ARTHROPOD DENSITY AND BIOMASS IN LONGLEAF PINES: EFFECTS OF PINE AGE AND HARDWOOD MIDSTORY

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Abstract: During a 2-year study we examined arthropod communities (density and biomass) on longleaf pines (*Pinus palustris*) in eastern Texas during spring, summer, and winter on trees in 3 age classes: 40–50, 60–70, and 130–150 years, as a potential food source for the red-cockaded woodpecker (*Picoides borealis*). We also examined arthropod density and biomass on the lower boles of 40–50 year-old longleaf pines in stands with and without a well-developed hardwood midstory. Pine age did not significantly affect total arthropod density on the lower boles of pines between the ages of 40 and 150 years during any of the 3 seasons examined. Total arthropod biomass, however, was significantly higher in 60–70-year-old pines than in 40–50 and 130–150-year-old pines during winter. During the breeding season, a period when adult red-cockaded woodpeckers are provisioning nestlings with food, total arthropod biomass increased steadily with pine age and was significantly higher in 130–150 year-old pines than in 40–50 year-old pines. During the post-breeding season, total arthropod biomass was unaffected by pine age. The presence or absence of hardwood midstory within 40–50 year-old pine stands had no significant effect on either total arthropod density or total arthropod biomass during any of the three seasons examined.

Key words: Arthropods, biomass, longleaf pines, red-cockaded woodpecker.

The red-cockaded woodpecker (*Picoides borealis*) is a keystone species within the southern pine ecosystem and is therefore crucial for the maintenance of biodiversity. It is the only species in North America that regularly makes cavities in living pines (*Pinus* spp.) (Ligon et al. 1986), and by doing so, provides cavities for many other cavity-using vertebrates and invertebrates in an otherwise relatively cavity-barren environment (Baker 1971, Dennis 1971*a*, Harlow and Lennartz 1983, Jackson 1978c, Rudolph et al. 1990a, Conner et al. 1997*a*). Provision of adequate foraging habitat is critical for the maintenance of viable populations of endangered species. The endangered red-cockaded woodpecker forages almost exclusively on invertebrates inhabiting living pines (Ligon 1968, Wood 1977, Miller 1978, Skorupa 1979, Hooper and Lennartz 1981, Porter and Labisky 1986, Repasky and Doerr 1991), but also uses pines infested by bark beetles when they are available (Conner et al. 2001*a*).

The red-cockaded woodpecker evolved in a fire-maintained pine ecosystem with an herbaceous groundcover and little hardwood midstory vegetation (Ligon, 1970, Jackson 1971, Hooper et al. 1980, Conner et al. 2001*a*). In the absence of natural fire or an effective prescribed burning regime, many areas of historic red-cockaded woodpecker habitat currently have a well-developed hardwood midstory. How hardwood midstory vegetation influences arthropod communities is largely unknown. Jackson (1979) speculated that increasing tree species diversity, such as hardwood midstory, might increase the diversity of arthropods in a forest community.

Few studies have attempted to quantify arthropod abundance and biomass in pine forests. Hooper (1996) examined winter arthropod biomass on boles, live limbs, and dead limbs on longleaf pine trees (*Pinus palustris*) of different age classes in the Francis Marion National Forest, South Carolina. He concluded that winter arthropod biomass on longleaf pines increased with tree age up to about 86 years of age and then declined. Hanula et al. (2000*a*) examined arthropod communities associated with longleaf pines during four seasons of the year and noted that arthropod biomass increased with increasing tree age up to about 65–70 years (see also Hanula and Horn 2004). They further suggest that arthropod biomass remains relatively constant as pines age beyond 70 years. Horn and Hanula (2002*a*) suggested that it was bark structure that was responsible for higher abundance and biomass of arthropods on longleaf pines than on loblolly pines (*Pinus taeda*).

Hanula and Franzreb (1998) examined arthropods on the boles of 50–70-year-old longleaf pines, and found that a majority of the arthropods originated from the forest floor. Studies of pine bole arthropod communities on loblolly and shortleaf pines in eastern Texas also indicated that arthropods on the boles of pines were coming primarily from the forest floor, and herbaceous layer vegetation composed primarily of grasses and forbs produced the greatest arthropod biomass on pine boles (Collins et al. 2002).

Male red-cockaded woodpeckers favor the upper bole, branches, and higher regions of pines as foraging sites, whereas females forage more on the lower boles of pines (Ligon 1968, 1971, Ramey 1980, Skorupa 1979, Hooper and Lennartz 1981, Jackson and Schardien-Jackson 1986, Engstrom and Sanders 1997). The presence of hardwood and pine midstory appears to displace female red-cockaded woodpeckers into the foraging niche of the socially dominant male (Rudolph et al. 2002).

Food supply has been shown to greatly influence reproductive success in other birds (Bryant 1975, 1978, 1979; Nolan and Thompson 1975; Sealy 1978; Quinney 1983; Blancher and Robertson 1987). Female red-cockaded woodpeckers appear to suffer weight loss from inadequate foraging habitat sooner than males (Jackson and Parris 1995). Thus, studies focusing on arthropod communities on the lower boles of pines, the region of the pine where female red-cockaded woodpeckers do most of their foraging, should be particularly valuable.

Past research on arthropod communities has evaluated arthropods on pines up to 127 years of age for winter arthropods (Hooper 1996) and during other seasons for ages up to about 95 years (Hanula et al. 2000*a*). We examined arthropod communities (density and biomass) on pines during spring, summer and winter on trees in three age classes: 40–50, 60–70, and 130–150 years in age. We also examined arthropod density and biomass on the lower boles of 40–50-year-old longleaf pines in stands with and without a well-developed hardwood midstory.

STUDY AREA AND METHODS

We selected 10 pines in each of 4 longleaf pine stands in 1997 on the southern portion of the Angelina National Forest (31°15'N, 94°15'W) in eastern Texas. Of the 2 youngest stands (40–50 years old), 1 had fairly dense hardwood foliage in both the understory and midstory, whereas the second stand had few hardwoods, and primarily grasses and forbs in the herbaceous layer (Table 1). The 2 additional stands were 60–70 years old and 130–150 years old, had little hardwood midstory, but had a well-developed herbaceous layer composed of grasses and forbs (Table 1).

Vegetation Structure Sampling

We measured vegetative characteristics in the 4 study areas because the vegetative structure within a pine stand might influence arthropod abundance on pine boles. We measured basal area of overstory pines, overstory hardwoods, midstory pines, and midstory hardwoods using a 1-factor metric basal area prism. We estimated foliage density at 0-1 m and 1-2 m in each cardinal direction from the base of each study tree using a foliage density board as described by MacArthur and MacArthur (1961). We used a hollow 4- x 12- cm tube as described by James and Shugart (1970) to determine groundcover percentage (monocot and dicot) and canopy closure percentage along 11.2-m transects extending from the base of each study tree in 4 cardinal directions. Each study tree was cored with an increment borer and the age determined in the lab.

Arthropod sampling

Arthropods were sampled on the pines for a 7-day period in January, May-June, and August during 1997 and 1998 at 3 heights on the bole: 3, 6, and 9 m. These 3 times of the year correspond to the red-cockaded woodpecker's winter, breeding season, and post-

Table 1. Habitat characteristics (mean ± SD) of 4 longleaf pine stands in which pine bole arthropod communities were examined on the Angelina National Forest, eastern Texas.

Habitat Variables[a]	Longleaf Pine Stands (n = 10 each) 40-50 y old with Midstory	40-50 y old without Midstory	60-70 y old	130-150 y old
Foliage Density 0-1 m (k)[b]	0.23 (0.09)^{A}	0.16 (0.10)^{A,B}	0.45 (0.13)^{B}	0.82 (0.33)^{C}
Foliage Density 1-2 m (k)	0.17 (0.06)^{A}	0.07 (0.05)^{B}	0.07 (0.05)^{B}	0.30 (0.08)^{C}
Foliage Density 0-1 m (k)	0.13 (0.08)^{A}	0.03 (0.01)^{B}	0.03 (0.01)^{B}	0.16 (0.07)^{A}
Herbaceous Dicot Groundcover (%)	13.8 (9.8)^{A,B}	11.5 (4.9)^{A}	26.9 (12.8)^{B,C}	29.9 (15.3)^{C}
Monocot Groundcover (%)	2.4 (2.3)^{A}	10.9 (8.5)^{B}	2.8 (2.8)^{A,B}	6.6 (10.3)^{A,B}
Canopy Closure (%)	84.5 (7.7)^{A}	61.6 (12.7)^{B}	55.0 (7.1)^{B}	53.5 (11.6)^{B}
Stand Height (m)	23.0 (0.0)^{A}	21.0 (0.0)^{B}	29.0 (0.0)^{C}	26.8 (2.0)^{D}
Overstory Pine Basal Area (m^2/ha)	10.7 (2.8)^{A}	16.5 (2.7)^{B}	21.5 (2.8)^{C}	12.2 (2.1)^{A}
Midstory Pine Basal Area (m^2/ha)	3.4 (2.2)^{A}	0.0 (0.0)^{B}	0.0 (0.0)^{B}	0.4 (0.7)^{B}
Overstory Hardwood Basal Area (m^2/ha)	1.5 (0.9)^{A}	0.9 (0.9)^{A,B}	0.2 (0.3)^{B}	0.3 (0.5)^{B}
Midstory Hardwood Basal Area (m^2/ha)	2.7 (2.1)^{A}	0.8 (0.8)^{B}	0.1 (0.3)^{B}	0.0 (0.0)^{B}

[a]ANOVA followed by Tukey's Test. Common letters across rows indicate non-significant differences at an alpha level of 0.05.
[b]See MacArthur and MacArthur (1961) for horizontal measurements of foliage (k).

breeding season, respectively. Thus, sampling was conducted during three seasons each year for 2 years on 40 trees, yielding 720 trap samples (3 heights × 40 trees × 3 seasons × 2 years).

Each arthropod trap was composed of a 5-cm-wide clear weatherproof tape with a 3- to 4-mm layer of Tangle Trap® (an insect trap coating made by the Tangle Foot Company) on the surface. To prepare for arthropod sampling, we shaved the bark ridges on the surface of the bole at each collection site (3, 6, and 9 m above the ground) approximately 15 cm wide to prevent arthropods from traveling under the trap tape. The tape was placed around the circumference of the tree at the three desired heights. After 7 days the traps and entrapped arthropods were removed and wrapped in a clear plastic film for freezer storage.

Arthropod Identification and Sorting

We examined arthropods through the clear plastic film and identified to taxonomic order or class (Borror and White 1970). We used a micrometer to measure length, and placed each arthropod into 1 of 3 size categories: <3 mm, 3-10 mm, and >10 mm. Because small arthropods (<3 mm) were so numerous, we randomly sub-sampled 3 10-cm segments on each trap for this size category. We divided the traps into numbered segments and used random number tables (n = 16) to select which segments to sample. All arthropod abundance data were converted to the number of arthropods per m^2 of trap surface. For most taxa, representative arthropods were captured for each of the 3 size classes, dried to constant weight, and averaged for each taxon size class. The weight coefficients were multiplied times the arthropod density

Table 2. The effects of longleaf pine age on the density and biomass (mean ± SD) of arthropod prey of red-cockaded woodpeckers on the Angelina National Forest, eastern Texas.

Arthropod Variables[a]	Longleaf Pine Age 40-50 years old	60-70 years old	130-150 years old
Breeding Season (May-June)			
Total Arthropod Density (no./m^2)	15443 (30604)^{A}	18101 (37216)^{A}	17156 (32977)^{A}
Total Arthropod Biomass (g/m^2)	2.06 (1.42)^{A}	2.49 (1.48)^{A,B}	2.98 (2.77)^{B}
Post-breeding Season (August)			
Total Arthropod Density (no./m^2)	7784 (11601)^{A}	10061 (14511)^{A}	9121 (13993)^{A}
Total Arthropod Biomass (g/m^2)	1.02 (0.76)^{A}	1.13 (0.67)^{A}	1.12 (0.60)^{A}
Winter (January)			
Total Arthropod Density (no./m^2)	1725 (2535)^{A}	1608 (2222)^{A}	1455 (2181)^{A}
Total Arthropod Biomass (g/m^2)	0.45 (0.48)^{A}	0.74 (0.56)^{B}	0.51 (0.56)^{A}

[a]Two-way ANOVA with interaction (pine age * year) calculated for each season followed by Duncan's Multiple Range Test. Common letters across rows indicate non-significant differences at an alpha level of 0.05. Pine stands examined contained minimal or no hardwood midstory.

values to estimate total biomass per m^2 for trap sample. Only taxa eaten by red-cockaded woodpeckers (Hess and James 1998, Hanula and Engstrom 2000, Hanula et al. 2000*a*) were included in the biomass estimate; samples of Diplopoda (millipedes) were not included because of their noxious taste/toxicity.

Statistical Analyses

We compared total arthropod density and total arthropod biomass between hardwood midstory treatments within each season with 2-way factorial analyses of variance (ANOVA, midstory condition × year) followed by Duncan's multiple range test (sample sizes across treatments were equal). A 2-way factorial ANOVA (pine age × year) within each season was also used to evaluate the effect of pine age on total arthropod density and total arthropod biomass. Data from all 40 pines were used to evaluate the effect of trap height on total arthropod density and total arthropod biomass (ANOVA, trap height × year). The criterion for significance in all statistical tests was a = 0.05.

RESULTS

A diverse array of arthropod taxa was captured in the traps on the boles of longleaf pines at all heights and during all 3 seasons (Appendices 1, 2, 3). The arthropod sampling method was very successful and, because traps were left on pine boles for the same 7 days on all treatments, variation due to time of day and temperature and humidity fluctuation, should have been equal among treatments. Only 1 taxonomic order was excluded from calculation of total arthropod biomass (Diplopoda) because millipedes are known to be distasteful/toxic and are not mentioned as red-cockaded woodpecker prey in previous studies on diet (Hess and James 1998, Hanula and Engstrom 2000, Hanula et al. 2000a). Removal of this taxon from biomass calculations affected results only during the winter. During the winter of 1998, a large downward movement of millipedes from the canopy was detected in the traps 9 m above the ground, primarily in the 40–50-year-old pines. Removal of this taxon resulted in the 60–70-year-old age class having the greatest arthropod biomass during winter (Table 2).

Pine age did not significantly affect total arthropod density on the lower boles of pines between the ages of 40 and 150 years during any of the 3 seasons examined (Table 2). Total arthropod biomass, however, was significantly higher in 60–70-year-old pines than in 40–50- and 130–150-year-old pines during winter. During the breeding season, a period when adults are provisioning nestlings with food, total arthropod biomass increased as pine age increased and was significantly higher in 130–150-year-old pines than in 40–50-year-old pines (Table 2, Figure 1). When the 40–50-year-old stand with hardwood midstory was excluded and only the 3 age classes with minimal hardwood midstory were examined, the increase of arthropod biomass with tree age during the breeding season coincided with a corresponding increase in monocots, herbaceous dicots, and vegetation density in the 0 to 1 m vegetation layer with tree age (Table 1). During the post-breeding season, total arthropod biomass was unaffected by increasing pine age (Table 2).

The presence or absence of hardwood midstory around 40–50-year-old pines had no significant effect on either total arthropod density or total arthropod biomass during any of the three seasons examined (Table 3). There was a tendency for arthropod biomass to be higher on pines where hardwood midstory was

Table 3. The effect of hardwood midstory on the density and biomass (mean ± SD) of arthropod prey of red-cockaded woodpeckers on 40-50 year-old longleaf pines on the Angelina National Forest, eastern Texas.

	Condition of Hardwood Midstory	
Arthropod Variables[a]	Hardwood Midstory Present	Hardwood Midstory Absent
Breeding Season		
Total Arthropod Density (no./m^2)	11993 (20134)[A]	15443 (30604)[A]
Total Arthropod Biomass (g/m^2)	2.42 (1.43)[A]	2.06 (1.42)[A]
Post-breeding Season		
Total Arthropod Density (no./m^2)	8439 (13756)[A]	7784 (11602)[A]
Total Arthropod Biomass (g/m^2)	1.03 (0.72)[A]	1.01 (0.76)[A]
Winter		
Total Arthropod Density (no./m^2)	1569 (2356)[A]	1725 (2535)[A]
Total Arthropod Biomass (g/m^2)	0.67 (0.76)[A]	0.45 (0.48)[A]

[a]Two-way ANOVA with interaction (midstory condition * year) calculated for each season followed by Duncan's Multiple Range Test. Common letters across rows indicate non-significant differences at an alpha level of 0.05.

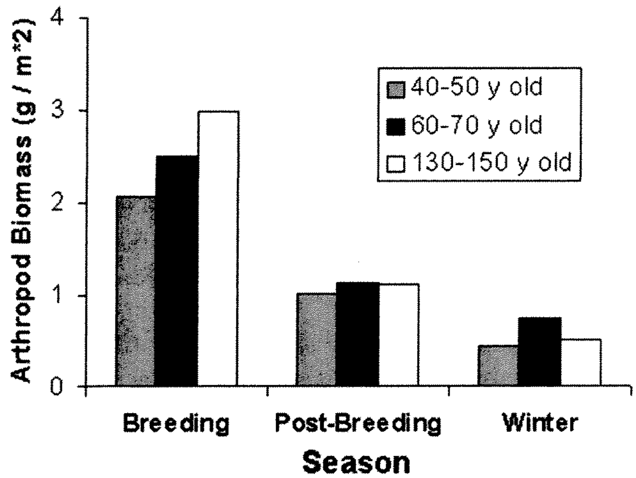

Figure 1. Mean arthropod biomass measured on the boles of three different age classes of longleaf pines during the red-cockaded woodpecker breeding and post-breeding seasons and winter on the Angelina National Forest in eastern Texas.

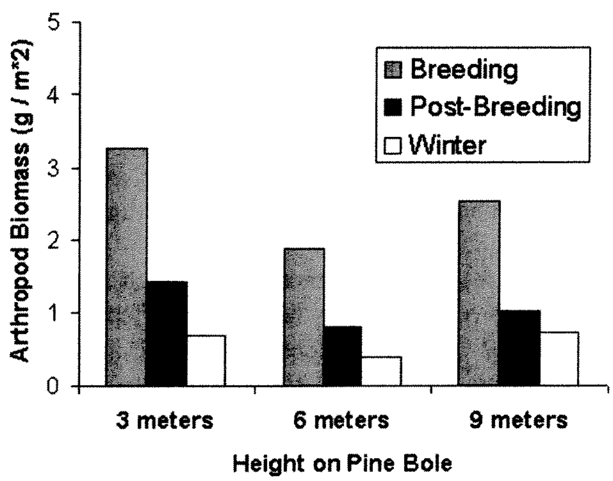

Figure 2. Mean arthropod biomass measured at 3, 6, and 9 m on the boles of longleaf pines during the red-cockaded woodpecker breeding and post-breeding seasons and winter on the Angelina National Forest in eastern Texas.

more abundant, but this tendency was not significant. None of the stands we examined in the present study had a dense growth of hardwood mid- and understory as is often present in loblolly pine (*Pinus taeda*) stands (see Collins et al. 2002).

Generally, both total arthropod density and total arthropod biomass were higher on the lower portion of the bole (3 m above the ground) than at 6 m or 9 m (Table 4, Figure 2). Only during winter was arthropod biomass at 9 m above the ground similar to biomass captured at 3 m above the ground.

Season had a strong effect on both total arthropod density and total arthropod biomass. Both measures of arthropods (density and biomass) were highest during the woodpecker's breeding season, significantly lower during the post-breeding season, and lowest during winter (Table 5).

DISCUSSION

Arthropod biomass was likely a better index of prey for red-cockaded woodpeckers than total mean density. Total number of arthropods fluctuated widely throughout the study and was greatly affected by seasonal blooms of numerous, small arthropods, whereas biomass was primarily determined by large, less mobile arthropods.

Our examination of arthropods on longleaf pines focused on the bole, which is the primary foraging location of the female red-cockaded woodpecker (Ligon 1968, 1970; Ramey 1980; Skorupa 1979; Hooper and Lennartz 1981). The energy requirements of the female for egg production emphasize the importance of this aspect of foraging habitat, and Jackson and Parris (1995) suggest that the female is the first to suffer weight loss when foraging habitat is insufficient. Our observation that higher arthropod densities and biomass were detected at the lower sampling site on pine boles, an important region of the bole for foraging female red-cockaded woodpeckers, is consistent with previous research. Hanula and Franzreb (1998), Hess and James (1998), Collins et al. (2002), James et al. (2001), and Hanula and Horn (2004) concluded that a significant portion of arthropods on the boles of pines came from forest floor vegetation and woody detritus.

Hooper (1996) and Hanula et al. (2000*a*) also examined arthropod biomass on pines to project their potential to provide food for red-cockaded woodpeckers. Our observations during winter closely matched those of Hooper (1996); both studies detected higher arthropod biomass in pines 60–70 years old than in the younger and older pines examined.

We were able to study arthropods on pines in an older age class (130–150 years old) than either Hooper (1996) or Hanula et al. (2000*a*), and unlike the previous studies, we were also able to evaluate annual differences in the availability of arthropods because of the 2-y duration of our sampling. Hooper (1996) and Hanula et al. (2000*a*) suggested the possibility that arthropod biomass on pines does not increase beyond pines 70–80 years in age. Although our study only evaluated multiple trees in 1 forest stand for each age class, we did observe highest arthropod biomass on the boles of 130–150-year-old longleaf pines during the breeding season, suggesting the possibility of increased foraging benefit for red-cockaded woodpeckers from longleaf pines older than 120 years.

The availability of arthropod prey during the breeding season is particularly important for the provisioning of nestlings. James et al. (1997, 2001) observed that red-cockaded woodpecker fitness (reproduction and group size) was positively related to the amount of herbaceous groundcover, low amounts of hardwood and pine midstory, and densities of large, old pines. Walters et al. (2002*b*) also observed that red-cockaded woodpecker group size was positively related to the density of old-growth pines. Our detection of higher prey biomass on older-growth pines during the breeding season suggests that the presence of these old pines and their higher prey biomass may be important for red-cockaded woodpecker reproductive attainment and large group size.

Even with the data provided by our study of 130–150-year-old longleaf pines, we still do not know how increasing pine age will affect arthropod availability. Longleaf pines can live in excess of 350 years with known ages beyond 500 years (Platt et al. 1988*a*). Thus, even the pines we examined had not attained half of their potential maximum age.

Red-cockaded woodpeckers tend to avoid pine stands with hardwood midstory for nesting and roosting (Conner and Rudolph 1989, Loeb et al. 1992) and foraging habitat (Rudolph et al. 2002, Walters et al. 2002*b*). We detected no differences in the numbers and biomass of arthropods in 40–50-year-old pine stands with and without hardwood midstory throughout the year. Thus, factors other than availability of prey may cause red-cockaded woodpeckers to favor pine stands with minimal hardwood midstory.

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Table 4. Density and biomass (mean ± SD) of arthropod prey of red-cockaded woodpeckers relative to height on the bole of longleaf pines on the Angelina National Forest, eastern Texas.

	Height on Longleaf Pine Boles		
Arthropod Variables[a]	3 m above ground	6 m above ground	9 m above ground
Breeding Season			
Total Arthropod Density (no./m^2)	27764 (26813)[A]	11365 (10842)[B]	9243 (6011)[B]
Total Arthropod Biomass (g/m^2)	3.26 (2.00)[A]	1.89 (0.88)[B]	2.53 (0.98)[C]
Post-breeding Season			
Total Arthropod Density (no./m^2)	12538 (5299)[A]	7532 (3444)[B]	6641 (3664)[B]
Total Arthropod Biomass (g/m^2)	1.43 (0.63)[A]	0.80 (0.38)[B]	1.01 (0.55)[C]
Winter			
Total Arthropod Density (no./m^2)	2276 (817)[A]	1354 (670)[B]	1138 (621)[C]
Total Arthropod Biomass (g/m^2)	0.68 (0.44)[A]	0.39 (0.38)[B]	0.72 (0.62)[A]

[a]Two-way ANOVA with interaction (bole height * year) calculated for each season followed by Duncan's Multiple Range Test. Common letters across rows indicate non-significant differences at an alpha level of 0.05.

Table 5. The effects of season on the density and biomass (mean ± SD) of arthropod prey of red-cockaded woodpeckers on the boles of longleaf pines on the Angelina National Forest, eastern Texas.

	Season		
Arthropod Variables[a]	Breeding	Post-breeding	Winter
Total Arthropod Density (no./m^2)	15673 (30775)[A]	8851 (13452)[B]	1589 (2315)[C]
Total Arthropod Biomass (g/m^2)	2.48 (1.88)[A]	1.07 (0.69)[B]	0.59 (0.61)[C]

[a]Two-way ANOVA with interaction (season * year) followed by Duncan's Multiple Range Test. Common letters across rows indicate non-significant differences at an alpha level of 0.05.

Appendix 1. Mean density and biomass of arthropods on longleaf pine in different-aged stands during red-cockaded woodpecker breeding seasons (May-June), 1997 and 1998.

	40-50 years old Hardwood Midstory Present		40-50 years old Hardwood Midstory Absent		60-70 years old		130-150 years old	
Arthropod Order	Mean Density (no/m^2)	Mean Biomass (g/m^2)	Mean Density (no/m^2)	Mean Biomass (g/m^2)	Mean Density (no/m^2)	Mean Biomass (g/m^2)	Mean Density (no/m^2)	Mean Biomass (g/m^2)
Araneae	209.9	0.504	266.0	0.505	272.4	0.542	220.0	0.489
Opiliones	27.75	0.422	13.31	0.202	16.27	0.247	29.82	0.453
Pseudoscorpiones	160.8	0.002	88.58	0.0009	150.9	0.002	141.1	0.001
Chilopoda	31.11	0.738	10.46	0.248	31.179	0.754	19.82	0.470
Diplopoda	3.467	0.109	1.031	0.032	0	0	2.216	0.070
Collembola	20312	0.609	27552	0.827	33973	1.019	33051	0.992
Orthoptera	5.688	0.122	2.185	0.096	5.239	0.101	4.856	0.126
Blattaria	23.39	0.390	10.48	0.180	18.55	0.351	35.87	0.763
Isoptera	9.108	0.038	1.066	0.004	13.50	0.038	52.14	0.138
Psocoptera	1437	0.043	918.6	0.028	1506	0.045	1237	0.037
Hemiptera	8.817	0.042	1.642	0.004	10.19	0.006	7.696	0.007
Homoptera	388.1	0.101	545.6	0.176	514.8	0.154	279.2	0.130
Coleoptera	276.8	0.347	166.8	0.173	185.5	0.165	291.1	0.332
Lepidoptera	4.579	0.015	5.402	0.004	5.903	0.012	5.970	0.019
Diptera	1976	0.287	3413	0.440	3602	0.453	3809	0.548
Hymenoptera	1780	0.117	1509	0.102	1594	0.114	988.8	0.085

Appendix 2. Mean density and biomass of arthropods on longleaf pine in different-aged stands during red-cockaded woodpecker post-breeding seasons (August), 1997 and 1998.

	40-50 years old Hardwood Midstory Present		40-50 years old Hardwood Midstory Absent		60-70 years old		130-150 years old	
Arthropod Order	Mean Density (no/m^2)	Mean Biomass (g/m^2)	Mean Density (no/m^2)	Mean Biomass (g/m^2)	Mean Density (no/m^2)	Mean Biomass (g/m^2)	Mean Density (no/m^2)	Mean Biomass (g/m^2)
Araneae	116.4	0.326	134.6	0.355	139.8	0.258	162.1	0.288
Opiliones	1.004	0.015	0	0	0	0	0	0
Pseudoscorpiones	131.2	0.001	150.9	0.002	114.8	0.001	121.4	0.001
Chilopoda	17.48	0.415	2.237	0.053	6.346	0.150	12.74	0.302
Diplopoda	0	0	1.200	0.038	0	0	0	0
Collembola	9167	0.275	5551	0.166	4314	0.129	5988	0.180
Orthoptera	0.607	0.031	2.109	0.108	3.850	0.090	4.701	0.116
Blattaria	2.902	0.029	1.812	0.006	1.284	0.004	1.178	0.012
Isoptera	0.473	0.002	0	0	0	0	0	0
Psocoptera	2106	0.063	2740	0.082	2113	0.063	1217	0.036
Hemiptera	0	0	1.313	0.003	0.285	0.014	0.731	0.012
Homoptera	272.0	0.058	284.3	0.063	385.9	0.098	208.8	0.093
Coleoptera	98.30	0.098	95.70	0.070	476.2	0.125	120.3	0.085
Lepidoptera	1.741	0.012	2.712	0.013	0.826	0.0006	0.784	0.0006
Diptera	1878	0.110	3269	0.223	5550	0.332	5399	0.300
Hymenoptera	2263	0.119	1179	0.069	1320	0.098	777.2	0.048

Appendix 3. Mean density and biomass of arthropods on longleaf pine in different-aged stands during January 1997 and 1998.

	40-50 years old Hardwood Midstory Present		40-50 years old Hardwood Midstory Absent		60-70 years old		130-150 years old	
Arthropod Order	Mean Density (no/m^2)	Mean Biomass (g/m^2)	Mean Density (no/m^2)	Mean Biomass (g/m^2)	Mean Density (no/m^2)	Mean Biomass (g/m^2)	Mean Density (no/m^2)	Mean Biomass (g/m^2)
Araneae	51.76	0.089	116.6	0.246	109.4	0.200	74.16	0.144
Opiliones	52.85	0.803	11.30	0.172	14.61	0.222	11.86	0.180
Pseudoscorpiones	3.281	0.00003	3.281	0.00003	0	0	3.281	0.00003
Chilopoda	27.13	0.643	5.222	0.124	36.39	0.863	26.91	0.638
Diplopoda	292.0	9.201	486.0	15.31	99.82	3.145	183.0	5.766
Collembola	1808	0.054	1893	0.057	1634	0.049	1552	0.047
Orthoptera	0	0	0	0	1.094	0.0001	0	0
Blattaria	0	0	0	0	0.760	0.002	0	0
Isoptera	0	0	0	0	0	0	0	0
Psocoptera	26.25	0.0008	19.68	0.0006	26.25	0.0008	6.562	0.0002
Hemiptera	2.203	0.003	0.674	0.002	0.256	0.012	0	0
Homoptera	25.89	0.009	15.37	0.006	32.35	0.013	15.091	0.005
Coleoptera	25.89	0.010	22.96	0.004	15.99	0.026	7.525	0.007
Lepidoptera	0.933	0.0007	3.019	0.002	3.498	0.020	0	0
Diptera	748.0	0.057	901.8	0.064	840.6	0.059	804.5	0.060
Hymenoptera	74.78	0.005	21.72	0.010	34.77	0.039	20.17	0.006

LITERATURE CITED

Baker, W. W. 1971. Observations on the foods habits of the red-cockaded woodpecker. Pages 100-107 *in* R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bur. of Sport Fish. and Wildl. and Tall Timbers Res. Stn., Tallahassee, Fl.

Blancher, P. J., and R. J. Robertson. 1987. Effect of food supply on the breeding biology of western kingbirds. Ecology 68:723-732.

Borror, D. J., and R. E. White. 1970. A field guide to the insects of America north of Mexico. Houghton Mifflin, Boston, Ma. 404pp.

Bryant, D. M. 1975. Breeding biology of house martins (*Delichon urbica*) in relation to aerial insect abundance. Ibis 117:180-216.

Bryant, D. M. 1978. Environmental influences on growth and survival of nestling house martins (*Delichon urbica*). Ibis 120:271-283.

Bryant, D. M. 1979. Reproductive cost in the house martin (*Delichon urbica*). J. Anim. Ecol. 48:655-675.

Collins, C. S., R. N. Conner, and D. Saenz. 2002. Influence of hardwood midstory and pine species on pine bole arthropods. For. Ecol. Manage. 164:211-220.

Conner, R. N., and D. C. Rudolph. 1989. Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. U.S. For. Serv. Res. Pap. SO-250. 15pp.

Conner, R. N., D. C. Rudolph, D. Saenz, and R. N. Coulson. 1997. The red-cockaded woodpecker's role in the southern pine ecosystem, population trends and relationships with southern pine beetles. Tex. J. Sci. 49:139-154.

Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. The red-cockaded woodpecker, surviving in a fire-maintained ecosystem. Univ. Texas Press, Austin. 363pp.

Dennis, J. V. 1971. Species using red-cockaded woodpecker holes in northeastern South Carolina. Bird-Banding 42:79-87.

Engstrom, R. T., and F. J. Sanders. 1997. Red-cockaded woodpecker foraging ecology in an old-growth longleaf pine forest. Wilson Bull. 109:203-217.

Hanula, J. L., and R. T. Engstrom. 2000. Comparison of red-cockaded woodpecker (*Picoides borealis*) nestling diet in old-growth and old-field longleaf pine (*Pinus palustris*) habitats. Am. Midl. Nat. 144:370-376.

Hanula, J. L., and R. T. Engstrom, and W. D. Pepper. 2000. Longleaf pine characteristics associated with arthropods available for red-cockaded woodpeckers. J. Wildl. Manage. 64:60-70.

Hanula, J. L., and K. E. Franzreb. 1998. Source, distribution and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker. For. Ecol. Manage. 102:89-102.

Hanula, J. L., and S. Horn. 2003. Availability and abundance of prey for the red-cockaded woodpecker *in* R. Costa and S. J. Daniels, eds. Red-cockaded woodpecker symposium IV, Hancock House Publishers, Blaine, Wa.

Harlow, R. F., and M. R. Lennartz. 1983. Interspecific competition for red-cockaded woodpecker cavities during the breeding season in South Carolina. Pages 41-43 *in* D. A. Wood, ed. Red-cockaded woodpecker symposium II proceedings. Fla. Game and Fresh Water Fish Commiss. Tallahassee, Fl.

Hess, C. A., and F. C. James. 1998. Diet of the red-cockaded woodpecker in the Apalachicola National Forest. J. Wildl. Manage. 62:509-517.

Hooper, R. G. 1996. Arthropod biomass in winter and the age of longleaf pines. For. Ecol. Manage. 82:115-131.

Hooper, R. G., and M. R. Lennartz. 1981. Foraging behavior of the red-cockaded woodpecker in South Carolina. Auk 98:321-334.

Hooper, R. G., A. F. Robinson, and J. A. Jackson. 1980. The red-cockaded woodpecker: notes on life history and management. U.S. For. Serv., Gen. Rep. SA-GR 9. 8pp

Horn, S., and J. L. Hanula. 2002. Comparison of arthropod prey of red-cockaded woodpeckers on the boles of longleaf and loblolly pines. Wildl. Soc. Bull. 30:131-138.

Jackson, J. A. 1971. The evolution, taxonomy, distribution, past populations, and currebt status of the red-cockaded woodpecker. Pages 4-29 *in* R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bur. of Sport Fish. and Wildl. and Tall Timbers Res. Stn., Tallahassee, Fl.

Jackson, J. A. 1978. Competition for cavities and red-cockaded woodpecker management. Pages 103-112 *in* S. A. Temple, ed. Endangered birds: management techniques for the preservation of threatened species. Univ. Wisconsin Press, Madison.

Jackson, J. A. 1979. Tree surfaces as foraging substrates for insectivorous birds. Pages 69-93 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll, eds. The role of insectivorous birds in forest ecosystems. Academic Press, New York, N.Y..

Jackson, J. A., and S. D. Parris. 1995. The ecology of red-cockaded woodpeckers associated with the construction and use of a multipurpose range complex at Fort Polk, Louisiana. Pages 277-282 *in* D. L. Kulhavy, R. G. Hooper, and R. Costa, eds. Red-cockaded woodpecker: recovery, ecology and management. Center for Applied Studies in Forestry, College of Forestry, Stephen F. Austin State Univ., Nacogdoches, Tx.

Jackson, J. A., and B. J. Schardien-Jackson. 1986. Why do red-cockaded woodpeckers need old trees? Wildl. Soc. Bull. 14:318-322.

James, F. C., C. A. Hess, and D. Kufrin. 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. Ecol. Appl. 7:118-129.

James, F. C., C. A. Hess, B C. Kicklighter, and R. A. Thum. 2001. Ecosystem management and the niche gestalt of the red-cockaded woodpecker in longleaf pine forests. Ecol. Appl. 11:854-870.

James, F. C., and H. H. Shugart. 1970. A quantitative method of habitat description. Aud. Field Notes 24:727-736.

Ligon, J. D. 1968. Sexual differences in foraging behavior of two species of *Dendrocopos* woodpeckers. Auk 85:203-215.

Ligon, J. D. 1970. Behavior and breeding biology of the red-cockaded woodpecker. Auk 87:255-278.

Ligon, J. D. 1971. Some factors influencing numbers of the red-cockaded woodpecker. Pages 30-43 *in* R. L. Thompson, ed. Ecology and management of the red-cockaded woodpecker. U.S. Bur. Sport Fish. and Wildl., and Tall Timbers Res. Stn., Tallahassee, Fl.

Ligon, J. D., P. B. Stacey, R. N. Conner, C. E. Bock, and C. S. Adkisson. 1986. Report of the American Ornithologists' Union committee for the conservation of the red-cockaded woodpecker. Auk 103:848-855.

Loeb, S. C., W. D. Pepper, and A. T. Doyle. 1992. Habitat characteristics of active and abandoned red-cockaded woodpecker colonies. South. J. Appl. For. 16:120-125.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

Miller, G. L. 1978. The population, habitat, behavior, and foraging ecology of the red-cockaded woodpecker (*Picoides borealis*) in southeastern Virginia. M.S. Thesis, William and Mary College, Williamsburg, Va. 132pp.

Nolan, V., Jr., and C. F. Thompson. 1975. The occurrence and significance of anomalous reproductive activities in two North American non-parasitic cuckoos (*Coccyzus* spp.). Ibis 117:496-503.

Platt, W. J., G. W. Evans, and S. L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Am. Nat. 131:491-525.

Porter, M. L., and R. F. Labisky. 1986. Home range and foraging habitat of red-cockaded woodpeckers in northern Florida. J. Wildl. Manage. 50:239-247.

Quinney, T. E. 1983. Tree swallows cross a polygyny threshold. Auk 100:750-754.

Ramey, P. 1980. Seasonal, sexual, and geographical variation in the foraging ecology of the red-cockaded woodpecker (*Picoides borealis*). M.S. Thesis, Mississippi State Univ., Starkville. 129pp.

Repasky, R. R., and P. D. Doerr. 1991. Home range and substrate use by two family groups of red-cockaded woodpeckers in the North Carolina Sandhills. Brimleyana 17:37-52.

Rudolph, D. C., R. N. Conner, and R. R. Schaefer. 2002. Red-cockaded woodpecker foraging behavior in relation to midstory vegetation. Wilson Bull. 114:235-242.

Rudolph, D. C., R. N. Conner, and J. Turner. 1990. Competition for red-cockaded woodpecker roost and nest cavities: effects of resin age and entrance diameter. Wilson Bull. 102:23-26.

Sealy, S. G. 1978. Possible influence of food on egg-laying and clutch size in the black-billed cuckoo. Condor 80:103-104.

Skorupa, J. P. 1979. Foraging ecology of the red-cockaded woodpecker in South Carolina. M.S. Thesis, Univ. California, Davis. 96pp.

Walters, J. R., S. J. Daniels, J. H. Carter, III, and P. D. Doerr. 2002. Defining quality of red-cockaded woodpecker foraging habitat based on habitat use and fitness. J. Wildl. Manage. 66:1064-1082.

Wood, D. A. 1977. Status, habitat, home range, and notes on the behavior of the red-cockaded woodpecker in Oklahoma. M.S. Thesis, Oklahoma State Univ., Stillwater. 61pp.