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Habitat Use And Avoidance by Foraging Red-cockaded Woodpeckers in East Texas

John N. Macey[1, 2,*], D. Brent Burt[1], Daniel Saenz[3], and Richard N. Conner[3]

Abstract - *Picoides borealis* (Red-cockaded Woodpecker) is an endangered bird endemic to the *Pinus* (pine) ecosystems of the southeastern US. Mature pine savannahs with a minimal midstory and lush herbaceous groundcover represent high-quality habitat. This study examines the foraging-habitat patterns of Red-cockaded Woodpeckers in East Texas. We present a logistic regression model that best differentiates between foraged and non-foraged habitat. Increases in hardwood-midstory basal area have the greatest negative impact on the probability of Red-cockaded Woodpeckers selecting a habitat patch for foraging. Five additional variables negatively impact foraging probability: shrub height, diameter at breast height (DBH) of pine midstory, canopy closure, density of pine midstory, and density of hardwood midstory. Our model shows a high degree of accuracy as to the probability of habitat-patch selection for Red-cockaded Woodpeckers foraging in East Texas forests composed of different pine species.

Introduction

Picoides borealis Vieillot (Red-cockaded Woodpecker) is an endangered species (USFWS 1970) endemic to the *Pinus* (pine) forests of the southeastern US (Conner et al. 2001, Ligon 1970). It is a cooperative breeder that lives in extended family groups (Walters 1990, Walters et al. 1988) that forage in open, pine savannahs composed of mature pines with herbaceous plants dominating the groundcover (Bradshaw 1995, Hooper and Harlow 1986, Hooper and Lennartz 1981, James et al. 2001, Ligon 1968, Morse 1972, Nesbitt et al. 1978, Walters et al. 2002). Males typically forage on larger branches higher in pines, while females forage lower on the tree bole (Engstrom and Sanders 1997, Franzreb 2010, Hooper and Lennartz 1981, Ligon 1968). Both sexes forage primarily on larger and older living and recently dead pines, but avoid long-dead trees (Doster and James 1998, Engstrom and Sanders 1997, Franzreb 2010, Hooper and Lennartz 1981, Jones and Hunt 1996, Ligon 1968, Morse 1972, Nesbitt et al. 1978, Porter and Labisky 1986, Zwicker 1999). They occasionally forage on large hardwoods located in mature pine forests (Delotelle et al. 1987, Doster and James 1998, Franzreb 2010, Skorupa and McFarlane 1976).

Historically, wildfires initiated by lightning strikes and indigenous peoples maintained pine-savannah forests and prevented the development of a dense midstory and thick leaf-litter layer (Conner et al. 2001, Van Lear et al. 2005). Most

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current pine-forest habitats within the Red-cockaded Woodpecker's range show significant midstory-hardwood encroachment and suppressed herbaceous groundcover (Conner and Rudolph 1989, Conner et al. 2001, Ligon et al. 1986). Nesting- and foraging-habitat suitability declines with increased midstory-hardwood encroachment, which results in nesting-tree–cluster abandonment and population declines (Conner and Rudolph 1989, 1991; Hovis and Labisky 1985; Jackson et al. 1986; Kelly et al. 1994; Ligon et al. 1986; Shackelford and Conner 1997). Extensive habitat restoration to reduce hardwood cover in the midstory is effective in improving Red-cockaded Woodpecker habitat quality; in some areas where extensive restoration has taken place, hardwoods no longer play a significant role in habitat selection (McKellar et al. 2015).

In this study, we examine the sensitivity of foraging Red-cockaded Woodpeckers to changes in midstory and other habitat characteristics in *Pinus taeda* L. (Loblolly Pine)–*P. echinata* Mill (Shortleaf Pine) forests. Although many previous studies have documented habitat factors related to Red-cockaded Woodpecker foraging-habitat quality, this study is unique in 3 ways. First, much of the research performed on the Red-cockaded Woodpecker foraging ecology pertains to *Pinus palustris* Mill (Longleaf Pine) forests. However 83% of the national forest land suitable for Red-cockaded Woodpeckers is comprised of pine species other than Longleaf Pine, such as the Loblolly–Shortleaf Pine forests of East Texas (James 1995). Second, previous studies examined the differences between habitat used by foraging Red-cockaded Woodpeckers and available habitat (Doster and James 1998, Franzreb 2010, Rudolph et al. 2002). We make direct comparisons and quantify the distinctions between habitat patches selected for forage and those actively avoided by the group (hereafter non-foraged patches). Third, many previous studies took a univariate approach to examine the individual characteristics of appropriate foraging habitats. Studies that used a multivariate approach examined how variation in foraging habitat affected group fitness or population growth (Davenport et al. 2000; Garabedian et al. 2014; James et al. 1997, 2001; McKellar et al. 2014). We examined the combinations of habitat variables that best distinguish foraged from non-foraged–habitat patches and the threshold values of each variable.

Understanding the foraging preferences of the Red-cockaded Woodpecker in more detail will provide greater insight into its habitat requirements and allow more effective management. To achieve this goal, we used habitat-selection and -avoidance patterns documented in this study to develop a habitat-quality–assessment model. Our objectives were to: (1) develop a predictive model land managers can use to better identify and maintain foraging habitat for Red-cockaded Woodpeckers in a Loblolly–Shortleaf Pine ecosystem and (2) determine habitat-variable thresholds that indicate declines in foraging-habitat quality.

Field-site Description

We studied the foraging behavior of 34 Red-cockaded Woodpecker groups during 2004 (August–October) and 2005 (January–April) in a Loblolly–Shortleaf Pine forest in the Davy Crockett National Forest (DCNF; 63,359 ha; 31°21'N, 95°07'W) in East Texas. We used these data to develop our foraging-habitat model. The forest structure of the DCNF is varied. Pine habitats included established pine savannahs with ~1% mature hardwoods (Macey 2005), fire-suppressed habitats with extensive midstory growth, dense regeneration stands, and habitat patches that had recently undergone hardwood-midstory reduction. The DCNF is located within the Neches and Trinity river basins, and therefore, also includes extensive hardwood bottoms. We studied 8 additional Red-cockaded Woodpecker groups during September and October 2005 to validate the accuracy of our model in the DCNF (Loblolly–Shortleaf Pine habitat; 4 groups) and the Angelina National Forest (ANF; 62,423 ha; 31º15'N, 94º15'W; Longleaf Pine habitat; 4 groups).

Methods

Data collection

We chose to observe foraging behavior and habitat selection for the first 3 h after the Red-cockaded Woodpeckers exited roosting cavities because this is usually a period of uninterrupted foraging (Rudolph et al. 2002). We recorded the first observation 30 min after Red-cockaded Woodpeckers left their cavity to allow time for group members to assemble and initiate foraging activity. We conducted subsequent observations at 30-min intervals. We flagged the tree on which the woodpecker group foraged and recorded its GPS coordinates. The period between samples helped preserve sample independence by allowing individuals sufficient time to move to other foraging locations. If individuals were not foraging at the time of a sample, we did not record a location, and we continued to watch woodpeckers until the next sample period. If individuals were foraging on multiple trees at the end of a sample period, then we chose as the focal individual the woodpecker with the longest foraging time in a tree. We attempted to maintain continuous visual contact with the foraging groups; we ended the survey if the group was lost and not relocated within 1 h. If we relocated the group within an hour, then we recorded a sample at the next 30-min interval. We defined foraging behavior as probing, bark flicking, or active searching of bark for prey. Red-cockaded Woodpeckers foraging during the non-breeding season typically make short flights between neighboring trees. We identified non-foraged plots each time the group made non-interrupted long-distance (>75 m) flights from one foraging location to the next. We established these non-foraging sample plots halfway between the beginning and end of each long-distance flight. Foraging and non-foraging plots never overlapped.

We collected vegetation data at foraged and non-foraged plots. We centered each 20-m-radius plot on the foraged tree (foraged plots) or the canopy tree closest to the center of each long-distance flight (non-foraged plots). At each plot, we sampled 4 categories of vegetation structure: overstory, midstory, shrub layer, and groundcover. We defined overstory as the mature trees of greatest height and the midstory as the trees from 3-m tall to the bottom of the overstory, and subcategorized these 2 vegetation layers into pine and hardwood components. We defined the shrub layer as woody vegetation from 1 to 3 m tall, and the groundcover layer as all plants ≤1 m in height.

For overstory and midstory trees located within each 20-m–radius plot, we recorded density (trees per ha; pine and hardwood), DBH (cm), and tree height (m). We used a clinometer to determine tree height and we calculated basal area (m^2/ha) following the methods outlined in Avery and Burkhardt (2002). We visually estimated percent canopy closure to the nearest 5% using a PVC pipe (3.18-cm inside diameter x 15.24 cm length) at 10 m from the plot center in each cardinal direction, and averaged the 4 values.

We measured foliage density and average height of the shrub layer. We used a density board to collect foliage-density data for the shrub layer at a height of 1 m (MacArthur and MacArthur 1961). We calculated foliage density using the formula outlined by Conner and O'Halloran (1986). We took foliage density and shrub-height measurements 10 m from the center of each plot at each cardinal direction, and averaged the 4 values. We recorded the percent groundcover of leaf litter, grass, forbs, and bare ground 10 m from the plot center in each cardinal direction and averaged the 4 values.

General site-data analyses

We compared the mean of each vegetation variable between foraged and non-foraged plots, although the pine midstory, hardwood midstory, and overstory strata were absent from some sites. We compared means for these variables only between foraged and non-foraged plots that had trees in the relevant category.

We used a permutation procedure to test the null hypothesis that habitat at foraged and non-foraged plots did not differ. For each comparison, we generated 9999 permutations of the data and calculated the absolute difference between means for each pair of permutated groups. We calculated a P value from the percentage of times the mean difference in permutations was greater than that seen in the original data. Permutation tests were completed in R (R, version 2.9.2, R Development Core Team 2009).

Logistic regression analyses

We conducted a Pearson correlation analysis of the 25 vegetation variables to reduce the number of variables used in logistic regression analyses. Following Davenport et al. (2000) and Garabedian et al. (2014), we selected the variable easiest to duplicate in the field for use in subsequent analyses in cases where a correlation coefficient (r) was ≥ 0.7.

We examined logistic regression models to find a combination of vegetation variables that best described the variation between foraged and non-foraged plots. Models were developed using JMP (version 8.0.2; SAS Institute 2009). We used the mixed-direction option in the stepwise procedure to select model variables with a 0.25 probability to retain or discard.

We determined locally optimal habitat parameters in each model by setting the prediction-profiler option in JMP to maximum desirability. This procedure identifies the habitat parameters that describe the hypothetically best-quality foraged habitat available in our study plots. We used the inverse-prediction option to determine hardwood-midstory thresholds associated with 95%, 75%, and 50%

foraging probabilities when assuming maximum desirability in the other model habitat-variables.

Model validation

We tested the classification accuracy and general utility of our model in 2 ways. First, we examined how accurate this model was in correctly classifying a plot from the original data set as either foraged or non-foraged. We used the logistic regression equation to calculate the probability that woodpeckers would use a plot for foraging:

$$P = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 + \dots \beta_i x_i)}}$$

A P-value greater than or less than 0.5 indicated either a foraged or non-foraged plot classification, respectively. The relative influence of the habitat variables used in our logistic model are indicated by each β; the associated x is the habitat measurement of each variable at the specific plot. Second, we used this equation to test the classification accuracy using data collected on groups not previously included in the original analyses. These additional data represent forests with the same (DCNF–Loblolly–Shortleaf Pine) and different (ANF–Longleaf Pine) dominant pine species.

Results

The sample of 34 Red-cockaded Woodpecker groups initially monitored for model development provided 129 and 20 foraged and non-foraged plots, respectively, for a total of 149. To avoid pseudoreplication, we excluded 18 foraged plots from analyses because they represented areas receiving multiple foraging bouts; thus, we included a total of 111 and 20 foraged and non-foraged plots, respectively in model development. None of the plots used in model development overlapped. The adjusted mean number of foraged plots per woodpecker group was 3.26 ± 0.10 (range = 1–5). The mean number of non-foraged plots per group was 0.59 ± 0.18 (range = 0–3).

General site-characteristics

Of the 25 habitat variables considered in this study, 10 were significantly different between foraged and non-foraged plots (Table 1). Basal area of pine overstory and percent grass and forb groundcover were all significantly greater in foraged plots. Total tree density, density and basal area of both pine and hardwood midstory, canopy closure, and percent leaf-litter groundcover were all significantly greater in non-foraged plots.

Logistic Regression Model

The logistic regression model with the greatest ability to describe differences between foraged and non-foraged plots, while minimizing the number of model parameters (AIC = 53.219, $R^2 = 0.650$, $P < 0.0001$), retained 6 habitat variables (basal area and density of hardwood midstory, DBH and density of pine midstory, shrub height, and canopy closure). Increases in each of these variables beyond threshold values (Table 2) decreased the probability of plot selection for foraging. Basal area of hardwood midstory had the largest contribution to this model. The odds ratio for this variable indicated the probability a plot would be used for foraging decreased by 81.5% for each unit increase (m^2/ha) in basal area of hardwood midstory. The remaining variables had a weaker impact on a plot being selected for foraging with each unit increase (62.1% for shrub height, 11.8% for DBH pine midstory, 6% for canopy closure, 3.4% for density of pine midstory, and 1.4% for density of hardwood midstory). Basal area of hardwood midstory is by far the most important variable in our model; thus, we calculated the values for this variable associated

Table 1. Means for density (trees/ha), basal area (m^2/ha), DBH (cm); tree height (m), canopy closure (%), ground cover (%), shrub height (m), and foliage density [UNITS? m^2/m^3?]. Permutation test *P*-values are given for each comparison. The variables indicated by * show significantly greater values in foraged sites while those indicated by ** show significantly greater values in non-foraged sites.

Parameter	Foraging sites	Non-foraging sites	*P*
Density (trees/ha)			
Total**	59.47	178.35	0.0001
Pine overstory	29.18	36.11	0.3402
Pine midstory**	8.17	58.49	0.0001
Hardwood overstory	0.31	0.30	0.9999
Hardwood midstory**	21.81	83.46	0.0001
Basal area (m^2/ha)			
Total	4.42	4.71	0.4183
Pine overstory*	4.05	2.47	0.0003
Pine midstory**	0.12	1.03	0.0001
Hardwood overstory	0.04	0.05	0.7814
Hardwood midstory**	0.22	1.16	0.0001
DBH (cm)			
Pine overstory	41.95	44.04	0.3828
Pine midstory	12.39	15.21	0.0761
Hardwood overstory	42.61	46.67	0.8193
Hardwood midstory	11.15	13.37	0.2819
Tree height (m)			
Pine overstory	28.60	28.37	0.8304
Pine midstory	12.43	13.70	0.4313
Hardwood overstory	26.71	25.00	0.6359
Hardwood midstory	8.95	11.31	0.1214
Canopy closure (%)**	45.11	77.44	0.0001
Ground cover (%)			
Grass*	33.30	15.50	0.0009
Forbs*	26.94	15.88	0.0460
Leaf**	37.65	67.81	0.0001
Bare	2.11	0.81	0.4558
Shrub height (m)	1.35	1.22	0.7851
Foliage density index	0.21	0.15	0.3978

with 95%, 75%, and 50% foraging probabilities. Assuming maximum desirability for all other habitat variables in the model (Table 2), 95%, 75%, and 50% foraging probabilities were associated with hardwood midstory basal area values of 0.98 m^2/ha, 2.07 m^2/ha, and 2.72 m^2/ha, respectively.

Model validation

Our model had an overall successful classification rate of 94.6% for plots in the original data. Seven of 131 plots were misclassified (2 foraged, 5 non-foraged; Fig. 1). For validation using independent data, we used foraging data from 4 Red-cockaded Woodpecker groups (21 plots, 17 foraged and 4 non-foraged) in Loblolly-Shortleaf Pine habitats (DCNF) and from 4 groups (20 plots, 15 foraged and 5 non-foraged) in Longleaf Pine habitats (ANF) to test classification accuracy. The model was 95.2% and 90.0% accurate in classification of foraged versus non-foraged plots in the DCNF and ANF, respectively. All misclassifications (1 DCNF, 2 ANF) represent cases where non-foraged plots were misclassified as foraged plots.

Discussion

The USFWS Recovery Plan (2003) states that quality Red-cockaded Woodpecker foraging habitat "has some large old pines, low densities of small and medium pines, sparse or no hardwood midstory, and a bunchgrass and forb groundcover." Results from our univariate analyses confirm these broad guidelines. Foraged plots were characterized by greater coverage of larger pine-overstory trees with groundcovers dominated by grasses and forbs. Non-foraged plots had greater densities and coverage of larger pine and hardwood midstory trees, and were characterized by dense, closed, forest patches with more leaf-litter groundcover.

Our logistic regression analysis provides information on the relative importance of 6 habitat variables to Red-cockaded Woodpecker foraging-habitat selection (Table 2). Combined, these variables paint a consistent picture of the habitat that

Table 2. Summary of the contributions of the 6 variables retained in the logistic regression model differentiating between foraged and non-foraged Red-cockaded Woodpecker habitats. Estimate = estimate of explanatory slope for habitat variables (β_x), SE = standard error of slope estimate, χ^2 = statistic testing H_0 (slope estimate = 0), $P > \chi^2$ = probability to reject H_0, odds ratio = odds of a site being a foraged versus non-foraged site per unit increase in a habitat variable, and variable threshold = threshold values for each habitat variable as determined by the prediction profiler in JMP (version 8.0.2, JMP 2009). Values greater than the thresholds indicate a decreasing probability of a habitat's suitability for foraging.

Variable	Estimate	SE	χ^2	$P > \chi^2$	Odds ratio	Variable threshold
Intercept	10.982	2.788	15.52	<0.0001	NA	NA
Basal area of hardwood midstory	-1.6862	0.835	4.08	0.0435	0.185	0.36 m^2/ha
Shrub height	-0.9696	0.374	6.71	0.010	0.379	1.3 m
DBH of pine midstory	-0.1250	0.074	2.83	0.093	0.882	7.8 cm
Canopy closure	-0.0624	0.029	4.73	0.030	0.940	50%
Density of pine midstory	-0.0341	0.013	6.55	0.010	0.966	15.8 trees/ha
Density of hardwood midstory	-0.0146	0.010	2.14	0.144	0.986	31.2 trees/ha

Red-cockaded Woodpeckers avoid: closed canopy, dense (at multiple vegetative levels) forests. We compare the importance of these 6 habitat variables with previous work below.

Hardwood-midstory encroachment is widely known to negatively impact Red-cockaded Woodpecker foraging (Conner and Rudolph 1989, Davenport et al. 2000, Doster and James 1998, Epting et al. 1995, Hooper and Harlow 1986, Kelly et al. 1994, Ligon et al.1986, Loeb et al. 1992, Provencher et al. 2002, Rudolph et al. 2002, Shackelford and Conner 1997, Walters et al. 2002). USFWS (2003) guidelines to enhance the species' habitat suggest the elimination of hardwood midstory or that it remain sparse. Davenport et al. (2000) indicated understory height of good- and poor-quality habitat was 1.89 m and 3.26 m, respectively. Our model indicates increased probabilities of habitat use for foraging when shrub heights are ≤1.3 m. Hardwood basal area of foraging habitat in other studies varied from 0.0 m^2/ha to 0.44 m^2/ha in Bowman et al. (1999), and 0.8 m^2/ha to 4.1 m^2/ha in Rudolph et al. (2002). Our model indicates increasing probability for habitat use for foraging when hardwood-midstory basal area is ≤0.36 m^2/ha with densities of 31.2 trees/ha or less.

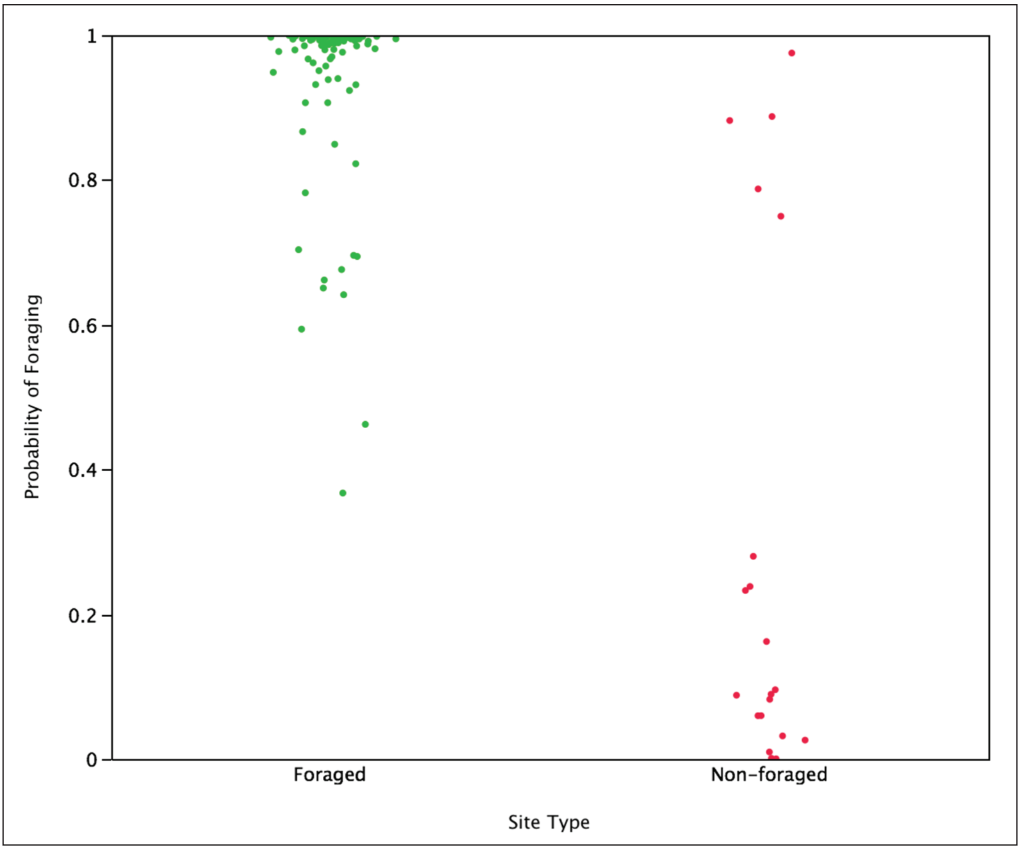

Figure 1. Foraged (n = 111) and non-foraged (n = 20) sites in this study with the associated probabilities of foraging indicated by our logistic regression model. Two foraged sites have probabilities below 50% (indicated by the dotted line), and 5 non-foraged sites have probabilities above 50%.

Foraging Red-cockaded Woodpeckers avoid dense stands of small pines (Engstrom and Sanders 1997, Hooper and Lennartz 1981, Porter and Labisky 1986, Walters et al. 2002), except in poor-quality habitats where they have few choices (Delotelle et al. 1987). Rudolph et al. (2002) determined foraged habitat had significantly lower pine-midstory densities in a Loblolly–Shortleaf Pine habitat. Our model indicates pine midstories with trees >7.83 cm DBH and >15.8 trees/ha decrease foraging probabilities (Table 2).

Red-cockaded Woodpeckers are also known to forage more often in habitats with open canopies (Doster and James 1998, James et al. 1997, Smart et al. 2012). The threshold canopy cover indicated by our analyses is 50% closure.

The Red-cockaded Woodpeckers' avoidance of dense, closed, forest patches may be partially explained by its effect on reducing arthropod density and diversity. Pine bark is a key microhabitat for many insects (e.g., *Paracoblatta* spp. [wood roaches]), and is an important pathway to the crown for others (Hanula and Franzreb 1998). Dense midstory and shrub layers inhibit light from reaching the forest floor, limiting herbaceous groundcover growth important for supporting an abundant arthropod community (Collins et al. 2002). However, variation in groundcover has had little impact on bole-arthropod abundance in other studies (Hanula et al. 2000). Burn history may shift groundcover vegetation toward plants that are more or less palatable to forest-floor insects and may partially explain inconsistencies among studies relating groundcover to bole-insect density and diversity (Provencher et al. 2002). Additionally, patterns of herbaceous groundcover growth may be tied to site-specific soil types (McKellar et al. 2014) and burn regimes (Hiers et al. 2007).

Management directed at improving foraging-habitat quality is likely to increase reproductive success and average group-sizes in Red-cockaded Woodpecker populations; however, population expansion (increases in the number of groups) is more closely tied to availability and distribution of cavity trees (Walters 1991). Recent studies suggest that pine and hardwood midstory have negative impacts on fitness and population growth across the species' range only when exceeding modest levels, and that current management guidelines may be too restrictive (Garabedian et al. 2014, McKellar et al. 2014). However, management of habitats should target optimal levels whenever possible (Conner 1979). Controlling woody understory and midstory vegetation benefits several other avian species of concern in addition to Red-cockaded Woodpeckers: *Aimophila aestivalis* Lichtenstein (Bachman's Sparrow), *Sitta pusilla* Latham (Brown-headed Nuthatch), *Meleagris gallopavo* L. (Wild Turkey), and *Colinus virginianus* L. (Northern Bobwhite). Indeed, the vast majority of the plant and animal biodiversity in southern pine forests is associated with the ground vegetation in regularly burned southern pine forest (Van Lear et al. 2005). The extent of woody understory and midstory reduction needed to benefit each of these species requires additional study.

Model validation indicates that our model is accurate at predicting foraged-habitat selection in both Loblolly–Shortleaf Pine and Longleaf Pine habitats in

East Texas. This model can therefore be used as a valuable assessment tool of Red-cockaded Woodpecker foraging habitat in East Texas. On sites within this range, the following formula can be used to calculate the probability that a habitat patch will be used by foraging woodpeckers:

$$P = \frac{1}{1 + e^{-(10.982 - 0.034 PineMidDens - 0.146 HWMidDens - 1.686 BasAreaHWMid - 0.125 PineMidDBH - 0.062 CanClos - 0.970 ShrHght)}}$$

Whether this model can be used in other areas of the species' range is unclear. Management needs may require population-specific alteration due to the subtle variations in habitat structure, life histories, and management histories seen in Red-cockaded Woodpecker populations across their range (Kelly et al. 1994).

This model also assumes the habitat in question has the major structural elements needed for foraging habitat (i.e., mature pine overstory of appropriate density). It is important to realize that our model does not necessarily describe optimum foraging habitat, but instead describes the key habitat variables Red-cockaded Woodpecker groups consider when selecting among potential foraging habitats in the DCNF. Red-cockaded Woodpeckers in the DCNF preferred to stay within the managed areas (improved habitat) surrounding their nest-tree clusters, and tended to avoid habitat that has not had midstory reduction. The size of these managed areas likely has a major impact on reproductive success.

Caution must also be used with regard to timing and extent of management activities. Midstory removal, particularly near the cluster site, can lead to site abandonment unless done outside the breeding season (Conner and Rudolph 1991, Jackson 1990). Our model does not indicate a need for complete midstory elimination. Clearly, growth of some small pines is needed to maintain recruitment. Growth of limited numbers of pyrophytic *Quercus* (oaks) in pine savannahs can be beneficial to the overall biodiversity of the habitat (Hiers et al. 2014), including arthropods that provide forage for Red-cockaded Woodpeckers (James et al. 2001). Woodpeckers use mature hardwoods while foraging, especially in winter, when these trees are scattered in pine-savannah habitats (Delotelle et al. 1987, Doster and James 1998, Franzreb 2010, Skorupa and McFarlane 1976).

Although we have identified threshold values for each habitat variable in our model, individual habitat variables must always be considered in the context of the cumulative effect of each variable. For example, hardwood-midstory basal area was the most important variable in our model—values above 0.36 m^2/ha reduce the probability of a site being foraged. However, when other model habitat-variables were at optimal levels, hardwood midstory basal areas of 0.98 m^2/ha, 2.07 m^2/ha, and 2.72 m^2/ha were associated with 95%, 75%, and 50% foraging probabilities respectively. The latter 2 basal-area values exceed the mean for non-foraged plots in our study, demonstrating how focusing on 1 habitat component can be misleading and why it is important to consider all relevant habitat variables when judging foraging-habitat quality.

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