

## HOME RANGES OF RED-COCKADED WOODPECKERS IN COASTAL SOUTH CAROLINA

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**ABSTRACT.**—Total observed ranges of 24 groups of Red-cockaded Woodpeckers (*Picoides borealis*) varied from 34 to 225 ha and averaged 86.9 ha. Groups defended portions of these ranges from adjacent groups year-round. Home ranges were derived from total observed ranges by subtracting extraterritorial areas and areas receiving limited use. The percentage of year-round home-range boundaries determined by intergroup conflicts varied from 0% to 54% and averaged 23.6%. Year-round home ranges averaged 70.3 ha and varied from 30 to 195 ha. The portion of year-round home ranges used in all sampling periods varied from 15% to 65% and averaged 30.5%. The amount of potential foraging habitat per group for all groups within 2,000 m of a study group's colony, a measure of population density relative to available habitat, accounted for 70% of the variation in size of year-round home ranges ( $P < 0.0001$ ). Various measures of group size and habitat quality were weakly related to size of year-round home ranges. Measures of group size and population density together accounted for 80% of the variation in size of year-round home ranges. Received 14 January 1982, accepted 2 March 1982.

THE Red-cockaded Woodpecker (*Picoides borealis*) is dependent upon live southern pines for nesting and roosting cavities (Jackson et al. 1979) and, to a large extent, for foraging sites (Hooper and Lennartz 1981). The scarcity and decline of pines suitable for cavity excavation are the major reasons the species was classified as endangered (Federal Register, 13 October 1970, 35, 199: 16047). A scarcity of suitable foraging habitat, however, may also limit the occurrence of the species. This has been indicated by colony abandonment where large areas of foraging habitat were clearcut from around colonies. Obviously the home range must encompass some minimal amount of suitable foraging habitat. Studies by Baker (1971), Crosby (1971), Skorupa and McFarlane (1976), Wood (1977), Nesbitt et al. (1978), and Sherrill and Case (1980) found that 17 seasonal ranges averaged 38.9 ha and varied from 14 to 91 ha. One year-round range in south Florida was 159 ha (Patterson and Robertson 1981). Considering

the extensive areas used by groups and the fact that forest management continually alters home ranges, a better understanding of home-range requirements is critical to the species' management and survival. The objective of this study was to examine relationships between home-range size, group size, population density, foraging resources, and habitat quality in order to test several hypotheses of why year-round home-range size varied in coastal South Carolina.

### METHODS

**Study areas.**—Eighteen of 24 home ranges studied were on the Francis Marion National Forest, in South Carolina. The area has at least 400 groups of Red-cockaded on about 64,000 ha of habitat (Oscar Stewart pers. comm.). This is one of the largest populations in existence. Major foraging areas consisted of loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pine stands. These stands have been periodically prescription burned since 1944 and have been under even-age management since 1950. Ages of pine stands ranged from less than 1 to 100 yr. Mixed stands of gum (*Nyssa* spp.), cypress (*Taxodium* spp.), oak (*Quercus* spp.), red maple (*Acer rubrum*), and other species were interspersed among the pine stands.

Six of 24 home ranges studied were on Hobcaw Barony, 3 km east of Georgetown, South Carolina.

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Hobcaw has about 3,000 ha of forest land, 3,000 ha of salt marsh, and 1,000 ha of fresh water and brackish marshes and abandoned rice fields. Forest vegetation was similar to that on the Francis Marion National Forest except that pine stands tended to be older. A detailed analysis of the vegetation was made by Barry and Batson (1969).

*Determination of ranges.*—Year-round ranges of 24 groups of Red-cockadedes were determined by following group members uniquely marked with colored plastic leg bands. Red-cockaded groups were family units consisting of a mated pair, their offspring of the year, and, in some groups, adult male helpers. A group traveled several kilometers daily but returned to its cavities each evening. After birds left their cavities in the morning, they were continuously monitored for 2–14 h. This was done on 627 days, for a total of 3,080 h of monitoring time. Sampling intensity was similar in all groups so that it would not be a variable in determining range size.

The locations of groups were recorded at 5-min intervals. On the Francis Marion, 1:24,000-scale aerial photographs were gridded to 15.2 m, with each tenth line shown on the photograph. Major (152 × 152 m) grid points were located in the forest when natural features could not be used for accurate plotting of the group's location. On Hobcaw Barony, group locations were plotted each 5 min on forest vegetation maps with a scale of 1:12,000.

On the Francis Marion, movements of six different groups were followed from May of one year to May of the next for 3 yr starting in 1976 and ending in 1979. On Hobcaw Barony, six groups were followed from September 1976 to September 1977. The year was divided into five sampling periods based on the behavior of the Red-cockaded and arbitrary division. These periods were nestling (1 May–15 June), postfledging (16 June–15 September), fall (16 September–31 December) and spring (1 January–30 April). Three of the 24 groups did not nest the year we studied their movements, and thus they did not have a nestling or postfledging period. For those three groups, movement was monitored during a comparable period called summer (1 May–15 September). Using observations for the nestling and postfledging periods, we determined a summer home range for the other 21 groups.

Total observed range was determined by connecting outermost points at which the group was observed. Territorial boundaries were determined from advances and retreats of respective groups during intergroup conflicts. Extraterritorial areas were portions of the total observed range that were across territorial boundaries. Limited-use areas were portions of the total observed range visited only once by the group. Home range was determined by subtracting extraterritorial and limited-use areas from total observed range.

*Measurement of vegetation.*—Vegetation was strat-

ified 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 from  $\geq 3$  to  $< 13$  cm dbh were recorded by species and dbh on a 0.02-ha plot. Stems  $\geq 13$  cm dbh were sampled with a 1-m factor wedge prism. Trees in the prism plot were recorded by dbh and species.

## RESULTS AND DISCUSSION

### TERRITORIAL BEHAVIOR

The 24 groups engaged in 146 conflicts with other groups. Intergroup conflicts varied in observed intensity and duration. Conflicts averaged 28.1 min for 87 timed encounters and had a range of about 1–200 min. In the overtly less agonistic conflicts, two groups would forage about 10–100 m apart and were silent or mildly vocal, as compared to more intense conflicts. The more aggressive conflicts were characterized by increased vocalizations, aerial chases, chases on the trunks of trees, wing spreading, and loud pecking (compared with normal foraging). At different times, breeding males and females, adult helper males, and juveniles were seen engaged in these activities during conflicts. Although both male and female Red-cockadedes drum, especially during encounters with single alien birds, they were not observed to do so during intergroup conflicts. In 17 cases, two birds from opposing groups made bodily contact by grasping bills or feet and fluttering toward the ground, sometimes landing there together. Conflicts ended when one of the groups withdrew.

Conflicts between groups occurred year-round (Table 1), but only three were seen when young were in the nest. Only one group had no observed intergroup conflict and three groups had only one. In contrast, another group engaged in 17 encounters with adjacent groups. The mean number of conflicts per group was statistically similar among sampling periods. There appeared to be a reduction in territorial encounters in spring, however, when fewer and significantly briefer conflicts were observed.

Typically, a group would not honor its territorial boundary if the adjacent group was not aware of its presence. During all periods, groups left their territory and traveled into adjacent ones. On these forays, the resident group was sometimes encountered, resulting in retreat by the trespassing group. The longest re-

TABLE 1. Frequency and duration of conflicts of 23<sup>a</sup> groups of Red-cockaded Woodpeckers with adjacent groups.

Intergroup conflicts	Summer (1 May–15 Sept.)	Fall (16 Sept.–31 Dec.)	Spring (1 Jan.–30 Apr.)
Number of conflicts			
Number per group <sup>b</sup>	2.3A	2.3A	1.7A
Minimum–maximum	0–6	0–6	0–7
Total	54	53	39
Duration of conflicts			
Mean per conflict <sup>c</sup> (min)	26.5A	38.8B	16.9C
Minimum–maximum (min)	0–123	0–200	0–50
Number conflicts timed	28	32	27

<sup>a</sup> One group out of 24 had no observed intergroup conflicts.

<sup>b</sup> Means followed by the same letters do not differ significantly ( $F = 0.95$ ;  $df = 2, 84$ ;  $P > 0.05$ ).

<sup>c</sup> Means followed by different letters differ significantly ( $F = 3.45$ ;  $df = 2, 84$ ;  $P < 0.05$ ).

treat was about 700 m. On other occasions, the resident group was not encountered. Twice, a trespassing group examined several cavities and pecked briefly at resin wells before returning to its own territory.

Movements across observed territorial boundaries averaged less than those into limited-use areas ( $\bar{x} = 180.8$  and 260.3 m, respectively;  $t = 2.12$ ,  $df = 84$ ,  $P < 0.05$ ). Probably one reason for this difference was the termination of extraterritorial forays upon encounter with the resident group. Many of the excursions into areas of limited use would probably have been shorter had the group being followed encountered the resident group. In other words, many of the limited-use areas were probably part of adjacent territories, but we failed to see intergroup conflicts at those locations. For example, in the second longest excursion (620 m) into a limited-use area, a group went 430 m beyond the cavity tree used by another group for nesting. Because both groups were still active for at least the two following breeding seasons, and because the two groups had one encounter in a different place before the above excursion, it seemed certain that a conflict and retreat would have occurred if the two groups had met.

Accounts of territorial behavior of Red-cockaded in the literature tend to support our observation that the species is strongly territorial (Ligon 1970, Lay et al. 1971, Nesbitt et al. 1978, Sherrill and Case 1980). Crosby (1971), Baker (1971), Patterson and Robertson (1981), Skorupa and McFarlane (1976), and Wood (1977), however, did not report intergroup conflicts. Crosby and Patterson and Robertson worked

with isolated groups, and Skorupa and McFarlane worked in an area with a low population density. Thus, the potential for intergroup conflicts appears to have been limited in their study areas.

#### SIZE OF RANGES

*Year-round ranges.*—The largest total observed range among the 24 groups of Red-cockaded Woodpeckers was 225 ha, and the smallest was 34 ha. Mean size of total observed range was 86.9 ha, with a standard deviation of 44.2 ha. Only one group we studied had a total observed range larger than the 159 ha reported for a group in south Florida (Patterson and Robertson 1981). Year-round home ranges averaged 70.3 ha, with a standard deviation of 35.7 ha. The largest year-round home range was 195 ha, and the smallest was 30 ha. On the average, year-round home ranges consisted of 82% of the total observed ranges, but this varied from 60% to 99%. The two measures of range were highly correlated (Pearson product-moment correlation coefficient = 0.98,  $P < 0.0001$ ).

Extraterritorial areas averaged 8.4 ha, and the largest was 24.7 ha. In two groups we did not observe an extraterritorial area, but those groups did have limited-use areas. Areas of limited use averaged 10.4 ha, and the largest was 31.0 ha. Seven groups had no observed limited-use area, but all seven of those had extraterritorial areas. It is possible that some portions of the limited-use areas were extraterritorial and that we simply failed to see conflicts in those areas.

TABLE 2. Mean and extreme values for size of home ranges of 24 groups of Red-cockaded Woodpeckers during different periods (ha).

Period	Mean <sup>a</sup>	Maximum	Minimum	Number of groups
Nestling (1 May–15 June)	27.8A	49	12	21
Postfledging (16 June–15 September)	43.1B	114	19	21
Summer <sup>b</sup> (1 May–15 September)	47.6B	115	22	24
Fall (16 September–31 December)	37.5A, B	77	16	24
Spring (1 January–30 April)	48.9B	151	22	24

<sup>a</sup> Means followed with different letters differ significantly ( $P < 0.05$ ) based on analyses of variance ( $F = 4.06$ ;  $df = 3, 86$ ;  $P < 0.01$ , and  $F = 1.83$ ;  $df = 2, 69$ ;  $P < 0.17$ ) and Duncan's multiple range tests. Note that the nestling and postfledging periods were not compared to the summer period.

<sup>b</sup> The summer period home range was the area used during the nestling and postfledging periods for groups that nested. For groups that did not nest, it was the area used during the comparable period.

Boundaries of year-round home ranges varied in length from 2.7 km to 8.3 km ( $\bar{x} = 4.4$  km). The percentage of these boundaries determined by intergroup conflicts varied from 0% to 54% and averaged 23.6%. Observed territorial boundaries were generally well defined, but we were unable to delineate entire territories for three possible reasons. First, home-range boundaries were extensive, and we might not have recognized the significance of a given intergroup conflict to the extent the woodpeckers did. Second, the low population density around some groups might have precluded the establishment of territorial boundaries. And third, we undoubtedly failed to see all territorial encounters that occurred during the year.

*Range size for different periods.*—Home ranges were similar in size during the summer, fall, and spring periods (Table 2). Of these three periods, home ranges in fall were on the average 21 and 23% smaller than in summer and spring, respectively, but the differences were not significant. Only three groups had their largest home range in fall, however, compared with 10 groups, each with their largest home ranges in spring and summer. One group had home ranges of equal size in fall and spring. These results are contrary to those of Skorupa and McFarlane (1976), who found home ranges to be smaller in summer.

In groups that nested, the summer period was divided into the nestling and postfledging periods. Home ranges were significantly smaller when young were in the nest than during the postfledging and spring periods (Table 2). Home ranges did not differ significantly during the nestling and fall periods.

Of the 18 total observed ranges reported in the literature, all but one were based on sample

periods of less than a year. Several of these ranges are of particular interest when compared with our data. A group monitored by telemetry for 4 days in October had a range of 91 ha (Nesbitt et al. 1978). The two largest total observed ranges that we measured in fall were 85 ha and 77 ha. Use of telemetry did not appear to account for the size of the range measured by Nesbitt and his coworkers, because they measured two other ranges by telemetry that were only 58 ha and 59 ha. Recently, Nesbitt (pers. comm.) studied five total observed ranges in south Florida during July–October that averaged 144 ha. He suggested the sparse distribution of suitable foraging areas accounted in part for the large size of those ranges. Crosby (1971) reported that a group studied in March–June had a range of 15 ha, and Skorupa and McFarlane (1976) reported ranges of 16 ha and 18 ha for two groups in June–July. These three ranges were smaller than any we studied during a comparable period.

Groups shifted the area they used within year-round home ranges among sampling periods. In the fall, groups used an average of 56% of their year-round home ranges, compared with 71% in summer and 69% in spring. For groups that nested, an average of 44% of the year-round home ranges was used when young were in the nest and an average of 60% after they fledged. The portion of the year-round home range used in all periods averaged only 30.5% and varied from 15% to 65%. Other studies involving more than one sampling period also reported shifts in ranges (Skorupa and McFarlane 1976, Wood 1977).

#### DETERMINANTS OF HOME RANGE SIZE

Before examination of the data, we framed four hypotheses that we could test about the

TABLE 3. Mean and extreme values for major vegetation characteristics in 24 year-round home ranges of Red-cockaded Woodpeckers.

	Mean	Maximum	Minimum
Total basal area of stems $\geq 13$ cm dbh (m <sup>2</sup> )			
Pine	831.7	2,310	210
Hardwood <sup>a</sup>	233.3	690	10
Total number of stems $>3$ but $<13$ cm dbh for all species ( $\times 1,000$ )	68.2	273	10
Hectares of pine and pine-hardwood stands by age class <sup>b</sup>			
$\leq 20$	6.0	44.6	0
21-40	7.6	70.0	0
41-60	19.3	90.7	0
$>60$	30.9	100.7	1.0

<sup>a</sup> Includes cypress.

<sup>b</sup> Stands where pine basal area  $>50\%$  of total basal for stems  $\geq 13$  cm dbh.

variation in range size among groups. The first was that home ranges contained approximately the same quantity of foraging resources even though they differed in size. Such a relationship was found for several nectar-feeding birds (Gass et al. 1976). Winter territories of Townsend's Solitaires (*Myadestes townsendi*), however, varied considerably in the amounts of food they contained (Salomonson and Balda 1977).

Our second hypothesis was that home range size was related to the density of the surrounding population. Compressible home ranges and territories have been reported for many vertebrates (Wilson 1975: 270). Although an inverse correlation between food density and territory size has been reported in several studies (Myers et al. 1979), in more recent studies this relationship was shown to result from intruder pressure (Myers et al. 1979, Ewald et al. 1980). Earlier, Krebs (1971) found that territory size in Great Tits (*Parus major*) was not related to food supply but was determined by the number of birds surviving. Settlement patterns of territory holders had a strong influence on territory size in Song Sparrows (*Melospiza melodia*) (Knapton and Krebs 1974). Sherrill and Case (1980) found a positive relationship between size of Red-cockaded home ranges and mean distance to nest trees of surrounding groups ( $r = 0.95$ ,  $n = 4$ ).

An association between habitat quality (usually stated in terms of food production and foraging efficiency) and territory size has been found for many species of birds (Schoener 1968, Southern 1970, Wiens 1973, Morse 1976, Best 1977, Seastedt and MacLean 1979). Because all

habitats within a home range of Red-cockaded were not of equal value to the birds, our third hypothesis was that home-range size was related to habitat quality. Possibly, the occurrence of young pine stands and hardwood stands increased home-range size because they took up space but contributed little in the way of food. Also, home ranges composed mostly of older pines might be smaller than those with mostly younger pines.

For some group-living birds, territory or home-range size increased directly with group size (Parry 1973, MacRoberts and MacRoberts 1976, Woolfenden and Fitzpatrick 1978). Thus, a fourth hypothesis was that group size was directly related to home-range size. Larger groups could possibly defend larger ranges or perhaps larger ranges could support larger groups.

TABLE 4. Results of regressions between year-round range size of study groups and the population density surrounding study groups;  $n = 24$  for all models.

Regression model	R <sup>2</sup>	P
1. Home range = 106.79 - 3.71 (number groups)	0.25	0.01
2. Home range = 26.42 + 0.3830 (ha habitat in 2 km <sup>2</sup> /number groups)	0.70	0.0001
3. Total range = 124.93 - 3.86 (number groups)	0.18	0.04
4. Total range = 37.65 + 0.4298 (ha habitat in 2 km <sup>2</sup> /number groups)	0.57	0.0001

<sup>a</sup> Hectares of pine and pine hardwood stands  $\geq 20$  yr old within 2 km of nest cavity. For the three groups that did not nest, the current nest cavity of the breeding male was used.

TABLE 5. Results of regressions between year-round home-range size of study groups and variables associated with habitat quality within ranges;  $n = 24$  for all comparisons.

Dependent variable	Independent variable	$R^2$	$P <$
1. Home range	pine basal area <sup>a</sup>	0.06	0.25
	total basal area		
2. Home range	pine basal area <sup>a</sup>	0.002	0.82
	home range		
3. Home range	nonpine basal area <sup>a</sup>	0.06	0.24
	home range		
4. Home range	ha pine stands <20 yr old	0.09	0.50
	home range		
5. Home range	ha pine stands >40 yr old	0.003	0.81
	home range		
6. Home range	ha pine stands >60 yr old	0.06	0.24
	home range		
7. Home range	number stems <13 cm <sup>b</sup>	0.21	0.03
	home range		

<sup>a</sup> Stems  $\geq 13$  cm dbh.

<sup>b</sup> Stems, all species, >3 but  $\leq 13$  cm dbh.

*Foraging resources and size of home ranges.*—As an index to the quantity of foraging resources in each range, we estimated basal area of pines  $\geq 13$  cm dbh in each year-round home range (Table 3). Red-cockadedes foraged almost exclusively on live pines and preferred those  $\geq 13$  cm dbh (Hooper and Lennartz 1981). Among year-round home ranges, there was an 11-fold difference in the minimum and maximum pine basal area. Also, a direct relationship was found between year-round home-range size and pine basal area ( $R^2 = 0.68$ ,  $P < 0.0001$ ). Thus, contrary to the foraging-resource hypothesis, pine basal area was highly variable among home ranges, and home-range size increased directly with basal area. These results are evidence against the hypothesis that year-round home ranges, regardless of size, contain essentially the same quantity of foraging resources. They support the alternative idea that some groups had more resources than needed for occupancy of their home ranges. Surplus resources, however, could possibly play a role in group size, reproductive success, and creation of new territories (Woolfenden and Fitzpatrick 1978).

*Population density and size of home ranges.*—The number of active groups within 2,000 m of the nest tree of each study group varied from 1 to 22. The relationship between home-range size and number of groups, however, was weak

(Table 4, model 1). Because salt marshes, open water, and large hardwood swamps occurred within some of the 2,000-m-radius circles surrounding study groups, it seemed reasonable to adjust the population density for these areas that had little or no value to the woodpecker. When this adjustment was made, 70% of the variation in home-range size was associated with population density (Table 4, model 2). These results support the hypothesis that home-range size was inversely related to population density, relative to available habitat. Thus, it appears that home-range size was primarily a result of the number of groups in an area dividing the amount of available habitat.

*Habitat quality and size of home ranges.*—Seven independent variables, possibly related to habitat quality, were derived from various measurements of the habitats within each home range. Means and ranges for these measurements are presented in Table 2, and the independent variables are defined in Table 5. The mean number of stems >3 but <13 cm dbh per ha had the only significant relationship to size of home range, but only 21% of the variation in home-range size was associated with this variable. No two-variable regression involving different measures of habitat quality was significant. In multiple regression models involving population density, however, both mean number of stems (for all species) per ha >3 but

TABLE 6. Multiple regression models of the form:  $y = a + b_1x_1 + b_2x_2$ ; where  $y$  is the year-round home range in ha,  $x_1$  is ha of habitat within 2 km of study group's nest cavity ÷ number of groups within 2 km, and  $x_2$  varies according to table;  $n = 24$  for all models.

	$x_2$	$a \pm SE^a$	$b_1 \pm SE$	$b_2 \pm SE$	$R^{2b}$	$P^c$
1.	$\frac{\text{pine basal area}^d}{\text{total basal area}}$	$86.78 \pm 23.33$	$0.3866 \pm 0.0475$	$-76.74 \pm 28.48$	0.77	0.01
2.	$\frac{\text{number stems } < 13 \text{ cm}^e}{\text{home range}}$	$10.77 \pm 8.78$	$0.3542 \pm 0.0489$	$21.85 \pm 8.16$	0.77	0.01
3.	Group size <sup>f</sup>	$-11.84 \pm 12.87$	$0.4057 \pm 0.0449$	$9.84 \pm 2.92$	0.80	0.003

<sup>a</sup> Standard error.

<sup>b</sup>  $R^2$  for  $y = a + b_1x_1$  was 0.70.

<sup>c</sup> Significance of  $x_2$  contribution in presence of  $x_1$ .  $P =$  probability of larger value of  $t$  if  $b_2 = 0$ .

<sup>d</sup> Basal area for stems  $\geq 13$  cm dbh.

<sup>e</sup> Number of stems, all species  $> 3$  but  $< 13$  cm dbh.

<sup>f</sup> Mean monthly group size.

$< 13$  cm dbh and pine basal area divided by total basal area (for stems  $\geq 13$  cm dbh) produced a significant reduction in the variation in size of home range (Table 6, models 1 and 2). Thus, we cannot reject the hypothesis that habitat quality influenced range size. At least as we measured it, however, habitat quality was not a very powerful determinant of home-range size of the groups we studied.

*Group size and size of home ranges.*—The groups we studied varied in size throughout the year. Following nesting, they averaged 4.3 birds, with 2–9 birds per group. Before nesting, groups averaged 2.6 birds, with 2–5 birds per group. Regression analysis did not reveal a linear relationship between mean monthly group size and year-round home-range size when other factors were not considered ( $R^2 = 0.06$ ,  $P > 0.36$ ,  $n = 24$ ). In addition, home ranges of groups with helpers averaged 72.4 ha ( $n = 12$ ), and ranges of groups without helpers averaged 68.2 ha ( $n = 12$ ). These means did not differ significantly ( $t = 0.29$ ,  $df = 22$ ,  $P > 0.50$ ).

Group size did appear to be significantly related to year-round home-range size when a measure of the surrounding population density was incorporated into the regression model (Table 6, model 3). In other words, if population densities were the same around all home ranges, group size by itself would probably have a significant effect on year-round home-range size.

Size of ranges for the different sampling periods did not appear to be related to group size in our study. Based on separate regression analyses, group size (maximum number of

birds in group during period) accounted for a nonsignificant amount of the variation in range sizes for each of the five periods ( $R^2 \leq 0.11$ ,  $P > 0.12$ ,  $n = 21$ –24). Skorupa (1979), however, reported a positive relationship between group size and size of fall home ranges ( $R^2 = 0.99$ ,  $n = 5$ ), and Sherrill and Case (1980) found a nonsignificant trend ( $r = 0.75$ ,  $n = 4$ ) between group size and home-range size for December–February. Combining their data to increase sample size resulted in a weak relationship ( $R^2 = 0.04$ ,  $n = 9$ ). Their data points fell within the clustering of our data points; thus, there is little evidence in our data or data in the literature that group size was related to size of home-ranges determined during different periods of the year.

#### CONCLUSIONS

Groups of Red-cockaded Woodpeckers were territorial toward adjacent groups throughout the year, and the observed territorial boundaries were generally distinct. Complete territories were not observed, however, possibly because of their large size and the probability that some groups had not established territorial boundaries in portions of their home range that lacked proximity to other groups. The size of year-round home ranges was apparently determined primarily by the groups in a local area dividing the available habitat within that area. Habitat quality and group size were weakly related to year-round home-range size. The quantity of foraging resources increased directly with size of home range, supporting the idea that some groups had access to more re-

sources than necessary for year-round occupancy.

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#### LITERATURE CITED

- BAKER, W. W. 1971. Progress report on life history studies of the Red-cockaded Woodpecker at Tall Timbers Research Station. Pp. 44-59 in *The ecology and management of the Red-cockaded Woodpecker* (R. L. Thompson, Ed.). Tallahassee, Florida, Bureau Sport Fish. and Wildl. Tall Timbers Res. Sta.
- BARRY, J. M., & W. T. BATSON. 1969. The vegetation of the Baruch Plantation, Georgetown, South Carolina in relation to soil types. *Castanea* 34: 71-77.
- BEST, L. B. 1977. Territory quality and mating success in the Field Sparrow (*Spizella pusilla*). *Condor* 79: 192-204.
- CROSBY, G. T. 1971. Home range characteristics of the Red-cockaded Woodpecker in north-central Florida. Pp. 60-73 in *The ecology and management of the Red-cockaded Woodpecker* (R. L. Thompson, Ed.). Tallahassee, Florida, Bureau Sport Fish. and Wildl. Tall Timbers Res. Sta.
- EWALD, P. W., G. L. HUNT, JR., & M. WARNER. 1980. Territory size in Western Gulls: importance of intrusion pressure, defense investments, and vegetation structure. *Ecology* 6: 80-87.
- GASS, C. L., G. ANGEHR, & J. CENTA. 1976. Regulation of food supply by feeding territoriality in the Rufous Hummingbird. *Can. J. Zool.* 54: 2046-2054.
- HOOPER, R. G., & M. R. LENNARTZ. 1981. Foraging behavior of the Red-cockaded Woodpecker in South Carolina. *Auk* 98: 321-334.
- JACKSON, J. A., M. R. LENNARTZ, & R. G. HOOPER. 1979. Tree age and cavity initiation by Red-cockaded Woodpeckers. *J. Forestry* 77: 102-103.
- KNAFTON, R. W., & J. R. KRIBBS. 1974. Settlement patterns, territory size, and breeding density in the Song Sparrow (*Melospiza melodia*). *Can. J. Zool.* 52: 1413-1420.
- KRIBBS, J. R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. *Ecology* 52: 2-22.
- LAY, D. W., E. W. MCDANIEL, & D. N. RUSSELL. 1971. Status of investigations of range and habitat requirements. Pp. 74-77 in *The ecology and management of the Red-cockaded Woodpecker* (R. L. Thompson, Ed.). Tallahassee, Florida, Bureau Sport Fish. and Wildl. Tall Timbers Res. Sta.
- LIGON, J. D. 1970. Behavior and breeding biology of the Red-cockaded Woodpecker. *Auk* 87: 255-278.
- MACROBERTS, M. H., & B. R. MACROBERTS. 1976. Social organization and behavior of the Acorn Woodpecker in central coastal California. *Ornithol. Monogr.* 21.
- MORSE, D. H. 1976. Variables affecting the density and territory size of breeding spruce-woods warblers. *Ecology* 57: 290-301.
- MYERS, J. P., P. G. CONNORS, & F. A. PITELKA. 1979. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. *Auk* 96: 551-561.
- NESBITT, S. A., D. T. GILBERT, & D. B. BARBOUR. 1978. Red-cockaded Woodpecker fall movements in a Florida flatwoods community. *Auk* 95: 145-151.
- PARRY, V. 1973. The auxiliary social system and its effect on territory and breeding in Kookaburras. *Emu* 73: 81-100.
- PATTERSON, G. A., & W. B. ROBERTSON. 1981. Distribution and habitat of the Red-cockaded Woodpecker in Big Cypress National Preserve, Homestead, Florida, Nat. Park Serv., South Florida Res. Center, Rep. T-613.
- SALOMONSON, M. G., & R. P. BALDA. 1977. Winter territoriality of Townsend's Solitaires (*Myadestes townsendi*) in a piñon-juniper-ponderosa pine ecotone. *Condor* 79: 148-161.
- SCHOENER, T. W. 1968. Sizes of feeding territories among birds. *Ecology* 49: 123-141.
- SEASTEDT, T. R., & S. F. MACLEAN. 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in arctic Alaska. *Auk* 96: 131-142.
- SHERRILL, D. M., & V. M. CASE. 1980. Winter home ranges of 4 clans of Red-cockaded Woodpeckers in the Carolina Sandhills. *Wilson Bull.* 92: 369-375.
- SKORUPA, J. P. 1979. Foraging ecology of the Red-cockaded Woodpecker in South Carolina. Unpublished M.S. thesis, Davis, California, Univ. California.
- , & R. W. MCFARLANE. 1976. Seasonal variation in foraging territory of Red-cockaded Woodpeckers. *Wilson Bull.* 88: 662-665.
- SOUTHERN, H. N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). *J. Zool.* 162: 197-285.
- WIENS, J. A. 1973. Interterritorial habitat variation in Grasshopper and Savannah sparrows. *Ecology* 54: 877-884.
- WILSON, E. O. 1975. *Sociobiology: the new synthesis*. Cambridge, Massachusetts, Belknap Press.
- WOOD, D. A. 1977. Status, habitat, home range, and notes on the behavior of the Red-cockaded Woodpecker in Oklahoma. Unpublished M.S. thesis, Stillwater, Oklahoma, Oklahoma State Univ.
- WOOLFENDEN, G. E., & J. W. FITZPATRICK. 1978. The inheritance of territory in group-breeding birds. *BioScience* 28: 104-108.