Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts

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Species respond to climate change in two dominant ways: range shifts in latitude or elevation and phenological shifts of life-history events. Range shifts are widely viewed as the principal mechanism for thermal niche tracking, and phenological shifts in birds and other consumers are widely understood as the principal mechanism for tracking temporal peaks in biotic resources. However, phenological and range shifts each present simultaneous opportunities for temperature and resource tracking, although the possible role for phenological shifts in thermal niche tracking has been widely overlooked. Using a canonical dataset of Californian bird surveys and a detectability-based approach for quantifying phenological signal, we show that Californian bird communities advanced their breeding phenology by 5–12 d over the last century. This phenological shift might track shifting resource peaks, but it also reduces average temperatures during nesting by over 1 °C, approximately the same magnitude that average temperatures have warmed over the same period. We further show that early-summer temperature anomalies are correlated with nest success in a continental-scale database of bird nests, suggesting avian thermal niches might be broadly limited by temperatures during nesting. These findings outline an adaptation surface where geographic range and breeding phenology respond jointly to constraints imposed by temperature and resource phenology. By stabilizing temperatures during nesting, phenological shifts might mitigate the need for range shifts. Global change ecology will benefit from further exploring phenological adjustment as a potential mechanism for thermal niche tracking and vice versa.

nesting | thermal niche | climate change | Sierra Nevada | birds

Global mean temperatures have warmed by approximately 1 °C over the past century, which has led to cascading and pervasive impacts across ecological communities (1, 2). Species are shifting their ranges poleward and to higher elevations (3–5), and phenological events of spring and early summer are advancing (6, 7). The consensus viewpoint is that range shifts occur when species distributions are directly or indirectly limited by shifting climatic gradients, such as temperature (8, 9). Phenological shifts occur because some taxa use temperature to cue life-history events (10, 11), while others adjust their phenology through plasticity or evolution to track peaks in biotic resources (12–14).

Range shifts are crucial mechanisms for species-level adaptation to changing temperature (1, 15), and species that do not shift geographically in response to a changing climate may risk population declines and extinction (16). However, latitudinal or elevational range shifts are not the only mechanism for thermal niche tracking. For example, steep temperature gradients across the vertical strata of tropical forests allow amphibians to avoid high temperatures by moving away from the canopy (17), and temperature gradients through the oceanic water column afford similar opportunities to marine organisms (5). Although phenological shifts in breeding dates are generally viewed as a mechanism for matching resource demand to availability

(18–20), they might also provide another opportunity to track temperature by shifting thermally constrained life-history events (e.g., nesting in birds) to colder times of year (Fig. 1). This might be the case even if the main adaptive significance of phenological shifts involves resource tracking.

However, species do not have unrestricted flexibility to adjust their phenology to track temperature. Phenological timing of life-history events is not always behaviorally plastic or evolutionarily labile (21). Moreover, consumers face demographic consequences if reproduction is not adequately timed with peaks in biotic resources (18–20). Because resource peaks do not necessarily shift in concert with breeding-season temperatures (6), consumers are not always free to shift phenologically by the appropriate amount to track temperature. Finally, phenological shifts are useful for thermal niche tracking only if critical life-history events that determine the thermal niche occur at a time of year when average temperatures are directionally changing with the passage of a season.

Several features of avian biology suggest that birds might be sensitive to temperatures during nesting, at a time of year when temperatures continue to rise with advancing Julian day (jday) in most nonequatorial areas. Demands of provisioning nestlings constrain adult energy budgets and preclude short-distance elevational or topographic movements to escape unfavorable weather (22, 23). Moreover, young nestlings cannot thermoregulate effectively; altricial young are ectothermic (24), and even precocial young have limited thermoregulatory capacity (25). Thus, avian phenological advancement might mitigate the need for range

Significance

Climate warming poses two major challenges for birds: exposure to higher temperatures and disruption of the synchrony between nesting and resource emergence. To cope, birds are expected to track temperature by moving to cooler areas and to track resource emergence by breeding earlier. We show that these two responses are intertwined. Earlier breeding can substitute for range shifts by reducing temperatures during critical breeding-season life-history events. We show that early-summer temperatures affect nesting success in North American birds and that Californian birds breed ~1 wk earlier today than a century ago. Thus, without shifting geographically, birds now nest at similar temperatures as they did a century ago, which might reshape both the need and the opportunity for range shifts.
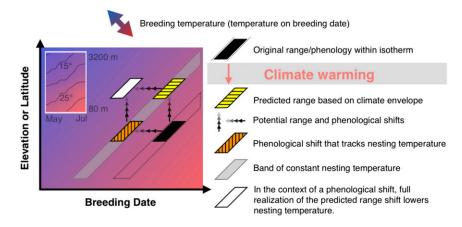
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Fig. 1. Species are widely predicted to respond to temperature mismatch by shifting geographically and to resource mismatch by shifting phenologically. In this stylized example, the prewarming population (black) breeds in a spatiotemporal window of constant temperature. Additional constraints (e.g., resource phenology, ecotones) prevent the population from occupying the full span of the isotherm. Range shifts and phenological shifts are both potential mechanisms for thermal niche tracking. If phenological advancement occurs, the range shift predicted by a spatial (i.e., nonphenological) climate envelope model would expose nests to colder temperatures. The interplay of additional constraints determines what region of the gray isotherm is ultimately occupied postwarming. (*Inset*) Empirical heat plot of average DMTs by date (May 15 to July 1) and elevation (86–3,216 m above sea level) in and near Yosemite National Park, California, in 1980–2015. Thermal contours with 5° of spacing range from 10 to 30 °C.

shifts (Fig. 1). At warm range limits, earlier breeding might allow nests and nestlings to escape high temperatures. At cold range limits, shifting resource peaks might provide resource-based incentives for birds to breed earlier, yet cause thermal stress as earlier breeding brings greater exposure to cold. This is possible especially when warming causes differential shifts in spring phenology and breeding-season temperatures (6).

In this study, we use data from the Grinnell Resurvey Project (3, 8), a model system for elevational range shifts, to estimate the phenological shift in the avifauna of California's Sierra Nevada (SN) and Coast Range (CR) concurrent with previously documented 20th century range shifts (26, 27). Statistical methods based on occupancy modeling provide an index of phenological shifts based on changes in avian detectability throughout the breeding season (28). Using our estimate of a community-wide phenological shift in avian breeding, we map the associated temperature change during nesting across California.

We then use a database of >47,000 monitored nests from Project NestWatch (29) to probe the association between temperatures during nesting (T_n) and nest success in the North American avifauna. If T_n impacts avian nesting biology sufficiently to influence thermal niches, we predict that warm temperature anomalies should increase nest success in the cold portions of a species' range but decrease nest success in the warm portions of the range. This effect should not be mediated by variation in resource phenology, and so should persist after accounting for any effects of earlier springtime temperature (T_s) anomalies (which influence resource phenology). Several previous studies have demonstrated associations between T_n and nest success or postfledging survival (30–36), and some of these have successfully isolated physiological and indirect mechanisms that underpin the effects; however, to our knowledge, none has tested for this telltale signal across large spatiotemporal or taxonomic scales.

We show that an index for breeding date in Californian birds has advanced by 5–12 d between initial surveys in 1911–1940 and resurveys in 2003–2010. We further show that the relationship between temperature and nesting success in North American birds strongly suggests that nesting biology constrains avian thermal niches. Together, these lines of evidence suggest that phenological shifts are a mechanism for thermal niche tracking that might dampen both the need and the opportunity to shift geographically (Fig. 1). This possibility suggests new hypotheses and research priorities for understanding the adaptive capacity of species to respond to climate change.
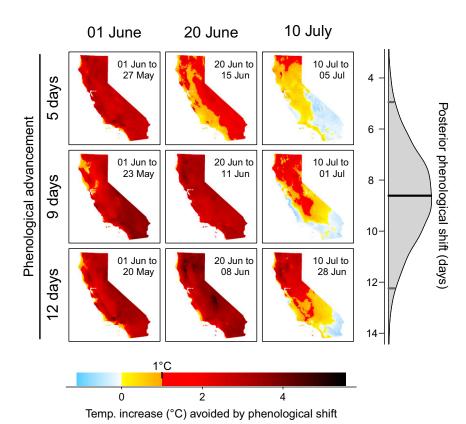
Results

Phenological Shift and Thermal Implications. An index of community-wide breeding phenology, measured across the entire avian species pool of the CR ($n = 150$) and SN ($n = 160$) from 1911–1940 to

2003–2010, has shifted earlier, with a posterior mean estimate of 8.6 d (95% Bayesian credible interval of 5–12 d; Fig. 2). This result is robust to various alternative model specifications and is unlikely to be confounded by slight differences in timing of bird surveys between sampling eras (*SI Appendix*, Fig. S1 and Table S2). Data were too sparse to produce precise species-specific estimates of phenological shifts. However, the strong signal for an entire community comprising 224 species across 6.5° latitude and 6.2° longitude represents a finding of widespread breeding-season phenological shifts across an unprecedented spatial and temporal scale.

The magnitude of the observed phenological shift is sufficient for breeding birds to track daily maximum temperatures (DMTs) through an increase of >1 °C across most of California (Fig. 2). By breeding earlier, nesting birds experience average temperatures >1 °C colder than they would experience had they not responded phenologically. This trend is strongest for phenological events in June (Fig. 2). While the trend is less consistent after July 10 in the last third of the nesting season, it still corresponds to temperature reductions of at least 1 °C at many of our sampled sites (*SI Appendix*, Fig. S2). The thermal reduction gained by a phenological shift with respect to average nightly minimum temperatures is similar, although the differences are generally smaller in magnitude (*SI Appendix*, Fig. S3).

Temperature Impacts on Nest Success. Phenological advancement is a plausible mechanism for thermal niche tracking only if demography responds to temperature at a time of year when temperature varies systematically with jday. Based on the Project NestWatch sample of 47,023 bird nests of 110 species, laid between May 15 and June 15, 1997–2015, we found that temperature anomalies at the nest site (45 d postlaying; T_n) interact with the range-standardized temperature of the nest site [temperature at the geographical location of the nest relative to the species' breeding range (RT)] to determine nest success. In particular, while also accounting for the influence of T_s anomalies (April 15 to May 15 during the nesting year) and their interaction with RT, warm T_n is associated with high nest success in the cold parts of a species' range, but with low success in the warm part of a species' range (Fig. 3 and Table 1). Interestingly, while we found no evidence for an interaction between T_s and RT, we did find a negative main effect of T_s, consistent with the established hypothesis that warm springs cause resource mismatches for birds that result in demographic consequences (Table 1).

The impacts of temperature on nest success are large enough to affect avian demography at range edges. The mean estimated T_n/RT interaction indicates that a 1 °C temperature change at range edges ($RT = \pm 3$) shifts the probability of a nest successfully fledging young by roughly 0.03 (95% confidence interval: 0.01–0.04; details are provided in *SI Appendix*). A temperature change of 2–3 °C

Fig. 2. Across the CR and SN, bird communities have advanced their breeding phenology by roughly 8.6 d (95% credible interval of 5–12 d) between 1911–1940 and 2003–2010. This advancement reduces the temperatures experienced during breeding-season life-history events. Across most of California, the 5- to 12-d shift is sufficient to track breeding temperature through climate warming greater than 1 °C. Differences in average DMT are shown; minimum nightly temperature reveals a similar pattern (*SI Appendix*). Temp., temperature.

(corresponding to the 5–12 d of phenological shift we estimated for California birds) would alter nest success probabilities by roughly the same amount as 5–12 d of phenological mismatch between resource peaks and great tit (*Parus major*) hatching dates, as reported by Visser et al. (18). In other words, temperature-mediated fitness consequences of phenological shifts are potentially similar in magnitude to the consequences of resource mismatch.
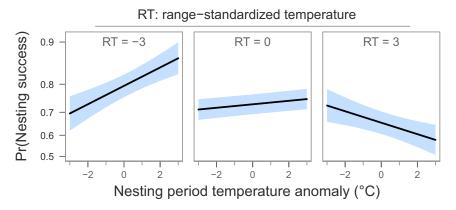
These results are robust to the inclusion or exclusion of species known to have unusual nesting phenology, and to nests that failed due to predation (*SI Appendix*, Table S3). A generalized additive modeling framework produces very similar results (*SI Appendix*, Fig. S4).

Discussion

Our results suggest that phenological shifts in the Californian avifauna, and likely elsewhere, can act as a mechanism for thermal niche tracking over time (Fig. 1). Nest monitoring data from across North America show that early summer temperatures can have substantial demographic impacts on bird populations via their impact on nest success (Fig. 3). Positive temperature anomalies during nesting reduce nest success in the warm part of the range but increase success in the cold part of the range, consistent with a role for nesting biology in constraining the thermal niche (Table 1). Historic weather data combined with bird resurveys over a century of climate change show that the magnitude of phenological shifts in the Californian avifauna lowers the ambient temperatures to which nests are exposed during breeding (Fig. 2) by at least as much as the total climate warming over the equivalent period (37). This result provides a parsimonious explanation for why, across upper and lower range limits combined, 16% of SN bird species and 37% of individual range margins did not show significant elevational changes over a century, despite strong regional climatic expectations to do so (26).

These results are consistent with contemporary understanding of avian responses to climate. Recent analyses of phenological

Fig. 3. Results of a logistic generalized linear mixed model (GLMM) for the probability (Pr) of nesting success. In the cold part of a species' range (low *RT*), warm T_n anomalies are associated with high nesting success. In the warm part of a species' range, the opposite is true. The model controls for the influence of early-spring temperatures and their interaction with *RT*. These results are fully consistent with the idea that nesting biology plays a role in setting avian thermal niches.

Table 1. Parameter estimates from a logistic generalized linear mixed model predicting nest success as a function of T_n anomaly, T_s anomaly, RT, and the interactions between RT and the temperature anomalies

Parameter	Estimate	P value
Intercept	1.00	<0.001
T_n	0.03	<0.001
T_s	−0.05	<0.001
RT	−0.12	<0.001
T_n/RT	−0.05	<0.001
T_s/RT	−0.01	0.36

change in breeding-season events for temperate birds, such as territorial singing, egg laying, and hatching, have reported estimated shifts of 2–5 d per decade (19, 20, 28). Our slightly lower estimate of ∼0.9 d per decade from 1911–2010 may reflect geographic or taxonomic variation, compensatory behavior through ongoing range shifts (26), or slower phenological advancement before 1980 when warming began to accelerate (38). Consequently, the large temporal extent of our dataset may produce estimates of average decadal shifts that are lower than rates from studies conducted over shorter, more recent time periods. Larger phenological shifts, as reported in other studies, could play even greater roles in thermal niche tracking.

The influence of temperature on nest success has been postulated for decades and supported through many fine-scale studies, but has rarely been tested at macroecological scales (30–36). Our macroecological test reveals the telltale signal of an interaction between temperature anomalies and position within the breeding range, strongly suggesting that nesting biology plays a role in setting avian thermal niches. Our approach cannot elucidate the mechanisms whereby temperature influences nest success, but some lines of evidence suggest that the effect might involve the direct impacts of temperature on avian physiology (36). Neotropical migrants might encounter colder temperatures early in the nesting period than at any other point in their lives. Similarly, facultative elevational migrants in North America might encounter both hot and cold temperature extremes while they are constrained to attend a nest. Moreover, the poor thermoregulatory ability of nestlings is a mechanism for temperature sensitivity across species. As predicted, T_s anomalies between April 15 and May 15 did not interact with RT to determine nest success. Instead, positive T_s anomalies were negatively related to nest success everywhere, consistent with the idea that, independent of thermal constraints, birds are negatively impacted by failure to fully track resource emergence during warm springs (19). These results are obtained primarily from cavity nesters in human-made nest boxes, which present unique opportunities for understanding the determinants of nest success in wild birds (*SI Appendix*). An exploration of these effects in a broader sample of species with diverse ecologies would be a valuable contribution.

The temperature consequences of the observed phenological shift pose a puzzle: Why have birds shifted phenologically by >1 °C in June, which is greater than the historical climate warming (∼0.8 °C)? One possibility is that birds are shifting to optimize temperatures over a protracted breeding window. A phenological shift that tracks 1 °C of temperature change in early July corresponds to larger temperature differences in June. A second possibility is that birds are responding primarily to shifting resource emergence, and only secondarily benefiting from thermal tracking. The phenology of resource emergence depends substantially on winter chill and early-spring warmth, which are partially decoupled from June temperatures (6). Even if the main adaptive significance of avian phenological shifts relates to resource tracking, the thermal consequences of those shifts could still alter the need to shift

geographically. If resource phenology advances faster than June temperatures, climate warming could hypothetically drive a geographical shift toward warmer temperatures (i.e., downslope or equatorial), potentially exacerbating the challenges of coping with high temperatures later in summer. Interestingly, previous analyses concluded that some SN birds are niche-tracking toward warmer temperatures (8).

Recognizing phenological shifts as a mechanism for thermal niche tracking leads to new mechanistic hypotheses for patterns of geographic range shifts. Range shifts that lag behind warming temperatures have been conceptualized as a climatic debt (39) and have been explained in terms of dispersal limitations, time lags in biotically mediated climate impacts, interacting effects of multiple climate drivers, or fundamental niches that extend beyond the realized thermal envelope (4, 26, 40–42). To this list, we add the hypothesis that some observed lags might be byproducts of phenological shifts of life-history events that are responding to thermal constraints, and might not reflect a climatic debt at all. The tendency for tropical animals to respond strongly to climate change through large elevational range shifts (43) has been attributed to narrow thermal tolerances in the tropics (44). Our alternative perspective suggests the aseasonal tropics might afford less potential for phenological shifts to buffer the need for shifting range limits. Work on temperate birds and butterflies has shown that warm range limits have remained more geographically stable than cold range limits (45–47, but 48), perhaps because extinctions are not instantaneous or because warm range limits are mediated by biotic interactions that vary unpredictably with global change (41, 42). In our montane system, an alternative explanation is that phenological advancement reduces maximum daily temperatures more quickly than minimum nightly temperatures (Fig. 2 and *SI Appendix*, Fig. S3); if maximum temperatures determine warm range limits and minimum temperatures determine cold limits, then we expect phenological advancement to buffer warm limits more strongly.

Whether phenological shifts play a major role in mediating geographic range shifts is still unclear, but our empirical results suggest that this mechanism operates in birds in California and likely throughout North America and beyond. Because phenological shifts mitigate temperature mismatch only when thermally constrained life-history events occur at a time of year when temperature varies systematically with jday, we call for more research into thermal constraints across the annual cycle (49, 50). As climate warming continues to alter communities and erode baselines, the interplay between phenological timing and the thermal niche provides species with overlooked flexibility as well as constraint in their responses. The implications of complementary axes of phenological and geographic response to thermal mismatch remain largely unknown.

Materials and Methods

Bird Surveys and Data Preparation. Bird observations were collected as part of the Grinnell Resurvey Project (3, 8), an ongoing endeavor to document distributions and populations of vertebrates throughout California. Historical bird observations were made by Joseph Grinnell and 23 other observers between the years of 1911 and 1940. A key feature of the historical dataset is that survey sites, ∼2-km line-transects, were visited and surveyed on multiple days within the historical period (26), providing repeat detection and nondetection suitable for robust analyses of range shifts (51). Modern resurveys began in 2003 and continued through 2010, focusing on distinct elevational gradients for 2-y periods. Details of historic and modern surveys in the SN are reported by Tingley et al. (8, 26) and Tingley and Beissinger (27).

CR surveys in California represent a heretofore unpublished dataset of the Grinnell Resurvey Project. Historically, surveys were conducted throughout the CR starting in 1911 and continuing up to 1940. While SN surveys were conducted within three distinct regions, each composed of an elevational gradient or transect, surveys along the CR were conducted along a continuous latitudinal gradient that sampled from sea level to ∼1,800 m. In total, 70 CR sites were surveyed, compared with the 77 sites surveyed across all three SN regions. Bird sampling procedures associated with historic and modern

surveys of the CR were nearly identical to those used and previously described for the SN (8).

To assess breeding-season phenology, we restricted our analysis to surveys performed between May 1 and August 25. This date range was well sampled by both historical and modern surveys in the SN. CR surveys do not extend beyond July 21 in either era. Some sites were visited exclusively before May 1 in the historical era; we removed these sites from the modern data as well. Because many species have arrived on territory by May 1, phenological variation in detectability in our data reflects behavior on the breeding grounds and not exclusively variation in arrival phenology.

Some CR sites were surveyed a large number of times over the span of multiple decades in the historical era, which is likely to violate closure assumptions in occupancy models (52). Previous occupancy models for the SN data assumed closure over 5-y time windows (8, 26, 27); therefore, we restricted the historical data at each site to the 5-y window with the greatest number of repeat visits. When multiple time windows contained equal visits or more than nine visits each, we used the oldest window. Further discussion of the closure assumption is provided in *SI Appendix*. Because a few CR sites were surveyed up to 96 times in the historical era, we removed all surveys in excess of the 10th visit to each site, retaining the oldest 10 visits for analysis. Doing so prevents a small subset of heavily visited sites from dominating estimates of detectability relationships in occupancy models, which could cause problems in the presence of unmodeled heterogeneity in detection probabilities.

After removing seabirds and nonbreeders from the dataset, we retained 202 bird species in the SN and 183 in the CR for occupancy modeling (*SI Appendix*, Table S1). Of these, 150 (SN) and 160 (CR) were recorded in both the historical and modern survey periods, and therefore were potentially informative for estimating shifts in the phenology of detection. Collectively, these informative species represented roughly 98% of the total detections in the dataset.

Community Occupancy Models for Phenological Shift. We analyzed detection/nondetection data from historical and modern surveys using community occupancy models (53, 54). These models introduce latent Bernoulli variables, Z_{ij}, to represent the true occupancy status of species i at survey site j. These true site occupancies are specified by logistic regression on site-specific occupancy covariates. Detection/nondetection data from each survey are conditioned on Z_{ij} and then modeled using logistic regression on site- and survey-specific detection covariates. In the community occupancy model, species-specific coefficient values for both occupancy and detection are drawn from Gaussian community-level hyperdistributions.

Tingley and Beissinger (27) presented a community occupancy model for the SN data. Modern site occupancy was assumed to be independent of historical site occupancy (8, 26, 27), and the logit occupancy probability was specified by an intercept and effects of era (historical or modern), elevation corrected for latitude [based on a study by Brock and Inman (55); linear and quadratic terms], the interaction of both elevation terms with era, and survey sector (one of three latitudinal zones of the SN). The logit detection probability is specified by an intercept and the effects of era and jday (linear and quadratic terms). To estimate phenological shifts, we took advantage of the fact that avian detectability in predominantly acoustic surveys varies predictably with events in the breeding cycle: arrival, territory establishment, nesting, fledging, and so on (28, 56–58). Therefore, interdecadal shifts in modeled jday-detection relationships yield an index for shifting phenology (28). To leverage this information, we made several modifications to the model of Tingley and Beissinger (27).

First, we changed the logit-quadratic specification for the jday-detectability relationship to a logit-quintic specification, which we expect to be sufficiently flexible to match the true relationship closely (28). We then allowed jday-detectability relationships to vary between eras with a horizontal offset parameter. We assume that the shape of the logit-quintic relationship remains constant but that the entire relationship can shift earlier or later between the historical and modern eras (the relationship can also shift up or down according to the direct effect of era on detectability, but it cannot change shape). By accounting for changing occupancy across a constant set of locations, and by focusing on the entire breeding-season phenology rather than single phenological events, this modeling framework avoids major pitfalls that may bias inference about phenological shifts (59).

We are interested in inference on the offset parameter, which is directly interpretable as the magnitude of the phenological shift. Given that our estimate for the offset parameter accounts for the full joint uncertainty in the quintic parameters, we are confident that the highly flexible quintic specification improves our inference (*SI Appendix*, Fig. S5). Results from models specified using a quadratic (rather than quintic) polynomial yielded similar overall results (*SI Appendix*, Table S2).

To perform inference about the phenological shift in detectability, we incorporated both the SN and CR data into an expanded model. First, we

constructed a separate community occupancy model for the CR data. Model specification was identical to the SN model except that we replaced "survey sector" with latitude and we used raw elevations rather than latitude-corrected elevations because the CR lacked a uniform latitudinal temperature gradient. We then assumed that species-specific phenological shifts in the SN and CR data were drawn from a single Gaussian hyperdistribution, and we fit the two submodels (SN and CR) jointly. We did not assume that any other parameters were related in this way (i.e., SN and CR coefficients for elevation and latitude came from independently parameterized hyperdistributions). Due to major ecological differences between the CR and SN, we did not assume that wide-ranging species would respond similarly to occupancy or detectability covariates in both regions. Therefore, we allowed SN and CR populations to respond independently to all covariates.

We analyzed the model under a Bayesian mode of inference with vague priors, using the statistical software JAGS 4.2.0 called from R 3.3.2 via the package dclone 2.1.2. We performed inference on posterior parameter estimates using 95% credible intervals. To confirm the robustness of our inference, we fit additional models using alternative specifications for jday-detectability relationships and the jday offset parameter (*SI Appendix, SI Methods*). Full specifications for all models are available in *SI Appendix, SI Methods*.

Climate Data and Visualization. We used historical weather data from Daymet (60) to visualize the average temperature differences that correspond to a phenological shift of a given magnitude on a given date. These temperatures are the amount of climate warming that might be avoided at a given point in the breeding cycle by shifting phenologically. Across California, we extracted DMTs from 1980 to 2015 at 1-km resolution using the R package FedData 2.4.0. We excluded the year 2005 from analysis due to missing data at some locations. We then averaged these temperatures across years and mapped the difference in average temperatures for nine pairs of date and shift magnitude. We repeated the process for nightly minimum temperatures.

Nest Success Model. To determine whether early summer temperatures influence nest success, we analyzed nest monitoring data from the Project NestWatch database (29). We restricted our analysis to nesting attempts with known species, known outcomes (success if at least one young bird fledged, failure otherwise), and known lay dates between May 15 and June 15. We further restricted our analysis to exclude failed attempts known to be caused by predation, brood parasitism, or invasive species management.

For each nesting attempt, we extracted DMTs from 1980 to 2015 from Daymet. We excluded attempts for which Daymet data were not available (generally nests that were plotted with geographic coordinates at barely offshore locations, indicating incorrect georeferences). For the year in which the nesting attempt was made, we calculated the T_n anomaly as the mean DMT during the 45 d following the lay date minus the mean across the equivalent jdays of all years from 1980–2015. Many North American birds have an interval of roughly 45 d between laying and fledging (61). We also calculated T_s anomalies at the nest locations from April 15 to May 15 of the year of the nesting attempt.

We hypothesized that warm temperature anomalies should be detrimental to nesting success in the warmest parts of a species range and beneficial in the coldest parts of the range. Therefore, we calculated an RT score for each nesting location as

$$RT = (tLoc - mtBBS)/sdtBBS,$$

where *tLoc* is the mean DMT at the nest location from May 15 to June 30 across all years, and *mtBBS* and *sdtBBS* are the mean and SD of the equivalent measurements taken at every survey route where the species has ever been recorded in the US Geological Survey Breeding Bird Survey (62). We excluded species that range substantially into the West Indies or lowland Mexico from analysis, as the Breeding Bird Survey does not fully capture the range of temperatures at sites where these species breed (*SI Appendix*, Table S4).

We then fit a logistic mixed-effects regression (R package lme4 1.1–12) to predict nest success based on T_n, T_s, RT, and the interactions of RT with both T_n and T_s. The inclusion of T_s mitigates the possibility that phenological mismatch due to warm springs might correlate with T_n, and thereby muddle inference on the effects of temperatures during nesting.

We confirmed that our results are robust to alternative model specifications by fitting a generalized additive mixed model to the nest success data, and we confirmed that results are consistent across species by fitting single-species logistic regressions for the 10 most common species in the dataset. At this stage, we observed strongly outlying and counterintuitive covariate relationships for only a single species, the purple martin (*Progne subis*), which we believe are explained by this species' unique early-spring phenology (*SI*

ECOLOGY

Appendix). Therefore, we report results based on data with purple martin nests removed. Including the purple martin data does not alter our conclusions, but some parameter estimates changed marginally (*SI Appendix, Table S3*). We also refit the model to data that included nest failures caused by predation or brood parasitism to confirm the robustness of our inference.

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