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Red-cockaded woodpecker habitat characteristics associated with partial brood loss in the Upper East Gulf Coastal Plain, USA

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ABSTRACT: Some red-cockaded woodpecker (RCW) *Dryobates borealis* populations remain understudied. This is notable because management that incorporates population demographics and site characteristics may benefit RCW recovery. The Oakmulgee Ranger District of the Talladega National Forest (Alabama, USA) has no wiregrass *Aristida stricta*, small forest stand sizes, rolling topography, and contains an understudied RCW population. Our goal in the Oakmulgee was to characterize RCW habitat, possibly identify ways in which habitat differed from other regions, and estimate associations between habitat and reproductive output. We found that 70.2 and 92.5% of sampled stands met recovery standard thresholds for small and large pine basal area (BA) as defined in the United States Fish and Wildlife Service (USFWS) RCW Recovery Plan. While 74.6% of longleaf pine *Pinus palustris*-dominated stands met the threshold for overstory hardwood canopy composition, 60.0% of loblolly pine *P. taeda*-dominated stands did not. Few stands met the recommended percentage of herbaceous understory (19.8%) or recommended absence of hardwood midstory. A lower rate of partial brood loss was associated with a greater area of large pines (≥25.4 cm diameter at breast height; DBH), a smaller area of small pines (≥10 and <25.4 cm DBH), a larger area burned in the dormant season, and higher RCW density. In our models, hardwood overstory and midstory did not influence egg or hatchling production. Hardwoods in the Oakmulgee could contribute to unfavorable habitat, as indicated in the USFWS RCW Recovery Plan, as well as relate to variation in habitat across the RCW's range. Regions of the RCW's range are understudied, and limited staffing and funding impede advances in understanding and conservation.

KEY WORDS: Prescribed fire · Hardwood overstory · Herbaceous understory · Nest success · Egg · Hatchling · Longleaf pine · Midstory

1. INTRODUCTION

The red-cockaded woodpecker (RCW) *Dryoxbates borealis* is a federally endangered species endemic to pine *Pinus* spp. forests across the southeastern United States. In general, RCWs are thought to select open pine stands with limited pine and hardwood midstory (Jones & Hunt 1996, Rudolph et al. 2002, Macey et al. 2016), moderate densities of older pine >60 yr (Conner et al. 1994, Zwicker & Walters 1999), and herbaceous ground cover (James et al. 1997). The RCW Recovery Plan (USFWS 2003) defines good quality foraging habitat based on recovery standards (Recovery Plan section 8I). Recovery standards identify threshold values for habitat metrics designating high-quality habitat. However, field studies suggest that relationships between reproductive success and habitat features may be inconsistent across RCW

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populations, and recommended threshold values may not be universally applicable (Garabedian et al. 2014, Martin et al. 2021). For example, the Recovery Plan has multiple recommendations about the distribution of pine size classes in RCW habitat (USFWS 2003). Research generally indicates that RCWs require large, old pines for foraging and nesting habitat (Conner et al. 2001), but studies that examined the effects of pine size class distributions on mean clutch size, nestling production, or fledgling production generated conflicting results, with some studies showing no effect and other studies showing small effects (Garabedian et al. 2014).

Effects of habitat features may be inconsistent across RCW populations because the historical range of the RCW spanned multiple diverse ecoregions (Kelly et al. 1994, Omernik & Griffith 2014, Weiss et al. 2019, Martin et al. 2021). Ecoregions have different climates and biological communities that may be associated with local adaptations in RCWs. Yet the recommendations in the Recovery Plan are not specific to ecoregions, and the recovery standard for habitat is based on studies that do not geographically represent the RCW's range (Martin et al. 2021). There have been few studies on RCW populations in the Upper East Gulf Coastal Plain recovery unit despite the presence of 2 populations with donor status (i.e. populations are robust enough to serve as a source of RCWs for translocation to other populations) (USFWS 2003). One population is in the Bienville National Forest in Mississippi, USA, and the other is in the Oakmulgee Ranger District of the Talladega National Forest in Alabama, USA (hereafter referred to as the Oakmulgee). Only 9 studies about RCWs in the Upper East Gulf Coastal Plain have been published; 8 took place in Bienville National Forest (Jackson 1985, Raulston et al. 1996, Samano et al. 1998, Wood et al. 2000, 2001, 2005, 2008, 2014). The one published study that was carried out in the Oakmulgee used structured decision making with stakeholders to model how different management strategies are expected to affect the RCW population (Brown & Ferguson 2019), but it did not use data collected from the Oakmulgee.

Research in the Oakmulgee is warranted because the Oakmulgee harbors the largest RCW population in Alabama with approximately 120 potential breeding groups (PBGs), i.e. a male and female occupying a cluster (a group of cavity trees) that may also contain one or more helpers (Walters et al. 1988, USFWS 2003). Despite managing for RCWs, the Oakmulgee population has not surpassed 130 PBGs for many years, but the Recovery Plan recommends the Oakmulgee contain a minimum of 250 PBGs at the time of delisting (USFWS 2003). Also, the Oakmulgee has distinctive habitat characteristics. For example, it encompasses areas of great topographic relief, lacks wiregrass *Aristida stricta* (a species that is often emblematic of quality RCW habitat), and primarily contains longleaf *Pinus palustris* and loblolly pine *P. taeda*-dominated stands. In contrast, loblolly and shortleaf *P. echinata*-dominated pine stands are common in the Bienville National Forest.

We investigated how vegetation composition, timing of prescribed burns, and RCW group density in the Oakmulgee related to RCW reproductive output. Our goal in the Oakmulgee was to characterize RCW habitat and estimate associations between RCW habitat and reproductive output. We expected results could provide insight into how RCW habitat associations in the Oakmulgee may compare to other regions and insight into the RCW population trajectory in the Oakmulgee. We collected vegetation data around RCW clusters, and we accessed RCW population data and burn records from United States Forest Service (USFS) biologists working in the Oakmulgee. While pursuing our research goal, we found important data gaps in Oakmulgee records; consequently, we also discuss how resource constraints (e.g. limited funding or personnel) affect data availability and inference about RCW conservation in the Oakmulgee.

2. MATERIALS AND METHODS

2.1. Study region

Our study was conducted in the Oakmulgee Wildlife Management Area (32.88° N, 87.38° W), a section of the Oakmulgee Ranger District of the Talladega National Forest in Bibb County and Hale County in west–central Alabama (Fig. 1). Mean annual precipitation is 144–200 cm, and mean summer temperature is 25.9–27.1°C, with a mean daily maximum of 32.1–33.3°C (USDA 2006, 2008). Elevation ranges from 24–177 m in Hale County (USDA 2006) and from 53–213 m in Bibb County, with higher elevations occurring more frequently in the northern sections of each county (USDA 2008). Soils in this area are characterized by a loamy subsoil and a sandy loam surface layer (Mitchell 2008), and topography consists of rolling to steep hills (USDA 2006, 2008). Within the Oakmulgee, longleaf pine *Pinus palustris*-dominated stands, loblolly pine *P. taeda*-dominated stands, and stands consisting of a mixture of pine and hardwood tree species are typically found along ridges and hill-

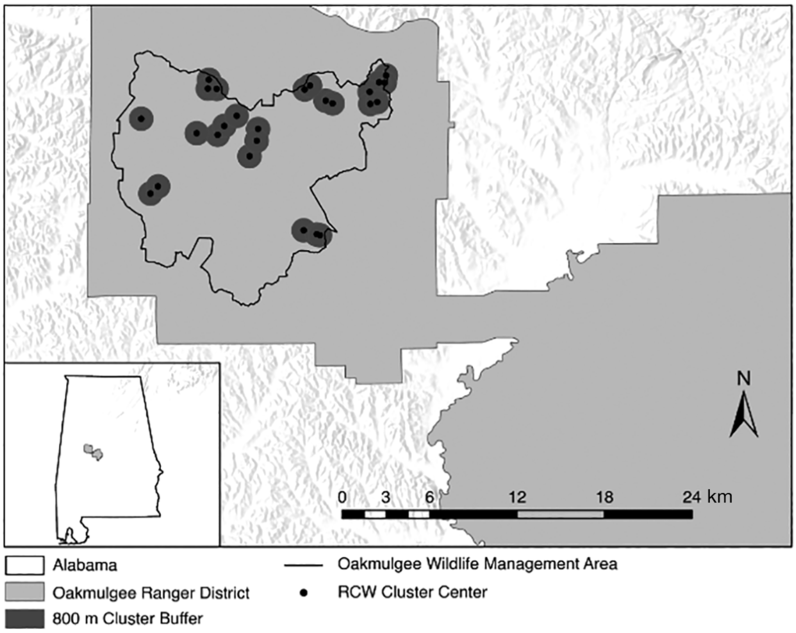

Fig. 1. Red-cockaded woodpecker (RCW) *Dryobates borealis* clusters surrounded by 800 m buffers for vegetation surveys within the Wildlife Management Area in the Oakmulgee Ranger District of the Talladega National Forest, Alabama, USA

sides with hardwood bottomland occurring at slightly lower elevations (USFS unpubl. data). Hardwood species in the area include hickory *Carya* spp., tulip poplar *Liriodendron tulipifera*, red oak *Quercus rubra*, walnut *Juglans* spp., and white oak *Quercus alba*. Common understory vegetation species include blue stem grasses *Andropogon* spp., bracken fern *Pteridium* spp., seedlings of the aforementioned hardwood species, honeysuckle *Lonicera japonica*, muscadine *Vitis rotundifolia*, and wild blueberry *Vaccinium* spp.

2.2. RCW cluster selection

During the summer of 2017, we identified RCW *Dryobates borealis* clusters within the Oakmulgee Wildlife Management Area that contained breeding groups that nested at least once from 2014 to 2017 (n = 72) and had cluster centers (i.e. the geographic center of all cavity trees used by an RCW group) in areas last burned in 2015 or 2016. We used this burn timing criterion because the USFS planned to conduct prescribed burns on a 2–3 yr rotation throughout the Oakmulgee (pers. comm. with M. Caylor, USFS), and consequently, we were interested in short-term (i.e. within the last 2–3 yr) effects of burning on RCWs. At the time of our data collection, the majority of the Oakmulgee Wildlife Management Area had been last burned either in 2015 or 2016. There were few clusters in areas that had most recently been burned in 2014 or prior years. Due to dry conditions, no RCW clusters were burned in 2017, prohibiting the sampling of clusters burned in that year. There were 15 clusters that were last burned in 2015 and nested between 2014 and 2017. We randomly selected 16 clusters that were last burned in 2016 and nested between 2014 and 2017 to have similar sample sizes between burn years. Of the 31 active clusters we initially selected, 26 attempted nesting in 2017 and therefore were included in this study (Figs. 1 & 2). All ethical research guidelines were followed, and all research was conducted in coordination with the USFS at the Oakmulgee. USFS personnel performed all RCW nest checks, and E. Martin conducted vegetation sampling, which did not require permitting.

2.3. Vegetation sampling

From mid-May to early August 2017, we collected vegetation data in the understory, midstory, and overstory of our sampled clusters (n = 26) to characterize RCW habitat at 2 spatial scales: a 400 m radius buffer and an 800 m radius buffer around each cluster center. We chose these spatial scales because the RCW Recovery Plan indicates that all RCW foraging habitat should be within 800 m of the cluster center with >50% of foraging habitat located within 400 m (USFWS 2003).

2.3.1. Selecting stands

We delineated stands using a 2016 GIS shapefile provided by the Oakmulgee USFS that characterized stands by dominant tree species and age. In our study area, the 400 and 800 m buffers often contained multiple stands with different vegetation (Fig. 2). When a stand within an 800 m buffer had ‘unknown’ listed in the USFS shapefile as its stand composition, we visited the stand to determine whether it fit sampling criteria based on diameter at breast height (DBH) and tree species composition (see details below).

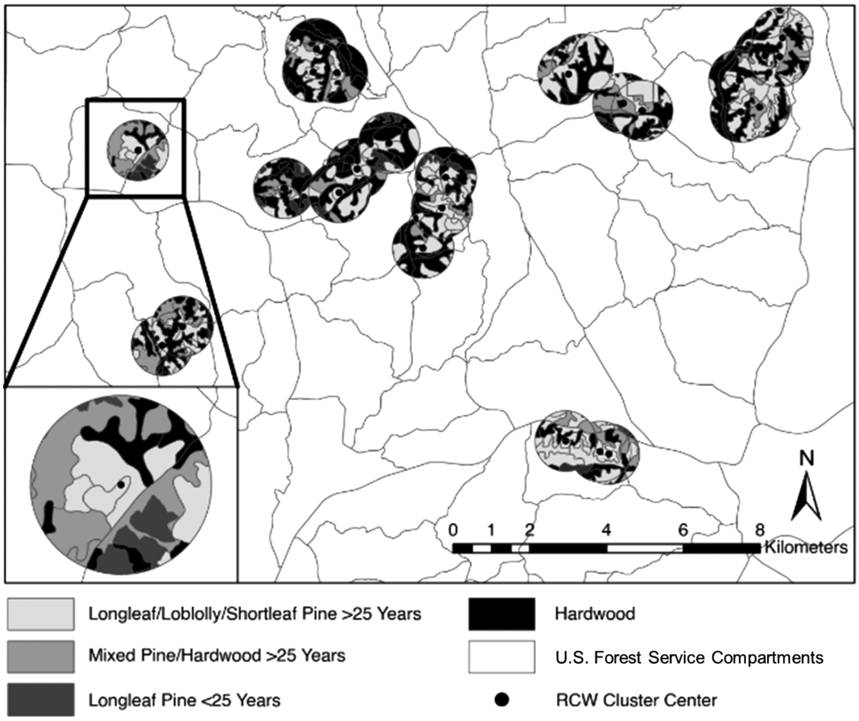

Fig. 2. Forest stands within 800 m of red-cockaded woodpecker (RCW) *Dryobates borealis* clusters in the Oakmulgee Ranger District of the Talladega National Forest, Alabama. Stand boundaries were determined by the United States Forest Service based on tree age and primary tree species. The Oakmulgee is divided into compartments to organize management activities. One stand is enlarged to illustrate an example of the diversity of stands that occurred within 800 m buffers

We used general information about stand composition extracted from the GIS shapefile to calculate a covariate for the total area of RCW habitat within either 400 or 800 m from the cluster center. We calculated total RCW habitat area as the summed area of all stands that were ≥25 yr old with ≥1 pine with DBH ≥25.4 cm and ≥50% pine (i.e. not hardwood-dominated) (USFS unpubl. data).

To characterize RCW habitat in more detail, we collected vegetation data in the field, but because the 800 m buffers included more stands than we could feasibly sample in the field, we focused on collecting detailed field data in stands that were expected to have suitable RCW habitat based on stand composition data in the GIS shapefile. We did not put field sampling effort into measuring stands that, based on stand composition data in the GIS shapefile, were unsuitable habitat for RCWs. However, the presence of stands with unsuitable habitat was captured in the covariate quantifying the area of RCW habitat in the buffer. We chose the field sampling criteria (stands within the 400 and 800 m buffers that were ≥25 yr old, had ≥1 pine with DBH ≥25.4 cm, and were ≥50% pine) because RCWs tend to avoid foraging in areas dominated by hardwoods (Hooper & Lennartz 1991, Repasky & Doerr 1991, Jones & Hunt 1996, Franzreb 2010) and preferentially forage in older pine stands (James et al. 1997, 2001, USFWS 2003), and USFS employees had observed RCWs foraging in the Oakmulgee in stands as young as 25 yr old (pers. comm. with M. Caylor, USFS).

Of the stands in the buffer that met sampling criteria (≥25 yr old with ≥1 pine with DBH ≥25.4 cm and ≥50% pine), we only sampled stands that were ≥1.8 ha because of time constraints and because a stand below this minimum size would comprise <1% of the 800 m buffer area around a cluster. Further, it often would not have been possible to fit sampling plots entirely within and ≥50 m from edges in stands that were <1.8 ha (see Section 2.3.2). We placed plots at least 50 m from stand edges for independence of plots in adjoining stands. If hardwood encroachment occurred in a large pine-dominated stand but ≥1.8 ha of mature pine remained, we redrew stand boundaries using GPS points collected during ground-truthing and sampled the remaining pine stand if it met sampling criteria.

2.3.2. Sampling random plots within stands

In each stand that met sampling criteria, we used ArcMap (v10.2.1, 2013) to randomly place one circular 0.4 ha plot ≥50 m from stand edges (Beyer et al. 1996, Addington et al. 2015). Given the number of stands within the 800 m buffers and time constraints, this was the largest area we could effectively sample. We recognize that there can be variation in vegetation within a stand, but we expected greater variation among stands than within stands. Within each stand, vegetation was managed via the same regiment (pers. comm. with M. Caylor, USFS), and during our field sampling, stand boundaries were evident based on vegetation differences among stands. Therefore, we chose to sample 1 plot per stand in stands selected according to methods described in Section 2.3.1. In some irregularly shaped stands, it was not possible to place a 0.4 ha circular plot at least 50 m from all edges. In these cases, we randomly placed a 0.4 ha circular plot at least 50 m from one stand edge.

Within each plot, we sampled understory vegetation (≤1 m in height) using the line intercept method on a transect that ran along the diameter of the plot from north to south (Outcalt & Brockway 2010). We measured percent cover of the following vegetation functional groups: forb, grass, shrub or hardwood, and vine (Table 1). We sampled these vegetation characteristics because, taken together, they describe the percentage of herbaceous understory within a plot, the RCW Recovery Plan recommends a recovery standard of ≥40% herbaceous understory (USFWS 2003, Table S1 in Supplement 1; all 4 Supplements are available at www.int-res.com/articles/suppl/n050p249_supp/), and previous studies indicated RCWs prefer to forage in areas with higher percent herbaceous understory (James et al. 1997, USFWS 2003). We measured vine cover because vines were prolific in the Oakmulgee, and we found little literature about vine cover and RCW foraging preferences or reproductive output.

In a 2 m wide belt transect along the length of each understory transect, we measured stem density of woody plants in the midstory with a height ≥1 m but a DBH <10 cm (Addington et al. 2015; Table 1). We measured woody midstory density because midstory stem density was negatively correlated with RCW clutch size in Wood et al. (2014), and the recovery standard describes a sparse to non-existent hardwood midstory (USFWS 2003, Table S1 in Supplement 1).

We used a 10-factor prism to estimate basal area (BA; m^2 ha^{-1}) of overstory trees and tallied trees within the limiting distance of the prism from the center of the plot. We measured DBH of each tree in the limiting distance and recorded whether trees were pine or hardwood (Table 1). If ≥50% of the trees in the limiting distance of the 10-factor prism were pine, then we classified the stand as pine-dominated. We measured DBH and BA of pine and hardwood trees because Butler & Tappe (2008) observed greater RCW nest success and fledgling recruitment in areas with lower hardwood BA. Also, greater pine DBH and mature pine BA was associated with more RCW fledglings (Garabedian et al. 2017). Both pine BA and percent hardwood overstory are described in the recovery standards as well (USFWS 2003; Table S1 in Supplement 1).

Measurements for the 400 m buffer were a subset of the 800 m buffer measurements. If a pine stand occurred in multiple 800 m buffers, we sampled one circular 0.4 ha plot and applied those measurements to all the 800 m buffers in which the stand occurred.

Table 1. Red-cockaded woodpecker (RCW) *Dryobates borealis* habitat covariates measured within a 400 and 800 m buffer from an RCW cluster center. DBH: diameter at breast height; BA: basal area

Covariate
Mean DBH of all hardwood with ≥10 cm DBH
Mean DBH of all pines with ≥10 cm DBH
Mean BA of pines with <25.4 cm DBH but with ≥10 cm DBH
Mean BA of pines with ≥25.4 cm DBH
Mean BA of hardwoods with ≥10 cm DBH
Midstory density calculated using the number of hardwood stems in an area with <10 cm DBH but ≥1 m high
Mean% understory cover (<1 m high) of shrubs and hardwood seedlings
Mean% understory cover (<1 m high) of vines
Mean% understory cover (<1 m high) of shrubs, hardwood seedlings, and woody vines
Mean% understory cover (<1 m high) of grasses
Mean% understory cover (<1 m high) of forbs
Mean% understory cover (<1 m high) of grasses and forbs
Mean fire return interval within the buffer
Mean fire return interval in RCW habitat within the buffer
Mean no. of days since RCW habitat has been burned
Mean no. of years since RCW habitat has been burned
% RCW habitat last burned during the growing season (April–September)
% RCW habitat last burned during the dormant season (October–March)
Total area of RCW habitat
Toral area of high-quality RCW habitat
No. of meters from the RCW cluster center to the nearest active RCW cluster center
No. of active RCW clusters within the buffer

Because we did not sample stands <1.8 ha, for buffer-level calculations we assumed that stands <1.8 ha had the same stand type as the stand type (i.e. pine or hardwood) with which the <1.8 ha stand shared the most border, and we assumed the <1.8 ha stand had the stand characteristics of the largest bordering stand of that stand type.

2.3.3. Calculating vegetation covariates

With our data collection protocol, we were able to evaluate the suitability of sampled stands for RCWs based on 4 recovery standards for good quality foraging habitat (Table 13 in USFWS 2003; Table S1 in Supplement 1): percent herbaceous ground cover, BA of small pines, BA of large pines, and percent hardwood canopy cover. If a stand met all 4 recovery standards, the stand was considered high-quality habitat. We summed the area of high-quality habitat within the 800 m buffer to calculate the quality habitat variable (Table 1).

To create covariates that represent habitat within the buffer surrounding an RCW cluster, we needed to summarize the diversity of stands within a buffer. We accounted for diversity in stands within the buffer by calculating a weighted mean (ω) where each stand-specific covariate measurement (M_i for stand i = 1, 2, …, n) was weighted by the percentage of RCW habitat within the buffer that was made up by that stand (H_i) (Supplement 1):

$$\omega = \sum_{i=1}^{n} (H_i \times M_i) \quad (1)$$

2.4. Prescribed fire data

We used burn history data from the USFS Oakmulgee Ranger District. The Oakmulgee is divided into compartments to organize timing of management activities such as prescribed burning. For prescribed burns before 2008, a GIS shapefile indicated the years in which a compartment was burned. We assumed that all stands in a compartment were burned because there were no records at a finer spatial scale. As support for this assumption, we note that for the prescribed fire data that included acreage, 62% of the time the entire compartment was burned.

For prescribed burns between 2008–2016, the USFS had burn prescription documents that indicated the day, month, and year the burn was conducted. Dormant season was defined as November 1–March 31, and growing season was defined as April 1–October 31 (pers. comm. with M. Caylor, USFS). No prescribed burns were conducted in 2017 due to dry conditions. Some burn prescription documents indicated specific stands within compartments that were burned. Other burn prescription documents only listed the compartment and the size of the area burned within the compartment. This created uncertainty about where the burn occurred relative to the RCW clusters because the 800 m buffers around RCW clusters did not cover entire compartments and often spanned multiple compartments (Fig. 2). Therefore, if records did not indicate which stands in a compartment were burned but the burned area was ≥50% of the compartment area, we assumed that all stands in the compartment within our 800 m buffers were burned. Uncertainty in the data required assumptions about the location of burns, and if records indicated the majority of the compartment was burned, then the part of the 800 m buffer in that compartment was most likely burned. Using similar logic, if the burned area was <50% of the compartment area, we assumed no stands in the compartment within our 800 m buffers were burned. We used the GIS shapefiles, burn prescription documents, and assumptions described above to generate a list of dates on which each stand within our 800 m buffers was burned.

We wanted to calculate a covariate for mean fire return interval because in previous studies the number of RCW fledglings produced per year was positively correlated with fire return intervals of 2–3 yr (Ramirez & Ober 2014). However, for many Oakmulgee burn dates, records included year but lacked a month or day. If only the year was recorded for a prescribed burn but a month, day, and year were recorded for a subsequent burn in the stand, we assigned the earlier burn the same month and day to compute the approximate time between burns. For each of i = 1, 2, …, n stands within a 800 m buffer, we calculated the mean number of years between burns T_i. To compute buffer-level variables, we weighted the stand-specific mean fire return intervals by the percent of the 800 m buffer that was made up by that stand (B_i) or by the percent of RCW habitat within the buffer that was made up by that stand (H_i).

$$\omega_B = \sum_{i=1}^{n} (B_i \times T_i) \quad (2)$$

$$\omega_H = \sum_{i=1}^{n} (H_i \times T_i) \quad (3)$$

We also calculated the mean number of days and years since RCW habitat within the buffer was burned (similar to Eqs. 1 & 3) as well as the percent of RCW habitat within the buffer that was most recently burned in the growing season and percent most recently burned in the dormant season. These 4 covariates depended only on the most recent burn date and therefore were not affected by the uncertainty in past burn dates.

2.5. Nest monitoring data

We partnered with the USFS to obtain RCW nest monitoring data. The USFS monitored nests during the 2017 RCW nesting season (late April–June) using cameras mounted on poles that could be maneuvered inside cavities. The USFS did not add flashing or other predator exclosures to active nest trees. RCWs begin incubation before the clutch is complete, incubation lasts 10–12 d, and eggs hatch asynchronously (Ligon 1970, Costa 2002). Optimum banding age is 5–10 d post-hatch (pers. comm. with C. Tindell, USFS), and RCWs normally fledge 24–27 d after hatching (Costa 2002). Based on this information, the USFS checked all historically active RCW clusters (approximately 110 clusters, 31 of which were included in this study) once a week until eggs or nestlings were observed in a nest. Once eggs or nestlings were observed, the USFS did not check the cluster again until they returned to band the hatchlings. Occasionally, nest cavities were found empty, either indicating predation or that not all groups attempted nesting. Consequently, the nest monitoring data collected by the Oakmulgee USFS consisted of number of eggs observed and number of hatchlings observed. The Oakmulgee does not have the funding or staffing to conduct fledge checks with regularity, so fledging success was uncertain (pers. comm. with C. Tindell, USFS). The limited capacity to check nests between finding eggs and banding hatchlings resulted in uncertainty about the total number of eggs laid and number of eggs that produced nestlings. Observers may have missed eggs that did not hatch or nestlings that did not survive to banding age. However, the existing data are the best available information, so we analyzed what was available and draw conclusions with limitations about the data in mind.

2.6. Statistical analysis

Because of the lack of published research on RCWs in the Oakmulgee, our models were exploratory (Tredennick et al. 2021). Our aim was to identify potentially important relationships between habitat features and reproductive output but avoid spurious relationships (Tredennick et al. 2021). Overall, we used Bayesian generalized linear models (GLMs) with vague priors to examine the influence of covariates at the 400 and 800 m scales on measures of RCW egg and hatchling production (Fig. 3). In the exploratory modeling, we formatted the nest monitoring data in multiple ways to avoid missing potentially important relationships. We used GLMs with a Poisson error distribution to model (1) the number of eggs, (2) the number of hatchlings, and (3) the number of eggs lost (i.e. did not hatch or depredated); GLMs with a binomial error distribution to model (1) whether any eggs were lost (i.e. if ≥1 egg did not hatch or was depredated) and (2) whether all eggs were lost; and GLMs with a beta error distribution to model the proportion of eggs that were lost (Venables & Ripley 2003). Because the log-likelihood for the GLM with a beta error distribution contains $\log(y)$ and $\log(1-y)$, it would be unbounded when $y = 0$ or $y = 1$ (i.e. clusters had no ($y = 0$) or all eggs ($y = 1$) lost). Therefore, we used the transformation $(y\,(n-1) + 0.5)/n$, where n is the sample size and y is the observed value of the response variable and used the transformed values in the beta regression models (Smithson & Verkuilen 2006).

In the exploratory modeling, we considered more covariates than suitable for a global model (van de Pol et al. 2016), so we first used stochastic search variable selection (SSVS) to assess which individual habitat covariates (Table 1) were relevant to RCW egg and hatchling output (George & McCulloch 1993, O'Hara & Sillanpaa 2009, Hooten & Hobbs 2015, Gilbert & Ferguson 2019). With SSVS, an indicator variable δ is included in the regression model to indicate if the covariate is informative (O'Hara & Sillanpaa 2009, Hooten & Hobbs 2015). The regression coefficient β was replaced by the product of a binary indicator variable and a regression coefficient, $\delta \times \beta$. We assigned the δ parameter a vague Bernoulli (0.5) prior. Conceptually, a posterior of δ approaching 1 indicates the covariate is important in the model, while a posterior approaching 0 essentially removes the effect of the covariate from the model. The prior for $\beta \mid \delta$ was $\delta\text{Normal}(0, c\tau^2) + (1-\delta)\text{Normal}(0, \tau^2)$, where c and τ^2 were tuned such that within each Markov Chain Monte Carlo (MCMC) iteration of the model, each β was given either a 'slab' prior centered at 0 with a large ($c\tau^2 = 2$) variance when $\delta = 1$ or a 'spike' prior centered at 0 with a small ($\tau^2 = 0.02$) variance when $\delta = 0$ (Hooten & Hobbs 2015, Cruz et al. 2019). For each measure of RCW egg or hatchling

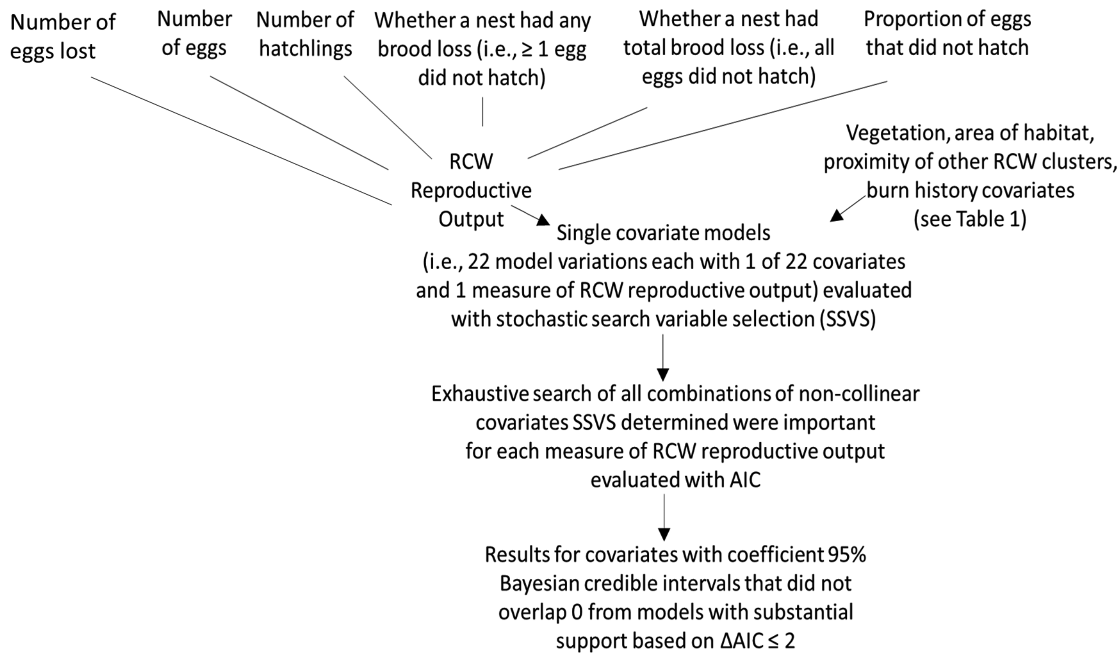

Fig. 3. Conceptual diagram of the modeling procedure. We modeled 5 measures of red-cockaded woodpecker (RCW) *Dryobates borealis* reproductive output. A measure of reproductive output was combined with covariates (see Table 1) first in single covariate models evaluated with stochastic search variable selection (SSVS). Then non-collinear covariates that SSVS determined were important were combined in an exhaustive search of covariate combinations and models were evaluated with Akaike's information criterion (AIC)

output, we standardized covariates to have a mean of 0 and variance of 1 and ran models with one covariate at a time noting which covariates had a posterior mean for δ (the binary indicator variable that is multiplied by β in the SSVS regression coefficient) ≥ 0.5. Covariates that had a δ with posterior mean <0.5 were eliminated from further consideration (because δ is an indicator variable where 1 indicates the covariate is important in the model and 0 essentially removes the covariate from the model), and covariates that had a δ with posterior mean ≥ 0.5 were used in the next modeling step.

Next, we included all combinations of non-collinear covariates (Pearson's $|r| < 0.7$) (Dormann et al. 2013) at both the 400 and the 800 m scale that had δ with posterior mean ≥ 0.5 in models for each measure of RCW egg or hatchling output. We used Akaike's information criterion (AIC) to rank models from this exhaustive search of covariates using R 4.0.5 and the package bestglm (McLeod et al. 2020, R Core Team 2021).

We fit all models that had substantial support based on ΔAIC ≤ 2 (Burnham & Anderson 2002) in OpenBUGS 3.2.3 using the R2OpenBUGS package (Sturtz et al. 2005, Lunn et al. 2009). Fitting Bayesian models facilitated the generation of uncertainty measures because posterior distributions are inferred for all unknown parameters in Bayesian models. We used vague normal (mean = 0, precision = 0.001) priors for the regression intercept and coefficient parameters, and for GLMs with a beta error distribution, we used a vague gamma (shape = 0.001, rate = 0.001) prior for the parameter that relates the response variable from the regression equation to the beta distribution's 2 shape parameters. We used 3 MCMC chains with 20 000 iterations, a burn-in of 10 000, and thinning of 5. We assessed convergence via visual inspection of trace plots and the Gelman-Rubin potential scale reduction factor (Rhat); chains with Rhat ≤ 1.04 were considered converged (Brooks & Gelman 1998). We present results for covariates with coefficient 95% Bayesian credible intervals that did not overlap 0.

Our use of diverse statistical methods (e.g. SSVS, AIC, examining posterior distributions) is consistent with the sense in Efron (2005), Little (2006), and Dorazio (2016) that modern statistical analyses will likely involve a combination Bayesian and frequentist ideas because Bayesian methods are most suitable for inferences and predictions (Dorazio 2016) while frequentist methods are most suitable for evaluating and comparing models (Box 1980, Rubin 1984, Draper 1996, Gelman et al. 1996, Little 2006, 2011, Gelman 2011). There is not consensus about the best approach for Bayesian model comparison (Royle & Dorazio 2008, Hooten & Hobbs 2015).

3. RESULTS

3.1. Egg and hatchling production

RCW *Dryobates borealis* clusters produced 2–7 eggs and 0–4 hatchlings (Fig. 4). The mean number of eggs per cluster was 3.2 (SD = 1.1), and the mean number of hatchlings per cluster was 2.3 (SD = 1.1). Half of the clusters had ≥1 egg lost. These clusters lost between 33 and 100% of eggs (1–4 eggs, mean = 1.77, SD = 1.01), and the mean proportion of eggs lost was 0.52 (SD = 0.30). Three clusters lost all eggs.

3.2. Vegetation composition in RCW habitat in the Oakmulgee

There was substantial variation in stand composition both within and among cluster buffers. For example, 23% of clusters had 2 types of stands within the buffer, 46% had 3, and 31% had 4. The mean percent of the buffer composed of longleaf *Pinus palustris* or loblolly *P. taeda* pine >25 yr old was 52% (SD = 12.3%) (Fig. 2). The stands we sampled averaged 8.71 ha (n = 342, SD = 8.64). Overall, the area in the 800 m buffers around the RCW clusters was 58% longleaf or loblolly pine >25 yr old, 4% longleaf pine <25 yr old, 7% mixed loblolly pine and hardwood, and 31% hardwood (Fig. 2).

Although 96.7% of sampled stands met at least 1 recovery standard (Table S1 in Supplement 1, USFWS 2003), only 13.6% of sampled stands met all 4 sampled recovery standards. Specifically, 70.2% of sampled stands met the small pine BA recovery standard, and 92.5% of sampled stands met the large pine BA recovery standard (Table 2). While 74.6% of longleaf-dominated stands met the recovery standard for overstory hardwood canopy composition, only 40.0% of loblolly-dominated stands met the recovery standard for overstory hardwood canopy composition. On average only 56% (SD = 0.19) of RCW habitat within 800 m of clusters contained a percentage of overstory hardwoods that was consistent with the recommended limit; the remaining habitat would not be considered suitable for foraging RCWs (Table 2). Stands that met all 4 recovery standards tended to be closer (mean = 494 m, SD = 248 m) to the RCW cluster center than stands that met <4 recovery standards (mean = 571 m, SD = 193 m), but only 40% of stands containing RCW cluster centers that we sampled met all 4 recovery standards.

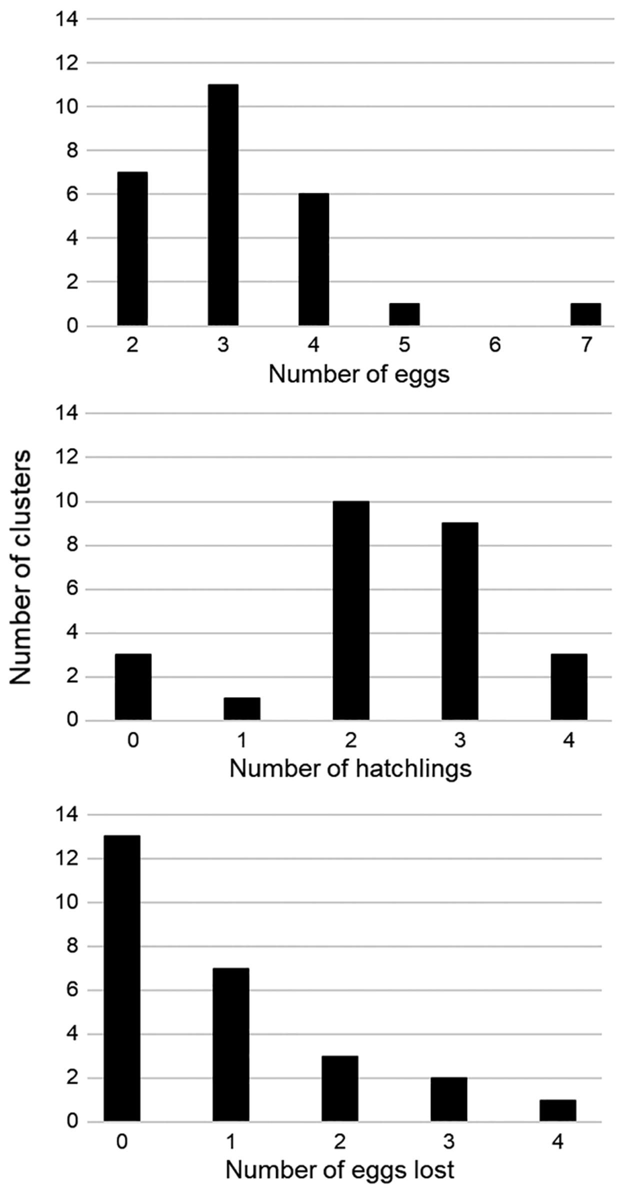

Fig. 4. Number of red-cockaded woodpecker (RCW) *Dryobates borealis* eggs, hatchlings, and eggs lost per cluster at 26 clusters in the Oakmulgee Ranger District of the Talladega National Forest, Alabama

Hardwood midstory density averaged 0.76 stems per m^2 (SD = 0.62, range = 0–3.34) in the 800 m buffers around the RCW clusters. We did not find recommended thresholds in the literature for hardwood midstory stem density, but Conner & Rudolph (1989) and Loeb et al. (1992) suggested a hardwood and pine midstory BA threshold of 5.7 m^2 ha^{-1}. We estimated that 23.5% of the 800 m buffers in the

Oakmulgee had hardwood midstory BA >5.7 m^2 ha^{-1} based on a conservative estimate of 2.5 cm DBH for an average midstory stem.

The Oakmulgee lacks wiregrass *Aristida stricta*, and 80.2% of stands did not meet the herbaceous groundcover recovery standard (Table 2). The proportion of RCW habitat within 800 m of a cluster that met the herbaceous groundcover recovery standard never exceeded 67%. On average, 24.7% of the understory in sampled stands was herbaceous (Table 2), while 57.2% of sampled stands had a woody understory composed of shrubs, hardwoods, or woody vines.

3.3. Association of vegetation and fire covariates with reproductive output

Of the 22 covariates (Table 1) included in the single-covariate models (i.e. 22 model variations with 1 covariate per model), SSVS identified important covariates for modeling the number of eggs lost, whether a nest had brood loss (i.e. if ≥1 egg lost), and the proportion of eggs lost (Table S2 in Supplement 1). No covariates were associated with the number of eggs or number of hatchlings. The models for whether all eggs in a nest were lost did not converge due to the small number of nests that experienced total brood loss (12% of nests; 3 out of 26 nests), so we do not report results from these models. Seven models of the number of eggs lost, 10 models of whether a nest had brood loss (i.e. if ≥1 egg lost), and 5 models of the proportion of eggs lost had substantial support based on ΔAIC ≤2 (Tables 3–5).

There was less egg loss in clusters with a greater area of large pines and in clusters with a smaller area of small pines (Tables 4 & 5, Figs. S1 & S2 in Supplement 1). The probability that ≥1 egg did not produce a hatchling was negatively associated with BA of pine trees with DBH >25.4 cm (Table 4, Fig. S1), and the proportion of eggs lost was positively associated with BA of pine trees with DBH >10 and <25.4 cm (Table 5, Fig. S2).

A greater percent of habitat burned in the dormant season (Table 3, Fig. S3 in Supplement 1) and a lower percent of habitat burned in the growing season were both associated with less egg loss (Table 3, Fig. S4 in Supplement 1) and a lower probability that ≥1 egg did not produce a hatchling (Table 4). Having another active cluster nearby was associated with less egg loss; the number of eggs lost was negatively associated with the number of RCW clusters within 400 m (Table 3, Fig. S5 in Supplement 1).

4. DISCUSSION

Because the nest monitoring protocol used by the USFS could not measure fledging success and because none of the covariates we examined were identified by SSVS to be important for the number of eggs or number of hatchlings, our analysis generated insights about partial brood loss in the Oakmulgee. Compared to previous studies, we observed similar numbers of eggs and hatchlings per nest, but we observed a higher rate of partial brood loss (Table S3 in Supplement 1). The Recovery Plan notes that rates

Table 2. Stand characteristics and proportion of area within 800 m buffers around red-cockaded woodpecker (RCW) *Dryobates borealis* clusters that met recovery standards from the RCW Recovery Plan. We sampled 26 RCW clusters; often there were multiple stands in the 800 m buffer around a RCW cluster. Proportion of habitat within 800 m buffers that met the recovery standard was determined by calculating the area of sampled stands that met a recovery standard threshold divided by the total area of sampled stands within the 800 m buffer. BA: basal area; LL: longleaf pine; LOB: loblolly pine; small pines: pines with a diameter at breast height (DBH) 10 cm but <25.4 cm; large pines: pines with a DBH ≥25.4 cm

Vegetation characteristic	Recommended threshold	Stand characteristics within 800 m buffers				Proportion of area within 800 m buffers meeting recovery standard threshold			
		Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
% herbaceous	>40%	24.69%	0.00%	100%	22.25%	0.26	0.03	0.67	0.19
BA small pines	<2.3 m^2 ha^{-1}	3.88 m^2 ha^{-1}	0.00 m^2 ha^{-1}	41.32 m^2 ha^{-1}	7.39 m^2 ha^{-1}	0.76	0.51	1.00	0.14
BA large pines	>2.3 m^2 ha^{-1}	16.78 m^2 ha^{-1}	0.00 m^2 ha^{-1}	41.32 m^2 ha^{-1}	8.03 m^2 ha^{-1}	0.94	0.65	1.00	0.10
% canopy hardwood	<10% LL-dominated <30% LOB-dominated	LL: 7.88% LOB: 36.33%	LL: 0.00% LOB: 0.00%	LL: 73.68% LOB: 66.67%	LL:15.07% LOB: 18.91%	0.56	0.09	0.88	0.19

Table 3. Generalized linear models of the number of red-cockaded woodpecker (RCW) *Dryobates borealis* eggs lost that had substantial support based on difference in Akaike's information criterion (ΔAIC). Mean and 95% Bayesian credible interval bounds (in parentheses) from posterior distributions for coefficients of covariates are shown. Whether the covariate was measured within 400 or 800 m of the cluster center is noted in parentheses is noted in the column headers. BA: basal area; DBH: diameter at breast height

Mean BA of pines with <25.4 cm DBH but ≥10 cm DBH (400 m)	% RCW habitat last burned during growing season (400 m)	% RCW habitat last burned during dormant season (400 m)	No. of active RCW clusters within the buffer (400 m)	% RCW habitat last burned during growing season (800 m)	% RCW habitat last burned during dormant season (800 m)	ΔAIC
0.29 (−0.03, 0.59)			−2.18 (−5.30, −0.21)	0.54 (0.03, 1.12)		–
0.29 (−0.03, 0.58)			−2.19 (−5.26, −0.24)		−0.54 (−1.12, −0.02)	0.03
0.30 (−0.01, 0.60)		−0.45 (−1.00, 0.05)	−2.15 (−5.23, −0.19)			1.08
0.30 (0.02, 0.60)	0.45 (−0.06, 1.01)		−2.15 (−5.25, −0.21)			1.08
			−1.99 (−5.09, −0.05)	0.69 (0.19, 1.26)		1.60
			−1.99 (−5.07, −0.06)		−0.69 (−1.24, −0.19)	1.63
0.41 (0.11, 0.69)			−2.14 (−5.27, −0.17)			1.98

of partial brood loss are highly variable (~30–60%) among years and populations (USFWS 2003). In the study by McCormick et al. (2003), the number of nestlings initially in the nest appeared to have the most important effect on partial brood loss. McCormick et al. (2003) observed partial brood loss in all nest with 4 initial nestlings, in no nests with 1 initial nestling, and at a greater rate in nests with 4 initial nestlings compared to nests with ≤3 initial nestlings. In our study, clusters with ≥4 eggs and clusters with 3 eggs had similar rates of brood loss (62.5 and 63.6% of clusters lost ≥1 egg, respectively), but only 14.3% of clusters with 2 eggs lost ≥1 egg. While our nest monitoring data included uncertainty because of constraints that limited the frequency of nest checks, it is noteworthy that previous studies found the failure rate was higher during egg laying than in the nestling stage and most brood loss occurred during incubation or soon after hatching (LaBranche & Walters 1994, Conner et al. 2001). In LaBranche & Walters (1994), few nestlings were lost between banding and fledging checks, and the mean number of nestlings and fledgling were highly correlated. Although our nest monitoring data did not include number of fledglings, our data likely captured a large percent of the reproductive failure.

4.1. RCW habitat and partial brood loss in the Oakmulgee

Habitat (specifically hardwood midstory) only influenced partial brood loss in nests with 3 initial nestlings in McCormick et al. (2003), but our models identified important covariates for the number of eggs lost, whether a nest had brood loss (i.e. if ≥1 egg lost), and the proportion of eggs lost. Our study and Wood et al. (2014) found a similar negative relationship between RCW *Dryobates borealis* group density and egg loss. However, whereas other studies (McCormick et al. 2003, Wood et al. 2014) found a link between increased hardwood midstory and increased egg loss, we did not detect a relationship. Interestingly, we did not find other studies in the literature that estimated relationships between partial brood loss and burn season.

There is evidence from the literature that habitat quality influences partial brood loss. Wood et al. (2014) found farthest foraging distance from the nest tree and large home range size, which is expected in areas with lower-quality habitat, were associated with greater egg loss, while higher cluster density, which is expected in areas with higher quality habitat, was associated with more eggs hatched (Wood et al. 2014). If habitat quality influences rates of partial brood loss, it is important to determine what habitat features influence quality for a particular RCW population. Because of variation in ecoregions, vegetation composition, and land use histories within the RCW's range, the effect of habitat features may not be constant throughout the RCW's range (Garabedian et al. 2014, Martin et al. 2021).

Our findings of less egg loss in clusters with a greater area of large pines *Pinus* spp. and a smaller area of small pines are consistent with previous research indicating that large pines contribute to high-quality RCW habitat. RCWs are thought to select the largest available pines for foraging and nesting (Zwicker & Walters 1999, Davenport et al. 2000, McKellar et al. 2016) and select older pine trees for cavity excavation (Jackson et al. 1979, Conner & O'Halloran 1987, DeLotelle & Epting 1988, Hooper et

Table 4. Generalized linear models of whether a red-cockaded woodpecker (RCW) *Dryobates borealis* nest had brood loss (i.e. if ≥1 egg lost) that had substantial support based on difference in Akaike's information criterion (ΔAIC). Mean and 95% Bayesian credible interval bounds (in parentheses) from posterior distributions for coefficients of covariates are shown. Whether the covariate was measured within 400 or 800 m of the cluster center is noted in parentheses in the column headers. BA: basal area; DBH: diameter at breast height

Mean BA of pines with <25.4 cm DBH but ≥10 cm DBH (400 m)	% RCW habitat last burned during growing season (400 m)	% RCW habitat last burned during dormant season (400 m)	Mean BA of pines with ≥25.4 cm DBH (800 m)	Mean no. of years since RCW habitat had been burned (800 m)	Mean no. of days since RCW habitat had been burned (800 m)	% RCW habitat last burned during growing season (800 m)	% RCW habitat last burned during dormant season (800 m)	ΔAIC
			−1.69 (−3.24, −0.47)			1.33 (0.18, 2.69)		–
			−1.69 (−3.28, −0.47)				−1.32 (−2.71, −0.18)	0.03
		−1.12 (−2.36, −0.05)	−1.54 (−3.00, −0.38)					0.89
	1.13 (0.08, 2.36)		−1.53 (−2.97, −0.37)					0.89
0.56 (−1.07, 2.42)			−1.62 (−3.32, −0.26)			1.30 (0.06, 2.80)		1.79
0.56 (−1.03, 2.40)			−1.61 (−3.29, −0.27)				−1.28 (−2.77, −0.07)	1.82
			−1.62 (−3.30, −0.21)	−0.45 (−2.40, 1.15)		1.38 (0.21, 2.79)		1.92
			−1.62 (−3.33, −0.24)	−0.45 (−2.40, 1.16)			−1.38 (−2.81, −0.20)	1.95
			−1.69 (−3.34, −0.35)		−0.36 (−2.21, 1.20)	1.43 (0.25, 2.89)		1.95
			−1.67 (−3.34, −0.33)		−0.37 (−2.21, 1.17)		−1.42 (−2.89, −0.24)	1.98

al. 1991, Rudolph &Conner 1991, Conner et al. 1994). If the habitat around a cluster is poor quality, RCWs may travel greater distances during foraging, potentially leaving less time for incubation; Wood et al. (2014) found a negative relationship between the maximum foraging distance of an RCW from its nest tree and the number of eggs that hatched. Franzreb (2010) also found that the number of fledglings per breeding pair was positively correlated with the number of pine stems ≥25.4 cm DBH within 800 m of the cluster core.

Pine stocking densities in the Oakmulgee were compatible with RCW management goals (Table 2), but hardwood overstory composition, especially in loblolly pine *P. taeda*-dominated stands, was higher than recommended (USFWS 2003). However, hardwood DBH and BA variables were not important covariates in our models; we did not find evidence that the prevalence of overstory hardwoods was associated with brood loss in the Oakmulgee. The topography in the Oakmulgee (i.e. high relief and steep slopes) is conducive to the persistence of hardwood stands in mesic drainages immediately adjacent to stands of loblolly or longleaf pine along xeric ridges (Fig. 2). Some of these upland sites harbor mature fire-tolerant hardwoods, such as turkey oak *Quercus laevis* or post oak *Q. stellata*, that occur naturally within southern pine ecosystems and thus do not indicate a lack of fire on the landscape (USFWS 2003, Hiers et al. 2014).

Although we observed prevalent woody species in the Oakmulgee midstory and previous studies found higher hardwood midstory presence (i.e. density, BA, and stem number) was associated with greater egg loss (McCormick et al. 2003, Wood et al. 2014), SVSS did not identify midstory hardwood stem density as an important covariate in our models. It is possible that RCWs in the Oakmulgee have adapted to higher amounts of hardwood midstory, but exceeding the recommended midstory BA threshold could be of concern because a woody midstory can cause RCWs to abandon a cluster to search for suitable habitat, resulting in a decline in PBGs (Conner & Rudolph 1989, Loeb et al. 1992, Wood et al. 2014). Also, woody species can generate hotter fires that can result in mature pine mortality (Varner et al. 2007). Therefore, continued management of midstory hardwoods in the Oakmulgee is advisable. For example, applying herbicidal or mechanical treatments could reduce midstory density and facilitate the application of fire according to management objectives (Lettow et al. 2014).

Percent herbaceous groundcover was not important for egg numbers, hatchling numbers, or brood loss in our study. Other studies also have

Table 5. Generalized linear models of the proportion of red-cockaded woodpecker (RCW) *Dryobates borealis* eggs lost that had substantial support based on difference in Akaike's information criterion (ΔAIC). Mean and 95% Bayesian credible interval bounds (in parentheses) from posterior distributions for coefficients of covariates shown. Whether the covariate was measured within 400 or 800 m of the cluster center in parentheses is noted in the column headers. BA: basal area; DBH: diameter at breast height

Mean BA of pines with <25.4 cm DBH but ≥10 cm DBH (400 m)	% RCW habitat last burned during growing season (400 m)	% RCW habitat last burned during dormant season (400 m)	% RCW habitat last burned during growing season (800 m)	% RCW habitat last burned during dormant season (800 m)	ΔAIC
0.63 (0.14, 1.16)			0.37 (−0.13, 0.88)		–
0.64 (0.13, 1.16)				−0.37 (−0.87, 0.13)	0.01
0.73 (0.23, 1.24)					0.29
0.64 (0.13, 1.17)		−0.33 (−0.82, 0.16)			0.37
0.64 (0.13, 1.17)	0.33 (−0.17, 0.82)				0.37

reported small effect sizes of herbaceous groundcover on RCW clutch size, group size, nestling production, and fledgling production (Garabedian et al. 2014). In fact, the herbaceous groundcover recovery standard (USFWS 2003) was based on 3 studies (Hardesty et al. 1997, James et al. 1997, 2001) that took place in an ecosystem with wiregrass *Aristida stricta* in the understory, but the Oakmulgee does not have wiregrass.

We found that presence of another RCW cluster within 400 m was associated with less egg loss, and similarly, Wood et al. (2014) found higher cluster density was associated with a greater number of eggs hatched (Wood et al. 2014). However, studies conflict about how RCW cluster density influences hatchling and fledgling production. Higher RCW cluster density can lead to larger RCW group sizes, which can increase RCW hatchling and fledgling production (Lennartz et al. 1987, Neal et al. 1993, Heppell et al. 1994, Beyer et al. 1996, Conner et al. 2004). The positive relationship between RCW group size and reproductive output is largely due to the presence of more helpers in larger groups (Lennartz et al. 1987, Neal et al. 1993, Beyer et al. 1996, Conner et al. 2004). Helper presence benefits nest success and breeder survival by reducing stress on breeding pairs, specifically decreasing their incubation time and number of feedings (Khan & Walters 2002). On the other hand, higher RCW cluster density could result in lower RCW hatchling and fledgling production due to increased effort expended in territorial defenses and reduced access to high-quality foraging areas (Garabedian et al. 2018, 2020).

As expected, a higher percent of RCW habitat last burned during the dormant season was associated with fewer eggs lost at the 800 m scale. James et al. (1997) and Ramirez & Ober (2014) found dormant season burns increased herbaceous understory, which was positively associated with RCW egg and fledgling production. As discussed above, we did not find a relationship between percent herbaceous understory and RCW partial brood loss, egg production, or hatchling production, so further investigation into the mechanism through which dormant season burns influence brood loss in the Oakmulgee would be valuable.

Contrary to expectations, a lower percent of RCW habitat last burned during the growing season was associated with fewer eggs lost at the 800 m scale. Our results are not consistent with Sparks et al. (1999) and Wood et al. (2014) that found growing season fires were more likely than dormant season fires to decrease hardwood midstory density (Sparks et al. 1999), which was negatively associated with the number of RCW eggs hatched and the number of fledglings (Wood et al. 2014). Our unexpected result is not due to correlation between years since burn and percent of RCW habitat last burned the growing season (Pearson correlation coefficient $\rho = -0.20$). Our results could be related to the particular understory and midstory composition in the Oakmulgee, which differs from some highly-studied regions in the RCW's range as discussed above.

SSVS did not identify the number of days or years since the previous burn or the mean fire return interval as important covariates in our models, but Ramirez & Ober (2014) found RCWs select for habitat that is burned every 2–3 yr. The assumptions we had to make during analysis because the Oakmulgee USFS did not always have records about which stands within compartments were burned or the month and day of burns could have influenced our results about the effects of fire return interval, time since the previous burn, or burn season.

4.2. Resource constraints, data availability, and implications for the Oakmulgee

Data scarcity is a perennial problem for endangered species conservation. Of the species assessed by the International Union for Conservation of Nature, 14% are classified as data deficient because of a lack of data about taxonomy, geographic distribution, population status, or threats (IUCN 2022). In this study, we found how, even for a heavily studied species, a lack of data in a region of the species' range can make conservation challenging. With the USFS nest monitoring data, there is uncertainty about the total number of eggs laid and number of eggs that produced nestlings and no information about the number of chicks that fledged. At this point, there is no information we can use to correct for this uncertainty in the data, so we analyzed the data as the best available data currently.

We and others (McCarthy et al. 2012, Coad et al. 2019, Burt et al. 2022) found that limited staffing and funding was the main barrier to conservation. The ability of the Oakmulgee USFS to collect more data is constrained by funding, number of staff, and time (pers. comm. with C. Tindell, USFS). With their limited resources, the USFS attempts to collect data types that are emphasized in the Recovery Plan, namely number of active clusters and number of PBGs. Group size and reproductive success are not a top priority for the Oakmulgee USFS's limited resources because this monitoring is recommended for small populations with <30 PBGs. Translocation is the rationale for the Oakmulgee USFS to band RCW chicks (pers. comm. with C. Tindell, USFS). Nevertheless, a lack of data about group size and reproductive success in the Oakmulgee hinders understanding about how local habitat and population features influence RCW demographics. The data gaps that most affected our analysis were detailed spatial and temporal data about some prescribed burns and RCW fledgling production data. We suspect these data gaps influenced which prescribed burn covariates were important in the models, affected estimation about the effect of burns in growing or dormant seasons, and limited which aspects of reproductive output we could analyze. More understanding could help direct management of the Oakmulgee RCW population to increase the number of PBGs from the ~120 seen during recent years towards the 250 PBGs recommended in the Recovery Plan.

With additional resources, the Oakmulgee USFS would like to install recruitment clusters, manage cavities, GPS and inventory RCW trees, conduct midstory removal, and conduct predator and kleptoparasite control (pers. comm. with C. Tindell, USFS). It would be interesting to predict which actions would provide the largest gains in knowledge and conservation if additional resources became available. Results could help the Oakmulgee USFS prioritize their resources for studying and managing the RCW population in the Oakmulgee.

5. CONCLUSIONS

The vegetation and RCW *Dryobates borealis* demographic data reported in our study are valuable because the Oakmulgee has a unique RCW habitat composition and because of the lack of RCW or habitat data previously published in a peer-reviewed journal from the Oakmulgee. Most sampled stands within 800 m of an RCW cluster met recovery standard thresholds for small pine BA and large pine BA. While most longleaf pine *Pinus palustris*-dominated stands met the threshold for overstory hardwood canopy composition, most loblolly pine *P. taeda*-dominated stands did not. Also, few stands met the recommended percentage of herbaceous understory or absence of hardwood midstory. Overall, few stands met all sampled criteria for high quality RCW habitat. In our models, hardwood overstory and midstory did not influence egg or hatchling production. Further investigation is needed to determine how overstory and midstory hardwoods in the Oakmulgee might influence other aspects of RCW demography, such as fledge success. The degree to which hardwoods contribute to unfavorable habitat conditions on the Oakmulgee versus how they relate to variation in habitat conditions across the RCW's range is unknown (Martin et al. 2021). We found evidence that habitat in the Oakmulgee with a greater area of large pines *Pinus* spp., less area of small pines, larger area burned in the dormant season, and higher RCW density was associated with a lower rate of partial brood loss. Unexpectedly, our models indicated that a smaller area burned in the growing season was associated with a lower rate of partial brood loss, but this result could be influenced by a lack of information about where prescribed burns were conducted. Although the RCW is a heavily studied species in general, regions of the RCW's range are understudied, and limited staffing and funding impede advances in understanding habitat requirements and approaches to RCW conservation in these regions.

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LITERATURE CITED

Addington RN, Greene TA, Harrison WC, Sorrell GG, Elmore ML, Hermann SM (2015) Restoring longleaf pine: effects of seasonal prescribed fire and overstory density on vegetation structure of a young longleaf pine plantation. For Sci 61:135–143

Beyer E, Costa R, Hooper RG, Hess CA (1996) Habitat quality and reproduction of red-cockaded woodpecker groups in Florida. J Wildl Manag 60:826–835

Box GEP (1980) Sampling and Bayes inference in scientific modelling and robustness (with discussion). J R Stat Soc [Ser A] 143:383–430

Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulations. J Comput Graph Stat 7:434–455

Brown E, Ferguson PFB (2019) A structured decision making analysis to increase a red-cockaded woodpecker population and balance stakeholder objectives for a National Forest. J Nat Conserv 48:77–90

Burnham KP, Anderson DR (2002) Model selection and inference: an information-theoretic approach, 2nd edn. Springer, New York, NY

Burt AJ, Nuno A, Bunbury N (2022) Defining and bridging the barriers to more effective conservation of island ecosystems: a practitioner's perspective. Conserv Sci Pract 4: e587

Butler MJ, Tappe PA (2008) Relationships of red-cockaded woodpecker reproduction and foraging habitat characteristics in Arkansas and Louisiana. Eur J Wildl Res 54: 601–608

Coad L, Watson JE, Geldmann J, Burgess ND and others (2019) Widespread shortfalls in protected area resourcing undermine efforts to conserve biodiversity. Front Ecol Environ 17:259–264

Conner RN, O'Halloran KA (1987) Cavity-tree selection by red-cockaded woodpeckers as related to growth dynamics of southern pines. Wilson Bull 99:398–412

Conner RN, Rudolph DC (1989) Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. USDA Forest Service Research Paper SO2500. New Orleans, LA

Conner RN, Rudolph DC, Saenz D, Schaffer RR (1994) Heartwood, sapwood, and fungal decay associated with red-cockaded woodpecker cavity trees. J Wildl Manag 58:728–734

Conner RN, Rudolph DC, Walters JR (2001) The red-cockaded woodpecker: surviving in a fire-maintained ecosystem. University of Texas Press, Austin, TX

Conner RN, Saenz D, Schaffer RR, McCormick JR, Rudolph DC, Burt DB (2004) Group size and nest success in red-cockaded woodpeckers in the West Gulf Coastal Plain: helpers make a difference. J Field Ornithol 75:74–78

Costa R (2002) Red-cockaded woodpecker. http://npshistory.com/brochures/nwr/red-cockaded-woodpecker-2002.pdf (accessed 9 September 2020)

Cruz J, Windels SK, Thogmartin WE, Crimmins SM, Grim LH, Larson JH, Zuckerberg B (2019) Top-down effects of repatriating bald eagles hinder jointly recovering competitors. J Anim Ecol 88:1054–1065

Davenport DE, Lancia RA, Walters JR, Doerr PD (2000) Red-cockaded woodpeckers: a relationship between reproductive fitness and habitat in the North Carolina Sandhills. Wildl Soc Bull 28:426–434

DeLotelle RS, Epting RJ (1992) Reproduction of the red-cockaded woodpecker in Central Florida. Wilson J Ornithol 104:285–294

Dorazio RM (2016) Bayesian data analysis in population ecology: motivations, methods, and benefits. Popul Ecol 58:31–44

Dormann CF, Elith J, Bacher S, Buchmann C and others (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

Draper D (1996) Utility, sensitivity analysis, and cross-validation in Bayesian model-checking. Stat Sin 6:760–767

Efron B (2005) Bayesians, frequentists, and scientists. J Am Stat Assoc 100:1–5

Franzreb KE (2010) Red-cockaded woodpecker male/female foraging differences in young forest stands. Wilson J Ornithol 122:244–258

Garabedian JE, Moorman CE, Nils Peterson M, Kilgo JC (2014) Systematic review of the influence of foraging habitat on wreproductive success. Wildl Biol 20:37–46

Garabedian JE, Moorman CE, Nils Peterson M, Kilgo JC (2017) Use of LiDAR to define habitat thresholds for forest bird conservation. For Ecol Manage 399:24–36

Garabedian JE, Moorman CE, Peterson MN, Kilgo JC (2018) Evaluating interactions between space-use sharing and defense under increasing density conditions for the group-territorial red-cockaded woodpecker *Leuconotopicus borealis*. Ibis 160:816–831

Garabedian JE, Moorman CE, Peterson MN, Kilgo JC (2020) Effects of group size and group density on trade-offs in resource selection by a group-territorial central-place foraging woodpecker. Ibis 162:477–491

Gelman A (2011) Induction and deduction in Bayesian data analysis. Ration Mark Morals 2:67–78

Gelman A, Meng XL, Stern H (1996) Posterior predictive assessment of model fitness via realized discrepancies (with discussion). Stat Sin 6:733–807

George E, McCulloch R (1993) Variable selection via Gibbs sampling. J Am Stat Assoc 88:881–889

Gilbert NA, Ferguson PFBF (2019) Landscape patterns associated with occupancy of disturbance-dependent birds in the Blackland Prairie Ecoregion of Alabama and Mississippi. Southeast Nat 18:381–404

Hardesty JL, Gault KE, Percival HF (1997) Ecological correlates of red-cockaded woodpecker (*Picoides borealis*) foraging preference, habitat use, and home range size in northwest Florida (Eglin Air Force Base). Final Report. Florida Cooperative Fish and Wildlife Research Unit, Gainesville, FL

Heppell SS, Walters JR, Crowder LB (1994) Evaluating management alternatives for red-cockaded woodpeckers: a modeling approach. J Wildl Manag 58:479–487

Hiers JK, Walters JR, Mitchell RJ, Varner JM, Conner LM, Blanc LA, Stowe J (2014) Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. J Wildl Manag 78:383–393

Hooper RG, Lennartz MR (1991) Roosting behavior of red-cockaded woodpecker clans with insufficient cavities. J Field Ornithol 54:72–76

Hooper RG, Lennartz MR, Muse HD (1991) Heart rot and cavity tree selection by red-cockaded woodpeckers. J Wildl Manage 55:323–327

Hooten M, Hobbs N (2015) A guide to Bayesian model selection for ecologists. Ecol Monogr 85:3–28

IUCN (2022) 2022 IUCN Red List of Threatened Species. Version 2021-3. IUCN, Gland. www.iucnredlist.org (accessed 6 April 2022)

Jackson JA (1985) An evaluation of aerial survey techniques for red-cockaded woodpeckers. J Wildl Manag 49:1083–1088

Jackson JA, Lennartz MR, Hooper RG (1979) Tree age and cavity initiation by red-cockaded woodpeckers. J Forestry 77:102–103

James FC, Hess CA, Kufrin D (1997) Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. Ecol Appl 7:118–129

James FC, Hess CA, Kicklighter BC, Thum RA (2001) Ecosystem management and the niche gestalt of the red-cockaded woodpecker in longleaf pine forests. Ecol Appl 11:854–870

Jones CM, Hunt HE (1996) Foraging habitat of the red-cockaded woodpecker on the D'Arbonne National Wildlife Refuge, Louisiana. J Field Ornithol 67:511–518

Kelly JF, Pletschet SM, Leslie DM Jr (1994) Decline of the red-cockaded woodpecker (*Picoides borealis*) in southeastern Oklahoma. Am Midl Nat 132:275–283

Khan MZ, Walters JR (2002) Effects of helpers on breeder survival in the red-cockaded woodpecker (*Picoides borealis*). Behav Ecol Sociobiol 51:336–344

LaBranche MS, Walters JR (1994) Patterns of mortality in nests of red-cockaded woodpeckers in the sandhills of southcentral North Carolina. Wilson Bull 106:258–271

Lennartz MR, Hooper RG, Harlow RF (1987) Sociality and cooperative breeding of red-cockaded woodpeckers, *Picoides borealis*. Behav Ecol Sociobiol 20:77–88

Lettow MC, Brudvig LA, Bahlai CA, Landis DA (2014) Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. For Ecol Manage 329:89–98

Ligon JD (1970) Behavior and breeding biology of the red-cockaded woodpecker. Auk 87:255–278

Little RJ (2006) Calibrated Bayes: a Bayes/frequentist roadmap. Am Stat 60:213–223

Little R (2011) Calibrated Bayes, for statistics in general, and missing data in particular. Stat Sci 26:162–174

Loeb SC, Pepper WD, Doyle AT (1992) Habitat characteristics of active and abandoned red-cockaded woodpecker colonies. South J Appl For 16:120–125

Lunn D, Jackson C, Best N, Thomas A, Spiegehalter D (2009) The BUGS book: a practical introduction to Bayesian analysis. Chapman & Hall/CRC, Boca Raton, FL

Macey JN, Burt DB, Saenz D, Conner RN (2016) Habitat use and avoidance by foraging red-cockaded woodpeckers in East Texas. Southeast Nat 15:76–89

Martin EJ, FN Gigliotti, PFB Ferguson (2021) Synthesis of red-cockaded woodpecker management strategies and suggestions for regional specificity in future management. Ornithol Appl 123:duab031.

McCarthy DP, Donald PF, Scharlemann JPW, Buchanan GM and others (2012) Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. Science 338:946–949

McCormick JR, Conner RN, Burt DB, Saenz D (2003) Influence of habitat and number of nestlings on partial brood loss in red-cockaded woodpeckers. In: Costa R, Daniels SJ (eds) Red-cockaded woodpecker: road to recovery. Hancock House Publ, Blaine, WA, p 624–629

McKellar AE, Kesler DC, Walters JR (2016) Resource selection reflects fitness associations for an endangered bird in restored habitat. Anim Conserv 19:131–138

McLeod FC, Xu C, Lai Y (2020) Best subset GLM and regression utilities.Version 0.37.3. https://cran.r-project.org/web/packages/bestglm/bestglm.pdf

Mitchell CC Jr (2008) Soil areas in Alabama: NRCS soils. https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/office/ssr7/?cid=nrcs142p2_047868 (accessed 20 May 2018)

Neal JC, James DA, Montague WG, Johnson JE (1993) Effects of weather and helpers on survival of nestling red-cockaded woodpeckers. Wilson Bull 105:666–673

O'Hara R, Sillanpaa M (2009) A review of Bayesian variable selection methods: what, how and which. Bayesian Anal 4:85–117

Omernik JM, Griffith GE (2014) Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environ Manage 54:1249–1266

Outcalt KW, Brockway DG (2010) Structure and composition changes following restoration treatments of longleaf pine forests on the Gulf Coastal Plain of Alabama. For Ecol Manage 259:1615–1623

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramirez EM, Ober HK (2014) Nest site selection and reproductive success of red-cockaded woodpeckers in Ocala National Forest. Am Midl Nat 171:258–270

Raulston BE, James DA, Johnson JE (1996) Effects of cavity-entrance restrictors on red-cockaded woodpeckers. Wildl Soc Bull 24:694–698

Repasky RR, Doerr PD (1991) Home range and substrate use by 2 family groups of red-cockaded woodpeckers in the North Carolina Sandhills. Brimleyana 1:37–52

Royle JA, Dorazio RM (2008) Hierarchical modeling and inference in ecology. Academic Press, Amsterdam

Rubin DB (1984) Bayesianly justifiable and relevant frequency calculations for the applied statistician. Ann Stat 12:1151–1172

Rudolph DC, Conner RN (1991) Cavity tree selection by red-cockaded woodpeckers in relation to tree age. Wilson Bull 103:458–467

Rudolph DC, Conner RN, Schaffer RR (2002) Red-cockaded woodpecker foraging behavior in relation to midstory vegetation. Wilson J Ornithol 114:235–242

Samano S, Wood DR, Cole J, Vilella FJ, Burger LW (1998) Red-cockaded woodpeckers ensnared in mesh snake traps. Wilson Bull 110:564–566

Smithson M, Verkuilen J (2006) A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol Methods 11:54–71

Sparks JC, Masters RE, Engle DM, Payton ME, Bunkenhofer GA (1999) Influence of fire season and fire behavior on woody plants in red-cockaded woodpecker clusters. Wildl Soc Bull 27:124–133

Sturtz S, Ligges U, Gelman A (2005) R2WinBUGS: a package for running WinBUGS from R. J Stat Softw 12:1–16
Tredennick AT, Hooker G, Ellner SP, Adler PB (2021) A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology 102:e03336
US Department of Agriculture (2006) Soil survey of Hale County, Alabama. U.S. Department of Agriculture Natural Resources Conservation Service. https://nrcs.app.box.com/s/dhxh9kcj1bhvjpgrgh3mmlm66bdcltq5/file/981386846288 (accessed 10 April 2018)
US Department of Agriculture (2008) Soil survey of Bibb County, Alabama. U.S. Department of Agriculture Natural Resources Conservation Service. https://nrcs.app.box.com/s/dhxh9kcj1bhvjpgrgh3mmlm66bdcltq5/file/981390555684 (accessed 10 April 2018)
US Fish and Wildlife Service (2003) Recovery plan for the red-cockaded woodpecker (*Picoides borealis*), 2nd revision. U.S. Fish and Wildlife Service, Atlanta, GA
van de Pol M, Bailey LD, McLean N, Rijsdijk L, Lawson CR, Brouwer L (2016) Identifying the best climatic predictors in ecology and evolution. Methods Ecol Evol 7:1246–1257
Varner JM, Hiers JK, Ottmar RD, Gordon DR, Putz FE, Wade DD (2007) Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. Can J For Res 37: 1349–1358
Venables WN, Ripley BD (2003) Modern applied statistics with S. Springer, New York, NY
Walters JR, Doerr PD, Carter JH (1988) The cooperative breeding system of the red-cockaded woodpecker. Ethology 78:275–305
Weiss SA, Toman EL, Corace RG III (2019) Aligning endangered species management with fire-dependent ecosystem restoration: manager perspectives on red-cockaded woodpecker and longleaf pine management actions. Fire Ecol 15:19
Wood DR, Burger LW Jr, Vilella FJ, Raulston BE (2000) Long-term effects of red-cockaded woodpecker cavity-entrance restrictors. Wildl Soc Bull 28:105–109
Wood DR, Vilella FJ, Burger LW Jr (2001) Red-cockaded woodpecker banding at Bienville National Forest, Mississippi. N Am Bird Bander 26:16–19
Wood DR, Burger LW Jr, Vilella FJ (2005) Red-cockaded woodpecker (*Picoides borealis*) behavior in a Mississippi loblolly-shortleaf pine forest. J Miss Acad Sci 50: 168–176
Wood DR, Burger LW Jr, Vilella FJ (2008) Red-cockaded woodpecker home range use and macrohabitat selection in a loblolly-shortleaf pine forest. Wilson J Ornithol 120: 793–800
Wood DR, Burger LW Jr, Vilella FJ (2014) Red-cockaded woodpecker *Picoides borealis* microhabitat characteristics and reproductive success in a loblolly-shortleaf pine forest. Open Ornithol J 7:49–54
Zwicker SM, Walters JR (1999) Selection of pines for foraging by red-cockaded woodpeckers. J Wildl Manag 63: 843–852

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