WINTER TERRITORIAL AND FORAGING BEHAVIOR OF RED-HEADED WOODPECKERS IN FLORIDA

DEBRA MOSKOVITS

Red-headed Woodpeckers (Melanerpes erythrocephalus) demonstrate conspicuous seasonal differences in foraging behavior, engaging primarily in flycatching in the spring and summer (Nauman 1960, MacRoberts 1970, Jackson 1976) and in storing acorns for winter consumption in the fall (Bent 1931, Kilham 1958a). Many migrate to suitable habitats for gathering acorns in the fall, and subsequently concentrate their winter activities in defending their stored mast (Kilham 1958a, Bock 1970, MacRoberts 1975). Kilham (1958a) describes these phenomena in Maryland, and MacRoberts (1975) briefly discusses the species’ wintering behavior in Louisiana.

I recorded activities and daily time budgets of 26 Red-headed Woodpeckers wintering in Highlands County, Florida, and describe in this report some behavioral changes that emerged during the study period. In addition, I analyze the interactions of Red-headeds with their sympatric congener, the Red-bellied Woodpecker (Melanerpes carolinus). I close with a brief discussion of the ecological relationships of these species and a comparison of the Red-headed with its western relatives, the Lewis’ Woodpecker (Melanerpes lewis) and Acorn Woodpecker (M. formicivorus).

STUDY AREAS AND METHODS

Study areas.—From 11 October 1975 to 2 January 1976 I observed 17 Red-headeds that had established territories in a 1.2 km² scrubby flatwoods area in Highlands Co., 11 km south of Lake Placid, Florida. The low vegetation in this study site consisted largely of fetterbush (Lyonia lucida) and saw palmetto (Serenoa repens). Scrub oak (Quercus inopina) was the dominant species in large sections of palmetto scrub; other sections also contained large numbers of turkey oak (Q. laevis). Chapman’s oaks (Q. chapmanii) and live oaks (Q. virginiana) were present, but less abundant. Most oaks were 1–1.5 m tall. The only other trees in the area were swamp bay (Persea palustris) and red bay (P. borbonia), about 2 m tall, and occasional 18–20 m slash pines (Pinus elliottii). A number of burned pine stubs remained from a 1968 fire. Dry ponds, covered with grass (Andropogon sp.) and St. John’s wort (Hypericum nudiflorum), were scattered throughout the scrub.

From 14 November 1975 to 2 January 1976, and from 14 February to 4 March 1977, I observed some additional Red-headeds in a recently burned, open scrubby-flatwoods section of the Archbold Biological Station, about 7.5 km S of the first site. The vegetation in this area was similar to the site described above, the main shrubs being live oak (1.5–2 m tall). Further description of this habitat, along with a summary of the resident avifauna, appears in Woolfenden (1969).

Observations on Red-bellied Woodpeckers were also made in these 2 scrubby-flatwoods,
and in 3 other pine-dominated habitats of the Archbold Station: slash pine-turkey oak, sand pine scrub, and low flatwoods (Wooffenden 1969). Red-headeds occupy most of these habitats during the spring and summer, but move away for the fall and winter.

Methods.—I followed Red-headeds in the 2 study areas for about 250 h and recorded 36 h of timed observations. Immature Red-headeds were individually identifiable by the emerging patterns of red on their heads. Adults were harder to distinguish, but also had characteristic markings (spots of black on their heads, black streaks on their white wing patches) visible at close range. After learning to recognize individuals, I followed them for intervals of 15-45 min. Observations were concentrated on 10 of the 26 individuals. They were mostly made during the fall and winter of 1975-76. I returned to the same areas for 1 week in May 1976, and again in February 1977 for observations on the birds' activities during their last month in winter territories.

Each Red-bellied Woodpecker was followed for 10–15-min intervals, or until the bird was lost. I visited different sections of the study area each day, recording about 180 h of observation with this species (30 h of timed observations). Results of the Red-bellied study are reported here only as they relate to the ecology of the Red-headeds.

The woodpeckers' activities were timed with a stop-watch, and divided into 3 main categories following Reller (1972): (1) foraging, when the birds were actually feeding or gathering mast; (2) maintenance, when they were engaged in resting, preening, or roost-hole excavating; and (3) territorial defense.

RESULTS

Dispersion in fall.—In late summer or early autumn, Red-headeds migrate to open areas containing abundant mast, where they establish individual territories (Kilham 1958a; pers. obs.). They will also remain on their breeding ground if they happen to nest by an open area or clearing where the mast crop is abundant the following fall (Bock 1970; pers. obs.). The latest records for Red-headeds on their summer territories in the denser pine-habitats of the Archbold Biological Station, from 1969–1977, range from 20–30 September (unpubl. records of Archbold Biological Station).

From 2–10 October, I followed 2 adult and 3 young Red-headeds that were foraging together in oak scrub on the primary study site. The juveniles occasionally foraged independently, but normally followed the adults, begging incessantly. However, rather than feeding the young, the adults chased them away, at times even pecking them. Only once did I see a Red-headed feed its young. In contrast, I saw Red-bellieds, which did not separate into individual territories, feed their young well into the first half of November.

Aggressive encounters between foraging Red-headeds were common during the early fall, with interactions between juveniles and adults being milder than those within the same age class. Interspecific squabbles also occurred at this period, especially at storage posts. Red-headeds had greater difficulty driving other species away during the early fall than they did later in the season, but throughout the study they dominated every interaction.

In early October, Red-headeds, Red-bellieds, and occasionally Common
Flickers (*Colaptes auratus*), fed from the same storage posts, and 3 times I saw all 3 species simultaneously on 1 stub. I could not be certain whether Red-headeds or Red-bellieds had originally cached the stores, or when, but I did see a few Red-headeds harvesting and storing acorns then. By 11 October, Red-headeds had spread out into individually occupied territories, and Red-bellieds had taken over the largely emptied storage posts.
Table 1

Sizes of 22 Red-headed Woodpecker Winter Territories in 2 Study Areas

<table>
<thead>
<tr>
<th>Size Range (ha)</th>
<th>Number</th>
<th>Adults</th>
<th>Juveniles</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.04-0.5</td>
<td></td>
<td>4</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>0.5-1.0</td>
<td></td>
<td>2</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>1.0-1.5</td>
<td></td>
<td>1</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>1.5-2.0</td>
<td></td>
<td>3</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>10</td>
<td>12</td>
<td>22</td>
</tr>
<tr>
<td>Mean Size (ha)</td>
<td></td>
<td>1.00</td>
<td>0.95</td>
<td>0.97</td>
</tr>
<tr>
<td>SD (ha)</td>
<td></td>
<td>0.20</td>
<td>0.37</td>
<td>0.30</td>
</tr>
</tbody>
</table>

Winter territories.—The main requirements for winter territories were the presence of dead trees for storage space, open vegetation for easy defense of the stored mast, and an abundant acorn supply nearby. Beyond these conditions, the woodpeckers showed no further preference for specific vegetation types. By late October, they were scattered in individual territories throughout the scrub (Fig. 1). Acorn-bearing oaks did not have to be within the woodpeckers’ territories. As did Kilham (1958a) and Bock (1970, Lewis’ Woodpeckers), I found birds harvesting acorns up to 100 m from their defended storage area. The woodpeckers did not defend their harvesting grounds, and individuals from different territories frequently harvested from the same oak patches (Fig. 1). This contrasts with MacRoberts’ (1975) observation in Louisiana, where Red-headeds gathered mast only from within their territories.

I plotted the territories of 22 individuals, taking the boundaries to be the outermost trees or posts visited regularly by each bird during the study. The 17 territories in the primary study site are shown in Fig. 1. Although the territories varied considerably in size (Table 1), they were larger than the ones measured by Kilham (1958b; Maryland, average territory 0.1–0.2 ha) and apparently comparable in size to those studied by MacRoberts (1975; Louisiana, 0.8–1.2 ha). This further supports MacRoberts’ view that territory size is compressible, probably correlated with the mast production of the habitat. While Kilham (1958a) found that adults held smaller, more easily defended, and more productive areas, I found no difference between adult and juvenile territory sizes (Table 1).

Aggressive interactions.—Red-headed Woodpeckers defended their territories against many species. Defense was most vigorous within the central
portion of their territory, where most of the stored cache and the roost hole were located (see also Kilham 1958b, MacRoberts 1975). All potential acorn robbers were chased, including Red-bellied Woodpeckers, Common Flickers, Scrub Jays (Aphelocoma coerulescens), and Common Grackles (Quiscalus quiscula). A few non-acorn feeders were also pursued such as American Robins (Turdus migratorius), Mockingbirds (Mimus polyglottos), Great Horned Owls (Bubo virginianus), and Red-shouldered Hawks (Buteo lineatus). In contrast, Loggerhead Shrikes (Lanius ludovicianus) were not only tolerated by the woodpeckers, but often were seen in close proximity, frequently using storage posts as hawking perches. These species did not seem to interact in any way. The single time I saw a Hairy Woodpecker (Picoides villosus) in the area, the shrike was even more aggressive and persistent than the Red-headed in chasing it away.

The rates of intra- and interspecific interactions throughout the study are summarized in Fig. 2. Each aggressive encounter was given an intensity factor, ranging from 0, when the birds were tolerated, to 3, when they grappled and fell to the ground. Bill-pointing and bobbing were given value 1; chasing and calling, 2. The average intensity of interactions for each species is given in Table 2, along with the percentage of acorns in the diet of Red-headeds and the species they interacted with. The table shows that the Red-headed aggression intensity increased with the degree of acorn consumption of the various species.

Intraspecific conflicts diminished markedly in October, once Red-headeds had established individual territories (Fig. 2). The few interactions I observed occurred along territorial boundaries. Twice I watched a bird lose an acorn it had stored just past the border of its territory. The woodpecker was chased away by its neighbor, which proceeded to store the acorn closer to the nucleus of its own territory. Such occurrences probably reinforce sharp territorial boundaries and induce the birds to store their mast toward the center of their territories. Intraspecific robbery is reported for Lewis' Woodpeckers (Constantz 1974) but I never saw Red-headeds steal stored mast from an unguarded post.

Beginning in mid-November, intraspecific conflicts started to increase again, after diminishing almost to zero (Fig. 2). By this time Red-headeds were moving around their territories more, in pursuit of emerging insects (see Flycatching, below), which resulted in more conflicts along their boundaries.

Red-bellied Woodpeckers were vigorously chased throughout the study (Table 2). The Red-bellieds seemed to search for inattentive Red-headeds and a few times succeeded in stealing morsels of stored mast from Red-headed territories. But Red-headeds were usually alert, and quickly chased any Red-bellied that even approached their territories. Frequently, Red-bellieds were
FIG. 2. Frequency of inter- and intraspecific interactions of Red-headed Woodpeckers in defending their storage posts. The dashed line in this and in subsequent figures marks the establishment of individual territories.

persistent, making several return attempts before being finally expelled. Because their large home ranges included several Red-headeds’ territories (see Fig. 1), Red-bellieds were able to return habitually to rob Red-headed storage posts. Red-bellieds do not keep close guard of their own stores, and this further facilitates their robbing behavior. When chased, Red-bellieds called loudly and flew away. I never saw them return a Red-headed’s attack.

Aggressive relationships between these species were not always clearcut: at times a Red-bellied was tolerated in areas from which it was customarily chased, or pursued from areas in which it normally roamed freely. The intruder’s activity probably had an effect on whether it would be ignored or pursued.

When given the opportunity, Red-bellieds took over their congener’s territory, and even though they had trouble extracting or finding a good portion of the stored mast, they eventually succeeded in depleting most of it. One
TABLE 2

<table>
<thead>
<tr>
<th>Date</th>
<th>RHW 1</th>
<th>RBW 2</th>
<th>Fl</th>
<th>SJ</th>
<th>Gr</th>
<th>Rb</th>
<th>Mb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct 1-10</td>
<td>1.3</td>
<td>1.7</td>
<td>1.5</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Oct 11-31</td>
<td>1.0</td>
<td>1.7</td>
<td>1.0</td>
<td>2.0</td>
<td>1.7</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Nov 1-14</td>
<td>2.0</td>
<td>2.6</td>
<td>1.0</td>
<td>--</td>
<td>1.5</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Nov 15-30</td>
<td>2.0</td>
<td>1.8</td>
<td>0.7</td>
<td>--</td>
<td>2.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Dec 1-14</td>
<td>1.0</td>
<td>1.0</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>0.8</td>
<td>--</td>
</tr>
<tr>
<td>Dec 15-31</td>
<td>2.0</td>
<td>2.0</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>Av. intensity</td>
<td>1.5</td>
<td>1.8</td>
<td>1.1</td>
<td>2.0</td>
<td>1.7</td>
<td>0.9</td>
<td>1.0</td>
</tr>
<tr>
<td>No. months chased</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>0.5</td>
<td>1.5</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>% acorns in diet 3</td>
<td>10-25</td>
<td>10-25</td>
<td>0.5-2</td>
<td>25-50</td>
<td>5-10</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>

1 See text.
2 From Martin, Zim and Nelson (1951).
3 RHW = Red-headed Woodpecker; RBW = Red-bellied Woodpecker; Fl = Common Flicker; SJ = Scrub Jay; Gr = Common Grackle; Rb = American Robin; Mb = Mockingbird.

Red-headed territory, for example, was abandoned late in November, when its owner disappeared. The following day, a neighboring male Red-bellied pecked all over the former owner's stores. This Red-bellied's mate, a frequent intruder even while the Red-headed was present, attempted to join the male, but was vigorously chased and forced to search the peripheral posts. I saw both Red-bellieds return on following days to eat the dwindling mast supply; I saw no Red-headed ever approach the area.

Florida Scrub Jay families held territories in both study areas. Conflicts with these birds occurred during a 2-week period just after the Red-headeds established winter territories. The fights were intense (Table 2), and normally involved several jays against a single woodpecker. After this brief period, however, Scrub Jays and Red-headeds occupied overlapping territories without aggression, even though acorns are also a major component of the jay's diet (Table 2).

Red-headed Woodpeckers were rarely successful in driving big flocks of robins or grackles away from their territories. The intruders ignored the woodpeckers' frantic calls, and only left after repeated attacks to the center of their flocks. Although the woodpeckers did not defend their harvesting grounds, they chased away any grackle approaching the oaks, possibly in response to the latter's large numbers. Mockingbirds were tolerated, and the few interactions I observed were very mild. Common Flickers were chased away at first, but later were mostly ignored. In the 2 conflicts I saw before winter territories were fixed, the flickers made several return attempts
before being finally driven away by the Red-headeds. However, once the Red-headeds' territories were set up, intruding flickers flew away immediately even at the call of the Red-headed. Flickers probably did not pose a serious threat to Red-headeds as their habits are markedly different and acorns account for only 1–2% of their diet.

Interspecific conflicts decreased progressively after November. This was seemingly caused by the Red-headeds' increasing tolerance of the intruders, especially robins, which they rarely chased after November, and flickers, which they came to ignore (flickers were using Red-headeds' posts as perches for courtship displays). Red-headed Woodpeckers also seemed less agonistic toward Red-bellieds, and a few times I saw the latter fly to Red-headed posts without provoking immediate attacks.

TIME BUDGETS AND FORAGING BEHAVIOR

Harvesting and storing acorns.—Figure 3 summarizes the foraging behaviors Red-headed Woodpeckers displayed during the fall and winter, illustrating the changes that occurred as the season progressed. Acorn related activities, which comprised the most important foraging event, are further broken down in Figure 4, which again shows the shifts in emphasis that developed during the study period. Harvesting, as described by Kilham (1958a), was the predominant behavior among Red-headeds during the first 10 days after establishing their territories. Harvesting, as described by Kilham (1958a), was the predominant behavior among Red-headeds during the first 10 days after establishing their territories. Shelling acorns and searching for suitable storage places were the most time consuming activities. Usually only 1 Red-headed visited a given harvesting area at a time. Clashes occurred only occasionally, and especially among juveniles or with grackles and Scrub Jays. Red-headeds maximized their harvesting time by only breaking the acorns in halves or by storing them whole when they found a sufficiently large crevice. Bock (1970) reports a similar behavior in the Lewis' Woodpecker, although, unlike the latter, Red-headeds use special dead branches, not storing posts, as "anvils" for cracking their acorns. I observed sporadic harvesting well into the first half of December.

For acorn storage, Red-headeds used dead stubs, dead branches of living trees, and, in some cases, even trunks of living slash pines. They did not excavate their own storage cavities. Like the Lewis' Woodpecker (Bock 1970), they used natural crevices and holes, occasionally enlarging a few (see also Kilham 1958a). I found only acorns, whole or in bits, stored in the holes. Kilham (1958a) also found a few insects when he inspected some of the storing branches.

Following the major harvesting period, the emphasis shifted to "re-storing." As Kilham (1958a) and Pinkowski (1977) describe, the woodpeckers ex-
extracted their acorns, carried them to an anvil, and broke them into tiny morsels which they distributed over their storing posts. Two factors might help explain the energy invested in this behavior: (1) several of the storage posts were extremely rotten, and a few of them were blown down by strong winds; (2) whenever Red-headeds were inattentive, Red-bellieds, and occasionally Common Flickers, robbed their stores (see also Pinkowski 1977). Thus, as Kilham (1958a) suggests, it would have been precarious to store the entire harvest in one spot.

Shell-less morsels are open to fungus attack, and I found several stored pieces that were rotting. Red-headed Woodpeckers often climbed their storage posts, lightly and rapidly picking at almost every hole, and apparently not feeding. The birds may have been turning their acorn morsels to dry them out and minimize fungal infections as Bock (1970) suggests for the Lewis'
Kilham (1958a) describes a habit of Red-headeds, apparently unique among the Picidae, of covering up storage holes with splinters of wood. MacRoberts (1975) and Pinkowski (1977) also report this phenomenon. Kilham observed this behavior after heavy rains, when the splinters were soft and manageable. Whenever I saw Red-headeds engaged in this behavior, they were using dry slivers, which they often had great difficulty fitting into the holes. The percent of time devoted to covering their stores increased greatly toward the end of December (Fig. 4).

It was difficult to estimate how much of the stored mast the Red-headeds were actually consuming. The birds usually ate bits of an acorn while pounding it, and I believe they also ate some while working over their stores. Until December, the birds ate mostly acorns they had just harvested, not ones they had extracted from storage. In February, feeding from storage
was much more common and obvious. The birds pounded at their holes and occasionally gleaned from their posts, eating the scattered bits of stored mast. When I checked some posts in May 1976, I found a few acorns still left in 8 of 10 stubs examined. After the winter of 1976–77, which was unusually cold, I found no mast remaining in any of the 6 posts I checked at the time the woodpeckers left their territories early in March.

Flycatching and gleaning.—Red-headed Woodpeckers devoted more time to flycatching once the active acorn harvesting period was over (Fig. 3). On warm days in November, December, and especially February, it was common to see all individuals in the population engaged solely in hawking flying insects.

Rarely, the woodpeckers gleaned from branches and trunks, or probed into clusters of ball moss (Tillandsia recurvata) and Spanish moss (T. usneoides), apparently catching surface prey. This type of foraging, in contrast, was the principal foraging mode displayed by Red-bellieds in the denser habitats that Red-headeds deserted in the fall. In the open scrub, where the 2 Melanerpes species co-existed during winter, M. carolinus gleaned limbs and posts much more frequently than did its congener.
Maintenance activities.—The amount of time spent foraging declined after the harvest period, when Red-headeds shifted to activities involved in maintenance and territorial defense. After the completion of roost holes in mid-November, maintenance consisted of quiet perching (Fig. 5). In February, 1977, I included most perching (76% of the total observation time) under "flycatching," as the birds constantly looked around and sallied whenever an insect flew by. In both habitats, Red-bellieds' maintenance activities also increased significantly after November, when the birds were no longer feeding their young.

DISCUSSION

Red-headed Woodpeckers in south-central Florida stop feeding their young early in the fall and intraspecific aggression becomes progressively more intense until the groups split up into individual winter territories. They then spend the majority of their time harvesting acorns, flying almost continually into and out of their territories, from oaks to "anvil" to storage posts. This active phase is followed by a more sedentary "re-storing" phase, when the birds remain at their storage posts, rearranging their mast and chasing away intruders. During these first weeks on the winter grounds, only a small fraction of time is spent actually feeding or resting. Thus, as in Lewis' Woodpeckers (Bock 1970), Red-headeds seem to spend most of the early fall working on preparing stores for use during the colder days of mid-winter. With the stores completed, they feed predominantly on fresh acorns while these remain available on the oaks, and they spend an increasing amount of time flycatching whenever conditions are favorable. The birds become even more sedentary later in the fall, and are frequently found quietly perched on one of their main posts. The bulk of the stored mast is consumed in late winter (Fig. 4).

Kilham's (1958a) and MacRoberts' (1975) reports on Red-headeds in Maryland and Louisiana, also reveal their close dependence on acorn crops in selecting their winter grounds. However, Willson's (1970) and Reller's (1972) observations of these woodpeckers in Illinois imply a very different behavior in that area. Willson describes the Red-headeds as "generalist" feeders, and Reller found that they were selective in their choice of species and portions of trees in which to forage, which suggests that they gleaned a large portion of their diet, relying less on mast. Willson and Reller found that M. erythrocephalus and M. carolinus segregated in feeding sites, and neither mentions differences in foraging techniques. However, in my study, the primary foraging mode observed for Red-bellieds was gleaning and probing (see also Stickel 1965, Kilham 1963), activities that Red-headeds rarely
engaged in. Pinkowski (1977) reports storing and re-storing behavior of Red-headeds during the summer in Michigan, which suggests that at least in part of their northern range, Red-headeds show their specialized foraging habits year-round.

Accounts (Kilham 1958b, Reller 1972) regarding Red-headeds’ aggressive behavior agree with my findings in Florida: (1) Intraspecific conflicts drop drastically once winter territories are set up, and (2) Red-bellieds are major competitors of Red-headeds. I did not observe the agonistic interactions between Red-headeds invading each other’s territories described by Kilham (1958b). This probably reflects the lower densities of Red-headeds in my study area (see also MacRoberts 1975).

Red-headed Woodpeckers seem to have specialized in their diet such that all of their seasonal activities revolve around it. Thus in the fall they must look for and move into suitably open, acorn-bearing habitats. Their behavior throughout the winter revolves around use and defense of their stored mast. In contrast, Red-bellieds have generalized foraging tactics, using a slight specialization in morphology. Their unusually versatile tongue allows them to reach and manipulate objects in holes and crevices to which most other birds have no access (Kilham 1963). With a more diverse diet, and no need to keep constant guard of their stores, Red-bellieds do not undergo the major shifts in behavior that are associated with the Red-headeds’ local migrations into individual, specialized winter territories.

Because individual Red-headed and Lewis’ woodpeckers do not necessarily return to the same winter territories each year, their winter foraging and territorial behavior is oriented toward short-term exploitation of their habitat. Cracking and fitting acorns into natural crevices requires considerably less energy than drilling holes for whole-acorn storage in special “granaries.” The risk of losing the cracked pieces to fungal rot is of little consequence for the 2 migratory species, as they depart from their territories and any remaining stores after a few winter months. In contrast, Acorn Woodpeckers may eat stored mast throughout the year (MacRoberts and MacRoberts 1976), hence it is to their advantage to spend the extra energy in keeping their stores edible for longer periods.

Aspects of short-term residency can also be seen in the different harvesting strategies. Red-headed Woodpecker families break up in the fall, and individuals simultaneously exploit the superabundant acorn crop as rapidly as possible. They do not defend the productive oak patches, but instead concentrate on quickly accumulating sufficient stored mast for their own winter use. Furthermore, except for the relatively brief harvest period (Fig. 4), they are not likely to return to the same area in the near future. Acorn
Woodpeckers, on the other hand, hold territories in habitats that are annually predictable, and that meet requirements for both winter and summer (MacRoberts and MacRoberts 1976). As a result, they defend their harvesting areas, in order to assert permanent dominance within these productive habitats.

The contrast in the social structures of the 3 mast-consuming *Melanerpes* species is again related to this permanent vs. short-term residency. Red-headed and Lewis' woodpecker individuals disperse to provide for themselves in unpredictable habitats, while Acorn Woodpecker groups remain intact and cooperate in mast storage, roost and granary maintenance, and defense of their permanent territories.

Red-headed and Lewis' woodpeckers have dull juvenal plumage lasting well into the winter, while immature Acorn Woodpeckers resemble adult males (Spray and MacRoberts 1975). The different Red-headed juvenal plumage presumably contributes to diminishing aggression from adults. The fact that juveniles engaged in fights among themselves considerably more often than did adults might also suggest that the bright pattern of the adults' plumage is itself an effective signal for territoriality. However, this bright head color is apparently effective mostly intraspecifically, as juveniles seemed to have no more trouble than adults keeping intruders away. The difference in juvenal plumage patterns may also be related to the difference in social systems among the 3 species. Juvenile Red-headed Woodpeckers may benefit from decreased aggression by adults during the establishment of individual territories, while, by resembling adults, young Acorn Woodpeckers may be more effective in the cooperative defense of the group's territory.

**SUMMARY**

I studied foraging and territorial behavior of Red-headed Woodpeckers in south-central Florida. In autumn the birds leave their breeding territories and migrate to productive patches of oak scrub, arriving as acorn crops mature. Each individual establishes a separate territory within open scrub habitat and defends an area surrounding several dead trees, which it uses for storing acorns and excavating roost holes. Behavior patterns change markedly as the winter season progresses: most of early autumn is spent harvesting mast, which is then rearranged and covered during late fall. Flycatching predominates on suitable days in mid-winter, and the bulk of the stored mast is consumed only in late winter. Both intra- and interspecific aggressive behavior changes with the progression of different foraging activities throughout the season.

Red-headed Woodpeckers resemble the congeneric Lewis' and Acorn woodpeckers in their dependence on mast harvesting and storage. Opportunistic Red-headed and Lewis' woodpeckers depend on sporadically abundant crops, and show specialized winter behavior associated with their seasonal movements. In contrast, Acorn Woodpeckers occupy habitats with more reliable acorn supplies, and the species is resident and highly social all year.
ACKNOWLEDGMENTS

I thank the late Mr. Richard Archbold for making available all the facilities at the Archbold Biological Station, and for supporting my stay there. James N. Layne and students visiting the Station were helpful with advice and support. I am sincerely grateful to Dean Amadon, Henry S. Horn, James N. Layne, Fred E. Lohrer, John W. Terborgh, and Glen E. Woolfenden for their constructive comments on the manuscript, and I owe special thanks to John W. Fitzpatrick, for his time, effort, and patience in reviewing and criticizing various versions of the manuscript.

LITERATURE CITED


