

RED-COCKADED WOODPECKER FORAGING BEHAVIOR IN RELATION TO MIDSTORY VEGETATION

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ABSTRACT.—Red-cockaded Woodpeckers (*Picoides borealis*) nest and forage in pine-dominated forests. Research indicates that substantial hardwood midstory encroachment is detrimental to Red-cockaded Woodpecker populations, although the exact mechanisms are unknown. We examined foraging behavior in relation to midstory between August 1989 and February 1990. Red-cockaded Woodpeckers foraged at greater heights in areas of taller and denser midstory in the loblolly-shortleaf pine (*Pinus taeda* and *P. echinata*, respectively) habitat, but not in longleaf pine (*P. palustris*) habitat with less-developed midstory vegetation than typical of loblolly-shortleaf pine habitat. In addition, Red-cockaded Woodpeckers concentrated foraging activities in or adjacent to forest stands or openings with reduced midstory vegetation. Overall, Red-cockaded Woodpeckers foraged disproportionately at heights and sites that minimized their exposure to dense midstory conditions. These results suggest that ecosystem management, preferably using prescribed fire, that reduces midstory vegetation will improve foraging habitat for Red-cockaded Woodpeckers. Received 15 June 2001, accepted 12 February 2002.

The Red-cockaded Woodpecker (*Picoides borealis*) is a federally listed endangered species endemic to fire-maintained pine forests of the southeastern United States (Jackson 1971, 1994). The Red-cockaded Woodpecker is a cooperatively breeding species, typically living in groups consisting of a breeding pair and one or more nonbreeding male helpers (Ligon 1970, Walters et al. 1988, Walters 1990). These groups occupy territories containing a cluster of one to several cavity trees and an adjacent foraging area (Hooper and Lennartz 1981, Hooper et al. 1982, DeLotelle et al. 1987, Walters 1990).

Populations of Red-cockaded Woodpeckers have declined drastically due primarily to loss of old growth pine habitat (Jackson 1971, Lennartz et al. 1983, Ligon et al. 1986, Conner and Rudolph 1989) and changes in the fire regime, resulting in increased midstory vegetation (Beckett 1971, Van Balen and Doerr 1978, Conner and Rudolph 1989). The species currently survives in small, typically isolated, and mostly declining populations in remaining areas of suitable habitat (James 1995).

The nearly complete elimination of wild-fires due to efficient fire suppression measures and inadequate prescribed burning regimes have led to pervasive changes in the structure of the vegetation. Woody vegetation has great-

ly increased as the original fire-maintained pine-dominated communities enter the initial stages of succession to hardwood forest (Platt et al. 1988, Conner and Rudolph 1991, Frost 1993). Consequently, the open, pine-dominated stands with well-developed herbaceous understory vegetation that Red-cockaded Woodpeckers once inhabited are in most cases now pine-dominated stands with a well-developed hardwood midstory and greatly suppressed herbaceous understory (Platt et al. 1988, Conner and Rudolph 1991, Streng et al. 1993).

Numerous studies have noted that increasing midstory vegetation reduces the apparent suitability of habitat for Red-cockaded Woodpeckers (Van Balen and Doerr 1978, Repasky 1984, Hovis and Labisky 1985, Jackson et al. 1986). Midstory vegetation has been shown to increase the probability of cluster abandonment (Conner and Rudolph 1989), to negatively impact foraging (Epting et al. 1995), and to be negatively associated with measures of fitness (Davenport et al. 2000). How midstory vegetation leads to negative impacts on Red-cockaded Woodpecker populations is not well understood.

We examined the foraging behavior of Red-cockaded Woodpeckers to determine how Red-cockaded Woodpeckers react to different levels of midstory vegetation in predominately longleaf pine (*Pinus palustris*) forests and in mixed loblolly-shortleaf pine (*P. taeda* and *P. echinata*, respectively) forests in eastern Texas.

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STUDY AREAS AND METHODS

We examined Red-cockaded Woodpecker foraging behavior on the Angelina (31° 15' N, 94° 15' W) and Davy Crockett (31° 21' N, 95° 07' W) national forests in eastern Texas. Red-cockaded Woodpecker habitat on the Davy Crockett National Forest and the northern portion of the Angelina National Forest is composed primarily of loblolly and shortleaf pine with a significant hardwood component, especially in the midstory. Habitat on the southern portion of the Angelina National Forest is composed predominately of longleaf pine with a minimal hardwood component. Silvicultural practices near the study sites have included a mix of clearcutting, and seed tree or shelterwood harvests in which some mature trees are left unharvested. See Conner and Rudolph (1989) for a more complete description of the study sites.

Red-cockaded Woodpecker habitat is managed on both national forests to reduce midstory vegetation that has increased due to fire suppression (Conner and Rudolph 1989, 1991). Cluster sites have been a higher management priority than the surrounding foraging habitat. The primary result has been a major reduction in midstory vegetation within woodpecker cluster areas by a combination of prescribed fire, herbicides, and mechanical means. Midstory reduction in the foraging habitat surrounding the clusters, primarily using prescribed fire, has been much less effective, especially in the less pyrogenic loblolly-shortleaf pine habitat.

We banded members of 12 Red-cockaded Woodpeckers groups (6 in loblolly-shortleaf pine habitat, 6 in longleaf pine habitat) with metal USGS-BRD bands and plastic color bands for individual recognition. We determined social status of individuals (breeding pair, helpers, juveniles) by observing birds during the course of this study, especially during nesting. We used binoculars or a 20× spotting scope to identify birds and observe foraging behavior.

We observed foraging behavior of and habitat use by the 12 Red-cockaded Woodpecker groups between 29 August 1989 and 19 February 1990. This period was chosen to avoid influences of the nesting cycle on foraging patterns. Individual groups were observed for 1–5 days with a mean of 3.75 days. All groups included the breeding pair, and helpers and young of the year often were present as well. We initiated observations as group members exited roost cavities at dawn, and continued for approximately 3 h thereafter, for a total of 138 h on 45 different days. This time interval was chosen because it is typically a period of uninterrupted foraging. During the period of observation two observers, working as a team, attempted to maximize the number of woodpecker group members whose identity and foraging locations could be determined simultaneously. Simultaneous observations were necessary to allow collection of additional data for other aspects of this study. Once we located and identified a sufficient number of group members, we recorded foraging data. To maximize the likelihood that successive sampling observations would be inde-

pendent, we maintained ≥ 10 min between sampling observations. This time interval was sufficient for individual birds to change foraging position in all cases, typically involving a change in foraging tree.

We measured the height above ground of individual birds using a clinometer. Trees in which the birds foraged were identified for subsequent relocation by recording unique characteristics and general location, supplemented by attaching plastic ribbon to the tree with identifying information.

Subsequently, we relocated foraging trees and obtained habitat measurements centered on the foraging tree. We recorded canopy and midstory basal areas of pine and hardwoods using a 1-factor metric prism. We also measured general canopy and midstory height, and foraging tree height using a clinometer, and estimated midstory density using a five-category scale, ranging from none (1) to very dense (5). We calculated standardized foraging heights as the percentage of tree height (foraging height/tree height $\times 100$) for each foraging observation.

We selected a stratified random sample of trees to allow comparison of available trees with those used for foraging. Five pine trees were randomly selected per forest stand, a management unit delineated by the U.S. Forest Service, and habitat variables comparable to those for foraging trees were measured.

We also recorded the location of each foraging observation. Locations were characterized as (1) within intact forest (>50 m from an edge) or (2) open forest/edge, i.e., within or adjacent to (<50 m from) a forest opening, or within open forest. We defined forest openings to include clearcuts, pine plantations <20 years of age, road and utility rights-of-way, and other non-forested areas. We defined open forests to include seed tree and shelterwood harvest areas, southern pine beetle (*Dendroctonus frontalis*) infestation areas, and woodpecker cluster areas that had received some type of midstory control. We determined the percentage of area ≤ 800 m of the nest tree for each group of woodpeckers (an estimate of the group's foraging area) that occurred in each of these categories using forest stand maps and aerial photographs.

We compared habitat variables using *t*-tests. Satterthwaite's correction was used in cases of unequal variance. To avoid pseudoreplication, all data pertaining to individual birds and individual forest stands were treated as a single sample and analyzed accordingly. Bonferroni's correction was used to account for repeated testing of the same data set.

RESULTS

Comparisons of habitat variables measured at random trees in the two forest habitats (Table 1) revealed that loblolly-shortleaf pine habitats were characterized by significantly greater canopy height, midstory density composed predominately of hardwoods, and midstory hardwood basal area. We did not detect a significant difference in midstory height,

TABLE 1. Means (SD) of habitat variables for randomly selected canopy trees in longleaf pine habitat ($n = 53$ sites) and loblolly-shortleaf pine habitat ($n = 44$ sites), eastern Texas, 1989.

Habitat variable	Longleaf pine	Loblolly-shortleaf pine	P^a
Canopy pine basal area ^b	16.8 (5.52)	15.4 (3.18)	0.1211
Midstory pine basal area	2.5 (1.88)	2.8 (2.22)	0.5412
Canopy hardwood basal area	0.3 (0.80)	0.8 (2.05)	0.1328
Midstory hardwood basal area	1.1 (1.87)	4.8 (2.97)	<0.0001
Canopy height ^c	22.2 (3.77)	27.1 (2.78)	<0.0001
Midstory height	8.3 (5.12)	10.7 (4.60)	0.0178
Midstory density	2.4 (0.97)	3.6 (1.32)	<0.0001

^a Critical value of t -test with Bonferroni's correction is 0.0167.^b Basal area measures in m²/ha.^c Height measures in m.

overstory pine basal area, midstory pine basal area, or hardwood overstory basal area between the forest habitats.

We obtained 944 foraging observations and corresponding habitat measurements for 41 individual Red-cockaded Woodpeckers from 12 groups, 510 in longleaf pine habitat and 434 in loblolly-shortleaf pine habitat. In longleaf pine habitat, the foraging sites used by Red-cockaded Woodpeckers had significantly greater canopy height compared to that measured at random trees (Table 2). Conversely, random sites had greater canopy pine basal area. In loblolly-shortleaf pine habitat, foraging sites had significantly lower canopy pine basal area and midstory density.

Red-cockaded Woodpecker foraging sites in longleaf pine habitats, compared to loblolly-shortleaf pine habitats, had significantly lower values for midstory hardwood basal area, canopy height, and midstory density (Table 3). Mean Red-cockaded Woodpecker foraging height was significantly greater in loblolly-shortleaf pine habitat (19.6 m) than in longleaf pine habitat (17.1 m). The corresponding standardized foraging height also was greater in loblolly-shortleaf pine habitat (72.5%) than in longleaf pine habitat (69.4%), although this difference was not significant.

In both longleaf and loblolly-shortleaf pine habitats, foraging height was positively correlated with canopy height (Table 4). In long-

TABLE 2. Means (ranges) of habitat variables for Red-cockaded Woodpecker (*Picoides borealis*) foraging trees and random trees in eastern Texas, 1989.

Habitat variable	Foraging trees	Random trees	P^a
Longleaf pine habitat	$n = 18$	$n = 53$	
Canopy pine basal area ^b	14.2 (3.00)	16.8 (5.52)	0.0148
Midstory pine basal area	2.8 (1.67)	2.5 (1.87)	0.5292
Canopy hardwood basal area	0.3 (0.30)	0.3 (0.80)	0.9753
Midstory hardwood basal area	0.8 (0.82)	1.1 (1.87)	0.4062
Canopy height ^c	24.6 (1.23)	22.2 (3.77)	<0.0001
Midstory height	8.4 (2.28)	8.3 (5.11)	0.8625
Midstory density	2.2 (0.38)	2.4 (0.97)	0.4077
Loblolly-shortleaf pine habitat	$n = 23$	$n = 44$	
Canopy pine basal area	12.2 (2.52)	15.4 (3.18)	<0.0001
Midstory pine basal area	2.3 (1.60)	2.8 (2.22)	0.4202
Canopy hardwood basal area	0.4 (0.37)	0.8 (2.05)	0.1787
Midstory hardwood basal area	4.1 (1.72)	4.8 (2.97)	0.2326
Canopy height	26.8 (1.82)	27.1 (2.78)	0.5594
Midstory height	8.2 (3.41)	10.7 (4.60)	0.0288
Midstory density	3.0 (0.70)	3.6 (1.32)	0.0148

^a Critical value of t -test with Bonferroni's correction is 0.0167.^b Basal area measures in m²/ha.^c Height measures in m.

TABLE 3. Means (ranges) of habitat variables and foraging heights for Red-cockaded Woodpecker (*Picoides borealis*) foraging sites in longleaf pine habitat ($n = 18$ sites) and loblolly-shortleaf pine habitat ($n = 23$ sites), eastern Texas, 1989.

Habitat variable	Longleaf pine	Loblolly-shortleaf pine	P^a
Canopy pine basal area ^b	14.2 (3.00)	12.2 (2.52)	0.0253
Midstory pine basal area	2.8 (1.67)	2.3 (1.60)	0.3744
Canopy hardwood basal area	0.3 (0.30)	0.4 (0.37)	0.5128
Midstory hardwood basal area	0.8 (0.82)	4.1 (1.72)	<0.0001
Canopy height ^c	24.6 (1.23)	26.8 (1.82)	<0.0001
Midstory height	8.4 (2.28)	8.2 (3.41)	0.8395
Midstory density	2.2 (0.38)	3.0 (0.70)	<0.0001
Woodpecker foraging height	17.1 (2.10)	19.6 (3.53)	0.0073
Standardized foraging height (%)	69.4 (8.53)	72.5 (10.17)	0.3039

^a Critical value of t -test with Bonferroni's correction is 0.0167.

^b Basal area measures in m^2/ha .

^c Height measures in m.

leaf pine habitat, foraging height was negatively correlated with midstory pine basal area and canopy hardwood basal area. In loblolly-shortleaf pine habitat, foraging height increased as canopy pine basal area, midstory height, and midstory density increased.

Red-cockaded Woodpecker foraging trees were not randomly located; Red-cockaded Woodpeckers used trees within or adjacent to forest openings, or within cluster areas where midstory removal had occurred (open forest/edge areas), significantly more than expected. In longleaf pine habitat, 38.8% of foraging lo-

cations were in open forest/edge areas compared to an occurrence rate of 16.6% of this habitat ($\chi^2 = 84.7$, $df = 1$, $P < 0.001$). In loblolly-shortleaf pine habitat, 67.8% of the foraging locations occurred in open forest/edge areas compared to an availability rate of 24.7% ($\chi^2 = 205.0$, $df = 1$, $P < 0.001$). Openings with no foraging substrate (i.e., clearcuts and young plantations) were not included in these area calculations. Because data collection was limited to the first 3 h of each day, the possibility exists that there was a bias toward foraging within the stand containing the

TABLE 4. Correlation coefficients of Red-cockaded Woodpecker (*Picoides borealis*) foraging heights in relation to habitat variables in longleaf pine and loblolly-shortleaf pine habitats, eastern Texas, 1989.

Habitat variable	r	P
Longleaf pine habitat		
Canopy pine basal area ^a	0.250	0.574
Midstory pine basal area	-0.103	0.020
Canopy hardwood basal area	-0.092	0.038
Midstory hardwood basal area	-0.022	0.624
Canopy height ^b	0.397	<0.001
Midstory height	0.023	0.510
Midstory density	-0.031	0.493
Loblolly-Shortleaf pine habitat		
Canopy pine basal area	0.018	<0.001
Midstory pine basal area	0.009	0.856
Canopy hardwood basal area	0.060	0.219
Midstory hardwood basal area	0.035	0.469
Canopy height	0.513	<0.001
Midstory height	0.133	0.006
Midstory density	0.113	0.020

^a Basal area measures in m^2/ha .

^b Height measures in m.

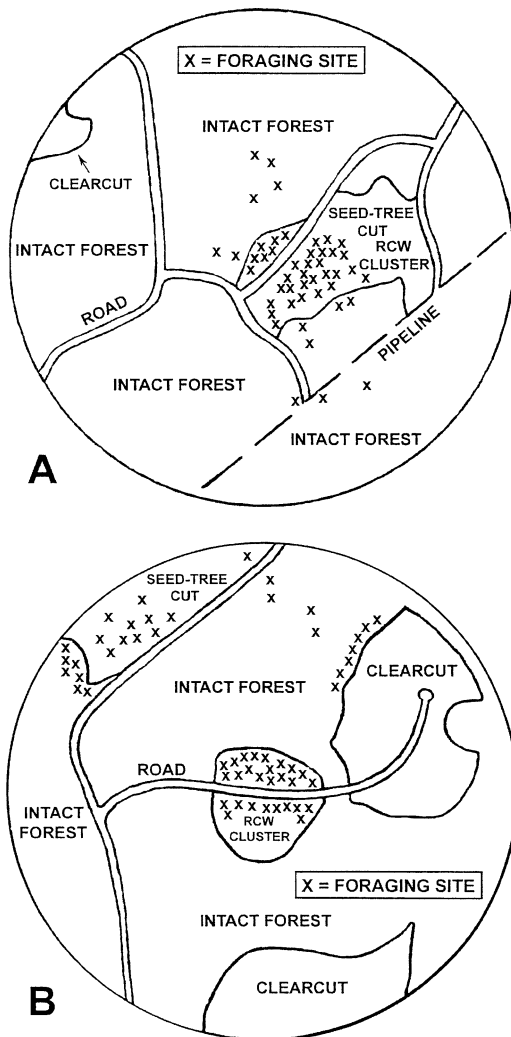


FIG. 1. Approximate locations of foraging sites of Red-cockaded Woodpeckers (*Picoides borealis*) on the Angelina National Forest in Texas, 1989. Examples from longleaf pine habitat (A) and loblolly-shortleaf pine habitat (B). Map circles are 800 m in radius centered on the woodpecker nest tree.

cavity tree cluster (see discussion). Removal of cavity tree cluster stands from the analysis eliminated the significant relationship in longleaf pine habitat ($\chi^2 = 7.73$, $df = 1$, $P = 0.26$), but not in loblolly/shortleaf pine habitat ($\chi^2 = 154.1$, $df = 1$, $P < 0.001$).

Foraging sites of two groups of woodpeckers illustrate habitat use by woodpecker groups in each pine habitat type (Fig. 1). The Red-cockaded Woodpecker group in the long-

leaf pine habitat concentrated their foraging in and adjacent to the seed tree harvest area containing the cavity tree cluster. Data from this group primarily were responsible for the different outcome with and without inclusion of the cavity tree cluster stand in the previous analysis. Surrounding intact interior forest habitat was closed canopy forest dominated by longleaf pine with moderate midstory development. The group of woodpeckers selected to illustrate habitat use in the loblolly-shortleaf pine habitat concentrated their foraging activities in and adjacent to a seed tree harvest area and adjacent to a recently planted clearcut, in addition to the cluster area where midstory removal had taken place.

DISCUSSION

Potential bias exists due to initiating observations in the cluster stands and the bird's periodic return to those stands. This potential bias was especially noticeable in the longleaf pine habitat due to timber harvest practices. The most open forest habitat available to several of the groups was the cluster area where the canopy had been thinned and midstory removed. In these instances the birds spent most of their foraging time in the cluster stand, unlike birds with additional open forest options available. Because birds with more options available frequently left the cluster area soon after exiting their roosts, and often returned later in the observation period, we believe that including the cluster area observations results in less bias than would result from deleting them.

The overall foraging behavior of Red-cockaded Woodpeckers in loblolly-shortleaf pine habitat indicated selection of foraging sites resulting in the avoidance of the typically dense midstory vegetation composed primarily of hardwoods. Red-cockaded Woodpeckers foraged in trees where the immediately adjacent habitat was characterized by significantly less dense midstory than what was available forestwide. In addition, Red-cockaded Woodpeckers foraged at greater heights at sites with greater midstory heights and densities.

These significant relationships were not detected in longleaf pine habitat. This may have been due to the significantly lower midstory density in the longleaf pine habitat than in the loblolly-shortleaf pine habitat. Midstory den-

sity at random points in longleaf pine habitat was less than midstory density adjacent to foraging trees in loblolly-shortleaf pine habitat.

Red-cockaded Woodpecker foraging height was positively correlated with canopy height in both habitat types, reflecting the increased range of potential foraging sites available in taller forest stands. In loblolly-shortleaf pine habitat, foraging height increased with canopy pine basal area, possibly due to a correlations among tree age, canopy height, and canopy pine basal area. In contrast, woodpecker foraging height was less in areas of longleaf pine habitat as midstory pine and canopy hardwood basal area increased. The relationship with midstory pine in longleaf pine habitat was the result of substantial amounts of woodpecker foraging directly on midstory pines in areas of relatively sparse midstory development, a behavior rarely noted in the loblolly-shortleaf pine habitat where midstory pines rarely occurred in areas of sparse midstory development. Many of the lower foraging heights observed in longleaf pine habitat with increased canopy hardwood basal area likely were due to substantial foraging in hardwood baygall habitats, which had lower canopy heights. The absence of a significant correlation between woodpecker foraging height and both midstory density and midstory height suggests that, in the longleaf pine habitats that we studied, midstory vegetation was not sufficiently developed to affect these aspects of woodpecker foraging behavior.

Canopy heights, both at foraging and random points, were significantly greater in loblolly-shortleaf pine habitat than in longleaf pine habitat. This difference was reflected in the overall significantly greater foraging height of Red-cockaded Woodpeckers in loblolly-shortleaf pine habitat.

In both habitat types, the distribution of foraging locations of Red-cockaded Woodpeckers suggests that midstory vegetation is a factor in foraging site selection across the landscape as well as within the vertical forest structure. In loblolly-shortleaf pine habitat, Red-cockaded Woodpeckers foraged disproportionately in forest stands that had reduced midstory vegetation, including cluster areas managed to reduce midstory vegetation and a variety of harvested areas where midstory as well as canopy vegetation had been reduced.

Foraging frequently occurred adjacent to forest openings or stands with reduced midstory. Although midstory vegetation at the location of foraging might be substantial, midstory conditions adjacent to the foraging location generally were much reduced. In longleaf pine habitat, this pattern typically did not occur, presumably due to reduced levels of midstory vegetation throughout the landscape. Only in the one Red-cockaded Woodpecker group with access to a large seed tree cut, including the cavity tree cluster, did a pattern similar to what was observed in loblolly-shortleaf pine habitat occur. We suggest that these foraging patterns indicate an avoidance of contiguous habitat with dense and tall midstory vegetation. In eastern Texas this vegetation structure occurs primarily in loblolly-shortleaf pine habitat.

Historically, the primary management emphasis has been on the effects of midstory vegetation within cavity tree clusters. A number of hypotheses have been suggested to account for the observed impacts of midstory vegetation on Red-cockaded Woodpeckers: (1) increased vulnerability of the cavity to predators (Dennis 1971), (2) increased competition for cavities with other species (Loeb and Stevens 1995), and (3) an open flight path increasing ease of access to cavities (Wood 1983). However, direct evidence in support of any of these hypotheses is lacking.

Recent studies have detected potentially negative effects of midstory in the foraging area (Epting et al. 1995, Davenport et al. 2000). Our observations support the view that midstory vegetation results in foraging patterns that reduce use of habitats, or portions of habitats, where hardwood midstory vegetation is well developed. The adaptive significance of this behavioral pattern remains to be demonstrated. Recent studies indicate that prey availability is higher in habitats with less midstory vegetation and more herbaceous vegetation (James et al. 1997, Collins 1998), and woodpecker group reproductive fitness declines as midstory development in foraging habitats increases (Davenport et al. 2000). Thus, it is likely that there are direct effects of midstory vegetation on foraging. The data presented above demonstrate that Red-cockaded Woodpeckers forage less in habitat with well-developed hardwood midstory vegeta-

tion. This behavior is consistent with the results indicating lower prey availability and lower reproductive fitness as a response to increasing midstory vegetation due to changes in the fire regime of southeastern U.S. pine forests.

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