

BEHAVIOR AND BREEDING BIOLOGY OF THE RED-COCKADED WOODPECKER

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THE Red-cockaded Woodpecker (*Dendrocopos borealis*) is one of the least studied North American members of its family. Although its overall range, from the southeastern Atlantic Coast to Oklahoma and Texas, is not small, it is almost entirely confined to areas where open pine forests predominate.

Many North American species with strict habitat requirements are in jeopardy as a result of modern man's activities. This woodpecker is no exception. The open pine forests it requires have been reduced by logging and the clearing of land for pastures. Further, fire, necessary for the maintenance of the open pinelands (Odum, 1959: 138), has been virtually excluded in much of the southern United States. Today the Red-cockaded Woodpecker is declining in parts of its range (Sprunt and Chamberlain, 1949; Burleigh, 1958) and even is thought by some to be a rare or endangered species (D. W. Lay, in litt.; Steirly, 1957).

STUDY SITES AND METHODS

I located several groups of Red-cockaded Woodpeckers near Gainesville, Alachua County, Florida, between early May and December 1962, and watched them frequently at irregular intervals from 4 May 1962 to 11 August 1963. I revisited the study sites briefly in June 1966 and December 1968. Observations totaling over 240 hours were made throughout the year, but were concentrated during the breeding season.

The study areas were at the east edge of Gainesville, on state lands managed in part by the Sunland Training Center (six groups of woodpeckers) and 2 miles east of Orange Heights, Florida (one group). Two groups near Waldo, Florida, also were observed on a few occasions. Habitat consisted primarily of second-growth longleaf pine (*Pinus palustris*) with a ground cover of palmetto (*Serenoa*) and grasses (Figure 1). In damp, poorly drained areas, slash pine (*P. elliottii*) was present, but it was not used extensively by the woodpeckers.

These woodpeckers are known to be gregarious at times, foraging in groups composed of several adults (Murphey, 1939). Six of the eight groups that I studied consisted of only a pair, while two groups had additional adults (one and three). As the sexes are virtually indistinguishable in the field, 16 were captured by frightening them from the roost cavity into a clear plastic bag and marked with airplane dope or colored leg bands. Sex was determined by presence or absence of cockades in adults and presence or absence of crown patch in juveniles. Statements concerning individuals and generalities about the behavior of each sex are in all cases based on observations of marked birds.

I investigated cavities with a small mirror and flashlight, and removed young from nests with a noose arrangement made of nylon leader attached to a sturdy wire. Chicks from five nests were weighed periodically for the first half of their

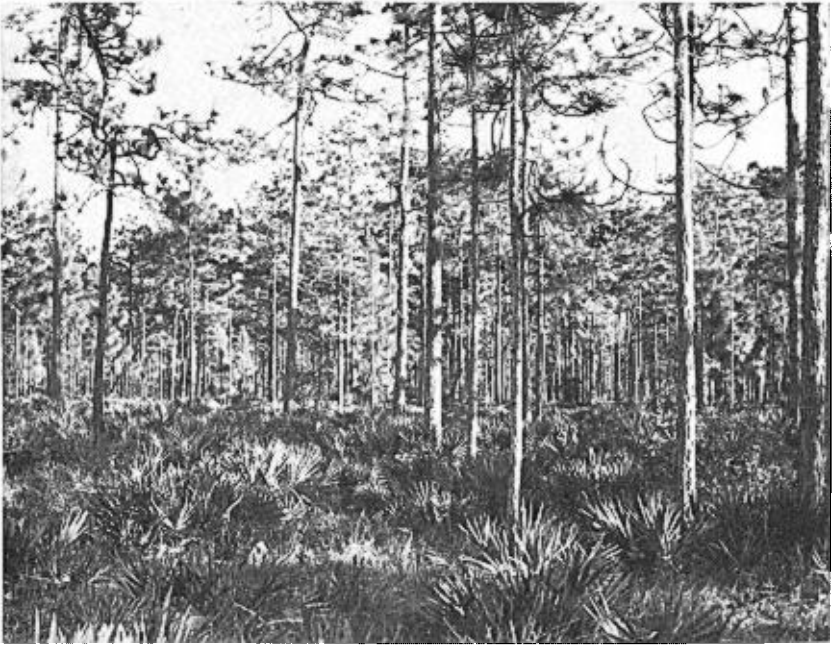


Figure 1. Open pine woodland near Gainesville, Alachua County, Florida. Photographed in December 1968.

nestling lives to the nearest tenth of a gram. Except for one bird weighed throughout its nest life, I stopped removing chicks from the nest after 13–18 days to avoid damage to the growing feathers.

I watched the first pair of woodpeckers that I located much more frequently than other groups. These are designated throughout this report as pair A (male A, female A, and a single female fledgling, juvenile A).

COMMUNICATIONS

Vocalizations.—These woodpeckers have an extensive vocal repertoire. Both sexes give most or all the calls described. Calls are phoneticized here and their significance, when known, is indicated. Most of these were heard many times, but I recorded a few only once.

(1) “Szrek” or “shrit.” A note indicative of low level excitement. The most commonly heard call, it is given when the birds are disturbed, as by man.

(2) “Whu-whu.” Soft notes uttered when the birds are calm and feeding near others of their group.

(3) “She-u,” “che-u,” or “whe-u.” A rapidly repeated call indicative of high excitement, given by adults when another Red-cockaded Woodpecker enters their territory. It is often accompanied by the open wing display (see below) and highly erratic corkscrew flight patterns.

(4) “Wic-a wic-a.” Another call indicative of excitement. It was once given by male A, as he called to the female while defending the nest cavity from a Red-bellied Woodpecker (*Centurus carolinus*).

(5) *Kingfisher-like rattle.* Given once by female A as she flew at high speed toward the nest.

(6) "Shurz-u." A soft note given when a hawk flew overhead. It apparently was a warning signal.

(7) "Churt." A deliberate note, given at intervals of 2-3 seconds as the bird flies to the nest or roost. It can sometimes be heard for many seconds before the woodpecker comes into sight. It was more often given by females.

(8) "Chit." A single low note given by a woodpecker being chased persistently by pair A whose territory it invaded.

(9) "Zrip." A soft note given near the cavity shortly before going to roost.

(10) "Deedle-deedle." A rarely given call, heard as the bird hovers before the entrance to the roost cavity just before entering for the night.

(11) "Wa-a-a" or "whe-he-he." A soft, barely audible begging note, given by recently fledged young when approached by an adult. Adults appear to be highly agitated when the young fledge and this note may suppress hostile behavior on the part of the parent.

(12) "Ruh-uh-uh-uh." Hunger calls of young nestlings. This call begins to change when they are about 11 days old.

(13) "Whew-whew." Loud demanding notes of fledged young for food. This is often given alternately with soft begging calls.

Drumming.—Drumming is apparently a less important means of communication in this species than in many other woodpeckers. This is in part because the habitat provides few structures with loud resonating qualities, such as a dead, hardened limb. I have seen drumming only when woodpeckers were perched on living pine trunks; their efforts did not produce a loud noise. Nevertheless, the functions of drumming appear to be similar to those of other species of woodpeckers, i.e. expressing excitement or establishing territorial rights. Both sexes of one pair drummed as I approached their nest. An intruder into a territory will sometimes drum, causing the owners to become greatly excited and to drum in response. A female that had recently mated with a male that had been established for a long period of time drummed repeatedly at different points in her new territory.

Wing-fluttering.—When agitated, Red-cockaded Woodpeckers make a fluttering or "galloping" sound with their wings as one bird flies to its mate.

Raised crest.—An expression of disturbance or restlessness. It may be seen while the birds are engaged in a variety of activities.

Open wing display.—Pairs of Red-cockaded Woodpeckers, when highly excited by an intruder into their territory, exhibit an impressive display of the wings that appears to serve primarily in intrapair recognition and as a pair-reinforcing mechanism. It was most often given first by the female, but either bird might initiate the display. For example, when the male had been pursuing the intruder for several minutes, the female intercepted the chase, landed on a pine trunk, gave the "she-u she-u" call, and fully extended her wings over her back (Figure 2). Her mate responded immediately by flying to her and landing below her on the vertical trunk. Thereupon both slowly extended and closed their wings several times, gave the "she-u" calls, and moved slowly up the trunk. Either or both then resumed pursuit of the intruder.

This display also was given to some extent by rivals involved in territorial conflicts. Both male and female owners extended their wings occasionally as they approached the intruder and the latter often partially extended its wings before retreating. In the Yellow-bellied Sapsucker (*Sphyrapicus varius*), and Downy (*Dendrocopos pubescens*) and Black-backed Three-toed (*Picoides arcticus*) Woodpeckers, the



Figure 2. Open wing display of a female Red-cockaded Woodpecker. Traced from a motion picture frame.

extended wings apparently serve only as a threat display (Kilham, 1962a, 1962b, 1966). Lawrence (1967: 50) illustrates the aggressive components of courtship behavior in the species she studied. The open wing display possibly also was originally entirely an aggressive action, but has been modified in this species to serve as a pair recognition or reinforcing mechanism.

ANNUAL CYCLE

The annual cycle is characterized by its uniformity. Pairs are completely sedentary after having excavated suitable roost and nest holes, unless the tree dies, they are driven away by the cutting of their trees, or by a similar calamity. Male A occupied the same tree for at least 4 years (1962-66), even though a fence was erected within a few feet of the tree and the area was converted into a park. Because of their sedentary nature the birds forage over the same trees throughout the year; an area used by these woodpeckers is often recognizable by the scaled appearance of the pines.

THE ROOST TREE AND CAVITIES

The roost tree is apparently the single most important feature in the life of the Red-cockaded Woodpecker and is a major factor influencing retention of the same territory over several years. The presence of suitable

trees for excavation may largely determine the distribution of the woodpeckers, the numbers in a group (my study area had only one bird per tree), the ability of the birds to attract and retain mates, and reproductive success. The vigorous defense of the cavity throughout the year against the larger, stronger, and more numerous Red-bellied Woodpecker is further indication of its importance.

Suitable trees may be used by several generations of woodpeckers. In December 1968 all but one of the 10 adult birds that I had banded in 1962 and 1963 were gone, but five of the same cavities were being used by Red-cockaded Woodpeckers.

Red-cockaded Woodpeckers excavate cavities in living pines that are infected with a fungal disease (*Fomes pini*) commonly known as red heart. The fungus attacks the heartwood of the tree and causes it to become soft and pithy through destruction of the cell walls (Steirly, 1957). All roost and nest trees I investigated appeared to be so infected. Red heart is said to be a disease associated with old age (Steirly, 1957) and in many areas Red-cockaded Woodpeckers are found principally in mature and over-mature pines (Steirly, 1957; D. W. Lay, in litt.). In the Gainesville area small and apparently younger pines are attacked by this fungus, as suggested by the difference in the range and mean heights of 13 holes used during this study (mean 10.0 feet, range 2.3–30.9 feet, see Table 1) and of five holes in Steirly's (1957) area in Virginia (mean 35.7 feet, range 23.6–50.0 feet). The average age of the five trees Steirly studied was 101 years, but he notes that occasionally symptoms of red heart appear in younger trees (40 years), especially those on poor sites. Most of the pines the woodpeckers used in the Gainesville area were probably about this age. Some of the smallest trees used may have been weakened by hot fires, making them susceptible to the fungus (J. V. Dennis, in litt.) and others may have been exposed to infection by cuts made for turpentine drainage. Only one other very low nest site has been reported; it was 5.6 feet above the ground (Hebard, 1950). Apparently infected trees are often in poor condition, as three living trees that contained nests in 1963 were dead in 1966.

Steirly (1957) considers these woodpeckers to be slightly colonial as several cavities are frequently in use within a small area. I, too, noticed this and assumed that it might reflect the distribution of infected trees and thus the availability of suitable trees. However, Steirly (1957) found suitable unused trees in all directions from a chosen group of trees. The percentage of second-growth pines with red heart in the Gainesville area needs to be determined, along with information on the minimum age and size of the trees when infection occurs.



Figure 3. Entrance to the roost cavity of a Red-cockaded Woodpecker.

How woodpeckers detect the diseased condition of trees before they excavate is unknown. Areas where cavities are located may sometimes have several trees showing the beginnings of excavations that are never completed.

Nest and roost trees are conspicuous and easily recognized. The birds peck many small chips through the bark and into the sapwood, often for several feet both above and below the cavity entrance, causing resin to flow freely. This is repeated frequently and results in a continuous flow of sap near the entrance (Figure 3). The birds usually engage in making fresh wounds shortly before entering the roost cavity for the night. This resin is alleged to prevent animals (i.e. ants, flying squirrels, snakes) from entering the hole (Pearson et al., 1942: 221; Steirly, 1957). As I have found both ants (in the nest with newly hatched young) and flying squirrels in cavities around which sap was flowing, this assumption is

somewhat dubious. Nevertheless, the resin probably does deter snakes and certain other animals.

Red-cockaded Woodpeckers live in extremely uniform habitat, particularly where man has not greatly altered the open pine forest. The hardened, whitish resin might serve to mark the tree conspicuously, making it easy to locate from a long distance.

Red-cockaded Woodpeckers flake much of the outer bark from their roost trees and adjacent ones, which causes these trees to appear reddish at a distance, in contrast to the deep gray of pine trunks not so scaled. The roost area of a pair or a group is usually thus marked with a few resin-covered trees, each containing one or more cavities, and others nearby with the outer layer of bark flaked away.

Limited data indicate that each bird excavates its own roost and that the work is done over a long period of time. On the morning of 16 December 1962, a family group of four returned to its roost area and one immature male worked on a new excavation (about 2 inches deep) that I had first noticed on 2 December. The other members of the family soon moved away, whereas this individual worked 20 minutes before flying to join the others. The hole was not completed on 9 March 1963, but was finished in late April 1963. This woodpecker remained with his parents and helped to rear their young of that year.

In two instances where there was only one cavity, the male roosted in it while the female passed the night high in the branches of a living pine.

When sap no longer flows in response to their chipping, Red-cockaded Woodpeckers either desert their roost tree or excavate a new hole in the same tree (Wayne, 1906). Fire is the primary factor in the development and maintenance of the longleaf pine woodlands (Stoddard, 1962). Prior to effective fire control probably few standing dead trees remained in the vast stretches of pine forest. The complete dependence of these birds on living pines for roosts and nests suggests that dead, more easily excavated wood was rarely available to them and that use of living trees was a requisite for existence in this habitat. The early desertion of dying trees further suggests that it is of survival value not to roost in such trees, possibly because of their susceptibility to fire. Adults roost in the open, high on living pines, rather than using cavities in dead trees, although this is not true of juveniles.

Most authors term all holes of this woodpecker "nest" cavities, but the majority probably never are used to rear young. For example, at one site only one of five actively used roost cavities was utilized as a nest. Typically roosts of mated adult males are also utilized as nests.

DEFENSE OF THE ROOST HOLE

The Red-bellied Woodpecker is the most important competitor of the Red-cockaded Woodpecker for the latter's roost sites. I found Red-bellied Woodpeckers attempting to obtain cavities of Red-cockaded Woodpeckers throughout the year, and, contrary to the statement of Pearson et al. (1942), cavities were not enlarged by Red-bellied Woodpeckers. Guarding their roost holes from Red-bellied Woodpeckers is, in some instances, an important part of the daily activities of Red-cockaded Woodpeckers. Often Group A became aware of the presence of a Red-bellied Woodpecker near their roosts well before I did and flew to their roosts immediately. Male A, in particular, flew to his roost hole, entered it, and faced outward at the first sign of a Red-bellied Woodpecker. Extreme alertness and quick response were most pronounced in those birds whose cavities were frequently threatened. Such defense was usually, but not always, successful. Occasionally, I shot Red-bellied Woodpeckers that had taken over holes of the smaller birds.

I also saw Red-cockaded Woodpeckers defend their cavities from Eastern Bluebirds (*Sialia sialis*) and Hairy Woodpeckers (*Dendrocopos villosus*). Red-headed Woodpeckers (*Melanerpes erythrocephalus*) took over one active cavity, and the smaller woodpeckers moved to a nearby tree.

TERRITORIALITY

Red-cockaded Woodpeckers maintain the same territories throughout the year and appear to recognize precise boundaries. The territory includes all activities of the birds (Type A of Hinde, 1956). Territory size and shape varied, although it was in all cases large. I did not measure the dimensions of territories. The greatest measured distance that I found these woodpeckers (a group of 4) from their roost area was 0.8 mile. Part of the foraging area of this group was composed of small, widely spaced pines that were probably poor in food resources. The birds did not range so far in the other direction although the habitat appeared to be excellent, as the territory of other Red-cockaded Woodpeckers formed a boundary. Boundaries were in general imposed both by habitat limitations and adjacent groups of woodpeckers. In this poor habitat these woodpeckers often traveled several miles in a day's movements.

In the two instances of territorial fighting noted, boundaries appeared to be recognized by both groups. Juveniles or yearling birds were actively involved in both conflicts. Conflicts were short-lived and terminated upon the withdrawal of the intruding pair or group. In one instance a group containing three adults (one a 1-year-old male helper) and two

recently fledged juveniles were driven from an adjacent territory held by only a pair. Numbers appeared to be of no advantage, as the larger group retreated to its own territory.

Both members of the pair attack a single intruder in the roost or nest area, unlike the situation found in many species of woodpeckers, where each member of a pair demonstrates hostility only towards intruders of the same sex (Lawrence, 1967: 30, 44). The action of the wings is the most conspicuous aspect of aggressive encounters. When attacking or repelling attack at close range the wings are opened and shut rapidly as the birds exchange jabs with the bill. I was unable to determine whether or not the wings themselves were used to strike an opponent. The tail is also spread and closed repeatedly, exposing the white outer rectrices.

A single unmarked bird (probably a male) invaded the territory of pair A almost daily from 11 to 30 May 1962. Despite the vigorous, almost continuous, pursuit by either or both members of pair A this intruder repeatedly perched near the nest cavity and remained in its vicinity. It also drummed frequently, greatly agitating the pair. Often, immediately after having been chased for some time, the intruder flew very close to the perched male, as if intentionally enticing the latter to chase him. Male A once caught the intruder and pulled several contour feathers from his body. On another occasion female A chased the intruder continuously for 11 minutes; both birds flew near the nest site during the entire chase. The intruder sometimes flew just above the palmettos, giving a single "chit" call when it appeared to be tired, repeated at intervals of several seconds.

The persistence of this lone individual is puzzling; perhaps pair A had earlier driven it away from this territory. The great amount of time and effort pair A expended in trying to drive this bird away might account in part for their poor reproductive success; only one of three young fledged.

In another instance a lone male was driven from the roost tree he had occupied for many months between 22 and 26 May, by a mated pair. The occupying pair laid their first egg in the newly acquired cavity on 4 June, 20 days later than at any other nest I observed. Possibly this pair recently had lost their nest and roost trees and had wandered until finding a potential nest site that was not strongly defended (one bird vs. two).

An incident observed on 11 August 1963 suggests that even juvenile Red-cockaded Woodpeckers recognize potential competitors. A captive juvenile was tethered within the territory of four adults and a single juvenile. The adults responded to the calls of the captive in a solicitous manner, as if an immature in their group had been captured. In contrast,

the juvenile repeatedly and viciously attacked the "intruding" bird, flying within a few feet of two human observers as he did so.

FEEDING BEHAVIOR

Adult Red-cockaded Woodpeckers demonstrate pronounced sexual differences in foraging sites during most of the year; males feed high on the trunk and on limbs and branches of pines, whereas females forage almost entirely on the trunk, largely at low elevations (Ligon, 1968). This behavior is thought to be adaptive in at least two ways: (1) it allows members of the pair to utilize the foraging potential of their territory more efficiently, and (2) it reduces potential competition for foraging sites that might have an adverse effect on the pair bond. Differences in feeding sites may decrease during the fall and winter months when members of both sexes feed in part on pine seeds.

Although Red-cockaded Woodpeckers forage on pine trees a vast majority of the time, they also visit other trees. One family group of four visited a cypress (*Taxodium distichum*) grove occasionally and a pecan (*Carya illinoensis*) orchard regularly. The trees in the orchard were widely spaced, as in pine woodland, and perhaps more importantly, the bark of the pecan trees, like that of the pines, was shingle-like and easily flaked away.

In addition to feeding on trunks and branches of pines in the manner described earlier (Ligon, 1968), Red-cockaded Woodpeckers also foraged in other ways. A male flew from a pine and captured an insect in the air in the manner of a flycatcher. On several occasions a single bird foraged among cut pine branches that had been raked into piles. On a few occasions Red-cockaded Woodpeckers ate berries. A female did so after first picking a single berry from a bush and pounding it. One male fed his nestlings large numbers of blueberries (*Vaccinium*). They also eat berries of the southern bayberry (*Myrica cerifera*), particularly during the winter. I saw drinking only once, from a small pool on the ground, on 19 January 1963.

BREEDING BIOLOGY

PAIR BOND FORMATION AND RETENTION

Most of the woodpeckers I located were mated, thus I had few opportunities to watch initial pair formation. Between 3 and 9 November 1962 the female of pair A died. The following suggests that Male A obtained a new mate with relatively little display. In adjacent territory B the male occupied the only roost cavity, while the female roosted high in a pine tree. By 16 November male A and female B were mated, occupying the territory of the former. After male A remated, juvenile A

left the area. Early on 17 November the newly mated pair was seen flying erratically in corkscrew patterns and giving the "szrek" call. Copulation occurred twice within a few seconds shortly thereafter. The female drummed several times at different points in her new territory, but the male did not. I suspect that female B had recently mated with male B and this (i.e. lack of a strong pair bond) together with the absence of a suitable roost caused her desertion. This pair was together when I revisited my study site 3½ years later in June 1966. Another pair also remained intact from 1963–1966.

Most Red-cockaded Woodpeckers, especially males, probably do not breed at 1 year of age. As young may remain with their parents until at least the following spring, they have little opportunity to locate a tree suitable for excavation, excavate the cavity, and attract a mate during that breeding season. First-year females perhaps become independent sooner than do males, wandering until they encounter an unmated male in possession of territory. Juvenile A became highly restless and excitable in mid-September, leaving her parents for long periods, although she was still fed occasionally by them. This behavior persisted through October, and in early November when male A remated, she disappeared. On 10 February of the following year she was found feeding peacefully in the company of this pair and was unmated.

COPULATION

Copulation or pseudocopulation was observed in March, May, November, and December. In some instances unsettling conditions, such as an intruder into the territory, seemed to be the primary factor triggering copulation. This was true in May after incubation had commenced. In the fall copulation appeared to strengthen the pair bond and was the most obvious manifestation of a general increase in sexual behavior.

In spring copulation may occur long before the eggs are laid. A pair whose first egg was laid on 5 May was seen to copulate on 23 March.

Copulation occurred with the female perched on a horizontal limb and either perpendicular or parallel to it. Typically the male slipped off to the left of the female with his tail tucked tightly beneath her. In one instance both birds toppled off the limb together and fell about 2 feet before flying back to the tree trunk.

THE NEST

No hole is excavated specifically as the nest site. In four instances the eggs were deposited in the roost cavity of the male. I saw no activity indicating that the cavity was prepared for deposition of the eggs. In one case, the eggs were deposited in what had been the female's roost

TABLE 1
MEASUREMENTS OF OCCUPIED NEST AND ROOST CAVITIES

	Height above ground ¹	Depth ²	Vertical diam- eter of entrance ²	Horizontal diam- eter of entrance ²
Nest	30.90	8.62	2.00	2.25
	11.90	8.50	2.25	2.00
	11.83	8.00	2.50	2.25
	11.75	7.25	2.13	2.13
	10.83	—	2.00	2.13
	3.90	9.25	2.00	2.25
Roost	10.91	—	—	—
	10.91	—	—	—
	9.58	—	—	—
	7.25	—	—	—
	5.50	—	—	—
	2.75	10.75	2.00	1.75
	2.33	—	—	—

¹ In feet.

² In inches.

cavity during the previous winter. The tree containing the male's roost was dead, although needless still clung to the branches. During incubation and the nestling period, this male spent the night in his mate's cavity while the female roosted in the cavity in the dead tree. This was my only observation of an adult roosting in a dead tree.

Table 1 gives dimensions of nest cavities, together with heights of nests and roosts.

EGGS AND CLUTCH SIZE

Fresh eggs are white, but they usually become spotted with pine resin. Eggs are laid daily until the clutch is complete and are deposited early in the morning; on at least three occasions eggs were laid before 06:00.

Clutch size in six nests was c/2-1, c/3-2, c/4-3; 19 of the 20 eggs in these nests hatched. The earliest egg was laid on or about 21 April, and the last on 4 June (the second of the two-egg clutch).

INCUBATION AND HATCHING

Incubation is performed by both members of the pair and apparently begins before the clutch is complete (see below). The male remains in the nest overnight, as is true of other woodpeckers. Incubation during the day is shared approximately equally by both members of the pair. I have no evidence that nest helpers participate in incubation.

At a nest where all eggs hatched, the fourth and last egg was laid by 06:55 on 16 May. The last egg to hatch was pipped by 07:15 on 26 May

and the young had emerged by 10:15 the same morning. Thus, the elapsed time from the laying of the last egg to the hatching of the last young was 10 days, 3-4 hours. This incubation period is as short as has been reported for any bird species. Another member of the genus *Dendrocopos*, *D. major*, also has a 10-day incubation period (Nice, 1953).

CARE OF THE YOUNG

Newly hatched nestlings are brooded almost continuously for 4 days. Helpers, when present, participate in this, at least after the 2nd day or so. For several days thereafter the chicks are brooded periodically, and some brooding may take place as late as the 12th day of nest life. Both parents and helpers removed fecal sacs. They are sometimes eaten near the nest, but more frequently are carried a long distance and presumably are dropped.

Feeding of nestlings.—Food is brought to the nest almost from the hatching of the first egg. At most nests feeding trips were equally divided between the parents (males-51, females-49, four pairs). However, at the nest of pair A the male brought food about twice as frequently as did his mate (83 vs. 40 trips observed). Female A brought food many fewer times than did other females. In a 1-hour period in the early morning, when the nestlings were of similar ages, female A brought food four times, whereas female B brought food eight times.

Equal feeding of the nestlings by both parents appears also to be the case in *D. villosus* and *D. pubescens* (Lawrence, 1967: 114, Table 13); however, in *D. major*, *D. minor*, and *D. leucotos*, the female left most of the care of the young to the male (Pynnönen, 1939 *in* Staebler, 1949). Kilham (1968) points out that in some woodpeckers the females are shier than their mates and do not feed their nestlings frequently when an observer stands too near the nest. This was not the case with Pair A.

Food items are primarily insects and other arthropods. Foods brought to the nestlings include: spiders, cerambycid beetles, moths, a damselfly, unidentified larvae and grubs, millipedes, and probably ants. In addition, one male fed his young many blueberries that he picked from bushes growing near the nest. On 5 June he took eight berries to the nestlings in 7 minutes.

Nestlings are fed most frequently early and late in the day and may not receive any food for periods of up to an hour at midday. Adults remain quiet in a sheltered spot and do not bring food during rainstorms.

Helpers at the nest.—One or more helpers were present at two of the six nests that I watched frequently. At one the single helper was a male offspring of the previous year. At the other the relationships of the three helpers (two males, one female) to the parents were not known.

TABLE 2
WEIGHTS¹ OF PAIRS OF RED-COCKADED WOODPECKER NESTLINGS IN FIVE NESTS

Age in days	No helpers ²	No helpers ³	No helpers	One helper	Three helpers
0			3.3-3.3	4.2-3.3	
1		4.3-4.2	4.6-4.0	5.2-4.0	
2	6.9-5.1	5.7-5.4	5.6-4.1	9.0-6.3	
3	9.6-7.1	8.8-7.8	9.4-6.4	9.6-8.1	13.9-11.1
4	11.0-10.3	11.6-10.2	12.7-7.5	12.2-11.0	
5	11.5-11.4		16.2-10.8	16.0-15.4	
6	14.9-12.5	18.6-16.5	18.4-15.0		22.5-22.7
7	17.5-13.9		19.6-15.7	22.0-20.9	
8	19.0-15.7	23.6-23.5			
9	24.4-18.1		28.4-26.4	28.7-26.5	34.5-35.5
10	27.2-20.0	32.2-31.5			
11	28.9-23.2		34.9-30.0	34.6-33.7	
12	32.3-22.3	38.5-36.2		38.6-37.8	
13	32.7-23.5	37.5-37.7	36.3-33.1		41.6-not weighed.
14				40.2-37.7	
15	38.1-gone		38.7-33.4		
16	38.4				
17					
18	43.0		45.0-37.7		
22	44.7				
24	43.3				
26	41.9			Fledged	Fledged
27	Fledged				
28					
29		Fledged			

¹ (g).

² Nest of Pair A, 1962. Female A not active in providing food.

³ C values in Figure 5.

I have no evidence that helpers participate in incubation, but their activity in feeding and brooding the nestlings, in nest sanitation, and in nest defense appears to equal that of the parents. During a 3-hour period at the nest with one helper, the male parent brought food four times, the female parent seven times, and the helper five times. Each brooded the 3-day-old nestlings until another adult arrived with food.

An observation concerning the male parent and single male helper is puzzling. I placed a stuffed Red-cockaded Woodpecker near the nest entrance when the nestlings were 9 days old, in order to observe its effects on the behavior of the three adults. All showed interest but not hostility, and the male parent tried to feed the dummy. Shortly thereafter, the helper *begged for and received* food from the male parent. The following morning the adult male gave a large insect to the helper (the dummy was not present), who then carried it about as if to take it to the nestlings. This behavior was not seen again, and was possibly a result of the earlier presence of the dummy.

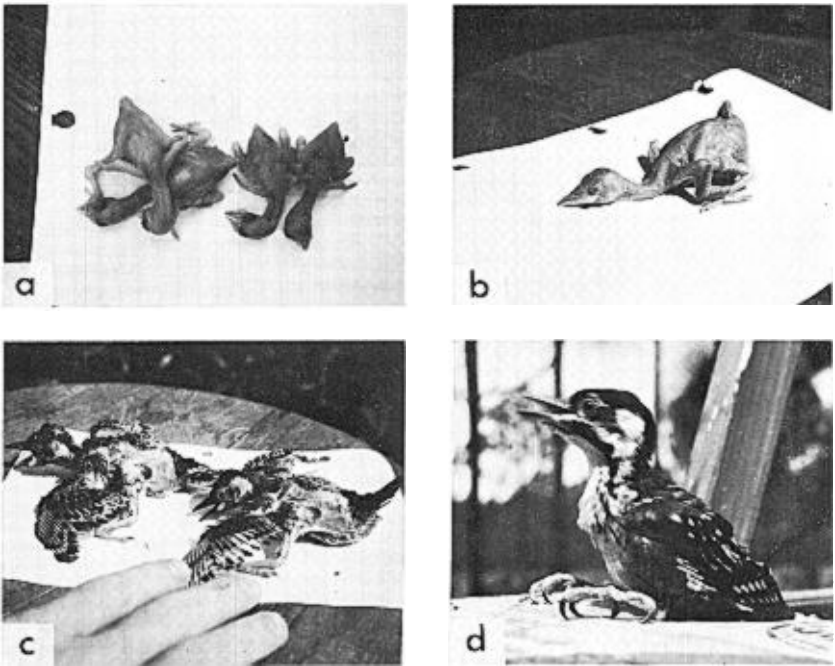


Figure 4. Nestling Red-cockaded Woodpeckers at different ages. a, the two on the left were 30 hours old; the bird third from the left was 22 hours old and was approaching starvation; the bird on the right was 4-5 hours old (see Table 3). b, 6 days old. c, 13 days old. d, 22 days old.

Development of nestlings.—I visited four nests as the eggs were hatching and marked each chick individually. Because incubation begins before the clutch is complete, the eggs hatch over a period of many hours. Table 2 summarizes the subsequent development of nestlings.

At hatching the skin of the naked young is bright pink, tarsi and feet are white, eyes and ear openings are closed, the rectrices appear as 10 bumps, and the heel pads are greatly developed (see Figure 4). By Day 5 feather tracts are visible on the wings, crown, most of the spinal, femoral, and ventral tracts, and on the scapular region. The bill has darkened and the ear passages are open. Feather tracts are well-developed on Day 10; feather tips are exposed on quills of rectrices, rump, and to a slight degree on the breast and lower abdominal tract. Quills of the middle and lesser wing coverts are apparent. The feet and tarsi are large and dark; the heel pads are decreasing in size and losing their knobs and tubercles; the eyes are open. By Day 18 the body is covered with feathers except for the abdominal and flank areas. Young are active and peck when removed

from the nest. Feather development of the body is complete by Day 26; remiges and rectrices are still ensheathed at their bases. Young are now of fledging age.

Fledging.—The young fledged from 26 to 29 days after they hatched. In the two instances in which it was watched the young left the nest in the early morning. This is accompanied by excitement on the part of the adults, who initially seem to be disturbed by the presence of the fledged juveniles. Soft calls given by the fledglings identify them to the parents, preventing possible hostile behavior from the latter.

A few hours before the young fledged at one nest, adults flew to the nest entrance three times and left without feeding either of the two nestlings. After leaving the nest both juveniles hitched up the nest tree before flying.

About 1 hour after juvenile A fledged, male A entered the female's roost cavity and remained there until I frightened him out. This behavior is somewhat similar to that Hebard (1950) reported, in which an alleged adult female carried food to an unoccupied cavity, apparently in an attempt to divert the watchers' attention from the hole containing nestlings. In the present case this was the first time that I saw the male enter this cavity but from the following night on he roosted in it.

Apparently the rectrices are not developed sufficiently at fledging to support the juvenile. The tail of a newly fledged male was 59 mm and of two juvenile males with rectrices fully grown, 71 and 73 mm. Juvenile A first used her tail as a prop 3 days after fledging.

Postfledging care.—Juvenile Red-cockaded Woodpeckers are dependent in part on their parents for food for an exceptionally long period, sometimes being fed by them for at least 5 months after fledging. I watched two immature males in complete first basic plumage unsuccessfully begging for food in December 1962, about 6 months after fledging. One of these later became a nest helper despite the efforts of its parents to drive it away in late April; the other disappeared at this time.

Helpers also care for fledglings. In one instance the parents left their two recently fledged young in the care of the helper for more than an hour. During this time the helper fed the two juveniles eight times and appeared to encourage them to forage in a clump of pine needles that he had found to be rich in insects.

Newly fledged young are not aided in locating or obtaining roosting sites. They roost high on trunks of pines for several weeks. Unlike adults, juveniles often investigate dead trees and may roost in holes in them until they excavate or otherwise obtain a cavity in a living tree.

I recorded two instances of cooperative feeding efforts between juvenile

A and female A. The latter offered a large insect to the juvenile that they jointly tore apart. Forty-eight days later these two cooperated in lifting a large slab of pine bark from the trunk. These observations suggest that the young learn foraging techniques from their parents. The extended dependency of juvenile Red-cockaded Woodpeckers suggests that they need a long learning period to gather food successfully in this habitat (Ligon, 1968). This agrees with the statement of Ashmole and Tovar (1968): "prolonged parental care should be especially common among birds that have small clutches and also use specialized feeding methods which can be perfected only by a prolonged learning process."

BREEDING SUCCESS

Although hatching rate was high in the six nests watched closely (95 per cent), fledging success was only 50 per cent, considerably less than the average of 66 per cent for hole-nesting passerines (Nice, 1957). None of eight nests produced more than two fledglings, and only one young fledged in four of these. Three other family groups located in June, shortly after the young had fledged, also contained either one or two juveniles. I know of no unequivocal evidence demonstrating that more than two young ever survive to fledging age. The age, adult or juvenile, of each individual in "family" groups of more than four must be known with certainty in order to do so, because of the possible presence of helpers.

The incubation pattern offers an explanation for this. Incubation normally begins with the laying of the second egg (based on five nests), as two young hatch almost simultaneously. At a nest containing four eggs, the third hatched about 12 hours after the first two, with the final egg hatching about 13 hours after the third. The pattern was similar at another nest, with the third egg hatching about 8 hours and the fourth about 26 hours after the first two. This difference of a few hours gives the older nestlings an insurmountable head start, and the younger ones starve about 24 hours after hatching (see Table 3 and Figure 4a). These apparently are discarded by the adults. I found one young dead in the nest about a day after it hatched, and another was found dead at the base of the nest tree at another site. Both of these birds were the last to hatch in their respective nests. This may explain the undocumented statement that disturbed pairs may throw their small young out of the nest (Murphey, 1939: 75). In other cases, the smallest nestlings simply disappeared. My visits to the nest did not appear to disturb the adults greatly. The older nestlings thrived despite my frequent intrusions and the adults soon became accustomed to my presence, waiting in a nearby tree to feed the nestlings after I examined them.

TABLE 3
WEIGHT CHANGES IN NEWLY HATCHED RED-COCKADED WOODPECKERS, FROM THE
HATCHING OF THE FIRST EGG¹

	1st hatched	2nd hatched	3rd hatched	4th hatched
Nest 1 (no helpers)				
Time 0	3.3	3.3	Unhatched	Unhatched
Time 8 hours	4.6	4.0	3.2	Unhatched
Time 26 hours	5.6	4.1	2.5	3.3
Time 47 hours	— ²	—	Gone	—
Time 49 hours	9.4	6.4		Gone
Nest 2 (one helper)				
Time 0 ³	4.3	4.2	3.3	Unhatched
Time 7 hours	5.3 killed	5.2	3.9	Unhatched
Time 33.5 hours		9.0	6.3	2.8
Time 48 hours		9.6	8.1	3.4
Time 73 hours		11.0	12.2	Dead at base of nest tree

¹ (g).

² Not weighed.

³ Two nestlings were apparently a few hours old; time 0 thus indicates first weighing.

At the nest of pair A the last of three nestlings to hatch quickly starved, whereas the second to hatch, smaller throughout its nestling life, disappeared at the age of 14 days, presumably a victim of starvation. At 13 days it weighed 23.5 g against its nest mate's 32.5 g. Neither was as large as other young of the same age (33.1–37.7 g) at nests with no helpers. Female A was not assiduous in providing food, as described earlier.

Why no more than two young survived even at nests with helpers seems puzzling at first. Apparently the first young to hatch obtain such an advantage, as a result of being fed almost immediately, that even helpers cannot increase the number of survivors. In addition, helpers which probably do not incubate, may not feed the nestlings for some time after they hatch. I first saw a helper feed young when they were 2 days old. If this is typical, helpers often would have little effect on the number of nestlings surviving. However, at the two nests with helpers 2.0 young fledged per nest, whereas at seven nests without helpers the average number of young fledged was 1.4 per nest. In addition, growth of surviving nestlings may be accelerated by the presence of helpers (Figure 5).

Asynchronous hatching is said to be of selective value in that it allows at least some young to survive when food is in short supply (Lack, 1954). If this is true of this woodpecker, one might expect more young to fledge in highly favorable habitat. Perhaps the habitat of my study area was suboptimal, and did not provide enough food for rearing more than two young; certainly the second-growth pines contrast strongly with mature

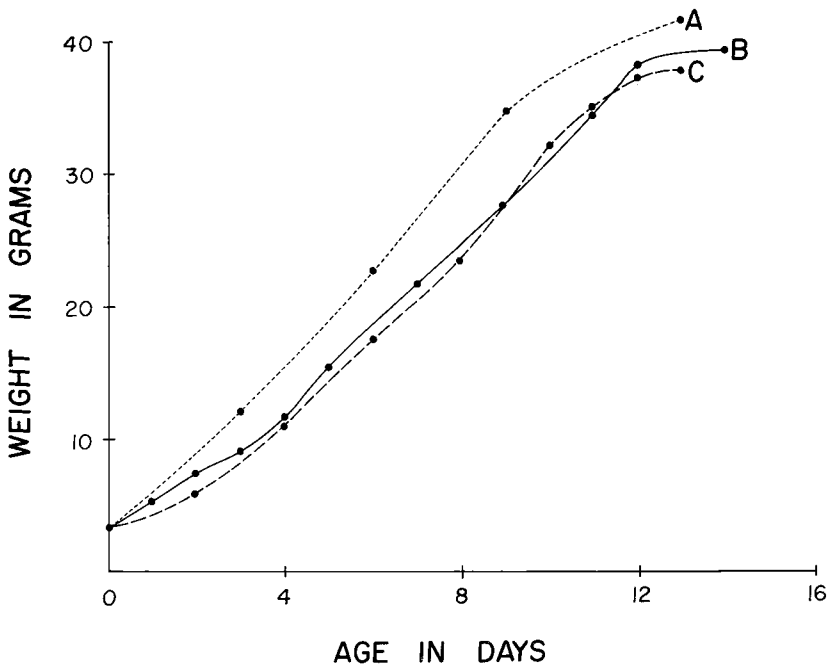


Figure 5. Mean growth of pairs of surviving Red-cockaded Woodpecker nestlings at nests with and without helpers. A, three helpers; B, one helper; C, fastest growing young at nest without helpers.

pine forest, such as that at Tall Timbers Research Station near Thomasville, Georgia, where Red-cockaded Woodpeckers are common.

SEXUAL DIMORPHISM

Voous (1947: 5) considered an extensive amount of red on the head as an ancient characteristic in the genus *Dendrocopos*, that tends to be reduced in the more highly developed forms. The frequent presence of widely distributed red-tipped crown feathers in juveniles of both sexes in most North American species of this genus, regardless of the pattern of red in the adult male, suggests that Voous' premise is valid and that this character is not subject to strong selective pressures in juvenile woodpeckers. Unlike all the other North American species, juvenile female Red-cockaded Woodpeckers never have red feathers on the crown, and the head pattern of the juvenile male differs strikingly from other members of the group in that the crown patch is small, distinct, and circular.

The Red-cockaded Woodpecker differs from most birds in that sexual dimorphism is more pronounced in juvenal than in adult plumage. If

Johnston's (1967) premise is valid, that sexual dimorphism in juvenile birds possibly has no adaptive value, this dimorphism can be considered a conservative character and the reduced dimorphism of adults a more recently derived condition.

The tiny cockades of males do not seem to be important in intraspecific relationships. The (apparently) essentially monomorphic plumage in adults may be related to the unusual means of territorial defense, in which both members of the pair actively attempt to drive away an intruder. Both may feel threatened, and the pair use a behavior pattern apparently agonistic in origin, the open wing display, as a recognition signal.

Reduction of the most conspicuous secondary sex character, the red on the males' heads, may have influenced the development of the unusual social nature seen in this species—presumably by reducing releasers of aggressive behavior. Various traits, such as gregariousness (including helpers and prolonged juvenile dependence) and the reduction of sexual plumage dimorphism form an interwoven complex of selective factors that cannot be analyzed at present.

MORTALITY AND PREDATORS

Mortality in established adults appears to be low. Of eight adults banded in 1962 and January 1963, I found five in the same places in June 1966. Two pairs had remained intact during this period, while at a third site the banded male had taken a new mate. Fidelity to an area is great as well. The third male had remained in the area, even though the nest and most of the roost trees were destroyed in a "clear-cutting" between 1963-66. The high survival rate of these birds, banded when they were probably at least 2 years old, may reflect their sedentary nature. Familiarity with the territory or range is almost certainly of great importance in reducing predation (Metzgar, 1967).

In December 1968 I saw only one of the eight mated adults that I had banded in 1962-63. At this time the territories, and in some cases the roost cavities, of the original birds were occupied by unmarked Red-cockaded Woodpeckers.

The long association of the juveniles with their parents, during which their foraging efforts are supplemented by the adults for several months, undoubtedly reduces their mortality as compared to species that become independent shortly after fledging. Lack (1966) considers starvation of independent juveniles a major source of mortality in many bird species.

Two incidents suggest that accipiters may be serious predators of Red-cockaded Woodpeckers, and that groups composed of several alert birds may serve as a defense against them. On 29 July 1962 juvenile A gave a single sharp call and "froze" on a pine trunk with her bill pointing

straight up, as did the two adults and a single Red-bellied Woodpecker that had been foraging in loose association with them. An immature Cooper's Hawk (*Accipiter cooperii*) soon flew towards both the woodpeckers and me, landed, and looked about for several minutes before flying away. All the woodpeckers remained completely motionless for 10 minutes after the hawk left. On another occasion a Sharp-shinned Hawk (*A. striatus*) almost caught an adult female as she scolded me from her roost tree.

Female A apparently died of natural causes. She disappeared in early November, 1962. I found her remains, including both bands, beneath her roost cavity on 12 January 1963. Apparently female B, then using this cavity, was only then able, as a result of its decomposition, to eject the body from the roost hole.

INTERSPECIFIC RELATIONSHIPS

Defense of the cavity was described earlier. Relationships with other species were otherwise peaceful, with a few exceptions. I recorded three aggressive encounters over foraging sites between Red-cockaded and Downy woodpeckers. The former initiated two of these, driving Downy Woodpeckers from trees in which both foraged, whereas in the third instance a single Downy Woodpecker tried unsuccessfully to drive away two Red-cockaded Woodpeckers feeding in a tree that had recently died. I never saw the two species feed peacefully in close proximity. As mentioned previously (Ligon, 1968), I could detect no differences in either foraging techniques or sites between Downy and male Red-cockaded Woodpeckers.

Hairy Woodpeckers were not common in my study area and I recorded only three incidents involving this species. On 12 May 1962 a Hairy Woodpecker perched at the entrance to the roost cavity of female A; neither she nor her mate were present. The following day male A (?) drove a Hairy Woodpecker from the same area. A female Red-cockaded Woodpecker displaced a Hairy Woodpecker from a foraging site in December.

Downy and Hairy woodpeckers possibly were even less common in open pinelands prior to modern man's exclusion of fire than they are today. Both species usually require dead standing timber for nesting (Howell, 1932) and, as suggested earlier, this probably was rare because of frequent fires. Consequently, the Red-cockaded Woodpecker may have been largely isolated from its congeners, at least during the breeding season. With the advent of extensive fire control, the Downy Woodpecker in particular may have become more common in the pinelands, with resulting competition between it and the Red-cockaded Woodpecker.

THE FUTURE

Statements of several authors, some of whom were cited earlier, suggest that the future of this species is dim, principally as a result of decreased habitat—mature and over-mature pine forests. My study shows these woodpeckers can use small second-growth pine stands and are adjusting to some degree to man-made changes. However, adjustments in habitat tolerance and behavior may not be enough to prevent increasing rarity of this species.

The extremely sedentary nature of this woodpecker works both for and against its survival. Individuals are not easily driven away by such disturbances as moderate lumbering or construction near their roost trees, and this faithfulness to a particular site decreases opportunities to populate unoccupied areas. Several areas in the vicinity of Gainesville that appeared suitable for Red-cockaded Woodpeckers were uninhabited by these birds.

The complete dependence on trees infected by *Fomes pini* for nest and roost sites indicates that eradication of this fungus would also eliminate the Red-cockaded Woodpecker. As Steirly (1957) indicates, a carefully managed pine forest would have no woodpeckers of this species, for such diseased trees would be removed. Infection by *Fomes pini* of young and small pines has made it possible for Red-cockaded Woodpeckers to utilize second-growth pinelands, as in the Gainesville area. Fortunately, in much of the south, pine forests are not yet managed carefully and infected trees will continue to be available in some areas for the indefinite future.

Open pinelands can be maintained only by recurring fire. The recent awareness of, and the willingness to use fires as an ecological tool (e.g. Tall Timbers Fire Ecology Conference) is encouraging. Only through the intelligent use of fire will the open pinelands, and thus the Red-cockaded Woodpecker, be preserved.

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SUMMARY

I studied Red-cockaded Woodpeckers (*Dendrocopos borealis*) near Gainesville, Alachua County, Florida, from May 1962 to August 1963 and briefly revisited the study area in 1966 and 1968. I observed the birds throughout the year, but investigated breeding biology in greatest detail. These woodpeckers center their activities about their cavities, which are

invariably located in living pines infected with a heartwood fungus, *Fomes pini*. Each bird uses the same cavity as a roost throughout the year and defends it from intruders, principally Red-bellied Woodpeckers (*Centurus carolinus*). Red-cockaded Woodpeckers are sometimes social, with one or more additional adults living close to the mated pair.

Territories are large and are defended by all members of a group. Unlike most other woodpeckers, both sexes defend the territory from a single intruder of their species.

Pair bonds usually are permanent and the female lays the eggs in the roost cavity of the male. Incubation is shared by both parents but apparently not by helpers. In one nest the incubation period was 10+ days. The nestlings hatch at staggered intervals and all but one or two young starve. Helpers care for the nestlings as diligently as do the parents, at least after the second day or so. The young fledge at about 27 days of age and are dependent on adults for food up to the age of 5 or 6 months.

Sexual plumage dimorphism in juveniles is greater than that of adults which suggests an evolutionary trend towards a reduction of sexual dimorphism in adults, with consequent development of the unusual social nature seen in this species (gregariousness, helpers at the nest, prolonged juvenile dependence).

The future of this species is intimately tied to the fungus *Fomes pini* and to fire-maintained open pinelands. Carefully managed forests, where all diseased trees are systematically removed, will not have Red-cockaded Woodpeckers. The recent awareness of the importance of fire in the ecology of the southern pinelands is encouraging to the survival of this species.

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