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# HABITAT USE AND TERRITORY CHARACTERISTICS OF RED-COCKADED WOODPECKERS IN CENTRAL FLORIDA

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ABSTRACT.—Habitat use and territory characteristics of six groups of Red-cockaded Woodpeckers (*Picoides borealis*) were studied in central Florida at the southern margin of the species' range. Compared to more northerly habitats, pine stands were lower in density, younger, or of smaller size class. A suite of foraging patterns compensates for the resource-poor habitat. An analysis of population density and available habitat indicates that Red-cockaded Woodpeckers in central Florida require larger territories and are more sensitive to population pressure in poorer-quality habitat. These results indicate that minimal territory size may vary depending on the quality of the habitat. A regression model of stand size, territoriality, cavity tree location, and stand structure effects accounts for 93% of pine stand use. Sensitivity analyses of model components indicate that, after the effect of stand size, stand use is most sensitive to the effects of territoriality, followed by stand age, stand density, and cavity-tree location. Thus, stand use depends simultaneously on the distance of the stand from the cavity trees and territorial interaction sites and pine stand age and density. *Received 13 June 1986, accepted 21 Oct. 1986.*

The Red-cockaded Woodpecker (*Picoides borealis*) is endemic to pine forests of the southeastern United States and is currently considered endangered because of loss of habitat. Red-cockaded Woodpeckers are nonmigratory and occupy territories that are defended year round and that contain nest sites and foraging habitats. Nesting habitat is associated with mature (≥70 years) pine, whereas foraging habitat is more variable and includes a broader range of age classes (Lennartz and Henry 1985).

Factors affecting habitat use and territory characteristics have been studied thoroughly in South Carolina near the middle of the species' distribution (Hooper et al. 1982, Lennartz and Henry 1985). Habitat use and home range characteristics have been described for populations in central and south Florida at the southern margin of the species' distribution (Nesbitt et al. 1978, 1983; Patterson and Robertson 1981). Compared to more northerly populations, habitats used by southern birds are of poorer quality (less dense and smaller size trees), and Nesbitt et al. (1983) suggested that habitat quality is important in determining home range size. No previous study has quantitatively evaluated the influences of population pressure and habitat quality on populations at the southern margin of the species' range in poor-quality habitats. Furthermore, the

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relative importance of pine stand age, density, territoriality, and cavity-tree location on foraging ecology has not been analyzed. This paper evaluates factors affecting habitat use and territory characteristics for six groups of Red-cockaded Woodpeckers from central Florida and compares this resource-poor population to more northerly populations occupying better habitat.

## METHODS

The 1328-ha study area, the Curtis H. Stanton Energy Center, is 21 km southeast of Orlando, Florida. Observations were conducted for 2 years, beginning in the fall of 1980, on group movements during the fall (September–December); winter (January–March); and summer (June–August) (DeLotelle et al. 1983). A total of 722 h of observations was made on six groups in the study area (Group A: 150 h; Group B: 75 h; Group C: 150 h; Group D: 149 h; Group H: 152 h; Group G: 46 h), averaging 7.8 h of observation per day. An additional 17 groups (1 group per 139 ha) occupied surrounding habitat. As suggested by Nesbitt (pers. comm.), groups were usually observed from morning to well into the late afternoon to ensure that we had observed the farthest point from the cavity trees the birds had reached on foraging trips. On other occasions groups were followed from near noon to roosting.

Here, we use the more traditional definitions of territory and home range (Burt 1943) to describe the defended area and total foraging range, respectively. The above two terms are analogous to home range and total observed range, respectively, used by Hooper et al. (1982) (Hooper, pers. comm.). Movements of groups, marked with color-coded plastic leg bands (N = 27), were recorded at 5-min intervals on photocopies of aerial photographs (scale 1:4800). Home ranges were estimated by connecting peripheral points of group movements. Group interactions were recorded on the photocopies, and territorial boundaries were determined following the procedure of Hooper et al. (1982). Territory size and configuration were based primarily on the locations of territorial boundaries. No territorial interactions were observed in certain segments of the home range. These areas were deleted from the territory if they were visited only once by the resident group. Disputes as determinants of territorial boundaries, and thus territory size, have been used in many avian studies (Myers et al. 1979, Hooper et al. 1982). Although Groups B and G were observed for fewer hours, each of these two groups shared three territorial boundaries with other groups studied. Interactions were observed involving Groups B or G with their neighbors along these shared boundaries, thus providing reliable estimates of their territory configurations.

Vegetation characteristics, including pine stand age and density, were determined by DeLotelle et al. (1983). A 1-in.$^2$ grid, representing a 1.5-ha plot, was traced on the aerial photographs, from which 72 grids were analyzed for tree density using a Leitz MS-27 2× and 3× stereoscope. Twenty-five plots were field-inspected for dbh, tree density, age, and basal area. Territory configurations were superimposed on the site vegetation map to obtain the stand characteristics of each territory. Stand use was determined by summing all observations for a particular pine stand.

To evaluate the effect of population density on territory size, territory size was regressed against area of suitable habitat within a 2000-m radius of cavity trees of each group divided by population density within the area (i.e., mean available habitat per group) (Hooper et al. 1982). Suitable habitat included all pine forests and all small cypress stands with all clearcuts and hardwood swamps excluded. Central Florida and South Carolina populations (Hooper et al. 1982) were compared using a 2-sample $t$-test for slopes of regression lines.

Indices of the influences of cavity-tree location and territorial behavior on stand use were measured as the distances from the midpoint of each stand to the cavity trees and the focal point of territorial activity, respectively. For each group, the focal point of territorial activity represented the mean of the coordinates for all observed group interactions. The midpoint of cavity-tree location was taken from DeLotelle et al. (1983). Cavity tree and territory distances were standardized by dividing by the average diameter of each territory.

Observed stand use, expressed as a percent of total foraging within the entire territory, was regressed against stand size using SAS (SAS Institute 1985). The residuals (observed minus predicted stand use) from this regression are independent of stand size and are used in further analysis (Afifi and Clark 1984). A regression model of differential stand use (observed stand use residuals) was constructed employing distance from the cavity-tree location to the midpoint of each stand, distance from the territorial focal point to the midpoint of each stand, and pine stand structure. Differential stand use as a dependent variable is not the same as stand preference based on use-availability ratios used elsewhere (see Wood et al. 1985).

Several procedures were used to solve violations of the nonlinearity, interaction, and multicolinearity assumptions of multiple linear regression. The natural logarithmic transformation was performed on stand characteristics, including age, density, and dbh. An interaction term often takes into account the non-additive effects of two regression factors (Afifi and Clark 1984). We evaluated a cavity-tree distance times territory distance (see above) interaction term and age or dbh times density interaction term. The model variables were then subjected to principal component analysis to remove the effects of multicolinearity. The principal component analysis used the correlation matrix which is equivalent to the use of standardized variables and allows the direct interpretation of the principal component loadings (Afifi and Clark 1984).

Evaluation of alternative models and transformations was based on plots of adjusted $R^2$ versus the number of variables in the model and on plots of residuals versus each of the regression factors in a given model. For models with the same number of regression factors, model selection was based on the best subset regression method (Afifi and Clark 1984).

To perform the sensitivity analyses, two regression equations of the original variables were obtained by multiplying the loadings for each principal component by their respective multiple regression parameters and re-collecting terms in original variable order. The two graphical sensitivity analyses, employing the standardized regression equations, were stand age versus density and territory focal point versus cavity-tree location at given levels of differential stand use. In both solutions the remaining variables were set to their mean values. Because of the use of the correlation matrix in the principal component analysis, the mean value of all variables is zero, so that only the pair of variables of interest remain in the solution to the regression equation. The whole-model sensitivity analyses solved the regression equation for the variable of interest and then varied each variable by a fixed amount (Smith 1970). The intercept form of the regression equation was obtained from the standardized equation by factoring the original variable means and standard deviations from the regression coefficients.

## RESULTS

*Home range and territory use.*—Group activity during daily foraging movements was similar to that reported by Nesbitt et al. (1983). This included a congregation period in the morning accompanied by much vocalization and flying about the cavity tree stand. Normally, group members followed a regular pattern consisting of a foraging trip away from the

TABLE 1

TERRITORY SIZE, AVAILABLE HABITAT, AND TERRITORIAL BEHAVIOR CHARACTERISTICS OF RED-COCKADED WOODPECKERS ON THE STANTON ENERGY CENTER, FLORIDA

| | | | | | | | Extraterritorial movements | |
|---|---|---|---|---|---|---|---|---|
| Group | Home range (ha) | Territory (ha) | Number of groups[a] | Available habitat[b] (ha) | Interval between interactions[c] (h) | Focal point distance from cavity tree (m) | Interval between trips[c] (h) | Mean length (m) |
| A | 198.8 | 154.9 | 4 | 170.6 | 30.0 | 763.2 | 25.0 | 368.2 |
| B[d] | 157.8 | 147.0 | 6 | 156.6 | 15.0 | 586.4 | 18.8 | 333.5 |
| C | 116.2 | 101.5 | 10 | 103.7 | 18.8 | 320.7 | 18.8 | 297.8 |
| D | 123.1 | 105.7 | 10 | 107.1 | 14.9 | 357.2 | 18.8 | 190.5 |
| G[e] | ND | 92.7 | 11 | 93.8 | 11.5 | 228.0 | 15.3 | 252.4 |
| H | 154.2 | 94.7 | 9 | 108.0 | 11.7 | 71.7 | 9.5 | 220.4 |
| Mean | 150.0 | 116.1 | 8.3 | 123.3 | 17.0 | 387.9 | 17.7 | 277.1 |
| SD | 32.9 | 27.5 | 2.7 | 31.9 | 6.91 | 249.5 | 5.1 | 196.3 |

[a] Number of groups within 2000-m radius of cavity trees.

[b] Hectares of mean available habitat within 2000-m radius of cavity trees (i.e., total suitable habitat/number of groups).

[c] Indicates the number of hours required to observe either a territorial interaction or extraterritorial movement.

[d] Group B abandoned cavity trees and territory prior to the nesting season in 1982.

[e] No home range data during fall and summer; not included in mean for home range.

cavity trees in the morning with a return to the vicinity of roosting sites later in the day. While in the vicinity of cavity trees, Red-cockaded Woodpeckers were engaged in cavity maintenance, protection of the cavities from intruders, and construction of new cavities. In stands farther from the cavity trees, Red-cockaded Woodpeckers' activities consisted primarily of foraging, resting, and scanning and listening for predators and neighboring groups of woodpeckers. In some of these more distant stands, birds often encountered other groups of Red-cockaded Woodpeckers or initiated forays into their neighbors' habitats.

Home range size averaged 150.0 ha (Table 1). Mean territory size was 116.1 ha and accounted for 77.4% of the mean home range. Habitats within territories consisted of pine flatwoods (88.1%), cypress domes and bayheads (8.6%), and wet prairie and open areas (3.3%). Mean amount of pine flatwoods per territory was 102.3 ha, which included a mean of 9768 pine stems ($\geq$6.0 cm dbh). Mean pine basal area per territory was 267.6 $m^2$ (range = 204.6–355.8 $m^2$). Cypress trees constituted about 40% of the total stems and basal area in the territories. Pine stands in the territories (Table 2) consisted mostly of younger trees ranging in age from approximately 17 years to 53 years. An older age class much lower in density and averaging 110 years in age was included in many stands. Of the pine stands in the territories, 59% were logged for pulpwood during

TABLE 2

PINE STAND AND FORAGING PARAMETERS FOR SIX GROUPS OF RED-COCKADED WOODPECKERS ON THE STANTON ENERGY CENTER, FLORIDA

| Group | No. stands in territory | Mean stand size (ha) | Mean stand density[a] (ha) | Mean dbh (cm) | Mean age of trees (years) | Mean % time observed foraging | Mean distance of stand from cavity trees (m) | Mean distance of stand from territorial focal point (m) |
|---|---|---|---|---|---|---|---|---|
| A | 6 | 20.5 ± 12.0[b] | 97.0 ± 86.5 | 17.4 ± 3.2 | 46.3 ± 26.1 | 16.7 ± 14.4 | 524.6 ± 229.6 | 770.1 ± 304.9 |
| B | 4 | 32.7 ± 30.6 | 154.9 ± 118.9 | 15.4 ± 2.6 | 34.8 ± 11.1 | 25.0 ± 25.8 | 556.7 ± 205.0 | 741.2 ± 270.1 |
| C | 5 | 19.3 ± 21.1 | 159.7 ± 131.8 | 18.1 ± 4.3 | 48.2 ± 31.7 | 20.0 ± 14.2 | 403.6 ± 174.0 | 495.3 ± 243.9 |
| D | 7 | 12.8 ± 16.0 | 167.1 ± 110.4 | 14.9 ± 3.7 | 45.1 ± 26.5 | 14.3 ± 18.3 | 479.0 ± 223.6 | 397.4 ± 161.8 |
| G | 5 | 17.3 ± 17.5 | 141.1 ± 111.2 | 19.9 ± 3.1 | 56.6 ± 28.3 | 20.0 ± 24.3 | 395.0 ± 139.1 | 384.3 ± 193.4 |
| H | 4 | 20.8 ± 22.6 | 185.2 ± 135.4 | 17.9 ± 4.8 | 52.0 ± 36.7 | 25.0 ± 24.1 | 465.5 ± 263.9 | 385.8 ± 192.1 |

[a] Includes all pine stems ≥6 cm dbh.

[b] Mean ± SD.

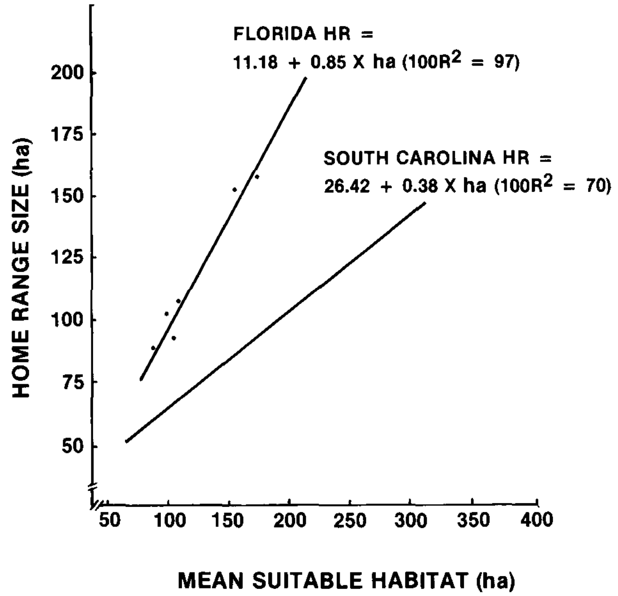

FIG. 1. Comparison of regressions for home range size versus area of mean suitable habitat within 2000 m for central Florida and South Carolina populations; N = 6 for central Florida and N = 24 for South Carolina (Hooper et al. 1982).

the past 10 years and had densities ranging from 32 to 122 stems/ha. The remaining stands were unlogged (densities from 92 to 319 stems/ha) and constituted 41% of the territories.

Territory sizes and surrounding population densities were variable (Table 1). Territories occupied almost all ($\bar{x}$ = 95%; range = 88–99%) of the available habitat, whereas home ranges overlapped and accounted for 119% of available habitat. Furthermore, especially in the denser population areas, home ranges overlapped surrounding territories. Territory size was positively related to the area of suitable habitat within a 2000-m radius of each group of cavity trees ($R^2 = 0.97$, $P < 0.0001$, N = 6). Thus, the relative amount of available habitat accounts for a significant percent of the variation in territory size in the central Florida populations (Fig. 1). Comparison of the two regression lines for central Florida and South Carolina (Hooper et al. 1982) indicates that the response to population density for the central Florida population was higher than in South Carolina and that it had a significantly steeper slope ($P = 0.005$).

Intergroup conflicts occurred throughout the year except when nestlings were present. Of the 45 group interactions, 94% occurred at or near observed territorial boundaries. The remaining 6% occurred well within territories, usually near the cavity trees. Most group interactions were between closest neighboring groups. The mean number of adjacent groups encountered by each group was 3.6 ± 1.14 [SD]; however, 51% of observed interactions were with a specific neighbor. Thus, the territorial focal point was generally near the territorial boundary with the most frequently encountered neighbor. On several occasions groups were observed to travel up to 950 m from within their territory to intercept an intruding neighbor at the territorial boundary. After interactions, groups usually resumed foraging in nearby stands within their respective territories. There were instances, however, in which territorial boundaries were not respected even when the boundary segment had already been estabished earlier that same day by interacting groups.

In addition, the six groups made a total of 45 forays outside their territories. Of the 45 extraterritorial movements, 37 (82%) were into adjacent territories, and 10 of these were into or approaching neighboring cavity trees. Of the 8 extraterritorial group movements into unoccupied habitat, 75% were into the abandoned territory of Group B and beyond previously observed interaction sites. Mean distance traveled outside the territory was 277.1 ± 196.3 m. The mean distance traveled outside the territory and into unoccupied habitat (465.7 ± 183.8 m) was significantly greater than the mean distance traveled into occupied habitat (217.3 ± 166.0 m) (2-sample $t$-test, $P = 0.006$).

*Habitat use.*—Longleaf pine stands were selected for foraging 90% of the time compared with 10% for cypress stands. Cypress domes were important seasonal foraging sites, and their use generally exceeded their availability for most of the study-site groups (10% use vs 6% availability). Small, open-canopied cypress domes (64% of the cypress area) accounted for 89% of the cypress foraging. Unlogged pine stands occupied 41% of the home ranges, but accounted for 59% of the foraging observations. Stand use was significantly correlated with pine stand size (use = 3.87 + 0.79 × size; $R^2 = 0.63$, $P = 0.0001$, $N = 31$).

The multiple regression (Table 3) of differential stand use on the principal components (PRIN 1–6) of age, density, age times density, cavity-tree location, territorial focal point, and cavity tree times territory was significant ($R^2 = 0.81$, $P = 0.0001$, $N = 31$). This model accounts for 81% of the 37% (100–63%) variability unexplained by size, so that 93% (63%+ 81% × 37%) of stand use is explained. The large value of adjusted $R^2$ (0.77) compared to unadjusted $R^2$ indicates an unbiased regression model and parsimonious choice of variables. Principal Components 1, 2, 4, and 5 are significant, and 3 is nearly significant. The variable loadings for the principal components appear to have readily defined biological interpretations (see Table 3). Cavity-tree location and territoriality are localizing

## TABLE 3
## MULTIPLE REGRESSION ON PRINCIPAL COMPONENTS

| | Principal components | | | | | |
|---|---|---|---|---|---|---|
| | PRIN 1 | PRIN 2 | PRIN 3 | PRIN 4 | PRIN 5 | PRIN 6 |
| Proportion | 0.4740 | 0.2705 | 0.1764 | 0.0726 | 0.0060 | 0.0004 |
| Eigenvectors | | | | | | |
| ln D[a] | 0.2078 | 0.7296 | −0.0476 | −0.1513 | −0.0357 | 0.6310 |
| ln A | −0.3856 | −0.3101 | 0.6170 | 0.1984 | −0.0433 | 0.5772 |
| ln D*ln A[b] | −0.1733 | 0.5504 | 0.6300 | 0.0672 | 0.0495 | −0.5129 |
| C | 0.5057 | 0.0044 | 0.0560 | 0.7790 | 0.3642 | 0.0400 |
| T | 0.4667 | −0.2269 | 0.3704 | −0.5711 | 0.5162 | 0.0288 |
| C*T | 0.5519 | −0.1307 | 0.2823 | −0.0142 | −0.7715 | −0.0563 |
| Interpretation[c] | C, T, C*T | D, D*A | A, D*A | C | T | D |
| | Multiple regression on principal components | | | | | |
| P value | 0.0001 | 0.0001 | 0.0594 | 0.0265 | 0.0001 | 0.4445 |
| Partial $R^2$ (Type II) | 0.2906 | 0.2856 | 0.0299 | 0.0426 | 0.1548 | 0.0046 |
| Parameter estimate | −3.6236 | 4.7554 | 1.9063 | 3.5466 | −23.7497 | 14.9198 |
| Standard error | 0.5887 | 0.7794 | 0.9650 | 1.5040 | 5.2258 | 19.2048 |

[a] ln = The natural logarithmic function.

[b] Interaction terms are denoted by an asterisk between symbols.

[c] A = Standard age (years); D = Stand density (stem/ha); C = Distance (m) from the cavity-tree location to the midpoint of a stand divided by home range diameter; T = Distance (m) from the territorial focal point to the midpoint of a stand divided by home-range diameters.

effects on stand use. Principal Components 1, 4, and 5 can be interpreted as a localizing aspect of differential stand use, whereas Principal Components 2 and 3 are habitat quality aspects of differential stand use. Based on the proportion of variance explained by each principal component, the partial $R^2$s, and parameter estimates for each principal component, the localizing aspect accounts for the majority of variation in the differential stand use regression model, whereas the habitat quality aspect is less important (Table 3). A regression of the residuals from this model versus stand size is not significant ($P = 0.34$), thus indicating that none of the model variables interacts with stand size. A regression model with dbh in place of age was similar in all respects, but provided a slightly poorer fit ($R^2 = 0.79$).

The original variable form of the standardized regression of differential stand use (DSU) is:

$$\begin{aligned}\mathrm{DSU} = {} & 0.0 + 12.34 \ln \mathrm{D} + 11.43 \ln \mathrm{A} - 4.13 \ln \mathrm{A} \ln \mathrm{D} - 6.90\,\mathrm{C} \\ & -15.78\,\mathrm{T} + 15.14\,\mathrm{CT} \qquad \text{(Eq. 1)}\end{aligned}$$

The regression equation for the intercept form of the original variables for differential stand use is:

$$\begin{aligned}\mathrm{DSU} = {} & -91.37 + 15.84 \ln \mathrm{D} + 21.87 \ln \mathrm{A} - 1.78 \ln \mathrm{D} \ln \mathrm{A} \\ & -29.63\,\mathrm{C} - 51.33\,\mathrm{T} + 39.47\,\mathrm{CT} \qquad \text{(Eq. 2)}\end{aligned}$$

(See Table 3 for explanation of symbols.)

Differential stand use is not equally sensitive to the original variables in the regression model (Eq. 2). For a 1% increase from the mean of each variable, the changes in differential stand use for density, age, cavity tree location, and territorial effects are 0.0919, 0.1318, −0.0361, and −0.1735, respectively, corresponding to relative sensitivities (Smith 1970) of 53.0, 76.0, 20.0, and 100%. Thus, although the localizing effects are more variable than habitat quality (Table 2), and the regression model accounts for proportionally more of this greater variability (Table 3), the model is, overall, slightly more sensitive to habitat quality.

The relative sensitivity implications of the two localizing and two quality aspects of the regression model (Eq. 1) best can be evaluated graphically. Differential stand use depends simultaneously on the distance of the stand from the cavity trees and the focal point of territory activity (Fig. 2) and simultaneously on pine stand age and density (Fig. 3). For each figure, the zero or positive and negative differential stand use lines correspond to the regression line or parallel lines for observed stand use versus stand size.

Differential stand use is not equally sensitive to stand distance from the cavity trees and territorial focal point (Fig. 2). Based on a differential

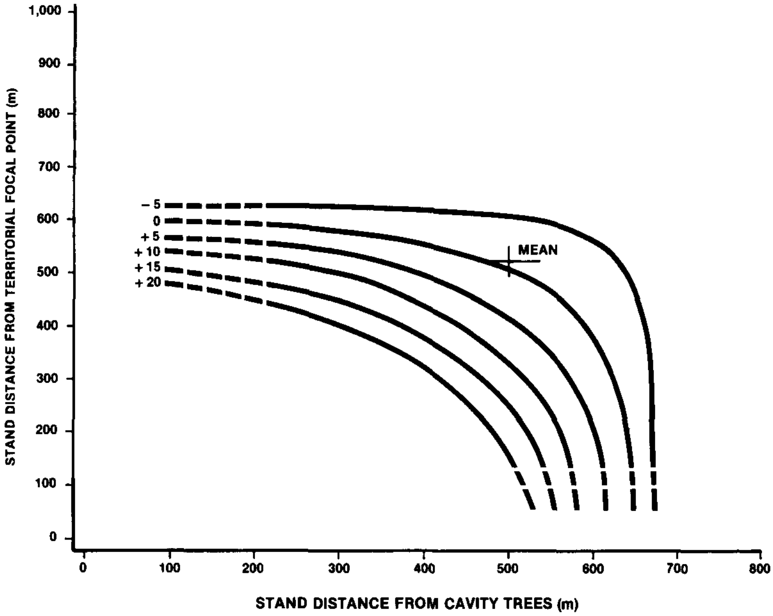

FIG. 2. Isoclines of differential stand use in relation to distance from the midpoint of a stand to the cavity trees and territorial focal point. Dashed line segments are beyond range of data.

stand use change from +5 to −5%, the changes in stand distance from the mean cavity tree location and mean territorial focal point are 315 and 645 m for cavity tree (81% change) and 432 and 599 m for territory (39% change). Thus, differential stand use is twice as sensitive to territorial focal point as it is to cavity tree location where the model can be expected to be most stable. For stands closer to the cavity trees, differential stand use is highly sensitive to territorial focal point. Conversely, for stands near the territorial focal point, differential stand use is more sensitive to cavity tree location. Differential stand use curves above −5% do not have the same form and are omitted from the figure.

Differential stand use is an inverse nonlinear function of pine stand age and density (Fig. 3). For a given age, differential stand use increases with density; for a given density, differential stand use increases with age. With respect to a given level of differential stand use, however, there is a wide range of combinations of pine stand ages and densities which are equivalent. For a change in differential stand use from +5 to −5%, the changes from the mean age and mean density are 166 and 89 stems ha for density (87% change) and 52 and 33 years for age (58% change). Thus, differential

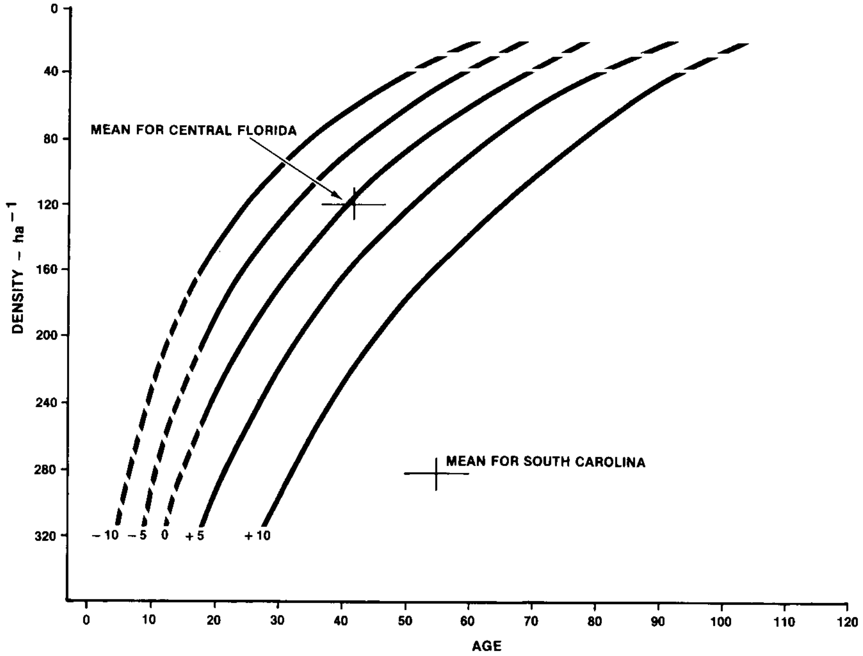

FIG. 3. Isoclines of differential stand use in relation to pine stand age and tree density. Note that the scale for density is inverted. Dashed line segments are beyond range of data.

stand use is 1.5 times more sensitive to age than it is to density. For denser stands, differential stand use is more sensitive to age. Conversely, for younger stands, differential stand use is slightly more sensitive to density.

## DISCUSSION

*Home range and territory use.*—The central Florida site, although similar to habitats in more northerly latitudes, supports less dense stands of pines and smaller trees (DeLotelle et al. 1983). In addition to lower site productivity, pine stands have been subjected to logging activity over the last century. Moreover, study site habitats are similar to habitats containing Red-cockaded Woodpeckers elsewhere in central and south Florida (Nesbitt, pers. comm.).

Red-cockaded Woodpeckers in this central Florida site compensate for occupying resource-poor habitat in several ways. Average home range and territory sizes in central Florida are larger than average home range and territory sizes in South Carolina (Hooper et al. 1982) where habitat is better. Home range sizes in this study are closer to those reported by

Nesbitt et al. (1978, 1983) and Patterson and Robertson (1981) in peninsular Florida, who described home ranges of 58.4 to 213.2 ha. Available pine basal area in the current study site is similar to that available to woodpecker populations in south Florida (Nesbitt et al. 1983), which ranged from 265 to 485 $m^2$ ($\bar{x} = 7.0$ $m^2$/ha). Central Florida group territories contained a mean pine basal area of 267.6 (2.3 $m^2$/ha), whereas Hooper et al. (1982) reported a mean pine basal area of 831.7 $m^2$ (11.8 $m^2$/ha) for 24 territories. Thus, territories and home ranges in central and south Florida are larger, but they contain less pine basal area than do those in South Carolina. Populations in north Florida (Porter 1984) appear intermediate, with home ranges somewhat smaller than central and south Florida and pine basal areas similar to those in South Carolina.

The larger territories and home ranges in central Florida incorporated 95% and 119% (i.e., 19% overlap) of available habitat, respectively, whereas the territories and home ranges in South Carolina incorporated only 64% and 75% of available habitat, respectively (Hooper, pers. comm.). This suggests that for the former, population density is near maximum. Under very similar average population densities (central Florida = 8.3; South Carolina = 8.8 groups/2000-m radius circle), central Florida groups require or use more habitat area for their territories compared to South Carolina groups and appear more constrained by population density in the poorer-quality habitat conditions found in central Florida.

As suggested by Wiens et al. (1985), habitat options for other bird species may become restricted at high population densities, resulting in occupancy of suboptimal territories. Conversely, individuals may use better habitats in areas with low population density (Wiens 1973). For Belted Kingfishers (*Megaceryle alcyon*) Davis (1982) found that habitat quality (i.e., the amount of preferred feeding habitat) had a significant inverse effect on both breeding and nonbreeding territory size, and that reduced population pressure resulted in individual kingfishers incorporating a greater resource base. The rate of incorporation of available habitat by the central Florida population of Red-cockaded Woodpeckers, which is 1.6 times that of the South Carolina population (Fig. 1), can be interpreted as a greater sensitivity of the central Florida population to poorer habitat conditions.

Two characteristics of foraging substrate selection can be interpreted as compensation effects for poor-quality habitat. Central Florida groups foraged on stems as small as 5 cm dbh (DeLotelle et al. 1983), whereas South Carolina groups were seldom observed on stems less than 13 cm dbh (Hooper and Lennartz 1981). More importantly, a larger proportion of foraging use occurred (21% use; 22% availability) on smaller size class stems (5–11 cm dbh) compared to the use of similar size classes (8% use;

55% availability) in South Carolina and north Florida (0.8% use; availability not reported) (Porter 1984). There are practical limits to this compensation, as woodpeckers were never observed to forage on pine stems <5 cm dbh, and those ≥10 cm dbh were preferred (DeLotelle et al. 1983). In addition, groups in central Florida made extensive seasonal use of cypress as an alternate foraging resource, whereas populations in northern Florida and South Carolina are seldom observed to use available hardwoods or cypress. During the fall of 1980, use of cypress was 20% (DeLotelle et al. 1983). Thus, in forests of substantially different densities and available tree sizes, foraging Red-cockaded Woodpeckers showed flexibility in their use of foraging habitats.

The higher frequency of observed extraterritorial foraging and group interactions can also be interpreted as an indication of resource-poor habitat. Myers et al. (1979) suggested that for Sanderlings (*Calidris alba*) it may be important for territorial residents to obtain part of their daily energy from sources away from their own territories. In our study, extraterritorial foraging and group interactions were 50% more common than in South Carolina (Hooper et al. 1982). Furthermore, in the current study groups averaged 277.1 m on extraterritorial trips, while the South Carolina groups averaged only 220.3 m.

*Habitat use.*—Nest- and roosting-site locations and territorial competition are factors influencing the use of habitat in many species. Defense behavior has been observed to influence territory use in other species (Eckhardt 1979, Myers et al. 1979). Territorial influences also affect Red-cockaded Woodpeckers in central Florida, which were observed to cross their territory in response to an intruding group. After such interactions, resident groups continued to forage in the area. In addition, the frequency of territorial interaction is greater in central Florida than South Carolina (Hooper et al. 1982). Thus, the relatively high sensitivity of stand use to territoriality reported here may be less important elsewhere. As inferred by Hooper (pers. comm.) and Seastedt and MacLean (1979), nest site location has an important influence on resource use. Although the effect of territoriality may be less pronounced in more optimal habitat, our results (Fig. 2) suggest that territoriality would remain more important than cavity tree location.

Despite the unbiased strong fit of the regression equation, the sensitivity analysis curves for cavity tree location and territorial focal point change form above −5% (Fig. 2). The change in form could result from behavior not accounted for by the model, or from measurement sources. The change in form may indicate a switch in foraging strategy due to distance effects as reported for the Gila Woodpecker (*Melanerpes uropygialis*) (Martindale 1983). When they were near roosting sites and territorial interaction sites, Red-cockaded Woodpeckers were engaged in foraging activities, but they also performed other activities, such as cavity defense or scanning and listening for neighbors. At greater distances from these two sites, these nonforaging behavioral patterns were less apparent, and foraging was the primary activity. Seasonal changes in foraging patterns may also have influenced the results as reported by Conner (1981) for other woodpeckers. Marked seasonal changes in the foraging use of cypress were observed (DeLotelle et al. 1983), which could have influenced pine stand use. Alternatively, there are several possible measurement sources for the change in form. As is often the case in survey research, there is not a complete distribution of values for each variable with respect to all other variables. Clearly, there is less precision in the measurement of the territorial focal point compared to other parameters. Also, uncertainty exists in the placement of territory boundary segments based on use alone.

The sensitivity analysis shows stand age to be more important than stand density in determining stand use. Analysis of stand preference suggests that age or dbh and density influence stand use (Wood 1983; Porter 1984; Hooper, pers. comm.). Our sensitivity analysis quantifies the greater relative importance of age versus density over most of the range of age and density; however, there exists a range of combinations of ages and densities that are equivalent (Fig. 3). Stand densities in our study were not sufficiently high enough to have the inhibiting effect on stand use that occurs in north Florida (Porter 1984) and South Carolina (Hooper, pers. comm.). For moderately young stands, it is probable that there is an optimum range of densities. Whether age or dbh is more descriptive of differential stand use (or preference) is unknown.

A model of observed habitat use employing multivariate statistical procedures explains 93% of the variation in stand use for a population of Red-cockaded Woodpeckers in central Florida. In addition, sensitivity analyses (Smith 1970) provide a procedure for obtaining further interpretive insight (Wiens and Innis 1974) into the information content of complex regression models. In particular, our sensitivity analysis reveals that differential stand use is most sensitive to the effects of territorality followed by stand age, stand density, and cavity-tree location. This result quantifies suggestions that habitat quality influences stand use (Hooper, pers. comm.; Porter 1984), and indicates clearly that interpretation of stand use requires consideration of the influences of territoriality and the location of cavity trees.

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