

Research



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Wind and rain are the primary climate factors driving changing phenology of an aerial insectivore

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While the ecological effects of climate change have been widely observed, most efforts to document these impacts in terrestrial systems have concentrated on the impacts of temperature. We used tree swallow (*Tachycineta bicolor*) nest observations from two widely separated sites in central Alaska to examine the aspects of climate affecting breeding phenology at the northern extent of this species' range. We found that two measures of breeding phenology, annual lay and hatch dates, are more strongly predicted by windiness and precipitation than by temperature. At our longest-monitored site, breeding phenology has advanced at nearly twice the rate seen in more southern populations, and these changes correspond to long-term declines in windiness. Overall, adverse spring climate conditions known to negatively impact foraging success of swallows (wet, windy weather) appear to influence breeding phenology more than variation in temperature. Separate analyses show that short windy periods significantly delay initiation of individual clutches within years. While past reviews have emphasized that increasing variability in climate conditions may create physiological and ecological challenges for natural populations, we find that long-term reductions in inclement weather corresponded to earlier reproduction in one of our study populations. To better predict climate change impacts, ecologists need to more carefully test effects of multiple climate variables, including some, like windiness, that may be of paramount importance to some species, but have rarely been considered as strong drivers of ecological responses to climate alteration.

1. Introduction

Climate change is a global phenomenon with well-documented effects, including increasing temperatures as well as changes in precipitation, humidity, snow pack depth and duration, storm frequency, and wind speed [1–4]. There is substantial evidence that climate change is causing or will cause range and phenology shifts in individual species and will alter the structure and composition of entire communities [5–14]. Determining what aspects of climate are driving these changes is challenging because of annual climate variation and the correlated shifts in multiple aspects of climate. To date, most analyses in terrestrial systems have implicitly or explicitly assumed that temperature is the major driver of ecological effects ([1,5–9,11,13,15–28], but see [10,12,29]) Better understanding and prediction of climate effects relies on testing this assumption, as populations, species, communities, and ecosystems are likely to be differentially buffered against changes in the many aspects of the physical environment. Indeed, paleo-ecological data emphasize the non-congruent responses of different species to climate change, potentially a result of differential sensitivity to different aspects of climate [30,31].

One of the most powerful approaches to inferring ecological effects of climate, and climate change, is to track phenological changes of local populations

[5,6,9–11,20,32–34]. Recent work has shown advanced phenology in both plant and animal species in marine, freshwater and terrestrial environments, especially at higher latitudes [18,35–41]. In particular, avian species have shown mounting evidence of earlier breeding phenology [5–10,23,42,43] which is often assumed to result from increasing temperatures. One of the best studied North American species, the tree swallow, *Tachycineta bicolor*, has shown a 5- to 9-day advancement in average lay date over 32 years in the contiguous United States and Southern Canada. This advance was strongly correlated with rising spring temperatures [34]. However, as with many other climate–phenology studies, additional climate factors were not tested as alternative explanations for this response.

We quantified changes in population and individual-level phenology of tree swallows breeding in subarctic Alaska, an area warming at twice the rate of the contiguous United States [44,45]. We tested whether breeding phenology was related to temperature as well as windiness or precipitation. Windiness and precipitation have been shown to influence breeding success and timing of tree swallows and other birds, and they are likely to be particularly important for aerial insectivores [10,46–49]. Our findings suggest that investigators should look beyond temperature as they examine how climate change may alter phenology and, in particular, pay close attention to how a species' biological needs and limitations may be disrupted by different climate factors.

2. Material and methods

(a) Study species

Tree swallows migrate from overwintering sites in southern United States, Mexico, Caribbean, and Central America to breed in temperate and subarctic regions of North America. Tree swallows are cavity nesting, diurnal, generalist aerial insectivores that forage almost continuously during daylight hours for the duration of the chick rearing period [47,50]. In Alaska, tree swallows appear at breeding sites and begin nest construction approximately one month prior to laying. Clutch size in our populations varies between three and seven eggs (mean clutch size across our populations = 5.65). Incubation periods in these populations range from 13 to 17 days, with an average of 14.5 days. Both populations are single brooded.

(b) Data collection

Data were recorded from 2000 to 2015 for tree swallows nesting in artificial boxes at Creamer's Field Migratory Waterfowl Refuge in Fairbanks, Alaska (henceforth CF: 64.861944N, -147.740833 W, 134 m elevation). Between 46 and 113 nest-boxes were available each year, with 11–44 successful nesting attempts (nests with a hatch date) recorded annually. Using the same methods, from 2006 to 2015 between 58 and 91 nest-boxes (15–29 successful nesting attempts per year) were followed at Long Lake, Alaska (henceforth LL: 61.378333N, -143.314444 W, 448 m elevation), a site 433 km from Fairbanks and separated from it by two major mountain ranges [47]. In 2012–2015, some of these boxes were located in McCarthy, an area 21 km from LL that is part of the LL population, indicated by regular recapture of banded individuals at both locations. In both populations, nests were generally checked at least every other day during the laying period. Near to hatching, nests were generally checked by mid-morning at least every other day at LL and every day at CF. At LL, nests containing chicks with dry, fluffy down on their heads were assumed to have hatched the previous day. Since hatching is

frequently asynchronous, a nest was said to have hatched the day that the first chick emerged.

Information used in our analyses includes date of first egg laid for each active nest-box (henceforth lay date, or clutch initiation), and the date chicks first hatched (hatch date). Some lay dates were estimated by counting backwards one egg per day from the date that the nest with an incomplete clutch was first examined. All methods for data collection follow established protocols for tree swallow research [34,51]. The final dataset includes 515 nest records from Creamers Field and 165 from the Long Lake population. Across all years, 80% of CF lay dates fell between 23 May and 2 June, while 80% of hatch dates were between 10 and 22 June; for LL, 80% lay dates ranged from 25 May and 6 June, and 80% of hatch dates fell between 14 and 25 June.

(c) Climate data

For the CF site, we used the Fairbanks NOAA station (GHCND:USR0000AFAI), located approximately 6 km away, for air temperatures, and the Fairbanks International Airport station (GHCND:USW00026411), approximately 8 km away, for all other climate data. For LL, we averaged data from three neighbouring meteorological stations that collectively represent local climate (see electronic supplementary material, methods). We consolidated annual climate data from May (encompassing nest construction and early laying at both sites) into five summary variables: average daily temperature, total precipitation (cm), number of days with measurable precipitation, average daily wind speed, and number of windy days (days with average speed greater than the average May wind speed plus one standard deviation over the years of swallow monitoring at each site). We performed initial statistical tests using these same five variables calculated over different time periods, including the entire laying and incubation periods and subsets of these periods; use of May data gave predictive power comparable to the best alternate periods and climate variables showed consistent effects regardless of time period used (see electronic supplementary material). We also tested the correlations between May climate variables at each site and two regional climate indices, the Pacific Decadal Oscillation and the Multivariate El Niño–Southern Oscillation Index [52,53].

(d) Data analysis

We first tested for trends across time in lay or hatch dates using mixed-effects linear models that included year as a continuous fixed effect and box ID as a random factor. We next compared a series of 28 alternative models to predict lay or hatch date; all models included box ID as a random factor and had different combinations of climate factors. We concentrate on the hatch date analyses, as this measure of phenology integrates the entire response period (lay and hatch dates are also strongly correlated within both sites: $r = 0.88$ and 0.93 for CF and LL, respectively). We included models that had both linear and quadratic precipitation effects, as a unimodal or saturating response to precipitation seemed likely. Support for each model was judged using AICc and AICc weights.

To gauge the explanatory power of the fixed effects in our climate-driven models, we compared the marginal r^2 value (r^2_{marginal}) from the best supported climate-driven models with r^2_{marginal} from a model with box ID as a random effect and year as a categorical factor. r^2_{marginal} from these latter models indicates the maximum explanatory power of inter-year differences, so serves as a benchmark of the predictive power offered by the best-supported climate models. We also used these models to conduct Tukey post hoc comparisons to look for significant outlier years for hatch dates.

To examine whether short-term climate variability influences the day of clutch initiation, we fit Cox proportional hazard

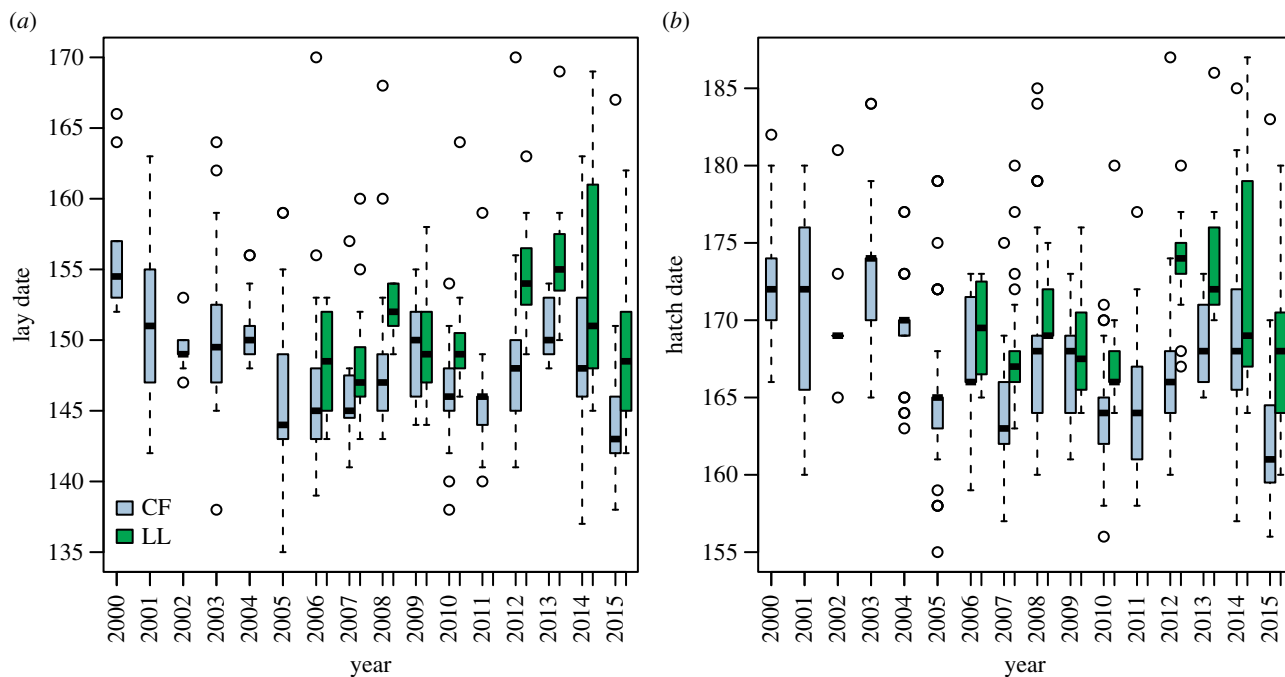


Figure 1. (a,b) Temporal patterns in hatch and lay dates at each study site. Box plots show the distributions of individual nest phenology at each site in each year. Mixed models including continuous year effects and box as a random factor show highly significant advances over time in lay ($p > 10^{-5}$) and hatch ($p < 10^{-13}$) dates at CF. At LL, lay dates have become significantly ($p = 0.00125$) and hatch dates marginally ($p = 0.060$) later through time. However, in all cases the inter-annual variability in phenology is more striking than these directional trends.

models to lay dates. Each model included a categorical year effect (to control for changing mean lay dates across years) and one of the five climate factors, using data from the 2nd to 7th day before each day at which laying could have been initiated (see [54] for rationale for 2-day delay in response). Use of 10 versus 5 day climate periods or periods with lesser or greater lags between climate and each day's lay/non-lay state did not change the qualitative results. In these models, each day from the earliest nest initiation for a site to the start of laying was included for a nest: days prior to first laying take the place of survival in a typical hazard model, while laying is equivalent to death. To show the effects of each climate variable on laying probability, we present $100 \times (\text{hazard ratio} - 1)$, with the hazard ratio calculated for the 80th and 20th percentile values of a climate variable. We also fit hazard models including year, lay date and climate to hatch dates, but no climate effects were significant in these models.

In order to compare relationships between phenology and climate variables at the two sites, and because of the different sampling durations, we conducted all analyses separately for CF and LL. All analyses were run in R [55]. Mixed models were fit using the lme4 package [56] and Cox models were fit in the survival package [57]. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

3. Results

We found strong support for advancing breeding phenology at CF (figure 1), with mean hatch date changing at -0.40 d yr^{-1} (table 1, $p < 10^{-13}$) and mean lay date changing at -0.24 d yr^{-1} ($p > 10^{-5}$), resulting in a 6-day and 4-day advancement, respectively, over the 16 year study. Though highly significant, the explanatory power of these trends was low for lay date ($r^2_{\text{marginal}} = 0.047$) and somewhat higher for hatch date ($r^2_{\text{marginal}} = 0.105$). The more rapid advancement of hatch dates is due to a decrease in average time between lay and hatch date during the study period (electronic supplementary material, figure S1). Advancing

phenology largely occurred between 2000 and 2005, with little evidence of directional change after 2005 (figure 1). At LL, where monitoring started in 2006, both hatch (table 1; $p = 0.060$) and lay ($p = 0.00125$) dates became later on average over the study period (figure 1), but in both cases with very low explanatory power ($r^2_{\text{marginal}} = 0.022$ and 0.062 , respectively). Hatch dates at LL varied synchronously with those at the CF site (figure 1; correlation between annual mean hatch dates across sites = 0.62), suggesting similar responses of swallows at both populations to annual climate variation.

All climate metrics showed substantial annual variation at both sites (figures 2 and 3). However, only windiness showed significant trends, declining over time at both sites ($p = 0.006$ and 0.008 at CF and LL, respectively). Average May temperature showed a non-significant increase at both sites, while trends in precipitation differed between sites. At neither site were temperature, windiness, or precipitation strongly correlated across time (electronic supplementary material, table S1).

The best-supported climate model for hatch date at CF (AICc wt = 0.57) included a negative effect of mean temperature, a positive effect of mean wind speed, and both linear and quadratic terms for precipitation days (table 1, figure 2). This model explained almost as much variation as the categorical year-effect model (climate $r^2_{\text{marginal}} = 0.25$; categorical year effect $r^2_{\text{marginal}} = 0.28$). The second best supported climate model retained wind speed and temperature, but included total precipitation rather than precipitation days. Across all models, variables with the strongest support included mean wind speed (summed AICc wt = 1.00) and the two precipitation variables (total precipitation AICc wt = 0.28 and precipitation days AICc wt = 0.72, for a total summed AICc wt = 1.00), and somewhat less support for temperature (summed AICc wts = 0.85; table 1 and electronic supplementary material, table S2). Partial coefficients of determination calculated from the best-supported model also indicate the

Table 1. Predictive models of hatch date. Linear mixed models of hatch date were run on year and on multiple combinations of climate variables. All models included box as a random effect. Here, we show the results from models including year as a continuous (with slope coefficient shown) or categorical effect (both shown in italics), and for the best supported climate models for each study site (all models with AICc weights > 0.05). Full climate model results are shown in electronic supplementary material, tables S2 and S3.

intercept	year	temp	ave wind	precip	precip ²	precip days	precip days ²	r^2_{marginal}	$r^2_{\text{conditional}}$	AICc	delta AICc	AICc weight
Greamer's Field:												
970.292	-0.3998							0.1050	0.1417	3128.07		
172.3902	<i>categorical</i>							0.2785	0.3101	3072.25		
151.7016		-0.3526	8.3907			-0.6300	0.0557	0.2457	0.2810	3051.55	0.0000	0.5741
151.6815		-0.4028	8.3115	-1.0983	0.3631			0.2340	0.2695	3053.20	1.6550	0.2510
143.9770			10.0376			-0.5895	0.0529	0.2356	0.2728	3054.61	3.0125	0.1273
Long Lake:												
-282.24	0.2248							0.02237	0.0224	942.06		
169.5003	<i>categorical</i>							0.2312	0.3912	897.49		
158.4984			6.6008			0.7492		0.1577	0.3979	916.61	0.0000	0.4571
164.9394		-0.3129	3.1688			0.6137		0.1602	0.4005	918.16	1.5484	0.2108

importance of windiness, with values of 0.054, 0.030, and 0.002 for wind, temperature, and precipitation, respectively.

We found very similar patterns of climate effects on hatch date at LL (table 1, figure 2). The best supported climate model (AICc wt = 0.46) included mean wind speed and the number of days with precipitation and had good fit (climate $r^2_{\text{marginal}} = 0.16$; categorical year effect $r^2_{\text{marginal}} = 0.23$). The second best model included these same factors and a negative effect of temperature. The summed AICc weights showed strongest support for wind (summed AICc wt of 0.86 for mean wind, and 0.91 for both wind variables) and precipitation (summed AICc wt of 0.84 for precipitation days and 0.97 for both precipitation variables) and markedly lower support for temperature (AICc wt = 0.38; electronic supplementary material, table S3). Partial coefficients of determination from the best-supported model indicate a greater importance of precipitation than of wind, with values of 0.011 and 0.122 for wind and precipitation, respectively. Lay date models showed similar effects as seen for hatch dates, with wind and precipitation having consistently strong effects; temperature also shows comparably strong effects at CF though not at LL (electronic supplementary material, tables S4 and S5). While there is substantial interannual variation in both hatch and lay dates, post hoc comparisons of annual hatch and lay dates did not show evidence of marked outlier years (electronic supplementary material, table S6).

The correlation in mean annual hatch dates between the two sites (figure 1) is driven entirely by correlated climate trends, as residuals from the best supported climate models for each site are not correlated with one another ($r^2 < 0.05$). Additionally, there are substantial correlations between May climate at both sites and two regional climate indices, the PDO and ENSO (electronic supplementary material, table S1 and figure S2), suggesting that regional climate variation drives the correlated phenology between the sites through its effects on local climate.

Daily probabilities of clutch initiation were strongly influenced by the weather immediately beforehand. Cox models show that at both sites higher temperatures in the preceding week led to greater likelihood of clutch initiation (figure 4), although this effect is likely due solely or in part to strong seasonal temperature trends: not surprisingly, temperature strongly increases over the range of possible lay dates at both sites ($p < 10^{-16}$ and 10^{-9} at LL and CF, respectively, from models including temperature and year effects). Windy conditions led to lower probabilities of clutch initiation at both sites and higher precipitation inhibited laying at LL but increased it at CF. In contrast to temperature, the effects of wind and precipitation are likely to reflect responses to short-term climate events. At LL, windy days increase over the laying period ($p = 0.007$) but windiness, precipitation and precipitation days did not trend significantly. At CF, both windiness and windy days declined over the lay period ($p = 0.0003$ and 0.017 , respectively), while precipitation increased ($p = 0.0017$) and precipitation days showed no trend. These same effects were seen when using other sets of days preceding possible lay dates (e.g. electronic supplementary material, figure S4).

4. Discussion

At CF, where our data extend back to 2000, we find substantial directional trends in phenology over time (figure 1,

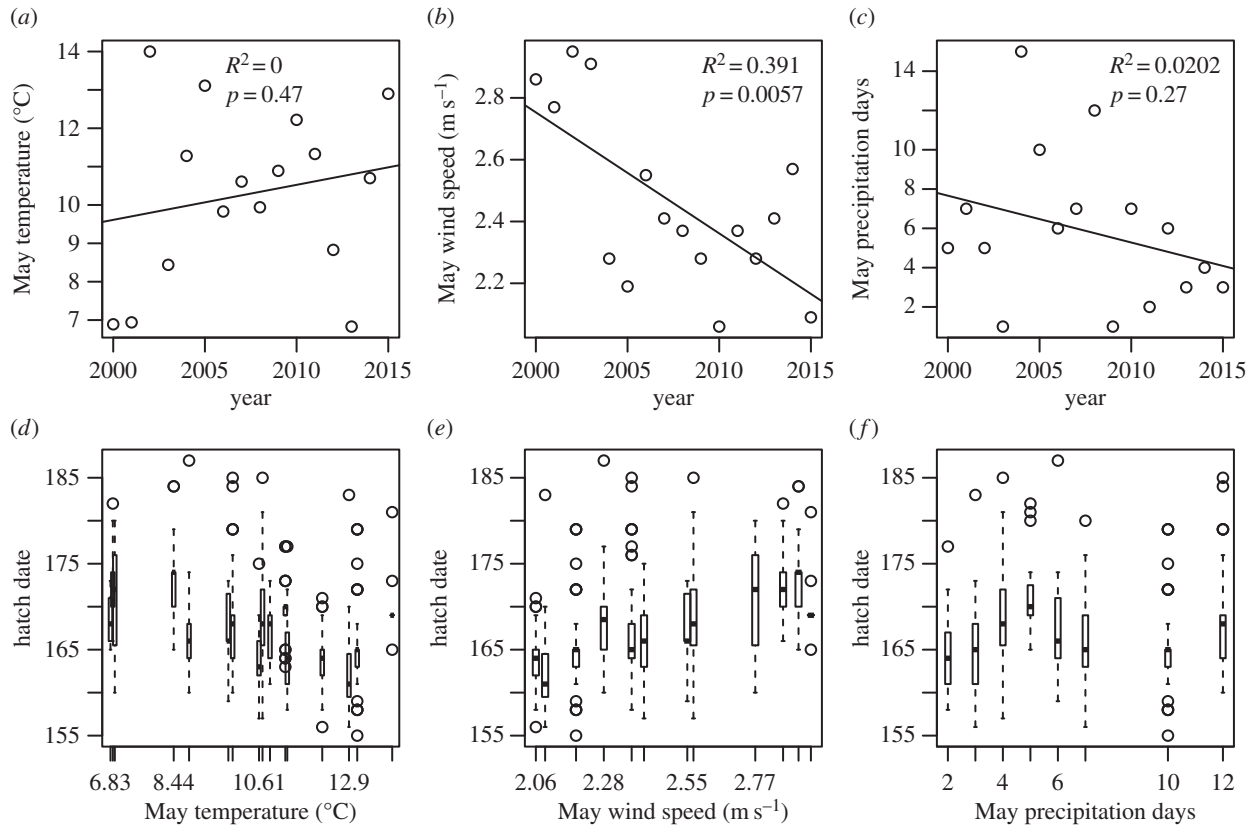


Figure 2. Multiple aspects of climate vary across years at the CF site, and these have had substantial effects on swallow hatch dates. While spring temperature and precipitation show substantial variation, only windiness has shown a significant trend over the study years, with declines through time (upper row of figures show adjusted r^2 value and significance values from linear regressions of each May climate variable against year). All three aspects of climate show relationships with hatch date (table 1): higher temperatures, as expected, result in earlier phenology, while declining windiness and precipitation also lead to earlier hatch dates.

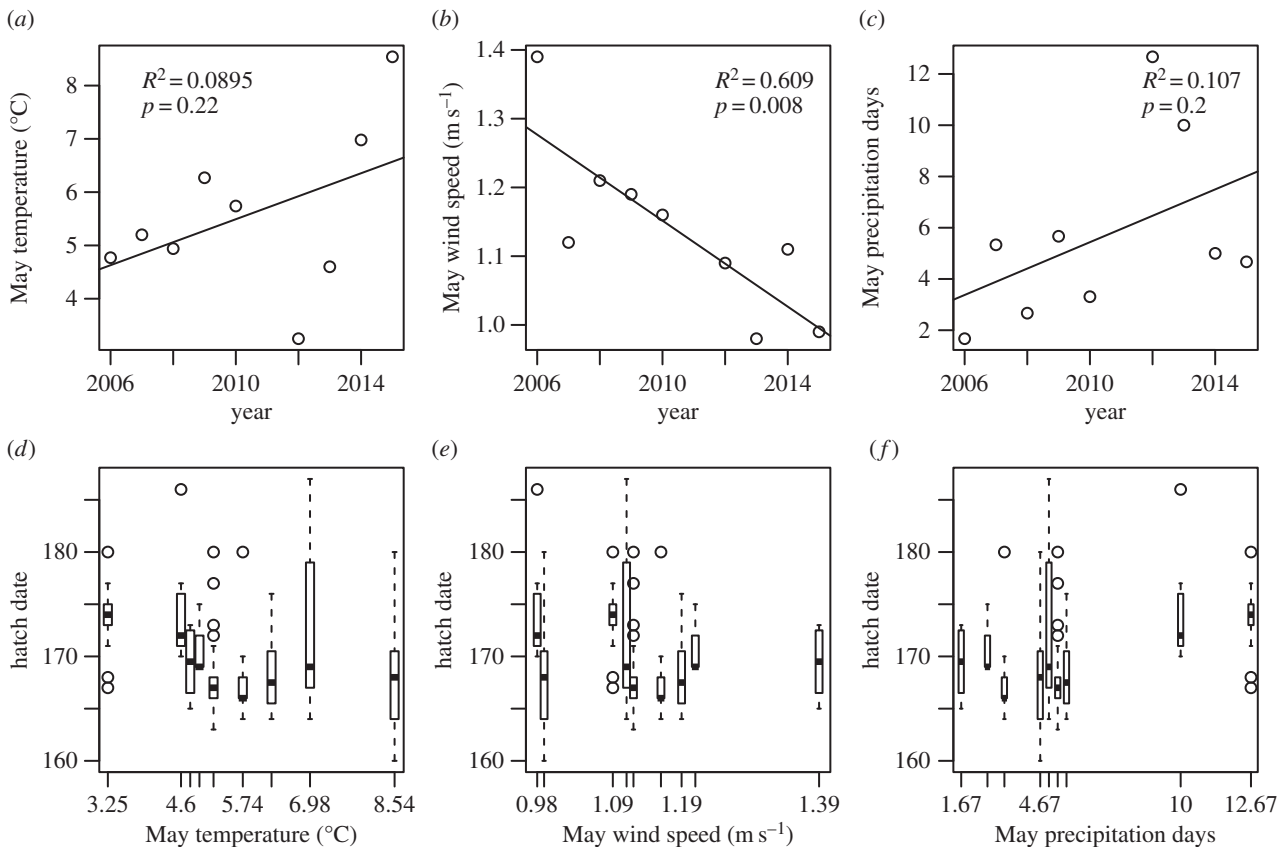


Figure 3. At the LL site, windiness has declined through time, with no other significant trends in May climate. All three aspects of climate show relationships with hatch date (table 1): higher temperatures and declining windiness result in earlier phenology, while higher precipitation tends to delay hatch dates. Statistics shown for climate trends are from linear regressions of annual May climate values on year.

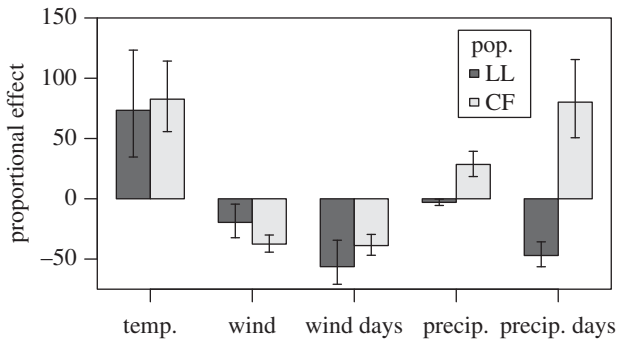


Figure 4. Cox proportional hazards models show strong effects of short-term weather on the probability of clutch initiation. Proportional effect is the change in probability of first laying (clutch initiation) on a given day, if the climate from 2 to 7 days preceding that date went from the 20th to the 80th percentile value for a given climate variable.

table 1). The rate of change for lay date we document is over twice the rate of 0.15 d yr^{-1} found in a comparable study of tree swallows across the continental United States and Southern Canada [34], and is consistent with the generally greater speed of climate change at northerly areas [36,44]. As also documented by Dunn and Winkler [34] in more southern latitudes, we found highly variable advancement over time. In addition, we see no clear trend in phenology over the last decade (figure 1). The shorter dataset from LL did not show earlier phenology over time, but the interannual variation in phenology matched that seen at CF, and this variation was well explained by annual differences in local climate at both sites, which is in turn correlated with regional climate indices.

More broadly, we find that local breeding site climate is an important factor in tree swallow phenology, explaining most of the observed annual variation in mean hatch dates between years, and operating both at the level of overall spring climate and in the days just prior to clutch initiation. However, temperature does not appear to be the sole or even primary driver of these shifts. At both sites, windiness and precipitation had stronger effects than temperature in explaining annual differences in hatch date, and models of both hatch and lay dates supported effects of these drivers more consistently than they did temperature. Furthermore, while temperature and precipitation show considerable annual variation, the only spring climate variables that showed significant trends over time during our study were measures of windiness. Thus, the long-term trends in hatch dates that we document at CF appear to be most strongly driven by declining wind, rather than by more usually assumed temperature effects. This ranking of effects is also likely to be a long-term one: there is a consistent 36-year decline in May windiness in Fairbanks ($p < 0.001$; electronic supplementary material, figure S3), while May precipitation has shown a weak declining trend ($p = 0.06$), and there has been no significant trend in May temperature ($p = 0.40$).

Dunn and Winkler [34] found a stronger effect of temperature on laying date ($r^2 = 0.75$) than we find in a comparable regression of mean annual values from CF ($r^2 = 0.37$), suggesting that the ranking of different effects on phenology may differ between regions. This is not surprising, as climate factors may differentially limit a species' ability to forage or perform other functions at the edge versus in the centre of its range [58]. In addition, the much longer migration route to

Alaskan breeding sites may play a larger role in driving phenology of the Alaska birds than they do for populations breeding at lower latitudes, making effects of breeding site climate less powerful. The correlation of climate at both our sites with both PDO and ENSO indices emphasizes that some effects of climate variation are widespread and could also influence birds on the way to breeding sites. However, our Cox hazard models also support the strength of local, immediate climate effects on breeding phenology, with weather conditions in the few days preceding laying having strong effects on clutch initiation. This result is not surprising, as birds are known to have the physiological ability to alter reproductive physiology over short timescales [54].

The mechanisms behind temperature, wind, and precipitation effects on breeding phenology of birds are not fully understood, and in many systems they may covary too strongly to fully untangle the effects of each. Ecologists have speculated that increasing temperatures, by advancing plant and insect phenology, will trigger advanced breeding by birds, due to earlier availability of prey [5,6,9,11,20,23,27]. Conversely, we speculate that wind and rain will either slow prey maturation or will hinder the ability of our aerially foraging study species to harvest food or maintain egg or nestling temperatures, slowing their breeding cycle (see also, [10]). In a study of tree swallows in California, Rose [50] found that average daily wind speed had a significant negative effect on the rate that adult tree swallows fed their young. Wet, cold, and windy conditions have also been seen to cause delays in egg laying and incubation in other tree swallow populations [48,49] as well as in other birds ([8,10], but see [7]). These studies, plus the concordance of climate effects at our two study sites, suggests that the effect of wind observed in this study is not spurious, but reflects an important aspect of climate for this species that is rarely considered in analyses of climate change. While the importance of windiness for an aerially hunting predator is not surprising, this result more broadly emphasizes the need to consider the natural history of a species when forming hypotheses about the most important routes by which climate change will influence phenology or other aspects of population ecology.

The ecological effects of climate change have received much attention in recent years, and numerous studies have been conducted to determine its effects on various species around the world. Fewer studies, however, have examined the effects of different aspects of climate, or looked at such a widely dispersed species as tree swallows. Our work shows the phenology of tree swallows in Alaska's subarctic regions has advanced rapidly in the past and that this effect is influenced more strongly by declines in windiness and precipitation than by increasing spring temperatures. In other areas, increases in inclement conditions have been shown to influence phenology in the opposite direction [10]. The specifics of when and how climate conditions will alter breeding phenology will depend both on how climate changes and the specific sensitivities of a species to the direct and indirect effects of different climate factors. Our results show that in future work, ecologists need to consider a broader range of climate variables in order to form more accurate and complete predictions of species' responses.

Data accessibility. Data used in analyses reported here are included in a single workbook in the electronic supplementary material of this article. These data include:

- hatch and lay dates and May climate summaries used in all analyses;
- annual climate data used in analyses, including Pacific Decadal Oscillation and the Multivariate El Niño–Southern Oscillation Index values; and
- climate summaries used in Cox models for daily probability of clutch initiation.

Authors' contributions. R.D.I. and D.F.D. carried out all data analyses, produced the figures and wrote the manuscript; A.P.R. collected all data at the LL site; J.C.H., A.H.S. and T.B. supervised and carried out data collection at the CF site. All authors edited the manuscript and gave final approval for publication.

Competing interests. We declare we have no competing interests.

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