CAVITY TREE SELECTION AND EFFECTS OF INTER-ANNUAL WEATHER VARIATION ON NESTING PHENOLOGY AND SUCCESS OF RED-COCKADED WOODPECKERS IN THE OUACHITA MOUNTAINS OF OKLAHOMA AND ARKANSAS

By

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Abstract: The Ouachita Mountains ecoregion in southeast Oklahoma and west-central Arkansas contains two populations of the red-cockaded woodpecker (*Dryobates borealis*, RCW), a federally endangered, cooperatively breeding species. Since the region is at the northwestern RCW range periphery, ecological thresholds are limiting for the species. To assess potential constraining factors for RCWs, we conducted a cavity tree selection analysis using data collected from 63 active cavity trees and 121 unused trees during 2017 - 2018. We also summarized attributes from active cavity trees and performed a chi-square analysis for directional cavity orientation. For cavity tree selection, we created single-variable generalized linear mixed models and used an AIC model comparison approach. Only one variable, canopy openness as measured from 0.5 m aboveground, was strongly supported. The χ^2 analysis indicated that cavity trees generally had a northwest orientation. We found cavity tree selection to be based on high levels of canopy openness, and to a lesser extent, large tree crown areas. However, tree age was unimportant, likely due to the abundance of mature trees in our study area.

Inter-annual weather variation is predicted to increase with climate change, causing potential range shifts for many species. RCWs may be susceptible to the effects of climate change, especially at the northwestern range periphery in the Ouachita Mountains ecoregion. We used 26 years of nesting data (1991 – 2016) from two RCW populations in the region to determine how inter-annual weather variation affects nesting date, clutch size, and number of nestlings fledged. For each population, we used daily temperature and precipitation data from Oregon State University’s PRISM® network for 3 periods (30 and 60 days before nesting and 40 days overlapping nesting) to determine effects at the population level. For a separate analysis, we created smaller windows for individual RCW nests to determine how extreme weather events (i.e. “heat waves” and high precipitation events) affected overall nest success and partial brood loss. Single-variable generalized mixed models were used for the longer windows, and mixed models were created for nest-specific windows. AIC model comparisons were conducted separately for population- and nest-level analyses. RCWs for both populations experienced shifts in nesting dates and clutch sizes in response to weather conditions leading up to nesting. RCWs also experienced reduced nestling survival to fledging with higher precipitation levels during the nesting period. For individual nests, high temperatures during the brooding period reduced the probability of nesting success for the Arkansas population, while high precipitation events reduced partial brood loss in Oklahoma. Our results indicate that RCWs are responding to inter-annual weather variation, though particular responses are complex and variable.

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CHAPTER I

RED-COCKADED WOODPECKER CAVITY TREE SELECTION IN THE OUACHITA MOUNTAINS OF OKLAHOMA AND ARKANSAS

Introduction

Understanding how wildlife species use and select habitat across spatial scales, through time, and throughout their geographic distribution, is crucial to habitat and population management efforts (Jones 2001; Mayor et al. 2009; Morris 2016). Many wildlife species that are critically endangered, threatened, or declining, are habitat-specialists and/or regionally endemic, occupying a narrow range of environmental conditions (Dobson et al. 1997; Flather et al. 1998; Preston et al. 2008). Managing the persistence and/or recovery of such species requires a thorough understanding of habitat use and selection. Gathering this information at the edges of species' distributions may be especially important because, relative to the range core, range margins are often characterized by unique climate regimes, anthropogenic stressors, and other habitat- and management-related conditions (Zhu et al. 2012; Niedzielski, Bowman 2014; Frick et al. 2018). Therefore, in addition to being important for species persistence, populations at range margins are important for determining species responses to regional and global sources of environmental change (Davis, Shaw 2001; Hampe, Petit 2005).

The red-cockaded woodpecker (*Dryobates borealis*, RCW) is a U.S.-federally endangered habitat-specialist that occupies pine-dominated savannas and woodlands in the southeastern U.S. (Ligon 1970; Jackson 1971). As with many bird species (Jones et al. 2001), RCWs appear to select habitat at multiple spatial scales, including landscape-, forest stand-, and tree-levels (Bailey, Thompson 1997; Mahon et al. 2007). RCWs excavate and occupy cavities in living, mature (60+ y/o) pine (*Pinus* sp.) trees often infected with fungal communities (e.g., *Porodaedalea pini)* that soften heartwood and expedite cavity construction (Jusino et al. 2016; Steirly 1957; Lay, Russell 1970; Jackson 1977; Conner, Locke 1982). Mature pines are essential to RCWs, as older trees contain heartwood amounts suitable for housing cavities (Clark 1993; Conner et al.1994). For example, longleaf pines (*P. palustris*) used for RCW cavities in Florida averaged 104 years old (Delotelle, Epting 1988); loblolly (*P. taeda*), pond (*P. serotina*), and longleaf pine cavity trees in South Carolina respectively averaged 75, 85, and 95 years old (Jackson et al. 1979); and shortleaf pine (*P. echinata*) cavity trees in Oklahoma averaged 149 years old (Wood, Lewis 1977). Aside from age, and compared to random trees, RCWs may select pines that are taller and with greater depth, volume, weight, diameter of the crown (i.e., the part of the tree with branches and foliage), and with less sapwood (Conner, O'Halloran 1987; Conner et al. 1994). Although tree age influences these features, surrounding forest stand conditions resulting from management practices like tree thinning and prescribed fire may influence them as well.

RCW habitat selection is well-studied in the longleaf and loblolly-shortleaf pine savannas in the species' range core (Jackson, Lennartz et al. 1979; Rudolph, Conner 1991); however, few studies have been conducted on the north and northwest edges of the RCW range, where savannas are dominated by shortleaf pine or a mix of other pines and hardwoods. In these areas, RCWs occupy forests that are much older and have a greater density of midstory and overstory hardwood stems compared to the range core (Masters et al. 1995; Doster, James 1998; Wood 1983; Kalisz, Boettcher 1991). In addition, limited information is available from anywhere in the RCW range regarding the orientation of cavity holes on cavity trees. Cavity orientation may influence thermal conditions—which may influence egg and nestling development and survival—visual concealment from predators, and/or other factors that influence nest success and reproductive fitness (Zwartjes et al. 1998; Wiebe 2001; Landler et al. 2014). Although descriptive accounts have indicated that RCWs may consistently orient their cavity holes westward (Jones, Ott 1973; Wood 1983; Locke, Conner 1983), quantitative analyses are lacking, including from the north and northwest range periphery.

We studied tree cavity selection and cavity orientation in two RCW populations at the northwest periphery of the species' range in the Ouachita Mountains of Oklahoma and Arkansas. Although RCWs select habitat at multiple spatial scales, we focused on tree-level selection because it may be an especially important process at the northwest range periphery, where mature pines are widely available across the landscape. Further, even the well-documented importance of tree age is based on studies from the core area of the RCW range, where relatively few mature pines remain due to historic forest clearing; other tree-level factors could be more important in regions with extensive stands of mature forest. Our specific objectives were to 1) quantify characteristics of active RCW cavity trees and compare them to cavity trees elsewhere in the range, 2) determine if RCWs select a particular orientation of cavity holes, and 3) compare characteristics of cavity trees to random trees to assess factors influencing cavity tree selection. For cavity trees, we hypothesized that in addition to age, other factors related to structure can predict suitability for RCW cavity excavation. Furthermore, we hypothesized that the directional orientation of cavity entrances would be random for active cavity trees in the Ouachita Mountains.

Methods

Study Species

Red-cockaded woodpeckers (RCWs) are highly social, living in groups composed of a breeding pair and up to five helper birds that assist the breeding pair in raising young, most of which are males from previous broods (Ligon 1970; Lennartz et al. 1987; Walters et al. 1988; Walters, Garcia 2016). RCWs excavate cavities in living pines (*Pinus* sp.) infected with fungi (e.g. *Porodaedalea pini*) that soften the heartwood and allow birds to more easily excavate cavities (Steirly 1957; Conner et al. 1976; Jackson 1977; Jusino et al. 2015). Each bird in a group inhabits its own cavity within a stand of cavity trees known as a "cluster" (Walters 1988). The breeding male is the dominant individual in the territory and occupies the newest cavity in the cluster, which serves as the nest for the breeding pair (Ligon 1970; Walters 1990; Conner et al. 1998). The Ouachita Mountains ecoregion forms part of western extent of *Pinus* spp. in the eastern USA. Shortleaf pine (*Pinus echinata*), a species known to tolerate dry, well-drained areas on slopes (Mattoon 1915; Masters et al. 1989), is the dominant native pine in the Ouachita Mountains available to RCWs for cavity excavation

Study Area

We conducted field research on state and federal lands in the Ouachita Mountains ecoregion in the south-central United States, an area composed of rugged topography and mixed pine-hardwood forests in southeastern Oklahoma and west-central Arkansas (Carter 1967; Burnside 1983; Masters 1995; Doster, James 1998). RCWs occur in two disjunct populations in this region, including one on the McCurtain County Wilderness Area (MCWA), managed by the Oklahoma Department of Wildlife Conservation (ODWC), and one on the Poteau / Cold Springs District of the Ouachita National Forest (ONF) in Scott and Polk counties, Arkansas, managed by the U.S. Forest Service (ODWC 2017; U. S. Department of Agriculture 2017) (Fig. 1.1). The ONF and MCWA harbor similar floral and faunal communities. However, they vary slightly from each other with regard to topography and average forest overstory age, with the MCWA having steeper slopes and greater expanses of old-growth trees. With respect to tree age, the MCWA is unique in that it has never experienced commercial timber harvest, thus the area has extensive stands of relict, mature shortleaf pine stands greater than 100 years old (Wood 1983). Although relict pine stands are scattered throughout the ONF, the majority of stands in the area used for our study, where RCW restoration activities are conducted (details in next paragraph), are composed of second-growth trees less than 100 years of age (Neal, Montague 1991; Bukenhofer et al. 1994).

Both ODWC and USFS formalized management plans in the 1990s to increase RCW populations on their respective lands, conducting activities such as prescribed burning, removing midstory hardwood trees, and intensive nest monitoring (ODWC 1991; Hedrick 2007). RCW management occurs at both the landscape level and at the level of cavity tree clusters. When new cavity trees are identified, agency personnel mechanically remove woody understory and midstory vegetation immediately surrounding the tree, both for habitat improvement and to improve accessibility for monitoring. In addition, prescribed burning is conducted on a three-year rotation at RCW cluster locations to reduce deciduous hardwood encroachment and maintain the structure of a pine-bluestem woodland / savanna (USDA 2005).

Tree Measurements

During 2017 and 2018, we obtained measurements from 63 occupied (active) RCW cavity trees and 121 unused, nearby trees. Both USFS and ODWC maintain the location coordinates (latitude and longitude) of all currently active RCW clusters, and we used their data to locate RCW cavity trees in the MCWA and ONF. We selected RCW clusters based on both accessibility and confirmation of recent RCW activity. We visited all clusters throughout the year to confirm that cavity trees were active based on the presence of an appropriate-sized cavity entrance and visible resin flow outside the cavity and along the bole of the tree (Ligon 1970). However, we avoided all active territories from mid-April through June to prevent disturbing the birds during nesting. To compare characteristics of active nest cavity trees and unused trees, we selected four unused trees near each active cavity using a variation of the Point-Centered Quarter Method (Cottam, Curtis 1956). Specifically, the cavity tree was at the center of a plot, the plot was divided into four quadrants based on cardinal directions, and a compass was used to identify the nearest shortleaf pine with a diameter at breast height (dbh) >25.4 cm in each of the four quadrants (Fig. 1.2a). To maintain systematic selection of unused trees, some active cavity trees shared an unused comparison tree due to their close proximity to each other within the cluster. The minimum dbh threshold was selected because there is no information in the literature suggesting that RCWs regularly occupy trees smaller than this diameter (Jones, Ott 1973; Kalisz, Boettcher 1991; Conner et al. 1994; Hooper et al. 1991). All selected trees were marked with a mobile GPS unit.

For a subset of active trees (32) and all 121 unused pines, we obtained 11 measurements that we used as predictor variables in our analysis of cavity tree selection, including (all details below): dbh; total height; height to live crown (i.e., height to the lowest live branch); diameter at average cavity height; crown area; percent canopy openness measured 0.5 m above ground; percent canopy openness measured 1.9 m above ground; tree age; basal area of deciduous hardwood trees; basal area of pine trees; and total basal area. Ages could not be obtained for some cavity trees, therefore analyses involving age include fewer (n = 32) active trees. For active cavity trees, we also obtained measurements for cavity height, diameter at the cavity, and compass bearing (in degrees) of the cavity entrance orientation.

All measurements for diameter were in nearest half centimeter (cm) and taken with Haglöf® 500 mm gator-eye laser calipers (Haglöf Inc., Madison, MS). Two measurements for dbh were obtained and averaged for each tree. The diameter at average cavity height measurement was based on the average cavity height of 10 randomly selected active cavity trees in our sample (8.8 m). For all height measurements, we used a TruPulse® laser hypsometer (Laser Technology Inc., Centennial, CO). To measure canopy cover, we used a Nikon® digital camera (Nikon Corporation, Minato, Tokyo, Japan) with a fish-eye lens to obtain hemispherical photos on the north side of each tree. To capture maximum canopy cover of deciduous trees and shrubs, we only obtained canopy photos during the growing season (May – September). Two photos were taken for each tree, one each at 1.9 m and 0.5 m above ground level, to capture characteristics of the tree canopy (photo at 1.9 m) and the tree canopy plus shrub/understory layer (photo at 0.5 m). We analyzed photos and extracted percent (%) canopy openness estimates using WinScanopy® 2006 (Regent Instruments, Quebec City, Quebec). For crown area, we measured crown diameter to the nearest decimeter with a measuring tape in both a north to south (labeled a in following equation) and east to west (b) direction, and then used the formula for an area of an ellipse ($A = \pi ab$) to estimate crown area (m^2). For basal area, we used a 10 Basal Area Factor (BAF) wedge prism to count the number of “in” trees, including separate counts for pine and hardwood trees, and we multiplied counts by 10 to calculate basal area in ft^2 ac^{-1}. We estimated tree age by first extracting tree cores with a 0.169” increment borer (Haglöf Inc., Madison, MS) and then counting growth rings for each core.

Data analysis

We conducted all analyses in R (R Core Team 2017). For the 63 active cavity trees, we calculated descriptive statistics (mean, range, and standard deviation) for all of the predictor variables. To assess whether RCW’s choose particular compass orientations for cavity openings, we re-grouped cavity entrance orientations into 4 categories that corresponded with cardinal directions: 0-90 (Northeast), 91-180 (Southeast), 181-270 (Southwest), and 271-360 (Northwest). We conducted a chi-square goodness-of-fit test (significance inferred at $\alpha = 0.05$) to compare numbers of observed cavities for each orientation grouping to expected proportions based on the null hypothesis that orientations are equivalently distributed among the above four orientation groupings.

To assess cavity tree selection, we constructed binomial generalized linear mixed models (GLMMs) using the “lme4” package (Bates et al. 2015). We set “status” (active or random) as the response and treated “cluster” as a random effect because trees within a cluster may not be entirely independent due to broader-scale (e.g., forest stand) characteristics and because of potential non-independence of the tree selection process for multiple birds in the same family group and cluster. To avoid multicollinearity in our model selection process, we conducted pairwise correlation tests among all 11 of the above-described predictor variables. Each predictor variable from a correlated pair was tested for correlation against the response variable, and the variable with the stronger correlation with the response was retained (a correlation matrix of all variables can be seen in Table 1.1). Following correlation tests, we constructed single-variable candidate models for each individual fixed effect. We then employed a model comparison approach using Akaike Information Criterion (AIC) corrected for small sample sizes (Burnham, Anderson 2002). We inferred that models were strongly supported when they had ΔAIC values ≤ 2 and at least 2 greater than the null (i.e., intercept-only) model. We also assessed coefficients from strongly supported models and only considered variables to have meaningful associations with response variables when the 95% confidence interval of their coefficient estimates did not overlap zero.

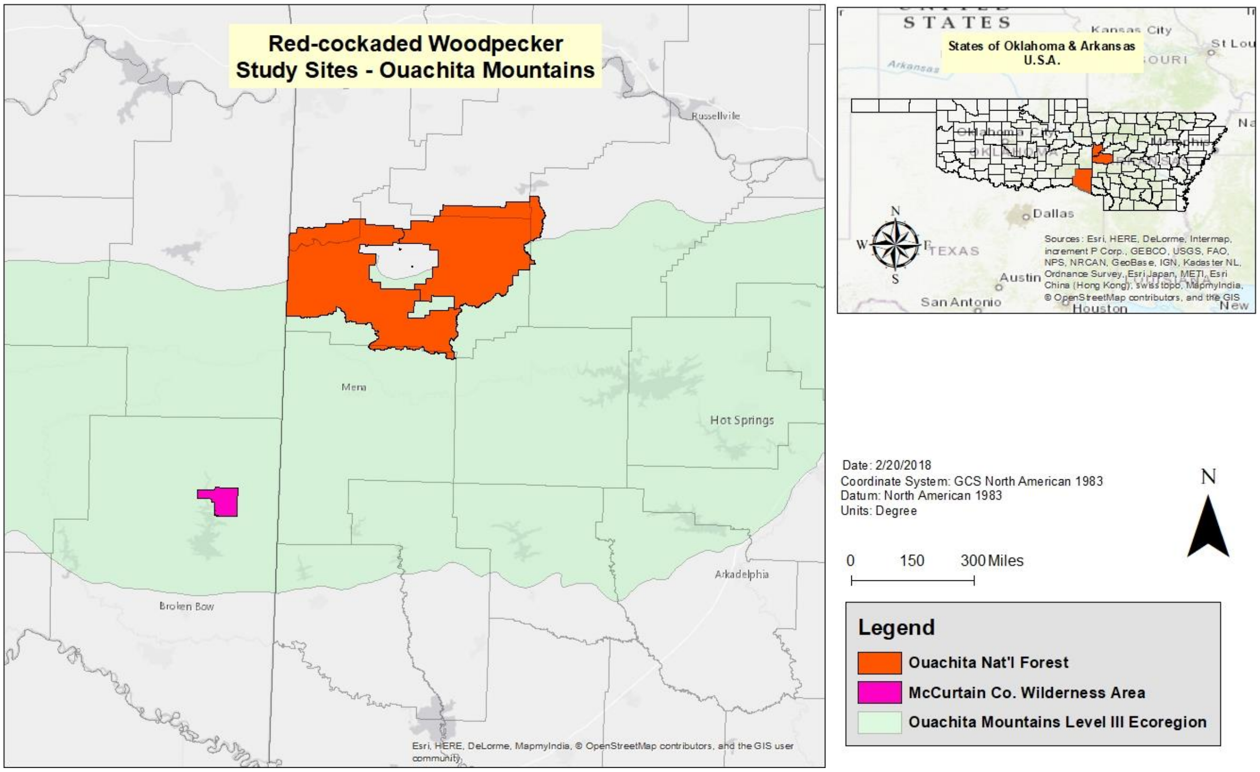


Figure 1.1 Map of study sites in the Ouachita Mountains ecoregion of the south-central United States, including the McCurtain County Wilderness Area (MCWA) in Oklahoma and the Poteau / Cold Springs District of the Ouachita National Forest (ONF) in Arkansas.

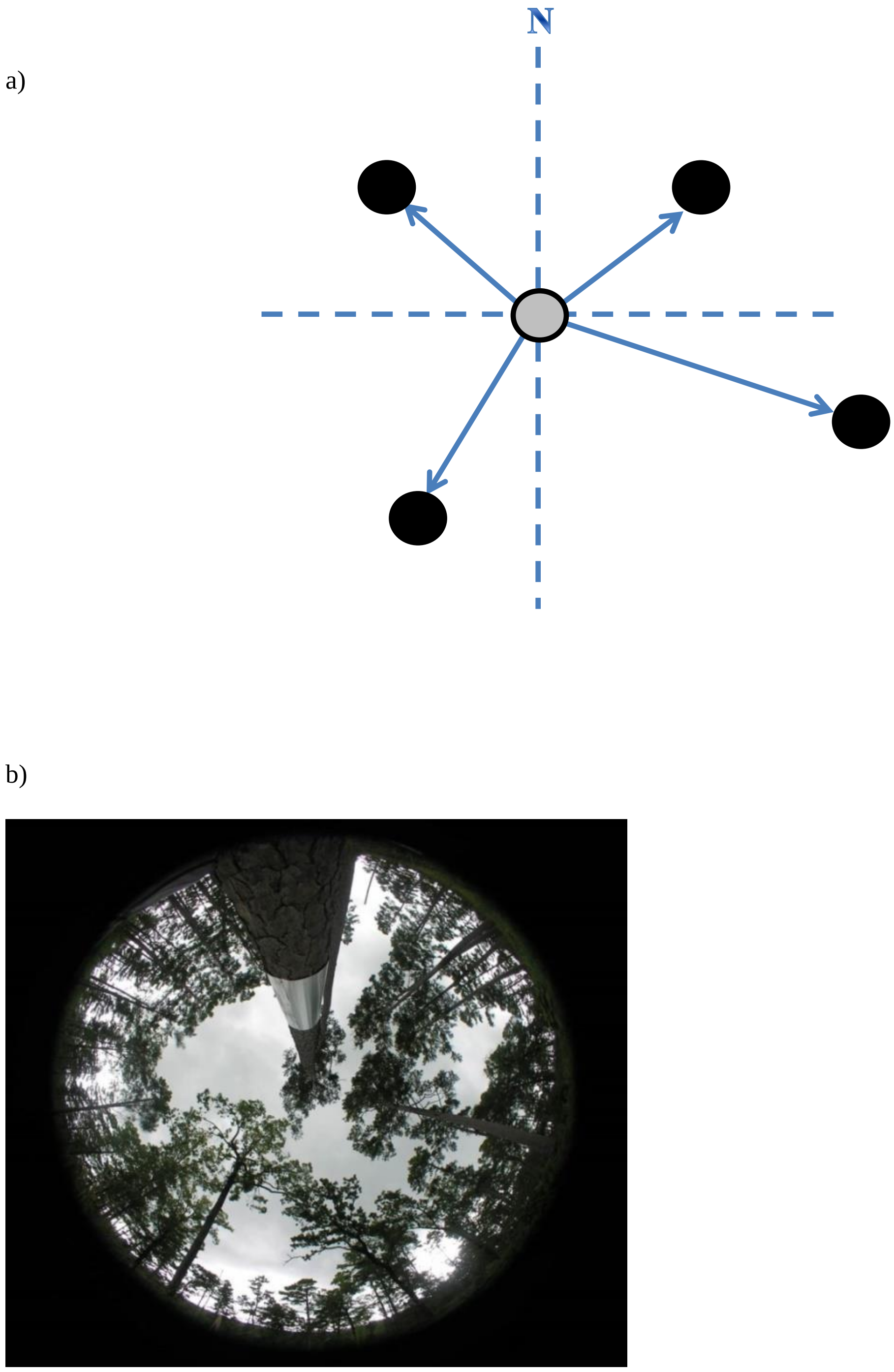


Figure 1.2 (a) Sampling design using Point-centered-quarter method (Cottam and Curtis 1956) to select unused trees (black circles) for comparison with active red-cockaded woodpecker (*Dryobates borealis*, RCW) cavity trees (gray circle at the center of the plot) in the Ouachita Mountains region of the southcentral U.S and (b) example of a hemispherical photo used to estimate percent canopy openness at active red-cockaded woodpecker cavity trees and unused comparison trees.

Results

A summary of descriptive statistics for all variables measured at cavity trees is in Table 1.2. Of particular relevance to the unique characteristics of pine forests in our study region, the average age of cavity trees (n = 32) was 101 years, average height was 25.6 m, and average dbh and diameter at cavity height were 44.6 and 41.9 cm, respectively. Regarding cavity orientation, 41% (26) of active cavities had a northwest orientation, 33% (21) had a southwest orientation, 9% (6) had a southeast orientation, and 15% (10) had a northeast orientation. The χ^2 analysis indicated that this is a statistically significant unequal distribution of orientations (n = 63, $\chi^2 = 16.556$; df = 3; p = 0.0008) (see Fig. 1.3). Analysis of χ^2 residuals (Table 1.3) indicated that, under a null hypothesis of an equal distribution of cavity orientations, the northwest orientation was almost 3 times more likely to occur than expected, the southwest orientation was one and a half times more likely than expected, the northeast orientation was one and a half times less likely than expected, and the southeast orientation was almost three times less likely than expected.

For the analysis of cavity tree selection, two pairs of predictor variables were strongly correlated with each other: (1) dbh and diameter at average cavity height (r = 0.92), and (2) total basal area and pine basal area (r = 0.73). We retained dbh and total basal area for further analyses due to their stronger correlations with the response variable. A summary of all top-performing models, along with associated coefficients and 95% CI's, is in Table 1.4. When comparing characteristics of active RCW cavity trees with random pine trees, only the model containing canopy openness as measured from 0.5 m aboveground was strongly supported ($\Delta AIC_c = 0.0$; $\omega_i = 0.93$), and this variable was positively associated with the response (Fig 1.4a). The only other model to rank higher than the null model contained a positive effect of crown area. Although support for this model was less than for the top model ($\Delta AIC_c = 5.1$; $\omega_i = 0.07$), the 95% CI of the coefficient for crown area did not overlap zero and indicated a positive association with the response (i.e., RCW cavity trees had greater crown area than random trees; Fig. 1.4b).

	Dbh	**Diam. (Avg. Cavity Height)**	**Height (Live Crown)**	**Total Height**	**Crown Area**	**Total Basal Area**	**Pine Basal Area**	**Decid. Basal Area**	**Age**	**Perc. Open (1.9 m)**	**Perc. Open (0.5 m)**
Dbh	1	**0.882**	0.114	0.386	0.469	-0.129	-0.147	0.026	0.372	-0.044	-0.039
Diam. (Avg. Height)	**0.882**	1	0.100	0.387	0.452	-0.101	-0.106	-0.005	0.327	-0.024	0.015
Height (Live Crown)	0.114	0.100	1	0.564	-0.146	0.196	0.233	-0.052	0.045	-0.099	-0.075
Total Height	0.386	0.387	0.564	1	0.004	0.112	0.152	-0.120	0.200	-0.047	-0.099
Crown Area	0.469	0.452	-0.146	0.004	1	-0.138	-0.169	0.039	0.161	0.048	0.153
Total Basal Area	-0.129	-0.101	0.196	0.112	-0.138	1	**0.886**	0.166	0.083	-0.444	-0.212
Pine Basal Area	-0.147	-0.106	0.233	0.152	-0.169	**0.886**	1	-0.210	0.063	-0.329	-0.184
Decid. Basal Area)	0.026	-0.005	-0.052	-0.120	-0.039	0.166	-0.210	1	0.043	-0.315	-0.104
Age	0.372	0.327	0.045	0.200	0.161	0.083	0.063	0.043	1	-0.137	-0.216
Perc. Open (1.9 m)	0.044	-0.024	-0.099	-0.047	0.0486	-0.444	-0.329	-0.315	-0.015	1	0.582
Perc. Open (0.5 m)	-0.039	0.015	-0.075	-0.099	0.153	-0.212	-0.184	-0.104	-0.216	0.582	1

Table 1.1. Correlation matrices (Pearson's) for tree variables measured at both occupied ("active") and unused comparison trees for red-cockaded woodpeckers (*Dryobates borealis*, RCW) in the Ouachita Mountains ecoregion in southeastern Oklahoma (MCWA) and western Arkansas (ONF).

Variable	$\bar{x}$		Median		σ	
	Active	Unused	Active	Unused	Active	Unused
dbh (cm)	44.6	44.8	44.2	44.2	7.06	8.59
Diameter at Cavity Height (cm)	41.9	NA	41.3	NA	5.95	NA
Cavity Height (m)	9.38	NA	9.3	NA	2.41	NA
Diameter (cm) at Average Cavity Height (8.8 m)	40.9	40.1	41	39.5	6.21	7.46
Height to Live Crown (m)	14.4	13.5	14.3	13.1	2.77	3.23
Total Height (m)	25.6	25.7	25.2	25.6	3.24	3.87
Age (years)	101 (n = 32)	97 (n = 121)	90	89	27.8	28.27
Crown Area (m^2)	60.3	49.6	55.64	45.3	26.01	22.07
Percent Canopy Openness (0.5 m)	40.4	33.4	39.9	34.4	8.27	9.81
Percent Canopy Openness (1.9 m)	42.3	41.6	41.7	40.6	6.86	6.82
Basal Area (Pine) (ft^2/ac)	49.2	45.4	50	40	18.60	13.9
Basal Area (Hardwood) (ft^2/ac)	3.4	3.05	0	0	7.65	6.81
Basal Area (Total) (ft^2/ac)	54.1	48.4	60	50	19.14	13.9
Cavity Orientation Bearing (Degrees)	222.5	NA	250	NA	94.21	NA

Table 1.2. Characteristics of occupied (“active”) red-cockaded woodpecker (*Dryobates borealis*, RCW) cavity trees (n = 63) and unused trees (n = 121) in the Ouachita Mountains ecoregion in southeastern Oklahoma and western Arkansas.

Directional Bearing	Residual
Northeast	-1.673004
Southeast	-2.836833
Southwest	1.527525
Northwest	2.982311

Table 1.3. Chi-square residuals for the analysis of cavity orientations of red-cockaded woodpecker (*Dryobates borealis*, RCW) cavity trees in the Ouachita Mountains ecoregion in southeast Oklahoma and western Arkansas (orientation bearing groupings include: northeast – 0-90 degrees; southeast – 91-180 degrees; southwest – 181-270 degrees; northwest – 271-360 degrees).

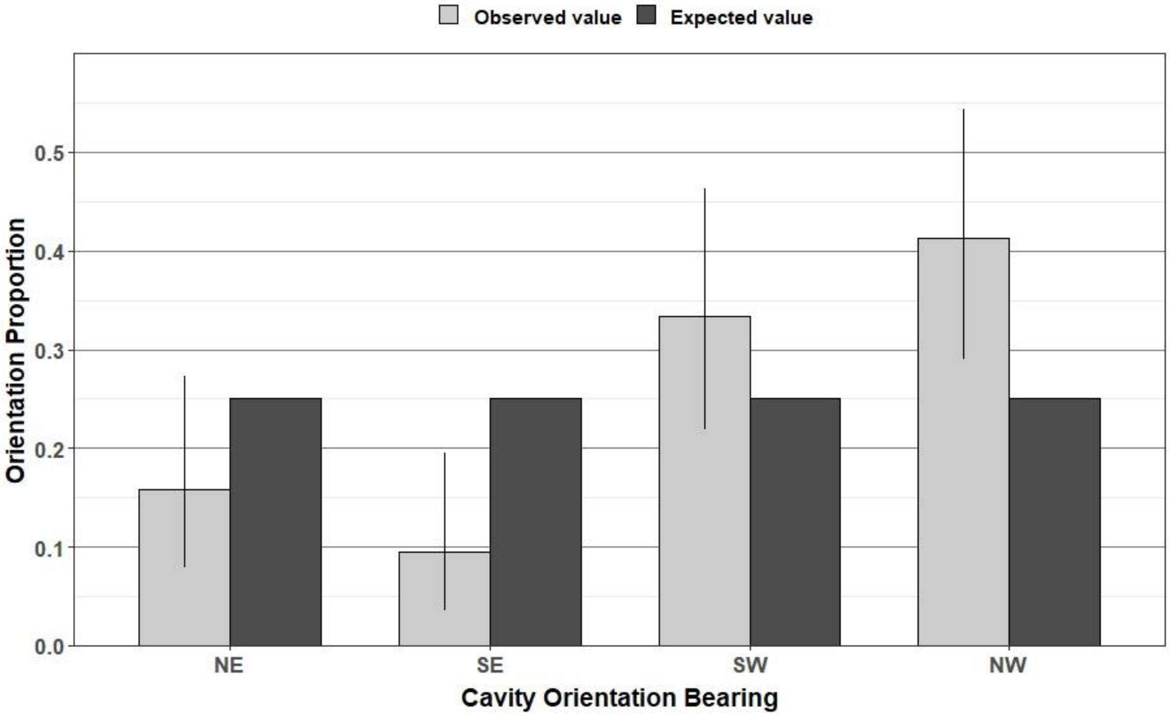
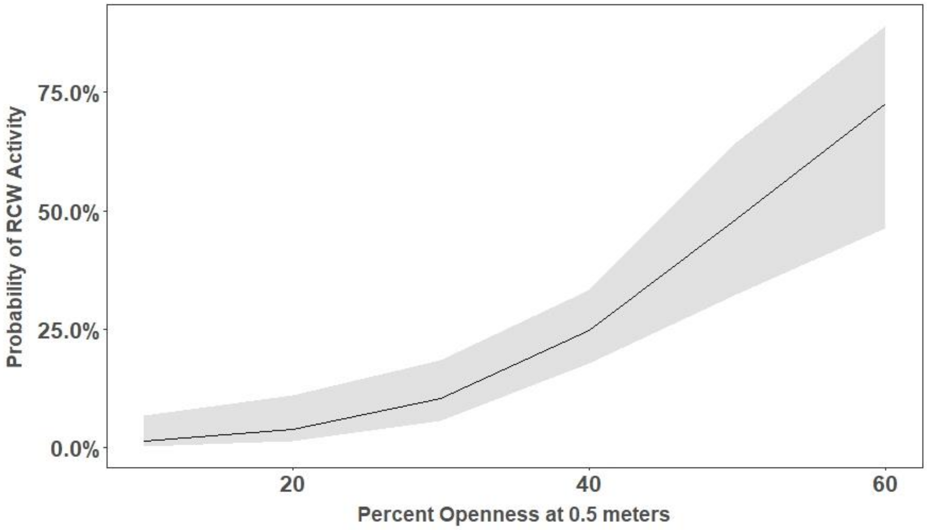


Figure 1.3. Observed and expected proportions of red-cockaded woodpecker (*Dryobates borealis*, RCW) cavity orientations for occupied ("active") trees in the Ouachita Mountains ecoregion in southeastern Oklahoma and western Arkansas. Expected proportions represent a null hypothesis that cavity orientations are equivalently distributed among compass bearing groups (orientation bearing groupings include: northeast – 0-90 degrees; southeast – 91-180 degrees; southwest – 181-270 degrees; northwest – 271-360 degrees)

a)



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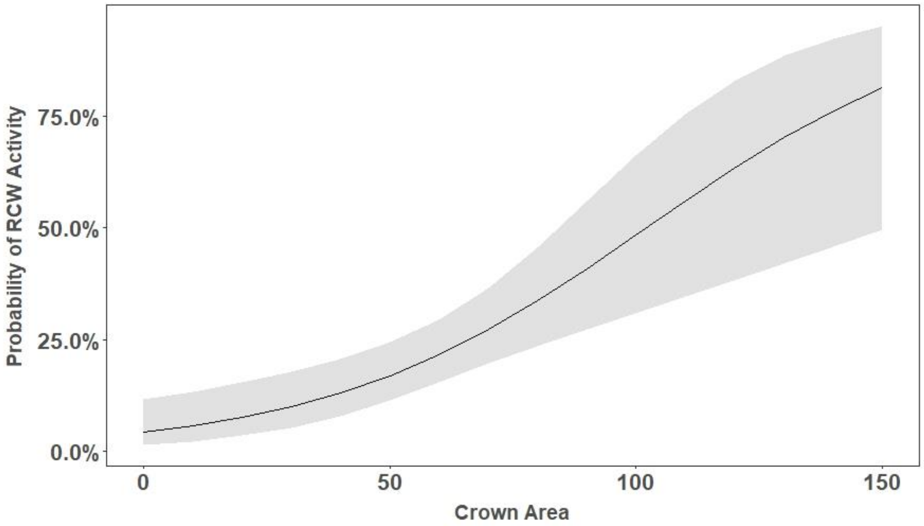

Figure 1.4. For red-cockaded woodpecker (*Dryobates borealis*) populations in the Ouachita Mountains ecoregion in southeast Oklahoma and western Arkansas, modeled relationship between probability of cavity use at a shortleaf pine tree and (a) percent canopy openness at tree as measured from 0.5 m above ground level and (b) crown area.

Discussion

At the northwest periphery of the RCW's range, we described characteristics of active cavity trees, analyzed the distribution of nest cavity orientations, and assessed which characteristics of trees and their surroundings influence cavity tree selection. Our descriptive summary confirmed that cavity trees in this region average older, but not necessarily larger, than in most other areas of the species' range. We also found that RCW nest cavities disproportionately face west, and especially northwest, which may shed light on thermal or concealment-related factors that influence cavity excavation and/or nest success. As in other portions of the RCW range, we found cavity tree selection to be based on high levels of canopy openness, and to a lesser extent, large tree crown areas; however, unlike most past studies, tree age was unimportant, likely due to the abundance of mature trees in our study area.

Characteristics of active cavity trees

Comparing our descriptive results to cavity trees studied elsewhere in the RCW range illustrates that cavity trees in our study area are older (average = 102 years) than in all previous studies, except one in Oklahoma that found cavity trees to average 149 years old (Wood 1983). Despite being older, RCW cavity trees in our study were not larger, as measured by factors such as dbh and height (Table 1.5). This pattern could result from the effects of site quality (i.e. soil composition, slope) and/or an interaction between stand-level disturbances that influence tree growth, heartwood width, and thus, suitability of pines for RCW excavation. Specifically, Conner and O'Halloran (1987) noted that RCW cavity trees exhibit evidence of growth suppression followed by a period of relatively fast growth compared to unoccupied trees. These authors also suggested such growth patterns were driven by natural and/or anthropogenic disturbances (e.g., timber harvest, tree mortality from storms and disease). Thus, in our study area, a prolonged period of growth suppression, possibly associated with decades of deciduous hardwood encroachment from 30+ years of fire suppression, may have led to stands of older, stunted trees with more heartwood and less sapwood relative to size (Conner et al. 1994; Masters et al. 1995). Furthermore, many shortleaf pine stands in the Ouachita Mountains may be growing on poor quality sites, thus influencing growth form and subsequently, the ratio of heartwood to sapwood.

Despite cavities being excavated in older trees, the observed average of cavity heights in our study (9.3 m) was within the range of heights for past studies. This may be because cavity height is influenced by multiple factors other than tree age, such as height of the midstory, proximity and size of surrounding cavity trees (Kelly et al. 1993; U.S. Fish and Wildlife Service 2003), and the above disturbance-related factors that influence tree growth, heartwood width, and thus the height at which heartwood can be excavated. A previous study in Oklahoma documented higher average cavity heights (12-13 m) at a time when habitat restoration efforts were not yet underway in RCW clusters. The initiation of midstory hardwood removal around active cavity trees starting in 1991 may have allowed RCWs to excavate cavities at lower heights compared to pre-management periods (ODWC 1991).

Model	**Variables**	**β**	**SE**	**Lower 95% CI**	**Upper 95% CI**	**ΔAIC**	**AIC Wt**
Canopy Openness	Canopy openness (%) measured from 0.5 m above ground	0.104	0.026	0.055	0.159	0.00	0.926
Crown Area	Crown Area (m^2)	0.030	0.008	0.014	0.047	5.1	0.073
Null	Intercept	-1.33	0.198	-1.73	-0.953	18.1	<0.001

Table 1.4. For top models in AICc model selection exercise, relationships between tree-related variables and binary response variable reflecting whether pine trees are occupied by red-cockaded woodpeckers (*Dryobates borealis*, RCW) in the Ouachita Mountains ecoregion in southeastern Oklahoma (MCWA) and western Arkansas (ONF).

Location	**Dbh (cm)**	**Age (years)**	**Cavity Orient. (mean bearing)**	**Total Height (m)**	**Cavity Height (m)**
Ouachita Mountains, OK & AR (Fullerton et al., 2019)	44.6 *n = 63*	101 *n = 33*	222° *n = 63*	25.6 *n = 63*	9.3 *n = 63*
Ouachita Mountains, OK (Wood 1983)	43.8 *n = 155*	149 *n = 49*	290° *n = 205*	24.8 *n = 154*	13.1 *n = 224*
Daniel Boone NF, KY (Kalisz, Boettcher 1991)	45.5 *n = 28*	NA	285°	28.8	12.2 *n = 56*
Angelina NF, TX (Conner & O'Halloran 1987)	52.7	86.9 *n = 61*	NA	28.1 *n = 61*	NA
Ft Benning/Rock Eagle/Emanuel Co., GA (Jones & Ott 1973)	43.9	76.7 *n = 4*	NA	24.6 *n = 4*	7.3

Table 1.5. Comparison of mean values for various samples of occupied (active) red-cockaded woodpecker (*Dryobates borealis*, RCW) shortleaf pine cavity trees from studies conducted at various locations.

Cavity Orientation

The majority of RCW cavities in our study had an opening facing westward, a result that matches descriptive observations in past studies, both in our study region and elsewhere in the RCW range (Hopkins, Lynn 1971; Jones, Ott 1973; Wood 1983; Locke, Conner 1983; Kalisz, Boettcher 1991). However, ours is the first region-specific analysis to statistically support that RCW cavities disproportionately face a certain direction. Several factors may have contributed to this pattern. For example, cavity orientation may be associated with the density and height of vegetation near the cavity tree (Kelley et al. 1993). Furthermore, west-facing cavities may allow increased exposure to afternoon sunlight, which may increase resin flow in and around cavity entrances, thus deterring nest predators (Dennis 1971). However, we observed no clear patterns of vegetation structure around canopy trees—likely due to midstory hardwood thinning conducted throughout RCW clusters—and confirmation of the thermal-related explanation requires assessing the amount of radiative heating at different tree orientations and times of day, as well as confirming the link between heating and resin flow. A meta-analysis of cavity orientations for woodpecker species across North America and Europe found a strong effect of latitude, suggesting that orientation is associated with thermal factors related to local climate (Landler et al. 2014). Many local studies of woodpeckers in North America and Europe have also found an equal distribution of cavity orientations (Kerpez, Smith 1990; Ćiković et al. 2014), which suggests RCW cavity orientations may be driven by ecological factors unique to the species. Since fungal-caused heartwood decay can vary throughout the tree bole (Conner, Locke 1982), one such factor could be variation in the degree to which red heart fungus causes heart rot on different tree aspects, which would influence ease of cavity excavation, and potentially, selection of cavity orientations. Further research is needed to test this explanation, as well as the potential that cavity orientation influences the microclimate of the cavity and surrounding tree bole.

Cavity Tree Selection

Previous RCW habitat selection studies in our study region and elsewhere have found that tree age, presence of red heart fungus, and stand basal area, strongly influence cavity tree selection (Jackson 1977; Delotelle, Epting 1988; Rudolph, Conner 1991). Many of these studies occurred at a time when RCW management programs were relatively new, and fewer, smaller tracts of mature pines existed where the species persisted (Jackson 1971; Lennartz et al. 1983). In our study area, restoration efforts initiated in the early to mid-1990s (Oklahoma Department of Wildlife Conservation 1991; Hedrick et al. 2007) expanded suitable RCW habitat in the Ouachita National Forest of Arkansas by increasing numbers of trees ≥60 years old in an open forest condition. Conversely, large stands of mature shortleaf pines have always been available on the MCWA in Oklahoma due to the area’s historic protection from timber harvest (Masters 1989; ODWC 1991). Our finding that tree age did not influence cavity tree selection suggests that tree age, and perhaps stand age, is less important when mature pines are widely available due to long-term restoration and/or the presence of extensive old growth forest. Similarly, the lack of a difference in basal area surrounding used and unused trees may reflect a wide availability of forest stands with an open midstory and canopy, conditions that benefit RCWs and result from regular prescribed fire and other stand- and landscape-level management.

Our results indicate that RCWs in the Ouachita Mountains select shortleaf pines in areas with greater canopy openness as measured from 0.5 meter above ground. This finding, combined with the result that cavity tree selection was not influenced by openness as measured from 1.9 m, suggests RCWs respond most strongly to vegetation density between 0.5 and 1.9 m above ground. Although forest canopy openness is important for RCW habitat selection at the cluster and landscape level (Locke et al. 1983b; Walters et al. 2000), open canopies may be less important at the tree level and/or more widely available in our study area (as described above), resulting in RCWs responding instead to variation in understory and shrub vegetation. Understory herbaceous plants provide habitat for many arthropod groups, some of which are RCW food sources (Hanula, Horn 2004). We also provide evidence that cavity trees have larger crown areas than unused pines. This finding may reflect a combination of stand- and tree-related factors. Specifically, pine savannahs are characterized by relatively open forest stands that allow individual tree crowns to spread more widely (Frost 1993; Ware et al. 1993). Broad-crowned canopy trees may also provide benefits to RCWs independent of stand characteristics, including increased resin flow (Novick et al. 2012) and more foraging opportunities (Doster, James 1998), especially in mature trees (Hooper 1996).

Our study focused on how RCWs select cavity trees based on characteristics of trees and their immediate surroundings (e.g., basal area, canopy openness around trees). However, other stand- and landscape-related factors are also likely to influence RCW habitat selection, including selection of cavity trees. Beyond stand age and stand-level density of hardwoods and small pines, little is known about RCW habitat selection at these larger scales. Previous studies show that high densities of large pines are beneficial for both cavity site selection (Bradshaw 1995; DeLotelle et al. 1987) and general foraging (Hooper, Harlow 1986; Walters et al. 2000); however, a threshold may exist beyond which too many large pines result in stands that are less than optimal for RCWs. Numerous other factors likely influence RCW habitat selection both rangewide and in our study region at the northwest range edge; these include, for example, topography, slope/aspect, predator communities, nest parasitism, food availability, anthropogenic disturbances, proximity to other populations, and landscape-scale density of pines and hardwoods. Understanding tree-level selection within the context of these multi-scale drivers will benefit RCW management. Additional research to clarify these factors could be framed under the hierarchical conceptual model of habitat selection that appears to accurately describe habitat selection by many bird species (Bailey and Thompson 1997; Saab 1999; Jones 2001). Specifically, RCW habitat selection could be envisioned as occurring across a hierarchy of scales, from landscape and regional scales at which habitat is perceived by RCWs pioneering new territories in unoccupied habitat, to landscape and/or stand scales associated with territory splits and "budding" of new territories (Hooper 1983), to landscape, stand, and tree-levels associated with selecting cluster locations, cavity trees, and foraging areas.

Our study is characterized by several limitations that must be considered when interpreting the above results. Although we believe there is sufficient prior evidence to indicate that RCWs may select cavity trees in areas with open understories, this pattern could have also arisen due to habitat management at and near occupied RCW cavity trees in our study. As a routine management activity, USFS and ODWC initiate management actions when new RCW cavity trees are identified, and this includes removal of hardwood trees and shrubs immediately surrounding cavity trees. Further, some clusters were in a management unit that received a prescribed burn during the study period, which resulted in removal of much of the midstory, shrub, and herbaceous understory foliage. An additional limitation is that we did not separate cavity trees used for nesting from those used for roosting by helper birds; however, many features that make trees suitable for nest cavity excavation should also apply to roosting trees. Further, we only examined factors influencing cavity tree selection, not those influencing if cavities produce fledglings. In shortleaf pine stands, male RCWs use the newest cavity in the cluster as the nest cavity, presumably due to high resin flow (Conner et al. 1998). However, nesting success has not been positively associated with characteristics of the occupied tree or cavity itself. Understanding how these and other habitat-related factors influence RCW population demographics is important for population sustainability and management.

Finally, other tree characteristics not measured in this study (e.g., ratio of heartwood to sapwood; chemical composition of resin) have been associated with RCW cavity tree selection in other areas of the species' range (Conner et al. 1994; Conner et al. 2003). These and other features of cavity trees, such as fungal communities and bark thickness, warrant further research at the RCW's northwest range periphery.

Conclusion and Implications for RCW Habitat Management

In a region with extensive mature trees and forest stands, tree age and stand basal area were less important for RCW cavity tree selection than understory/shrub layer openness and tree crown width. This result provides novel insight into habitat selection in the understudied northwest periphery of the RCW range, and may provide a window of insight into future RCW cavity tree selection in other regions as forests continue to mature. Our results are also important to managing a species at its range periphery, where habitat conditions and climate are different from in the more well-studied range core. Further, we documented consistent westward cavity orientations, suggesting a potential benefit to RCWs of placing cavities in a particular direction; this information is useful for land managers responsible for installing artificial cavities for the establishment of RCW recruitment stands (U.S. Fish and Wildlife Service 2003). Managers would be well advised to pay attention to cavity directional orientation trends in their respective populations and mimic them as closely as possible when establishing such sites. Understanding habitat selection across the entire range of threatened and endangered species, including peripheral populations, is critical to conservation efforts as global change stressors like climate change, urbanization, and habitat loss continue to increase.

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CHAPTER II

WEATHER EFFECTS ON NESTING PHENOLOGY AND SUCCESS OF THE RED-COCKADED WOODPECKER AT THE NORTHWESTERN PERIPHERY OF ITS RANGE

Introduction

The effects of climate change, including increases in average, minimum, and maximum temperatures, and abnormal precipitation patterns including prolonged droughts and intense precipitation events, are expected to profoundly alter ecosystems and impact biodiversity from global to local scales (Dawson et al. 2011; Bellard et al. 2012; IPCC 2013). Over the last two decades, the number of studies measuring climate change impacts on wildlife has increased substantially, and birds are particularly well-studied (Crick et al. 1999, Dunn, Winkler 1999, Wann, Aldridge et al. 2016). Weather patterns strongly influence avian behavior, phenological events (e.g., migration timing and breeding events), survival rates, and reproductive output (Dunn, Winkler 1999, Jenni, Kerry 2003, Pipoly et al. 2013, Wann et al. 2016). Such impacts are of substantial concern to researchers and conservation organizations seeking to mitigate climate change effects, including agencies responsible for managing bird populations and habitats under a changing climate (e.g., U.S. Forest Service 2008, Oklahoma Department of Wildlife Conservation 2015).

The occupied ranges of many bird species are expected to shift as increasing 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, Yohe 2003; Sekercioglu et al. 2008; Morin, Thuiller 2009). Populations on the edge of a species' range may be the most vulnerable to climate-related effects because they are often constrained by suitable habitat and temperature-tolerance thresholds (Geber 2008; Hardie, Hutchings 2010). Further, many aspects of a species' foraging ecology and habitat selection can differ at the range periphery as compared to the majority of the occupied range (Zhu et al. 2012; Niedzielski, Bowman 2016). Changes in avian breeding phenology and reproductive success in response to climate change, and including at range peripheries, are of particular interest to researchers and conservation managers because such demographic changes may greatly influence the risk of population decline and extinction at a variety of spatial scales (Martin et al. 2017; Pipoly et al. 2013).

The red-cockaded woodpecker (*Dryobates borealis*, RCW) is a federally endangered, cooperatively-breeding species that inhabits mature pine, fire-maintained savannas and woodlands in the southeastern United States (Ligon 1970; Jackson 1971; Lennartz et al. 1987; Walters et al. 1988; U.S. Fish and Wildlife Service 2003). At the westernmost periphery of its range in the southcentral U.S., two populations of RCWs occur, one in Oklahoma and one in Arkansas, with both on state and federal lands within the Ouachita Mountains Ecoregion (Carter 1967; Wood, Lewis 1977; Masters et al. 1989). RCWs are social, exhibit high site-fidelity, and excavate cavities almost exclusively in living, mature pines (Steirly 1957; Ligon 1970; Walters et al. 1988). With its unique life history and specialized habitat requirements, the RCW may be highly susceptible to the effects of climate change, and the populations in the Ouachita Mountains may be especially threatened because historic conditions on their northwestern range periphery may already represent climatic tolerance thresholds for the species. Although the effects of weather-specific events (Neal and James 1993, Conner et al. 2005) and climate change (Schiegg et al. 2002; Williamson et al. 2016; Garcia 2014) have been measured for RCW populations in the eastern and southern portions of the range, no research has addressed possible effects on the northwestern edge of the RCW range. Most RCW ecology studies have been conducted in longleaf or mixed pine forests (Lennartz et al. 1987; Conner, Rudolph 1991; Ross et al. 1997, Ramirez, Ober 2014) within the species' range core. However, less is known about RCW ecological constraints in shortleaf pine-dominated systems. Furthermore, impacts of climate change along the range periphery are particularly important to establishing range-wide patterns for the species' long-term viability.

We addressed this research gap using long-term datasets (1991 – 2016) of RCW nesting phenology and reproduction for the Oklahoma and Arkansas populations. Our specific objectives were to (1) at the population level, assess how changes in average weather conditions (average temperature and precipitation) influence nest initiation date, clutch size, and number of nestlings fledged, and (2) at the individual nest level, assess how climate-associated extreme weather events (maximum and minimum temperatures and extreme precipitation events) influence 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 would advance RCW nest initiation dates and increase clutch sizes; 2) At the population level, below average temperatures and above average wet periods during the brooding period (i.e., an extended number of days with high precipitation) would reduce numbers of nestlings fledged, and 3) At the individual nest level, extreme low and high temperatures and extreme precipitation events (i.e., high single-day precipitation totals) would negatively affect nest success and increase the number of nestlings lost to partial brood loss. We hypothesized that warmer temperatures before the nesting period will advance nesting dates and increase clutch sizes. Furthermore, we hypothesized that cooler and wetter conditions during the brooding period will reduce the number of nestlings fledged.

Methods

Study Area

We conducted field research in two study sites, one in southeastern Oklahoma and one in west-central Arkansas (Fig. 2.1). The study sites are separated by approximately 50 km, and both areas are in the Ouachita Mountain ecoregion of the southcentral U.S., which is characterized by small mountains, large hills, and steep, rugged topography with elevations ranging from 183 to 415 meters (Burnside 1983; Kelly et al. 1994; 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 (*Pinus echinata*) more prevalent on drier, south-facing slopes (Carter 1967; Masters 1995).

In the Oklahoma study site at the southern edge of the Ouachita Mountains ecoregion, we conducted research in the 5700 ha McCurtain County Wilderness Area

(MCWA), the largest contiguous tract of old-growth shortleaf pine forest in the United States (Stahle et al. 1985). After designation as a state Wilderness Area by the Oklahoma Department of Wildlife Conservation (ODWC) in 1918, very little active land management was conducted for over 70 years. In 1991, and to benefit the MCWA's population of RCWs, the ODWC entered into a formal agreement with the U.S. Fish and Wildlife Service (USFWS) to begin implementing mechanical removal of hardwood trees and reinstating prescribed fire (on a 3-yr dormant-season burn rotation) in and around active RCW clusters (ODWC 1991).

The Arkansas study site was located at the northern edge of the Ouachita Mountain ecoregion in the Ouachita National Forest (ONF). Here, the U.S. Forest Service (USFS) began a large-scale pine-bluestem habitat restoration effort in 1994 for the purposes of recovering the RCW population present in the Poteau/Cold Springs District of the ONF (Hedrick 2007). Similar to the MCWA, this restoration area has received a three-year fire rotation supplemented by selective thinning of hardwoods and small pines in areas with RCW family groups (USDA 2005). Although the Oklahoma and Arkansas study sites are very similar with regards to plant community composition and structure, they vary slightly from each other in topography, with the MCWA characterized by more complex topography and steeper slopes. The overall age of the forest overstory also differs; some shortleaf pine stands in the MCWA have a mean age of nearly 150 years, as they were never harvested commercially for timber (Wood 1983), while the majority of stands in the ONF restoration area are composed of second-growth trees less than 100 years of age (Neal, Montague 1991).

Data Collection

To examine the effects of climate variation on RCW nest initiation dates, nest success, and nest productivity, nesting data were obtained for both the ONF and MCWA populations. Arkansas and Oklahoma data were originally collected by USFS and ODWC biologists, respectively. At ONF, USFS began conducting intensive RCW nest and population monitoring in 1991, while ODWC started gathering complete MCWA nesting data in 1992 (W. Montague, pers. comm, Oklahoma Department of Wildlife Conservation 1992). Although ODWC has continued to monitor and record RCW nesting attempts through the present day, the ONF significantly reduced population monitoring in 2013; thus, annual nesting data used for this analysis ranged from 1991 to 2013 for the Arkansas population and from 1992 to 2016 for the Oklahoma population. In both sites, population monitoring was conducted in accordance with established USFWS guidelines, with nests checked weekly from egg-laying to fledging (USFWS 2003). Data collected for each year included estimated date of nest initiation for the first nesting attempt (approximate date first egg was laid), clutch size, number of nestlings hatched, number of nestlings present when banded at approximately 7 days of age, and estimated number of nestlings fledged at 26 days after hatching (26 days is the average length of the RCW incubation period; Jackson 1994). Additionally, USFS personnel recorded both group size (breeding pair plus any helper birds in the territory) and age of the breeding pair for each RCW cluster in ONF.

For both populations, we estimated the mean center point across all active RCW cluster locations using the Mean Center tool in ArcMap (ESRI 2011) and GPS coordinates for clusters. Climate data were then downloaded from the PRISM Climate

Group website (Oregon State University 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 4 km resolution, and time series data were obtained for each 4km 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 of the following analyses were conducted separately for MCWA and ONF. To capture potential effects of inter-annual weather variation on RCW reproduction at the population level, we averaged nesting variables across all nests for each year and treated years as replicates. Nesting variables assessed at this population level included median nest initiation date (treated as Julian dates for purposes of analyses; Chi 1979), clutch size, and estimated number of nestlings fledged. To assess effects of weather conditions during different time periods relevant to RCW nesting, we created several 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 nests and years for each study site. 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 nest initiation date as above. This 40 day period was selected to capture the average RCW egg-laying period (3 days), average incubation period (11 days), and average period from hatching to fledging (26 days) (Jackson 1994).

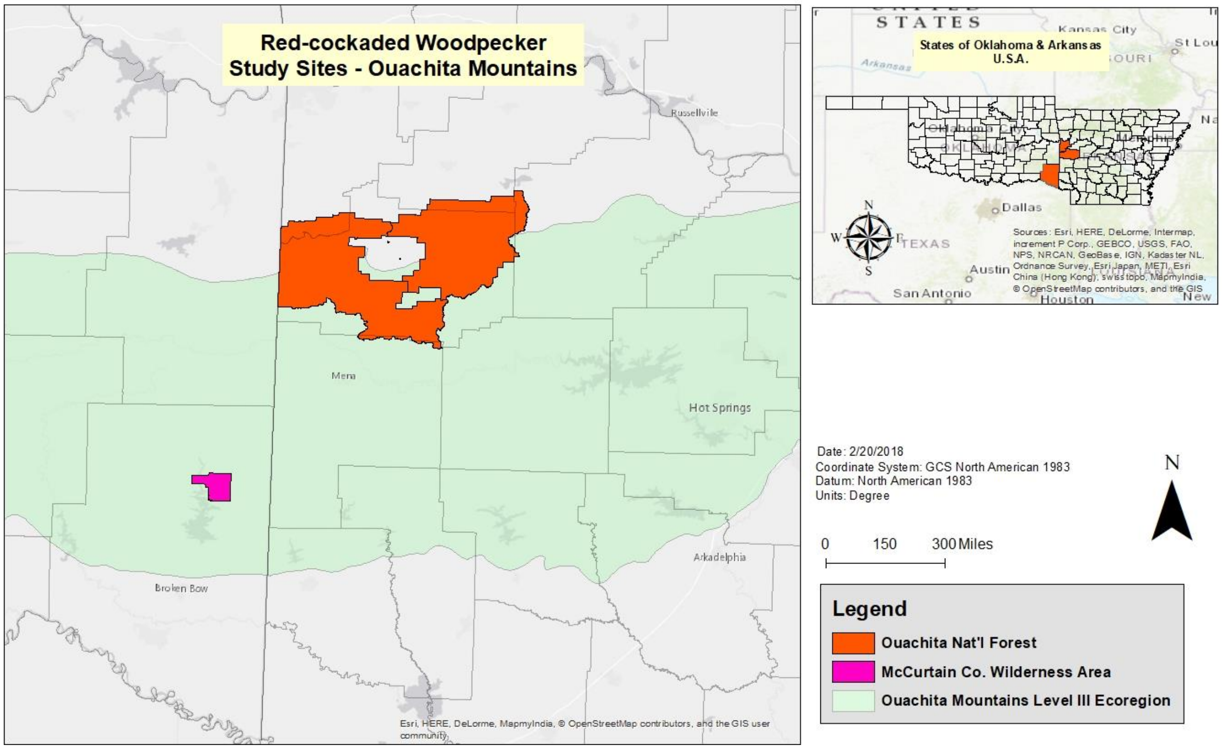
We conducted all analyses in R (R Core Team 2017). For the population-level analyses, we created generalized linear models (GLMs) with climate variables as fixed effects and using a Gamma distribution with a log link (Pescim, Nadarajah 2015) because all values of the response variables were greater than zero and distributions were generally right-skewed. Specifically, for the nest initiation and clutch size analyses, we only tested weather variables for the two windows (30 and 60 days) prior to median nest initiation. For the fledgling analysis, we only tested the weather variables for the 40 day window from nest initiation to fledging. Pairwise correlation tests among all predictor variables were conducted for each site and analysis (Tables 2.1-2.2). Before creating a global model, each predictor variable from a correlated pair was tested for correlation against the response variable of interest, and to reduce multicollinearity in models, we only retained the predictor variable that was more strongly associated with the response variable. Using the "stepAIC" function in the R package "MASS", we then used a backwards stepwise approach to model selection, beginning with the global model containing all uncorrelated predictor variables and removing one variable at a time.

For the individual nest-level analyses, we constructed Generalized Linear Mixed Models (GLMMs) using the "lme4" package (Bates et al. 2015) because multiple nests were included for each year. Therefore, we treated "year" as a random effect. Before testing weather variables at the nest level, we first conducted preliminary analyses for both nest success and partial brood loss on ONF using only breeder age and group size as fixed effects in separate binomial GLMMs because previous research has shown that group size and breeder experience, especially in cooperatively breeding species, can positively influence reproductive success (Mumme 1992; Lennartz et al. 1987; Conner et al. 2001; McCormick et al. 2003; Walters, Garcia 2016). This “RCW demographics” analysis was only conducted for the ONF because breeding male age and group size data were only available for this study site, but only for a subset of years. Both age of the breeding male and group size were each statistically significant and had positive relationships with nest success. However, neither variable had a strong influence on partial brood loss for individual nests on ONF.

To capture potential effects of extreme weather events on nesting success (i.e., whether nests successfully fledged at least one nestling) and partial brood loss (i.e., the number of nestlings lost from the egg stage to nestling day 7, when nestlings were typically banded), we also conducted analyses at the individual nest level (i.e., individual nesting attempts treated as replicates). For this analysis, we used initiation dates for individual nests to define unique weather windows for each nest, with the objective of determining whether absolute maximum and minimum temperatures and extreme precipitation events cause nest failure and partial brood loss. Since conditions several weeks prior to nesting can affect RCW incubation and nestling periods (Schiegg et al. 2002), and because smaller time windows may be more appropriate for capturing single extreme events, we defined 2 windows prior to nest initiation for each nest (7 and 14 days). To assess the effect of extreme weather events while nests are active, we also defined 3 windows after nest initiation. These included 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 nest-level analyses, we treated partial brood loss as a count variable modeled using a Poisson distribution and nest success as a binary variable modeled using a binomial distribution. As with the preliminary demographics analysis, we used GLMMs with “year” treated as a random effect and extreme climate event variables (absolute maximum and minimum temperature, and absolute maximum daily precipitation value) as fixed effects. As with the population-level analyses, we only tested weather variables for time windows considered relevant to the reproductive event of interest. Specifically, for the partial brood loss analysis, we only included the weather variables for the 11 day incubation window and 7 day window between hatching and nestling banding age. We excluded all four pre-nest initiation windows for the partial brood loss analysis because we speculated that extreme events occurring prior to RCW nesting would have little measurable effect on partial brood loss, a loss of some nestlings in a brood from several potential causative factors (e.g. parental brood reduction, predation, siblicide, etc.) (Mock 1994). Assuming that conditions both before and during nesting likely influence nesting success, we used all 7 nest-specific windows for the nest success analysis, including all those before and after nest initiation (see Table 2.3). Breeding male age was included as a covariate in all models for the nest-level analyses for overall success and partial brood loss on ONF-PD (see Tables 2.3b – 2.4b)

For all response variables assessed at the individual nest level, we used a similar approach to identifying and excluding correlated predictor variables as described for the population-level analysis. For the GLMM analysis, we employed a model comparison approach using Akaike Information Criterion (Burnham, Anderson 2002) rather than a stepwise AIC approach, due to computational challenges of applying the latter to mixed models (Bolker et al. 2009). We inferred that models were strongly supported when they had ΔAIC values ≤2 and at least 2 greater than the null (i.e., intercept-only) model, and when they did not include uninformative parameters (Arnold 2010). We also assessed coefficients from strongly supported models and only considered variables to have meaningful associations with response variables when the 95% confidence interval of their coefficient estimates did not overlap zero (see Tables 2.3-2.4 for list of compared models).



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Date: 2/20/2018
Coordinate System: GCS North American 1983
Datum: North American 1983
Units: Degree

Figure 2.1 Map of study sites within the Ouachita Mountains ecoregion in Oklahoma and Arkansas, USA.

a)

	60d avg tmax	**60d avg tmin**	**60d total ppt**	**30d avg tmax**	**30d avg tmin**	**30d total ppt**
60d avg tmax	1	0.682	-0.127	0.575	0.316	-0.218
60d avg tmin	0.682	1	-0.033	0.459	**0.727**	-0.238
60d total ppt	-0.127	-0.033	1	-0.081	0.104	**0.846**
30d avg tmax	0.575	0.459	-0.081	1	0.608	-0.379
30d avg tmin	0.316	**0.727**	0.104	0.608	1	-0.156
30d total ppt	-0.218	-0.238	**0.846**	-0.379	-0.156	1

b)

	40d avg tmax	**40d avg tmin**	**40d total ppt**
40d avg tmax	1	0.429	-0.565
40d avg tmin	0.429	1	0.171
40d total ppt	-0.565	0.171	1

Table 2.1. Correlation matrices (Pearson's) for pre-nesting (a) and post-nesting (b) climate window variables used for the red-cockaded woodpecker (*Dryobates borealis*. RCW) population on the McCurtain County Wilderness Area (MCWA), Oklahoma.

a)

	60d avg tmax	**60d avg tmin**	**60d total ppt**	**30d avg tmax**	**30d avg tmin**	**30d total ppt**
60d avg tmax	1	**0.901**	-0.188	**0.762**	0.683	-0.572
60d avg tmin	**0.901**	1	-0.051	0.619	**0.766**	-0.428
60d total ppt	-0.188	-0.051	1	-0.22	0.051	0.637
30d avg tmax	**0.762**	0.619	-0.22	1	**0.797**	**-0.724**
30d avg tmin	0.683	**0.766**	0.051	**0.797**	1	-0.439
30d total ppt	-0.572	-0.428	0.637	-0.724	-0.439	1

b)

	40d avg tmax	**40d avg tmin**	**40d total ppt**
40d avg tmax	1	0.719	-0.423
40d avg tmin	**0.719**	1	-0.448
40d total ppt	-0.423	-0.448	1

Table 2.2. Correlation matrices (Pearson's) for pre-nesting (a) and post-nesting (b) climate window variables used for analysis of climate change effects on population-level nesting variables for red-cockaded woodpecker population (*Dryobates borealis*. RCW) on the Ouachita National Forest – Poteau/Cold Springs District (ONF), Arkansas.

a)

Model	**Variables**
Absolute 7d Max T Pre-nesting	7d abs tmax
Absolute 7d Min T Pre-nesting	7d abs tmin
Absolute 7d Precip. Pre-nesting	7d abs ppt
Absolute 14d Max T Pre-nesting	14d abs tmax
Absolute 14d Min T Pre-nesting	14d abs tmin
Absolute 14d Precip. Pre-nesting	14d abs ppt
Absolute 11d Incubation Max T	11d abs tmax
Absolute 11d Incubation Min T	11d abs tmin
Absolute 11d Incubation Precip.	11d abs ppt
Absolute 7d hatching-to-banding Max T	7d-hb abs tmax
Absolute 7d hatching-to-banding Min T	7d-hb abs tmin
Absolute 7d hatching-to-banding Precip.	7d h-b abs ppt
Absolute 19d banding-to-fledge Max T	19d abs tmax
Absolute 19d banding-to-fledge Min T	19d abs tmin
Absolute 19d banding-to-fledge Precip.	19d abs ppt
Absolute 19d banding-to-fledge and 11d Inc. Max T	19d abs tmax + 11d inc. tmax
Abs. 7d Max T Pre-nesting and 11d inc. Max T	7d abs tmax + 11d inc. ppt
Absolute 7d Pre-nesting All Variables	7d abs tmax + 7d tmin + 7d ppt
Absolute 7d and 14d Pre-nesting Max T / Min T	7d abs tmax + 7d abs tmin + 14d abs tmax + 14d abs tmin

b)

Model	**Variables**
Absolute 7d Max T Pre-nesting & Male	7d abs tmax + Breeding Male Age
Absolute 7d Min T Pre-nesting & Male	7d abs tmin + Breeding Male Age
Absolute 7d Precip. Pre-nesting & Male	7d abs ppt + Breeding Male Age
Absolute 14d Max T Pre-nesting & Male	14d abs tmax + Breeding Male Age
Absolute 14d Min T Pre-nesting & Male	14d abs tmin + Breeding Male Age
Absolute 14d Precip. Pre-nesting & Male	14d abs ppt + Breeding Male Age
Absolute 11d Incubation Max T & Male	11d abs tmax + Breeding Male Age
Absolute 11d Incubation Min T & Male	11d abs tmin + Breeding Male Age
Absolute 11d Incubation Precip. & Male	11d abs ppt + Breeding Male Age
Absolute 7d hatching-to-banding Max T & Male	7d-hb abs tmax + Breeding Male Age
Absolute 7d hatching-to-banding Min T & Male	7d-hb abs tmin + Breeding Male Age
Absolute 7d hatching-to-banding Precip. & Male	7d h-b abs ppt + Breeding Male Age
Absolute 19d banding-to-fledge Max T & Male	19d abs tmax + Breeding Male Age
Absolute 19d banding-to-fledge Min T & Male	19d abs tmin + Breeding Male Age
Absolute 19d banding-to-fledge Precip. & Male	19d abs ppt + Breeding Male Age
Absolute 19d banding-to-fledge Min T, 14d Max T, & Male	19d abs tmin + 14d abs tmax + Breeding Male Age
Abs. 19d banding-to-fledge Max T, 11d inc. precip. & Male	19d abs tmax + 11d abs ppt + Breeding Male Age
Absolute 19d Max / Min T, 11d inc. precip. & Male	19d abs tmax + 19d abs tmin + 11d abs ppt + Breeding Male Age
Abs. 19d Max / Min / Precip., Abs. 11d inc. Max / Min / Precip. & Male	19d abs tmax + 19d abs tmin + 19d abs ppt + 11d abs tmax + 11d abs tmin + 11d abs ppt + Breeding Male

Table 2.3. Models with associated variable combinations used for red-cockaded woodpecker (*Dryobates borealis*, RCW) nesting success analysis on the McCurtain Co. Wilderness Area (MCWA), Oklahoma (a) and on the Ouachita National Forest – Poteau/Cold Springs District (ONF), Arkansas (b).

a)

Model	**Variables**
Absolute 11d Incubation Tmax	11d abs tmax
Absolute 11d Incubation Tmin	11d abs tmin
Absolute 11d Incubation Precip.	11d abs ppt
Absolute 7d hatching-to-banding Tmax	7d-hb abs tmax
Absolute 7d hatching-to-banding Tmin	7d-hb abs tmin
Absolute 7d hatching-to-banding Precip.	7d-hb abs ppt
Abs. 7d hatching-to-banding Tmin & Precip	7d-hb abs tmin + 7d-hb abs ppt
Abs. 11d Incubation Precip. & 7d hatch-band Tmin	11d abs ppt + 7d-hb abs tmin
Abs 11d Incubation Max / Min / Precip.	11d abs tmax + 11d abs tmin + 11d abs ppt

b)

Model	**Variables**
Absolute 11d Incubation Tmax & Male	11d abs tmax + Breeding Male Age
Absolute 11d Incubation Tmin & Male	11d abs tmin + Breeding Male Age
Absolute 11d Incubation Precip. & Male	11d abs ppt + Breeding Male Age
Absolute 7d hatching-to-banding Tmax & Male	7d-hb abs tmax + Breeding Male Age
Absolute 7d hatching-to-banding Tmin & Male	7d-hb abs tmin + Breeding Male Age
Absolute 7d hatching-to-banding Precip. & Male	7d-hb abs ppt + Breeding Male Age
Abs. 7d hatching-to-banding Tmin & Precip. & Male	7d-hb abs tmin + 7d-hb abs ppt + Breeding Male Age
Abs. 11d Incubation Precip.,7d hatch-band Tmin & Male	11d abs ppt + 7d-hb abs tmin + Breeding Male Age
Abs 11d Incubation Max / Min / Precip. & Male	11d abs tmax + 11d abs tmin + 11d abs ppt + Breeding Male Age

Table 2.4. Models with associated variable combinations used for red-cockaded woodpecker (*Dryobates borealis,* RCW) partial brood loss analysis on the McCurtain Co. Wilderness Area (MCWA), Oklahoma (a) and on the Ouachita National Forest – Poteau/Cold Springs District (ONF), Arkansas (b).

Results

Population-level analysis of climate effects on nest initiation, clutch size, and fledgling number

For MCWA, the median earliest nesting date across all years (1992 – 2016) was April 24th, while the median earliest nesting date for all years for ONF (1991 – 2013) was April 22nd. Among other correlated pairs of predictor variables (all correlations shown in Table 2.5), we found that total precipitation values for the 30 and 60 day windows preceding nest initiation were highly correlated for MCWA (r > 0.7) and that average minimum and maximum daily temperatures for the 30 day window preceding nest initiation were correlated for ONF. The most strongly supported variables for each analysis, as well as the estimated coefficients (±95% confidence intervals [CI]) are shown in Table 2.6.

Of the six predictor variables for the MCWA, two were eliminated (average minimum daily temperature and total precipitation for the 60 day window) following correlation tests with the median nest initiation date response variable. For the MCWA, the top model for nest initiation date contained four variables, including average maximum daily temperature for both the 30 and 60 day windows preceding nest initiation, the average minimum daily temperature for the 30 day window, and total precipitation for the 30 day window. However, assessment of model coefficients (Table 2.6) illustrated little support for an effect of average maximum daily temperature for either the 30 or 60 day windows (i.e., 95% CI's of coefficient estimates overlapped zero). Average minimum daily temperature during the 30 day window preceding nesting had a negative effect (i.e. earlier nesting date with warmer minimum temperature), and total precipitation during the same window had a positive effect (i.e. delayed nesting with increased total precipitation) (Figure 2.2).

For ONF, three of the six predictor variables were removed (average daily minimum, maximum temperature and total precipitation during 30 day window; and average daily minimum and maximum temperature during 60 day window) following the correlation test with the median nest initiation date response variable. The top model for nest initiation date in the ONF contained two variables, including total precipitation for the 60 day window (positive effect indicating delayed nesting with more precipitation) and average minimum daily temperature for the 30 day window (negative effect indicating earlier nesting with warmer temperatures) (Table 2.6 & Figure 2.3).

For the MCWA, two of the six predictor variables were removed (average minimum daily temperature and total precipitation during 60 day window) following correlation tests with clutch size. The top model for average clutch size contained two variables, including average maximum daily temperature and total precipitation for the 30 day window preceding nest initiation. The top model indicated a positive effect of average maximum daily temperature during the 30 day window (larger clutch sizes with higher temperatures) and a negative effect of total precipitation for the 30 day window (smaller clutch sizes with higher total precipitation) (Table 2.6 & Figure 2.4).

For the ONF, three of the six predictor variables were removed (total precipitation and average maximum daily temperature values for 30 and 60 day windows) following correlation tests with clutch size. The top model for clutch size contained one variable, average minimum daily temperature for the 60 day window. This variable had a positive effect on clutch size, indicating that warmer temperatures during the 60 day period preceding nest initiation resulted in larger clutches (Table 2.6 & Figure 2.5).

For the MCWA, no strong correlations existed among the three predictor variables for the 40 day nesting window; thus, all three were retained for the fledgling number analysis (Table 2.1b). For MCWA, the top model for fledgling number included total precipitation for the 40 day nesting period (negative effect), and both average minimum and maximum daily temperatures for the same period (positive effects of both) (Table 2.6 & Figure 2.6). For the ONF, both average minimum and maximum daily temperature during the 40 day nesting period were highly correlated ($r > 0.7$) (Table 2.2b); therefore, average maximum daily temperature for the 40 day nesting window was excluded following a correlation test with the response variable for fledgling number. The top model for fledgling number for ONF included total precipitation during the 40 day nesting window (negative effect) and average minimum daily temperature during the 40 day window (positive effect) (Table 2.6 & Figure 2.7).

Nest–level analysis of extreme event effects on brood reduction and nest success

Correlation tests for nest level predictor variables indicated that only two variables were correlated for both the MCWA and ONF (absolute maximum daily precipitation for the 7 and 14 day windows preceding nest initiation). A summary of all top-performing models and associated coefficients and 95% CI's for nest-level analyses is in Table 2.7.

For the analysis of how weather extremes influenced nesting success in the MCWA, the top model included one variable (absolute maximum temperature for the 7 day period preceding nest initiation); however, we interpreted little support for this variable because the 95% CI for its coefficient overlapped zero and the null model had $\Delta AIC < 2$. For the ONF analysis of nest success, three models were supported and collectively contained five variables, including absolute maximum and minimum temperatures for the 19 day window between banding age and fledging, absolute maximum daily precipitation for the 11 day incubation window, and age of the breeding male. However, only absolute maximum temperature for the 19 day window had a model coefficient with a 95% CI that did not overlap zero, and the coefficient for this variable indicated a negative effect on nest success (i.e., lower probability of nest success with warmer maximum temperatures) (Table 2.7 & Figure 2.8).

For the partial brood loss analysis for the MCWA, two models were supported and collectively contained two variables: absolute maximum daily precipitation for the 11 day incubation window and absolute minimum temperature for the 7 day window between hatching and banding. However, the 95% CI for this latter variable overlapped zero. Absolute maximum daily precipitation during the 11 day window had a negative effect on partial brood loss (i.e., higher number of nestlings lost with more intense single-day precipitation events) (Table 2.7 & Figure 2.9).

For the partial brood loss analysis for ONF, no models out-performed the null model, indicating that none of the climate-related factors we measured explained brood loss for this study site.

60d prenest tmin	Average Daily Minimum Temperature in 60 day period before median first nest initiation date for all years for each site
60d prenest tmax	Average Daily Maximum Temperature in 60 day period before median first nest initiation date for all years for each site
60d prenest ppt	Total precipitation in 60 day period before median first nest initiation date for all years for each site
30d prenest tmin	Average Daily Minimum Temperature in 30 day period before median first nest initiation date for all years for each site
30d prenest tmax	Average Daily Maximum Temperature in 30 day period before median first nest initiation date for all years for each site
30d prenest ppt	Total precipitation in 30 day period before median first nest initiation date for all years for each site
40d nesting tmin	Average Daily Minimum Temperature in 40 day period following median first nest initiation date for all years for each site
40d nesting tmax	Average Daily Maximum Temperature in 40 day period following median first nest initiation date for all years for each site
40d nesting ppt	Total precipitation in 40 day period following median first nest initiation date for all years for each site
14d abs tmin	Absolute lowest daily temperature value within 14 day period preceding nest initiation date for a specific nest
14d abs tmax	Absolute highest daily temperature value within 14 day period preceding nest initiation date for a specific nest
14d abs ppt	Absolute highest daily precipitation value within 14 day period preceding nest initiation date for a specific nest
7d abs tmin	Absolute lowest daily temperature value within 7 day period preceding nest initiation date for a specific nest
7d abs tmax	Absolute highest daily temperature value within 7 day period preceding nest initiation date for a specific nest
7d abs ppt	Absolute highest daily precipitation value within 7 day period preceding nest initiation date for a specific nest
11d abs tmin	Absolute lowest daily temperature value within 11 day period following nest initiation date for a specific nest
11d abs tmax	Absolute highest daily temperature value within 11 day period following nest initiation date for a specific nest
11d abs ppt	Absolute highest daily precipitation value within 11 day period following nest initiation date for a specific nest
7d-hb abs tmin	Absolute lowest daily temperature value within 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 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 7 day period following the 11th day after nest initiation date for a specific nest
19d abs tmin	Absolute lowest daily temperature value within 19 day period following the 18th day after nest initiation for a specific nest
19d abs tmax	Absolute highest daily temperature value within 19 day period following the 18th day after nest initiation for a specific nest
19d abs ppt	Absolute highest daily precipitation value within 19 day period following the 18th day after nest initiation for a specific nest

Table 2.5. Description for all climate variables used for each analysis that correspond with time periods both before and during nesting for red-cockaded woodpecker (*Dryobates borealis*, RCW) populations in the Ouachita Mountains ecoregion.

1)

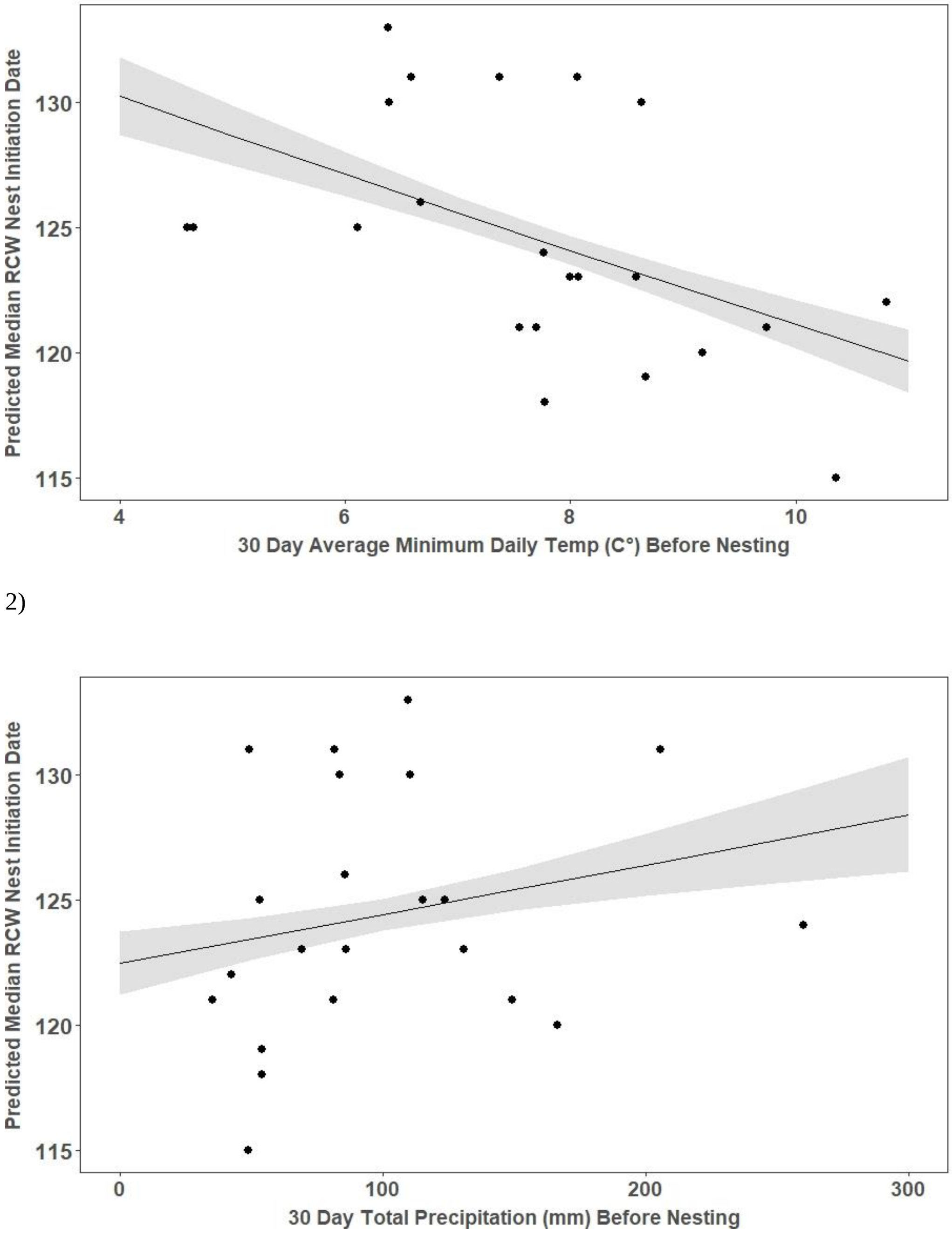
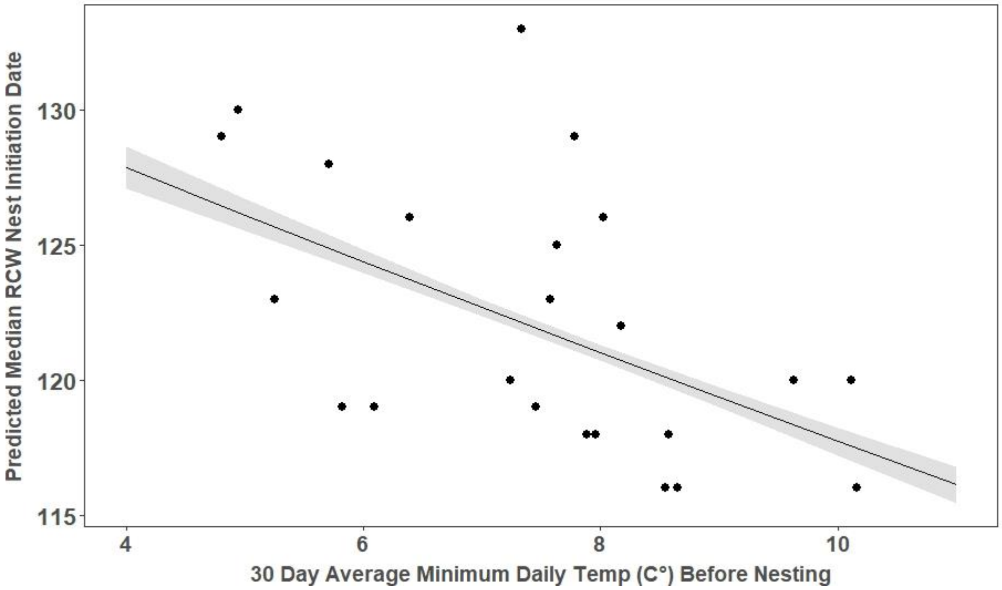


Figure 2.2. Effects of average minimum daily temperature (C°) (1) and total precipitation (mm) (2) during the 30 day window preceding nest initiation on median initiation date for red-cockaded woodpecker (*Dryobates borealis*, RCW) nests on the McCurtain Co. Wilderness Area (MCWA), Oklahoma.

1)



2)

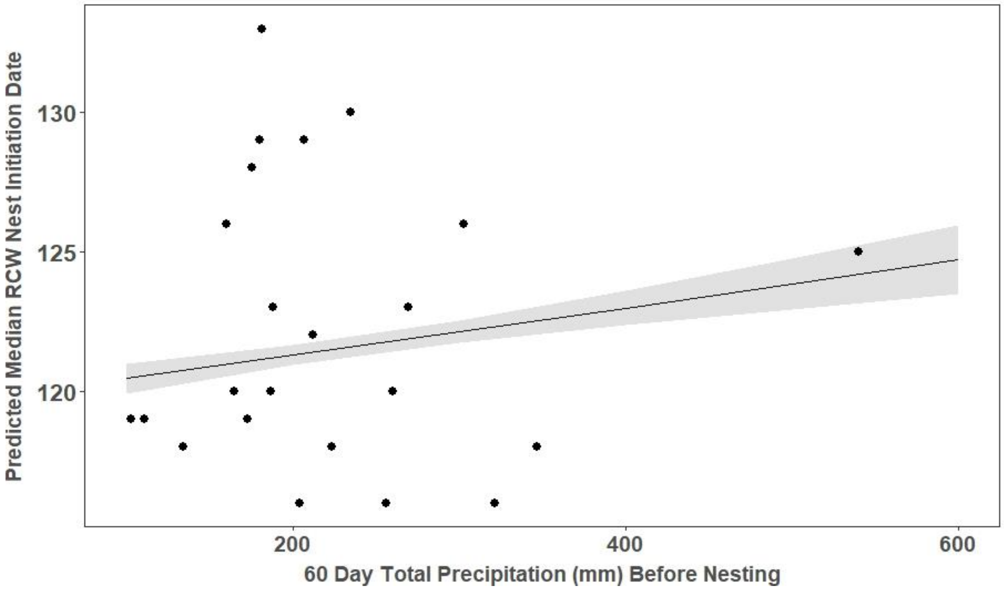
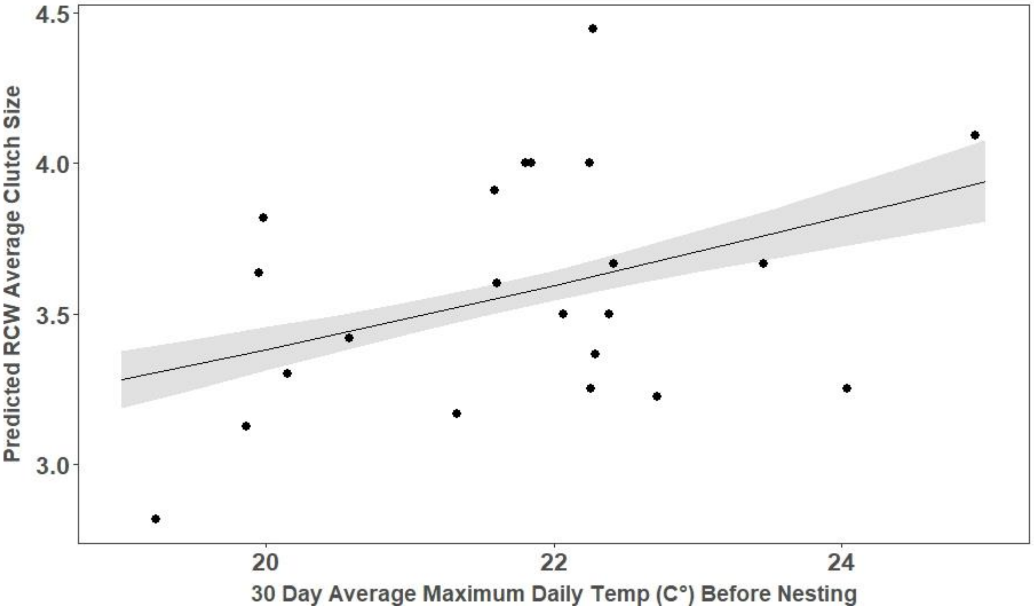


Figure 2.3 Effects of average minimum daily temperature (C°) during the 30 day window preceding nest initiation (1), and total precipitation (mm) during 60 day window preceding nest initiation (2) on median initiation date for red-cockaded woodpecker (*Dryobates borealis*, RCW) nests on the Ouachita National Forest – Poteau/Cold Springs District (ONF), Arkansas.

1)



2)

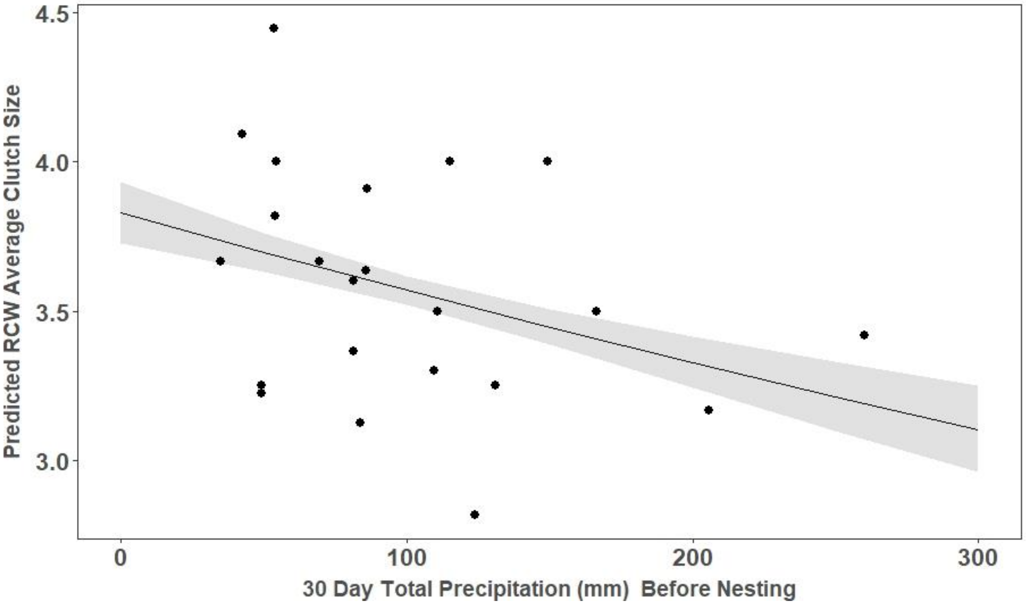


Figure 2.4. Effects of average maximum daily temperature (C°) (1) and total precipitation (mm) (2) during the 30 day window preceding nest initiation on average clutch size for red-cockaded woodpecker (*Dryobates borealis*, RCW) nests on the McCurtain Co. Wilderness Area (MCWA), Oklahoma.

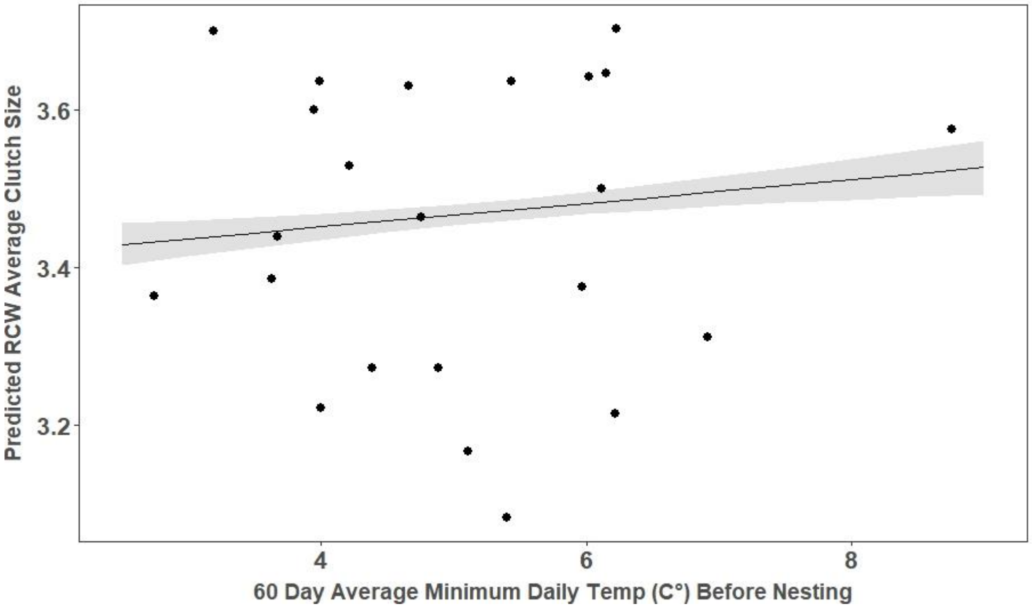
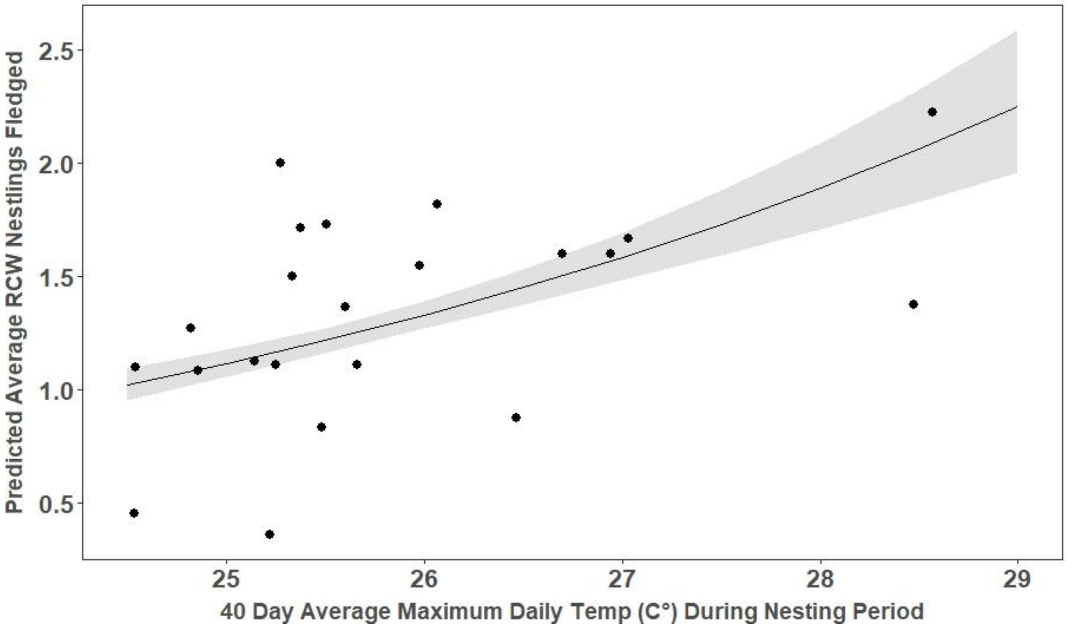
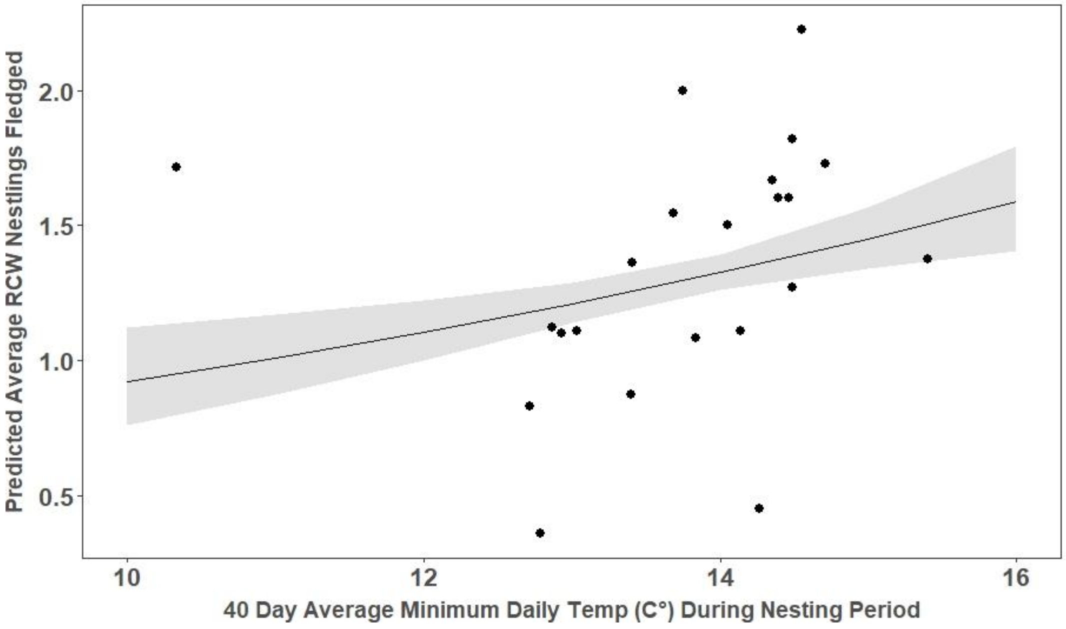


Figure 2.5. Effect of average minimum daily temperature (C°) during 60 day window preceding nest initiation on average clutch size for red-cockaded woodpecker (*Dryobates borealis*, RCW) nests on the Ouachita National Forest – Poteau/Cold Springs District (ONF), Arkansas.

1)


Predicted Average RCW Nestlings Fledged
2.5
2.0
1.5
1.0
0.5
25
26
27
28
29
40 Day Average Maximum Daily Temp (C°) During Nesting Period

2)


Predicted Average RCW Nestlings Fledged
2.0
1.5
1.0
0.5
10
12
14
16
40 Day Average Minimum Daily Temp (C°) During Nesting Period

3)

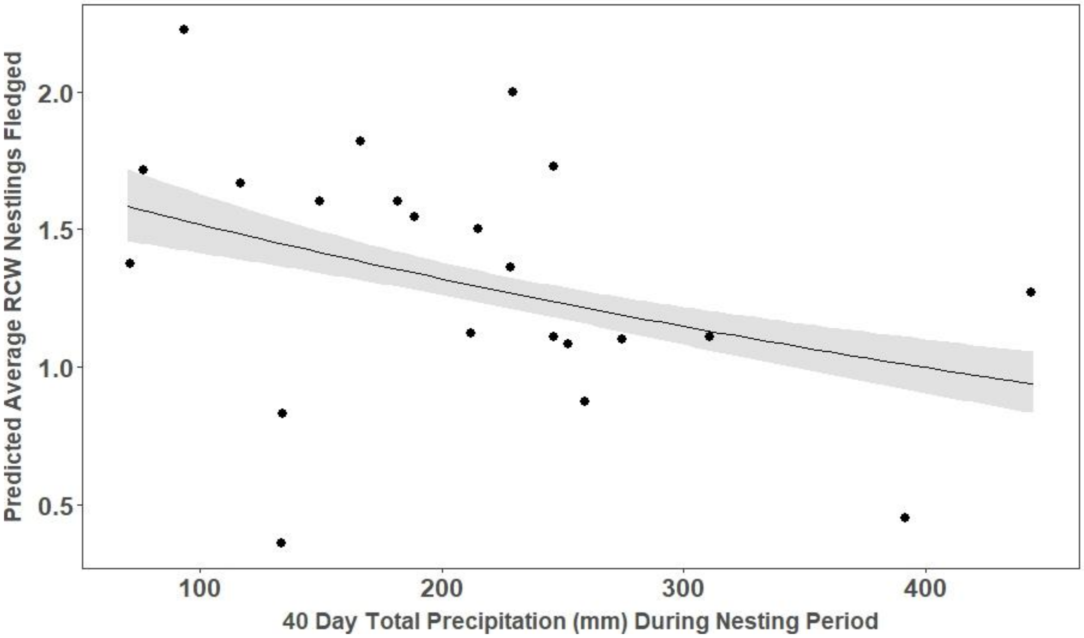
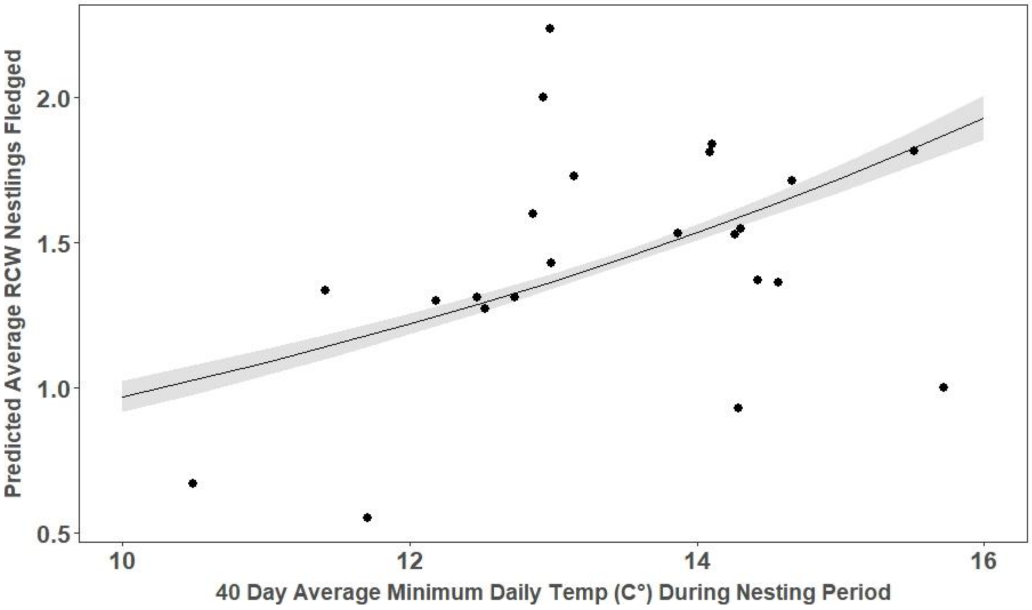


Figure 2.6. Relationship between average number of nestlings fledged and average maximum daily temperature (C°) (1), average minimum daily temperature (2) and total precipitation (mm) (3) during the 40 day nesting period for red-cockaded woodpecker (*Dryobates borealis*, RCW) nests on the McCurtain Co. Wilderness Area (MCWA), Oklahoma.

1)



2)

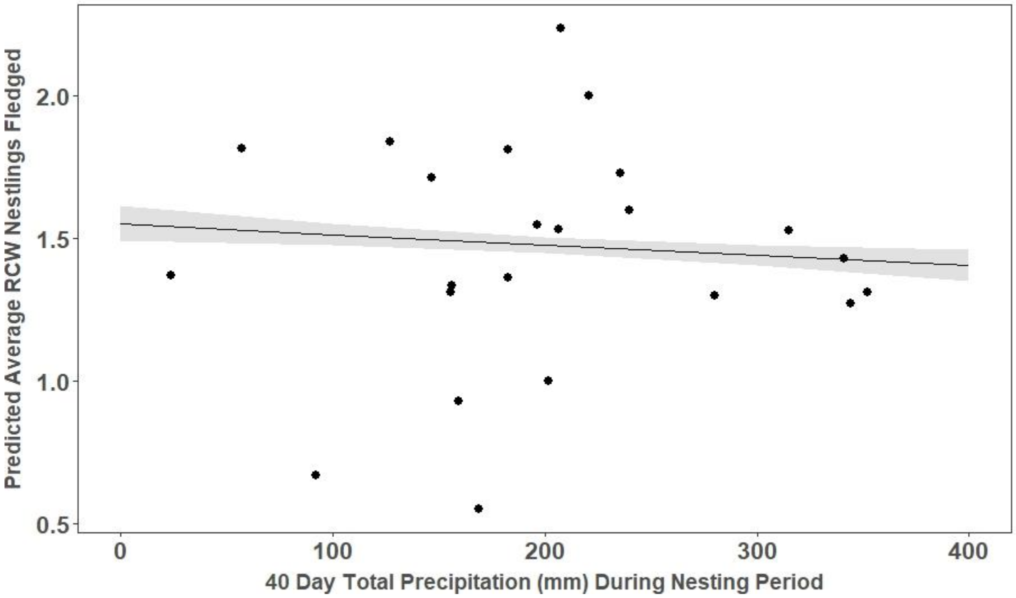


Figure 2.7. Predicted average number of nestlings fledged as a function of average daily minimum temperature (C°) (1) and total precipitation (2) during the 40 day nesting period for red-cockaded woodpecker (*Dryobates borealis*, RCW) nests on the Ouachita National Forest – Poteau District (ONF), Arkansas.

Trait	Site	Climate Window Variables	β	SE	Lower 95% CI	Upper 95% CI	AIC
Median Nest Date	MCWA	60d avg tmax	-0.00292	0.00190	-0.00666	0.00082	1174.2
		30d avg tmax	0.00419	0.00275	-0.00125	0.00963	
		30d avg tmin	-0.01310	0.00206	-0.01719	-0.00902	
		30d total ppt	0.00015	0.00004	0.00006	0.00023	
	ONF	60d total ppt	0.00008	0.00001	0.00006	0.00010	3222.1
		30d avg tmin	-0.01402	0.00077	-0.01553	-0.01251	
Clutch Size (Average)	MCWA	30d avg tmax	0.02260	0.00505	0.01257	0.03263	142.57
		30d total ppt	-0.00050	0.00012	-0.00073	-0.00026	
	ONF	60d avg tmin	0.00431	0.00122	0.00193	0.00670	-497.95
Number fledged (Average)	MCWA	40d avg tmax	0.10368	0.02956	0.04436	0.16373	366.78
		40d avg tmin	0.06300	0.02877	0.01021	0.11517	
		40d total ppt	-0.00078	0.00034	-0.00146	-0.00008	
	ONF	40d avg tmin	0.13990	0.00849	0.12182	0.15784	378.76
		40d total ppt	0.00054	0.00009	0.00034	0.00073	

Table 2.6. Effects of climate variables on nest initiation, average clutch size, and average number of nestlings for red-cockaded woodpecker (*Dryobates borealis*, RCW) populations in the Ouachita Mountains; results are shown for the top Generalized Linear Models (GLMs) identified using a stepwise model selection approach

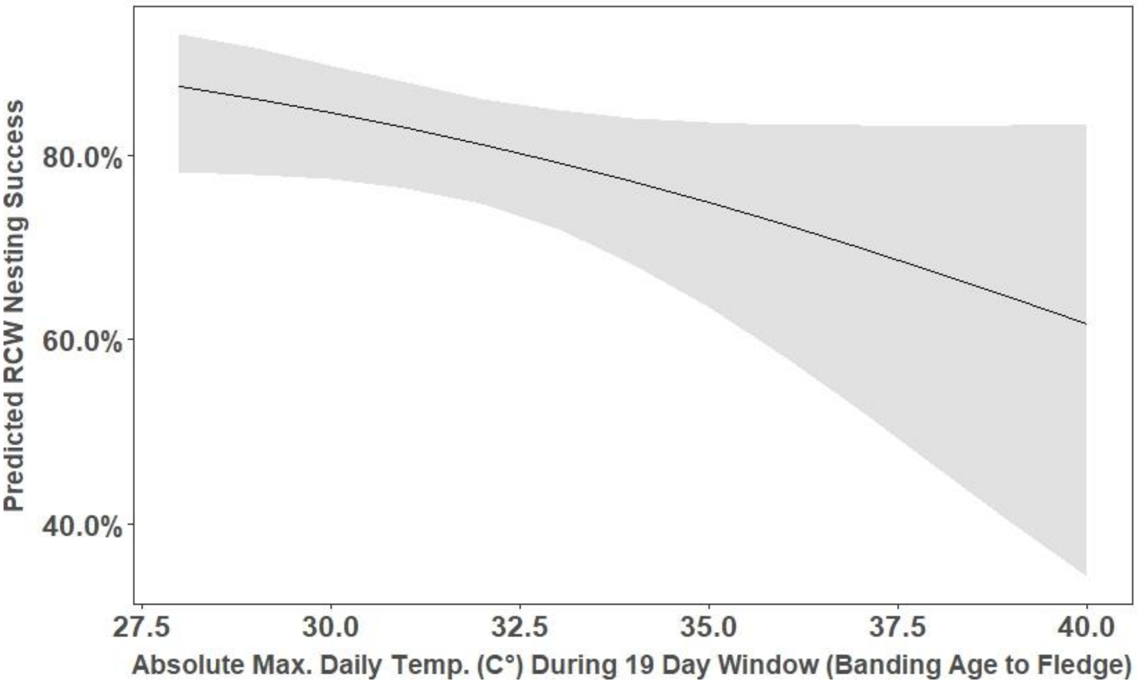


Figure 2.8 Nest success as a function of the absolute maximum daily temperature (C°) value during the 19 day period between banding age and fledging for individual red-cockaded woodpecker (*Dryobates borealis*, RCW) nests on the Ouachita National Forest – Poteau/Cold Springs Districts (ONF), Arkansas.

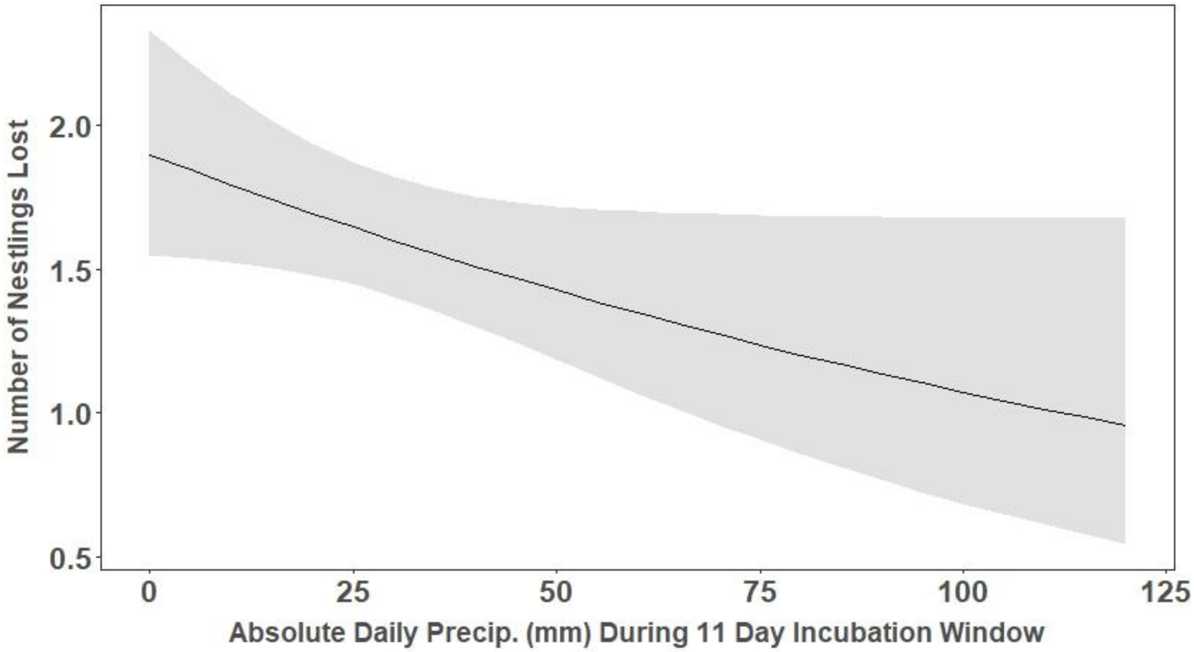


Figure 2.9 Effect of the absolute maximum daily precipitation (mm) value during the 11 day incubation period on partial brood loss of red-cockaded woodpecker (*Dryobates borealis*, RCW) nests on the McCurtain Co. Wilderness Area (MCWA), Oklahoma.

Trait	Site	Model	Variables	β	SE	Lower 95% CI	Upper 95% CI	ΔAIC	AIC Wt
Nest Success	MCWA	Abs. 7d Tmax	7d abs tmax	-0.139	0.098	-0.341	0.049	0.00	0.098
	ONF	Abs. 19d banding-to-fledge Tmax & Male	19d abs tmax	-0.283	0.129	-0.566	-0.041	0.00	0.260
			Br. Male Age	0.132	0.077	-0.013	0.294		
		Abs. 19d banding-to-fledge Tmax, 11d inc. precip. & Male	19d abs tmax	-0.234	0.123	-0.573	-0.009	0.80	0.173
			11d abs ppt	0.016	0.015	-0.012	0.046		
			Br. Male Age	0.132	0.078	-0.014	0.295		
		Abs. 19d Max / Tmin, 11d inc. precip. & Male	19d abs tmax	-0.191	0.139	-0.485	0.083	1.70	0.113
			19d abs tmin	-0.068	0.063	-0.196	0.057		
			11d abs ppt	0.016	0.015	-0.013	0.047		
			Br. Male Age	0.122	0.078	-0.024	0.286		
Partial Brood Loss	MCWA	Abs. 11d inc. precip.	11d abs ppt	-0.006	0.003	-0.012	-0.00001	0.00	0.334
		Abs. 11d inc. precip. & 7d hatch-band Tmin	11d abs ppt	-0.006	0.003	-0.012	-0.00002	1.80	0.139
			7d h-b tmin	0.010	0.020	-0.030	0.050		
	ONF	Null	Intercept	0.307	0.060	0.187	0.423	0.0	533.1

Table 2.7. Effects of climate window variables and breeding male age on nesting success and partial brood loss for specific red-cockaded woodpecker (*Dryobates borealis*, RCW) nests on the McCurtain Co. Wilderness Area (MCWA), Oklahoma, and the Ouachita National Forest – Poteau/Cold Springs District (ONF), Arkansas. Additive variables for each model are grouped together by row. Only models with a ΔAIC < 2 are summarized.

Discussion

Based on 20+ years of data for two red-cockaded woodpecker (RCW) populations at the northwestern periphery of the species' range, we documented several apparent effects of weather variation on both population- and nest-level nesting variables. Weather effects varied somewhat between populations and depending on the response variable, but several consistent patterns emerged. For example, both RCW populations experienced shifts in nesting dates in response to weather conditions during periods leading up to the nesting season, with nesting occurring earlier with warmer average temperatures and later with greater precipitation. RCW populations also experienced reduced nestling survival to fledging with higher precipitation levels during the nesting period. For both populations, average daily minimum temperature appeared to have a stronger overall influence than maximum temperature, suggesting that warm nights may be more important than hot days in influencing multiple nesting variables. Weather extremes also influenced individual nesting; intense precipitation events during the incubation period increased partial brood loss (number of nestlings lost) in Oklahoma (MCWA) while high temperature extremes during the brooding period reduced nest success in Arkansas (ONF). Our results collectively indicate that RCWs are responding to inter-annual variation in weather, that these responses are complex and variable, and that the nature of responses will likely influence the future persistence and adaptability of these peripheral populations in response to climate change, with important implications for the range-wide persistence and management of the species.

Population-level analysis of climate effects on nest initiation, clutch size, and fledgling number

Effects of variation in temperature and precipitation on RCW population-level nesting variables were generally similar for both MCWA and ONF. Warmer temperatures (specifically average minimum daily temperatures) prior to nesting were associated with earlier nest initiation dates and larger clutch sizes, while greater total precipitation before nesting delayed nest initiation and reduced clutch sizes. These same factors during the nesting period influenced numbers of fledglings produced (i.e., warmer temperatures and greater precipitation respectively increased and decreased numbers of fledglings). We also provide some evidence that the 30 day window prior to nesting may be most important in influencing nest timing and clutch size, as more variables were supported for this window than for the 60 day window. Overall, average temperature variables appeared 7 times in population-level nesting analyses, and warmer temperatures were always associated with earlier nesting and/or greater productivity. Total precipitation variables appeared 5 times in population-level analyses, with higher precipitation always associated with delayed nesting and reduced number of nestlings fledged.

Our finding that RCWs initiate nests earlier when conditions are warm in the days preceding the nesting season matches similar studies of this species on the northeastern periphery of its range in North Carolina (Schiegg et. al 2002; Garcia 2014). This pattern may be driven by RCWs responding to temperature cues that correlate with plant phenology and increased insect abundance, thus facilitating earlier nesting (Lack 1954; Dunn, Winkler 1999; Both 2004). The link between higher precipitation and delayed nesting is less clear. Previous studies (Ligon 1970; Baker 1971), as well as anecdotal observations by ODWC staff in the MCWA (C. Barnes, *pers. comm.*), have suggested that during both nesting and non-nesting periods, RCWs may have difficulty foraging and/or spend greater time in their cavities during extended periods of precipitation. High levels of average precipitation during key pre-productive periods (e.g. the 30 days before nesting) could signal poor conditions for breeding, thus delaying the onset of optimal reproductive condition for females and/or induce laying of smaller clutches (Neal et al. 1993; Conner et al. 2005).

For both the MCWA and ONF, warmer temperatures preceding nesting increased average clutch size while greater precipitation reduced clutch size; however, the most important time window for temperature effects was different for the two study areas (30-day window for MCWA; 60-day window for ONF; see below discussion of potential reasons for this difference). As with nest initiation, we suspect that warmer temperatures and greater precipitation before nest initiation signal optimal conditions for breeding, thus affecting clutch size and indirectly affecting foraging and/or reproductive condition. Warmer temperatures during spring are likely used as a favorable environmental cue to RCW females before the onset of egg-laying, thus increasing the average clutch size (Lack 1947). Conversely, effects of extended periods of rainfall on foraging and physiological condition of RCW females could reduce numbers of eggs laid in addition to delaying nest initiation. Further research should seek to validate such mechanisms of climate effects on RCW clutch size because links between precipitation, reproduction, and population demographics vary among different bird species (Winkler, Allen 1996; Sheldon 2003; Chase et al. 2005; Cady et al. 2019).

As with nest initiation and clutch size, warmer temperatures and greater precipitation during the nesting period respectively increased and decreased numbers of nestlings fledged for both sites; however only minimum temperature was important in the ONF while both minimum and maximum temperature were important in the MCWA. The negative effect of precipitation may reflect reduced parental foraging opportunities, and thus provisioning of nestlings, during rainy periods, as has previously been shown for RCWs in Texas (Conner et al. 2005) and more broadly for many bird species (Pasinelli 2001; Radford et al. 2001; Öberg et al. 2015). Additionally, these findings could reflect that RCW nestlings may be sensitive to cool temperatures and moist conditions during the brooding period (Neal et al. 1993), which could lead to increased nestling mortality. Aside from climatic variables, RCW fledgling survival has been linked to several direct and indirect factors, including breeder experience, group size, and habitat quality (Lennartz et al. 1987; Walters 1990; Ramirez, Ober 2014). However, our below-discussed nest-level analysis suggests that, at least in our study areas, climate variables may be more important than breeder age in influencing nest success probability, and this may also be the case for population-level productivity.

Although the direction of the effects for temperature and precipitation was similar for both sites, conditions during the 60 day period preceding nesting were associated with ONF nesting variables, but only conditions during the 30 day period were important for MCWA. Differences between sites in forest structure (e.g., age and tree density), topography (e.g., slope and aspect), and management approaches (e.g., fire and thinning intervals) could mediate differential effects of temperature and precipitation on food availability and RCW reproductive physiology. For example, in the MCWA, where the forest structure (both over- and midstory) may be denser with a less-open canopy and thus more shading, warmer air temperatures may only impact RCW foraging and reproductive condition during the warmest period of spring immediately prior to nesting. In the ONF site, USFS maintains an open forest midstory by reducing midstory and managing for 60 – 80 square feet of pine-hardwood basal area per acre in and around RCW clusters (U.S. Forest Service 2005), potentially allowing even marginally warm air temperatures earlier in spring to cause substantial radiative warming effects on RCWs due to more limited shading. For precipitation, which may influence the frequency of RCW foraging, as well as vegetation greenness and arthropod abundance at both sites, different time windows could capture different arthropod and/or vegetation responses to precipitation. Cady et al. (2019) documented that different bird species in the southern Great Plains respond to precipitation and drought as measured at different time scales and suggested that these different temporal scales of response reflect complex effects of different drought lengths on food and vegetative structure, with associated implications for foraging, habitat selection, and population abundance. If RCWs in our two sites select habitat or forage differently, then they could have population-specific responses to precipitation during different time windows. No RCW foraging studies have been conducted at either of our sites, so dietary composition for the two populations can only be deduced from previous gut sampling (Hanula et al. 1998; Hanula, Horn 2004) and ongoing DNA analysis (Jusino et al. 2018; J. Walters, *pers. comm*) conducted elsewhere in the range. Ongoing research is assessing whether the different populations select cavity trees differently, and this and similar research would further clarify how RCW populations respond to precipitation and temperature as measured over different time windows.

Nest–level analysis of extreme event effects on brood reduction and nest success

For individual nest-level analyses—in which we considered weather extremes instead of averages and tailored time windows to initiation dates of each nest—the effects of weather variables on RCW nesting were less consistent across sites and analyses. No weather extremes were associated with nest success for the MCWA; however, absolute maximum temperature during the 19 day window between day 7 and 26 in the nestling period had a negative effect on nest success in the ONF. This apparent negative effect of maximum temperatures on nestling survival is the opposite of the consistent positive effect of warm temperatures on population-level averages of clutch size and fledgling number. The differing results between the two study sites may relate to the above-described differences in topography and density of over- and midstory trees (Masters et al. 1989); specifically, denser tree canopies and greater shading in the MCWA may increase the ability of RCWs to tolerate extreme heat. The differential effect of warm conditions on clutch size and nest success could reflect that RCWs are less able to track phenology as they base clutch size on anticipated conditions, whereas nest success reflects actual conditions. Garcia (2014) documented such an inverse relationship between RCW nestling size and clutch size in response to warming spring temperatures. Further, and as is the case for many other bird species (Magrath 1991, Mock and Parker 1997, Cleasby et al. 2010), RCW nestling mass may be positively correlated with survival to fledging, as suggested by past correlations between RCW nestling mortality and mass at banding age (Delotelle et al. 2003). Because of the different scales at which we assessed clutch size (populations) and nest success (individual nests), we did not specifically test for a relationship between the two variables and are therefore uncertain if they are related. Additional research is needed to investigate how habitat-related differences, as well as effects of clutch sizes on nest success, mediate RCW nesting responses to climate change.

Interpretation of the effects of weather variables on partial brood loss (i.e., the number of nestlings dying between hatching and nestling day 7) was not straightforward for either site. None of the 7 predictor variables were associated with partial brood loss for the ONF. For the MCWA, high single-day rainfall totals during the 11 day incubation period were associated with reduced partial brood loss. Past research suggests potential mechanisms behind this unintuitive result. Brood reduction, or loss of nestlings directly caused by either parental adjustment or sibling competition (Mock 1994), has been documented in previous studies (Ligon 1970; Lennartz et al. 1987; DeLotelle et al. 2003; LaBranche, Walters 1994), and may be related to reduced food availability due to suboptimal environmental conditions. Evidence exists that fewer RCW nestlings are lost through brood reduction when clutch sizes are smaller (McCormick et al. 2003), and therefore, our finding could reflect an indirect effect of high levels of precipitation on reduced brood loss via decrease in clutch size (see above clutch size discussion). Furthermore, incubation constancy may be higher during wet periods, allowing for more eggs to hatch. Due to the nature of our data sources, we were unable to separate brood loss from brood reduction, but the above explanation could be valid if brood losses largely occur due to brood reduction. Contrary to our result, Garcia (2014) found higher precipitation to increase RCW partial brood loss in North Carolina. They speculated that unpredictable weather due to climate change may alter the ability of nesting RCWs to time nesting with ideal foraging conditions, thus resulting in more partial brood loss due to nestlings being exposed to cool and wet conditions, especially during the first days after hatching (Dyrcz, Halupka 2008; Anctil et al. 2014). Although some of the aforementioned explanations are possible, further research is needed to determine the exact relationship between precipitation and partial brood loss during the 11 day incubation period.

Conclusion and Implications for RCW Population Ecology and Management

Effects of weather averages and extremes on several nesting variables for RCWs in the Ouachita Mountains suggest complex, and potentially population-specific, responses to inter-annual weather variation. At the population level, warmer temperatures in early spring advanced nesting and increased clutch size, implying that predicted warming trends during this time of year (IPCC 2013) may benefit RCW population recovery if these effects translate to increased population-level fecundity. Although warmer temperatures will likely advance nest dates and increase clutch sizes, our results also suggest that high precipitation amounts will have opposite effects. Combined, these results suggest that the exact combination of weather conditions that RCWs experience under a future climate (e.g., hotter and wetter conditions versus hotter and drier conditions) will have important implications for reproduction and overall persistence of this species. Throughout the RCW range, precipitation amounts are projected to become more variable with higher frequencies of extreme rainfall events (U.S. Global Change Research Program, 2018). This suggests that prediction of RCW responses to climate change may remain difficult even with increased knowledge about how weather influences nesting. Ours and past research suggests that RCWs have some adaptive ability or plasticity to shift nesting dates in response to weather variation; however, the degree to which they will be able to shift nest initiation as climate continues to change and weather extremes become more frequent remains uncertain. Nonetheless, the potential emergence of mismatches between timing of nesting, vegetation phenology, and insect availability would have important implications for future population recovery efforts for the species (Garcia 2014). At the nest level, extreme temperature and precipitation events had a weaker link to nest success, suggesting that factors other than climate (e.g., habitat quality and predation) may have a stronger influence on whether individual nests successfully fledge any young. This result indicates the continued importance of managing RCW habitats and clusters in ways that not only moderate climatic impacts but also target other population-limiting factors (e.g. hardwood density, pines of suitable age, etc.).

Our analysis provides a useful first approximation of how RCWs may respond to climate change at their northwestern range periphery, but several other aspects of climate that we did not account for likely also influence RCW nesting and demography. For example, climate variables related to drought can influence occupancy and abundance of bird species, with species responding differently to drought as measured over varying temporal scales (e.g., from 1-12 months before breeding seasons; Cady et al. 2019); this suggests the possibility that weather conditions during periods earlier than 2 months before nest initiation may also influence RCW nesting phenology. These potential carry-over effects, such as precipitation from the previous season influencing food availability in the current nesting season, may also influence RCW fecundity, breeding phenology, and nesting success (Fantle-Lepczyk 2016). Although we measured the effect of temperature and precipitation extremes on RCW nesting, we speculate that the frequency of such extremes is also an important driver of vegetation characteristics, insect abundance, and other ecological processes that influence RCWs both before and during nesting. Regardless of these uncertainties, our results indicate that RCW nesting ecology is influenced by climatic conditions as measured for different time windows and at different temporal scales; this information is a critical first step toward understanding RCW population responses to future climate change.

In conclusion, we found that timing of nesting and nest productivity for RCWs in the Ouachita Mountains, at the northwest periphery of the species' range, are influenced by temperature and precipitation averages and extremes both before and during the nesting period. Because the association between climate and RCW nesting had only been shown in the northeastern portion of the species' range, such information is critical in assisting government agencies and other land managers with regionally-tailored recovery planning for this endangered species. RCW habitat is dependent upon active forest management practices such as the use of prescribed fire and midstory hardwood removal (Hopkins, Lynn 1971; Hovis, Labisky 1985; Kelly et al. 1993). Warmer global temperatures from climate change are expected to alter many ecosystems throughout the world and necessitate adaptation and/or range shifts for many species (Parmesan, Yohe 2003; Forero-Medina et al. 2011; Sunday et al. 2015). While unknown if RCWs will be able to shift their range, areas along the northern range periphery may become increasingly important as projected warming trends continue, potentially making areas along southern edge unsuitable for the species to occupy. In addition, understanding how weather and projected climate change may affect RCW reproduction can benefit efforts to identify and prioritize locations that may be suitable for future reintroduction and/or population expansion, as well as currently-occupied areas that may become unsuitable for RCWs. Further research is needed to integrate information about how RCWs are likely to respond to climate change with other interrelated factors that influence nesting and population ecology, such as predation risk, food availability, and characteristics of land cover and vegetation structure from the scale of entire landscapes to individual nesting trees. Such information will be beneficial for conserving RCWs and other at-risk, declining, and endangered species in the face of a changing climate.

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VITA

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