

## RED-COCKADED WOODPECKER FORAGING BEHAVIOR

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**ABSTRACT.**—We studied Red-cockaded Woodpeckers (*Picoides borealis*) to examine the effect of status and gender on foraging behavior. Foraging behavior of breeding pairs extended beyond separation by foraging height to include zones (bole, trunk in crown, primary limb, secondary limb) of the tree used and foraging methods (scaling, probing, excavating). Helper males and juvenile females maintained partial spatial separation from breeding adults. Helper males maintained spatial separation from breeding adults by exploiting limbs within tree crowns in both longleaf (*Pinus palustris*) and loblolly-shortleaf (*P. taeda*, *P. echinata*) pine forests, but also increased use of boles in loblolly-shortleaf pine in concert with reduced use of boles by adult females. Breeding males tended to forage less by scaling, probably due to the reduced proportion of foraging on boles of trees where scaling tends to predominate. Received 29 June 2003. Accepted 31 August 2006.

The genus *Picoides* is particularly rich in species that show behavioral differences in foraging niches. Details of niche separation have been described for most species in the genus including Downy Woodpecker (*P. pubescens*; Jackson 1970, Peters and Grubb 1983), Hairy Woodpecker (*P. villosus*; Kilham 1965), White-headed Woodpecker (*P. albolarvatus*; Ligon 1973), Three-toed Woodpecker (*P. tridactylus*; Hogstad 1976), Ladder-backed Woodpecker (*P. scalaris*; Austin 1976), Nuttall's Woodpecker (*P. nuttallii*; Jenkins 1979), and Red-cockaded Woodpecker (*P. borealis*; Ligon 1968). Behavioral differences in foraging niches in these studies generally involve differences in height and diameter of stems used, and in specific foraging methods. Grubb and Woodrey (1990) reviewed behavioral differences in foraging within species of *Picoides* woodpeckers and found no consistent patterns; behavior varied across species and geographically within species. Several hypotheses have been proposed to account for behavioral differences in foraging behavior within bird species including morphological specializations, size differences, social dominance, and reduction in competition for food resources (Selander 1966, Slatkin 1984)

The Red-cockaded Woodpecker is a cooperatively breeding species that lives in groups composed of breeding pairs and male helpers

(Ligon 1970, Walters et al. 1988). Sexual dimorphism in size, although limited, has been detected (Pizzoni-Ardemani 1990). Behavioral differences in foraging behavior of Red-cockaded Woodpeckers have consistently been found when color-banded birds have been observed (Ligon 1970, Skorupa 1979, Ramey 1980, Hooper and Lennartz 1981). Females tend to forage lower on the tree (often on the bole) and males tend to forage higher. Because of the complex social system of Red-cockaded Woodpeckers, there is potential for status-based as well as gender-based differences in foraging behavior among individuals, unlike in other *Picoides* species. J. A. Jackson (pers. comm.) suggested that abundant mid-story vegetation might force female Red-cockaded Woodpeckers into the foraging zone of males. He further suggested that females might suffer detrimental foraging impacts due to increased competition with presumably dominant males.

We examined the foraging biology of Red-cockaded Woodpeckers with particular emphasis on differences in foraging position and behavior of individuals differing in gender and social status. We hypothesized that Red-cockaded Woodpeckers might differ in foraging position and behavior, based not only on gender, but also on social status. We examined aspects of Jackson's hypothesis concerning shifts in foraging niche with presence of abundant midstory vegetation, and looked for evidence of male dominance maintaining niche separation between males and females.

### METHODS

*Study Area.*—We observed foraging woodpeckers on the Angelina (31° 15' N, 94°

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15°W) and Davy Crockett (31° 21' N, 95° 07' W) National forests in eastern Texas. Woodpecker habitats on the Davy Crockett National Forest and the northern portion of the Angelina National Forest are composed predominantly of loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines with a significant component of hardwoods, especially in the midstory. The southern portion of the Angelina National Forest is predominantly longleaf pine (*P. palustris*) with a minor hardwood component (Conner and Rudolph 1989).

**Data Collection.**—We banded Red-cockaded Woodpeckers ( $n = 42$ ) present as regular members of 12 groups—six in longleaf pine forest and six in loblolly-shortleaf pine forest—with a federal band on one leg, and two color bands on the other leg. We began adding a white band to the leg with the federal band later in the study to facilitate reading bands in the field. Capture and banding of woodpeckers was initiated in late summer, which allowed us to identify juveniles prior to the post-juvenile molt (Jackson 1979). Band combinations were identified using binoculars or a 20X spotting scope during foraging observations.

Individual birds were assigned to one of six social status categories. The breeding male was the adult male roosting in the nest cavity, the breeding female was the only adult female present prior to the breeding season, and helper males and females were all non-breeding adults, with the exception of the breeding pair, in excess of 1 year of age. Juveniles were individuals less than 1 year of age, even though they had attained adult plumage.

We obtained foraging observations during 1–5 days for each of the 12 groups. Numbers of observations were fairly evenly split between two periods; 29 August to 2 November 1989 (57%), and 28 December to 19 February 1989–90 (43%). Ten groups were observed for either 4 or 5 days, and no group was observed for more than 1 day in any given month. Contact was initiated each day as woodpeckers exited roost cavities shortly after dawn. We attempted to maintain contact with each group for approximately 3 hrs. This was usually accomplished, although we occasionally lost contact for up to 45 min. This generally coincided with a period of intense foraging. Foraging is interspersed with other ac-

tivities later in the day (i.e., cavity maintenance, loafing) and we did not examine foraging behavior at these times.

We needed to obtain data simultaneously on two or more individuals to obtain foraging data when positions of individuals relative to others in the group were known. This precluded methods commonly used to avoid biases, such as taking samples at set time intervals or at a set time after an individual was located. A minimum of 10 min was maintained between observations to minimize lack of independence between successive samples. The same two observers, working as a team, attempted to identify and track individuals. We initiated data collection when two or more woodpeckers were simultaneously identified. We collected data for single individuals if we were experiencing difficulty identifying multiple individuals. Identification of pairs without helpers or juveniles was much easier and, consequently, data accumulated more rapidly for pairs than for larger groups. We recorded time and location within the home range, foraging method (scaling, probing, excavating, other), foraging zone (bole, trunk in crown, primary limb, secondary limb, other), diameter of stem at foraging site, height of foraging site above ground, and total tree height for each individual woodpecker. The condition of the foraging substrate was recorded as (1) live, (2) dead portion of live tree, (3) dying tree, or (4) dead tree. Diameter of the stem at the foraging position was visually estimated using the known dimensions of the woodpecker as a gauge; heights (m) were estimated using a clinometer.

Foraging tree species, tree diameter at breast height (DBH) and canopy height, and distances between any multiple trees involved in simultaneous foraging observations were recorded after foraging observations were terminated for the day. We calculated standardized foraging heights as a percent (foraging height/tree height  $\times$  100) of total tree height for each foraging observation.

**Data Analysis.**—Data were combined for the late August through mid-February period to obtain an adequate sample size. We used a two-way factorial ANOVA with Bonferroni's MRT to investigate the relationships among forest type (loblolly-shortleaf, longleaf), bird status, and bird foraging locations (foraging

height, standardized foraging height, stem diameter, tree height, tree DBH, and canopy height). We looked for differences among bird status categories within forest types if there was a significant interaction ( $P \leq 0.10$ ) between forest type and bird status. Statistical significance of remaining tests was set at  $P < 0.05$ .

Observation periods when only the breeding male and breeding female were present were used to explore dominance of breeding males in relation to foraging position of breeding females. Pairs either shared a tree or foraged in different trees. Vertical separation was calculated as breeding male foraging height minus breeding female foraging height. Two-way factorial ANOVA was used to examine effects of forest type and sharing of trees on vertical separation.

We used three-way tests of independence ( $G$ ) to examine the relationships among forest types, bird status, and behaviors (foraging zone, foraging substrate, and foraging method; Sokal and Rohlf 1995:737–759). Forest type, bird status, and foraging zone ( $G = 114.18$ ,  $df = 24$ ,  $P < 0.001$ ), foraging substrate ( $G = 80.69$ ,  $df = 17$ ,  $P < 0.001$ ), and foraging method ( $G = 66.01$ ,  $df = 17$ ,  $P < 0.001$ ) were not independent. Therefore, we conducted two-way tests of independence between bird status and foraging behavior within each forest type. We used simultaneous test procedures (STP, Sokal and Rohlf 1995:722–724) to examine which bird status categories differed.

## RESULTS

Red-cockaded Woodpecker groups for which foraging data were obtained consisted of pairs ( $n = 3$ , 2 in longleaf and 1 in loblolly-shortleaf) and pairs with 1–3 helpers and/or juveniles ( $n = 9$ ). Breeding males were assumed to be those individuals roosting in the 1989 nest cavity and their identities were confirmed during the 1990 breeding season. Breeding females were the only adult-plumaged females present at the time of initial banding. All remaining adult-plumaged males (late summer) were designated as helpers. Group membership was highly stable during the duration of the study, with only the replacement of a breeding female and the disappearance of one juvenile female.

We logged 125 contact hrs during the data collection period. Data were obtained on 42 individual birds on 460 separate occasions. We recorded 946 individual foraging observations, 512 in longleaf pine and 448 in loblolly-shortleaf pine. Of the 946 observations, 7% involved single birds, 64% involved two birds, and 28% involved three or more birds.

*General Foraging Behavior.*—Red-cockaded Woodpecker group members aggregated in the general vicinity of the roost trees, usually at the roost tree of the breeding male, after exiting roost cavities. An extended period of foraging ensued after a brief period of social interaction. This usually lasted throughout our approximately 3-hr observation period. Foraging was occasionally interrupted by work on cavities or resin wells, and interactions with neighboring groups.

Foraging was predominantly on pines (94.2%). Limited foraging (5.8%) occurred on eight species of hardwoods, primarily oaks (*Quercus* spp.). Various arthropods were the primary object of foraging activities. The major exception observed was foraging for seeds from longleaf pine cones. This behavior was recorded six times during foraging observations and an additional 49 times during periods between observations. All observations of foraging on seeds were between late October and early January, most in early November. This period corresponds to the opening of longleaf pine cones and dispersal of seeds. Red-cockaded Woodpeckers typically perched on an open cone, removed the seed, and flew to the bole or large limb of the pine. The seed and attached wing were wedged between the stem and the breast feathers, the wing was removed by pecking, and the seed was consumed. Red-cockaded Woodpeckers were not observed to feed on available seeds of loblolly or shortleaf pines. They also extracted tip moth larvae (*Dioryctria* sp.) from green longleaf pine cones (12 times during Aug and Oct) and flycatching behavior was observed twice.

Woodpecker groups foraged extensively on pines dying of southern pine beetle (*Dendroctonus frontalis*) and engraver beetle (*Ips* spp.) infestation when these were available. Red-cockaded Woodpeckers foraged on dead and dying pine-bark-beetle-infested trees during 9.3 and 13.4% of the observations, respectively, in longleaf and loblolly-shortleaf pine

habitats. Trees infested by pine bark beetles did not preferentially attract the attention of foraging Red-cockaded Woodpeckers early in the beetle's developmental cycle. Eggs and larvae are present at the depth of the vascular cambium at this time, but were not excavated by Red-cockaded Woodpeckers. Infested trees began to be preferentially visited only late in the infestation cycle after pupae and callow adults were present within the outer layers of bark. The pines were essentially dead at this point with all needles reddish and drying. Red-cockaded and other woodpeckers often completely stripped the outer layers of bark from the infested portions of the bole to expose the beetles. Slightly later in the cycle, more substantial excavations were directed at arthropods involved in secondary infestations of the beetle-killed pines. Red-cockaded Woodpeckers greatly curtailed their foraging activities on infested trees when substantial shedding of dead needles and loosening of the bark commenced.

Red-cockaded Woodpeckers appeared to obtain prey items more frequently, and secured items of larger average size, when foraging on trees infested by southern pine beetles. Groups often moved directly to infested trees early in the morning. Typically, all group members foraged together in the infested tree(s) for substantial periods. The mean time individual Red-cockaded Woodpeckers foraged on a southern-pine-beetle-infested tree was 21.3 min ( $n = 68$ ), compared with a mean of 6.8 min for a randomly selected sample of living trees ( $n = 50$ ).

*Foraging Behavior in Relation to Gender, Age, and Social Status.*—Sample sizes for helper females (zero in longleaf pine and 14 in loblolly-shortleaf pine) and juvenile males (28–30 in longleaf pine and 3 in loblolly-shortleaf pine) were too small to be considered representative of the bird status category and were deleted from analyses. The cone foraging method was dropped from analyses because it was used only in longleaf pine forest and was restricted to a limited time period.

*Foraging and Tree Measures.*—There were no interactions among forest type, bird status category, and foraging location for tree DBH ( $F = 0.86$ ,  $P = 0.46$ ) and canopy height ( $F = 2.05$ ,  $P = 0.11$ ). Tree DBH was similar in both forest types ( $F = 1.86$ ,  $P = 0.17$ ) and

across all bird status categories ( $F = 0.87$ ,  $P = 0.46$ ; mean = 40 cm, SE = 0.41). Canopy height was greater in loblolly-shortleaf pine forest than in longleaf pine forest (26 m, SE = 0.2 vs. 25 m, SE = 0.1;  $F = 31.84$ ,  $P < 0.001$ ), but did not differ ( $F = 1.30$ ,  $P = 0.27$ ) among bird status categories.

Interactions occurred among forest type, bird status category, and foraging location for stem diameter ( $F = 2.22$ ,  $P = 0.084$ ) and height of tree ( $F = 3.53$ ,  $P = 0.015$ ). Diameter of stems within both forest types differed among bird status categories ( $P < 0.001$ ; Fig. 1A). Breeding and helper males in longleaf pine forest foraged on significantly smaller diameter stems than breeding and juvenile females. Breeding males in loblolly-shortleaf pine forest also foraged on significantly smaller diameter stems than breeding and juvenile females. However, helper males were observed on larger stems, similar in diameter to those used by both females and breeding males.

Height of tree in loblolly-shortleaf pine forest did not differ among bird status categories (mean = 26 m, SE = 0.2;  $F = 0.58$ ,  $P = 0.63$ ). However, in longleaf pine forest, height of tree differed among bird status categories ( $F = 6.63$ ,  $P < 0.001$ ); helper males foraged in shorter trees (22 m, SE = 0.7) than other bird status categories (25 m, SE = 0.2; Fig. 1B).

*Foraging and Bird Location.*—There was no interaction between forest type and bird status category for woodpecker foraging height ( $F = 0.22$ ,  $P = 0.89$ ). However, when foraging height was standardized by height of tree, the interaction was significant ( $F = 4.28$ ,  $P = 0.005$ ). Overall, woodpeckers foraged at greater heights in loblolly-shortleaf pine forest than in longleaf pine forest (20 m, SE = 0.3 vs. 17 m, SE = 0.3,  $F = 32.97$ ,  $P < 0.001$ ). Foraging heights differed between breeding males and breeding females with forest types combined due to lack of interaction ( $F = 11.64$ ,  $P < 0.001$ ); breeding males foraged higher in the tree than breeding females (20 m, SE = 0.3 vs. 17 m, SE = 0.3) (Fig. 1C).

The difference in standardized foraging heights of males and females in longleaf pine was pronounced ( $F = 11.14$ ,  $P < 0.001$ , Fig. 1D) when foraging height was standardized by height of tree. Breeding males also had a

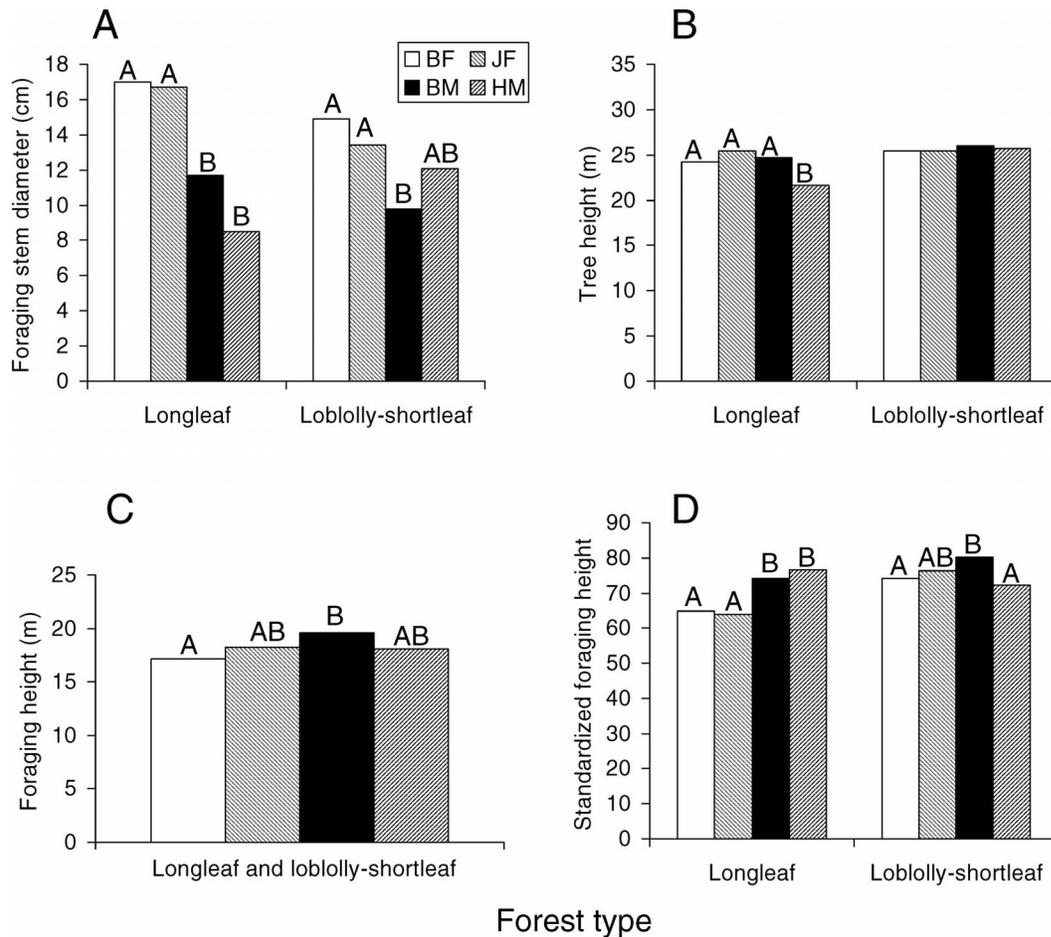


FIG. 1. Red-cockaded Woodpecker foraging stem diameters (A), foraging tree heights (B), foraging heights (C), and standardized foraging heights (D) in longleaf and loblolly-shortleaf pine habitats in eastern Texas, 1989–90 (BF = breeding females, longleaf  $n = 192$ –206 and loblolly-shortleaf  $n = 150$ –153; BM = breeding males, longleaf  $n = 174$ –182 and loblolly-shortleaf  $n = 139$ –141; HM = helper males, longleaf  $n = 24$ –26 and loblolly-shortleaf  $n = 41$ ; and JF = juvenile females, longleaf  $n = 50$ –51 and loblolly-shortleaf  $n = 72$ –73). Different letters above bars indicate differences ( $P < 0.05$ ) between birds of different status within forest types.

greater standardized foraging height than breeding females in loblolly-shortleaf pine forest ( $F = 6.83$ ,  $P < 0.001$ ).

There was no interaction between forest type and sharing of trees for vertical separation of breeding males and breeding females ( $P = 0.18$ ). Pairs in different trees ( $n = 110$ ) were spaced farther apart vertically than pairs in the same tree ( $n = 68$ ) (4.4 vs. 3.0 m,  $P = 0.012$ ). Vertical separation of pairs was greater in longleaf pine forest than in loblolly-shortleaf pine forest (4.4 vs. 2.8 m,  $P = 0.006$ ).

Bird status and frequency of foraging by

zone within the tree were not independent in longleaf ( $G = 46.29$ ,  $df = 9$ ,  $P < 0.001$ ) or loblolly-shortleaf pine forest ( $G = 47.87$ ,  $df = 9$ ,  $P < 0.001$ ), (Fig. 2A, B). Breeding males and helper males in longleaf pine forest had similar distributions among zones within the tree; breeding females and juvenile females were also similar (Fig. 2A). Helper males in loblolly-shortleaf pine forest were more similar to breeding females and juvenile females (Fig. 2B) due primarily to increased foraging on the boles of trees.

At least one member of the breeding pair

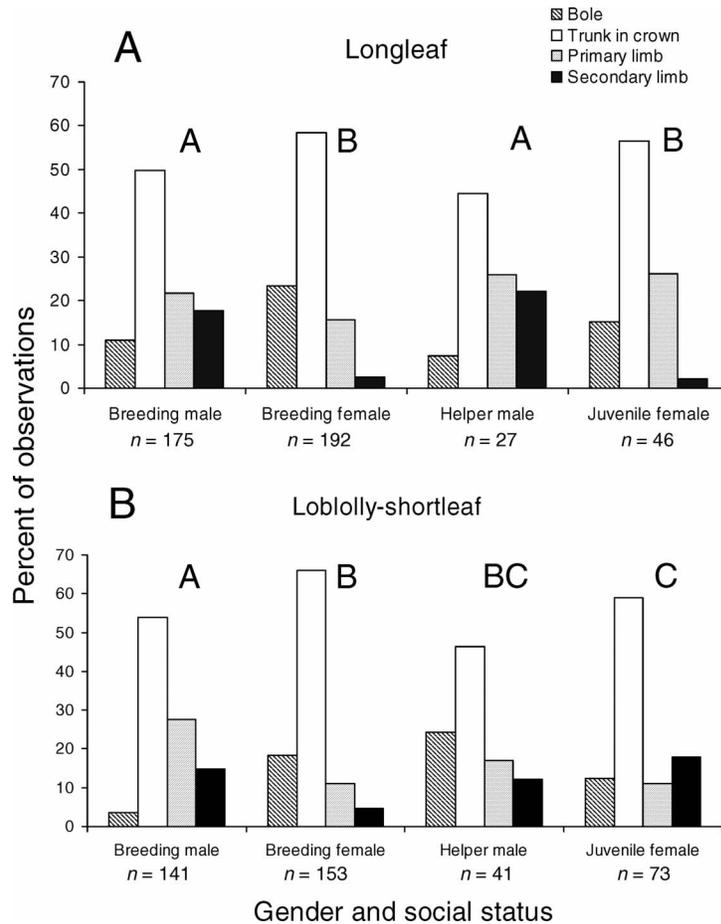


FIG. 2. Red-cockaded Woodpecker foraging frequencies by tree zone in longleaf (A) and loblolly-shortleaf (B) pine habitats in eastern Texas, 1989–90. Different letters above distributions of bird types indicate differences ( $P < 0.05$ ) within forest types.

was present in the same tree when helper males foraged on the boles of trees ( $n = 7$ ) in loblolly-shortleaf forest. In contrast, when helper males foraged in other zones within the tree, at least one member of the breeding pair was present in the same tree during only 47% of the observations ( $n = 19$ ).

Bird status and use of foraging substrate in longleaf pine forest were not independent ( $G = 34.75$ ,  $df = 6$ ,  $P < 0.001$ ), (Fig. 3A). Breeding males and helper males had similar distributions among substrates; breeding females and juvenile females were also similar. Bird status and use of foraging substrate were independent ( $G = 12.29$ ,  $df = 6$ ,  $P = 0.056$ ; Fig. 3B) in loblolly-shortleaf pine forest.

*Foraging Method.*—Bird status and forag-

ing method in longleaf pine forest were independent ( $G = 9.46$ ,  $df = 6$ ,  $P = 0.15$ ), implying that foraging methods did not differ by gender and social status (Fig. 4A). In contrast, bird status and foraging method were not independent ( $G = 42.11$ ,  $df = 6$ ,  $P < 0.001$ ) in loblolly-shortleaf pine forest (Fig. 4B). The proportion of time spent using different foraging methods was similar for breeding males and breeding females, whereas helper males were similar to breeding females, but differed from breeding males.

## DISCUSSION

The differences we noted between forest types resulted primarily from differences in forest structure and tree species. Greater hard-

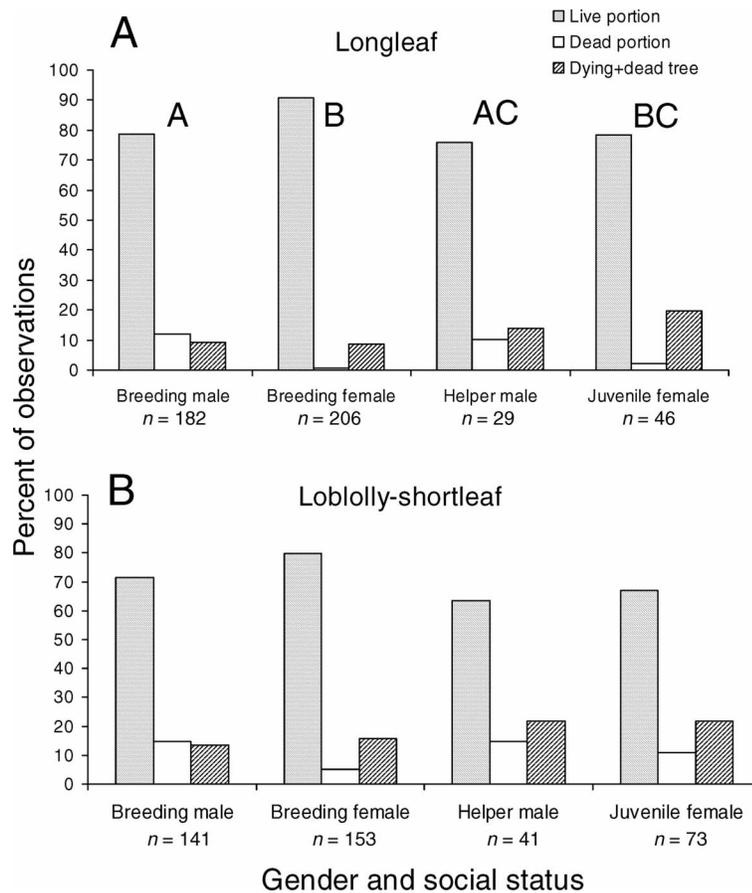


FIG. 3. Red-cockaded Woodpecker foraging frequencies by tree substrate in longleaf (A) and loblolly-shortleaf (B) pine habitats in eastern Texas, 1989–90. Different letters above distributions of bird types indicate differences ( $P < 0.05$ ) within forest types.

wood midstory in loblolly-shortleaf pine forest was associated with greater foraging heights in pines, especially for females (Rudolph et al. 2002). The generally greater abundance of hardwoods in loblolly-shortleaf pine forest was also associated with consistently greater use of hardwoods for foraging than in longleaf pine forest (Rudolph et al. 2002).

Dead and dying pines composed a greater proportion of Red-cockaded Woodpecker foraging sites than previously reported (Ligon 1970, Baker 1971, Nesbitt et al. 1978, Hooper and Lennartz 1981). This is almost certainly due to the generally high southern pine beetle populations in eastern Texas (Hedden 1978, Price and Doggett 1978). Greater use of bark beetle infested pines in loblolly-shortleaf pine habitats compared to longleaf pine habitats

was presumably due to the greater prevalence of southern pine beetle infestations in the more susceptible loblolly and shortleaf pines (Hodges et al. 1979).

Use of pine seeds was restricted to longleaf pine (Ramey 1980, Hooper and Lennartz 1981, this study), as was the excavation of green cones to obtain arthropod prey. Hooper and Lennartz (1981) noted that foraging birds perched directly on the cones and hypothesized the larger size of longleaf pine cones may have influenced their use. However, larger size and nutritional benefit of longleaf pine seeds may be the primary factor. The average weight of longleaf pine seeds is approximately 93 mg versus 25 mg for loblolly pine and 9.8 mg for shortleaf pine (Schopmeyer 1974). Excavation on cones was also restricted to long-

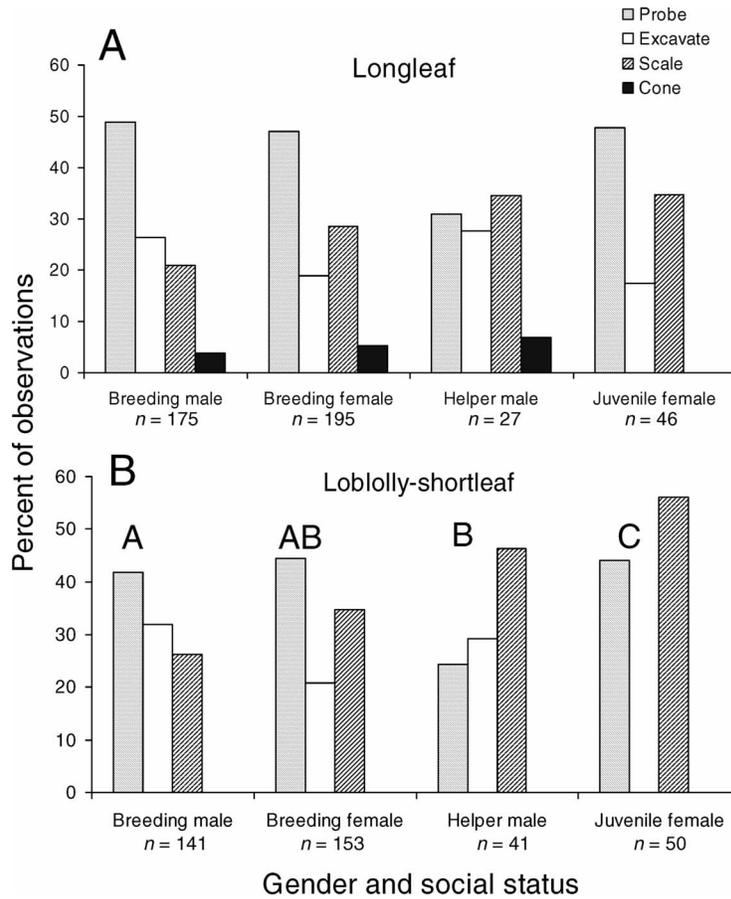


FIG. 4. Foraging frequencies of Red-cockaded Woodpeckers by foraging method in longleaf (A) and loblolly-shortleaf (B) pine habitats in eastern Texas, 1989–90. Different letters above distributions of bird types indicate differences ( $P < 0.05$ ) within forest types.

leaf pines. Birds appeared to be excavating for tip moth larvae in both Texas (this study) and South Carolina (Hooper and Lennartz 1981).

All members of social groups typically forage together, which limits the potential for differential use of overall habitat, or even individual trees, by birds of different social status or age. We found no significant differences in overall habitat or tree characteristics (tree height, tree DBH, canopy height) among birds of different social status or age, with one exception. Helper males in longleaf pine habitat foraged in shorter trees than did other social classes of Red-cockaded Woodpeckers.

Ligon (1968) first reported behavioral differences in foraging behavior in Red-cockaded Woodpeckers. Males were observed to forage mainly on limbs and upper trunks, while

females foraged mainly on upper and especially lower trunks. Similar results, differing only in minor details, have been reported in subsequent studies (Skorupa 1979, Ramey 1980, Hooper and Lennartz 1981). Studies that have not detected gender differences have failed to present data (Beckett 1971), or did not involve marked birds (Morse 1972, Miller 1978).

Our results confirmed the general pattern of spatial separation of male and female Red-cockaded Woodpeckers. However, additional differences between birds of differing age and social class were also found. In longleaf pine forest, breeding and helper males foraged at greater heights than females, especially if standardized foraging heights were considered. A similar pattern occurred in loblolly-

shortleaf pine forest for breeding males and females, but at greater absolute heights, presumably due to greater canopy heights and the restriction of foraging space. Helper males foraged at significantly lower standardized heights due to increased foraging on the boles of pines. The well-developed midstory in this forest type may constrain foraging to lower levels, especially for females.

Significant differences were consistently found between breeding males and breeding females in relation to foraging stem diameters, zone within the tree, and foraging substrate in both forest types. Breeding males exhibited a greater propensity to forage on smaller diameter stems, more often on branches and less often on boles, and more often on dead portions of living trees consisting of self-pruning limbs, compared to breeding females. Each of these differences is consistent with the vertical separation maintained between breeding males and breeding females.

Juvenile females were intermediate between breeder classes and resembled breeding females for these measures. The pattern is more complex for helper males. Helper males closely resembled breeding males in longleaf pine forest. However, helper males in loblolly-shortleaf forest differed significantly from breeding males in relation to zones used within the tree, more closely resembling breeding females. This was a result of greater use of tree boles by helper males. This results in a reversal of the pattern of foraging stem diameters used by helper males compared with breeding males; helper males used larger stems in loblolly-shortleaf pine forest and smaller stems in longleaf pine forest.

Our results confirm the tendency for gender separation of foraging position reported in previous studies (Ligon 1968, Hooper and Lennartz 1981). Our data suggest that helper males maintain some separation in foraging position from breeding adults. Breeding adult males and females concentrate much of their foraging activities on the trunk in the crown. Secondarily, breeding males use limbs and breeding females use boles to a greater extent than the other gender. Helper males are similar to breeding males in their general choice of foraging position, but show a consistent tendency to shift from the foraging niche of breeding males. Helper males in longleaf pine

forest forage to a greater extent on primary and secondary branches and less on boles than breeding males. However, helper males in loblolly-shortleaf pine forest also increased foraging on boles of pines, contrary to the situation in longleaf forest. This may be a result of the reduced use of boles by breeding females in loblolly-shortleaf pine forest, presumably due to the greater amount of hardwood midstory vegetation compared to longleaf habitats. Concurrent observations (Rudolph et al. 2002) suggest that Red-cockaded Woodpeckers tend to avoid foraging in situations with dense midstory vegetation.

The foraging positions and behaviors of breeding male and female Red-cockaded Woodpeckers are consistent with the assumed social dominance of breeding males (Ligon 1970) and limited dimorphism (Pizzoni-Ardemani 1990). We suspect that social dominance is the mechanism driving differential foraging positions, but clearly more information is required concerning this aspect of foraging. Red-cockaded Woodpeckers exhibit some plasticity in foraging behavior due to habitat (i.e., encroaching midstory; Rudolph et al. 2002, this paper). The behavior of helper males is more complex, suggesting reduction in competition among group members may also be involved. Helper males in longleaf pine forest foraged in portions of trees most similar to that of the breeding male, maintaining significant spatial separation. However, in loblolly-shortleaf pine forest where encroaching midstory resulted in more intense foraging by the breeding pair in tree crowns, consistent with Jackson's (pers. comm.) hypothesis, helper males also increased foraging on tree boles that were partially vacated by breeding females. This observation suggests that morphological differences between males and females do not completely constrain foraging position.

Social dominance and reduction in competition for prey appear to be important, although overt aggression was rarely observed among established group members, especially between members of the breeding pair. Hooper and Lennartz (1981) reported a similar lack of conflict between adult group members. This lack of aggression is expected in these typically well-established social groups. Regardless of the mechanisms controlling foraging

behaviors, Red-cockaded Woodpeckers maintain a sophisticated separation of foraging space in relation to gender and social status.

The observed foraging behavior of Red-cockaded Woodpeckers in eastern Texas differed between loblolly-shortleaf and longleaf pine habitats. The observed differences were presumably related to differences in vegetation structure (amount of midstory vegetation), bark beetle abundance, and pine species. Differences between Red-cockaded Woodpeckers of differing gender, age, and social status were detected for several aspects of foraging behavior. These results are consistent with the frequent pattern of gender variation in foraging behavior within the genus *Picoides*. The occurrence of cooperative breeding and consequent existence of larger social groups, which frequently remain intact for several years (Walters et al. 1988), presumably allows for development of more complex partitioning of the foraging niche in this cooperatively breeding species.

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