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RESEARCH ARTICLE

Interannual climate variation influences nest initiation date and nest productivity of the Red-cockaded Woodpecker at the northwestern edge of its range

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ABSTRACT

Climate change, including directional shifts in weather averages and extremes and increased interannual weather variation, is influencing demography and distributions for many bird species. The Ouachita Mountains ecoregion in southeast Oklahoma and west-central Arkansas contains 2 populations of the Red-cockaded Woodpecker (*Dryobates borealis*, RCW), a federally endangered, cooperatively breeding species. Since this region is at the RCW's northwestern range periphery, ecological thresholds likely are limiting for the species. Therefore, populations in this region may be more sensitive to climate change-associated weather variation and unpredictability. We used 26 years of nesting data (1991–2016) from the 2 RCW populations to determine if interannual weather variation has affected nesting phenology and productivity. For each population, we used daily temperature and precipitation data for 3 periods (30 and 60 days before nesting; 40 days overlapping the nesting period) to determine how weather influences median nesting date and average clutch size and numbers of fledglings. In a separate analysis, we used shorter time windows with individual nests as replicates to determine how discrete weather events (e.g., minimum and maximum temperatures and intense precipitation events) affect nest success and partial brood loss. For both Oklahoma and Arkansas populations, warmer early spring temperatures generally advanced nesting and increased clutch size and fledgling number. However, the effects of average precipitation varied depending on the amount and duration of precipitation in different time periods. At the nest level, most variables reflecting discrete temperature and precipitation events were unrelated to nest success and brood loss, suggesting that factors other than weather (e.g., habitat quality and predation) more strongly influenced the nesting output of individual RCW broods. Our results indicate RCWs are responding to interannual weather variation in complex and variable ways. However, warming trends may generally be having positive effects on the species at the northwestern edge of its range.

Keywords: climate change, nesting phenology, range periphery, Red-cockaded Woodpecker

LAY SUMMARY

- Climate change is influencing distributions and demography for many bird species. Understanding effects on populations at the edge of species' ranges will be crucial for adapting management to prevent climate-caused declines and extinctions.
- For the endangered Red-cockaded Woodpecker, we used 26 years of nest monitoring data to evaluate how interannual climate variation has affected nesting timing and productivity at the northwestern edge of the species' range.
- Warmer temperatures in early spring generally advanced Red-cockaded Woodpecker nesting dates and increased nest productivity. Precipitation effects were variable, depending on the amount and duration of rainfall in different time periods before and during the nesting season.
- Although climate effects on Red-cockaded Woodpecker nesting ecology appear complex, conditions may be changing in ways that increase nest productivity at the northwestern edge of the species' range. Managing habitat in this part of the range may become increasingly important to Red-cockaded Woodpecker conservation as climate change continues.

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La variación climática interanual influencia la fecha de inicio del nido y la productividad del nido de *Dryobates borealis* en el borde noroeste de su rango

RESUMEN

El cambio climático, incluyendo los cambios direccionales en los promedio y extremos climáticos y el aumento en la variación climática interanual, está influenciando la demografía y las distribuciones de muchas especies de aves. La ecorregión de las Montañas de Ouachita en el sudeste de Oklahoma y el centro-oeste de Arkansas contiene dos poblaciones de *Dryobates borealis*, una especie de reproducción cooperativa en peligro a nivel federal. Debido a que esta región está en la periferia noroeste del rango de *D. borealis*, hay umbrales ecológicos que probablemente son una limitante para la especie. Por ende, las poblaciones en esta región pueden ser más sensibles al cambio climático-variación climática e imprevisibilidad asociada. Usamos 26 años de datos de anidación (1991–2016) provenientes de dos poblaciones de *D. borealis* para determinar si la variación climática interanual ha afectado la fenología y la productividad de anidación. Para cada población, usamos datos diarios de temperatura y precipitación para tres períodos (30 y 60 días antes de la anidación; 40 días superpuestos al período de anidación) para determinar cómo el clima influencia la fecha mediana de anidación y el promedio del tamaño de la nidada y del número de volantones. En un análisis separado, usamos ventanas temporales más cortas con nidos individuales como réplicas para determinar cómo eventos climáticos discretos (e.g., temperaturas mínimas y máximas y eventos de precipitación intensos) afectan el éxito de anidación y la pérdida parcial de la nidada. Para las poblaciones de Oklahoma y Arkansas, las temperaturas más cálidas de inicios de la primavera generalmente adelantaron la anidación y aumentaron el tamaño de la nidada y el número de volantones. Sin embargo, los efectos de la precipitación promedio variaron dependiendo de la cantidad y duración de la precipitación en diferentes períodos de tiempo. A nivel del nido, la mayoría de las variables que reflejaron los eventos discretos de temperatura y precipitación no estuvieron relacionadas con el éxito del nido y la pérdida de la nidada, sugiriendo que otros factores además del clima (e.g., calidad de hábitat y depredación) influenciaron más fuertemente el resultado de las nidadas individuales de *D. borealis*. Nuestros resultados indican que *D. borealis* está respondiendo a la variación climática interanual de modos complejos y variables. Sin embargo, las tendencias de calentamiento pueden estar teniendo en general efectos positivos en la especie en el borde noroeste de su rango.

Palabras clave: cambio climático, *Dryobates borealis*, fenología de anidación, periferia del rango

INTRODUCTION

Climate change, including increasing temperatures, changing frequency and severity of droughts and precipitation events, and increased weather variability, is profoundly altering ecosystems and biodiversity (Dawson et al. 2011, Bellard et al. 2012, Intergovernmental Panel on Climate Change [IPCC] 2013). Over recent decades, the number of studies measuring climate change impacts on wildlife has increased greatly, and birds are particularly well-studied (Crick et al. 1999, Dunn and Winkler 1999, Wann et al. 2016). Climate change and weather strongly influence avian behavior, phenology (e.g., timing of migration and breeding events), survival, and reproduction (Dunn and Winkler 1999, Jenni and Kéry 2003, Pipoly et al. 2013, Wann et al. 2016). Such impacts are of concern to conservation organizations and agencies seeking to mitigate climate change effects and to manage bird populations and habitats under a changing climate (e.g., United states Department of Agriculture [USDA] Forest Service 2008, Oklahoma Department of Wildlife Conservation [ODWC] 2016a).

The occupied ranges of many bird species are expected to shift as warming temperatures, altered precipitation patterns, and shifting disturbance regimes change biomes and ecosystems, placing many rare, declining, and specialist species at further risk of decline and/or extinction (Walther et al. 2002, Parmesan and Yohe 2003, Sekercioglu et al. 2008, Morin and Thuiller 2009, DeMay and Walters 2019). Populations on the edge of species' ranges may be especially vulnerable to climate-related effects because they are often constrained by suitable habitat and temperature-tolerance thresholds (Geber 2008, Hardie and Hutchings 2010). Furthermore, aspects of a species' foraging ecology and habitat associations can differ at range margins (Zhu et al. 2012, Niedzielski and Bowman 2016). For example, at the southern edge of its range, Greater Sage-Grouse (*Centrocercus urophasianus*) selects higher-elevation areas with greater precipitation, compared to other parts of the range (Picardi et al. 2020). Changes in breeding phenology and reproductive success in response to climate change, including at range peripheries, may influence the risk of decline and extinction at a variety of spatial scales (Pipoly et al. 2013, Martin et al. 2017).

The Red-cockaded Woodpecker (*Dryobates borealis*, hereafter "woodpecker") is a federally endangered, cooperatively breeding species inhabiting mature, fire-maintained pine savannas and woodlands in the southeastern United States (Ligon 1970, Walters et al. 1988, U.S. Fish and Wildlife Service [USFWS] 2003). At the northwest edge of its range in the southcentral United States, 2 woodpecker populations occur, one each in Oklahoma and Arkansas, with both on public land in the Ouachita Mountains Ecoregion (Carter 1967, Masters et al. 1989). Red-cockaded Woodpeckers are social, exhibit high site fidelity, and excavate cavities almost exclusively in living, mature pines (Steirly 1957, Ligon 1970, Walters et al. 1988). This unique life history and specialized habitat requirements likely preclude range shifts except on very long (i.e. century) time scales. Thus, the woodpecker

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and other specialist species that must adapt in place are especially susceptible to climate change. Woodpecker populations in peripheral areas of the range, like the Ouachita Mountains, may be especially affected because historic conditions on the range edge may already represent climatic tolerance thresholds. Effects of discrete weather events (Neal and James 1993, Conner et al. 2005) and climate change (Schiegg et al. 2002, Garcia 2014, Williamson et al. 2016, DeMay and Walters 2019) have been studied for woodpecker populations in the eastern and southern parts of the range, where longleaf pine (*Pinus palustris*) and mixed pine forests dominate and are preferentially used (Lennartz et al. 1987, Conner and Rudolph 1991, Ross et al. 1997, Ramirez and Ober 2014). These studies show that woodpeckers tend to nest earlier in response to warming spring temperatures; whereas high precipitation levels delay nest initiation and reduce foraging opportunities and nestling provisioning (Conner et al. 2005). Productivity appears to be increasing in response to climate change in the northeastern part of the range, but declining in the southwestern part of the range (DeMay and Walters 2019).

At the northwest range periphery, where woodpeckers use shortleaf pine (*Pinus echinata*) dominated systems, little is known about woodpecker ecological constraints, including effects of climate on demography and phenology. Mean temperature and precipitation are projected to change greatly in the Ouachita Mountains ecoregion in the next century, with average annual temperatures projected to increase by ≥4°C by 2071, and precipitation coming in fewer, more intense events, with longer intervening droughts (Wang et al. 2016). Understanding how weather and climate change affect woodpecker reproduction, and the species' capacity to adapt to changes in climate, can benefit efforts to manage the species' habitat and identify currently occupied areas that may become unsuitable in the future. Furthermore, investigating such climate effects in this portion of the woodpecker distribution is important to understand the species' long-term viability because the location of these populations on both the northern and western edges of the range makes it unclear if climate change will have negative or positive demographic effects.

We addressed this research gap using long-term datasets (spanning 1991 to 2016) for woodpecker nesting phenology and reproduction in the Oklahoma and Arkansas populations. At the level of each population, we assessed how interannual variation in average temperature and precipitation influenced nest initiation date, clutch size, and the number of nestlings fledged. At the level of individual nests in each population, we assessed how discrete weather events (maximum and minimum temperatures and maximum daily precipitation during particular time windows) influenced nest success (i.e. whether a nest fledges any young) and partial brood loss (i.e. when nestling loss occurs during the brooding period). We hypothesized that (1) at the population level, warmer temperatures leading up to nesting have advanced woodpecker nest initiation dates and increased clutch sizes; (2) at the population level, cooler temperatures and high levels of precipitation during the brooding period have reduced numbers of nestlings fledged; and (3) at the nest level, maximum or minimum temperatures and high amounts of daily precipitation have negatively affected nest success and increased the number of nestlings lost to partial brood loss.

METHODS

Study Area

We conducted field research in 2 study sites, one in southeast Oklahoma and one in west-central Arkansas (Figure 1). The sites are separated by ~50 km, and both are in the Ouachita Mountains ecoregion of the southcentral United States, which is characterized by small mountains, large hills, and steep, rugged topography, with elevations in study sites ranging from 183 to 415 m (Burnside 1983, Kelly et al. 1993, Masters 1995). Throughout the ecoregion, vegetation is dominated by mixed hardwood and pine forests, with hardwoods (primarily oaks; *Quercus* spp.) dominating relatively moist north-facing slopes and shortleaf pines more prevalent on drier south-facing slopes (Carter 1967, Masters 1995). Year-round average temperatures and precipitation for the region include daily maximum temperatures of 11°C, 23°C, 33°C, and 24°C; and daily minimum temperatures of −1°C, 8°C, 20°C, and 8°C for the months of January, April, July, and October, respectively, with 139.7 cm of precipitation annually (United States Department of Agriculture [USDA] Forest Service 1999).

The Oklahoma study site was at the southern edge of the Ouachita Mountains in the 5,700 ha McCurtain County Wilderness Area, the largest contiguous tract of old-growth shortleaf pine forest in the United States (Stahle et al. 1985). After designation as a Wilderness Area by the ODWC in 1918, little active land management was conducted for over 70 years. In 1991, to benefit the site's woodpecker population, the ODWC entered into an agreement with the USFWS to begin implementing mechanical removal of hardwood trees and to reinstate prescribed fire (on a 3-year dormant-season burn rotation) in and near active woodpecker clusters (ODWC 1991).

The Arkansas study site was at the northern edge of the Ouachita Mountains in the Ouachita National Forest. Here, the U.S. Forest Service began a large-scale pine-bluestem habitat restoration effort in 1994 to recover the woodpecker population in the Poteau/Cold Springs District of the National Forest (Hedrick 2007). Similar to the Oklahoma site, this restoration area has received a 3-year fire rotation supplemented by selective thinning of hardwoods and small pines in areas with woodpecker family groups (USDA Forest Service 2005). Although the Oklahoma and Arkansas sites have similar plant community composition and structure, they vary slightly from

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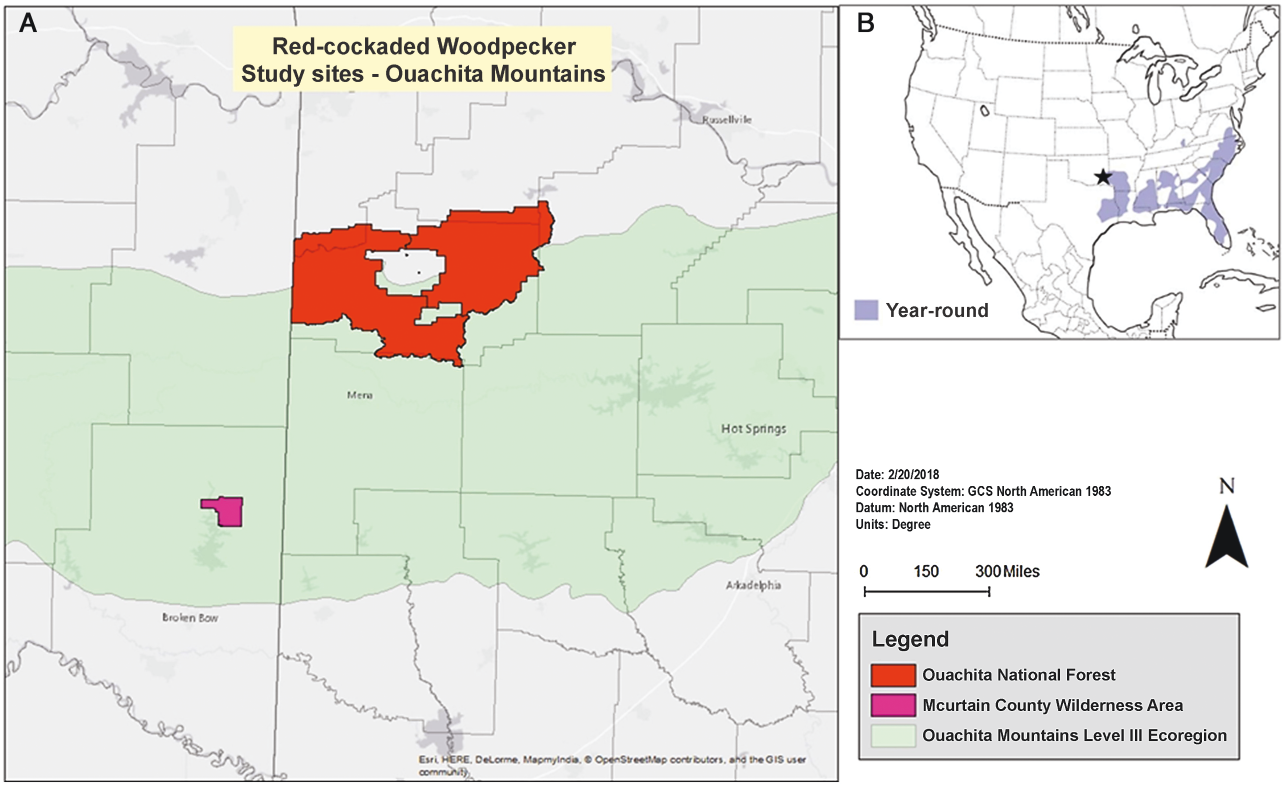

FIGURE 1. (**A**) Map of study sites in the Ouachita Mountains ecoregion, United States; Arkansas and Oklahoma populations of the Red-cockaded Woodpecker (RCW) were in the Ouachita National Forest and McCurtain County Wilderness Area, respectively; (**B**) location of the study area within the woodpecker range (source of range-wide distribution map: Cornell Lab of Ornithology 2019).

each other in topography, with the former having more complex topography and steeper slopes. The overall age of the forest overstory also differs; some shortleaf pine stands in the Oklahoma site have a mean age of nearly 150 years, as they were never harvested commercially for timber (Wood 1983), whereas the majority of stands in the Arkansas site are composed of second-growth trees <100 years of age (Neal and Montague 1991).

Long-term monitoring (see "Data Collection") indicates that woodpecker populations have increased in both intensively managed study sites over the last few decades. However, the overall distribution of woodpeckers in the region has retracted greatly from its historical extent (Wood 1983, Neal and Montague 1991). The Oklahoma population has grown slowly (from 9 groups in 1991 to 15 in 2016), while the Arkansas population has increased substantially over the same period (from 13 groups in 1991 to 64 in 2013; ODWC 2016b; W. Montague personal communication).

Data Collection

To examine the effects of climate variation on woodpecker nest initiation dates, nest success, and nest productivity, we obtained nesting data for both the Arkansas and Oklahoma populations (data for these 2 populations were originally collected, respectively, by U.S. Forest Service and ODWC biologists). In Arkansas, intensive woodpecker nest and population monitoring began in 1991; in Oklahoma, the collection of nesting data began in 1992 (W. Montague personal communication, ODWC 1993). Although nest monitoring in Oklahoma has continued through the present day, monitoring in Arkansas was greatly reduced in 2013; thus, annual nesting data used for this analysis ranged from 1991 to 2013 for Arkansas and from 1992 to 2016 for Oklahoma. In both sites, population monitoring was conducted following USFWS guidelines, with nests checked at least weekly from egg-laying to fledging (USFWS 2003). Ligon (1970) and Jackson (2020) have recorded woodpecker incubation time to be 10–12 days with a brooding period (hatching to fledging) of ~26 days. Data collected for each year included the estimated date of nest initiation for the first nesting attempt (approximate date first egg was laid; estimated by counting backward from the day a full clutch or nestling(s) was first observed, assuming 1 egg laid per day), clutch size, number of nestlings hatched, number of nestlings present when banded at ~7 days of age, and estimated number of nestlings fledged at 26 days after hatching (assuming the number

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of nestlings observed at or near the cavity at day 26 represented the number successfully fledged). Additionally, both group size (breeding pair plus any adult helper birds in the territory) and age of the breeding pair were recorded for each woodpecker cluster in the Arkansas population.

For both populations, we estimated the mean center point across all active woodpecker cluster locations using the *Mean Center* tool in ArcMap (Environmental Systems Research Institute 2011) and GPS coordinates for clusters. Climate data were downloaded from the PRISM Climate Group website (PRISM Climate Group 2018) via the Explorer application. Because our analyses focused on temporal changes in climate variables from year to year, and not fine-scale spatial variation, we used the daily weather data product with the 4-km resolution, and time series data were obtained for the 4-km grid cell that contained the mean center location for each study site. Specifically, time series values for daily minimum temperature, daily maximum temperature, and daily total precipitation were accessed for 1991 to 2013 for Arkansas and 1992 to 2016 for Oklahoma.

Data Analysis

All analyses were conducted separately for Oklahoma and Arkansas. To capture the potential effects of interannual weather variation on woodpecker reproduction at the population level, we combined data for nesting variables across all nests for each year and treated years as replicates (n = 25 years for Oklahoma; n = 23 years for Arkansas). Nesting variables assessed at this population level included, for first nests (i.e. excluding renests following nest failure), median nest initiation date (median date first egg was laid across all nests for a given year; treated as Julian date for analyses; Chi 1979), average clutch size, and average estimated number of nestlings fledged. We used the median for nest initiation date because the distribution of values for this variable was more-skewed than for other nesting variables. To assess the effects of weather conditions during different time periods relevant to woodpecker nesting, we defined 3 time windows for which all weather variables—including average daily maximum and daily minimum temperatures, as well as total precipitation—were separately calculated. To capture effects of weather conditions for time periods prior to nesting, we defined 30- and 60-day windows preceding the median first nest initiation date across all years for each population. To capture possible weather effects during the incubation and nestling periods, we defined a 40-day window with a start date based on the same median first nest initiation date as above. This 40-day period was selected to capture the average woodpecker egg-laying period (3 days), the incubation period (11 days), and the period from hatching to fledging (26 days; Jackson 2020). For a visual representation of all time windows assessed for each nesting response variable in both this and the following nest-level analysis, see Figure 2.

We conducted analyses in R 3.6.1 (R Core Team 2019). For population-level analyses, we used generalized linear models with weather variables as fixed effects and a Gamma distribution with a log link (Pescim and Nadarajah 2016) because values of response variables were greater than zero and distributions were right-skewed. For nest initiation and clutch size analyses, we tested weather variables for the 2 windows (30 and 60 days) prior to nest initiation. For the fledgling analysis, we tested weather variables for the 40-day window from nest initiation to fledging. We conducted pairwise correlation tests among all predictor variables for each population and analysis. Before creating a global model, each predictor variable from a correlated pair was tested for correlation against the response variable of interest; to reduce multicollinearity in models, we only retained the predictor variable that was more strongly associated with the response variable. Furthermore, we only tested independent effects of predictor variables because there was no a priori evidence suggesting interactive effects of multiple climate-related factors on woodpecker nesting variables; this approach also maintains the simplicity of model interpretation and management applications. Using the *stepAIC* function in the R package *MASS*, we used a backward stepwise model selection approach, beginning with the global model containing all uncorrelated predictor variables and removing one variable at a time. This procedure only retains variables when their removal results in ΔAIC (Akaike's Information Criterion) increasing by >2.

We also conducted analyses at the individual nest level (i.e. individual nesting attempts treated as replicates; n = 232 nests for Oklahoma; n = 612 nests for Arkansas) to assess effects of discrete weather events on nesting success (i.e. whether nests fledge at least one nestling) and partial brood loss (i.e. number of offspring lost from the egg stage to nestling day 7, when nestlings were typically banded). For these analyses, we used generalized linear mixed models (GLMMs) in the *lme4* package (Bates et al. 2015), with year and cluster as random effects, and binomial and Poisson distributions for nest success and brood loss analyses, respectively. Although past studies indicate important effects of the year on woodpecker nesting (DeMay and Walters 2019), we sought to focus on the effects of weather and thus treated year as a random effect, not a fixed effect. We treated cluster as a random effect to account for variation arising from woodpecker breeding group-related factors and habitat differences among groups/clusters. For nest success analyses, we did not account for exposure days (i.e. number of days each nest was observed) because the intensive nature of nest monitoring in both study sites ensured that all active nests used in analyses were found within 3 days of the first egg being laid. We

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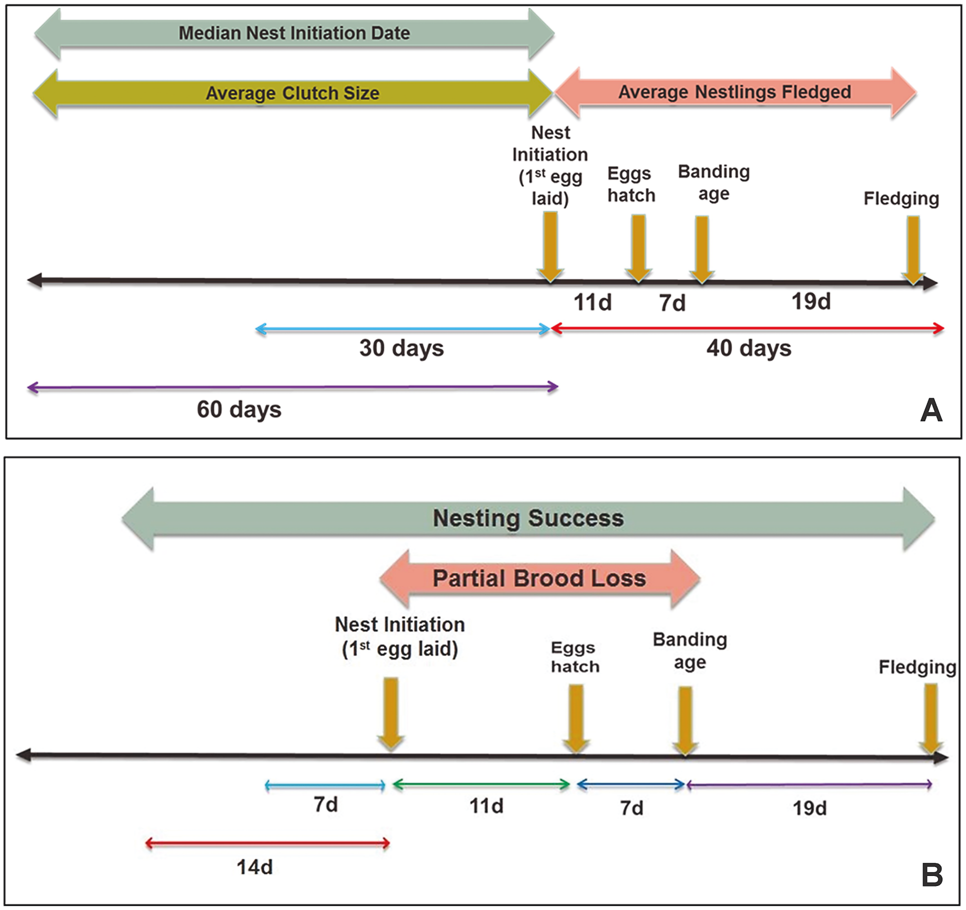

FIGURE 2. Visual representation of analyses to assess effects of (**A**) average weather conditions on population-level nesting variables for Red-cockaded Woodpeckers; (**B**) discrete weather events on nest-level nesting variables. Arrows at the bottom of each image indicate time windows for which weather data were summarized; arrows at the top of each image encapsulate time windows for which weather variables were analyzed for each response variable.

conducted preliminary analyses for the Arkansas population to test effects of breeder age and group size on nest success and partial brood loss because past research indicates these factors can positively influence reproductive success in cooperatively breeding species (Lennartz et al. 1987, Mumme 1992, Conner et al. 2001, McCormick et al. 2004, Walters and Garcia 2016). This preliminary analysis was only conducted for Arkansas because breeding male age and group size data were only available for this site and only for a subset of years. Both breeding male age and group size had statistically significant ($P < 0.05$, 95% confidence intervals [CIs] of coefficients not overlapping zero) positive relationships with nest success, but neither variable was related to partial brood loss.

We used initiation dates for individual nests to define unique, nest-specific time windows, with the objective of determining whether absolute maximum and minimum temperatures and discrete precipitation events cause nest failure and partial brood loss. Since conditions prior to nesting can affect woodpecker incubation and nestling periods (Schiegg et al. 2002), and because smaller time windows may be more appropriate for capturing short-term heat, cold, and precipitation events, we defined 2 windows prior to nest initiation for each nest (7 and 14 days). To assess the effect of discrete weather events while nests are active, we also defined 3 windows after nest initiation, including the 11-day incubation period, the 7-day nestling period before nestlings were banded and brood reduction events were identified, and the 19-day nestling period between banding age and fledging at day 26.

For all nest-level analyses, we used the above-described GLMM structure, and for fixed effects, we included nest initiation date (because this factor has been shown to influence woodpecker reproductive success; Schiegg et al. 2002) and weather variables (absolute maximum and minimum temperature, and absolute maximum daily precipitation value for each time window). Based on the results of the above preliminary analysis, both breeding male age and group size were also included as

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covariates in all nest-level models for Arkansas (Table 1). As with population-level analyses, we only tested weather variables for time windows considered relevant to the reproductive event of interest. For the partial brood loss analysis, we included variables for the 11-day incubation window and 7-day window between hatching and nestling banding age. We excluded pre-nest initiation windows for the partial brood loss analysis because we assumed that extreme events occurring before woodpecker nesting have a little measurable effect on this process. However, assuming conditions both before and during nesting likely influence nest success, we used all 5 time windows for this analysis (Figure 2).

For all response variables assessed at the nest level, we used a similar approach to identify and exclude correlated predictor variables as described for population-level analyses, and again, we only considered independent effects of predictors (i.e. no interactions). Unlike the population-level analyses, we did not use a stepwise AIC approach due to computational challenges of using this method for mixed models (Bolker et al. 2009). Instead, we used AIC to compare an a priori set of candidate models (Burnham and Anderson 2002). We first constructed single variable models; based on rankings for these models, we then systematically built models containing more than one variable. We inferred that models were strongly supported when ΔAIC values were between 0 and 2 and at least 2 less than the null (i.e. intercept-only) model and when they did not include uninformative parameters (Arnold 2010). For both population- and nest-level analyses, we considered variables from strongly supported models to have meaningful associations with response variables if the 95% CI of their coefficient estimates did not overlap zero (see Supplementary Material Tables 4 and 5 for all compared models).

RESULTS

Population-Level Analyses of Nest Initiation Date, Clutch Size, and Fledgling Number

For both populations, numbers of nests for each year and descriptive summaries of clutch sizes, nestlings fledged, and successful nests can be found in Supplementary Material Tables 6 and 7. For Oklahoma, the median earliest nesting date across years (1992–2016) was April 24, while the median earliest nesting date across years for Arkansas (1991–2013) was April 22. Several pairs of predictor variables were strongly correlated with each other for population-level analyses (Supplementary Material Tables 8 and 9), and we only included the variable that was more strongly associated with the response variable in each analysis. Strongly supported variables for each analysis as well as estimated coefficients are given in Supplementary Material Table 10.

The top model for nest initiation date for Oklahoma contained 4 variables, including average maximum daily temperature for both the 60-day (β = –0.002, 95% CI: –0.006 to 0.0008) and 30-day (β = 0.004, 95% CI: –0.001 to 0.009) windows preceding nest initiation and average minimum daily temperature (β = –0.013, 95% CI: –0.017 to –0.009) and total precipitation (β = 0.0001, 95% CI: 0.00006 to 0.0002) during the 30-day window. However, only the latter 2 variables had coefficients with 95% CIs not overlapping zero; this model's coefficients (Table 2) indicate that warmer minimum temperatures and greater precipitation during the 30-day window advance and delay nest initiation, respectively (Figure 3). The top model for nest initiation date for Arkansas contained average minimum (β = –0.007, 95% CI: –0.011 to –0.004) and maximum (β = 0.004, 95% CI: 0.001 to 0.008) daily temperature for the 60-day window, average maximum daily temperature for the 30-day window (β = –0.0112, 95% CI: –0.013 to –0.009), and total precipitation for the 60-day window (β = 0.00003, 95% CI: 0.00001 to 0.00005; Table 2 and Figure 4). Effects suggested in this model are similar to the Oklahoma nest initiation model (i.e. warmer minimum temperatures and greater precipitation advance and delay nesting, respectively), except maximum temperature also had meaningful, window-specific effects. Specifically, warmer maximum temperatures for the 60- and 30-day windows were associated with delayed and advanced nesting, respectively.

The top model for average clutch size for Oklahoma contained 3 variables, including total precipitation for the 60-day window (β = –0.0005, 95% CI: –0.0008 to –0.0002) and average maximum daily temperature (β = 0.033, 95% CI: 0.022–0.044) and total precipitation (β = 0.0003, 95% CI: –0.0001 to 0.0009) for the 30-day window preceding nest initiation (Table 2 and Figure 5). However, the effect of the latter variable was relatively weak as evidenced by the 95% CI overlapping zero. The top model for clutch size for Arkansas contained 3 variables, including average minimum daily temperature for the 60-day window (β = 0.007, 95% CI: 0.005–0.010) and total precipitation for the 30-day (β = 0.0002, 95% CI: 0.001–0.0003) and 60-day (β = –0.00006, 95% CI: –0.0001 to –0.00001) windows preceding nest initiation (Table 2 and Figure 5). These models indicate that clutch size increases with warmer temperatures and that precipitation before the nesting period may have effects that differ by time window and location (i.e. for Arkansas, negative and positive effects of precipitation during 60- and 30-day windows, respectively; for Oklahoma, negative effect of precipitation during 60-day window). Despite relatively small coefficient estimates for the above clutch size analyses, effects

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TABLE 1. Description of predictor variables used to analyze effects of average weather conditions and discrete weather events on population- and nest-level nesting variables, respectively, for Red-cockaded Woodpecker (*Dryobates borealis*) populations in Arkansas and Oklahoma.

Analysis level	Name	Description
Population	60d prenest tmin	Average daily minimum temperature in the 60-day period before median first nest initiation date for all years for each site
	60d prenest tmax	Average daily maximum temperature in the 60-day period before median first nest initiation date for all years for each site
	60d prenest ppt	Total precipitation in the 60-day period before median first nest initiation date for all years for each site
	30d prenest tmin	Average daily minimum temperature in the 30-day period before median first nest initiation date for all years for each site
	30d prenest tmax	Average daily maximum temperature in the 30-day period before median first nest initiation date for all years for each site
	30d prenest ppt	Total precipitation in the 30-day period before median first nest initiation date for all years for each site
	40d nesting tmin	Average daily minimum temperature in the 40-day period following median first nest initiation date for all years for each site
	40d nesting tmax	Average daily maximum temperature in the 40-day period following median first nest initiation date for all years for each site
	40d nesting ppt	Total precipitation in the 40-day period following median first nest initiation date for all years for each site
Nest	14d abs tmin	Absolute lowest daily temperature value within the 14-day period preceding nest initiation date for a specific nest
	14d abs tmax	Absolute highest daily temperature value within the 14-day period preceding nest initiation date for a specific nest
	14d abs ppt	Absolute highest daily precipitation value within the 14-day period preceding nest initiation date for a specific nest
	7d abs tmin	Absolute lowest daily temperature value within the 7-day period preceding nest initiation date for a specific nest
	7d abs tmax	Absolute highest daily temperature value within the 7-day period preceding nest initiation date for a specific nest
	7d abs ppt	Absolute highest daily precipitation value within the 7-day period preceding nest initiation date for a specific nest
	11d abs tmin	Absolute lowest daily temperature value within the 11-day period following nest initiation date for a specific nest
	11d abs tmax	Absolute highest daily temperature value within the 11-day period following nest initiation date for a specific nest
	11d abs ppt	Absolute highest daily precipitation value within the 11-day period following nest initiation date for a specific nest
	7d-hb abs tmin	Absolute lowest daily temperature value within the 7-day period following the 11th day after nest initiation date for a specific nest
	7d-hb abs tmax	Absolute highest daily temperature value within the 7-day period following the 11th day after nest initiation date for a specific nest
	7d-hb abs ppt	Absolute highest daily precipitation value within the 7-day period following the 11th day after nest initiation date for a specific nest
	19d abs tmin	Absolute lowest daily temperature value within the 19-day period following the 18th day after nest initiation for a specific nest
	19d abs tmax	Absolute highest daily temperature value within the 19-day period following the 18th day after nest initiation for a specific nest
	19d abs ppt	Absolute highest daily precipitation value within the 19-day period following the 18th day after nest initiation for a specific nest
	Male age	Age (in years) of breeding male in the territory
	Group size	Number of individuals in the territory (nesting pair + helper birds)

of precipitation and temperature appear to be biologically meaningful (Figure 5). As an example, for the Oklahoma population, average clutch size was estimated to decrease by ~18% from the lowest to highest observed levels of precipitation for the 60-day window (Figure 5E), a magnitude of change likely to have important implications at the population level.

For Oklahoma, the top model for fledgling number included total precipitation for the 40-day nesting period ($\beta = -0.0007$, 95% CI: −0.001 to −0.00008), and both average minimum ($\beta = 0.063$, 95% CI: 0.010–0.115) and maximum ($\beta = 0.103$, 95% CI: 0.044–0.163) daily temperatures for the same period (Table 2 and Figure 6). The top model for a fledgling number for Arkansas included total precipitation

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TABLE 2. Variables from top models for population-level analyses of effects of weather averages on median nest initiation date, average clutch size, and average number of nestlings fledged for Red-cockaded Woodpeckers (*Dryobates borealis*) in Oklahoma (OK) and Arkansas (AR). For a description of weather variables, see Table 1, Figure 2, and text. For AIC values,[a] see Supplementary Material Table 10.

Response variable	Study site	Weather variables
Nest initiation date	OK	60d avg tmax
		30d avg tmax
		30d avg tmin
		30d total ppt
	AR	60d avg tmin
		60d avg tmax
		60d total ppt
		30d avg tmax
Clutch size	OK	60d total ppt
		30d avg tmax
		30d total ppt
	AR	60d avg tmin
		60d total ppt
		30d total ppt
Number fledged	OK	40d avg tmax
		40d avg tmin
		40d total ppt
	AR	40d avg tmin
		40d total ppt

[a] Value of Akaike's Information Criterion for top model assessed for each response variable.

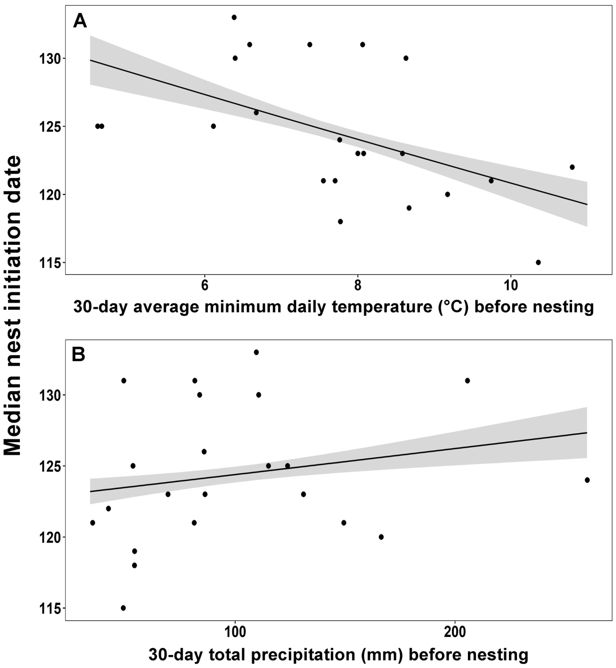

FIGURE 3. Relationships between pre-nesting weather conditions and population-level median nest initiation date (Julian date) for Red-cockaded Woodpeckers in the Oklahoma population. Supported predictors included (**A**) average minimum daily temperature (**B**) and total precipitation, both during the 30-day period preceding nest initiation.

during the 40-day nesting window ($\beta = 0.0005$, 95% CI: 0.0003–0.0007) and average minimum daily temperature ($\beta = 0.139$, 95% CI: 0.0003–0.0007) during the 40-day window (Table 2 and Figure 6). These models indicate that the number of fledglings increases with increasing temperatures and either increases or decreases (depending on the study site) with increasing precipitation during the nesting period.

Some of the modeled relationships in population-level analyses included apparent outlier values of predictor variables. However, in most cases (Figures 5B and 6D), removal of such values would result in an even stronger modeled effect of the predictor variable in the same direction (e.g., in Figure 6D, an even stronger positive effect of temperature on the number of fledglings, as opposed to a negative effect or lack of any effect).

Nest-Level Analyses of Discrete Weather Event Effects on Brood Reduction and Nest Success

For the Oklahoma nest success analysis, no models outperformed the null model (Table 3). For the Arkansas nest success analysis, 4 models were supported ($\Delta\text{AIC} < 2$) and contained 6 variables. However, only absolute maximum temperature for the 19-day window had a coefficient with a 95% CI that did not overlap zero ($\beta = -0.250$, 95% CI: -0.548 to -0.002), indicating that nest success probability was lower with warmer maximum temperature. For both Oklahoma and Arkansas brood loss analyses, no models out-performed the null model. Notably, despite breeder age and group size having significant effects on nest success in the preliminary analysis, these factors were not supported as meaningful predictors of nest success or partial brood loss once weather variables were included in analyses (see Supplementary Material Tables 11–14 for full AIC model rankings).

DISCUSSION

Based on 20+ years of data for 2 Red-cockaded Woodpecker populations at the northwest edge of the species' range, we documented apparent effects of climate variation on population-level nesting variables (nest initiation date, clutch size, number of fledglings) and a limited effect of discrete weather events on individual nesting attempts. Our results indicate that woodpecker demography is responding to interannual variation in weather and that the nature of responses may influence the persistence and adaptability of these peripheral populations in response to climate change.

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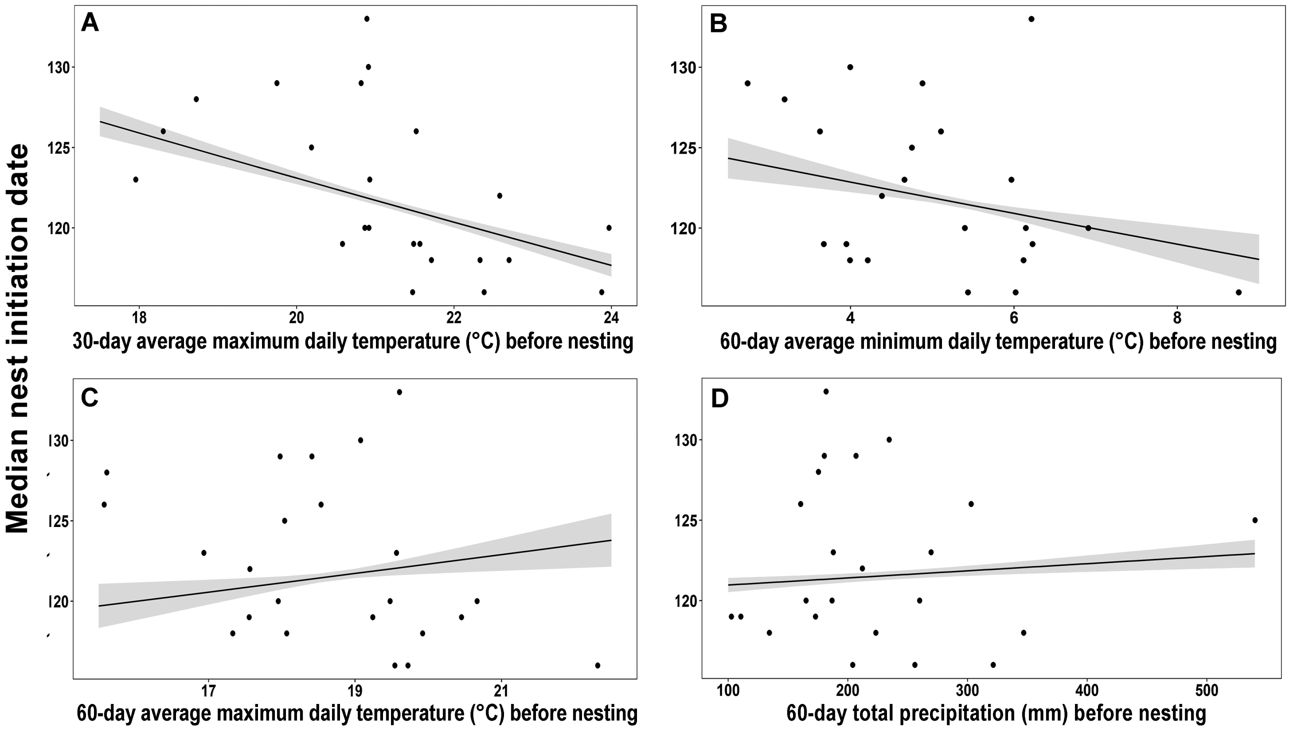

FIGURE 4. Relationships between pre-nesting weather conditions and population-level median nest initiation date (Julian date) for Red-cockaded Woodpeckers in the Arkansas population. Supported predictors included (**A**) average maximum daily temperature during the 30-day period preceding nest initiation, (**B** and **C**) average minimum and maximum daily temperature during the 60-day period preceding nest initiation, and (**D**) total precipitation during the 60-day period preceding nest initiation.

Population-Level Analyses of Nest Initiation Date, Clutch Size, and Fledgling Number

Effects of temperature on woodpecker population-level nesting variables were relatively consistent, while precipitation effects were variable. Average temperature variables were supported 9 times in population-level analyses. Warmer temperatures were generally associated with earlier nest initiation (a pattern shown for 3 of 4 temperature variables related to nest initiation) and had consistent positive effects on clutch size and fledgling number. Total precipitation variables were supported 7 times in population-level analyses. Greater precipitation was associated with delayed nesting (both populations) and generally associated with reduced clutch size (shown for 2 of 3 precipitation variables related to clutch size). Precipitation was negatively and positively associated with the fledgling number for the Oklahoma and Arkansas populations, respectively.

Red-cockaded Woodpeckers in both populations tended to initiate nests earlier with warmer early spring temperatures, a finding that matches other studies of this species at the northeastern edge of its range in North Carolina (Schiegg et al. 2002, Garcia 2014). This pattern may reflect woodpecker responses to temperature cues that correlate with the phenology of arthropod prey critical to successful nesting (Lack 1954, Dunn and Winkler 1999, Both 2004). The link between greater precipitation and delayed nesting was consistent for both populations and may be associated with the effects of precipitation on food supply and/or foraging opportunities. Past studies (Ligon 1970, Baker 1971) and anecdotal observations by ODWC staff (C. Barnes personal communication) suggest that in both nesting and non-nesting periods, woodpeckers may have difficulty foraging and/or spend more time in their cavities during extended periods of precipitation. High levels of average precipitation during preproductive periods (e.g., 30–60 days before nesting) could signal poor conditions for breeding (e.g., depressed insect populations), thus delaying the onset of optimal reproductive condition for females (Neal et al. 1993).

Pre-nesting temperatures had a consistent positive association with clutch size for both populations. This finding indicates that warmer temperatures prior to nesting may signal optimal conditions for breeding, potentially resulting in effects on reproductive condition and/or providing a cue to adjust clutch sizes (Lack 1947). Effects of precipitation were variable, with greater precipitation during the 60-day window reducing clutch size for both populations and greater precipitation during the 30-day window increasing clutch size for Arkansas.

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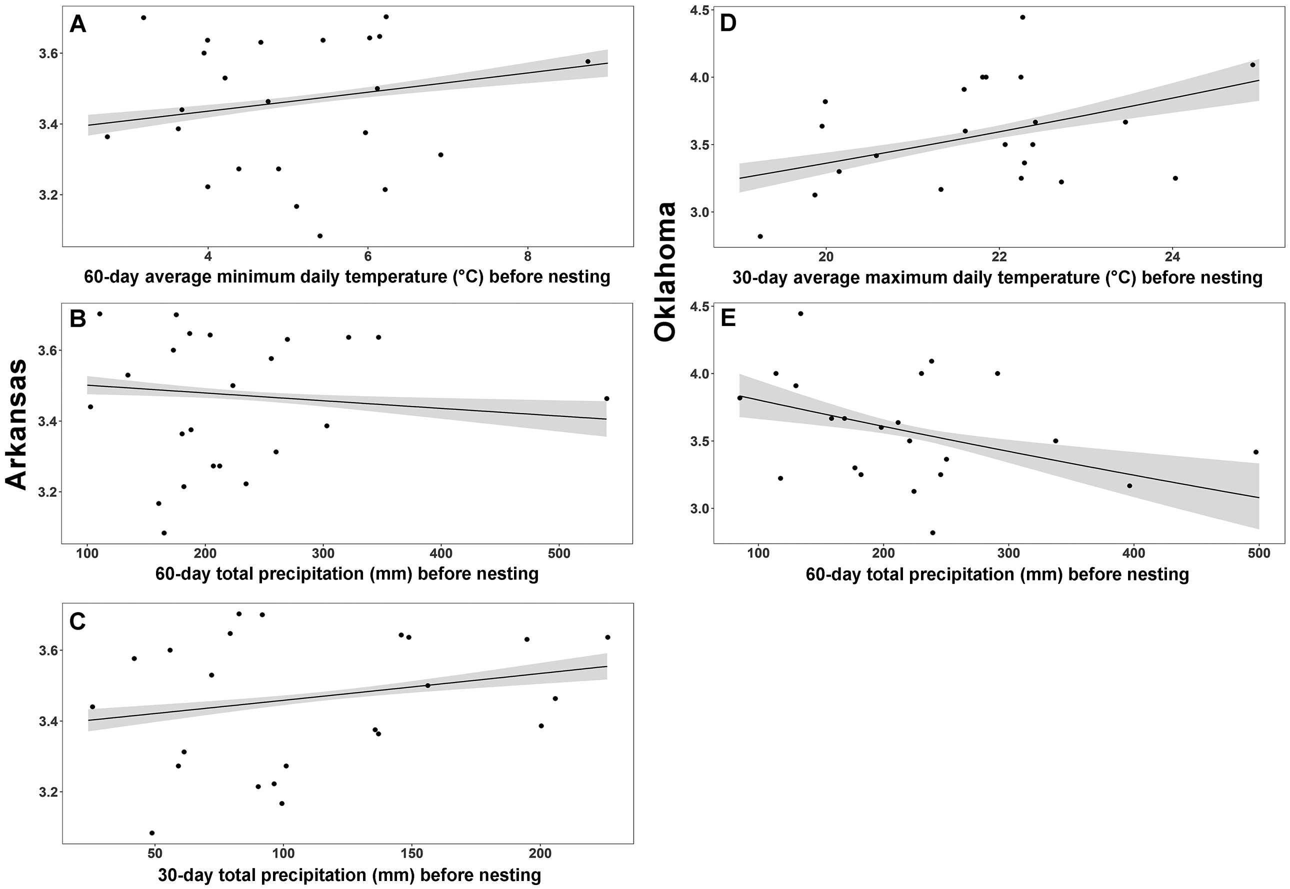

FIGURE 5. Relationships between pre-nesting weather conditions and population-level average clutch size for Red-cockaded Woodpeckers. Supported predictors for the Arkansas population included (**A**) average minimum daily temperature during the 60-day window preceding nest initiation and (**B** and **C**) total precipitation during the 60- and 30-day windows preceding nest initiation. Predictors for the Oklahoma population included (**D** and **E**) average maximum daily temperature and total precipitation during the 30- and 60-day windows preceding nest initiation.

This difference in the effect of precipitation may relate to mechanisms specific to different time windows, populations, and amounts of precipitation. For example, opposing patterns may arise because different maximum levels of precipitation occurred in different time windows and populations. Precipitation only had a positive effect on clutch size when the maximum observed value of total precipitation was ~200 cm; whereas precipitation effects were negative in both cases with much higher levels of maximum precipitation (~500 cm; Figure 5). Perhaps up to a point, increased rainfall preceding nesting increases arthropod abundance, creating good nesting conditions and allowing woodpecker females to attain suitable physiological condition for egg-laying (Cady et al. 2019), but very high levels of precipitation may outweigh the positive effects of increased food supplies by limiting foraging opportunities (as suggested for nest initiation).

The consistent effect of warmer temperatures resulting in more fledglings for both populations may reflect increased parental foraging opportunities and thus provisioning of nestlings. As with clutch size, precipitation effects were site-specific, with the fledgling number decreasing and increasing, respectively, with greater precipitation during nesting in Oklahoma and Arkansas. As these patterns mirror the context-specific effects of precipitation on clutch size, we suggest similar mechanisms may be at play (i.e. mechanisms related to different time windows, populations, and/or amounts of precipitation). In particular, fledgling numbers may increase with increasing precipitation up to a point (as evidenced by the positive relationship for Arkansas when the maximum observed value of total precipitation during nesting was ~325 cm), but very high precipitation levels may decrease fledgling number (as evidenced by the negative relationship for Oklahoma with a maximum precipitation value >400 cm). During the nesting period, very cool and rainy conditions may reduce foraging opportunities, as has been shown for woodpeckers in Texas (Conner et al. 2005) and more broadly

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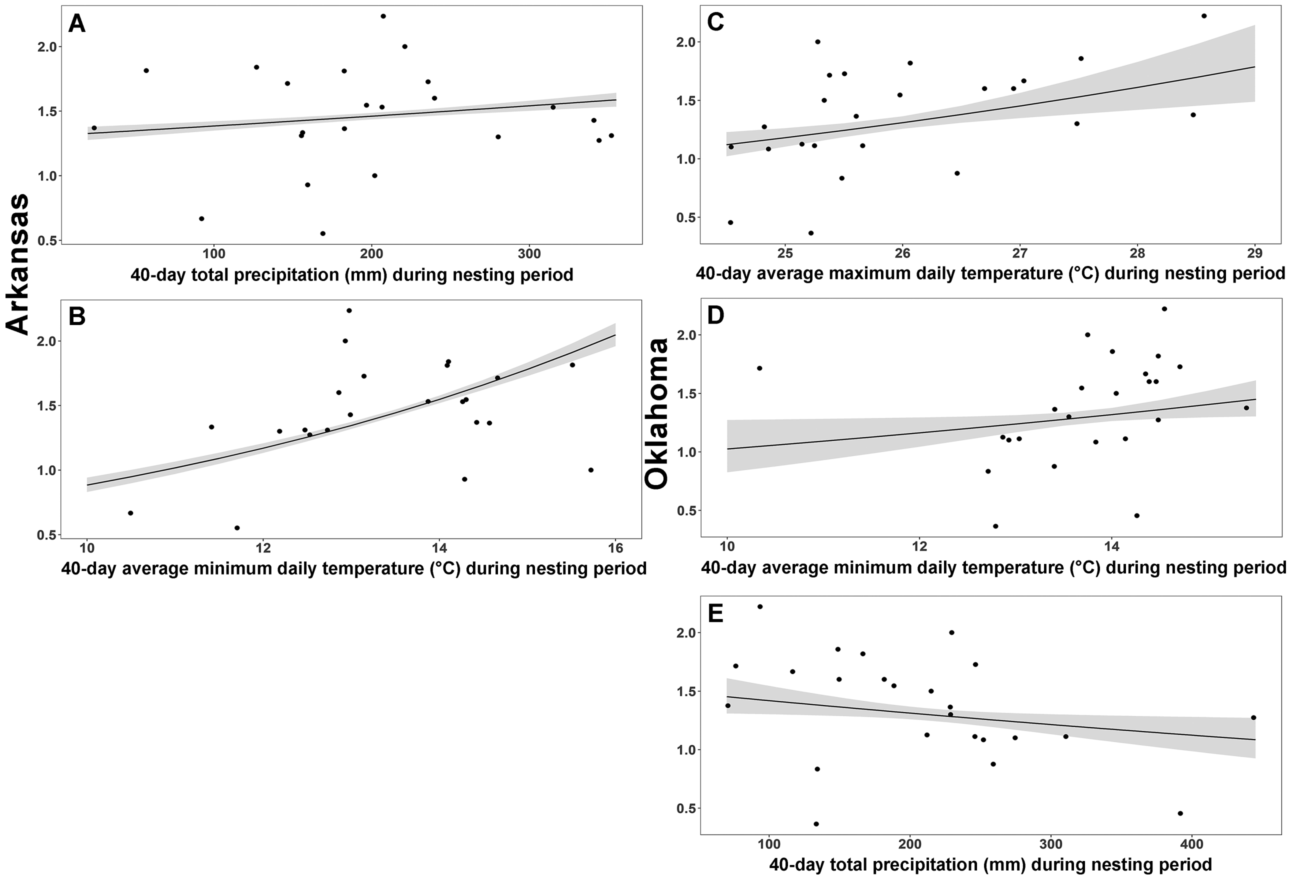

FIGURE 6. Relationships between weather conditions during the 40-day nesting period and population-level average number of nestlings fledged for Red-cockaded Woodpeckers. Supported predictors for the Arkansas population included (**A** and **B**) total precipitation and average minimum daily temperature during the 40-day nesting period. Predictors for the Oklahoma population included (**C**–**E**) average maximum daily temperature, minimum daily temperature, and total precipitation for the same time period.

TABLE 3. Top models for nest-level analyses of discrete weather event effects on nesting success and partial brood loss for Red-cockaded Woodpeckers (*Dryobates borealis*) in Oklahoma (OK) and Arkansas (AR). Standard deviation of year and cluster random effects is also shown. For a list of all models ranked and used for inference, see Supplementary Material Tables 11–14. For a description of weather variables, see Table 1, Figure 2, and text.

Response variable	Study site	Weather variables	AIC	ΔAIC	w_i	Year (σ^2)	Cluster (σ^2)
Nest success	OK	Intercept	256.3	0.00	0.196	0.271	$3.43e^{-8}$
	AR	19d abs tmax + Male age + Group size + Nesting date	232.1	0.00	0.192	0.213	0.00
		19d abs tmax + 11d abs ppt + Male age + Group size + Nesting date	232.9	0.90	0.124	0.251	0.00
		11d abs ppt + Male age + Group size + Nesting date	233.3	1.30	0.102	0.248	0.00
		19d abs tmax + 19d abs tmin + 11d abs ppt + Male age + Group size + Nesting date	233.7	1.70	0.084	0.258	0.00
Partial brood loss	OK	11d abs ppt + Nesting date	432.9	0.0	0.278	0.00	0.004
	AR	Intercept	535.1	0.0	0.569	$1.84e^{-15}$	0.00

for many bird species (Pasinelli 2001, Radford et al. 2001, Öberg et al. 2015). Reduced food supplies and unfavorable thermal conditions during rainy periods could cause increased mortality for woodpecker nestlings (Neal et al. 1993). Notably, since we only used the first nesting attempts for our analysis (i.e. we excluded re-nest attempts), our results are not a reflection of total productivity for each breeding season.

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Nest-Level Analyses of Discrete Weather Event Effects on Brood Reduction and Nest Success

For nest-level analyses—in which we sought to capture discrete weather events instead of averages and tailored time windows to initiation dates of each nest—effects of the weather variables we measured were limited. No weather variables were associated with nest success for the Oklahoma population; however, the absolute maximum temperature during the 19-day window from day 7 to 26 in the nestling period had a negative effect on nest success for the Arkansas population. The differing results between sites may relate to differences in topography and density of overstory and midstory trees described under "Study Area" (Masters et al. 1989); denser tree canopies and greater shading in Oklahoma, as compared to Arkansas, may better moderate effects of heat and precipitation on nestlings and outcomes of individual nests. The negative effect of temperature on nest success opposes the general positive effect of temperature on population averages of clutch size and fledgling number. This differential effect of warm conditions suggests that the factors causing nests to fail differ from those affecting the timing of nesting and the ability to raise young. Whereas we have speculated that the latter is related to foraging conditions, the former might relate to factors influenced by maximum temperatures (e.g., heat stress in woodpeckers and activity of nest predators such as rat snakes).

For both populations, no weather variables were associated with partial brood loss (i.e. number of nestlings dying between hatching and nestling day 7), indicating that discrete weather events may have little influence on the loss of nestlings in the first week after hatching. Garcia (2014) found higher precipitation to increase woodpecker partial brood loss in North Carolina, but this study included loss of nestlings after the first week after hatching in the measure of partial brood loss. The speculated cause for this pattern was that unpredictable weather due to climate change may alter the ability of woodpeckers to time nesting with ideal foraging conditions, resulting in lower nestling weights and more partial brood loss due to nestling exposure to cool and wet conditions (Dyrcz and Halupka 2009, Anctil et al. 2014, Garcia 2014). It may be that this explanation applies to nestling loss after, but not during, the first week. Indeed, in North Carolina, loss of nestlings after the first week was once rare (LaBranche and Walters 1994) but has increased greatly over time (Garcia 2014). Alternatively, other unmeasured aspects of intense weather may have greater effects on partial brood loss, as well as on nesting success. Examples of other factors that could be incorporated into similar future analyses include the number of intense temperature and/or precipitation events and the deviation in the intensity of such events from long-term averages (e.g., deviations in precipitation as captured using indices like the standardized precipitation evapotranspiration index, Vicente-Serrano et al. 2010).

Although woodpecker group size and breeder age had significant influences on nest success when these factors were evaluated in preliminary analyses, neither factor was supported as a predictor of nest survival or brood loss when temperature and precipitation variables were included in analyses. This finding is unexpected because positive effects of both breeder age and group size on reproductive success are well documented in woodpeckers (Lennartz et al. 1987, Mumme 1992, McCormick et al. 2004, Walters and Garcia 2016). One possible explanation for this result is that, while group size and breeder age do appear to influence outcomes of individual woodpecker nests, interannual climate variation may have greater effects on nesting at the northwestern edge of this species range.

Conclusions and Management Implications

Peripheral populations may play a crucial role in determining the degree to which species are able to persist, adapt, and/or shift their geographic distribution in response to climate change (Hampe and Petit 2005, Rehm et al. 2015). Compared to populations at the core of the species' range, often these edge populations face unique climate conditions, are genetically distinct and/or spatially isolated, and have unique habitat associations and interspecific interactions (Geber 2008, Hardie and Hutchings 2010, Jiguet et al. 2010, Razgour et al. 2013, Picardi et al. 2020). Understanding the ecology of peripheral populations, including the demography of so-called "leading edge" populations at high-latitude edges of species' ranges (Gibson et al. 2009), is therefore important for developing and implementing conservation measures that prevent or limit climate change-caused population declines and extinctions.

This study adds to the growing body of literature regarding the effects of climate change on peripheral populations. At the northwestern edge of the woodpecker range in Arkansas and Oklahoma, we found evidence that interannual weather variation is influencing multiple aspects of woodpecker demography in ways that have implications for conservation and habitat management. At the population level, warmer temperatures in early spring generally advanced nesting and increased clutch size and fledgling number, implying that ongoing and predicted warming trends at this time of year (IPCC 2013) may benefit woodpeckers in this region if these effects translate to increased population fecundity in the future. In contrast, our results suggest that effects of precipitation changes will depend on the amount and duration of precipitation in different time periods. Combined, these results suggest that the exact combination of conditions woodpeckers experience under a future climate (e.g., hotter and wetter vs.

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hotter and drier conditions) will have important implications for reproduction and overall persistence of populations of this species at the northwestern edge of its range and elsewhere. Throughout the woodpecker range, precipitation is projected to become more variable with more frequent intense rainfall events (United States Global Change Research Program 2018). This suggests that prediction of woodpecker responses to climate change may remain difficult even with increased knowledge of weather influences on nesting.

Nevertheless, our results suggest that conditions may be improving for woodpeckers at the northwestern edge of the range, as they are in the northeastern part of the range (DeMay and Walters 2019). Although correspondence between the ranges of southern pines and woodpecker strongly suggests the species' range is limited by habitat (Conner et al. 2001), it appears that past climate at the northern range limit was also less than optimal for the species. This understanding can benefit management planning for this endangered species. Because woodpeckers depend on old-growth pine, they will be strongly limited in their ability to shift their range northward. Yet, areas along the northern range edge may become increasingly important as projected warming trends continue. There is potential to identify locations that may be suitable for reintroduction and/or population expansion north of the current range that contain suitable habitat or in which new habitat can be established. Such efforts may be essential for conserving woodpeckers and other at-risk, declining, and endangered habitat specialists in the face of a changing climate.

Several other aspects of climate that we did not account for likely also influence woodpecker nesting and demography at their northwestern range periphery. For example, climate variables related to drought can influence the occupancy and abundance of bird species, with species responding differently to droughts occurring over varying temporal scales (e.g., from 1 to 12 months before breeding; Cady et al. 2019). This suggests that weather conditions in periods earlier than 2 months before nest initiation (e.g., precipitation from the previous breeding season) may also influence food, habitat, and perhaps woodpecker physiology, in ways that affect nesting phenology, nest success, and fecundity (Fantle-Lepczyk 2016). Also, we did not assess the effects of weather in the non-breeding season on survival or other aspects of demography. Winter climate may be another factor limiting the northern extent of the woodpecker range. Ours and past research (Schiegg et al. 2002, Garcia 2014, DeMay and Walters 2019) suggest that woodpeckers have considerable plasticity that allows adjustment to weather variation, which bodes well for their ability to adapt in place to a changing climate. However, the limits to this plasticity are unknown. Our demonstration that woodpeckers adjust to climatic conditions as measured for different time windows is just the first step to understand how this species will respond to climate change. Future research should seek to determine mechanisms responsible for the demonstrated effects of temperature and precipitation on woodpecker nesting parameters. Links between climate, reproduction, and demography take many forms among bird species (Winkler and Allen 1996, Sheldon 2003, Chase et al. 2005, Cady et al. 2019). Understanding these mechanisms will be especially important to preserving populations in portions of the species' range where conditions may be deteriorating (e.g., at the southwestern range periphery; DeMay and Walters 2019).

SUPPLEMENTARY MATERIAL

Supplemental material is available at *Ornithological Applications* online.

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Ethics statement: No birds were handled throughout the duration of this study. In addition, no nests were disturbed within the course of field work.

Author contributions: M.R.F., S.R.L., and J.R.W. conceived the study. M.R.F., S.R.L., J.R.W, and R.E.W. developed and designed the methods. M.R.F. led the writing of the manuscript and conducted analyses. M.R.F., S.R.L., J.R.W., and R.E.W designed the study. M.R.F. collected the data and assisted in securing funding through his employer. All authors contributed critically to manuscript edits.

Data availability: Analyses reported in this article can be reproduced using the data provided by Fullerton et al. (2021).

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