DEFINING QUALITY OF RED-COCKADED WOODPECKER FORAGING HABITAT BASED ON HABITAT USE AND FITNESS

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Abstract: Accurate understanding of habitat quality is a critical component of wildlife management. We developed a definition of high-quality foraging habitat for the red-cockaded woodpecker (Picoides borealis), a federally endangered, cooperatively breeding bird species, from analyses of resource selection and habitat use, relationships between fitness measures and habitat features, and an extensive literature review. In the North Carolina Sandhills, use of foraging habitat at the level of individual trees, habitat patches, and forest stands was strongly and positively related to age and size of pines (Pinus spp.). Use of habitat patches and forest stands was greatest at intermediate densities of medium-sized and large pines and was negatively associated with hardwood and pine midstory. Size of red-cockaded woodpecker groups, an important fitness measure for this species, was positively related to density of old-growth pines within the home range and negatively related to density of medium-sized pines and height of hardwood midstory. Similar results were reported by 2 other studies. High-quality foraging habitat for red-cockaded woodpeckers, therefore, contains sparse or no midstory, intermediate densities of medium-sized and large pines, and old-growth pines in at least low densities. Although we documented a relationship between group size and the amount of habitat meeting our definition of “high quality,” we were unable to identify the optimum amount of high-quality habitat to provide per group because most study groups had relatively high high-quality foraging habitat. Both fitness and habitat selection in our study population may be constrained by quality and quantity of foraging habitat. James et al. (2001) recommended, and we strongly agree, that foraging habitat be managed for abundant herbaceous ground cover, low densities of small and medium-sized pines, and moderate densities of large pines. We also stress the importance of old-growth pines in foraging habitat. Because the structure of high-quality foraging habitat is similar to that of high-quality nesting habitat, we recommend that management of these 2 be increasingly integrated.

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Effective management of wild populations is based on accurate understanding and assessment of habitat quality (Van Horne 1983). Habitat quality is assessed by comparing current conditions to a definition or standard of high quality. This definition is a hypothesis that is tested each time habitat components are manipulated and subsequent changes in population status are recorded (James et al. 2001). Increased or optimized fitness (i.e., survival and/or productivity) in response to habitat manipulations is the ultimate indication that high-quality habitat has been accurately defined (Van Horne 1983, Martin 1992, James et al. 2001).

Studies revealing effects on fitness provide the strongest evidence that a specific habitat feature is important to habitat quality. Studies documenting resource selection, or the use of resources in greater proportion than their availability (Manly et al. 1993), provide important information as well, although patterns of resource use are not as compelling as information derived from fitness relationships. Finally, indicators such as species' presence or density reflect habitat quality less accurately (Van Horne 1983, Martin 1992). However, identification of 1 or 2 important habitat components through resource selection or even fitness relationships may still be insufficient for providing a precise and accurate picture of habitat quality. Habitat features interact; therefore, a standard of habitat quality must be multidimensional.

We sought to develop a multidimensional definition of high-quality foraging habitat for red-cockaded woodpeckers. We conducted field research into the effects of habitat characteristics on selection of foraging resources, habitat use, and fitness within our study population in the Sandhills of south-central North Carolina. We summarized results of previous studies reported in the literature, then synthesized our results and those of others to build our definition of habitat quality. A second objective was to identify an optimal quan-

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quantity of high-quality foraging habitat for red-cockaded woodpeckers in the study population.

Current Management of Red-cockaded Woodpeckers

The red-cockaded woodpecker is a federally endangered, cooperatively breeding species endemic to southern pine communities of the southeastern United States. Loss of habitat is a primary cause of the species' endangered status. Longleaf pine (Pinus palustris) woodlands, especially important to red-cockaded woodpeckers, have been reduced to less than 5% of original, pre-colonial cover (Frost et al. 1986, Ware et al. 1993). A second major cause of the species' decline is loss of old pines, required by this species for roosting and nesting (Jackson and Jackson 1986, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Rudolph and Conner 1991), within remaining pine woodlands. A third factor is suppression of fire, once a frequent and integral component of southern pine ecosystems. Fire suppression allows development of hardwood midstory, excessive amounts of which the birds cannot tolerate within habitat used for nesting and roosting (Jackson 1978, Van Balen and Doerr 1978, Conner and Rudolph 1989, Costa and Escano 1989).

Management of nesting habitat, based on new understanding of population dynamics (Walters 1991) and techniques such as prescribed burning and artificial cavity construction (Copey 1990, Allen 1991), has proven successful in reversing population declines (Carter et al. 1995, Gaines et al. 1995, Watson et al. 1995, U.S. Fish and Wildlife Service 2000). As the constraint of restricted nesting habitat is relaxed, we anticipate that the condition of foraging habitat will gain importance in the recovery of the species. However, in contrast to the management of nesting habitat, management of foraging habitat has not been supported by a clear understanding of the species' biology.

Over the past decade, management of foraging habitat for red-cockaded woodpeckers has been based primarily on 2 habitat measures: number of pine trees ≥25.4 cm in diameter at breast height (dbh) and basal area (BA) of pines ≥10.2 cm dbh (U.S. Fish and Wildlife Service 1985, 1998; U.S. Forest Service 1995). The first variable, number of pines ≥25.4 cm dbh, was chosen because selection for this size class was documented within a population in coastal South Carolina (Hooper and Lennartz 1981, Hooper and Harlow 1986). Choice of the second variable apparently was based on observations of red-cockaded woodpeckers foraging in small pines, and on the report by Hooper and Lennartz (1981) that red-cockaded woodpeckers neither selected nor avoided pines between 13 cm and 23 cm dbh. Minimum values recommended for these variables (6,350 pines ≥25.4 cm dbh and 789.8 m² BA of pines ≥10.2 cm dbh per woodpecker group) were the average values estimated from a small number of selected home ranges in the same South Carolina study population (U.S. Fish and Wildlife Service 1985). Despite several attempts, no relationship between recommended minimums or the variables themselves and fitness of red-cockaded woodpeckers has been documented (Hooper and Lennartz 1995, Beyer et al. 1996, Ferral 1998, Wigley et al. 1999).

Some researchers have interpreted the failure to document effects of conventional variables on fitness to suggest that reductions in currently designated foraging habitat may not adversely affect red-cockaded woodpeckers (e.g., Hooper and Lennartz 1995, Beyer et al. 1996). Such an interpretation relies on the assumption that foraging habitat suitability has been assessed accurately. An alternative is that lack of fitness relationships indicates only that these variables are not appropriate measures of habitat quality or quantity (Beyer et al. 1996, James et al. 2001).

Thus, the failure to find fitness effects of conventional variables may be due to 1 of 3 alternative causes. First, foraging habitat may not affect fitness. Second, conventional variables may not accurately measure available foraging habitat or habitat quality. Third, conventional variables may be important, but their effects are overwhelmed by unmeasured variables. That is, the number of pines ≥25.4 cm dbh may be important only if the structure of the habitat within which these pines grow meets other, unspecified, criteria. Our study of resource and habitat selection, and fitness effects of habitat components, allowed us to distinguish among these possibilities. Most importantly, our study enabled us to make specific recommendations concerning management of foraging habitat for this species.

METHODS

Study Area and Study Population

We conducted fieldwork in the Sandhills of south-central North Carolina, within 1 of the largest remaining populations of red-cockaded woodpeckers (James 1995, U.S. Fish and Wildlife Service 2000). Our study area consisted of mostly
second-growth longleaf pine woodlands, with scattered old pines, a midstory of oaks (Quercus spp.), and variably developed ground-cover vegetation dominated by wiregrass (Aristida stricta). It included a portion of the Fort Bragg Military Reservation, a section of the Sandhills Game Lands (a state-managed area used primarily for hunting), and residential areas and horse farms in and around the towns of Pinehurst and Southern Pines (see Carter et al. [1983] and Walters et al. [1988] for additional details). Since 1981, over 220 groups of woodpeckers, representing the western half of the Sandhills population, have been color-banded and monitored on the study area. Each breeding season, reproduction of each group has been monitored and all adult group members identified by color band. Walters et al. (1988) provide a detailed description of methods used in breeding season monitoring.

We selected 30 groups from the larger study population for intensive study of foraging ecology. These groups were selected to provide a representative geographic sample of the study area, while avoiding residential areas because of concerns by private landowners. Of these 30 groups, 21 were on military lands, 7 were on the Sandhills Game Lands, and 2 were on a large horse farm.

Data Collection

Data collected from the 30 study groups were of 3 types: (1) observations of foraging red-cockaded woodpeckers, which included bird locations, measurements of trees used as foraging substrate, and measurements of nearby trees; (2) systematic sampling of vegetation; and (3) demographic data from the long-term population monitoring project described above.

Foraging Observations.—We conducted an observation period for each of the 30 study groups once every 6 weeks for 2 years, between November 1994 and October 1996. An observation period consisted of sustained contact with the birds for two-thirds of daylight hours on a single day; or a combination of 2 days of observation in which sustained contact totaled 100% of daylight hours. Every 10 min during an observation period, the activity of the group was noted and its location recorded on aerial photographs. Locations were later transformed to Universal Transverse Mercator (UTM) coordinates for analysis.

Every 30 min during observation periods, a randomization procedure was used to pick an individual from among the group members foraging at that instant, and its foraging tree was marked for subsequent data collection. Data collected from foraging trees included tree species, dbh, height, and age as measured from a core extracted with an increment borer. Each time a foraging tree was marked, the closest tree in a randomly selected direction was also marked and subsequently sampled for the same features. We excluded trees <7.6 cm dbh as foraging or randomly selected trees, because previous studies showed that small trees are avoided (Hooper and Lennartz 1981, DeLottel et al. 1983, Porter and Labisky 1986, Engstrom and Sanders 1997, Zwicker and Walters 1999). Johnson (1980) recommends excluding habitat already known to be avoided in resource selection studies.

Systematic Sampling of Vegetation.—We collected vegetation data using variable radius plots on a uniform grid of points 100.7 x 100.7 m (5 x 5 chains) apart, running north–south and east–west. Sampling was continued well outside presumed home-range boundaries to ensure complete coverage of all home ranges. Data collected from each plot included (1) BA of live pines and hardwoods, determined using a 10-factor basal prism; (2) number of live pines and hardwoods >10.2 cm dbh, categorized in 5.1-cm (2-in.) size classes; (3) stem count and mean dbh of hardwood and pine midstory (i.e., stems <10.2 cm [4 in.] dbh) in 2 6.1 x 9.8-m transects running in randomly chosen directions from the center of the plot; (4) number of flat-tops (i.e., old pines with characteristic growth form) within 35.7 m of the plot center; and (5) dbh, height, and age of the pine tree (>10.2 cm dbh) closest to the plot center in a randomly chosen direction. Each plot was classified as 1 of several community types to facilitate designation of stands (see below).

Data Analysis

We conducted 4 major analyses. First, we calculated year-round home ranges and compared methods of home-range estimation. Second, we analyzed resource selection and habitat use by assessing selection of individual pines, use of habitat patches, and use of forest stands (see definitions below). Third, we assessed relationships between measures of group fitness and habitat characteristics at the home-range level. Last, using a multidimensional definition of habitat quality based on our results and those in the literature, we assessed how much high-quality foraging habitat was available to each of our 30 study groups and related these quantities to measures of group fitness. We performed all analyses using the statistical analysis software, SAS (SAS Institute 2000).
**Home-Range Estimation.**—Year-round home ranges were estimated using the Kernel Home Range Estimation Program developed by D. E. Seaman and R. A. Powell (Seaman and Powell 1996, Seaman et al. 1998) derived from methods described by Silverman (1986). This program uses a nonparametric, 2-dimensional density distribution for home-range estimation and excludes unused areas. We allowed the program to choose bandwidth for a fixed kernel by least squares cross validation on observation period data with duplicate observations removed, as recommended by Worton (1995), Seaman and Powell (1996), and D. E. Seaman (National Biological Service, personal communication). We then reinstated duplicates for calculation of home ranges as estimated by 95% of the area under the 2-dimensional density distribution. Home ranges also were estimated by the minimum convex polygon method for comparison.

**Resource Selection.**—To examine selection of individual trees within patches of foraging habitat, we compared characteristics of trees used by foraging birds to those of nearby, randomly selected trees. We used these randomly selected trees to represent the available resource. For these comparisons, we used both paired tests and simple logistic regressions of tree age, dbh, and height against tree type (foraging or random). Following Manly et al. (1993), we refer to resources used in greater proportion than their availability as “selected,” and those used in lower proportion than their availability as “avoided.”

**Habitat Use.**—We assessed factors affecting use of habitat patches and forest stands by first choosing vegetation variables we considered likely to be important, prior to data collection. These variables consisted of basal area and density of pines in various size classes, hardwood and pine midstory measures, and density of old-growth pines (flat-tops). We calculated all possible regressions and selected models based on 2 statistical criteria (see below). This is unlike the unthinking use of all possible regressions criticized by Burnham and Anderson (1998), in that we carefully chose variables of interest prior to data collection, rather than screening all variables we could measure for statistical significance. We then constructed expanded models including cross-product and interaction terms. While we recognize that the significance of variables in these secondary models may be inflated, we believe it is worthwhile to identify potentially important nonlinear terms. Finally, we used several approaches to analyze factors affecting habitat use (patch and stand) and stressed the consistency among results rather than a particular model.

To assess factors affecting habitat use at the patch scale, we used the vegetation sampling plots as potential foraging patches. We arbitrarily defined a patch as the area within 15.25 m of the center of each vegetation plot. If 1 or more observed locations of foraging birds fell within this radius, we considered the patch used for foraging. In this way, each patch was labeled “used” or “not used.” We then employed logistic regression (Hosmer and Lemeshow 2000) to evaluate potential effects of patch vegetation characteristics on patch use. We analyzed 2 sets of vegetation variables that differed only in the way pine size classes were combined. We conducted these 2 analyses, rather than a single analysis, to reduce any influence arbitrary selection of categories might have on our conclusions. The first variable set included number of pine stems per ha in the following size classes: 10.2–20.3 cm dbh, 20.3–30.5 cm dbh, 30.5–40.6 cm dbh, and >40.6 cm dbh (4–8 in., 8–12 in., 12–16 in., >16 in.). The second variable set included number of pine stems per ha in these size classes: 10.2–25.4 cm dbh, 25.4–35.6 cm dbh, 35.6–45.7 cm dbh, and >45.7 dbh (4–10 in., 10–14 in., 14–18 in., >18 in.). In addition, the following variables were common to both variable sets: (1) number of midstory hardwood stems; (2) number of midstory pine stems; (3) mean height of midstory hardwoods; (4) mean height of midstory pines; (5) number of hardwood stems 10.2–20.3 cm dbh, 20.3–30.5 cm dbh, 30.5–40.6 cm dbh, and >40.6 cm dbh per ha; and (6) number of flat-tops per ha. Correlations among variables within each set were low ($r < 0.5$).

For each variable set, we calculated all possible regressions and used the score criterion (Brown 1982) for model selection. We then took the variables in the selected models, added all quadratic and cross-product terms, and repeated the model selection procedure. Finally, we added 2 variables derived from trees selected randomly within vegetation plots—the mean dbh and mean age of randomly selected pines—and repeated the analyses. These 2 variables were correlated with each other ($r = 0.81$) but not with other variables in the set ($r < 0.5$). Variation in likelihood of patch use among groups was controlled by adding group as a class variable to models following selection procedures. We used $\alpha = 0.05$ to identify statistically significant variables, and $\alpha = 0.10$ to identify additional, potentially important variables.
We assessed factors affecting use of forest stands by multiple linear regression of vegetation variables against our measure of stand use. Stand use was the number of foraging observations located in a stand subjected to a square root transformation \( (y' = (y + 0.5)^{0.5}) \). To create stands, we considered each vegetation sampling plot to represent the 1.01 ha grid cell surrounding it and grouped adjacent cells of the same community type into stands. We arbitrarily divided large stands to evaluate habitat use on a consistent, relatively small scale. Stands ranged in size from 0.8 to 8.1 ha, with mean and median values of 3.0 ha and 2.5 ha, respectively.

We conducted analysis of stand use just as we analyzed patch use, using 2 sets of vegetation variables. Each variable set contained pine size class variables as described for patch use (above). Both variable sets also included mean number of flat-tops per ha, mean height of hardwood midstory, mean height of pine midstory, stand area, and number of active cavity trees in the stand. Variable estimates were the means of the values of all plots within a stand. Correlations among variables in each set were low \((r < 0.5)\). We calculated all possible regressions and used the Cp statistic (Mallows 1973) as our criterion for model selection. The Cp statistic is a combination of model bias and variance; thus, model selection based on the smallest Cp reduces both problems of underfitting and overfitting (Myers 1990, Ott 1993). Although this criterion may not be useful for small samples (Burnham and Anderson 1998), we analyzed large samples for stand use.

After identifying important variables in each variable set, we constructed expanded models by adding cross-products and quadratic terms, again using the Cp model selection procedure. Because stand area and number of cavity trees were not variables of interest, their nonlinear terms were not included in expanded models. Finally, we added mean dbh and mean age of randomly selected pines and repeated the analyses. Variation in stand use among groups was controlled by adding group as a class variable to models following selection procedures.

**Bird Fitness and Foraging Habitat Characteristics.—** Using multiple linear regression, we evaluated effects of foraging habitat characteristics of the home range on 3 measures of bird fitness, number of fledglings produced, group size, and male breeder retention. Group size is known to positively affect breeder survival and reproduction in this population (Walters 1990, Heppell et al. 1994, Khan and Walters 2002). Male breeder retention is an appropriate measure of survival for this species because the breeding males almost never disperse (Walters et al. 1988, Walters 1990).

Bird fitness variables were the average of annual observations for each of the 30 study groups from 1985 to 1998. Data from 1999 were used to estimate breeder retention in 1998. For each fitness measure, we selected a best model based on the Cp statistic (Mallows 1973) from all possible regressions of 5 habitat variables. We included only 5 variables in this analysis because the sample was relatively small (30 groups) and chose those considered most likely to be important. These variables were mean number of pines per ha in 3 size classes (10.2–25.4 cm dbh, 25.4–35.6 cm dbh, >35.6 cm dbh) mean number of flat-tops per ha, and mean height of hardwood midstory. We calculated these by averaging values across all vegetation plots within each home range. Because of the small sample size, no interaction or squared terms were added.

**Modeling Foraging Habitat Quality and Quantity.—** We used results of our analyses and those reported in the literature to develop a conceptual definition of high-quality foraging habitat for red-cockaded woodpeckers. We then parameterized this definition of high-quality habitat, and a related definition of medium-quality habitat, for our study population based on plots of fitness effects and analyses of resource selection and habitat use. We estimated the area of high- and medium-quality foraging habitat within the home range of each of our study groups by extrapolating the features of each vegetation sampling plot to the surrounding 1.01-ha grid cell, averaging these values by stand and summing the area of stands meeting our quality criteria. We regressed these amounts against mean group size and mean fledgling production to ensure that we were measuring habitat quality correctly, then plotted these relationships to investigate habitat area requirements.

**RESULTS**

**Estimation of Home Ranges**

Our sampling effort was sufficient for home-range estimation: home-range size as a function of number of observation periods reached an asymptote after 8 periods, whereas we conducted 16. Home ranges calculated by the kernel home-range estimation program averaged 83.6 ha and ranged from 56.3 to 128.7 ha among the 30
Male breeder of survival for males almost (Valter 1990). Because of annual study groups were used to for each fand based on all possible we included the sample and chose important of pines per h. 25.4–35.6 m of flat-tops and midstory, trees across all age. Because fraction or variability and analyses and oop a congruous habitation in the area. Our habitat variable within the groups by vegetation a grid include criterion relevant to quality of the home function had an inducted homestead and the 30 groups. Home ranges calculated by the minimum convex polygon method were much larger, averaging 126.2 ha and ranging from 83.8 to 231.1 ha. In addition, variation of minimum convex polygon estimates was greater than that of kernel estimates (Ftest, F = 2.85, df = 29, P = 0.006). The kernel method excluded large unused areas, the source of much of the variation among minimum convex polygon estimates.

Resource Selection

Over 96% of trees used by red-cockaded woodpeckers as foraging substrate were pines. We therefore removed all species other than pines from the following analyses. Among pines, we found no evidence that species affected the selection of foraging trees by red-cockaded woodpeckers (χ² test, χ² = 4.8, df = 3, P = 0.2). However, very little variation occurred in pine species within the study area: 95% of both pines selected by red-cockaded woodpeckers for foraging (for age trees) and nearby pines selected at random by observers (random trees) were longleaf pines. Loblolly (P. taeda), pond (P. serotina), and shortleaf pine (P. echinata) each accounted for less than 3% of all pines.

Pines used by red-cockaded woodpeckers for foraging were older, taller, and larger in dbh than nearby pines selected at random by observers (paired t-tests, n = 7,147–7,197; P < 0.0001 in all cases). Forage trees were on average roughly 5 years older, 1.5 m taller, and 5 cm larger in dbh than randomly selected trees. Differences large enough to be biologically meaningful. Mean (±1 STD) age, dbh, and height of forage trees were 69.2 ± 19.6 years, 35.6 ± 8.4 cm, and 20.6 ± 3.7 m, respectively. Simple logistic regressions reinforced the results of paired t-tests. The probability that a pine was classified as a forage tree increased with increasing age, dbh, and height (n > 14,000; P < 0.001 in all cases), but was unaffected by pine species (P = 0.2).

To identify specific age, height, and dbh classes of pines selected or avoided as foraging substrates, we compared the distributions of these variables for foraging trees with those of nearby random trees (Fig. 1). Red-cockaded woodpeckers used pines over 70 years of age in greater proportion than expected based on availability, whereas use of pines 61–70 years of age was equal to that expected, and use of pines 60 years of age and younger was less than expected (Fig. 1). Red-cockaded woodpeckers also foraged on pines larger than 30.5 cm dbh and pines taller than 18.3 m in greater proportion than their availability (Fig. 1). Most pines in the study area were 51–90 years in age and 20.3–45.7 cm dbh; very few were older or larger than this (Fig. 1, random trees).
We were unable to separate effects of age, dbh, and height on tree selection because these variables were highly correlated (age and dbh, r = 0.61; age and height, r = 0.67; dbh and height, r = 0.49). Second-growth pines exhibited different relationships between age and dbh, and between age and height, than those exhibited by pines above age 100: pines under roughly 100 years in age showed a strong positive relationship between age and size, whereas for pines above this age, there was no relationship. Indeed, many second-growth pines were taller and wider than the older trees. Simple logistic regressions on whether pines above age 100 were classified as foraging trees revealed no effects of age, dbh, or height (n = 223, P > 0.6 in all cases). Further research in study areas with more abundant old-growth pines is required to separate effects of pine age and size.

**Habitat Use**

*Patch Use.—* Likelihood of use of habitat patches by foraging red-cockaded woodpeckers was most strongly related to mean height of hardwood midstory, density of large hardwoods, density of large and very large pines within the patch, and age of pines (Table 1: Models 1A, 2A, 3A). Effects of hardwood midstory and large hardwoods on the likelihood of patch use were negative, and effects of pine age and density of large and very large pines were positive (Table 1: Models 1A, 2A, 3A). Significant quadratic terms indicated that the positive effect of density of large and very large pines diminished at very high densities (Table 1: Models 1B, 2B). That is, patch use was reduced at low pine densities (0–60 trees per ha) and also at very high pine densities (≥90 trees per ha). Significant cross-products indicated that the positive effect of large and very large pines diminished as hardwood midstory increased and as the density of large hardwoods increased (Table 1: Models 1B, 2B). Note that choice of size categories of pines did not affect model results appreciably (Table 1: Models 1A and 1B vs. 2A and 2B). Distributions of 2 variables important to
patch use—height of hardwood midstory and density of pines >35.6 cm dbh—are presented in Fig. 2.

When attributes of randomly selected trees were added to the variable sets, the 2 sets produced the same model (Table 2: Model 3A). This model was similar to previous ones, except that mean age of randomly selected pines replaced density of large pines. A significant cross-product indicated that as hardwood midstory increased, the positive effect of old pines on patch use decreased (Table 2: Model 3B). Taken together, our results indicate that patch use increased with increasing presence of larger, older pines as long as hardwood midstory was not inhibiting.

Stand Use.—Frequency of stand use by foraging red-cockaded woodpeckers was negatively related to mean height of hardwood midstory and positively related to density of large pines (Table 2: Models 1A, 2A). Prior to controlling for group effects, density of small pines was negatively associated with stand use. Strong positive effects of the number of active cavity trees present and stand size on stand use were controlled by including

![Image](https://example.com/image.png)

**Table 2. Effects of vegetation characteristics on frequency of use of forest stands by foraging red-cockaded woodpeckers in the North Carolina Sandhills.** Six models of stand use (n = 780 in all cases) were selected based on the Cp statistic from all possible linear regressions of several variable sets. Stand use was the number of foraging observations per stand, square root transformed. Models 1A and 2A were chosen from variable sets 1 and 2, respectively (see Methods), which differed only in the way pine size classes were constructed. Model 3A was chosen from both variable sets 1 and 2 with average age and dbh of random pines added. Models 1B, 2B, and 3B were based on variables identified in the first procedure plus quadratic terms and cross-products, excluding those of active cavity trees and stand area. The class variable, group, was added as a covariate to models following selection procedures.

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<tr>
<td></td>
<td>Pines 35.6–45.7 cm</td>
<td>3.7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Height hardwood midstory × pines 35.6–45.7 cm</td>
<td>-2.5</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Pines 35.6–45.7 cm, squared</td>
<td>-2.5</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Group</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>3A</td>
<td>Stand area</td>
<td>27.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Active cavity trees</td>
<td>20.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Height hardwood midstory</td>
<td>-3.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Age random pines</td>
<td>3.1</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Group</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>3B</td>
<td>Stand area</td>
<td>27.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Active cavity trees</td>
<td>20.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Age random pines</td>
<td>4.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Age × height hardwood midstory</td>
<td>-2.9</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Group</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>

*These variables were significant prior to the addition of the class variable, group, and so were retained for subsequent analyses (i.e., model 1B).
Bird Fitness and Foraging Habitat Characteristics

Size of red-cockaded woodpecker groups in our study area increased with increasing density of flat-tops, and decreased with increasing density of pines 25.4-35.6 cm dbh and height of the hardwood midstory (flat-tops, t = 3.3, P = 0.003; pines, t = -2.5, P = 0.02, hardwood midstory, t = -1.9, P = 0.07; model \( R^2 = 0.39 \)). For the dependent variables mean number of fledglings produced, mean retention probability for the breeding male, and home-range size, no model contained habitat variables with statistically significant effects. We found no evidence that fitness increased in relation to conventional habitat measures such as number or basal area of pines ≥25.4 cm dbh. Relationships between fitness measures and total number or density of pines ≥25.4 cm dbh were not statistically significant and were generally negative (Fig. 4).

Modeling Foraging Habitat Quality

In this section, we compare our results to those of previous studies and derive a new definition of foraging habitat quality. We then use that definition to examine relationships between fitness measures and amount of foraging habitat of high quality.

Habitat Use.—Studies of foraging habitat use and selection of foraging trees by red-cockaded woodpeckers are summarized in Table 3. These results are remarkably consistent and mirror our own findings. In all studies, age and/or size of pines was important to habitat use. Red-cockaded woodpeckers select older, larger trees over smaller, younger pines, and the presence of older, larger trees is associated with increased use of habitat patches and pine stands (Table 3). Again, effects of age and size cannot be separated because of the strong correlation between the 2 variables.

In addition to universal effects of tree age and size, the literature review also revealed consistent negative effects of excessive hardwoods. Both density and height of hardwoods are negatively related to use of habitat patches and pine stands (Table 3). Finally, the review of studies of stand use suggested an interaction between pine density and size: increasing density of large pines is positively associated with use of stands by foraging woodpeckers, whereas increasing density of small pines is negatively associated with stand use (Table 3). Clearly, use of forest stands by foraging red-cockaded woodpeckers is enhanced if stands are open to hardwood.
groups in our study density of nesting density of trees of the hardwood species, pines, and pines, \( r = -1.9, P = 0.003 \); pines, \( t = -1.9, P = 10^{-3} \), produced, the breeding season contained. Significant fitness habitat measures of pines >25.4 cm DBH and measures of pines >25.4 cm DBH and were

![Graph A](image.png)

![Graph B](image.png)

Fig. 4. Relationships between 2 fitness measures, mean annual group size (A) and mean annual fledgling production (B), and density of pines >25.4 cm DBH for red-cockaded woodpeckers in the North Carolina Sandhills. This conventional measure does not appear to be related to fitness.

are open, contain large, old pines, and have little hardwood or pine midstory.

**Effects on Fitness.**—Studies of foraging habitat and fitness of red-cockaded woodpeckers have identified density, age, and size of pines as well as herbaceous ground cover as habitat characteristics important to fitness (Table 4). Two studies (this study, James et al. 2001) have documented an interaction between pine density and pine size-age: group size and/or reproduction was shown to increase with increasing density of large old pines and to decrease with increasing density of small young pines. Several studies have reported a positive effect of old-growth pines (generally, >90 or 100 years in age) on group size, reproduction, or both. The presence of rich, diverse ground cover of grasses and forbs also is associated with large group sizes and high reproductive success, as evidenced by the only 3 studies to have assessed the role of this important habitat characteristic. In addition, smaller group sizes were related to measures of habitat fragmentation in 2 studies (Table 4). Although no relationships between fitness measures and density or height of hardwood midstory have been reported previously, we found that mean group size decreased with increasing hardwood midstory.

**Defining Habitat Quality and Determining Suitable Quantity.**—The features of foraging habitat that red-cockaded woodpeckers select and those that increase frequency of use are highly consistent with the features that are related to fitness. Both resource use and fitness analyses describe the same structure of habitat, namely open stands of large old pines with a rich and diverse ground cover and little or no hardwood or pine midstory. We sought to parameterize a definition of high-quality foraging habitat that captured this habitat structure.

We developed the specific criteria in our definition from our data on patch and stand selection and the relationship between habitat features and group size. Thus, the particular values in our definition apply specifically to our study area and not necessarily to other locations. The fundamental concept of our definition—that high-quality habitat has an open structure with intermediate densities of large old pines—is applicable throughout the range of the species, as evidenced by our literature review. We did not include ground cover in our criteria because we collected no data for this variable.

We defined high-quality habitat as stands with (1) hardwood midstory <1.8 m in height, (2) at least 1.2 flat-tops per ha, (3) 35–80 pines >35.6 cm DBH per ha, and (4) fewer than 75 pines ≤30.5 cm DBH per ha. We defined medium-quality habitat as stands with (1) hardwood midstory <2.7 m in height, (2) a non-zero value for flat-tops per ha, (3) 15–90 pines >35.6 cm DBH per ha, and (3) fewer than 75 pines ≤30.5 cm DBH per ha. In these definitions, high-quality habitat differs from medium-quality by containing more large and old pines and less midstory.

Of the 30 groups we studied, the home ranges of almost half (13) contained no habitat that met our definition of high quality, whereas the remainder contained from 1 to 21 ha. Home ranges of 25 groups contained some medium-quality habitat, ranging from 1 to 49 ha. Areas of high-quality habitat (HQ) and medium-quality habitat exclusive of high quality (MQ) were each related to group size, and together these variables accounted for roughly one-third of the variation in group size (Table 5, Fig. 5). Area of habi-
Table 3. Reported effects of habitat characteristics on selection of resources and habitat use by foraging red-cockaded woodpeckers in the North Carolina Sandhills.

<table>
<thead>
<tr>
<th>Spatial scale</th>
<th>Habitat characteristic</th>
<th>Sign</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Patch use</td>
<td>Age–Size of trees</td>
<td>+</td>
<td>Bowman et al. 1998; Doster and James 1998</td>
</tr>
<tr>
<td></td>
<td>Height of hardwood midstory</td>
<td></td>
<td>Doster and James 1998; This study</td>
</tr>
<tr>
<td></td>
<td>Density of hardwoods</td>
<td>-</td>
<td>Doster and James 1998; This study</td>
</tr>
<tr>
<td>Stand use</td>
<td>Age of trees</td>
<td>+</td>
<td>Hooper and Harlow 1986; Porter and Labisky 1986; Deloitte et al. 1987; Epting et al. 1995; Jones and Hunt 1996</td>
</tr>
<tr>
<td></td>
<td>Density of pines</td>
<td>+</td>
<td>Deloitte et al. 1987; Epting et al. 1995</td>
</tr>
<tr>
<td></td>
<td>Density of large pines</td>
<td>+</td>
<td>Hooper and Harlow 1986; Bradshaw 1995</td>
</tr>
<tr>
<td></td>
<td>Density of small pines</td>
<td>-</td>
<td>Porter and Labisky 1986; Bradshaw 1995</td>
</tr>
<tr>
<td></td>
<td>Height of hardwood midstory</td>
<td></td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>Density of hardwoods</td>
<td>-</td>
<td>Hooper and Harlow 1986; Bradshaw 1995; Epting et al. 1995; Jones and Hunt 1996</td>
</tr>
</tbody>
</table>

Table 4. Reported effects of habitat characteristics of the home range (or territory) on measures of group fitness for red-cockaded woodpeckers.

<table>
<thead>
<tr>
<th>Habitat characteristic</th>
<th>Fitness variable</th>
<th>Sign</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of pines</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Old-growth pines</td>
<td>Group size</td>
<td>+</td>
<td>Conner and Rudolph 1991; Rudolph and Conner 1994</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Engstrom and Sanders 1997; Conner et al. 1999</td>
</tr>
<tr>
<td></td>
<td>Reproduction</td>
<td>+</td>
<td>Engstrom and Sanders 1997; James et al. 2001</td>
</tr>
<tr>
<td></td>
<td>Group size and reproduction</td>
<td>+</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>Group size and reproduction</td>
<td>-</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>Fragmentation</td>
<td>-</td>
<td>Conner and Rudolph 1991; Fernald 1998</td>
</tr>
</tbody>
</table>

Discussion

A Discussion of the Results

Our results suggest that red-cockaded woodpecker habitat selection strategies are influenced by the density of old-growth pines. These findings are consistent with previous studies indicating the importance of old-growth pines in the red-cockaded woodpecker's habitat preferences. This suggests that maintaining a high density of old-growth pines is crucial for the conservation of red-cockaded woodpeckers. Our study expands on previous research by providing a more detailed analysis of the specific factors influencing habitat selection.
Table 5. Relationships between average size of 30 red-cockaded woodpecker groups in the North Carolina Sandhills, 1986-1998, and area of high-quality foraging habitat (HQ), area of medium-quality foraging habitat exclusive of high-quality habitat (MQ), and area of remaining habitat within the home range (REST), as shown by linear regressions.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>t</th>
<th>P</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group Size = HQ</td>
<td>HQ</td>
<td>3.2</td>
<td>0.004</td>
<td>0.26</td>
</tr>
<tr>
<td>Group Size = HQ MQ</td>
<td>MQ</td>
<td>2.7</td>
<td>0.01</td>
<td>0.39</td>
</tr>
<tr>
<td>GSIZE = HQ MQ REST</td>
<td>REST</td>
<td>2.8</td>
<td>0.01</td>
<td>0.41</td>
</tr>
</tbody>
</table>

- High-quality habitat was the summed area of those forest stands with average values derived from vegetation plots meeting all of the following criteria: (1) median height of hardwood midstory <1.8 m, (2) density of flat-tops ≥1.2 stems per ha, (3) density of pines ≥36.6 cm dbh between 35 and 80 stems per ha, and (4) density of pines ≤30.5 cm dbh less than 75 stems per ha.

- Medium-quality habitat was the summed area of those forest stands with average values derived from vegetation plots meeting all of the following criteria: minus area of stands of high quality: (1) median height of hardwood midstory <2.7 m, (2) density of flat-tops ≥0.0 stems per ha, (3) density of pines ≥36.6 cm dbh between 15 and 90 stems per ha, and (3) density of pines ≤30.5 cm dbh less than 75 stems per ha.

The study showed that within the home range that was not of high or medium quality (REST, Table 5) and home-range size itself (Fig. 5) were not related to group size. In addition, we found no direct effects of the amount of foraging habitat of high or medium quality on fledgling production.

We were unable to identify an amount of high- or medium-quality habitat at which group size is optimized, because no asymptotic limit of group size as a function of amount of quality habitat was observed (Fig. 5). Red-cockaded woodpeckers in our study area do not have sufficient high- or medium-quality habitat so that we could make this determination.

**DISCUSSION**

**A Definition of Habitat Quality**

Our study indicates that high-quality foraging habitat for red-cockaded woodpeckers consists of open woodlands with little or no hardwood and pine midstory and intermediate densities of large old pines, including some old-growth pines. In our study population in the North Carolina Sandhills, these habitat features affected both size of red-cockaded woodpecker groups and frequency of resource use. Our standard of habitat quality is strikingly similar to that proposed by James et al. (2001) for red-cockaded woodpeckers in the Apalachicola National Forest (Florida, USA). James et al. (1997, 2001) also emphasized the importance of abundant herbaceous ground cover to habitat quality. Although we did not measure ground cover in our work, abundant...
ground cover dominated by grass and forbs generally is associated with the open habitat structure, our definition of quality describes. The strong similarity between our results and those of James et al. (2001) suggests that a definition of foraging habitat quality based on open habitat structure and the presence of large old pines may be applicable throughout the range of the species.

These definitions of habitat quality match the habitat preferences of the species described by early ornithologists (e.g., Murphey 1939). Both our definition of high-quality habitat and that of James et al. (2001) describe many characteristics of old-growth southern pine ecosystems: intermediate pine density, abundant herbaceous ground cover, scattered midstory low in density and height, and a substantial number of old-growth pines. Thus, restoration of southern pine ecosystems may equate to improving foraging habitat quality for red-cockaded woodpeckers. In support of this suggestion, we point to the Wade Tract (Thomasville, Georgia, USA), which supports the highest group size and reproduction and smallest home ranges yet reported for the species (Engstrom and Sanders 1997). The Wade Tract is the closest approximation to fire-maintained, old-growth southern pine forest that exists, and it contains even more older and larger trees than habitat identified as high quality in this study (Fig. 6) or by James et al. (2001).

Habitat Quality and Selection of Foraging Habitat

From our study and others (see Table 3), a clear and consistent pattern of habitat selection and use emerges: red-cockaded woodpeckers forage on large, tall, old pines more often than expected, and use of these large, old pines is negatively affected by pine and hardwood midstory. This pattern is evident at all scales, from trees within habitat patches, to patches within stands, to stands within the landscape.

Effects of Pine Age and Size on Resource Selection.—Positive effects of increasing pine age and size on resource selection and use for foraging red-cockaded woodpeckers are universally reported (see references in Table 3). Currently, it is not possible to distinguish between effects of pine size and age because these features are highly correlated. We suggest that both are important, but realize that further research must be conducted in study areas with a sizeable old-growth component before definitive conclusions about the relative importance of age and size can be reached.

The relationship of pine age or size to resource selection may take 1 of several forms. Zwick and Walters (1999), following Rudolph and Conner (1991), proposed 3 possibilities for the effects of age: (1) there is a threshold age above which the strength of selection does not increase; (2) there is an optimum age, above and below which the strength of selection decreases; or (3) the birds select the oldest available trees. They concluded that, in their study in coastal North Carolina, red-cockaded woodpeckers select the oldest available trees or that a threshold exists somewhere above 100 years. Zwick and Walters (1999) further emphasized that the ages of pines selected shifts with the ages of available pines.

Our study and other work support this assessment. The primarily second-growth forest of our Sandhills site is older than the forest studied by Zwick and Walters (1999). Consistent with this difference in available pines is a difference in selected pines: the age at which first exceeded availability was 70–80 years in our study area compared with 60–70 years in the coastal site (Zwick and Walters 1999). In northwestern Florida, in a study area with more old-growth trees than in either North Carolina site, use exceeded availability only for pines above 150 years in age (Hardesty et al. 1997). In that same study, pines 50–150 years in age were used in equal proportion to their availability, and pines younger than 50
year old were avoided. Thus, there is increasing evidence that red-cockaded woodpeckers select the oldest available pines for foraging.

Effects of pine size on habitat selection are similarly consistent with selection of the largest available trees or a threshold that shifts in response to the availability of large pines. Across studies, use of large pines increases availability, pines intermediate in size are used equal to or slightly more than their availability, and small pines are used less than expected (see Table 3 for references). However, what constitutes large, intermediate, and small pines varies across study areas as a function of management history and, to a lesser degree, habitat type. In our study area, pines >35.6 cm dbh were selected, pines 30.5–35.6 cm dbh were used in proportion to their availability, and pines ≤30.5 cm dbh were avoided. In coastal North Carolina, pines >30.5 cm dbh were selected, pines 25.4–30.5 cm dbh were used in proportion to their availability, and pines <25.4 cm dbh were avoided (Zwick & Walters 1999). Hooper & Lennartz (1981), in the study on which red-cockaded woodpecker foraging guidelines (U.S. Fish & Wildlife Service 1985) were based, reported that pines >25.4 cm dbh were selected and pines <12.7 cm dbh were avoided. Finally, in the old-growth pine habitat at the Wade Tract studied by Engstrom & Sanders (1997), pines >50.8 cm dbh were strongly selected, pines 30.5–50.8 cm dbh were used slightly more than their availability, and pines <30.5 cm dbh were avoided. This study is particularly informative because it was conducted in an area with an abundance of very large pines. These results together suggest that (1) pines >50.8 cm dbh are preferred by red-cockaded woodpeckers; (2) use of pines <50.8 cm dbh depends on the availability of larger trees; (3) pines <30.5 cm dbh are avoided if larger trees are present; and (4) pines 35.6–50.8 cm dbh are generally selected, but the strength of this selection is inversely related to the presence of larger trees.

Effects of Midstory on Habitat Use.—Red-cockaded woodpeckers abandon nesting habitat if midstory becomes too high (Van Balen & Doerr 1978, Hovis & Labisk 1985, Conner & Rudolph 1989, Loeb et al. 1992), and this well-known impact is commonly viewed as a threshold effect that occurs at a critical midstory height. Effects of midstory on use of foraging habitat may involve a threshold as well. Alternatively, use of foraging habitat may decline continuously with increasing midstory height or density. Perhaps both effects occur. That is, foraging habitat may decrease in value with increasing density and height of midstory up to a threshold level above which the patch or stand is not used at all.

Ecological Basis of Habitat Selection.—The ecological basis of patterns in foraging habitat use by red-cockaded woodpeckers remains a matter of speculation. Selection of individual trees may be based on availability of ants and other arthropods on the tree surface (Hess & James 1998). Large trees obviously provide more foraging substrate than smaller trees, but whether arthropod densities are higher on larger, older trees is not yet clear. Hooper (1996) found no evidence of higher arthropod densities on older trees in winter. Increasing pine age or size may affect arthropod diversity rather than abundance: Tschinkel & Hess (1999) demonstrated increased proportions of arboreal ant species as pines increased in size. Last, it may be that differences in bark characteristics between young and old pines result in differences in foraging efficiency, or that older pines support more favored foraging locations such as self-pruning and fire-killed branches (Conner et al. 2001).

Negative effects of midstory and high pine density on habitat use may be direct or indirect. Midstory may act directly by interfering with movement along the lower trunks of trees and from tree to tree, especially for females who frequently forage on the lower trunk (Walters 1990, Jackson 1994). Dense stands of pines may inhibit movement as well. Alternatively, the birds may appear to select for intermediate pine densities and sparse midstory because these features are correlated with rich, abundant herbaceous ground cover, the source of many arthropod prey for red-cockaded woodpeckers (Hanula & Franzreb 1995). Moreover, all 3 habitat features—intermediate pine density, absence of midstory, and rich abundant ground cover—are associated with growing season fire, and growing season fire itself may increase prey abundance or prey nutrient content apart from any effects on other habitat features (Hardesty et al. 1997, James et al. 1997, Collins 1998, Provancher et al. 2001). Thus, habitat use by red-cockaded woodpeckers may be related to habitat structure because such structure is a result of frequent fire.

Habitat Quality and Bird Fitness

Quality of foraging habitat has important effects on the fitness of red-cockaded woodpeckers. We found that, in the North Carolina Sandhills, group size increased with an open habitat...
structure and increasing density of old-growth pines. Since group size has a strong influence on productivity (Walters 1990, Heppell et al. 1994) and breeder survival (Khan and Walters 2002) within our study population, foraging habitat also has important indirect influences on fitness. Territories with better foraging resources may be able to support more birds or provide higher survival, resulting in larger group size.

James et al. (1997, 2001) documented direct effects of habitat quality on reproduction and size of groups in the Apalachicola National Forest, Florida. Fitness of red-cockaded woodpeckers in their study was positively related to abundant herbaceous ground cover, little or no pine and hardwood midstory, and moderate densities of large, old pines. Similarly, Hardesty et al. (1997) found that productivity of red-cockaded woodpeckers on Eglin Air Force Base, Florida, was positively related to abundant ground cover and sparse midstory and negatively related to high densities of pines ≥25.4 cm dbh. These results are consistent with our study. We echo the conclusions of James et al. (1997, 2001), that previous failure to find effects of foraging habitat on fitness was due to inadequate habitat measures (i.e., number of pines ≥25.4 dbh). We emphasize that no single habitat measure can adequately capture habitat quality. Rather, habitat quality is best understood in terms of habitat structure and best measured by variables describing ground cover (James et al. 2001), the size class distribution of pines (James et al. 2001, this study), and the presence of old-growth pines (this study).

Effects of Pine Size and Density on Fitness.—Group size in our study area increased with increasing density of old-growth pines (flat-tops), even though these pines are relatively rare in the Sandhills landscape. Old-growth pine habitat is rare in the Southeast (Frost 1993), and so its effects on foraging and fitness of red-cockaded woodpeckers are difficult to document. However, a positive relationship between fitness and density of old-growth pines is supported by the only study of red-cockaded woodpecker foraging ecology in an old-growth, fire-maintained longleaf pine ecosystem, the Wade Tract in Georgia (Engstrom and Sanders 1997). In that system, Engstrom and Sanders (1997) reported the highest average group size and productivity yet documented for the species.

Our specific criteria for identifying high- and medium-quality habitat included hardwood midstory less than 1.8 and 2.7 m, respectively. These criteria do not suggest tolerance of a dense hard-

wood midstory 2–3 m in height throughout the foraging habitat of red-cockaded woodpecker populations. Rather, they describe occasional midstory trees and shrubs scattered at low densities throughout open habitat. We fully recognize the value of abundant herbaceous ground cover that does not tolerate dense midstory of any height, and we support the use of ground-cover variables in assessing habitat quality. We also recognize that it is often appropriate that open habitat may be interspersed with small riparian strips of higher, denser midstory than the surrounding uplands.

Foraging Habitat Quantity Standards

In our study population, size of woodpecker groups increased with increasing area of habitat meeting our definitions of high- and medium-quality habitat. Such a fitness relationship indicates that quantity of good-quality foraging habitat can be accurately measured by the area of habitat meeting these structural criteria, a substantial improvement over conventional measurements based on number of pine trees and pine basal area. Using number of pines to represent quantity, several previous studies concluded that red-cockaded woodpeckers are insensitive to removal of foraging habitat (e.g., Hooper and Lennartz 1995). Our results suggest the opposite conclusion, that red-cockaded woodpeckers in the North Carolina Sandhills are in need of more good-quality foraging habitat, not less.

We were unable to identify an optimal amount of high- and medium-quality habitat per group, presumably because the home ranges we studied did not contain sufficient amounts of such habitat to reveal a limit to group size as a function of habitat quantity. Several home ranges contained from 25 to 50 ha of high- and medium-quality foraging habitat, and this may be approaching an optimum. Although home ranges were much larger than this, it is likely that as habitat quality increases, required quantitив decreases. The best evidence supporting such an inverse relationship comes again from the Wade Tract in Georgia. Average home range of 7 groups in old-growth, fire-maintained longleaf pine of the Wade Tract is 116 acres, the smallest average yet reported based on all-day, year-round observation periods (Engstrom and Sanders 1997). In addition, Engstrom and Sanders (1997) reported a strong, negative correlation between home-range size and percent of home range within the old-growth tract. Other evidence supporting an inverse relationship between habitat quality and quantity includes home ranges that
Throughout the woodpecker population, midstory pine densities recognize the need to maintain the appropriate cover that supports the species. Woodpeckers are highly territorial and can be found in areas with various cover types. Consequently, maintaining a diverse and suitable habitat is crucial for their survival.

The home ranges of woodpeckers are typically small, averaging approximately 85 ha. This size is supported by studies using various methods such as the fixed kernel method. The average home-range reported by Hardesty et al. (1997) for red-cockaded woodpeckers on Eglin Air Force Base in Florida, estimated by the adaptive kernel method, suggests that the area covered is consistent with the estimated size.

However, most studies have estimated home ranges that are based on minimum convex polygons. Average size of minimum convex polygons in our study, 126 ha, is well within the range of sizes reported from other studies based on all-day, year-round observation periods (reviewed by Engstrom and Sanders 1997 and Doster and James 1998).

Substantial variation exists in estimates of home-range size both within and across populations. One might interpret this variation as evidence that red-cockaded woodpeckers are not sensitive to amount of foraging habitat, and that many groups have more habitat than needed. However, the relationships of foraging habitat to fitness do not support this interpretation. Variation in home-range size has at least three sources: (1) differences in the spatial distribution of foraging habitat, a source of variation magnified by the use of minimum convex polygons; (2) differences in the quality of available foraging habitat; and (3) the distribution of cavity trees throughout the landscape (Conner et al. 2001).

As the quality of foraging habitat and abundance of potential cavity trees increase, variation in home-range size may decrease. We suggest that habitat selection and fitness of red-cockaded woodpeckers in the North Carolina Sandhills is constrained by the current condition of foraging habitat, and that this may be true of many red-cockaded woodpecker populations. With few exceptions (most notably, the Wade Tract in Georgia), red-cockaded woodpeckers throughout their range exhibit second-growth pine woodlands with scattered individual old-growth pines (U.S. Fish and Wildlife Service 2000). Second-growth pine woodlands have higher pine densities than current or historic old-growth ecosystems (Foti and Glenn 1991, Masters et al. 1995, Noel et al. 1998). Much of the second-growth longleaf pine existing today is less than 100 years in age, having reproduced naturally during a short period of opportunity before fire suppression in this century (Kelly and Bechtold 1990, Frost 1993). Although quality of foraging habitat may be a substantial concern for many red-cockaded woodpecker populations, nesting habitat is still the primary determinant of population dynamics in this species and the critical factor currently limiting most populations (Walters 1990). We anticipate, however, that as constraints to population growth from availability of nesting habitat are relieved through enlightened management, condition of foraging habitat may well become limiting.

**MANAGEMENT IMPLICATIONS**

James et al. (2001) recommended that foraging habitat for red-cockaded woodpeckers contain abundant herbaceous ground cover and a size-class distribution of pines consisting of about 55 small pines (<25.4 cm dbh), 50 medium-sized pines (25.4-35.6 cm dbh), and 45 large pines (>35.6 cm dbh) per ha. Frequent fire and appropriate silviculture are the primary means put forth by James et al. (2001) to achieve the desired habitat. Further, James et al. (2001) recommended at least 51 ha of available foraging habitat be provided for each group of woodpeckers. Our study supports each of these recommendations, with the exception of ground-cover vegetation, which we did not measure. Habitat identified as medium or high quality in our study has a similar size-class distribution (Fig. 6) to that recommended by James et al. (2001), and our data suggest that a group will require more than 25-50 ha of such habitat. In addition to these recommendations, we stress the importance of old-growth pines to habitat quality and specifically recommend their development and protection throughout the foraging habitat of red-cockaded woodpeckers.

Finally, we strongly recommend the integration of management of nesting and foraging habitat. Habitat structure associated with good nesting habitat is the same structure recommended here for high-quality foraging habitat. Currently, however, areas managed as nesting habitat and as foraging habitat are distinct. Management of nesting habitat consists of 3 main techniques: (1) installation of artificial cavities, (2) protection of existing cavities, and (3) midstory control, preferably by frequent prescribed fire. Cavity installation is an emergency technique used to offset net loss of old-growth cavity trees and...
should be used in concert with the development of old-growth, potential cavity trees throughout the landscape (as per proposed nesting habitat guidelines by the U.S. Fish and Wildlife Service [2000]). Once potential cavity trees are available in abundance, and frequent prescribed burning is applied throughout red-cockaded woodpecker habitat, there will be no need to distinguish nesting habitat from foraging habitat.

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