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Shifting correlations among multiple aspects of weather complicate predicting future demography of a threatened species

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Abstract. Most studies of the ecological effects of climate change consider only a limited number of weather drivers that could affect populations, though we know that multiple weather drivers can simultaneously affect population growth rate. Multiple drivers could simultaneously increase/decrease one vital rate, or one may increase a vital rate while another decreases the same vital rate. Considering the impact of multiple weather drivers on vital rates is particularly important in a changing climate, in which correlations among drivers may not be preserved in the future. We used a long-term dataset on the endangered red-cockaded woodpecker (*Dryobates borealis*) to understand how multiple weather drivers jointly affect survival and reproductive vital rates and then assessed the contributions of individual weather drivers to historical trends in vital rates over time. We found that vital rates were often influenced by more than one weather driver and that weather drivers most commonly exerted opposing effects. For instance, some weather drivers increased vital rates over time, while others acted in the opposite direction, decreasing vital rates over time. Importantly, the historical correlations among weather drivers are almost always projected to change in the future climate, such that future trends in vital rates may not match historical trends. For example, we do not find historical trends in adult survival, but changing correlations among weather drivers could generate future trends in this vital rate. Our work provides an example of how multiple weather drivers can control a variety of vital rates and also illustrates how changes in the correlation structure of weather drivers through time might substantially affect future trends in individual and population performance.

Key words: climate change; correlation; directional trend; vital rate; weather.

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INTRODUCTION

In the face of rapid climate change, ecologists are now widely engaged in the task of identifying the components of weather that drive species' population dynamics in order to project how climate change will alter the distribution and abundance of those species. This is a challenging task, because many weather variables (e.g., mean temperature, maximum temperature, total annual precipitation, growing season precipitation, and wind speed) can affect populations (van de Pol et al. 2016). In particular, more than one weather variable may independently influence each vital rate (including survival, reproduction, and recruitment), all of which contribute to composite metrics of performance such as population growth rate and extinction risk. Studies that have tested for the simultaneous effects of multiple weather variables commonly find that vital rates can be controlled by multiple weather variables (e.g., Doak and Morris 2010, Dalgleish et al. 2011, Peery et al. 2012), though most studies consider only one or two weather drivers at a time (van de Pol et al. 2016).

If multiple weather drivers affect a single vital rate and adaptation to changing climate trends is minimal or slow (as has been shown by Quintero and Wiens 2013), then past trends in all of those drivers, perhaps resulting from climate change, have affected trends in vital rates. Trends in weather drivers could have worked either in concert with one another, or in opposition to one another, with respect to trends in the vital rate (similar to the demographic effects of single weather drivers that affect multiple vital rates; e.g., Doak and Morris 2010, Nicolè et al. 2011). For example, if temperature and precipitation both decrease survival, and both temperature and precipitation have increased over time, survival should also have declined. In contrast, if temperature has increased but precipitation has decreased, survival may have shown little change over time, depending on the relative strength of temperature and precipitation effects on survival and the temporal trends in temperature and precipitation. In order to assess the role of weather in past vital rate changes when multiple weather drivers influence a single vital rate, we need to know both the strength of the relationship between the vital rate and each weather driver and the direction and magnitude of past change in each weather driver. While a variety of studies have quantified trends in vital rates over time (e.g., Parmesan and Yohe 2003, McMahon et al. 2010, Garcia 2014, see also Dunne et al. 2004), most only look for effects of one weather driver at a time (van de Pol et al. 2016), limiting our ability to quantify effects of multiple weather drivers.

Yet another complication is that past trends in multiple weather drivers affecting one vital rate may not continue into the future, with important consequences for future vital rates. If weather drivers that have trended in opposite directions in the past, buffering a vital rate against change, begin to trend in concert in the future, this new positive correlation between the drivers could cause a vital rate to suddenly decline, possibly leading to extinction (although sudden increases in a vital rate are also possible). For example, the negative correlation between annual temperature and precipitation has intensified under recent climate change, resulting in a doubling of the likelihood of 100-yr hot–dry event in some areas (Kong et al. 2020). Empirical work suggests that changes in the correlations among weather drivers are common and also shows that these changes make it difficult to predict effects of each weather driver alone when using observational data (Crimmins et al. 2011, McCain and Colwell 2011, Tingley et al. 2012). Thus, if we are to use observational data to project how vital rates, and thus population growth rates, are likely to change in the future, we need to know whether past trends in multiple weather drivers will continue and whether the correlations among weather drivers will change in a future climate.

In this work, we use a long-term dataset on survival and reproduction in the red-cockaded woodpecker (*Dryobates borealis*) to rigorously quantify the effect of multiple weather drivers on each vital rate that comprises population growth across multiple locations. *Dryobates borealis* is a flagship, umbrella species that drives conservation and management of millions of hectares of pine forest in the southeastern United States (Conner et al. 2001, USFWS 2003). Thus, the impact of climate change on its vital rates, and the possibility that opposing trends in weather might buffer those rates, is of great interest to managers. Garcia (2014) found positive effects of spring and summer temperatures, and both positive and negative effects of winter temperatures and spring rainfall, on reproductive vital rates in this species. However, Garcia did not consider weather effects on adult survival, which also contributes to population growth, or simultaneous effects of multiple weather drivers. Here, we examine more complex relationships between weather and all vital rates that contribute to population growth rate, including multiple simultaneous weather drivers and year-round weather conditions. We use the dataset to test three key hypotheses: (1) Temporal trends in vital rates are primarily attributable to changes in weather rather than other factors; (2) Temporal trends in weather drivers tend to act in opposition to influence trends in vital rates, rather than operating in the same direction; (3) Historical correlations between weather drivers will change in the future, and these changes have the potential to dampen or exacerbate trends in vital rates, suggesting that changing correlation structures might limit the predictive ability of models fit with observational data.

Materials and Methods

Dryobates borealis is a cavity-nesting bird that lives in cooperatively breeding, territorial family groups consisting of a breeding pair and 0–6 non-breeding adult helpers (Walters and Garcia 2016). In addition to breeders and helpers, adult (≥1 yr old) birds can also act as floaters (non-breeding adults not part of a group). The demographic data used in this analysis come from long-term studies at three locations, the Sandhills region in south-central North Carolina (1980–2015), Marine Corps Base Camp Lejeune on the central coast of North Carolina (1986–2015), and Eglin Air Force Base on the Gulf Coast in the western panhandle of Florida (1996–2015; hereafter, "Sandhills," "Lejeune", and "Eglin", respectively). Sandhills is the largest site, with 313 groups of birds monitored in 2017, whereas Lejeune and Eglin are smaller and had 115 and 39 monitored groups in 2017, respectively. The data collection methods are much the same at all three sites and are described in detail in Walters et al. (1988); briefly, we conducted complete sampling of populations of marked birds at each site via annual observations of the populations during each breeding season (May–June, Appendix S1). Locating and monitoring all of the groups in a study area are facilitated by the long-term stability of the territories and conspicuous cavity trees. Reproductive vital rates are assessed by visiting territories in March and early April; occupied territories are then visited every 7–9 d from April to mid-July to check for nesting activity (using a camera mounted on a telescoping pole). Most birds are banded as nestlings, and fledglings per brood are determined by following groups after the expected fledging date. Adult survival and status ("breeders" are breeding adults affiliated with a territory, "helpers" are non-breeding adults that are members of a group, and "floaters" are non-breeding adults that do not belong to a group) are assessed using nesting checks, group follows, and evening visits. Detection probability is very high, so birds not seen in a given year were assumed to have died, unless they were seen in subsequent years (a small fraction, 30 birds out of 18,455, were resighted after having gone missing one or more years). See Appendix S1 for more details.

We synthesized the demographic data into 11 response variables. We focus here on the four we found to depend on weather: annual adult survival (including data from both males and females), survival from fledging to the following breeding season (including data from both males and females, hereafter, "fledgling survival"), probability of a female breeder attempting a first nest, and number of eggs in first nest (given a first nest was attempted and successful; hereafter, clutch size). We present data and results on the weather-independent vital rates in Appendix S1. Appendix S1: Table S1 shows sample sizes for each vital rate.

Non-weather drivers of vital rates

To obtain functional forms for vital rates, we used Akaike's information criterion corrected for sample size (AIC$_c$; Hurvich and Tsai 1989) to select a best-fit generalized linear model for each vital rate, comparing the fit of a global model to all possible subsets of this global model. For the adult survival model, our global model included site (categorical: Eglin, Sandhills, or Lejeune), number of non-breeders in a group (hereafter "group size"), status, age, age squared (reflecting senescence, Conner et al. 2001), and sex (Walters 1990, Conner & Walters 2002, Khan and Walters 2002, Walters and Garcia 2016). For fledgling survival, our global model only included site and sex (Walters 1990); we exclude group size and maternal and paternal age because they have minimal effects on fledgling survival (Appendix S1). For reproductive vital rates, our global model included site, maternal age, paternal age, maternal age squared, paternal age squared (both squared terms reflecting senescence), and group size (Walters 1990, Walters 2001, Walters and Garcia 2016). In all models, we included site to control for systematic differences among sites, such as habitat quality (models did not consistently converge when using site or individual-level random effects). All vital rates were fit with the glm function in R (version 3.3.2, R Core Team 2016), using binomial errors for all models except clutch size, which was fit with Poisson errors (Appendix S1: Table S2). We did not use a "hurdle" model as we wanted to dissect effects of weather on the component vital rates; see Appendix S1. Hereafter, "significant" indicates $P \leq 0.05$.

Weather drivers of vital rates

We used the best-fit model lacking weather drivers for each vital rate as a baseline model to look for additional weather effects. We obtained observed daily weather data (daily maximum and minimum temperatures, precipitation, and mean wind velocity 10 m above the ground surface, hereafter "windspeed") over the period 1979–2016 at a resolution of 4 km^2 from the GRIDMET dataset (Abatzoglou 2013; Appendix S1). We calculated daily mean temperatures as the average of the maximum and minimum daily temperatures. We assumed that all individuals occupying each territory experienced the same weather as the 4 km^2 weather grid cell overlaying the territory center.

We then used the R package climwin (Bailey and van de Pol 2016, van de Pol et al. 2016) to identify which of the 5 weather variables impacted each vital rate, and over which time period(s). Briefly, climwin allows users to test for the effect of weather conditions over a wide range of time periods using a sliding window approach and rigorously controls for Type I and II errors (Bailey and van de Pol 2016, van de Pol et al. 2016). Our analyses assumed that both the census occurred and the breeding season began on May 1. We used a sliding window at a weekly time scale, considering all possible combinations of consecutive weeks between breeding seasons (for survival), or for the 365 d prior to the initiation of the breeding season (for reproductive rates). We quantified linear effects of the weekly mean of temperature and windspeed variables and of weekly cumulative precipitation over a given interval. Note that we did not allow for quadratic effects of weather variables, as preliminary analyses suggested a linear effect was sufficient. Consistent with the approach outlined by Bailey and van de Pol (2016) and van de Pol et al. (2016), we conducted randomization tests and cross-validation to ensure that support for our weather signals was not due to overfitting (Appendix S1). Throughout this manuscript, "weather variable" denotes a distinct aspect of weather (mean temperature, maximum temperature, minimum temperature, windspeed, or precipitation), "weather window" denotes a distinct time period that varies in duration and timing, and "weather signal" indicates a specific weather variable and window combination present in the best-fit model for a vital rate.

We then assessed support for including multiple weather signals in the best-fit model for a vital rate. First, for each weather variable individually, we ensured that adding additional windows to our best-fit weather model did not improve fit (Appendix S1). Next, we combined variables that were present in the baseline model (site, group size, age, etc.) with the best window (s) for each weather variable into one global model (McLean et al. 2018). For example, if the best-fit adult survival model included both mean temperature January 1–7, mean temperature February 1–7, and precipitation March 1–7, and had site and group size in the baseline model, the global model would be: Prob. of adult survival ~ site + group size + January 1–7 mean temperature + February 1–7 mean temperature + March 1–7 precipitation. We then used model selection to determine which of the weather signals present in the full model should be retained (always including non-weather baseline effects) and used the subsequent best-fit model in our results. If weather variables were collinear ($r > 0.6$), we always kept them in the same models when testing various combinations of weather variables (recommended by Freckleton 2010, McLean et al. 2018, Appendix S1). This approach results in unbiased parameter estimates and also allows the effects of correlated (and thus indistinguishable) weather signals to be measured together so that their effects can be compared with other weather signals or correlated sets of weather signals. Our analytical approach is outlined in Appendix S1: Fig. S1.

Changes in vital rates and weather drivers over time

We then assessed how changes in weather signals over time contributed to changes in vital rates over time. To estimate temporal trends in vital rates, we obtained annual values for each weather-dependent vital rate at each site from the demographic data. For each site, we then regressed vital rates against year using general linear models and used the slope as an estimate of dv_i/dt where v_i is vital rate i and t is time (Appendix S1: Fig. S2). Similarly, we regressed site-specific weather signals against year to get dw_j/dt, where w_j is weather signal j present in the best-fit model for a particular vital rate (Appendix S1).

Contributions of weather signals to change in vital rates over time

According to the chain rule, the trend in vital rate i driven by trends in all weather signals is given by.

$$\frac{dv_i}{dt} \approx \sum \frac{\partial v_i}{\partial w_j}\frac{dw_j}{dt}$$

Each weather signal can contribute positively or negatively toward dv_i/dt, depending on the signs of $\partial v_i/\partial w_j$ and dw_j/dt, and weather signals can either act in the same direction if their contributions, $(\partial v_i/\partial w_j)(dw_j/dt)$, have the same sign, or in opposite directions if their contributions have different signs. Our summation assumes that the relationships between the vital rates and weather signals are linear and that weather signals change linearly over time (a reasonable assumption; Appendix S1: Fig. S2–S4).

To obtain the contribution of each weather signal to dv_i/dt, we calculated the site-specific analytical partial derivatives of the fitted vital rate functions with respect to each weather signal, $\partial v_i/\partial w_j$, evaluated at the mean site-specific values of all weather signals, and multiplied each by its associated dw_j/dt. We calculated the $\partial v_i/\partial w_j$s at the mean values of all non-weather continuous drivers, and in the case of categorical drivers, we took the weighted average of category-specific $\partial v_i/\partial w_j$ values. For example, if $\partial v_i/\partial w_j$ depended on status, we calculated a status-specific$\partial v_i/\partial w_j$, then took the weighted average of these $\partial v_i/\partial w_j$ values, where weights were the proportion of individuals of each status.

Correlations among historical and future weather signals

We assessed the correlations among historical (1980–2015) weather signals and among future (2016–2096) weather signals using, respectively, the METDATA dataset and a comparable suite of statistically downscaled global weather models (GCMs) based on the multivariate constructed analogue (or MACA; Abatzoglou 2013) approach (Appendix S1). We averaged the results from 19 downscaled GCMs for a realistic future scenario for the windspeed, temperature, and precipitation weather variables (Appendix S1: Table S3). We confined this analysis to vital rates with multiple weather signals in the best-fit model, because only changes in historical vs. future correlations among these weather signals had the potential to result in changes in historical vs. future vital rate trends.

Using the average of occupied weather grid cells at each year × site combination (for the future, grid cells occupied in 2015; Appendix S1), we then calculated the correlation between annual weather signals at each site, which accounts for both interannual variability and long-term trends in weather signals. To quantify whether correlations differed in historical vs. future weather conditions, we used Mantel tests to assess whether the correlations of weather signals controlling the three vital rates with multiple weather signals in the best-fit model (adult survival, hatchling survival, and probability of initiating a first nest) were significantly different in the historical vs. future weather data for each site separately. Finally, we used piecewise linear regression to ask whether the slope of a weather signal vs. time differed in current vs. future weather conditions.

RESULTS

We found support for including non-weather variables as predictors of vital rates (Table 1); all of our four weather-dependent vital rates had group characteristics, age, status, or other non-weather variables in the best-fit model. Reproductive performance usually increased with breeders' age, but we found evidence for reproductive senescence: both reproductive vital rates increased and then decreased with both male and female adult age (Table 1). Unsurprisingly,

Table 1. Best-fit vital rate functions for our four vital rates that include weather signals.

Predictor variable	Response variables Probability of attempting a first nest	Clutch size (first attempt)	Fledgling survival	Adult survival
Intercept	−16.99 (11.91)	**1.37 (0.11)**	**21.47 (3.38)**	−16 (9.78)
Group size	**0.27 (0.07)**		N/A	**0.0402 (0.0199)**
Maternal age	**2.47 (0.18)**	**0.19 (0.04)**	N/A	N/A
Maternal age^2	**−1.66 (0.16)**	**−0.12 (0.03)**	N/A	N/A
Site (EG)	**−0.58 (0.29)**		**0.24 (0.09)**	0.0747 (0.146)
Site (CL)	**−0.33 (0.14)**		**0.40 (0.05)**	**0.361 (0.0817)**
Age	N/A	N/A	N/A	**0.337 (0.0594)**
Age^2	N/A	N/A	N/A	**−0.417 (0.0468)**
Paternal age	**1.49 (0.16)**		N/A	N/A
Paternal age^2	**−1.27 (0.16)**		N/A	N/A
Sex (M)	N/A	N/A	**0.54 (0.03)**	**0.54 (0.0369)**
Status (floater)	N/A	N/A	N/A	**−0.67 (0.0757)**
Status (helper)	N/A	N/A	N/A	**−0.27 (0.0531)**
Max. temp.	**Max. temp February 27–April 23: 0.30 (0.08)**		*Max. temp. August 7–August 13: −0.04 (0.02)*	Max. temp. October 9–January 8: −0.048 (0.0445)
Min. temp.			**Min. temp. March 6–March 19: −0.03 (0.01)**	Min. temp. May 8– January 29: 0.0208 (0.0423)
Mean temp.	**Mean temp. February 27–April 23: −0.24 (0.10)**		Mean. temp. August 7–August 13: −0.002 (0.02)	*Mean temp. October 9 – January 8: 0.0911 (0.0535)*
Precip.	**Precip. January 6–January 29: 0.03 (0.01)**			**Precip. September 11–April 9: −0.00406 (0.000988)**
Windspeed	**Windspeed March 6–March 19: −0.26 (0.09)**	*Windspeed January 18–April 2: −0.05 (0.03)*	**Windspeed June 26–July 23: −0.15 (0.04)**	**Windspeed July 10–August 20: −0.2 (0.0541)**

Notes: For categorical variables, we indicate the coefficient for each categorical variable (note that the missing categorical variable's coefficient is estimated at zero), and for numeric variables, we indicate the magnitude of the coefficient. Standard errors are shown in parentheses. Bolded coefficients indicate significance at the $P \geq 0.05$ level, italics indicate marginally significant coefficients ($P \geq 0.1$). All non-weather numeric predictor variables are scaled, such that the magnitudes of the coefficients are comparable. Absence of a coefficient indicates that effect was not present in the best-fit vital rate model, and "N/A" indicates we did not test for that effect. While the weather effects are the same as those in Fig. 1, we show them in this table to facilitate comparison. Correlations among weather signals in the raw data used to fit these models are presented in Appendix S1: Table S5.

larger group size at a given territory was correlated with higher reproduction (Table 1). For both adults and fledglings, males had higher survival rates, and breeders had highest adult survival rates, followed by helpers, then floaters. Similar to reproductive rates, adult survival increased with group size, and we saw evidence for higher survival rates in older individuals but declining survival rates in very old individuals, suggesting senescence (see the positive linear, but negative quadratic, terms for age, Table 1).

We also found support for including weather signals in the best-fit models for vital rates (Fig. 1). High winter precipitation and spring windspeed were correlated with higher probability of initiating a first nest. Spring maximum and mean temperatures were positively and negatively correlated, respectively, with the probability of initiating a first nest. High winter and spring wind speeds were correlated with low clutch size of the first nest (January 18–April 2, Fig. 1). Fledgling survival was negatively correlated with warmer summer and spring temperatures and high summer winds. Temperature was correlated with adult survival rates, but different metrics of temperature had opposing correlations. Specifically, higher fall maximum temperatures were associated with lower adult survival, though higher mean and minimum temperatures over similar time periods were

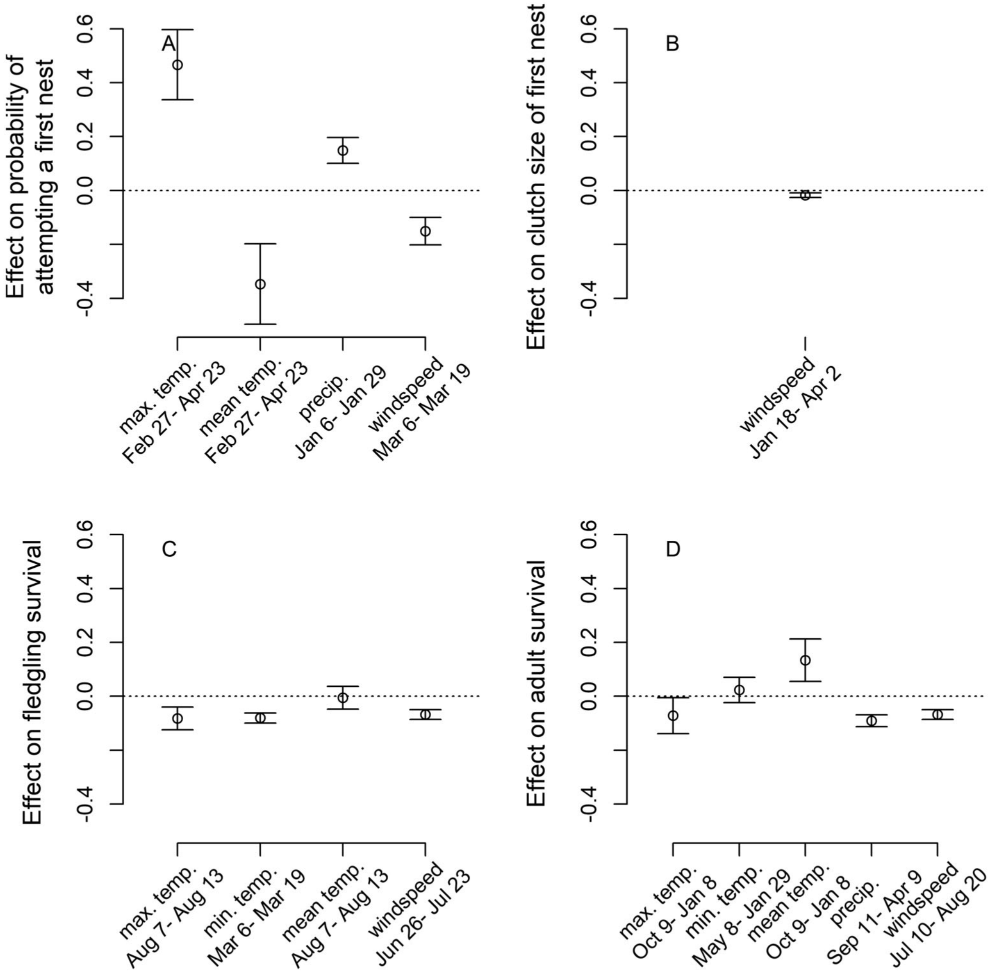


Fig. 1. Coefficients of weather signals in the best-fit model for each weather-driven vital rate. Bars indicate SE of coefficients. In order to render effect sizes of weather variables roughly comparable, we show here best-fit models using scaled weather signals. Temperature and windspeed values represent the mean of the indicated metric of daily temperature (mean, maximum, or minimum) or mean daily windspeed over the time period indicated; precipitation values represent the cumulative amount over the time period indicated. Plots of vital rates vs. weather signals are shown in Appendix S1: Fig. S5. Max. stands for maximum, temp. for temperature, precip. for precipitation, and min. for minimum.

associated with increased survival. High precipitation (over much of the year) and high summer wind speeds were correlated with low adult survival.

Across all vital rates, several patterns emerge. First, all weather variables were correlated with one or more vital rates, suggesting that all are important. Maximum temperature, mean temperature, and windspeed were correlated with the highest number of vital rates. Further, a variety of time periods were present in the best-fit models for vital rates. Both weather-dependent reproductive vital rates were correlated with conditions during spring and winter (Fig. 1), just before the breeding season, and fledgling survival was strongly correlated with spring and summer conditions, both just before the breeding season and during the time period of fledging. A variety of conditions throughout the year were present in the best-fit model for adult survival, with no one time period most commonly included in the best-fit model. Finally, we often see different signs of correlations for different temperature metrics, with both positive and negative correlations of maximum, minimum, and mean temperatures, with one vital rate, even over the same time periods.

A few weather-driven vital rates and weather signals showed significant trends over the course of the demographic study. The probability of initiating a first nest significantly increased over time at both Sandhills and Lejeune, and clutch size of the first nest increased significantly over time at Sandhills and Eglin, despite the fact that density was increasing at all sites. Fledgling survival also significantly increased over time at Eglin (Table 2). Though we did see significant shifts in some weather signals over time, for none of the weather-driven vital rates did the weather signal change significantly in the appropriate direction to account for the change in the vital rate over time (Table 2). For example, of the four weather signals that were correlated with the probability of initiating a first nest (Fig. 1), only January 6–29 precipitation changed significantly over time (at Sandhills and Lejuene; Table 2). However, because January 6–29 precipitation was positively correlated with the probability of initiating a first nest, the significant decrease in precipitation over this window actually acted to reduce the probability of initiating a first nest over time, rather than contributing to the significant positive trend (Table 2). This example illustrates that we cannot directly attribute significant shifts in weather-driven vital rates through time to significant shifts in the weather signals. We see similar effects for other significant trends in vital rates over time.

Table 2. Trends in weather-dependent vital rates and weather signals over time.

Response variable	Sandhills	Lejeune	Eglin
Vital rates			
Probability of initiating a first nest (PF)	0.0059*	0.0047*	−0.0044
Clutch size (CS)	0.0120*	0.0014	0.0360*
Fledgling survival (FS)	−0.0006	−0.0014	0.0101*
Adult survival (AS)	0.0003	0.0005	−0.0008
Weather signal			
Max. temp. February 27–April 23 (PF, +)	0.029	−0.016	−0.006
Mean temp. February 27–April 23 (PF, −)	0.032	−0.004	−0.001
Precip. January 6–January 29 (PF, +)	−0.021*	−0.040*	−0.043
Windspeed March 6–March 19 (PF, −)	0.008	−0.012	−0.006
Windspeed January 18–April 2 (CS, −)	0.007	−0.018	0.005
Max. temp. August 7–August 13 (FS, −)	0.025	0.042	0.054
Min. temp. March 6–March 19 (FS, −)	0.025	0.045	0.059
Mean temp. August 7–August 13 (FS, −)	0.019	0.034	0.042
Windspeed June 26–July 23 (FS, −)	0.005	0.0218*	0.002
Max. temp. October 9–January 8 (AS, −)	0.004	−0.018	0.013
Min. temp. May 8–January 29 (AS, +)	0.023*	−0.004	−0.029
Mean temp. October 9–January 8 (AS, +)	−0.001	−0.012	−0.021
Precip. September 11–April 9 (AS, −)	−0.321	0.272	−1.313
Windspeed July 10–August 20 (AS, −)	0.007	0.014	0.017

Notes: We show slopes of regressions of vital rates or weather signals against year; asterisks indicate significant ($P < 0.05$) relationships. Units are follows: temperature, °C/yr; precipitation, mm/yr; and windspeed, (m/s)/yr. For vital rates, we show the abbreviation of each vital rate after its name, and then for each weather signal, we show the name of the vital rate that was correlated with that weather signal and the direction of the correlation (+/−) in parentheses after the weather signal's name.

Trends in vital rates over time tended to be influenced by both weather signals operating in the direction of the overall temporal trend in a vital rate and by weather signals operating in the opposite direction (Fig. 2, note that few of the weather signals trended significantly through time; Table 2). For example, at Lejeune, non-significant trends over time in February 27–April 23 mean temperature and March 6–19 windspeed contributed to the increase in probability of initiating a first nest over time. By contrast, a non-significant trend in February 27–April 23 maximum temperature and a significant trend in January 6–29 precipitation acted in the opposite direction (Fig. 2), dampening the significant net positive trend in probability of initiating a first nest over time (Table 2). For only one vital rate, fledgling survival, multiple weather signals acted in concert in their influence on temporal trends in vital rates. Namely, at all sites, all weather signals acted to decrease fledgling survival over time, contributing to the negative non-significant trend in fledgling survival at Sandhills and Lejeune (but reducing the significant positive trend at Eglin; Fig. 2).

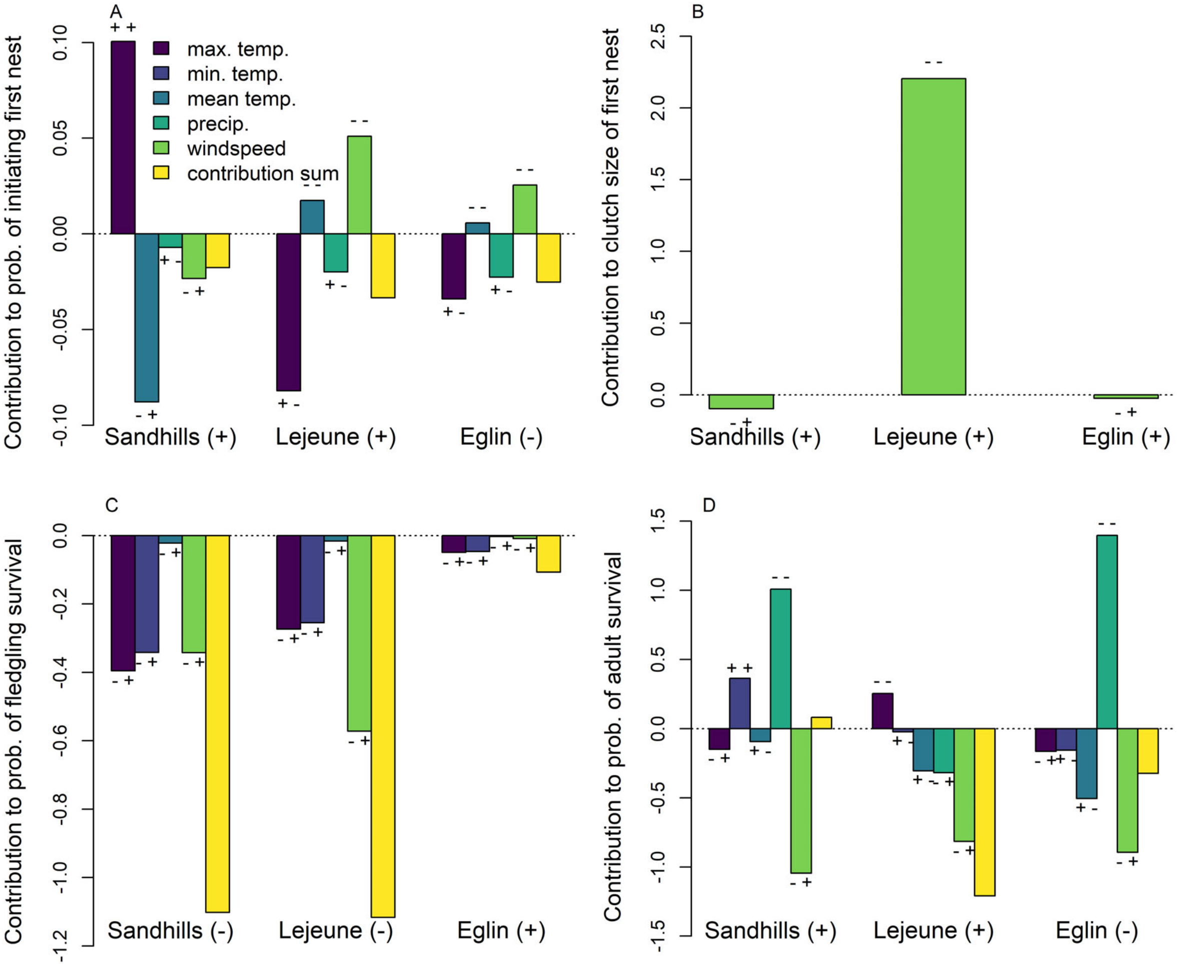


Fig. 2. Contributions of weather signals to changes in weather-dependent vital rates at the three sites. Namely, for each site we show vital rate contributions $((\partial v_i/\partial w_j)(dw_j/dt)$, the change in vital rate i with a change in weather signal j × the change in weather signal j over time) for each weather signal present in the best-fit model for that vital rate, and the sum of weather signals' contributions. Values are normalized by the absolute value of dv_i/dt (the change in empirical vital rates over time), with the sign of dv_i/dt shown in parentheses after the site name. Thus, if dv_i/dt is positive, a value of 1 indicates that a contribution or sum of contributions explains the entire effect, and if dv_i/dt is negative, a value of -1 indicates explanation of the entire effect. For singular contributions, the sign of the elements comprising each bar is shown just above or below each bar, $\partial v_i/\partial w_j$ first, then dw_j/dt. Note change in scale across panels. Prob. stands for probability, max. for maximum, temp. for temperature, precip. for precipitation, and min. for minimum.

Non-weather variables and/or weather signals not tested in this study often contributed substantially to trends in vital rates over time. At Sandhills, for example, three weather signals acted to reduce the overall significant increase in probability of initiating a first nest through time (see negative contributions in Fig. 2). These effects were counterbalanced by positive contributions of February 27–April 23 maximum temperature and apparently, strong positive contributions from other factors not included in this study (not shown in Fig. 2). For all site × vital rate combinations, we saw similar effects: The contribution of weather variables never sums to unity (Fig. 2, contributions of 1 or −1 indicate explanation of the entire dv_i/dt). Supporting the importance of the contribution of other factors to trends in vital rates over time, we found that the correlation between $\sum_j \frac{\partial v_i}{\partial w_j}\frac{dw_j}{dt}$ (predicted change in a vital rate over time based only on weather signals) and dv_i/dt (true, observed change in a vital rate over time) was quite poor (correlation = −0.23 across all vital rates and sites).

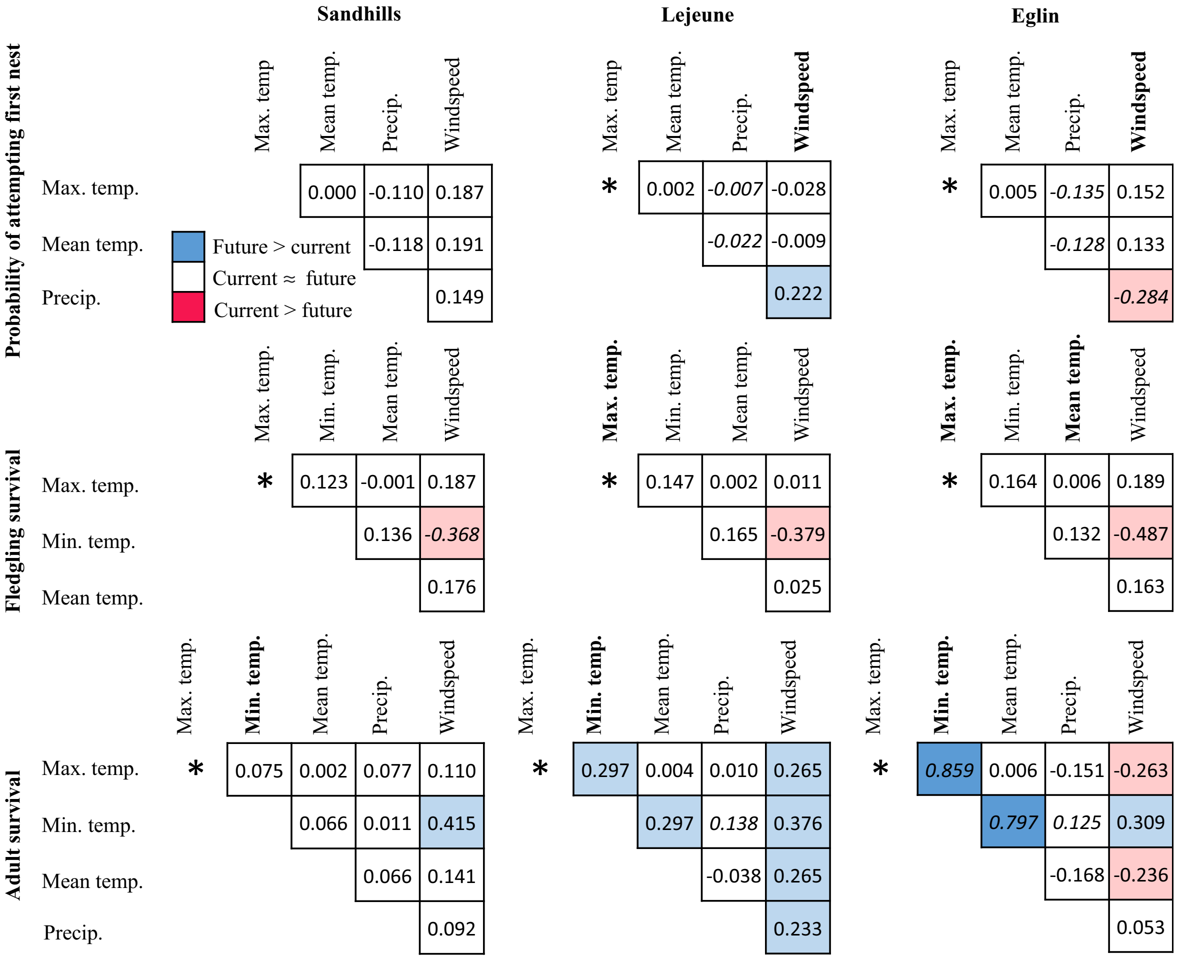
The correlation structure for the historical weather signals differed from that for the future weather signals across almost all site × vital rate combinations, suggesting that future trends in vital rates might not mirror historical trends. Correlations among historical weather signals were almost always significantly different than the correlations among future weather signals; 8 of the 9 correlation matrices for the vital rate × site combinations that we were able to test were significantly different (Mantel tests, Appendix S1: Table S4; only the probability of initiating a first nest at Eglin was not significantly different). Some differences between historical and future correlations were drastic. For example, the correlation among historical weather signals changed sign in the future projections in 4 of 30 correlations for adult survival, 5 of 18 correlations for probability of initiating a first nest, and 1 of 18 correlations for fledgling survival. More subtle changes in historical vs. future weather signal correlations were also present: the slopes of many weather signals against time were significantly different under historical vs. future weather conditions (8 of 39 weather signals, roughly equally arrayed across vital rates; Fig. 3). The changes in correlation structures were not always consistent across sites, with probability of initiating a first nest and adult survival showing substantial differences in the change in correlation matrices across sites (Fig. 3). Predicting vital rates using models fit with these historical data assumes that correlations among weather signals are the same in the historical data as in the data used for prediction, suggesting that predictions of future vital rates will be inaccurate.

DISCUSSION

Multiple weather signals over multiple seasons, including temperature, precipitation, and windspeed, were correlated with both survival and reproductive rates of the threatened red-cockaded woodpecker. Future changes in correlations among weather signals will have important implications for future weather-generated trends in vital rates, with substantial variability in future weather impacts across sites. Reflecting these differences, over the historical period, multiple weather signals rarely operated in the same direction in terms of their effects on vital rates over time. Effects of weather signals also varied with site over the historical period. Overall, trends in vital rates over time could not be explained by directional shifts in the underlying weather controls on these vital rates that we uncovered, but rather must have been due to other factors, either non-weather drivers or weather signals not tested in this study.

Both survival and reproductive rates were correlated with weather signals. The vital rates for which we had the most data (i.e., survival rates, probability of initiating, and clutch size of first nest, Appendix S1: Table S1), conveying the most power to detect a weather signal, tended to be correlated with weather. Consistent with other studies showing strong effects of weather (Robinson et al. 2007, Cox et al. 2014), specifically drought (Yackel Adams et al. 2006), on post-fledging survival in other bird species, we found negative correlations between spring/summer temperatures and fledgling survival (Fig. 1). Similarly, consistent with previous work finding that winter temperatures often affect survival in birds (Altwegg et al. 2006, Oro et al. 2010), we found that winter temperatures were positively correlated with adult survival, perhaps via direct negative effects of colder temperatures on physiology. Negative correlations between fall/winter precipitation and adult survival (as found in Salewski et al. 2013) may arise because excessively wet winter conditions decrease food availability. The causes of other correlations are unknown.

Overall, our finding that windspeed was correlated with many vital rates was surprising. We initially hypothesized that high winds could destroy cavity trees, resulting in correlations between windspeed and probability of initiating nests or success of nests (both of which might be affected by loss of cavity trees). There was a negative correlation between windspeed and probability of initiating a first nest, which may indeed reflect the loss of cavity trees. However, our findings of correlations between windspeed and



Probability of attempting first nest

Sandhills

	Max. temp	Mean temp.	Precip.	Windspeed
Max. temp.		0.000	-0.110	0.187
Mean temp.			-0.118	0.191
Precip.				0.149

🟦 Future > current
☐ Current ≈ future
🟥 Current > future

Lejeune

	Max. temp	Mean temp.	Precip.	**Windspeed**
Max. temp.	*	0.002	*-0.007*	-0.028
Mean temp.			*-0.022*	-0.009
Precip.				0.222

Eglin

	Max. temp	Mean temp.	Precip.	**Windspeed**
Max. temp.	*	0.005	*-0.135*	0.152
Mean temp.			*-0.128*	0.133
Precip.				*-0.284*

Fledgling survival

Sandhills

	Max. temp.	Min. temp.	Mean temp.	Windspeed
Max. temp.	*	0.123	-0.001	0.187
Min. temp.			0.136	*-0.368*
Mean temp.				0.176

Lejeune

	Max. temp.	Min. temp.	Mean temp.	Windspeed
Max. temp.	*	0.147	0.002	0.011
Min. temp.			0.165	-0.379
Mean temp.				0.025

Eglin

	Max. temp.	Min. temp.	**Mean temp.**	Windspeed
Max. temp.	*	0.164	0.006	0.189
Min. temp.			0.132	-0.487
Mean temp.				0.163

Adult survival

Sandhills

	Max. temp.	**Min. temp.**	Mean temp.	Precip.	Windspeed
Max. temp.	*	0.075	0.002	0.077	0.110
Min. temp.			0.066	0.011	0.415
Mean temp.				0.066	0.141
Precip.					0.092

Lejeune

	Max. temp.	**Min. temp.**	Mean temp.	Precip.	Windspeed
Max. temp.	*	0.297	0.004	0.010	0.265
Min. temp.			0.297	*0.138*	0.376
Mean temp.				-0.038	0.265
Precip.					0.233

Eglin

	Max. temp.	**Min. temp.**	Mean temp.	Precip.	Windspeed
Max. temp.	*	*0.859*	0.006	-0.151	-0.263
Min. temp.			*0.797*	*0.125*	0.309
Mean temp.				-0.168	-0.236
Precip.					0.053

Fig. 3. Comparison of historical (1980–2015) vs. future (2016–2096) weather signal correlations involved in each of the three weather-driven vital rates controlled by multiple weather signals. Values show the difference between future and current correlations among the weather signals, coded by color; italics indicate that the correlation changes sign. Weather signals listed in bold indicate that dw_j/dt was significantly different in a future climate ($P < 0.05$). Asterisks indicate a significant difference between the correlation matrix of future vs. current weather signals. Max. stands for maximum, temp. for temperature, precip. for precipitation, and min. for minimum.

clutch size and fledgling survival were unexpected. We speculate that high wind speeds may correlate with stormy weather, which could make conditions for foraging poorer, and perhaps wind chill during spring storms may further reduce performance.

Garcia's (2014) work on this same species often finds somewhat different correlations, though these results are not directly comparable due to differences in the data included and statistical methodology. For example, Garcia found a positive correlation between spring temperatures and clutch size, while we found only negative correlations with spring windspeed (perhaps arising from a shared mechanism, reduction in core body temperature). She also found correlations between weather and partial brood loss, whereas we found no weather signals for our related vital rate, fraction of eggs surviving to fledging. Garcia's methodology differed than ours in important ways that likely contribute to these differences. First, we built on her analysis by correcting for the possibility of overfitting due to fitting a high number of competing models and explicitly accounted for the fact that a correlation between weather and a vital rate may be detected by chance due to testing so many models (using the climwin approach; Bailey and van de Pol 2016, van de Pol et al. 2016). In addition, she included only the two (colder) Northern sites, used different weather windows than ours, only used data up to 2013, and fit models for site-specific vital rates (we fit vital rates using data from all sites). She also explicitly accounted for laying date (earlier laying date increases reproduction; Verhulst and Nilsson 2008), while we looked for correlations of weather and vital rates, without considering the intermediary effect of weather on laying date.

If vital rates are controlled by multiple weather signals, the changing correlations among those signals can have important consequences for predicting future vital rate responses. Namely, using the model fits derived from historical data to predict future vital rates assumes that the correlation among weather signals present in model is preserved under a future climate, even for correlations that were weak in a historical climate. We find that historical correlations among weather signals will change drastically in the future (Fig. 3, Appendix S1: Table S4). Such changing correlations could be generated by a shift from two weather signals trending in the same direction in the historical period (leading to a positive correlation) to those two weather signals trending in opposite directions in the future (leading to a negative correlation; change in sign of correlation occurs in 10/39 instances). Alternatively, less extreme shifts could occur, such as a reduction in the strength of positive (or negative) correlation (change in strength occurs in 8/39 instances). Echanges in the correlation among weather signals could have large impacts on future vital rates. For example, our results suggest that precipitation and maximum temperature were positively correlated with the probability of initiating a first nest (Fig. 1). In the historical data, these weather signals were positively correlated at Eglin (Appendix S1: Table S4), such that they both acted in the same direction, increasing the probability of initiating a first nest through time (Fig. 2). In the future, though, these weather signals are projected to be negatively correlated at this site (Appendix S1: Table S4), meaning that they will act in opposite directions to influence trends in this probability over time, potentially leading to future trends in vital rates that were not present in the historical data. Importantly, changes in the correlation structure are not consistent across sites: At Sandhills, for example, these same two weather signals were positively correlated and will continue to be positively correlated in the future. Thus, our work suggests that this type of no-analog climate condition, where the correlation among weather signals might differ from historical data, could have substantial consequences for species' future population dynamics, but that the changes in weather differ geographically, potentially leading to very different responses to future climate change at different locations. Studies that use historical weather effects on vital rates to predict vital rates under future climate conditions assume, perhaps incorrectly, that any historical correlation among weather signals will be preserved in the future (e.g., Doak and Morris 2010, Dalgleish et al. 2011).

In our study, significant shifts in vital rates over time could never be explained exclusively by significant shifts in the underlying weather signals over time, despite significant vital rate/ weather signal relationships. We therefore infer that shifts in weather-driven vital rates over time occurred as a result of changes in non-weather drivers, some of which we may not have tested for (e.g., habitat fragmentation or burn regimes), or perhaps from changes in weather signals not tested in this study (Fig. 2). Untested weather signals could include signals outside of the tested 12-month period, or signals not easily summarized using the sliding window approach, such as the total number of winter days below freezing. The weak effect of weather trends in generating trends in vital rates is consistent with only weak trends in the Southeastern U.S. weather (shown for temperature by Trenberth et al. 2007 shown for precipitation and windspeed in this study). In our study, non-weather drivers affecting vital rate trends surely include changes in habitat availability and quality due to widespread habitat restoration efforts, including prescribed burning of *D. borealis* habitat and construction of artificial cavities known to increase reproduction and survival (Walters

1991, USFWS 2003, Rudolph et al. 2004, McKellar et al. 2014, Walters and Garcia 2016). Increases in group size over time have also surely increased reproduction and survival (Walters and Garcia 2016), as is common in cooperative breeding systems (e.g., Lloyd et al. 2009, Preston et al. 2016, Van de Loock 2017).

Opposing effects of weather signals could also have contributed to the overall lack of weather control over vital rate trends. Namely, when we found a weather-driven vital rate to be correlated with multiple weather signals, these weather signals usually operated in opposing directions. For example, in the case of adult survival at Sandhills, two out of four weather signals operated in the direction of an overall positive trend in adult survival over time, but the other two weather signals contributed to a reduction in this positive trend, acting to reduce adult survival over time (Fig. 2). We see similar patterns across most multiple vital rate × site combinations (Fig. 2). Further complicating matters, the contribution of weather signals to vital rate trends is sometimes, but not always, in the same direction among the 3 sites, due to geographic variability in weather trends over time (Table 2, Trenberth et al. 2007). For example, February 27–April 23 maximum temperature increased over time at Sandhills, contributing to the positive trend in probability of initiating a first nest over time (Fig. 2). By contrast, this same weather signal decreased over time at Lejeune, acting against the positive trend in probability of initiating a first nest over time (Fig. 2). This example illustrates that changes in weather signals through time were not consistent across different locations (Appendix S1: Table S4), which resulted in geographic variability in historical trends in vital rates across sites. While our modeling approach assumed that the effect of a weather signal on a vital rate was the same across sites, even stronger cross-site differences in vital rate trends might be possible if this assumption were relaxed.

Our analytical approach has at least two limitations concerning our use of historical data to infer future responses. Perhaps most importantly, a species' current response to weather will not necessarily continue under future conditions that are different than what they have experienced over the historical record. While we do see substantial overlap between our current and future weather conditions, there may also be nonlinear effects of temperature or precipitation once they surpass current extremes. Ideally, future studies will pair observations of responses to historical weather conditions with experimental studies that increase temperature (or modify precipitation and windspeed) to simulate realistic future climate conditions. Another more subtle problem with using historical data to infer future response concerns collinearity of historical weather signals. For example, if two weather signals have historically been positively correlated, but have subadditive effects, analyses of historical observational data may find no response of vital rates to either weather signal, because one signal masks the effect of the other. But their independent effects may become important should the signals become negatively correlated or uncorrelated in the future. Similar arguments apply to any vital rate that is affected by multiple weather signals. Disentangling the effect of positively correlated weather signals can only be done using experimental factorial manipulations of multiple weather drivers (Freckelton et al. 2010).

To accurately predict future vital rates (and thus future abundance and geographical distribution) based on climate model projections, future studies must first look for multiple weather signals controlling vital rates (van de Pol et al. 2016) and then must use realistic correlations among weather signals to predict future vital rates. Using realistic correlations among weather signals requires using climate model projections that are able to simulate realistic and possibly evolving correlation structures among climate signals (e.g., McCain and Colwell 2011), rather than assuming that trends in weather signals over time will continue into the future. However, these studies are limited by their use of historical observational data. Thus, robust predictions of how vital rates could change in the future under a changing climate require: (1) looking for multiple weather signals using long-term historical data; (2) experimentally modifying weather signals in a realistic setting to levels consistent with future weather conditions; (3) using factorial experimental manipulations of weather designed to break positive correlations among drivers to better quantify their separate and interactive effects; (4) climate model projections that are able to simulate realistic and possibly evolving correlation structures among weather signals to project future changes in vital rates. Note that 2 and 3 are not possible or feasible for many rare, threatened, or long-lived species, including the species outlined in this manuscript. Thus, to date, we lack all of these ingredients for any one system.

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DATA AVAILABILITY STATEMENT

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.15157602.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3740/full