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Schaefer, Richard R.; Conner, Richard N.; Rudolph, D. Craig; and Saenz, Daniel, "Red-Cockaded Woodpecker Nestling Provisioning and Reproduction in Two Different Pine Habitats" (2004). *Faculty Publications*. Paper 446.
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RED-CKOKADED WOODPECKER NESTLING PROVISIONING AND REPRODUCTION IN TWO DIFFERENT PINE HABITATS

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ABSTRACT—We obtained nestling provisioning and reproductive data from 24 Red-cockaded Woodpecker (*Picoides borealis*) groups occupying two different pine habitats—longleaf pine (*Pinus palustris*) and a mixture of loblolly (*P. taeda*) and shortleaf pine (*P. echinata*)—in eastern Texas during 1990 and 1991. **Habitat data** were collected within 800 m of each group's cavity-tree cluster. Feeding trips per nest and prey biomass per feeding trip were significantly greater in loblolly-shortleaf pine habitat. There were few significant correlations between reproductive/provisioning and habitat variables in either pine habitat. Pines dying from infestation by southern pine beetles (*Dendroctonus frontalis*) were more common in loblolly-shortleaf than in longleaf pine habitat. In addition, adult male Red-cockaded Woodpeckers weighed more in loblolly-shortleaf pine habitat. **Indices of southern pine beetle abundance in loblolly-shortleaf pine habitat were negatively correlated with number of feeding trips per nestling, but positively correlated with prey biomass delivered to nestlings. We hypothesize that the greater abundance of southern pine beetles and associated arthropods in loblolly-shortleaf pine habitat, and the resulting higher frequency of dying pines containing an abundant food source, were associated with an elevated prey biomass available to both nestling and adult Red-cockaded Woodpeckers. Received 29 June 2003, accepted 20 April 2004.**

The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperatively breeding species that lives in family groups of two or more individuals (Ligon 1970, Walters et al. 1988). Groups include a breeding pair, young of the year, and often one to three other adults, which serve as "helpers." Helpers are usually male offspring from previous nestings and assist the breeding pair with caring for nestlings (Ligon 1970, Lennartz and Harlow 1979). Red-cockaded Woodpeckers are endangered (U.S. Department of Interior 1970) and inhabit open, mature pine (*Pinus* spp.) habitats of the southeastern United States. Populations have become fragmented and isolated due to severe habitat alterations (Costa and Escano 1989, Rudolph and Conner 1994). Cutting of old-growth pine forests and elimination of recurring fire across most of the woodpecker's range are major causes of the species' decline (Jackson 1971, Lennartz et al. 1983). Historically, fire maintained suitable foraging and nesting habitat. Several studies have reported positive indirect effects of fire on Red-cock-

aded Woodpecker fitness through increased arthropod abundance (Provencher et al. 1998, 2001), increased grass and/or forb ground cover (James et al. 1997), and reduced hardwood midstory vegetation (Walters et al. 2002).

Red-cockaded Woodpeckers are known to select larger and older pines as foraging substrates (Engstrom and Sanders 1997, Zwicker and Walters 1999, Walters et al. 2002); such pines are believed to support more arthropods (Hanula et al. 2000), particularly during the breeding season (Conner et al. 2004). Young pine forests may offer suboptimal foraging habitat by providing a reduced prey base, especially in areas surrounding cavity tree clusters (stands of cavity trees occupied by Red-cockaded Woodpecker groups) that have been clearcut or contain dense plantations of young (<30 years) pines. Foraging and provisioning of nestlings may be more difficult in young pine forests, which could have a negative effect on the survivorship of adults and nestlings (Ligon 1970, 1971).

Logically, prey availability during the nesting season has an impact on Red-cockaded Woodpecker reproductive success and adult nutrition. There is little information regarding comparisons of arthropod densities and biomass between longleaf pine (*Pinus palustris*) and loblolly-shortleaf pine (*P. taeda*-*P. echin-*

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ata) habitats. During nesting season, differences in prey availability among habitats dominated by different pine species can impact both reproduction and adult nutrition of Red-cockaded Woodpeckers.

The southern pine beetle (*Dendroctonus frontalis*) is responsible for considerable pine mortality, especially during cyclic epidemics (Conner et al. 2001). Infestations can potentially destroy Red-cockaded Woodpecker foraging habitat and cavity trees. However, during non-epidemic beetle years, woodpeckers can benefit by concentrating foraging activity on dying pines that provide an arthropod-rich food source (Hooper and Lennartz 1981, Schaefer 1996, Bowman et al. 1997). Such ephemeral food sources, while unpredictable, can provide nutritional benefits to both nestlings and adults.

Our objectives were to (1) compare reproductive and provisioning effort in longleaf pine and loblolly-shortleaf pine habitats, (2) determine whether habitat variation affected reproduction and nestling provisioning, and (3) use body mass of adults to assess nutritional status of birds in longleaf pine and loblolly-shortleaf pine habitats.

METHODS

Study areas.—We collected reproductive, nestling provisioning, and vegetation data during the 1990 and 1991 nesting seasons. Study sites were on the Davy Crockett National Forest (DCNF) and the Angelina National Forest (ANF) in eastern Texas (see Conner and Rudolph 1989 for area descriptions). We chose 24 study sites (i.e., 24 woodpecker groups), 8 at DCNF and 16 at ANE Sites were selected based on the dominant pine species; 11 sites were located in longleaf pine and 13 were located in loblolly-shortleaf pine habitat.

Reproduction and nestling provisioning.—All Red-cockaded Woodpeckers captured at each of the 24 study sites were banded (U.S. Fish and Wildlife Service band and 2-3 color bands) for individual recognition. Birds were visually identified in the field with the aid of binoculars and a 20× spotting scope mounted on a tripod.

Nest monitoring began during the first week of April, about 2 weeks before nesting was expected to commence. If an adult occupied the nest cavity when checked, the tree was

climbed using sectional aluminum ladders; eggs were then counted. If the clutch did not appear complete (normally two to four eggs comprise a complete clutch), it was checked again in a few days. When nestlings were detected, the nest tree was again climbed and young were counted and aged (Ligon 1971).

Provisioning data were collected when nestlings were 8, 20, and 23 days of age. The nest cavity of each woodpecker group was observed for a 3-hr period in the morning, beginning when the breeding male exited the nest. We recorded identity of the adult bringing food, size of each prey item, and time of each feeding. Prey size was visually estimated and categorized as small, medium, or large. An item was considered small if barely visible in the adult's beak. A medium-sized item was estimated at less than one-half of the beak's length. A large item was estimated at more than one-half of the beak's length. We assume that any bias toward larger prey inherent in this procedure was equal among the two pine habitats.

We attempted to obtain a biomass value for each size category. Since it was not possible to collect samples of prey items delivered to nestlings, we collected arthropods similar to those observed being provided in both pine habitats. Samples were obtained from the boles of dead loblolly and shortleaf pines killed by southern pine beetles. These arthropods were separated into small, medium, and large size categories using the same criteria used during provisioning observations. We collected 30 individuals of each size category, determined wet weight (mg), and calculated average weight for each size category. Relative values for prey biomass were calculated using the mean weight of each size category (small = 11.3 mg, medium = 45.6 mg, large = 197.4 mg).

Vegetation and stand area measurements.—Habitat data were collected at each study site within an 800-m radius centered on each woodpecker group's cluster of cavity trees. Forest compartment stand maps were obtained from the ANF and DCNF district offices for those compartments falling within the 800-m radius. Each compartment is comprised of forest stands of varying size. Five dominant or codominant pines were selected within each forest stand within the 800-m radius by

choosing the nearest tree in a random direction from five arbitrary points well-dispersed within the stand. Habitat measurements were taken within an 11.2-m radius (0.04-ha circular plot) centered on each of these live trees (Conner 1980), and means were used to characterize habitat within the forest stand.

Stand age was determined by coring each central tree at breast height (1.3 m) with an increment borer and counting growth rings of the cores. We added 3 years for loblolly pine and shortleaf pine, and 5 years for longleaf pine to account for growth to breast height (Conner and O'Halloran 1987). Stands were categorized as 0–20, 30–49, 50–69, 70–89, or >90 years old. Tree diameter (cm) was measured at breast height (dbh) with calipers and categorized into 0–30, 30.1–40, 40.1–50, or 50.1–70 cm. Surrounding canopy height and midstory height (m) were measured with a range finder. Canopy height was placed into categories of 0–12, 12.1–21, 21.1–27, or 27.1–33 m.

Midstory density was visually estimated and placed into one of five categories: none, sparse, moderate, dense, or very dense. Midstory conditions were considered suitable if height was ≤ 3 m regardless of density, or if density was none to sparse regardless of height. A one-factor metric basal area prism was used to measure basal area (m^2/ha) of pine overstory, hardwood overstory, pine midstory, and hardwood midstory. Pine and hardwood overstory basal areas were placed into categories of 0–9, 9.1–15, 15.1–20, 20.1–25, or 25.1–30 m^2/ha . Pine and hardwood midstory basal areas were categorized as 0–3, 3.1–6, 6.1–9, or 9.1–12 m^2/ha . The area (ha) of each forest stand within 800 m of each nest tree was measured from compartment stand maps with a digitizer, and the percentage of area occupied by each habitat category calculated.

Measurements of southern pine beetle abundance.—Data on southern pine beetle abundance during 1990 and 1991 were obtained from the U.S. Forest Service for each forest compartment where study sites were located. All other causes of mature pine mortality were assumed to be equal between longleaf and loblolly-shortleaf pine habitats. Three variables were used as indices of southern pine beetle abundance in comparing beetle ac-

tivity in longleaf pine versus loblolly-shortleaf pine: (1) the number of active beetle spots (one or more contiguous beetle-infested trees), (2) the number of trees infested (dying pines with fading or red needles, and all or most bark remaining), and (3) the number of hectares affected by infestation. A total for each variable was calculated for the entire forest compartment, even if only a portion of the compartment fell within the 800-m radius circle.

Adult Red-cockaded Woodpecker body mass.—Each adult woodpecker was weighed to the nearest 0.5 g with a 100-g spring scale. Body mass was obtained throughout the year, except during nesting; each bird was weighed once. Birds were captured either in the morning just before exiting the roost cavity, or in the evening just after entering. We realize there is both seasonal and temporal (24-hr) variability in the body mass of a given individual. For each of the two pine habitats, body masses were pooled by sex.

Data analysis.—Data were analyzed using SAS (SAS Institute, Inc. 1988). A significance level of $P = 0.05$ was used in all hypothesis testing. In tests involving habitat variables, stands 0–29 years old, most of which were clear-cuts and young pine plantations, were not included in evaluations of available foraging habitat because these stands are considered unsuitable for Red-cockaded Woodpecker foraging (U.S. Fish and Wildlife Service 2003). However, the 0–29 year stand age category is included for comparative purposes.

The 24 Red-cockaded Woodpecker groups observed produced a total of 37 successful (i.e., one or more fledglings) nests during the two nesting seasons. For statistical analyses, a 2-year average of each reproductive variable was used for each group to avoid a repeated measures violation. Comparisons of reproductive variables between pine habitats using repeated measures analyses were not possible because of instances of small sample sizes within years due to some groups not nesting for various reasons, especially in longleaf pine habitat.

Pearson correlation coefficients were used to explore relationships of reproductive and provisioning variables with habitat variables. Two-tailed *t*-tests were used to compare reproductive performance and provisioning ef-

fort between longleaf and loblolly-shortleaf pine. A medium effect size of 0.5 (Cohen 1988) was used in power analyses for statistically non-significant variables.

Two-way ANOVAs (pine type X habitat variable) on ranked data were used to compare category distribution of each habitat variable (tree age, diameter at breast height, canopy height, suitable/unsuitable midstory, pine overstory basal area, hardwood overstory basal area, pine midstory basal area, and hardwood midstory basal area) between longleaf ($n = 11$) and loblolly-shortleaf ($n = 13$) pine habitats. If the interaction indicated different distributions between the pine habitats, Wilcoxon rank-sum tests were used for each habitat variable category to test for differences between longleaf and loblolly-shortleaf pine.

Two-tailed t-tests were used to compare southern pine beetle abundance and body mass of adult Red-cockaded Woodpeckers between the pine habitats. Pearson correlation coefficients were used to examine relationships between southern pine beetle abundance, and provisioning effort and reproductive performance, within each pine habitat. Adult male body mass, including that of both helpers and breeders, was treated separately from adult female body mass due to differing foraging strategies (Ligon 1968, Hooper and Lennartz 1981).

RESULTS

Nesting effort in relation to pine habitat.—During the two nesting seasons, 24 Red-cockaded Woodpecker groups had a total of 37 successful (i.e., one or more fledglings) nests. For various reasons, not all groups successfully nested. One longleaf clutch was depredated and the group did not re-nest. One loblolly-shortleaf group disappeared altogether between years. Eggs at three nests failed to hatch (one in longleaf, two in loblolly-shortleaf). Breeding pairs at five longleaf sites appeared to forgo nesting during 1 of the 2 years. Although unlikely, some clutches may have been initiated and then depredated immediately before we detected them. If so, the birds did not appear to re-nest.

Twelve (80%) of 15 successful nests in longleaf pine habitat lacked helpers, and only one helper was present at the remaining 3 (20%) nests. Eleven (50%) of 22 successful

nests in loblolly-shortleaf pine habitat lacked helpers. Of the remaining 11 nests, 10 (45%) had one helper and 1 (5%) had two helpers (one male and one female). For all 24 groups (2 years combined) the average number of helpers per group was 0.4.

During the two nesting seasons, 17 clutches were produced in longleaf pine and 24 in loblolly-shortleaf pine. Clutch size was not recorded in two instances, once in each habitat. The remaining 16 longleaf nests produced a total of 51 eggs ($\bar{x} = 3.19$ eggs/clutch), and 23 loblolly-shortleaf nests produced a total of 78 eggs ($\bar{x} = 3.39$ eggs/clutch). Hatching success based on clutch size was 75% in longleaf pine and 87.3% in loblolly-shortleaf. Hatching success, as measured by the number of nestlings hatched from eggs surviving through the incubation period, was 85.7% (36 nestlings from 42 eggs; $n = 13$ nests) in longleaf habitat and 89.9% (62 nestlings from 69 eggs; $n = 20$ nests) in loblolly-shortleaf habitat. Two clutches in each pine habitat failed to hatch, leaving a total of 15 and 22 broods produced in longleaf and loblolly-shortleaf, respectively. The 15 broods in longleaf produced 24 fledglings ($\bar{x} = 1.60$ fledglings/nest), and the 22 in loblolly-shortleaf produced 42 fledglings ($\bar{x} = 1.91$ fledglings/nest). The initial number of nestlings could not be counted for two broods in each pine habitat. Fledging success subsequent to hatching was 55.6% for the remaining 13 broods in longleaf, and 62.9% for the remaining 20 broods in loblolly-shortleaf habitat.

Considering only woodpecker groups that produced one or more fledglings, all nest productivity measures (with the exception of partial brood loss) and number of adults were slightly higher in loblolly-shortleaf than in longleaf pine habitat; only feeding trips per nest and prey biomass per feeding trip were statistically greater (Table 1). Power analyses revealed that sample sizes in each pine habitat were too small to detect biological significance (medium size effect of 0.5, power = 0.2) for statistically non-significant variables.

A two-way ANOVA was calculated to evaluate the contribution of group size to the number of feeding trips to nests in loblolly-shortleaf and longleaf pine habitats. There was no significant interaction ($F_{2,16} = 0.43$, $P = 0.66$) between group size and pine habitat in relation

TABLE 1. Red-cockaded Woodpecker nesting effort^a (mean \pm SD) in longleaf ($n = 10$)^b and loblolly-shortleaf ($n = 13$) pine habitats in eastern Texas during 1990 and 1991.^c

Nesting variable	Longleaf	Loblolly-shortleaf	<i>t</i>	<i>P</i>
Group size	2.3 \pm 0.4	2.5 \pm 0.5	1.43	0.17
Clutch size	3.3 \pm 0.6	3.5 \pm 0.5	0.91	0.37
Initial brood size ^d	2.9 \pm 0.7	3.0 \pm 0.6	0.53	0.61
Brood size ^e	1.7 \pm 0.5	2.0 \pm 0.4	1.68	0.11
Feedings per nest ^e	31.4 \pm 0.7	43.3 \pm 11.3	2.66	0.015
Feedings per nestling ^e	19.7 \pm 7.1	22.7 \pm 5.4	1.15	0.26
Prey biomass per trip (mg) ^f	73.2 \pm 31.0	116.7 \pm 36.3	3.03	0.006
Number of fledglings	1.7 \pm 0.5	1.9 \pm 0.4	1.41	0.17
Partial brood loss ^g	0.3 \pm 0.2	0.2 \pm 0.2	0.59	0.56

^a Only groups that produced at least one fledgling are included in these analyses.

^b Sample size = 10 because one longleaf pine group did not produce at least one fledgling during either year.

^c The total number of nests producing fledglings was 15 at longleaf pine and 22 at loblolly-shortleaf pine sites over the two nesting seasons. The 2 years were averaged for each nesting variable, for each group.

^d Initial brood size and partial brood loss are each unknown in one instance in longleaf pine habitat. Therefore $n = 9$ in longleaf for these two nesting variables.

^e Means based upon observations at 8, 20, and 23 days of nestling age at each nest.

^f Nestling loss between hatching and day 8.

to the number of feeding trips per nest, and group size alone did not influence ($F_{3, 16} = 0.41$, $P = 0.75$) number of feeding trips per nest. These results indicate that differences between the two pine habitats, and not group size, were responsible for the greater number of feeding trips made to nests in loblolly-shortleaf pine habitat.

Mean number of feeding trips per nest was significantly greater in loblolly-shortleaf pine habitat, but mean number of feeding trips per nestling was similar, indicating that individual nestlings were fed at about the same frequency in both pine habitats (Table 1). However, average prey biomass per feeding trip was significantly greater in loblolly-shortleaf than in longleaf pine (Table 1), indicating that nestlings in the former received more food. There were few significant correlations among reproductive/provisioning variables and habitat variables in either pine habitat. Of note was the lack of significant relationships between any of the habitat variables and prey biomass within either pine habitat. Thus, the habitat variables we measured had little or no relationship with size of prey items delivered to nestlings.

Comparison of longleaf and loblolly-shortleaf pine habitats.—The percentage of area occupied by forest stands <30 years old was greater in loblolly-shortleaf than in longleaf pine habitat ($Z = -3.22$, $P = 0.001$; Fig. 1A). This was the result of extensive clear-cutting that occurred during the 1970s and 1980s, as

well as southern pine beetle control cuts in loblolly-shortleaf pine study sites. Cutting seldom occurred in longleaf pine study sites. Forest stands in the 30–49 year ($Z = 2.71$, $P = 0.007$) and SO-69 year ($Z = 2.12$, $P = 0.034$) age categories occupied more area in longleaf pine habitat, whereas stands in the 70–89 year ($Z = -3.62$, $P < 0.001$) age category occupied more area in loblolly-shortleaf pine habitat (Fig. 1A). There was no difference between pine habitats in the percentage of area occupied by the 90–120 year age category ($Z = -1.50$, $P = 0.13$; Fig. 1A). This oldest stand-age category constituted only a small percentage of area within the 800-m radius in both pine habitats.

Loblolly-shortleaf pine contained a higher frequency of stands in the largest dbh category of SO. 1–70 cm ($Z = -2.78$, $P = 0.006$) and highest canopy height category of 27.1–33 m ($Z = -3.72$, $P < 0.001$) than did longleaf pine (Figs. 1B and 1C). Conversely, the smaller dbh category of 30.1–40 cm ($Z = 3.63$, $P < 0.001$) and shorter canopy height categories of 12.1–21 m ($Z = 2.11$, $P = 0.035$) and 21.1–27 m ($Z = 2.32$, $P = 0.021$) were more common in longleaf pine (Figs. 1B and 1C).

Comparison of midstory between pine habitats revealed that the percentage of area with suitable midstory conditions was greater in longleaf pine ($Z = 3.74$, $P < 0.001$) and the percentage of area occupied by unsuitable midstory conditions was greater in loblolly-

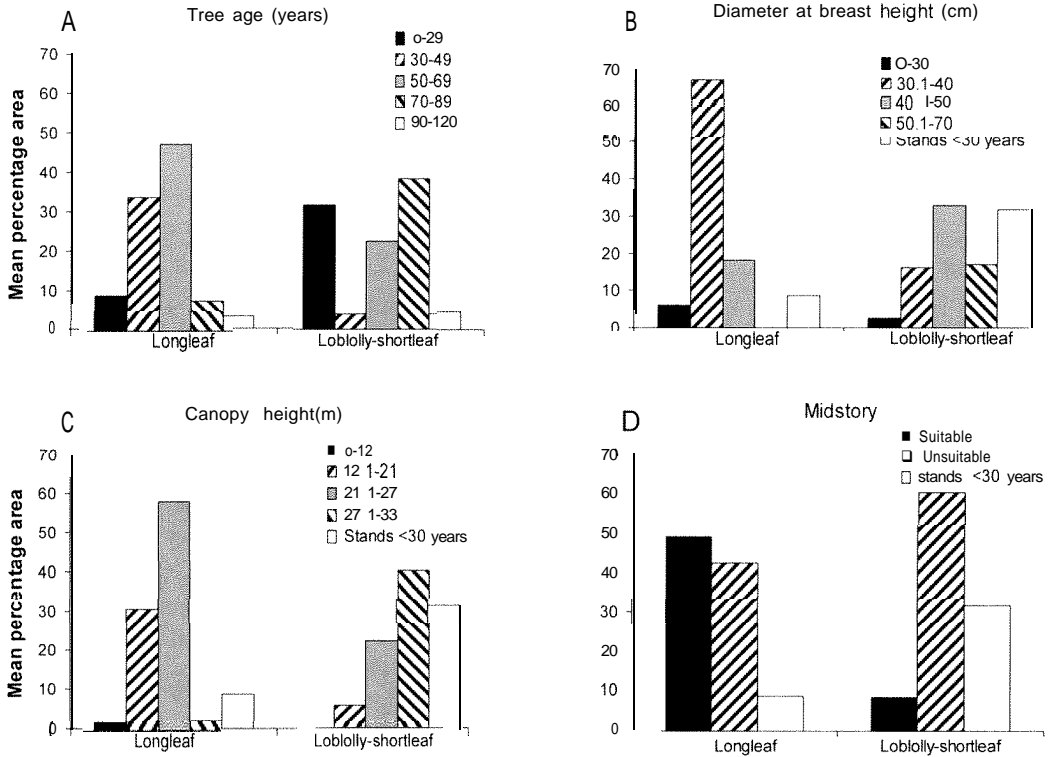


FIG. 1. Mean percentage of area within 800 m of Red-cockaded Woodpecker cavity-tree clusters occupied by each category of (A) tree age, (B) diameter at breast height, (C) canopy height, and (D) midstory in longleaf pine ($n = 11$) and loblolly-shortleaf pine ($n = 13$) sites in eastern Texas, 1990–1991.

shortleaf pine ($Z = -2.17, P = 0.030$; Fig. 1D). When habitat of all ages (i.e., including stands <30 years old) within 800 m of woodpecker nest trees was considered, the average percentage of area with unsuitable midstory was 51% for longleaf and 93% for loblolly-shortleaf pine.

Pine overstory basal area was similar between pine habitats with the exception of the 20.1–25 m²/ha category, which occupied a greater percentage of area in longleaf pine ($Z = 2.62, P = 0.009$; Fig. 2A). Trees in the 0–9 m²/ha hardwood overstory basal area category occupied a greater percentage of area in longleaf than in loblolly-shortleaf pine ($Z = 3.05, P = 0.002$). Few forest stands containing overstory hardwoods were within any basal area category greater than 0–9 m²/ha in either pine habitat (Fig. 2B).

No significant differences were found in any pine midstory basal area category between the two pine habitats ($F_{3, 88} = 1.96, P$

$= 0.13$; Fig. 2C). The percentage of area occupied by the relatively low hardwood midstory basal area category of 0–3 m²/ha was greater in longleaf pine ($Z = 3.07, P < 0.001$). The percentage of area occupied by the greater hardwood midstory basal area categories of 3.1–6 m²/ha ($Z = -2.89, P = 0.004$), 6.1–9 m²/ha ($Z = -2.13, P = 0.033$) and 9.1–12 m²/ha ($Z = -1.96, P = 0.050$; Fig. 2D) were all greater in loblolly-shortleaf pine.

Southern pine beetle influence.—The number of active beetle spots, beetle-infested trees, and total hectares infested with beetles were all significantly greater in loblolly-shortleaf pine habitat (Table 2). At loblolly-shortleaf nests in which at least one fledgling was produced ($n = 22$), number of active beetle spots ($r = 0.48, P = 0.022$), beetle trees ($r = 0.45, P = 0.036$), and infested hectares ($r = 0.67, P < 0.001$) were positively correlated with prey biomass delivered to nestlings. Number of beetle spots ($r = -0.57, P = 0.006$), beetle

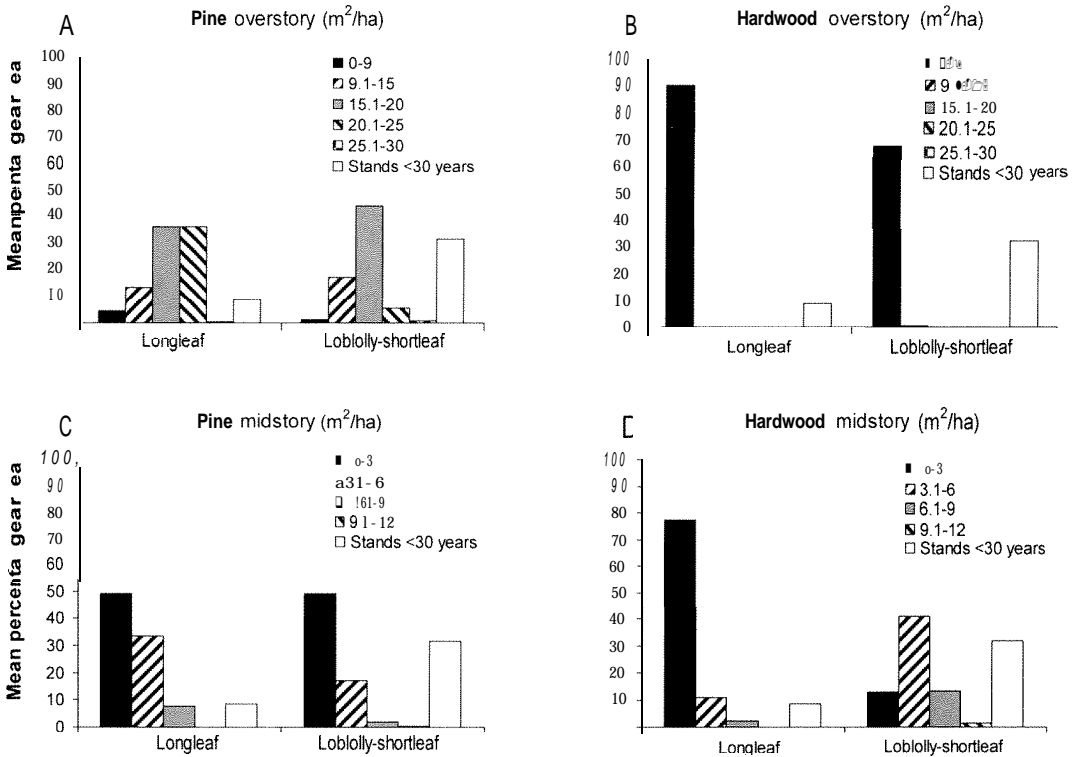


FIG. 2. Mean percentage of area within 800 m of Red-cockaded Woodpecker cavity-tree clusters occupied by each category of (A) pine overstory basal area, (B) hardwood overstory basal area, (C) pine midstory basal area, and (D) hardwood midstory basal area in longleaf pine ($n = 11$) and loblolly-shortleaf pine ($n = 13$) sites in eastern Texas, 1990–1991.

trees ($r = -0.60$, $P = 0.003$), and infested hectares ($r = -0.51$, $P = 0.016$) were negatively correlated with number of feeding trips per nestling. No significant correlations were found between indices of beetle abundance and the remaining reproductive and provisioning variables. At longleaf nests in which at least one fledgling was produced ($n = 15$), no significant correlations were found between indices of beetle abundance and any of the reproductive and provisioning variables.

Adult nutritional status.—Body mass was used to compare separately the nutritional status of adult male and female Red-cockaded Woodpeckers in longleaf and loblolly-shortleaf pine habitats. Body mass of adult males was significantly greater ($t = -2.25$, $P = 0.030$) in loblolly-shortleaf ($\bar{x} = 48.5$ g \pm 2.3 SD, $n = 27$) than in longleaf pine ($\bar{x} = 46.9$ g \pm 2.7 SD, $n = 18$). Adult females averaged only slightly heavier in loblolly-shortleaf ($\bar{x} = 46.6$ g \pm 2.2 SD, $n = 17$) than in longleaf

pine ($\bar{x} = 45.3$ g \pm 2.0 SD, $n = 13$), and the difference was not statistically significant ($t = -1.59$, $P = 0.12$).

DISCUSSION

Canopy trees in loblolly-shortleaf pine habitat were generally older, taller, and larger in diameter than in longleaf pine. Suitable midstory conditions for Red-cockaded Woodpeckers were more widespread in longleaf than in loblolly-shortleaf pine. Soil-type differences and more effective prescribed burning in longleaf pine areas had a strong influence on differences in midstory condition between the two pine habitats (Conner and Rudolph 1989). Red-cockaded Woodpeckers are known to have an aversion to a well-developed stratum of midstory vegetation associated with both nesting (Conner and Rudolph 1989, Loeb et al. 1992) and foraging habitat (Rudolph et al. 2002; Walters et al. 2000, 2002). Thus, it might be expected that nest productivity of

TABLE 2. Southern pine beetle abundance (mean \pm SD) at longleaf ($n = 22$) and loblolly-shortleaf ($n = 25$) pine sites in eastern Texas during 1990 and 1991.^a

Variable	Longleaf	Loblolly-shortleaf	<i>t</i>	<i>P</i>
Number of beetle spots	0.32 \pm 0.57	2.80 \pm 2.80	4.33	<0.001
Number of infested trees	2.91 \pm 5.13	65.32 \pm 65.58	4.74	<0.001
Number of infested hectares	0.01 \pm 0.04	0.63 \pm 0.80	3.84	<0.001

^a The 2 years were not combined for southern pine beetle analyses due to the potential for substantial year-to-year changes in beetle abundance indices

woodpeckers in habitat with an abundance of midstory vegetation (i.e., loblolly-shortleaf pine) would be lower than in longleaf pine.

Despite less suitable midstory conditions in loblolly-shortleaf pine habitat, woodpecker groups there performed at least as well reproductively as groups in longleaf pine, but only feeding trips per nest and relative prey biomass delivered to nestlings were significantly greater in the former. Our sample sizes were too small to detect biologically significant differences between pine habitats for the remaining reproductive and provisioning variables.

Helpers were more common in loblolly-shortleaf groups, but only once was there > 1 per group. Other studies indicate that groups with helpers fledge significantly more young than groups without helpers (Lennartz et al. 1987, Walters 1990). In this study, increased group size did not significantly influence the number of feeding trips per nest even though helpers assisted with nestling provisioning. However, helpers may enhance reproductive success by assisting with incubation, brooding and feeding nestlings, territory defense, and defense against predators.

The relative biomass of arthropod prey delivered to nestlings was significantly greater in loblolly-shortleaf than longleaf pine habitat. At those loblolly-shortleaf sites where southern pine beetles were more abundant, adult Red-cockaded Woodpeckers made fewer feeding trips per nestling but delivered larger prey items. Access to larger prey items may benefit adults by reducing nestling provisioning effort.

The smallest mean for provisioned biomass per feeding trip (76.9 mg) for any nest in loblolly-shortleaf habitat was greater than that for 9 of the 15 nests in longleaf habitat. We know from field observations that adults from at least three of the six nests in longleaf habitat with large values for mean prey biomass per

feeding trip had access to one or more (exact number unknown) nearby dying pines. These trees were often loblolly pines located on wetter sites (i.e., streams or baygalls) within longleaf pine habitat, and were dying from either lightning strikes or southern pine beetle infestations. During provisioning observations, we noticed adults spending considerable time traveling between the direction of the dying pines and the nest. Thus, the high values of biomass provisioned to nestlings appear to be at least partially dependent on the local availability of dying pines that have an abundant supply of arthropod prey. A great number of arthropod species are attracted to such dying pines, which provide an abundance of food for Red-cockaded Woodpeckers (Ligon 1968, Hooper and Lennartz 1981, Conner et al. 2001).

Adult and larval southern pine beetles are fairly small prey items for Red-cockaded Woodpeckers. However, the adults and larvae of larger wood boring beetles (e.g., Cerambycidae and Buprestidae), which are attracted to pines infested by southern pine beetles, provide much larger prey items for foraging woodpeckers. Red-cockaded Woodpeckers have been observed to forage for as long as 55 min on small groups of dying pines infested with arthropods before moving on to a healthy tree (Schaefer 1996). Dying pines provide an important food source for Red-cockaded Woodpeckers throughout the year, particularly during the nesting season when young woodpeckers are being fed.

We suggest that the greater abundance of southern pine beetles in loblolly-shortleaf pine habitat and the resulting higher frequency of dying pines containing a diverse and abundant arthropod community are associated with elevated prey biomass. Dying pines were comparatively rare in longleaf pine habitat because this species is more resistant to southern

pine beetle infestation; this is due to its ability to produce copious amounts of resin and to the different physical properties of its resin (Hodges et al. 1979). Increased prey availability, in terms of biomass, is one indication of increased territory quality. Thus, the quality of foraging habitat at our loblolly-shortleaf pine study sites was greater than that at longleaf pine sites. That adult male Red-cockaded Woodpeckers weighed more in loblolly-shortleaf pine habitat suggests, at least in eastern Texas, that they are nutritionally more fit than those in longleaf pine habitat.

The abundant food source available to Red-cockaded Woodpeckers in dying pines is transient. During epidemic years southern pine beetles can devastate large areas of pine forest, including Red-cockaded Woodpecker foraging habitat and entire cavity-tree clusters. However, during non-epidemic years, when southern pine beetle attacks are confined to single trees or small groups of pines, prey availability may increase for Red-cockaded Woodpeckers. Territory quality influenced by the presence of ephemeral southern pine beetle infestations will fluctuate and can be unpredictable.

ACKNOWLEDGMENTS

We thank C. K. Evans, P. Fenci, S. W. Lower, C. E. Shackelford, and M. Watson for assistance with field work, and C. E. Braun, R. T. Engstrom, F. C. James, B. R. Pappasol, F. J. Sanders, J. R. Walters and an anonymous reviewer for constructive comments on an early draft of the paper. We also thank N. E. Kocrt for statistical and editorial assistance.

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