*), although this hypothesis remains to be tested directly in our system (*30*, *31*).

A new dimension of ecological change

Taken together, these results show that environmental change can affect demographic performance not only through shifts in mean timing but also through changes in the reliability of seasonal timing. By jointly analyzing changes in means and variances, our study reveals a previously underappreciated dimension of climate impact in this system. Environmental predictability significantly declined (Fig. 2B), phenological synchrony weakened (Fig. 2D), and reproductive performance decreased (Fig. 2E–F), even though mean timing remained relatively stable (Fig. 2A, C). This demonstrates that analyses that explicitly model temporal variation in both means and variances can detect biologically important change that is not apparent from mean trends alone. For seabirds and the marine systems they represent, these findings suggest that loss of predictability is a plausible pathway linking environmental change to demographic decline. Seabirds are widely used as indicators of ocean conditions and contribute importantly to coastal ecosystem functioning and nutrient transfer (*32*). Re-examining long-term datasets with explicit tests of temporal change in variance, rather than mean timing alone, may therefore reveal hidden pathways by which climate change erodes synchrony and demographic performance.

References and Notes

1. C. Parmesan, G. Yohe, A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
2. W. Lang, Y. Zhang, X. Li, F. Meng, Q. Liu, K. Wang, H. Xu, A. Chen, J. Peñuelas, I. A. Janssens, S. Piao, Phenological divergence between plants and animals under climate change. *Nature Ecology & Evolution 2024 9:2* **9**, 261–272 (2024).
3. K. Keogan, F. Daunt, S. Wanless, R. A. Phillips, C. A. Walling, P. Agnew, D. G. Ainley, T. Anker-Nilssen, G. Ballard, R. T. Barrett, K. J. Barton, C. Bech, P. Becker, P.-A. Berglund, L. Bollache, A. L. Bond, S. Bouwhuis, R. W. Bradley, Z. M. Burr, K. Camphuysen, P. Catry, A. Chiaradia, S. Christensen-Dalsgaard, R. Cuthbert, N. Dehnhard, S. Descamps, T. Diamond, G. Divoky, H. Drummond, K. M. Dugger, M. J. Dunn, L. Emmerson, K. E. Erikstad, J. Fort, W. Fraser, M. Genovart, O. Gilg, J. González-Solís, J. P. Granadeiro, D. Grémillet, J. Hansen, S. A. Hanssen, M. Harris, A. Hedd, J. Hinke, J. M. Igual, J. Jahncke, I. Jones, P. J. Kappes, J. Lang, M. Langset, A. Lescroël, S.-H. Lorentsen, P. O. Lyver, M. Mallory, B. Moe, W. A. Montevecchi, D. Monticelli, C. Mostello, M. Newell, L. Nicholson, I. Nisbet, O. Olsson, D. Oro, V. Pattison, M. Poisbleau, T. Pyk, F. Quintana, J. A. Ramos, R. Ramos, T. K. Reiertsen, C. Rodríguez, P. Ryan, A. Sanz-Aguilar, N. M. Schmidt, P. Shannon, B. Sittler, C. Southwell, C. Surman, W. S. Svagelj, W. Trivelpiece, P. Warzybok, Y. Watanuki, H. Weimerskirch, P. R. Wilson, A. G. Wood, A. B. Phillimore, S. Lewis, Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nat. Clim. Chang.* **8**, 313–318 (2018).
4. M. Paleczny, E. Hammill, V. Karpouzi, D. Pauly, Population Trend of the World's Monitored Seabirds, 1950-2010. *PLoS One* **10**, e0129342 (2015).
5. W. J. Sydeman, D. S. Schoeman, S. A. Thompson, B. A. Hoover, M. García-Reyes, F. Daunt, P. Agnew, T. Anker-Nilssen, C. Barbraud, R. Barrett, P. H. Becker, E. Bell, P. D. Boersma, S. Bouwhuis, B. Cannell, R. J. M. Crawford, P. Dann, K. Delord, G. Elliott, K. E. Erikstad, E. Flint, R. W. Furness, M. P. Harris, S. Hatch, K. Hilwig, J. T. Hinke, J. Jahncke, J. A. Mills, T. K. Reiertsen, H. Renner, R. B. Sherley, C. Surman, G. Taylor, J. A. Thayer, P. N. Trathan, E. Velarde, K. Walker, S. Wanless, P. Warzybok, Y. Watanuki, Hemispheric asymmetry in ocean change and the productivity of ecosystem sentinels. *Science (1979).* **372**, 980–983 (2021).

6. M. E. Visser, C. Both, Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences* **272**, 2561–2569 (2005).

7. M. E. Visser, P. Gienapp, Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* **3**, 879–885 (2019).

8. J. M. Mcnamara, Z. Barta, M. Klaassen, S. Bauer, Cues and the optimal timing of activities under environmental changes. *Ecol. Lett.* **14**, 1183–1190 (2011).

9. A. Charmantier, R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, B. C. Sheldon, Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science (1979).* **320**, 800–803 (2008).

10. S. J. Thackeray, P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helaouet, D. G. Johns, I. D. Jones, D. I. Leech, E. B. MacKay, D. Massimino, S. Atkinson, P. J. Bacon, T. M. Brereton, L. Carvalho, T. H. Clutton-Brock, C. Duck, M. Edwards, J. M. Elliott, S. J. G. Hall, R. Harrington, J. W. Pearce-Higgins, T. T. Høye, L. E. B. Kruuk, J. M. Pemberton, T. H. Sparks, P. M. Thompson, I. White, I. J. Winfield, S. Wanless, Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**, 241–245 (2016).

11. W. J. Sydeman, E. Poloczanska, T. E. Reed, S. A. Thompson, Climate change and marine vertebrates. *Science (1979).* **350**, 772–777 (2015).

12. W. Cai, A. Santoso, M. Collins, B. Dewitte, C. Karamperidou, J.-S. Kug, M. Lengaigne, M. J. McPhaden, M. F. Stuecker, A. S. Taschetto, A. Timmermann, L. Wu, S.-W. Yeh, G. Wang, B. Ng, F. Jia, Y. Yang, J. Ying, X.-T. Zheng, T. Bayr, J. R. Brown, A. Capotondi, K. M. Cobb, B. Gan, T. Geng, Y.-G. Ham, F.-F. Jin, H.-S. Jo, X. Li, X. Lin, S. McGregor, J.-H. Park, K. Stein, K. Yang, L. Zhang, W. Zhong, Changing El Niño–Southern Oscillation in a warming climate. *Nat. Rev. Earth Environ.* **2**, 628–644 (2021).

13. J. M. Cohen, M. J. Lajeunesse, J. R. Rohr, A global synthesis of animal phenological responses to climate change. *Nat. Clim. Chang.* **8**, 224–228 (2018).

14. P. K. Thornton, P. J. Ericksen, M. Herrero, A. J. Challinor, Climate variability and vulnerability to climate change: A review. *Glob. Chang. Biol.* **20**, 3313–3328 (2014).

15. D. Li, M. Belitz, L. Campbell, R. Guralnick, Extreme weather events have strong but different impacts on plant and insect phenology. *Nature Climate Change 2025 15:3* **15**, 321–328 (2025).

16. M. Stemkovski, J. R. Bell, E. R. Ellwood, B. D. Inouye, H. Kobori, S. D. Lee, T. Lloyd-Evans, R. B. Primack, B. Templ, W. D. Pearse, Disorder or a new order: How climate change affects phenological variability. *Ecology* **104** (2023).

17. G. Domínguez-Hernández, J. Cepeda-Morales, L. Soto-Mardones, J. P. Rivera-Caicedo, D. A. Romero-Rodríguez, E. A. Inda-Díaz, O. U. Hernández-Almeida, C. Romero-Bañuelos, Semi-annual variations of chlorophyll concentration on the Eastern Tropical Pacific coast of Mexico. *Advances in Space Research* **65**, 2595–2607 (2020).

18. A. M. McInnes, P. G. Ryan, M. Lacerda, J. Deshayes, W. S. Goschen, L. Pichegru, Small pelagic fish responses to fine-scale oceanographic conditions: implications for the endangered African penguin. *Mar. Ecol. Prog. Ser.* **569**, 187–203 (2017).

19. P. M. Cury, I. L. Boyd, S. Bonhommeau, T. Anker-Nilssen, R. J. M. Crawford, R. W. Furness, J. A. Mills, E. J. Murphy, H. Österblom, M. Paleczny, J. F. Piatt, J. P. Roux, L. Shannon, W. J. Sydeman, Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. *Science (1979).* **334**, 1703–1706 (2011).

20. S. Bonamour, L.-M. Chevin, C. de Franceschi, A. Charmantier, C. Teplitsky, Age-Specific Phenology and Reproductive Success Senescence Vary with Environmental Age in a Wild Bird. *Am. Nat.* **205**, 76–89 (2025).

21. G. F. Ball, E. D. Ketterson, Sex differences in the response to environmental cues regulating seasonal reproduction in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 231–246 (2008).

22. S. Nakagawa, S. Ortega, E. Gazzea, M. Lagisz, A. Lenz, E. Lundgren, A. Mizuno, Location–scale models in ecology and evolution: Heteroscedasticity in continuous, count and proportion data. *Methods Ecol. Evol.* **00**, 1–13 (2025).

23. A. J. Miller-Rushing, R. B. Primack, GLOBAL WARMING AND FLOWERING TIMES IN THOREAU'S CONCORD: A COMMUNITY PERSPECTIVE. *Ecology* **89**, 332–341 (2008).

24. R. P. Kovach, S. C. Ellison, S. Pyare, D. A. Tallmon, Temporal patterns in adult salmon migration timing across southeast Alaska. *Glob. Chang. Biol.* **21**, 1821–1833 (2015).

25. S. J. Thomalla, S. A. Nicholson, T. J. Ryan-Keogh, M. E. Smith, Widespread changes in Southern Ocean phytoplankton blooms linked to climate drivers. *Nature Climate Change 2023 13:9* **13**, 975–984 (2023).

26. D. E. Castillo-Loeza, D. Romero, A. Quesada-Román, Tropical Cyclones in Mexico: A Comparative Analysis and a Composite Socioeconomic Damage Index. *Economics of Disasters and Climate Change 2025 9:3* **9**, 495–517 (2025).

27. Tropical Cyclone Climatology. https://www.nhc.noaa.gov/climo/.

28. T. E. Reed, L. E. B. Kruuk, S. Wanless, M. Frederiksen, E. J. A. Cunningham, M. P. Harris, Reproductive Senescence in a Long-Lived Seabird: Rates of Decline in Late-Life Performance Are Associated with Varying Costs of Early Reproduction. *Am. Nat.* **171**, E89–E101 (2008).

29. G. Beauplet, C. Barbraud, W. Dabin, C. Küssener, C. Guinet, Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos* **112**, 430–441 (2006).

30. A. Velando, C. Alonso-Alvarez, Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *Journal of Animal Ecology* **72**, 846–856 (2003).

31. M. Guerra, H. Drummond, Reversed Sexual Size Dimorphism and Parental Care: Minimal Division of Labour in the Blue-Footed Booby. *Behaviour* **132**, 479–496 (1995).

32. H. P. Jones, J. Appoo, C. E. Benkwitt, S. B. Borrelle, R. E. Dunn, H. E. Epstein, L. A. Fowlke, N. D. Holmes, L.-L. Jeannot, Y. Malhi, L. L. Rankin, S. Steibl, C. N. Wails, D. J. Will, N. A. Graham, The circular seabird economy is critical for oceans, islands and people. *Nature Reviews Biodiversity*, 1–14 (2025).

33. E. Morales-Bojórquez, V. M. Gómez-Muñoz, R. Félix-Uraga, R. Alvarado-Castillo, Relation between recruitment, sea surface temperature, and the density-independent mortality of the Pacific sardine (Sardinops caeruleus) off the southwest coast of the Baja California Peninsula, Mexico. *Sci. Mar.* **67**, 25–32 (2003).

34. S. E. Lluch-Cota, C. Salvadeo, D. B. Lluch-Cota, R. Saldívar-Lucio, G. P. Díaz, "Impacts of Climate Change on Mexican Pacific Fisheries" in *Climate Change Impacts on Fisheries and Aquaculture* (Wiley, ed. 1, 2017; https://onlinelibrary.wiley.com/doi/10.1002/9781119154051.ch9), pp. 219–238.

35. F. Mayani-Parás, R. M. Kilner, M. C. Stoddard, C. Rodríguez, H. Drummond, Behaviorally Induced Camouflage: A New Mechanism of Avian Egg Protection. *Am. Nat.* **186**, E91–E97 (2015).

36. S. Ortega, C. Rodríguez, B. Mendoza-Hernández, H. Drummond, How removal of cats and rats from an island allowed a native predator to threaten a native bird. *Biological Invasions 2021 23:9* **23**, 2749–2761 (2021).

37. H. Drummond, C. Rodríguez, D. Oro, Natural 'poor start' does not increase mortality over the lifetime. *Proceedings of the Royal Society B: Biological Sciences* **278**, 3421–3427 (2011).

38. A. Castillo, C. Chavez-Peón, "Ecología reproductiva e influencia del comportamiento en el control del número de crias en el bobo de patas azules Sula nebouxii en la Isla Isabel, Nayarit," thesis, Universidad Nacional Autónoma de México (1983).

39. H. Drummond, R. Torres, V. V. Krishnan, Buffered Development: Resilience after Aggressive Subordination in Infancy. *Am. Nat.* **161**, 794–807 (2003).

40. ASAB Ethical Committee, ABS Animal Care Committee, Guidelines for the treatment of animals in behavioural research and teaching. *Anim. Behav.* **183**, I–XI (2022).

41. C. Hu, Z. Lee, B. Franz, Chlorophyll aalgorithms for oligotrophic oceans: A novel approach based on three-band reflectance difference. *J. Geophys. Res. Oceans* **117** (2012).

42. NASA Ocean Biology Processing Group, Aqua MODIS Level-3 Global Mapped Chlorophyll (CHL) Data, version 2022.0 (2025). https://doi.org/10.5067/AQUA/MODIS/L3M/CHL/2022.0.

43. H. Weimerskirch, S. Shaffer, Y. Tremblay, D. Costa, H. Gadenne, A. Kato, Y. Ropert-Coudert, K. Sato, D. Aurioles, Species- and sex-specific differences in foraging behaviour and foraging zones in blue-

footed and brown boobies in the Gulf of California. *Mar. Ecol. Prog. Ser.* **391**, 267–278 (2009).

44. C. B. Zavalaga, S. Benvenuti, L. Dall'Antonia, S. D. Emslie, Foraging areas of breeding blue-footed boobies Sula nebouxii in northern Peru, as determined by direction recorders. *J. Avian Biol.* **39**, 405–412 (2008).

45. D. A. Siegel, S. C. Doney, J. A. Yoder, The North Atlantic Spring Phytoplankton Bloom and Sverdrup's Critical Depth Hypothesis. *Science (1979).* **296**, 730–733 (2002).

46. S. A. Henson, J. P. Dunne, J. L. Sarmiento, Decadal variability in North Atlantic phytoplankton blooms. *J. Geophys. Res. Oceans* **114** (2009).

47. M.-F. Racault, C. Le Quéré, E. Buitenhuis, S. Sathyendranath, T. Platt, Phytoplankton phenology in the global ocean. *Ecol. Indic.* **14**, 152–163 (2012).

48. M. van De Pol, S. Verhulst, Age-Dependent Traits: A New Statistical Model to Separate Within- and Between-Individual Effects. *Am. Nat.* **167**, 766–773 (2006).

49. R Core Team, R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing 4.5.2 [Preprint] (2025). https://www.R-project.org/.

50. P. C. Bürkner, brms: An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).

51. A. Vehtari, A. Gelman, J. Gabry, Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**, 1413–1432 (2017).

52. F. M. Hollenbach, J. M. Montgomery, Bayesian Model Selection, Model Comparison, and Model Averaging. *The SAGE Handbook of Research Methods in Political Science and International Relations*, 937–960 (2020).

53. H. Wickham, ggplot2. *WIREs Computational Statistics* **3**, 180–185 (2011).

54. M. Kay, tidybayes: Tidy Data and "Geoms" for Bayesian Models. R 3.0.7 (2024). https://doi.org/10.32614/CRAN.package.tidybayes.

55. M. Kay, ggdist: Visualizations of Distributions and Uncertainty in the Grammar of Graphics. *IEEE Trans. Vis. Comput. Graph.*, 1–11 (2023).

56. T. Pendersen, patchwork: The Composer of Plots. 1.3.2.9000 (2025). https://doi.org/10.32614/CRAN.package.patchwork.

57. S. Ortega, C. Rodriguez, A. Mizuno, L. Arroyo, H. Drummond, S. Nakagawa, The collapse of environmental predictability erodes reproductive success in a Tropical seabird (2026). https://doi.org/10.5281/ZENODO.19208182

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Data, code, and materials availability:

All data, code, and materials needed to evaluate the conclusions of this paper are publicly available. The project GitHub repository and companion website provide a fully documented, step-by-step workflow for reproducing all analyses and figures. The GitHub repository is available at https://github.com/Santiago-0rtega/Collapse_environmental_predictability_erodes_reproductive_success, and the companion site is available at https://santiago-0rtega.github.io/Collapse_environmental_predictability_erodes_reproductive_success/. A Zenodo archive (57) provides a permanent versioned release of the datasets and fitted model .rds files underlying the analyses.

Supplementary materials

Materials and Methods

Supplementary Text

Figs. S1 to S5.

Tables S1 to S5

References (*33-57*)