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RED-COCKADED WOODPECKER FORAGING ECOLOGY IN AN OLD-GROWTH LONGLEAF PINE FOREST

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ABSTRACT.—Most Red-cockaded Woodpecker (*Picoides borealis*) populations are in pine forests that have been harvested at least once and are relatively young compared to old-growth stands. We quantified foraging behavior, year-round home range, and woodpecker productivity for groups within and proximal to an old-growth longleaf pine (*Pinus palustris*) stand from late 1992 to late 1993 in southwestern Georgia. Average year-round home range size for seven woodpecker groups in and adjacent to the old-growth stand based on minimum 95% convex polygons was 47.1 ha. Year-round home range was negatively correlated with the percentage of the home-range located within old-growth forest. In the old-growth stand the size class distribution of trees selected by woodpeckers for foraging was different than the distribution of trees available in size classes >30 cm dbh. As in other studies, males and females differed in foraging height and parts of the trees used. Clutch size and fledging rates of the seven study groups were also higher than reported in other studies. Red-cockaded Woodpeckers preferentially forage on large (and presumably old) trees. The small year-round home range, high density, large group size, and high productivity indicate that this old-growth longleaf forest is high quality habitat. We suggest that forest management intended to provide an adequate number of replacement cavity trees and quality foraging habitat for the Red-cockaded Woodpecker should have old trees across the landscape. *Received 14 May 1996, accepted 15 Jan. 1997.*

Longleaf pine (*Pinus palustris*) forest dominated an estimated 27 million ha (Wahlenberg 1946) of the southeastern coastal plain before extensive logging in the early 1900s. Today, approximately 5% of the original longleaf pine ecosystem remains in such forests, although most of this is second- or third-growth (Kelly and Bechtold 1990, Outcalt and Outcalt 1994). Based on preliminary estimates, only 3900 ha of old-growth longleaf forest remains (Means 1996). Much of the younger forest lacks important characteristics of old-growth longleaf, such as old trees, vertical and horizontal heterogeneity, and persistent snags (Engstrom, pers. obs.). The importance of the structure and composition of old-growth to organisms that presumably evolved in longleaf pine forests is largely unexplored. This paper documents some of the life history characteristics of one bird species of the longleaf pine ecosystem, the Red-cockaded Woodpecker (*Picoides borealis*).

Habitat requirements of the Red-cockaded Woodpecker have become centrally important to forest management planning for public lands such

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as National Forests and military installations in the southeastern United States (Lennartz 1985, McWhite 1993, Meier 1993). Basic needs of the woodpecker include large areas of pine forest for foraging (Henry 1989), trees an average of 90–130 years old or older for cavities (Rudolph and Conner 1991), and contiguity of habitat to facilitate successful dispersal of individuals among groups (Anonymous 1990). Ecosystem management planning for National Forests in the Southeast has focused on providing these habitat features (Meier 1993). Old-growth forest plays an important role in the development of ecosystem management because it serves as a model for understanding natural disturbance and regeneration cycles (Thomas et al. 1988, Sharitz et al. 1992). Additionally, study of the behavior of organisms in old-growth may be instructive because the full suite of forest structural characteristics is available. Most of the research that has been conducted on the Red-cockaded Woodpecker to establish habitat preferences has occurred on forests that have been managed for timber production for decades. Study of woodpecker behavior in old-growth provides information for deciding which old-growth characteristics are important and should be maintained or mimicked in forests for woodpecker management (Lennartz and Lancia 1989).

Our objectives for this study were to measure, for seven Red-cockaded Woodpecker groups, year-round home range and foraging behavior in relation to habitat structure and composition in or near an old-growth longleaf pine forest. We also measured group size, clutch size, and fledging rate for the study groups.

METHODS

The Wade Tract is an 80-ha old-growth longleaf pine forest preserve in southwestern Georgia (30°46′30″N, 84°00′W) that has been preserved in a long-term conservation easement since 1979. The easement is privately owned, but it is managed by Tall Timbers Research Station for research purposes. For a study of forest structure and dynamics the easement was gridded with permanent metal stakes at 100-m intervals, all trees ≥1.5 m in height were given numbered aluminum tags, and tree locations were surveyed on 39.4 ha of the easement (Platt et al. 1988).

The forest is characterized by a negative exponential size class distribution and considerable patchiness (Platt et al. 1988, Engstrom and James 1981). Tree species composition of the canopy is >90% longleaf pine with scattered hardwoods and other pine species. Hurricanes, fires, and small gaps caused by death of an individual or small groups of trees are disturbances that shape the forest. As far as known, only individual trees that were killed by lightning or insects were harvested for salvage before the area was made into an easement. Canopy trees are 200–400 years old (Platt et al. 1988, Engstrom, pers. obs.).

Currently, each half of the Wade Tract (the plot is roughly bisected by a dirt road that runs from cluster 3 to cluster 2 in Fig. 1) is burned biannually in the lightning season (May–June) on an alternating schedule. Previous to the establishment of the conservation easement, the entire preserve was burned annually during the dormant season (usually early March). The preserve is bounded to the east by a 30-m wide paved road and grassy shoulder with

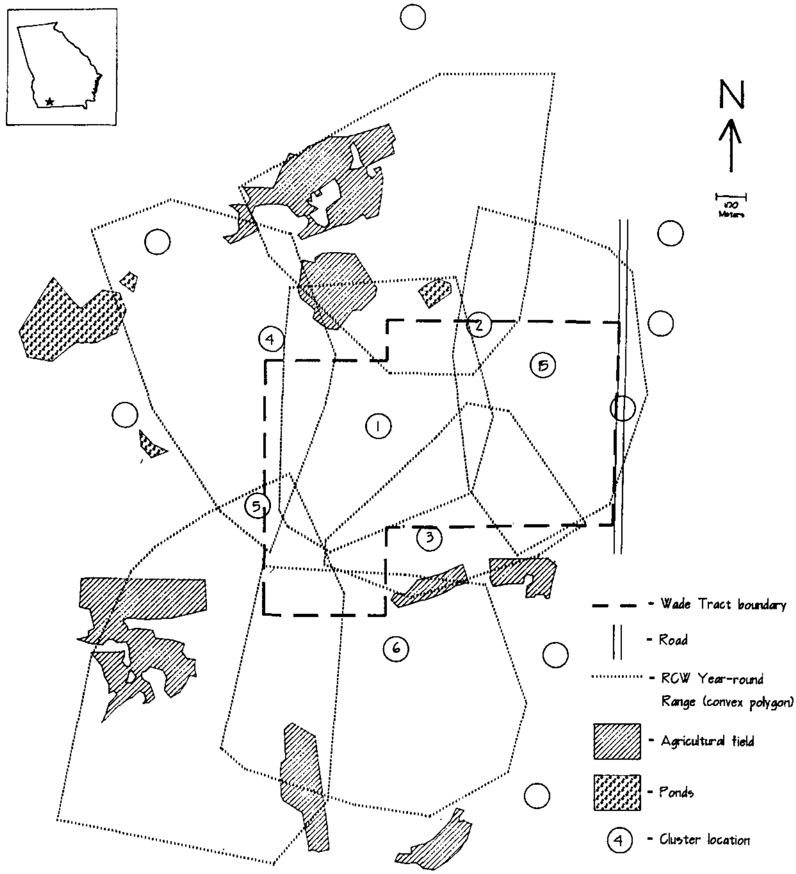

FIG. 1. Year-round home ranges of seven Red-cockaded Woodpecker study groups in old-growth longleaf pine forest indicated as convex polygons. The numbers within circles identify the study groups and the eight empty circles represent active clusters surrounding the study clusters.

similar old-growth habitat to the east of the road. Longleaf pine forest that is managed with single-tree selection silviculture is the habitat on all sides of the preserve. Fields and ponds are interspersed within this area (Fig. 1).

Some or all of the cavity trees of eight clusters are on the preserve. Seven of the groups that lived in these clusters were included in this study. The eighth group lived primarily on adjacent property (unnumbered circle that straddles the paved road in Fig. 1) and was not included in the study. Seven additional active clusters surround the preserve in the managed forest. Outside the preserve, old trees are retained within the clusters and scattered throughout the forest that is managed for quail hunting, aesthetics, timber production, and conservation of native flora and fauna (Engstrom and Baker 1995). Woodpecker cavity trees and potential cavity trees are retained within clusters in local timber management practices. The timber management approach includes selective tree harvest on an approximately 10-year cutting cycle in the managed forest (Neel 1971, Lindeman 1994). All clusters in this regional population (179 active clusters) are located on privately owned land (Engstrom and Baker 1995).

Each of the seven study groups was followed for as long as possible on at least one day in almost every month for a total of 476 h from December 1992 through December 1993. The number of hours per group for the entire year ranged from 57 to 78, and the average number of hours followed per group per month ranged from 4.8 to 6.0. Three groups (1, 2, and 6) were not followed during May, and Group 5 was not followed during March and April.

We plotted locations of the groups on 1:7200 scale aerial photographs, transferred them to base maps, and eventually digitized them into Generic CADD 6 (Anonymous 1993). Significant features of the landscape, such as agricultural fields, ponds, roads, and the preserve boundary, also were digitized and entered into Generic CADD 6. We determined areas of convex polygons of year-round home ranges and suitable and unsuitable habitat with Generic CADD 6. We calculated minimum convex polygons (95%) for each year-round home range (Program Home Range, Ackerman et al. 1990). A Pearson product moment correlation coefficient was calculated between the 95% convex polygon of each year-round home range and the percent of the home range in the Wade Tract (Zar 1984, Minitab 1991).

Linear distances from the center of cavity tree clusters (estimated visually) to foraging locations were measured on the base maps to determine the extent of movements in relation to time of day. LOWESS (Locally Weighted Scatterplot Smoothing) was used to display graphically the relationship between time of day and distance from cluster (SYSTAT Version 5.03: Wilkinson 1990a).

We took single-point observations of foraging behavior of individuals in the seven study groups using a 25× spotting scope. Single-point observations were used to avoid inter-observation dependence (Hejl et al. 1990). One foraging behavior was noted per individual on a given tree immediately after the identity of the individual was established. Foraging behavior categories, excavating (making a hole by removing wood), probing (using the bill to search beneath the surface of the bark), gleaning (search in foliage), scaling (removal of flakes of bark), and moving and looking, are described in Hooper and Lennartz (1981). After we recorded identity of each individual and foraging behavior, we noted tree diameter at breast height (dbh), height of the woodpecker on the tree, tree height, substrate used (trunk, live branch, dead branch, and cone), and position on the tree. To categorize position, the tree was divided into crown (area with the majority of limbs) and upper, middle, and lower thirds of the trunk (below the crown, but sometimes with a few limbs). Height of the woodpecker on the tree and tree height were measured with a clinometer. If the tree being used by a woodpecker was located within the part of the conservation easement in which all trees were tagged, the tree number was recorded.

After the year-round home ranges were determined, the area that comprised the home ranges was divided into stands of similar structure and composition as determined by visual evaluation. A grid was laid over the photo of each stand, and at least six points were randomly selected within each stand. Circular samples (0.04-ha) were taken at each point (James and Shugart 1970). Diameters of all trees ≥4 cm were measured and species identity determined within each circle.

Almost all adult and nestling woodpeckers in the seven woodpecker groups in the study area were banded with U.S. Fish and Wildlife Service aluminum bands and plastic color bands. Group size was established during the nesting season.

Cavity trees in the study clusters were monitored from early April in 1993 and 1994 to establish (1) the nest tree, (2) nesting initiation, (3) clutch size, (4) number of nestlings

TABLE 1
RED-COCKADED WOODPECKER YEAR-ROUND HOME RANGE IN AND AROUND THE WADE TRACT

Group	Year-round home range (ha)	Area of suitable habitat	Percentage in Wade Tract	95% convex polygon
1	55.4	52.3	83	42.6
2	74.5	60.4	11	55.4
3	33.9	32.4	76	23.2
4	60.3	59.0	15	45.4
5	91.3	78.5	11	61.9
6	69.5	66.3	10	56.8
15	58.3	55.9	63	44.6
Mean	63.3	57.8		47.1

when the nestlings were approximately 8 days old, and (5) the number of fledglings within 30 days after the departure from the nest.

RESULTS

The areas of 95% minimum convex polygons of the year-round home ranges of the seven Red-cockaded Woodpecker groups in and proximal to the old-growth longleaf pine forest ranged from 23.2 to 61.9 ha, with a mean of 47.1 ha (Table 1). The percentage of the home range within the Wade Tract had a significant negative Pearson product moment correlation coefficient ($r = -0.781$) with home range area. Using total year-round home range for comparability, the Wade Tract areas were smaller than those reported for other studies, except for Wood (1983), who measured home range for only one group (Table 2). When unsuitable habitat, such as agricultural fields, ponds, and roads were excluded, the mean amount of suitable habitat within the home range for the seven study

TABLE 2
TOTAL YEAR-ROUND HOME RANGE AREAS (HA) FROM OTHER STUDIES IN COMPARISON WITH THIS STUDY

Citation	Location	Mean (N)	Range
Wood (1983)	OK	53 (1)	—
Hooper et al. (1982)	SC	87 (24)	34–225
Porter and Labisky (1986)	FL	129 (4)	85–157
DeLotelle et al. (1987)	FL	150 (6)	116–199
Jackson and Parris (1995)	LA	pre-clearing 135 (3)	109–170
		post-clearing 253	115–413
This study	GA	63 (7)	34–91

groups was 57.8 ha. One complication was that some of the agricultural fields, which were included as unsuitable habitat, were corn fields. Red-cockaded Woodpeckers have been noted to eat corn ear worms and other arthropods on corn in the past (Baker 1971), and groups were seen to forage on corn in this study. Thus, corn fields provided an ephemeral food supply during the critical fledgling period, but the fields were unusable for most of the year.

Considerable overlap occurred in the home ranges. For example, 31% of the 52.3 ha home range of Group 1 overlapped with other groups (Fig. 1). Estimating the percentage of overlap of the other study groups was not possible, because each of these groups have additional neighboring groups whose home ranges were not measured. Observations of one group of woodpeckers entering the cluster area of another group were made on several occasions. Territorial interactions, such as wing displays, calling, and looping flights (Ligon 1970) were observed when two groups came into contact, but the intensity of the displays varied considerably. Occasionally, two groups that were foraging in the same area mingled with very little display.

The groups tended to move the maximum distance from the cluster by five hours after sunrise (determined by visual estimate of the asymptote of the LOWESS line in Fig. 2); however, this relationship varied considerably. For example, by the seventh hour after sunrise, distance from the cluster ranged from 0.1 to 1.1 km.

A total of 1380 observations of foraging behavior of individuals in the seven study groups were collected simultaneously with the year-round home range data from December 1992 through December 1993. The number of observations per group ranged from 150 to 242. Excavations and probes made up 69 percent of all foraging behaviors recorded. Scaling (15%), hitching and looking (10%), other (5%), and gleaning (2%) made up the rest of the observations. The frequency of gleaning may have been underestimated because of the difficulty of observing this behavior in clumps of needles high in the trees. Both excavations and probes have a strong seasonal component (Fig. 3), with excavations more common in the spring and summer than in the fall and winter. A few observations were made of woodpeckers feeding on ears of corn, but the groups were not followed closely in the corn fields.

As in other studies of Red-cockaded Woodpecker foraging behavior, males tended to forage higher in trees than females (mean height: males = 16.4 m, N = 945; females = 15.1 m, N = 404; $P \leq 0.001$, Mann-Whitney U-test). This was also reflected in the position on the tree (Table 3) and the substrate used by the sexes (Table 4). Males tended to forage in the crown more than females, and females spent more time than males

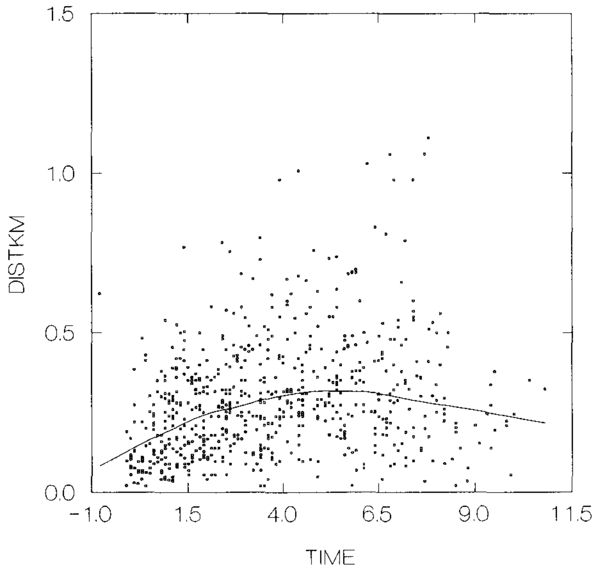

FIG. 2. Distances (km) that Red-cockaded Woodpecker study groups moved from the home cluster as a function of the number of hours since sunrise. The line through the points is a LOWESS plot.

on the lower and middle parts of the trunk. Males also made 35% more foraging visits to branches, living and dead, than did females. The area included within all seven woodpecker year-round home ranges was divided into nine stands based on forest structure and composition. Between

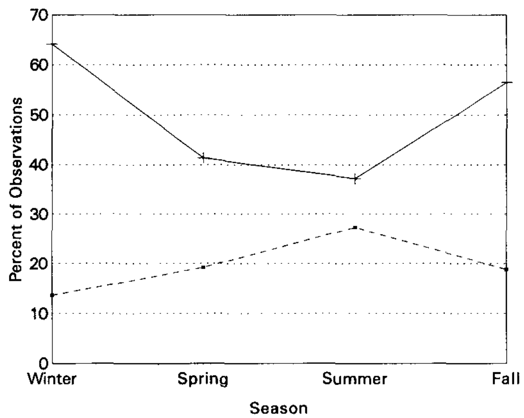

FIG. 3. Seasonal variation in the frequency of foraging behaviors.

TABLE 3

DIFFERENCES BETWEEN THE SEXES IN THE PERCENTAGE OF THE NUMBER OF OBSERVATIONS OF FORAGING BEHAVIOR FOR DIFFERENT POSITIONS ON A TREE

	CR	LOW	MID	UPP	OTH	TOTAL	N
F	65.13	12.35	9.20	12.11	1.21	100.00	413
M	79.32	2.69	5.27	11.27	1.45	100.00	967
N	1036	77	89	159	19	—	1380

[a] CR = crown; LOW, MID, UPP = thirds of trunk.

six and 38 0.04-ha circular samples were taken in the stands for a total of 129 samples. When all stands were combined within a year-round home range, the estimated numbers of pines (all species) ≥25.4 cm dbh ranged from 2341 to 5729 per group ($\bar{x}$ = 4504, SD = 1169, Table 5).

Based on 38 0.04-ha vegetation samples within the old-growth stand (39.4 ha plot), the size class distribution of trees was approximately an inverse J shape. Stems were most common in the 1–10 and 10–20 cm dbh size classes, underrepresented in the 20–40 cm dbh classes, and about as expected in the >40 cm dbh classes (Fig. 4).

Nearly 80% of the trees selected for foraging by Red-cockaded Woodpeckers in the old-growth forest were between 35 and 65 cm dbh. Using tree distribution and woodpecker foraging data from the old-growth stand only (nine 10-cm size classes: 1–10, . . . 81–90), a Chi-square test of the null hypothesis that the woodpeckers were selecting trees in relation to their availability can be rejected (χ^2 = 351, df = 8, P < 0.001). The number of trees used in the smallest size classes (1–10, 11–20 cm dbh) were used less than the 95% confidence intervals for the number of trees available in those classes, and trees in size classes from 31 cm dbh and higher were used in excess of the 95% confidence intervals for those classes (Wilkinson 1990b). When the two smallest size classes were deleted and the top two intervals combined, the null hypothesis was still

TABLE 4

DIFFERENCES BETWEEN THE SEXES IN THE PERCENTAGE OF THE NUMBER OF OBSERVATIONS OF FORAGING BEHAVIOR FOR DIFFERENT PARTS OF A TREE

	BR	CON	DBR	OTHER	ROOTS	TR	TOTAL	N
F	16.95	3.15	3.63	0.73	0.24	75.30	100.00	413
M	32.16	3.72	23.16	0.93	0.00	40.02	100.00	967
N	381	49	239	12	1	698		1380

[a] BR = branch; CON = cone; DBR = dead branch; TR = trunk; ROOTS = upturned roots.

TABLE 5

SUMMARY OF THE NUMBER OF TREES IN EACH YEAR-ROUND HOME RANGE[a]

	Longleaf		Other pine		Hardwoods		Hardwood snag		Pine snag	
Group	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large
1	4424	3742	41	93	1137	8	466	6	69	142
2	2377	5314	26	352	1510	83	1687	0	9	22
3	3483	2315	0	26	703	57	201	0	133	83
4	2993	4347	288	614	1436	33	322	74	173	64
5	11,407	4467	5907	1262	4540	712	656	0	365	136
6	10,566	4287	828	281	205	1080	142	0	172	115
15	3924	4323	77	101	1266	33	926	0	59	115

[a] Large = ≥25.4 cm and small = ≥2, and <25.4 cm.

rejected ($\chi^2 = 20.16$, df = 5, $P < 0.005$). Trees used exceeded the 95% confidence interval of trees available in the 61–70 cm dbh size class in this reduced data set.

Group sizes of the seven study groups ranged from two to five individuals when nestlings were being fed (Table 6). In 1994 groups were larger, nested earlier, had a higher clutch size, more nestlings, but fewer fledglings. In both years one of the seven groups failed to produce any fledglings.

DISCUSSION

Year-round home ranges of the seven Red-cockaded Woodpecker groups in and around the Wade Tract were smaller than home ranges

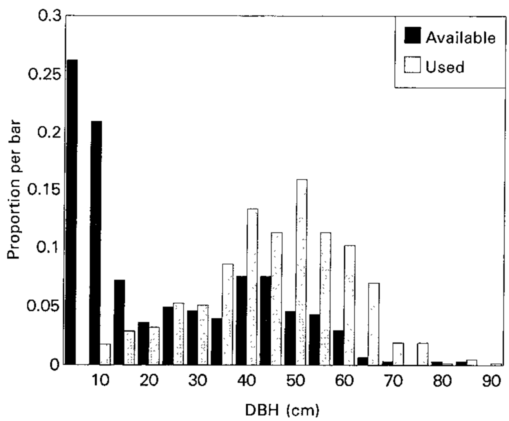

FIG. 4. Size class distribution of trees in the Wade Tract compared to the size class distribution of trees used by Red-cockaded Woodpeckers for foraging.

TABLE 6

SIZE AND PRODUCTIVITY OF SEVEN RED-COCKADED WOODPECKER GROUPS IN AND AROUND THE WADE TRACT

	1993	1994
Mean number of adults	3.0	3.6
Mean date of first egg	25 April	19 April
Mean clutch size	3.3	3.6
Mean number of nestlings	2.5	2.5
Mean number of fledglings	2.5	2.3
Percent of failed nests	14	14

measured in most other studies (Table 2). R. Hooper (in Lennartz 1985) reported 22 clans in an approximately 1000-ha expanse of mature heavily stocked longleaf pine forest. This equaled an estimated density of one group in 45 ha, but this may underestimate year-round home range because of overlap. We found that home ranges overlapped widely. Over 30 percent of the home range of Group 1, which held the most central position within the Wade Tract (Fig. 1), was shared by other groups. Amount of overlap for the peripheral study groups could not be determined because groups beyond the periphery were not followed. We did not determine defended territory size as a subset of home range.

Although the Red-cockaded Woodpecker is described as having a Type A territory (Ligon 1970), we and other authors (Hooper et al. 1982, DeLotelle et al. 1987), have noted movements by groups into the home range and even the cavity tree clusters of neighboring groups. DeLotelle et al. (1987) determined territory sizes of Red-cockaded Woodpeckers in central Florida based on locations of territorial encounters, but observed the same number of extraterritorial movements as territorial defenses. Porous home range boundaries are probably a function of the difficulty of defending such large foraging areas.

Determination of home range size is partly a function of how many hours a group is followed by observers during the day (e.g., Nesbitt et al. 1978). Some of the longest distances that groups moved away from the center of the home cluster were late in the day (Fig. 2). These long distance movements, although relatively rare, can strongly affect overall home range size. Usually, however, the maximum distance the groups traveled during a day tended to be within the first five hours. Using a different approach, Hooper and Harlow (1986) also found that woodpeckers followed for five hours provided unbiased estimates of territory size when compared to whole-day samples. Given the difficulty in obtaining whole-day samples, we recommend five-hour sampling periods for estimating home range size.

Inter-sexual foraging behavior of the woodpecker in old-growth forest was similar to behavior described in other studies. Males foraged higher in the trees, more in the crown (Table 3), and used more branches (Table 4) than females. This is consistent with the results of Ligon (1968) and Hooper and Lennartz (1981). We also found a strong seasonal component to foraging: excavations tended to be more frequent in the spring and summer and probes more frequent in the fall and winter (Fig. 3). This is somewhat consistent with the observations of Hooper and Lennartz (1981), but they divided the year into three sections; therefore, the results are not directly comparable to ours. Conner (1981), however, described different seasonal patterns of foraging for Downy (*Picoides pubescens*), Hairy (*P. villosus*), and Pileated (*Dryocopus pileatus*) woodpeckers. In all three species, excavations were more common in the winter than in the breeding or post-breeding seasons, and "peer-and-poke," which is similar to our "probe," was more common in the breeding and post-breeding seasons than in the winter. Higher use of limbs by females in this study (20.6%) compared to 4.3% in Hooper and Lennartz (1981) may be a function of larger crowns in the old trees at the Wade Tract.

Although the Wade Tract study groups are few in number and not randomly sampled, it is noteworthy that average group size tended to be three or larger in the two years of study (Table 6). Also, no single males were found defending clusters in the Wade Tract. The presence of helpers may be partially a function of habitat saturation (Walters 1990). The Wade Tract study groups have 32 active groups within 3.2 km (median dispersal distance of first year females, Walters et al. 1988), which is a very high population density (Engstrom and Mikusinski, unpub. data).

Productivity of fledglings (2.3–2.5 per nest per year, exclusive of failed nests) at the Wade Tract is also relatively high. LaBranche and Walters (1994) reported a mean number of young fledged per successful nest of 1.9 in 929 nests monitored from 1980 to 1985 in North Carolina. DeLotelle et al. (1995) reported mean fledging rates of 0.4–1.4 (grand mean = 1.0) and mean group size of 2.3 for a 12-year study in central Florida. High productivity in a region of high density indicates that density is not a misleading indicator of habitat quality (Van Horne 1983).

The Red-cockaded Woodpecker has declined precipitously in response to land use changes in the southeastern coastal plain in the twentieth century. Recovery of this species should be grounded in an ecosystem management approach that mimics natural forms of disturbance (e.g., Sharitz et al. 1992). In theory, this approach will provide habitat for plants and animals that are most adapted to the ecosystem, even species that are not and probably never will be studied, as well as the Red-cockaded Woodpecker.

Probably more than any other bird species, the Red-cockaded Woodpecker depends on some old-growth characteristics of southeastern pine forests. Although extensive old-growth pine forests have been eliminated from the southeastern landscape, scattered remnant trees and patches of old-growth likely provided a crucial bridge for the Red-cockaded Woodpecker into a second-growth forest. Red-cockaded Woodpecker life history requirements are pivotal considerations in National Forest and other public land management in the southeastern United States (Lennartz et al. 1983, Meier 1993). Foraging guidelines for the woodpecker have been based largely on research that was conducted in forests that have significantly modified tree species composition, age structure, and landscape arrangement. Public land managers must address what old-growth characteristics should be retained within managed forest and in what spatial arrangement (Lennartz and Lancia 1989).

High local population density, high productivity, and small year-round home range size indicate that the Wade Tract old-growth longleaf pine forest is excellent habitat for the Red-cockaded Woodpecker. The exact contribution of foraging habitat quality to productivity is not clear. For example, the abundance and quality of cavity trees also may have played a role. Although the Wade Tract may be an unusually productive forest, Red-cockaded Woodpeckers in this study, as in other studies, tended to forage on the largest (and probably oldest) trees in the forest (e.g., DeLotelle et al. 1983). At the stand level, Hooper and Harlow (1986), however, found no evidence that the occurrence of large pines affected stand selection for foraging. They also concluded that pines 24 to 35.6 cm dbh appear to be as valuable as trees ≥ 36 cm dbh for foraging. Our results indicate that large and old trees are used preferentially.

We disagree with the conclusion by Hooper and Harlow (1986) that "thinnings, superior stock, fertilization, initial spacing at regeneration, and site index may be as important as age in providing quality foraging habitat." These silvicultural techniques may provide larger trees faster at the expense of trees that are of high value to wildlife, especially the Red-cockaded Woodpecker. Old, co-dominant or suppressed trees may have microhabitats, such as dead limbs, that are important to ants and other arthropods. We recommend that management for Red-cockaded Woodpeckers include retaining old trees throughout the landscape, not just in the cluster to serve as replacement cavity trees.

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