

FORAGING BEHAVIOR OF THE RED-COCKADED WOODPECKER IN SOUTH CAROLINA

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ABSTRACT.—Foraging Red-cockaded Woodpeckers (*Picoides borealis*) selected live pines (96% use; 71% availability) over hardwoods (1% use; 25% availability). Use of recently dead pines (3%) was the largest departure from use of live pines. Mast was rarely consumed, although abundant at times. Live pine stems greater than 23 cm in diameter at breast height represented only 19% of the available pines but received 65% of the use. The sexes exhibited strong divergence in foraging behavior. Most important was the partitioning of foraging sites on live pines. Males foraged on dead and live limbs of the crown and midtrunk 54% of the time and females only 4%. On the lower trunk, females foraged 38% of the time and males only 3%. On the midtrunk, females foraged 29% and males 12%. On the trunk-in-crown, females foraged 28% and males 32%. Mean foraging height of males was 14.1 m and that of females 8.7 m ($P < 0.001$). The sexes used tree sizes, tree types, and methods for capturing prey with similar frequencies. Within each sex, there were between-season differences in use of foraging sites and in methods used at each site. Received 9 July 1980, accepted 5 January 1981.

ENDEMIC to mature pine forests of the southeastern United States, the Red-cockaded Woodpecker (*Picoides borealis*) is considered endangered due to loss of nesting habitat. Its use of mature, live pines for nesting and roosting cavities is well known (Jackson et al. 1979). The scarcity and decline of suitable pines for cavity excavation is the major reason the species was classified as endangered (Federal Register, 13 October 1970, 35, 199: 16047). Red-cockaded also use large areas of 30–100 ha and more of pine and pine-hardwood forests for foraging (Baker 1971a, Skorupa and McFarlane 1976, Wood 1977, Nesbitt et al. 1978, Sherrill and Case 1980, Hooper pers. obs., G. W. Wood pers. comm.). Because of the extensive areas used for foraging and the fact that forest management continually alters foraging habitats, information on the species' foraging behavior is critical to its management and prospects for survival.

We report year-round observations made on foraging Red-cockaded in coastal South Carolina. Prior to our work, Ligon (1968) studied foraging behavior of the Red-cockaded in Florida, and Morse (1972) looked at foraging during winter in Louisiana. Contemporaneously with our study, Skorupa (1979) and Ramey (1980) examined year-round foraging behavior in South Carolina and in Mississippi and South Carolina, respectively.

METHODS

Study area.—The study was conducted on the Francis Marion National Forest, Berkeley County, in coastal South Carolina. This area was chosen because of its large population of Red-cockaded Woodpeckers, an indication of good habitat. Oscar Stewart (pers. comm.) estimates at least 400 breeding groups on about 64,000 ha of habitat. Hooper (pers. obs.) found 22 groups on 1,000 ha, the most dense population thus far examined. The study area was also chosen for its diversity of habitat. Pine stands were interspersed with mixed stands of gum (*Nyssa* spp.), cypress (*Taxodium* spp.), oaks (*Quercus* spp.), red maple (*Acer rubrum*), and other species. Loblolly (*Pinus taeda*) and longleaf (*P. palustris*) were the most common pines. Since 1944, the pine stands have been periodically control burned; they have been under even-age timber management since 1950. Ages of pine stands ranged from less than 1 to 100 yr.

Sampling of foraging behavior.—From early May 1976 to mid-March 1977 we quantified foraging

behavior of 6 adult females, 6 breeding males, and 3 adult helper males in 6 separate groups. Red-cockaded groups are family units consisting of a mated pair, their offspring of the year, and, in some groups, auxiliary adult male helpers. All birds were uniquely marked with colored plastic leg bands. Although four of the groups had juvenile birds during at least part of the study period, we collected data only on adults. Red-cockaded birds with little or no human contact respond to human presence and act wildly. The birds we studied were conditioned by periodic exposure to humans, however, and we do not believe our presence affected foraging behavior.

An electronic metronome, modified from Wiens et al. (1970), giving an audible tone each minute, was used to determine a possible instant for recording foraging behavior. Recordings were seldom made every minute for any extended period, because movement of the birds created problems in identifying bands. Red-cockaded birds commonly foraged at several sites on the same tree and changed both foraging height and method as they moved over the tree. Direct contact was temporarily lost with specific birds when we measured foraging heights and tree diameters. Also, foraging was frequently interrupted by other behavior, and considerable time was involved merely in following and maintaining contact with the birds. If we had identified a bird and could judge its activity at the tone, we recorded the following: (1) foraging method, (2) foraging site, (3) foraging height measured with range finder and clinometer, (4) tree species, (5) tree condition, and (6) tree diameter at breast height (dbh, 1.4 m) measured with a caliper. A total of 3,172 observations was made on 69 different days. An average of 17 and maximum of 81 observations per bird were made per day. A group was followed for several hours each day, and observations were spread throughout the period.

Analyses.—Because several observations were made of the same bird on a given day, we cannot assume all observations to be independent. Consequently, only subsets of observations assumed to be independent were used for statistical comparisons. The subsets of observations assumed to be independent were derived as follows. Table 1 and Fig. 1 are based on one foraging observation for each individual tree used for foraging (about 50% of the total observations). Subsequent or additional foraging observations from the same tree are not included. Chi-square tests were made on numerical values, not the percentages shown in Table 1 and Fig. 1. Data in Table 2, and associated comparisons on foraging heights and diameters made in the text, were derived by randomly selecting one observation for a male and one for a female for each of the 69 sample days (about 4% of the total observations). Because such data are commonly treated as independent observations, we made χ^2 and *t*-tests on these data in numerical form. Cells with zero entries were deleted for χ^2 tests. Division of the total observations for other comparisons results in samples too small to compare reliably with the χ^2 test. Thus, in Figs. 2, 3, and 4 and Tables 3, 4, and 5 and for some means in the text, we included our total observations and presented the frequency data without statistical comparisons.

We calculated overlap in foraging behavior of males and females with Schoener's (1970) equation:

$$\% \text{ overlap} = 100(1 - 0.5 \sum |P_{x,i} - P_{y,i}|),$$

where $P_{x,i}$ and $P_{y,i}$ are the respective frequencies for males and females in each class for a given type of behavior. An overlap of 100% indicates that the sexes acted identically in regard to the type of behavior examined, whereas 0% overlap indicates completely different behavior.

General observations.—From May 1976 to April 1979, we followed the activity of birds in 18 different groups (6/yr) for 2,300 h. These observations served as a check on the validity of our sampling of apparently rare foraging behavior, e.g. use of hardwoods, fruit, and water.

Tree availability.—We determined the density of trees within the six territories used for the quantitative study. Vegetation was stratified into stands of similar species composition, age, and density. Depending on stand size, 3–20 plot centers were located systematically from a random starting point. At each plot center, stems equal to or greater than 3 to less than 13 cm dbh were recorded by species and dbh on a 0.02-ha plot. Stems equal to or greater than 13 cm dbh were sampled with a 1-m factor wedge prism. Trees selected by the prism were recorded by dbh and species. Availability values in Table 1 and Fig. 1 were adjusted by multiplying the number of stems for each diameter class or tree type in a territory by the proportion of foraging observations made in the territory.

RESULTS

Comparison of breeding and helper males.—Two groups we studied had helper males in addition to breeding males. A comparison of breeding and helper males showed nearly identical foraging behavior. The mean sizes of live pines selected by

TABLE 1. Types of trees (≥ 13 cm dbh) used by foraging Red-cockaded Woodpeckers and availability of trees (≥ 13 cm dbh) in the territories, May 1976–March 1977.

Sex	n	Pine		Hardwood		Cypress
		Live	Dead	Live	Dead	Live
<i>Percent of stems selected^a</i>						
Female	944	96.0	3.4	0.3	0.0	0.2
Male	756	96.0	2.9	0.9	0.0	0.1
<i>Percent of stems available^b</i>						
	21,861 ^c	71.3	2.8	24.6	0.4	1.9

^a No significant difference in the frequency with which males and females foraged on live and dead pines ($\chi^2 = 0.3$, $P > 0.50$). Overlap in use of tree types by sexes = 99%.

^b Sexes pooled, dead hardwoods and cypress excluded: the frequency with which tree types were selected differed significantly from the availability of tree types ($\chi^2 = 584.7$, $P < 0.0001$).

^c Value is adjusted n , see text. Actual estimate of total number of stems in the six territories was 143,157.

breeders and helpers were 28.1 cm ($n = 172$) and 28.3 cm ($n = 108$), respectively. Foraging heights were 13.9 m and 14.3 m for breeders and helpers. Use of sites on live pines for breeders and helpers were: limbs = 58% and 58%; trunk-in-crown = 27% and 28%; mid-trunk = 13% and 12%; lower trunk = 2% and 2%. We thus lumped data on breeding and helper males in all the following comparisons.

Trees selected for foraging.—Red-cockaded showed a strong preference for living pines as a foraging substrate (Table 1). Although there were only 3 times more live pines than live hardwoods within the territories, pines were selected 163 times more frequently than hardwoods. If observations made after the quantitative study are included, Red-cockaded foraged 18 times on oaks, 7 on gum, and 2 on sweetgum (*Liquidambar styraciflua*). Cypress was rarely foraged upon by the six groups in the quantitative study (Table 1). Later, for 140 h, we followed a group that spent about 12% of its foraging time on cypress. That group had considerably less pine available than groups we observed during the quantitative study.

Males and females foraged on living pines with similar mean diameters of 29.5 cm and 29.8 cm, respectively ($df = 136$, $t = 0.2$, $P > 0.5$). There was no difference in the frequency with which tree sizes were used by the sexes (Fig. 1). Both sexes showed a strong preference for pines greater than 23 cm dbh and avoidance of pines less than 13 cm (Fig. 1). Red-cockaded generally avoided stands of trees with diameters less than 11 cm and foraged on trees of that size mostly in stands of larger trees.

The next most frequently used trees were dying or recently dead pines, most of which had been struck by lightning (Table 1). Most of these trees still had dead needles and bark. Dead pines with extensively exposed wood were avoided, except once when three birds foraged on a long-dead pine that had only 50% of its bark. The frequency of use of live and dead pines was similar for males and females (Table 1).

Foraging sites.—Combining all seasons or sampling periods, we found that males and females foraged at different sites on live pines with strikingly different frequencies (Table 2). Males spent a major part of their foraging time (58%) in the crown and generally avoided the lower trunk, where females did 38% of their foraging. Although both sexes used the midtrunk frequently (males, 39% of the time; females, 32%), each tended to select different specific foraging sites within that zone. Males foraged more on limbs (28%) than on the trunk (12%), while females foraged more

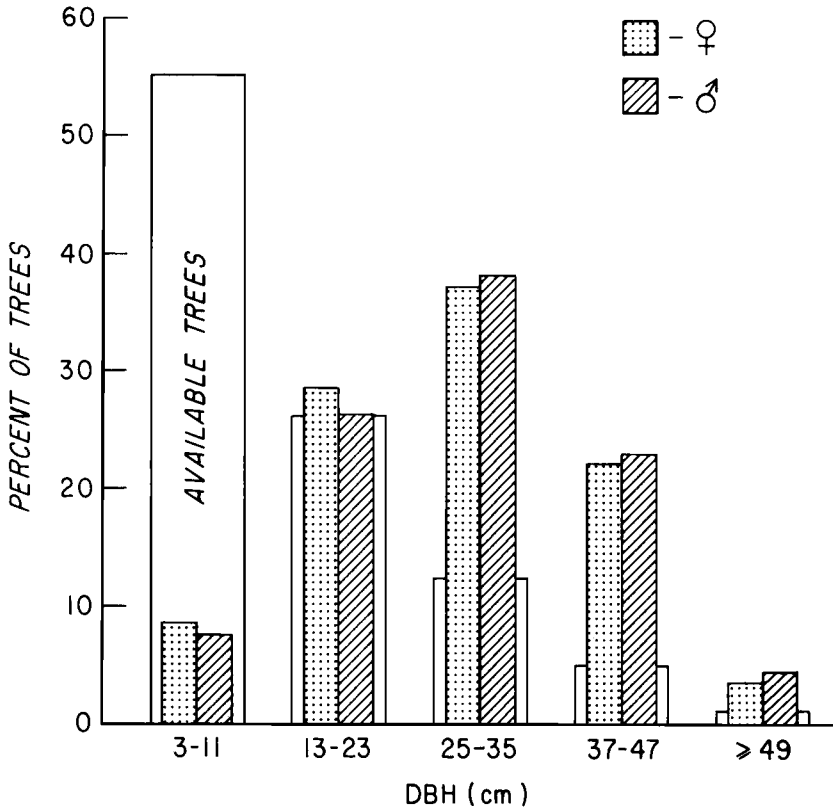


Fig. 1. Diameter (dbh) classes of live pines used by foraging Red-cockaded Woodpeckers compared to availability of diameters in the territories. By diameter class, there was no significant difference in the frequency with which males and females used trees of different sizes ($\chi^2 = 2.8$, $P > 0.5$). Sexes combined, the frequency with which trees were used, by diameter classes, differed significantly from the availability of trees within diameter classes ($\chi^2 = 2,758.6$, $P < 0.0001$); $n_{\text{males}} = 726$, $n_{\text{females}} = 906$. Overlap in use of tree diameters by sexes = 97%.

on the trunk (29%) than on limbs (3%). Females spent time within the crown (28%), but their foraging activities, as at the midtrunk zone, were primarily on the trunk. In contrast, males, when foraging in the crown, spent 45% of their time on limbs. The differential use of limbs and trunk by the sexes is more striking when observations of the crown, midtrunk, and lower trunk are combined. While males divided their foraging almost equally between limbs (46%) and the trunk (54%), females restricted their foraging almost exclusively to the trunk (94%).

Partitioning of foraging sites by the sexes was reflected in their relative foraging heights. On live pines males foraged at a mean height of 14.1 m and females at 8.7 m. Thus, the sexes were separated by a mean vertical distance of 5.4 m ($df = 136$, $t = 4.9$, $P < 0.001$). The range in foraging heights overlapped substantially, because both sexes used the same sites but at different frequencies. Females foraged from near ground level on the lower trunk to 29 m into the crown. Males foraged between 1 and 37 m. Occasionally females foraged higher than males, even when they were on the same tree. The foraging heights of females were skewed toward the lower height classes, but those of males were more symmetrically distributed about the mean (Fig. 2).

TABLE 2. Methods and sites used on live pines by foraging Red-cockaded Woodpeckers, May 1976–March 1977. Data (percentage of n) are from one randomly selected observation per day for each sex from 3,054 observations collected on 69 days ($n_{\text{males}} = 69$, $n_{\text{females}} = 69$).

Site	Method								Site total ^a	
	Probe		Excavate		Scale		Glean			
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Crown										
Trunk	17.4	10.1	0.0	5.8	14.5	11.6	0.0	0.0	31.9	27.5
Live limbs	8.7	1.4	2.9	0.0	2.9	0.0	1.4	0.0	15.9	1.4
Dead limbs	1.4	0.0	8.7	0.0	0.0	0.0	0.0	0.0	10.1	0.0
Cones	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	1.4
Midtrunk										
Trunk	7.3	15.9	1.4	7.3	2.9	4.4	0.0	1.4	11.6	29.0
Live limbs	0.0	2.9	0.0	0.0	2.9	0.0	0.0	0.0	2.9	2.9
Dead limbs	4.4	0.0	20.3	0.0	0.0	0.0	0.0	0.0	24.7	0.0
Lower trunk										
Trunk	1.4	14.5	1.4	17.4	0.0	5.8	0.0	0.0	2.8	37.7
Method totals ^b	40.6	44.8	34.7	31.9	23.2	21.8	1.4	1.4	99.9	99.9

^a Significant difference in frequency with which males and females used sites ($\chi^2 = 30.9$, 5 df, $P < 0.005$). Overlap in use of sites by sexes = 46%.

^b No significant difference in frequency with which males and females used methods ($\chi^2 = 0.3$, 2 df, $P > 0.75$). Overlap in use of methods by sexes = 96%.

Within each sampling period, males and females differed in the frequencies with which they used sites on live pines (Fig. 3). Primary foraging sites for males in all periods were live and dead limbs and the trunk-in-crown. Females foraged primarily on the trunk, making negligible use of limbs. The lower trunk, a major foraging site for females, was usually avoided by males. The midtrunk and trunk-in-crown were important sites for both sexes and are the only two sites where there was considerable overlap in foraging activity between the sexes. The period of least overlap, or greatest separation of the sexes, was January–March (Fig. 3). During that period, females spent most of their foraging time (61%) on the lower trunk and only 12% of the time in the crown. In contrast, males spent most of their foraging time in the crown (57%) and on the midtrunk (42%) and little time on the lower trunk (2%). The greater separation of the sexes during January–March was also apparent in mean foraging heights. During January–March, females foraged lower ($\bar{x} = 5.1$ m) than in May–August ($\bar{x} = 8.1$ m) and September–December ($\bar{x} = 8.0$ m). Mean foraging heights of males differed little throughout the year (12.5 m, January–March; 13.2 m, May–August; and 12.7 m, September–December).

Within each sex, the frequency of foraging at sites on live pines varied between sampling periods (Fig. 3). Between periods, males varied the most in the frequencies with which they foraged on dead limbs, live limbs, and the trunk-in-crown. Between periods, females varied most in the frequencies with which they used the lower trunk and trunk-in-crown. The lower trunk was the principal foraging site for females during January–March and May–August. During September–December, however, the lower trunk received the least use, except for limbs, and the trunk-in-crown received the most use.

Both sexes avoided green loblolly cones. Males were seen on green longleaf cones nine times and females five times. Our general observations suggest that in some years both sexes made greater use of green cones. We suspect that birds were preying on coneworms (*Dioryctria* spp.).

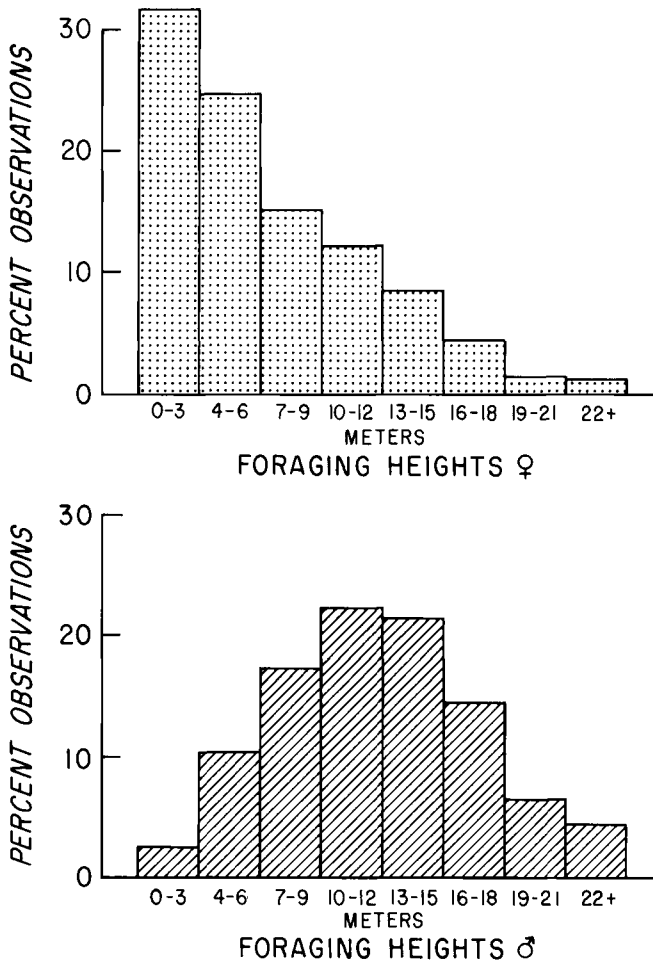


Fig. 2. Foraging heights of male and female Red-cockaded Woodpeckers on live pines, May–March; $n_{\text{males}} = 1,317$, $n_{\text{females}} = 1,737$. Overlap in foraging heights of sexes = 56%.

Males and females also differed in the frequency with which foraging sites on dead pines were used (Table 3). Their partitioning of sites on dead pines was similar to that on live pines, females using the lower and midtrunk more than males and males using the trunk-in-crown and limbs more.

During the quantitative study we did not see Red-cockaded Woodpeckers forage on the ground. Later, we saw a Red-cockaded Woodpecker foraging on a gravel road and suspect it was eating ants. We saw a group forage briefly on limbs cut from longleaf pines; Ligon (1968) reported similar behavior.

Foraging methods.—The sexes used methods with equal frequency for securing prey from live pines (Table 2). Also, when foraging on dead pines, males and females used foraging methods with similar frequencies (Table 3).

Four methods were used to capture prey: probing, excavating, scaling, and gleaning. We did not see Red-cockaded Woodpeckers flycatching. When probing, the birds hopped along trunks and limbs, appeared to inspect the surface visually, then probed be-

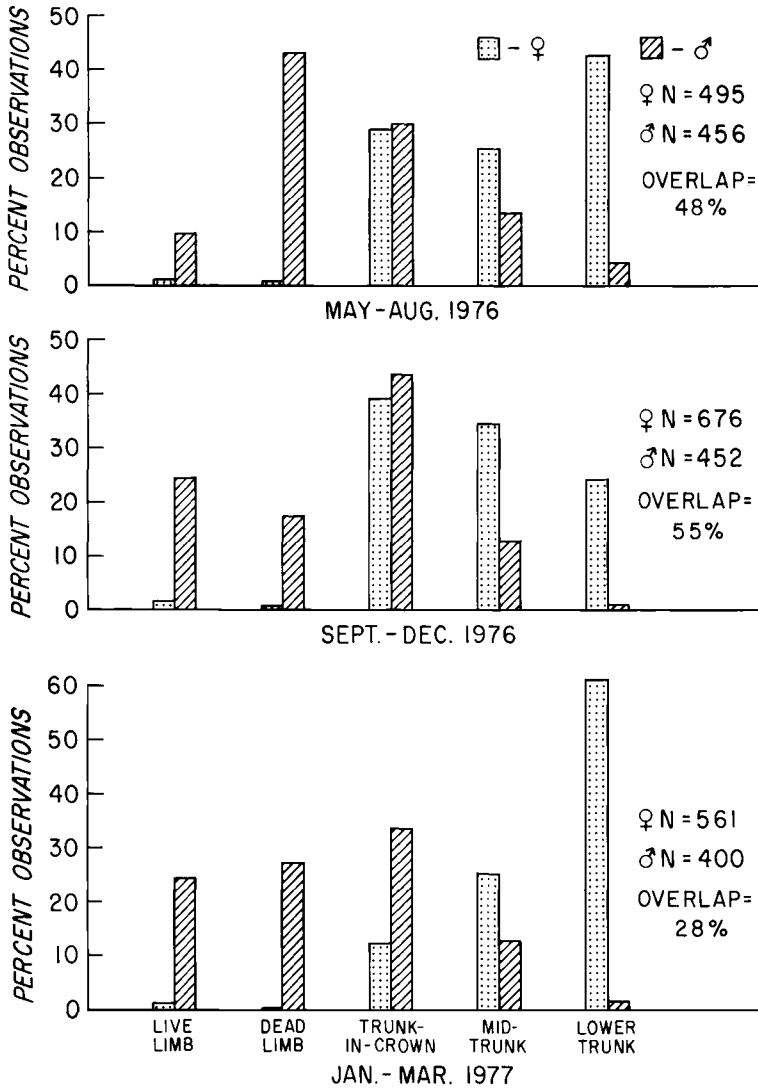


Fig. 3. Intersexual use of foraging sites on live pines by Red-cockaded Woodpeckers in different periods.

TABLE 3. Foraging activity of Red-cockaded Woodpeckers on dead pines, May 1976–March 1977.

Sex	n	Method (% of n) ^a			Site (% of n) ^b			
		Excavate	Probe	Scale	Limb	Trunk-in-crown	Mid-trunk	Lower trunk
Female	56	48.2	42.9	8.9	0.0	21.4	44.6	33.9
Male	41	56.1	36.6	7.3	22.0	41.5	17.1	19.5

^a Overlap in use of sites by sexes = 50%.

^b Overlap in use of methods by sexes = 92%.

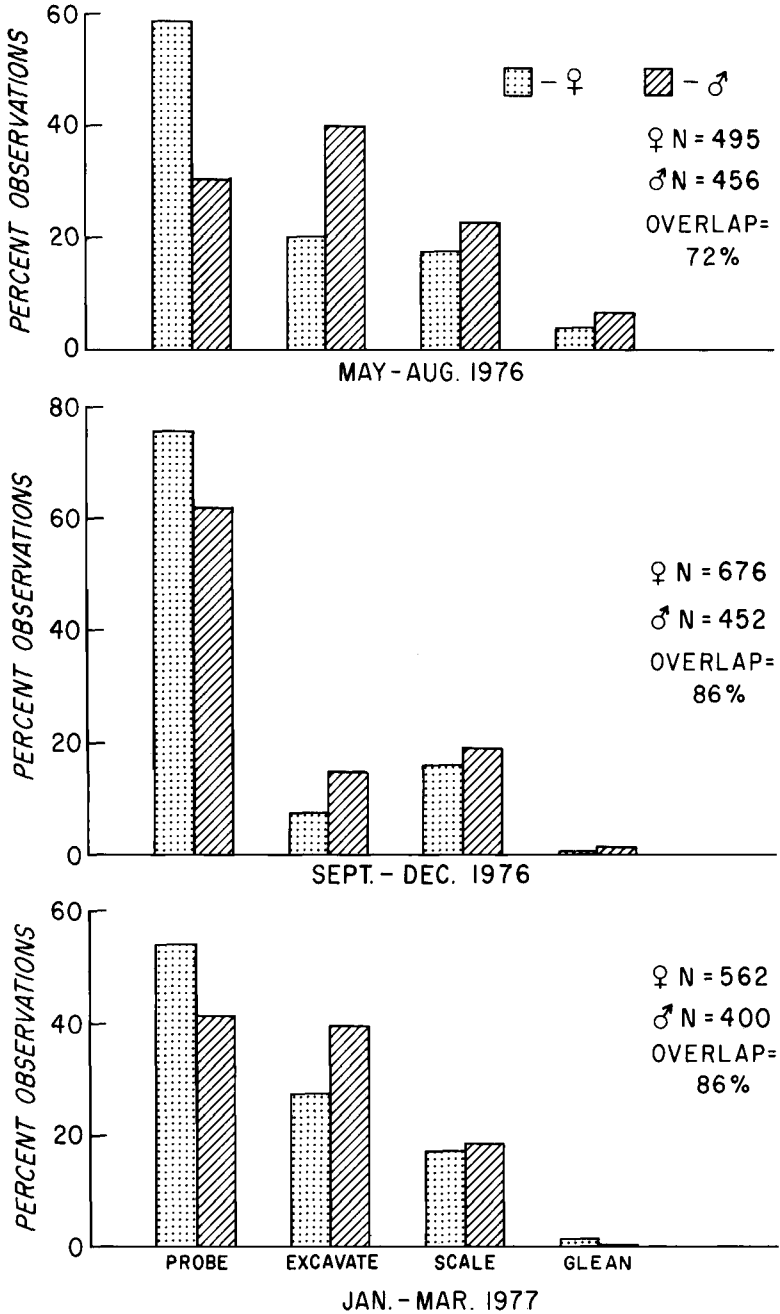


Fig. 4. Foraging methods used by male and female Red-cockaded Woodpeckers on live pines in different periods.

tween bark plates with their bills. Compared to scaling, only small amounts of bark were removed by probing. When probing, birds seemed to cover a larger area of foraging substrate per unit of time than when other methods were used. Year-round, probing was the most frequently used method of both sexes on live pines (Table 2)

TABLE 4. Relative use (percentages of *n*) of foraging methods by Red-cockaded Woodpeckers at foraging sites on live pines, May 1976–March 1977. Only sites receiving major use are considered.

Foraging method	Male			Female		
	May–August	September–December	January–March	May–August	September–December	January–March
	<i>Trunk-in-crown</i>					
Scale	48.9	28.8	23.7	32.2	23.4	32.4
Probe	35.8	61.6	60.7	49.6	68.7	52.9
Excavate	11.7	7.1	14.8	17.5	7.2	14.7
Glean	3.6	2.5	0.7	0.7	0.7	0
<i>n</i>	137	198	135	143	265	68
	<i>Midtrunk</i>					
Scale	42.6	8.6	21.6	15.7	15.4	31.2
Probe	41.0	82.8	51.0	61.4	77.2	51.8
Excavate	11.5	8.6	27.4	20.5	7.3	16.3
Glean	4.9	0	0	2.4	0	0.7
<i>n</i>	61	58	51	127	233	141
	<i>Live limbs</i>			<i>Lower trunk</i>		
Scale	18.6	21.6	31.6	8.3	3.0	7.0
Probe	46.5	71.2	46.9	63.4	87.2	56.4
Excavate	4.6	6.3	21.4	20.8	8.5	34.6
Glean	30.2	0.9	0	7.4	1.2	2.0
<i>n</i>	43	111	98	216	164	344
	<i>Dead limbs</i>					
Scale	0	0	0			
Probe	18.5	32.5	5.5			
Excavate	79.0	67.5	94.5			
Glean	2.6	0	0			
<i>n</i>	195	80	109			

and the second most used method on dead pines (Table 3). Red-cockaded excavated in order to expose subsurface arthropods and eggs in bark and dead wood. On live pines, males and females excavated with near equal frequency, and it was the second most used method year-round (Table 2). On dead pines, excavation was the primary method used by both sexes (Table 3). Scaling involved concentrated removal of superficial flakes of bark with the bill. Both sexes scaled with nearly equal frequencies (Tables 2 and 3) and rarely gleaned prey from the surface of the bark without first scaling.

Within each sampling period, the sexes overlapped considerably when foraging on live pines in the frequencies with which methods were used (Fig. 4). Observed differences in seasonal use of methods were not of the magnitude found in similar comparisons of seasonal use of foraging sites (Fig. 3). Males and females tended to use methods with similar frequencies at the two sites they both used regularly (Tables 4 and 5).

At foraging sites receiving major use, there were differences between sampling

TABLE 5. Percentage overlap in methods used by foraging male and female Red-cockaded Woodpeckers at two sites on live pines used frequently by both sexes. See Table 4 for frequencies.

Site	May–August	September–December	January–March
Midtrunk	80	93	89
Trunk-in-crown	71	93	91

periods in the frequencies with which both sexes used the four methods for capturing prey (Table 4). For example, when on the midtrunk, males scaled five times more often during May–August than during September–December (Table 4). Females were as variable as males. For example, when on the lower trunk, females excavated four times more often during January–March than during September–December (Table 4).

Use of vegetable matter.—We saw Red-cockadedes take fruit only once during the quantitative study. Including other observations, we saw 17 cases of Red-cockadedes feeding on fruits and seeds: wax myrtle (*Myrica cerifera*), 7 times; blueberry (*Vaccinium* spp.), 4; longleaf pine, 3; sweetbay (*Magnolia virginiana*), 2; and poison ivy (*Rhus radicans*), 1. Both wax myrtle and blueberry produced abundant fruit in 1976–1978. Longleaf pine is a sporadic seed producer, with good crops about 5–7 yr apart (Wahlenberg 1946: 72). Seed yield was light during 1976–1978. Loblolly pine is a more consistent seed producer and had good yields in 1976–1977 but a light yield in 1978 (O. Gordon Langdon, pers. comm.). We did not see Red-cockadedes foraging on loblolly seeds.

Use of water.—We observed 14 cases of Red-cockadedes drinking water. On four occasions Red-cockadedes drank from hollows in hardwood trees and on one occasion from one of their flooded cavities. Birds drank water from puddles on the ground on seven occasions. In one case the birds were perched on the base of a tree, but in the others they stood on the ground. When drinking from the ground, both males and females would back down a tree trunk and step off onto the ground. Twice we saw birds licking dew from pine needles. Drinking was observed from October to April, with nine of the cases in November and December. During the hottest part of the year, 28 June–8 September, we followed groups for 9 full days and 53 partial days and did not see the birds drink. Water was probably available to the groups year-round, and it is possible that birds, on occasion, drank without being detected.

Interspecific conflicts.—Overt interspecific conflicts at foraging sites appeared to be rare. Red-cockadedes supplanted Downy Woodpeckers (*Picoides pubescens*) four times from foraging perches and were in turn supplanted once. Red-bellied Woodpeckers (*Melanerpes carolinus*) supplanted Red-cockadedes seven times. A Red-cockadede was supplanted once by a Red-headed Woodpecker (*M. erythrocephalus*). Yellow-bellied Sapsuckers (*Sphyrapicus varius*) were supplanted six times by Red-cockadedes and in turn supplanted a Red-cockadede once. One Brown-headed Nuthatch (*Sitta pusilla*) was supplanted by a Red-cockadede. Some of these interactions may have been harassment not associated with foraging competition. In only one case did a Red-bellied Woodpecker forage at the usurped site. Another time the Red-bellied examined the site for a few seconds and then left, and the Red-cockadedes returned and resumed foraging. Red-cockadedes foraged at half the sites usurped from Downy Woodpeckers.

Intersexual conflicts.—Conflicts between adult members of Red-cockadede groups at foraging sites were rarely seen. Males and females commonly foraged close together on the trunk or passed each other with no overt aggression or other discernible interaction. The one case of intersexual conflict that might be related to foraging sites occurred when a breeding female, foraging on a limb in the crown, was jabbed and supplanted by her mate. Agonistic behavior among juveniles was fairly common. We saw adults take over the foraging sites of juveniles, but it was more common to see adults yield sites to juveniles with no overt signs of aggression.

DISCUSSION

Tree selection.—The Red-cockadedes we studied foraged almost exclusively on live pines. Birds did not avoid stands with a high percentage of hardwood trees, but in such areas they foraged on scattered pines. Other workers have not compared the frequency to the availability of trees foraged upon by Red-cockadedes, but they have reported extensive use of live pines in Florida (Ligon 1968, 1970; Nesbitt et al. 1978), Louisiana (Morse 1972), Oklahoma (Wood 1977), Virginia (Miller 1978), Mississippi (Ramey 1980), and South Carolina (Skorupa and McFarlane 1976; Skorupa 1979, Ramey 1980; G. W. Wood pers. comm.). Some use of hardwoods was reported by the above workers, except Nesbitt et al. (1978). Skorupa and McFarlane (1976) found exclusive use of pine in summer but 10% use of hardwoods in winter. Wood (1977) reported about 15% use of hardwoods, and Miller (1978) 4% use. Skorupa (1979) reported that only males foraged on hardwoods, 1% in summer and 3% in winter. In Mississippi Ramey (1980) reported 22% use of hardwoods by males but only 6% use by females, and in South Carolina the percentages were 12 and 1, respectively.

The major departure from foraging on live pines, albeit small, was in the use of recently dead or dying pines. Ligon (1970), Baker (1971b), Nesbitt et al. (1978), and G. W. Wood (pers. comm.) have also reported use of recently dead pines. We overestimated the availability of dead pines suitable for foraging because unsuitable pines were included in the vegetation sample. Thus, selection for recently dead pines was probably strong, even though little use was made of them compared to live pines.

A group that occupied a territory from which much of the pine had been cut spent about 12% of their foraging time on cypress. While this seems to indicate some adaptability in the selection of foraging habitats, the data from groups that had the opportunity to forage on pine or other species indicated a clear preference for pines.

We found that Red-cockaded foraging on larger pines was disproportionate to the quantity available. Skorupa (1979) obtained similar results. Preference for larger trees could indicate more (or different) food per unit area because of thicker, more fissured bark and larger dead limbs. Use of larger trees might also be energy conservative in that more foraging area per tree could reduce time spent flying between trees.

Use of vegetable matter.—We saw very little use of fruit and seeds by Red-cockadedes. In the same study area Harlow and Lennartz (1977) likewise did not observe fruits and seeds being brought to nestlings. Beal et al. (1941), however, collected 99 stomachs representative of every month and found 14% of the diet to be vegetable matter. Pine seeds were found in 45% of the stomachs, constituting the major portion of the plant material.

Red-cockadedes we studied excavated green longleaf cones, presumably for larvae, but we never saw them on loblolly cones. The birds perched directly on longleaf cones when excavating for insects and when taking seeds; thus, the size of the cone may have influenced its use. Longleaf cones are 15–25 cm long, but loblolly cones are only 5–13 cm long. Perhaps Beal et al. (1941) collected stomachs during good seed years, and we might have seen greater use of pine seeds under similar conditions. Morse (1972), however, did not see Red-cockadedes make regular use of an unusually heavy longleaf seed crop, and one stomach contained only arthropods. Ramey (1980) saw only minor use of cones. Baker (1971b) reported that Red-cock-

adedes fed heavily on wild cherry (*Prunus serotina*) and wax myrtle. Our study area had almost no wild cherry. Wax myrtle was common and had good fruit yields but received little use. Blueberry had abundant yields and was common but likewise received little use. It appears that Red-cockadedes, on some occasions, make considerable use of fruit and seeds (Beal et al. 1941, Baker 1971b), yet on other occasions use is casual, even when mast is common (Morse 1972, this study). It seems possible that use of mast could be related to the relative abundance of arthropods.

Intersexual foraging differences.—Divergent foraging behavior between sexes has been reported for most North American *Picoides*: Hairy (*villosus*) (Kisiel 1972, others), Downy (Williams 1975, others), White-headed (*albolarvatus*) (Koch et al. 1970, but not Ligon 1973), Strickland's (*stricklandi*) (Winkler 1979, others), Nuttall's (*nuttallii*) (Jenkins 1979), Ladder-backed (*scalaris*) (Austin 1976, others), Red-cockaded (Ligon 1968, Skorupa 1979, Ramey 1980, but not Morse 1972), and Northern Three-toed (*tridactylus*) (Massey and Wygant 1954, but not Short 1974). No sexual difference in foraging was reported for Black-backed Three-toed (*arcticus*) (Short 1974).

Ligon (1968) found intersexual foraging differences in the Red-cockaded in Florida. Obtaining results similar to those of our study, he found that males foraged mainly on limbs and upper trunk of pines, while females foraged mainly on the lower trunk and, to a lesser extent, the upper trunk. Ramey (1980) reported similar partitioning of pine trees by Red-cockadedes in Mississippi. Working on an area in South Carolina where young trees predominated, Skorupa (1979) and Ramey (1980) found that females made greater use of limbs (9 and 15%, respectively) than in Mississippi (4%) or in our study (4%), where mature trees predominated. In addition, they found that females used the trunk above limbs more than the trunk below limbs, contrary to the Mississippi data and our study. In Louisiana, Morse (1972) reported no sexual differences in foraging behavior in winter. Unfortunately, Morse's data are inconclusive because he did not use banded birds, and Red-cockadedes cannot be sexed out-of-hand. Also, several birds are usually found together. Two birds in relatively close proximity are frequently an adult-juvenile combination or two adult males and not necessarily an adult male-female pair, as assumed by Morse. It appeared to Miller (1978) that there were no intersexual differences in foraging behavior of Red-cockadedes in Virginia. He pointed out, however, the limitations of his data due to his inability to sex unmarked birds consistently. Beckett (1971) reported no difference in feeding sites of the sexes in South Carolina but did not present data.

In our study area, male and female Red-cockadedes clearly exhibited divergent foraging behavior. Differential use of foraging sites, especially the limited use of limbs by females and the limited use of the lower trunk by males, appeared to be the most important factor in the sexual partitioning of foraging habitat. It is possible that selection of foraging sites was predetermined by the observed vertical stratification of males and females. Evidence against this hypothesis, however, is provided by Ramey (1980). She found that Red-cockadedes foraging in young habitat averaged only 1.2 m difference in foraging heights of males and females but that they still maintained a significantly different intersexual use of sites. We found little evidence of intersexual partitioning of foraging resources by the methods that were used for capturing prey. These results are similar to those of Ramey (1980).

Significance of divergent foraging behavior.—Intersexual foraging differences ap-

pear to be widespread among woodpeckers. The most frequently cited presumed advantages of this adaptive behavior are a reduction in intraspecific competition for food and concomitant reduction in intersexual aggression (Selander 1966, Ligon 1968, Wallace 1974, Jackson 1970, Hogstad 1978, others). These adaptive advantages may be of major significance to the Red-cockaded. This species is a cooperative breeder, and a group of 2–9 birds maintains a mutual all-purpose territory throughout the year. Group members forage together, and they cooperate in such activities as incubation, feeding nestlings and fledglings (Lennartz and Harlow 1979), excavating cavities, and territorial defense. In their daily activities, group members maintain close contact. As suggested by Wallace (1974) for other species, sexual partitioning of the foraging resource is possibly one mechanism facilitating the social organization of the Red-cockaded by reducing intersexual aggression and competition.

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