ELSEVIER

Forest Ecology and Management 164 (2002) 21 l-220

Forest Ecology and Management

www.elsevier.com/locate/foreco

Influence of hardwood midstory and pine species on pine bole arthropods

Christopher S. Collins*, Richard N. Conner, Daniel Saenz

Wildlife Habitat and Silviculture Laboratory, Southern Research Station, U.S. Forest Service, Nacogdoches, TX 75962, USA

Received 26 February 2001; accepted 14 May 2001

Abstract

Arthropod density on the boles of loblolly pines (*Pinus taeda*) was compared between a stand with and stand without hardwood midstory and between a stand of loblolly and shortleaf pines (*P. echinata*) in the Stephen F. Austin Experimental Forest, Nacogdoches Co., Texas, USA from September 1993 through July 1994. Arthropod density was greatest ($t = 5.67$, 10 d.f., $P < 0.001$) in an open pine stand nearly devoid of hardwood midstory than in a pine stand with dense hardwood midstory. Loblolly pine had greater ($t = 2.34$, 10.9 d.f., $P = 0.040$) arthropod densities than shortleaf pine. Vegetative characteristics within a pine stand rather than bark rugosity appear to be the dominant factor determining arthropod density on the boles of pines. The red-cockaded woodpecker (*Picoides borealis*) should benefit from greater abundances of arthropods on the boles of pines particularly during the nesting season. In order to provide prime foraging habitat for the red-cockaded woodpecker, land managers should consider the vegetative community structure within foraging habitat. Published by Elsevier Science B.V.

Keywords: Arthropods; Bark rugosity; Foraging habitat; Lohlolly pine; Midstory: *Picoides borealis*; Pine holes; Pine species; *Pinus echinata*; *Pinus taeda*; Red-cockaded woodpeckers: Shortleaf pine

1. Introduction

Adequate foraging habitat is critical for maintenance of viable populations of all animal species. The endangered red-cockaded woodpecker forages almost exclusively on living pines (Ligon, 1968; Wood, 1977; Miller, 1978; Skorupa, 1979; Hooper and Lennartz, 1981; Porter and Labisky, 1986; Repasky and Doerr, 1991; and others). Currently, the red-cockaded woodpecker recovery plan (USFWS, 1985) specifies that a minimum of 50 ha of prime foraging habitat should be provided for each red-cockaded woodpecker group. However, the final red-cockaded woodpecker environmental impact statement of the U.S. Forest Service (1995) explains that these requirements are based on the "average foraging needs" of a single red-cockaded woodpecker population (Francis Marion National Forest). The statement also acknowledges that red-cockaded woodpeckers may not need as much foraging habitat as is currently specified by the USFWS (1985) for all pine timber types and conditions.

The red-cockaded woodpecker is thought to have evolved in a fire-climax, open-pine forest ecosystem (Conner and Rudolph, 1989) with an herbaceous understory, and little hardwood midstory vegetation

"Corresponding author. Present address: Southern Research Station, U.S. Forest Service, 506 Hayter St., Nacogdoches, TX 75961, USA. Tel.: +1-936-569-7981; fax: +1-936-569-9681.
E-mail address: ccollins@fs.fed.us (C.S. Collins).

0378- 1 127/02/$ - see front matter. Published by Elsevier Science B.V.
PII: S0378-1127(01)00595-3

(Conner and Rudolph, 1995). In the absence of an effective prescribed burning regime and a midstory reduction effort, many areas of historic red-cockaded woodpecker habitat currently have well-developed hardwood midstories. Information of how hardwood midstory vegetation and pine species influence 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 arthropod biomass on longleaf pines increased with tree age up to about 86 years and then declined. Hanula and Franzreb (1998) also 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.

Considerable research has been conducted on red-cockaded woodpecker foraging ecology (Ligon, 1968; Skorupa and McFarlane, 1976; Miller, 1978; Ramey, 1980; Hooper and Lennartz, 1981; Hooper and Harlow, 1986). Male red-cockaded woodpeckers appear to 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, 198 I ; Jackson and Jackson, 1986; Engstrom and Sanders, 1997). Controversy still exists as to whether the presence of hardwood and pine midstory displaces female woodpeckers into the foraging niche of the socially dominant male.

Food supply has been shown to greatly influence clutch size and other aspects of reproduction in other birds (Bryant, 1975, 1978, 1979; Nolan and Thompson, 1975; Sealy, 1978; Quinney, 1983; Blancher and Robertson, 1987). Past research has suggested that female red-cockaded woodpeckers suffer weight loss from inadequate foraging habitat sooner than their male counterparts (Jackson and Parris, 1995). Therefore, studies focusing on arthropod abundance on the lower boles of pines, the region of the pine where female red-cockaded woodpeckers do much of their foraging should be particularly valuable.

We tested the null hypotheses that arthropod density on the boles of loblolly pines was equal in a stand with and stand without a well-developed hardwood midstory, and arthropod density was equal on the boles of loblolly and shortleaf pines. In addition, we explore the effects of seasonal variation on pine bole arthropod communities and the possible influence of bark rugosity.

2. Experimental methods

2.1. Area description

Two relatively mature (>50 years), even-aged pine stands were chosen in upland sites on the Stephen F. Austin Experimental Forest (3 1°29′N, 94°47′W), an adjunct portion of the Angelina National Forest in southern Nacogdoches County, Texas. Currently, no red-cockaded woodpeckers inhabit the Experimental Forest, but they were found within a few miles as late as the 1970s (Johnson, 1971). Each stand contained both loblolly and shortleaf pines. The first stand was a moderately dense pine stand (27.3 m^2/ha overstory pine) with a well-developed hardwood midstory component (10.0 m^2/ha); hence, this area is referred to as the midstory present pine stand. This hardwood midstory formed a dense sub-canopy shading the forest floor and leaving it virtually bare of any herbaceous or hardwood understory vegetation. This stand had not been burned in the last 50 years. Arthropods were sampled from 10 loblolly pines within this stand.

The other pine stand, midstory absent, did not have a well-developed hardwood midstory (no stems detected with prism). This was an open pine stand (17.05 m^2/ha overstory pine) where sunlight penetrated to the forest floor, resulting in a thick herbaceous layer of grasses, forbs, and young woody vegetation. This stand had been burned at least three times in the last 20 years. In this stand, arthropods were sampled from 10 loblolly and 10 shortleaf pines.

2.2. Techniques

Arthropods were sampled from 10 loblolly pines within each pine stand to compare relative arthropod densities between midstory treatments. We also compared relative arthropod densities between pine

species (loblolly and shortleaf) within the stand where hardwood midstory was absent. We chose trees with similar diameters at breast height (dbh) between 40 and 50 cm to reduce the effect of tree size as a possible confounding factor of arthropod density. Arthropods were sampled on the trees for a 7-day period every other month for a year at three heights on the bole: 3, 6, and 9 m. Sampling was conducted from September 1993 to July 1994, yielding 540 trap samples (3 heights x 6 months x 30 trees).

Each arthropod trap was made of 5 cm wide clear weatherproof tape with a 3-4 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 1.5 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 clear cellophane for freezer storage.

We examined arthropods through the cellophane and identified to taxonomic order or class (Borror and White, 1970). We used a micrometer to measure length, and placed each arthropod into one of three size categories: <3, 3-7, and >7 mm. Because arthropods <3 mm were so numerous, we randomly sub-sampled three 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. We also placed each taxon into one of two categories based on its primary mode of locomotion, flying or non-flying, to determine how the arthropods in each treatment potentially disperse onto pine boles. All arthropod abundance data were converted to the number of arthropods per square meter of trap surface.

2.3. Vegetation structure sampling

We measured vegetative characteristics in the two 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 one-factor metric basal area prism. We estimated foliage density at O-1 and 1-2 m in each cardinal direction 11.2 m from the base of each study tree using a foliage density board as described by MacArthur and MacArthur (1961). We used a hollow 4 cm x 12 cm tube as described by James and Shugart (1970) to determine ground cover percentage (monocot and dicot) and canopy closure percentage along 11.2 m transects extending from the base of each study tree in four cardinal directions. Each study tree was cored with an increment borer and the age determined in the lab. Finally, we used a carpenter's contour gauge to reproduce the bark surface outline (rugosity) horizontally and vertically (Jackson, 1979; Adams and Jackson, 1995) at each of the three collecting heights on the tree from unscraped areas near each sampling height. The length of each bark surface outline was then traced on a note card and measured with a digital map measurer to the nearest millimeter.

2.4. Statistical analyses

We compared arthropod density between treatments (for each sampling height and each month) with two-tailed t-tests because each sampling height is not independent from other sampling heights on each tree. To evaluate effects of sampling heights on total arthropod density within each treatment, we ran a one-way ANOVA using a general linear model with a Tukey's Studentized Range Test. We used two-tailed t-tests to compare flying arthropod density to non-flying arthropod density by sampling height within each treatment. We ran a one-way ANOVA using a general linear model with a Tukey's Studentized Range Test to compare flying and non-flying arthropods densities by sampling heights within treatments. We used two-tailed t-tests to compare vegetative characteristics and bark rugosity between treatments. All statistical analyses were performed using SAS release 6.03 (SAS Institute Inc., 1988). Statistical analyses for tests of significance were all conducted at $\alpha = 0.05$.

3. Results

Approximately 65,280 arthropods were identified from all treatments from the classes Arachnida (four orders), Insecta (16 orders), Diplopoda, and Chilopoda (Table 1). Diplopoda and Chilopoda specimens were identified only to class level.

Table 1
Arthropod taxa sampled from the boles of pines and their primary mode of locomotion. 1993-1994

Class	Order	Common name	Locomotion
Arachnida	Araneae	Spiders	Non-flying
	Acari	Mites	Non-flying
	Chelonethida	Pseudoscorpions	Non-flying
	Opiliones	Harvestmen	Non-flying
Diplopoda		Millipedes	Non-flying
Chilopoda		Centipedes	Non-flying
Insecta	Collembola	Springtails	Non-flying
	Thysanura	Silverfish	Non-flying
	Phasmida	Walkingsticks	Non-flying
	Orthoptera	Grasshoppers	Flying
	Mantodea	Mantids	Flying
	Blattaria	Roaches	Non-flying
	Isoptera (alates)	Termites	Flying
	Psocoptera	Barklice	Non-flying
	Hemiptera	True bugs	Non-flying
	Homoptera	Cicadas, Hoppers, and Aphids	Flying
	Thysanoptera	Thrips	Non-flying
	Neuroptera	Net-winged insects	Non-flying
	Coleoptera	Beetles	Flying
	Diptera	Flies	Flying
	Lepidoptera	Butterflies and moths	Flying
	Hymenoptera	Ants, bees, and wasps	Flying

3.1. Midstory present versus midstory absent

3.1. I. Arthropod density

Arthropod density, combined over the three sampling heights and entire sampling period, was greater ($t = 5.67$, 10 d.f., $P < 0.001$) on the boles of loblolly pines where hardwood midstory was absent ($\bar{x}$ = 156,897 m^{-2}, S.D. = 35,646, $n = 10$) than in the stand where midstory was present ($\bar{x}$ = 91,205 m^{-2}, S.D. = 8435, $n = 10$). Similar results were observed independently at each of the three sampling heights (Table 2). We detected no differences ($F = 0.22$, 2 d.f., $P = 0.804$) among the three sampling heights in the stand where midstory was present (Table 2). However, where midstory was absent, significantly more arthropods/m' occurred at 3 m than at 6 and 9 m (F = 14.80, 2 d.f., $P < 0.001$) (Table 2). Arthropod density was not different at 6 and 9 m within the midstory absent stand.

Arthropod densities (three heights combined) on loblolly pine boles fluctuated monthly (Table 3). The stand with midstory absent had significantly greater

Table 2
Mean arthropod density (arthropods/m') per sampling height collected on sticky traps around loblolly pine boles with hardwood midstory present or absent, 1993–1994 (for each height n = IO)

Height (m)	Midstory present		Midstory absent		t	d.f.	P
	4	S.D.	$\bar{x}$	S.D.			
3	3 1075 A[a]	3997	71654 A	15479	8.03	10.2	<0.001
6	29712 A	4336	44315 B	15169	2.93	10.5	0.0 1.5
9	30418 A	5354	4092X B	10278	2.87	18.0	0.010

[a] Means followed by different letters are different (P < 0.05) among sampling heights within each midstory treatment, one-way ANOVA and Tukey's Studentized Range Test.

Table 3
Mean arthropod density (arthropods/m') on sticky traps around loblolly pine holes with hardwood midstory present or absent per month, 1993-1994 (for each month $n = 10$)

Month	Midstory present		Midstory absent		t	d.f.	P
	$\bar{x}$	S.D.	$\bar{x}$	S.D.			
September 1993	15886	2186	16554	2960	0.57	18.0	0.573
November 1993	12941	3098	45425	23710	4.30	9.3	0.002
January 1994	1x39	416	2409	840	1.92	13.2	0.077
March 1994	10595	1947	14266	303 1	3.22	18.0	0.005
May 1994	27762	4467	40232	12304	3.01	11.3	0.008
July 1994	221x1	269X	3x010	9072	5.29	10.6	<0.001

arthropod densities than the stand with midstory present every month except September 1993 and January 1994 (Table 3). During November 1993, there was a sharp increase in arthropod density in the stand without hardwood midstory. Upon analysis, it was determined that the increase in arthropod density was due to large numbers of Collembola (73% of total arthropod density in November 1993).

3.1.2. Flying versus non-flying arthropods

Where hardwood midstory was present, flying arthropods were significantly more abundant than non-flying arthropods at each of the three sampling heights (Table 4). Flying arthropods were similar ($F = 1.69$, 2 d.f., $P = 0.204$), among each of the sampling heights from lower to higher on the bole. Non-flying arthropods were significantly more abundant ($F = 17.21$, 2 d.f., $P < 0.001$) at 3 m than at 6 and 9 m (Table 4).

Where hardwood midstory was absent, flying arthropods were significantly more abundant at each sampling height than non-flying arthropods (Table 4). Flying arthropods ($F = 10.28$, 2 d.f., $P = 0.001$) and non-flying arthropods ($F = 6.81$, 2 d.f., $P = 0.004$) were significantly more abundant at 3 m than 6 and 9 m. (Table 4).

3.2. Loblolly pine versus shortleaf pine

3.2.1. Arthropod density

Comparison of arthropod densities between pine species in the midstory absent stand, combined over the three sampling heights and entire sampling period, revealed greater ($t = 2.34$, 10.9 d.f., $P = 0.040$) arthropod densities for loblolly pine ($\bar{x} = 156{,}897$ m^{-2}, S.D. = 35,646, $n = 10$) than shortleaf pine ($\bar{x} = 329{,}208$ m^{-2}, S.D. = 11,613, $n = 10$). Mean density

Table 4
Mean density of flying and non-flying arthropods (arthropods/m') per sampling height collected on sticky traps around loblolly pine boles with hardwood midstory present and midstory absent, 1993–1994 (for each height $n = 10$)

Height (m)	Treatment				t	d.f.	P
	Flying		Non-flying				
	$\bar{x}$	S.D.	$\bar{x}$	S.D.			
Midstory present							
3	21593 A[a]	386 1	9334 A	2529	8.40	18.0	<0.001
6	24002 A	3x37	5630 B	1194	14.46	10.7	<0.001
9	25016 A	4883	5222 B	1062	12.53	9.85	<0.001
Midstory absent							
3	4075X A"	x777	30738 A	14415	1.88	18.0	0.077
6	27513 B	5669	16736 B	12195	2.53	12.7	0.025
9	27771 B	7632	13091 B	5085	5.06	1X.0	<0.001

[a] Means followed by different letters are different ($P < 0.05$) among sampling heights within each, mode of locomotion one-way ANOVA and Tukey's Studentized Range Test.

Table 5
Mean arthropod density (arthropods/m') per sampling height collected on sticky traps around loblolly and shortleaf pine boles with hardwood midstory absent, 1993-1994 (for each height $n = 10$)

Height (m)	Loblolly		Shortleaf		t	d.f.	P
	$\bar{x}$	S.D.	$\bar{x}$	S.D.			
3	71654 A"	15479	58344 A	6474	2.51	12.1	0.027
6	44315 B	15169	36781 B	9225	1.34	18.0	0.196
9	40928 B	10278	34083 B	3817	1.97	11.4	0.073

"Means followed by different letters are different ($P < 0.05$) among sampling heights within each pine species treatment, one-way ANOVA and Tukey's Studentized Range Test

was greater at 3 m for loblolly pine than shortleaf pine (Table 5). Although arthropod density was not significantly different at 6 or 9 m, loblolly pine did have greater mean values than shortleaf pine (Table 6). Both loblolly and shortleaf pines had significantly more arthropods/m' at 3 m than at 6 and 9 m ($F = 14.80$, 2 d.f., $P < 0.001$; $F = 37.46$, 2 d.f., $P =< 0.001$), respectively (Table 5).

Monthly comparisons also showed seasonal fluctuations in arthropod densities across both species of pines. Arthropod densities on loblolly and shortleaf pines were similar every month except March (Table 6).

3.3. Habitat results

Loblolly pine study trees in both stands (midstory present and midstory absent) had similar dbh (Table 7). However, loblolly pines, in the stand with midstory present were significantly older than those in the stand where midstory was absent (Table 7). Basal area of overstory pines was significantly higher in the stand with hardwood midstory than the stand without hardwood midstory (Table 7). Basal area of overstory hardwoods and midstory pines was low to nonexistent in both pine stands (Table 7). Percent canopy closure was significantly higher in the stand where hardwood midstory was present (Table 7). A well-developed hardwood midstory occurred in the stand with midstory and was absent in the other stand (Table 7). Foliage density from 0 to 1 and 1 to 2 m was significantly greater in the stand without hardwood midstory than the stand with hardwood midstory (Table 7). Percent dicotyledonous and monocotyledonous ground cover was also significantly higher in the stand without hardwood midstory (Table 7).

Diameters (dbh) of loblolly ($\bar{x} = 43.60$, S.D. = 2.63, $n = 10$) and shortleaf ($\bar{x} = 44.30$, S.D. = 2.41, $n = 10$) pine study trees were not significantly different ($t = 0.62$, 18 d.f., $P = 0.543$) in the open stand where we compared arthropod density between loblolly and shortleaf pine tree species. However, shortleaf pines ($\bar{x} = 74.90$, S.D. = 12.95, $n = 10$) were significantly older ($t = 4.65$, 9.6 d.f., $P = 0.001$) than loblolly pines ($\bar{x} = 55.50$, S.D. = 2.46, $n = 10$).

Table 6
Mean arthropod density (arthropods/m') on sticky traps around loblolly and shortleaf pine boles with hardwood midstory absent per month, 1993-1994 (for each month $n = 10$)

Month	Loblolly		Shortleaf		t	d.f.	P
	$\bar{x}$	S.D.	$\bar{x}$	S.D.			
September 1993	16554	2960	16560	3724	<0.01	18.0	0.997
November 1993	45425	23710	31356	10477	1.72	12.4	0.111
January 1994	2409	x40	1934	561	1.49	18.0	0.154
March 1994	14266	3031	11020	1921	2.86	18.0	0.010
May 1994	40232	12304	32727	5166	1.78	12.1	0.101
July 1994	3x010	9072	35613	10524	0.55	18.0	0.592

Table 7
Vegetation characteristics around loblolly pines with hardwood midstory present or absent using each loblolly pine arthropod study tree as a center point in a 0.04 ha vegetation plot, 1993-1994 (for each variable n = IO)

Variable	Midstory present		Midstory absent		t	d.f.	P
	$\bar{x}$	S.D.	4	S.D.			
Diameters (dbh) of study trees	45.30	2.9X	43.60	2.63	1.35	18.0	0.193
Study tree age	78.70	5.23	55.50	2.46	12.69	12.8	<0.001
Overstory pines (BA)[a]	27.30	4.60	17.05	1.91	6.51	12.0	<0.001
Midstory pines (BA)"	1.35	3.2X	0.00	0.00	N/A	N/A	N/A
Overstory hardwoods (BA)[a]	0.10	0.32	0.00	0.00	N/A	N/A	N/A
Midstory hardwoods (BA)[a]	10.00	3.83	0.00	0.00	N/A	N/A	N/A
Percent canopy closure	74.55	9.05	28.33	5.X2	13.5X	18.0	4.00 1
Foliage density index O-l m (m^2/m^3)	0.02	<0.01	0.42	0.14	x.9x	9.0	<0.001
Foliage density index l-2 m (m^2/m^3)	0.02	10.0 l	0.26	0.02	27.09	9.0	<0.001
Percent dicotyledonous ground cover	2.73	5.71	46.45	24.21	5.56	10.0	<0.001
Percent monocotyledonous ground cover	0.00	0.00	11.30	9.66	N/A	N/A	N/A

[a] All basal area (BA) measurements are in m^2/ha.

Table 8
Mean bark rugosity indices (cm) of loblolly pine arthropod study trees with hardwood midstory present or absent and loblolly and shortleaf pine arthropod study trees with hardwood midstory absent, 1993-1994 (for each variable n = 10)

Variable	Treatment comparison				t	d.f.	P
	Midstory present		Midstory absent				
Horizontal	16.71	0.58	16.62	0.60	0.35	1X.0	0.733
Vertical	15.62	0.54	15.43	0.37	0.92	18.0	0.368
	Loblolly		Shortleaf				
Horizontal	16.62	0.60	16.20	0.51	1.70	18.0	0.107
Vertical	15.43	0.37	15.36	0.33	0.46	18.0	0.65 l

3.4. *Rugosity results*

Horizontal and vertical rugosity measurements on loblolly pines in midstory present and midstory absent stands were not significantly different (Table 8). Although bark rugosity of loblolly pine visually appeared to be greater than shortleaf pine, we failed to detect a difference (Table 8).

4. Discussion

4.1. Arthropod communities and hardwood midstory

We rejected the null hypothesis that arthropod density was equal in a stand with and stand without a well-developed hardwood midstory. Arthropod density was significantly greater in the open pine stand that lacked a hardwood midstory, but contained a thick understory vegetation of monocots and dicots. As in Jackson's (1979) investigation, the majority of arthropods collected were not pine-bole residents, but either landed or crawled onto the pine bole. Many arthropods use the bark as a pathway to the canopy (Moeed and Mead, 1983; Hanula and Franzreb, 1998). A few arthropods, such as Psocopterans and some species of spiders, are permanent residents (Hanula and Franzreb, 199X), probably using the bark surface to either feed on organic matter or ambush transient arthropods. Many arthropods trapped on the pine boles may have used bark surfaces for over-wintering or egg-laying, but most of the arthropods' daily activities were likely carried out on other vegetation (Jackson, 1979) or on the forest floor.

The vegetation structure in the surrounding forest affected the density of arthropods on pine boles. Most arthropods trapped on pine boles appeared to come from other forest vegetation and the forest floor. In the stand where hardwood midstory was present arthropod density was similar at all collecting heights (Table 2). As adjacent hardwood foliage was uniformly distributed along the bole, the majority of trapped arthropods likely flew from adjacent midstory foliage and landed on the pine boles (Table 4). The paucity of non-flying arthropods on these pines was likely a result of a well-shaded, bare-forest floor, created by the thick midstory and overstory vegetation.

In contrast, vegetation in the stand without hardwood midstory was not stratified but occurred only in a dense understory layer near the forest floor (Table 7). Densities of non-flying and flying arthropods on the boles were greatest at the lowest sampling height in this area (Table 4). Apparently, most arthropods trapped on pine boles originated from the herbaceous understory vegetation and forest floor. Hanula and Franzreb (1998) found similar results on the boles of longleaf pines in red-cockaded woodpecker foraging habitat in South Carolina.

Nicolai (1986, 1989) found differences in bark rugosity between tree species and explored the effects of rugosity on arthropod communities. We failed to detect a relationship between bark rugosity and arthropod abundance. Our methods of measuring rugosity, however, were not as rigorous as in other studies and additional measurements, such as bark thickness, may have yielded different results.

4.2. *Effects of pine species on arthropods*

Loblolly pine had greater arthropod densities than shortleaf pine at the 3 m sampling height. Both pine species had similar patterns of arthropod distributions with the greatest density of arthropods on the lowest portions of the pine boles. Because both tree species had similar diameters and were located in the same open pine stand, differences in arthropod density may be a function of some variation in pine species, such as bark rugosity. However, we failed to detect a difference in bark rugosity between pine species.

A potentially confounding factor for arthropod densities was tree age. Shortleaf pines, which averaged nearly 20 years older than loblolly pines, may have supported more dead branches because of self-pruning, which could have provided habitat for bark-resident arthropods.

4.3. *Red-cockaded woodpecker foraging implications*

The red-cockaded woodpecker's intolerance of hardwood midstory in their cavity-tree clusters is well known (Hopkins and Lynn, 1971; Van Balen and Doerr, 1978; Locke et al., 1983; Hovis and Labisky, 198.5; Conner and Rudolph, 1989; Loeb et al., 1992). However, less is known about their response to hardwood midstory in their foraging habitat. Crosby (197 1) observed red-cockaded woodpeckers foraging in pine stands with thick midstory vegetation 3–4.5 m high, but the woodpeckers would not forage on the pine boles lower than the tallest midstory vegetation. Hooper and Harlow (1986) observed that red-cockaded woodpeckers forage less in pine stands as hardwood midstory basal area increased. These observations suggest that red-cockaded woodpeckers avoid hardwood midstory in foraging habitat. The results of the present study suggest that an established hardwood midstory may reduce the availability of arthropod prey for red-cockaded woodpeckers.

Many of the arthropods trapped during this study were very small, or were flying insects. Small arthropods, like Collembola, may not be major prey items for red-cockaded woodpeckers because they may be difficult to catch or provide a marginal energy reward. However, Beckwith and Bull (1985) analyzed pileated woodpecker *(Dryocopus pileatus)* feces and found parts of parasitic Hymenoptera, Acari, and Collembola all of which are very small. If the larger pileated woodpecker were capable of preying on such arthropods, the smaller red-cockaded woodpecker would have no difficulty doing so as well.

Arthropod densities were highest in March, May, and July (Tables 3 and 6) a time period that coincides with the red-cockaded woodpecker nesting season. Greater density of arthropods on the boles of pines could be particularly important during the nesting season, when adult woodpeckers provision nestlings.

Our results suggest that managers may be able to increase the abundance of arthropods on the boles of pines for red-cockaded woodpeckers with an

aggressive prescribed fire program that reduces the amount of hardwood midstory within foraging habitats as well as areas used by the woodpecker for nesting. Further research is needed to address the effect of pine tree age and bark rugosity on pine bole arthropod communities.

Acknowledgements

We thank R.E. Brown and C.E. Shackelford for their exceptional assistance in the field throughout this study. We thank Nancy E. Koerth for her assistance with statistical analyses and suggestions on early drafts of this manuscript. We also thank R.R. Schaefer and T. Trees for their help identifying arthropods in the lab. We would like to give a special thanks to R.R. Fleet, K.E. Franzreb, J.L. Hanula, C.A. Hess, and EC. James for helpful suggestion on early drafts of this manuscript.

References

Adams. C.D., Jackson, J.F., 1995. Estimating the allometry of tree bark. Am. Midland Nat. 134, 99–106.

Beckwith, R.C., Bull, E.L., 19X5. Scat analysis of the arthropod component of pilcated woodpecker diet. Murrelet 66, 90-92.

Blancher, P.J., Robertson, R.J., 19X7. Effect of food supply on the breeding biology of western kingbirds. Ecology 68, 723-732.

Borror, D.J., White, R.E., 1970. A Field Guide to the Insects of America North of Mexico. Houghton Mifflin, Boston, MA, 404 pp.

Bryant, D.M., 1975. Breeding biology of house martins (*Delichon urbica*) in relation to aerial insect abundance. Ibis 117, 1 x0-2 16.

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. Anirn. Ecol. 48, 655–675.

Conner, R.N., Rudolph, D.C., 1989. Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. US Department of Agriculture, Forest Service Research Paper SO-250, 15 pp.

Conner, R.N., Rudolph, D.C., 1995. Excavation dynamics and USC patterns of red-cockaded woodpecker cavities: relationships with cooperative breeding. In: Kulhavy, D.L., Hooper, R.C.. Costa, R. (Eds.), Red-Cockaded Woodpecker: Recovery, Ecology and Management. College of Forestry Stephen F. Austin University, Nacogdoches. TX, pp. 343-352.

Crosby, G.T., 1971. Ecology of the red-cockaded woodpecker in the nesting season. M.S. Thesis, University of Florida, Gainesville, FL, 44 pp.

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

Hanula, J.L., Franzreb, K.E., 199X. Source, distribution and abundance of macroarthropods on the bark of longleaf pine: potential prey of the red-cockaded woodpecker. For. Ecol. Manage. 102, X9-102.

Hooper, R.G., 1996. Arthropod biomass in winter and the age of longleaf pines. For. Ecol. Manage. X2, 115–131.

Hooper, R.G., Harlow, R.F., 1986. Forest stands selected by foraging red-cockaded woodpeckers. US Department of Agriculture, Forest Service, Research Paper SE-259, 10 pp.

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

Hopkins, M.L., Lynn, Jr., T.E., 1971. Some characteristics of red-cockaded woodpecker cavity trees and managetnent implications in South Carolina. In: Thompson, R.L. (Ed.), The Ecology and Management of the Red-Cockaded Woodpecker. US Bureau of Sport Fisheries and Wildlife and Tall Timbers Research Station, Tallahassee, pp. 140–169.

Hovis, J.A., Labisky, R.F., 1985. Vegetative associations of red-cockaded woodpecker colonies in Florida. Wildlife Soc. Bull. 13, 307–314.

Jackson, J.A., 1979. Tree surfaces as foraging substrates for insectivorous birds. In: Dickson, J.G., Conner, R.N., Fleet, R.R., Jackson, J.A., Kroll, J.C. (Eds.), The Role of Insectivorous Birds in Forest Ecosystems. Academic Press, New York, NY, pp. 69-93.

Jackson, J.A., Jackson, B.J.S., 1986. Why do red-cockaded woodpeckers need old trees? Wildlife Soc. Bull. 14, 31X-322.

Jackson, J.A., Part-is, S.D., 1995. The ecology of red-cockaded woodpeckers associated with construction and use of a multi-purpose range complex at Fort Polk, Louisiana. In: Kulhavy, D.L., Hooper, R.G., Costa, R. (Eds.), Red-Cockaded Woodpecker: Recovery, Ecology and Management. College of Forestry Stephen F. Austin University, Nacogdoches, TX, pp. 277-2X2.

James, EC., Shugart, H.H., 1970. A quantitative method of habitat description. Audubon Field Notes 24, 727-736.

Johnson, T.B., 1971. Niche segregation of sympatric woodpeckers (Picidae) in east Texas. M.S. Thesis, Stephen F. Austin State University, Nacogdoches, TX, 53 pp.

Ligon, J.D., 196X. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. Auk 85, 203–215.

Ligon, J.D., 1971. Some factors influencing numbers of the red-cockaded woodpecker. In: Thompson, R.L. (Ed.), The Ecology and Management of the Red-Cockaded Woodpecker. US Bureau of Sport Fisheries and Wildlife and Tall Timbers Research Station, Tallahassee, pp. 30–43.

Locke, B.A., Conner, R.N., Kroll, J.C., 1983. Factors influencing colony site selection by red-cockaded woodpeckers. In: Wood, D.A. (Ed.), Proceedings of the Red-Cockaded Woodpecker Symposium II. Florida Game and Fresh Water Fish Commission, Tallahassee, pp. 46–50.

Loeb, S.C., Pepper, W.D., Doyle, A.T., 1992. Habitat characteristics of active and abandoned red-cockaded woodpecker colonies. Southern J. Appl. For. 16. 120-I 25.

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

Miller, G.L., 197X. The population, habitat, behavioral and foraging ecology of the red-cockaded woodpecker (*Picoides borealis*) in southeastern Virginia. M.A. Thesis, The College of William and Mary, Williamsburg, VA, 108 pp.

Moeed, A., Mead, M.J., 1983. Invertebrate fauna of four tree species in Orongorongo Valley New Zealand, as revealed by trunk traps. N.Z. J. Ecol. 6, 39-53.

Nicolai, V., 1986. The bark of trees: thermal properties, microclimate and fauna. Oecologia 69, 148-160.

Nicolai, V., 1989. Thermal properties and fauna on the bark of trees in two different African ecosystems. Oecologia 80, 421430.

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

Porter, M.L., Labisky, R.F., 1986. Home range and foraging habitat of red-cockaded woodpeckers in northern Florida. J. Wildlife Manage. SO, 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 red-cockaded woodpeckers (*Picoides borealis*). MS. Thesis, Mississippi State University, Mississippi State, MS, 129 pp.

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

SAS Institute Inc., 1988. SAS User's Guide: Statistics, Version 6th Edition. SAS Institute. Inc., Cary, NC, 1028 pp.

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. MS. Thesis, University of California, Davis, 95 pp.

Skorupa, J.P., McFarlane, R.W., 1976. Seasonal variation in foraging territory of red-cockaded woodpeckers. Wilson Bull. *88,* 662–665.

U.S. Fish and Wildlife Service, 1985. Red-cockaded woodpecker recovery plan. US. Fish and Wildlife Service, Atlanta, GA, 88 pp.

U.S. Forest Service, 1995. Final environmental impact statement for the management of the red-cockaded woodpecker and its habitat on national forests in the southern region. Management Bulletin R8-MB 73. US Department of Agriculture, Forest Service, Region 8, Atlanta, GA.

Van Balen, J.B., Doerr, P.D., 1978. The relationship of understory vegetation to red-cockaded woodpecker activity. In: Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies, Vol. 32. pp. 82-92.

Wood, D.A., 1977. Status, habitat, home range and notes on behavior of the red-cockaded woodpecker in Oklahoma. M.S. Thesis, Oklahoma State University, Stillwater, 66 pp.