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RED-COCKADED WOODPECKER NESTING SUCCESS, FOREST STRUCTURE, AND SOUTHERN FLYING SQUIRRELS IN TEXAS

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ABSTRACT.—For several decades general opinion has suggested that southern flying squirrels (*Glaucomys volans*) have a negative effect on Red-cockaded Woodpeckers (*Picoides borealis*) through competition for cavities and egg/nestling predation. Complete removal of hardwood trees from Red-cockaded Woodpecker cavity tree clusters has occurred on some forests because southern flying squirrel abundance was presumed to be associated with the presence and abundance of hardwood vegetation. In some locations, southern flying squirrels have been captured and either moved or killed in the name of Red-cockaded Woodpecker management. We determined southern flying squirrel occupancy of Red-cockaded Woodpecker cavities in loblolly (*Pinus taeda*)–shortleaf (*P. echinata*) pine habitat (with and without hardwood midstory vegetation) and longleaf pine (*P. palustris*) habitat (nearly devoid of hardwood vegetation) during spring, late summer, and winter during 1990 and 1991. Flying squirrel use of Red-cockaded Woodpecker cavities was variable and was not related to presence or abundance of hardwood vegetation. Woodpecker nest productivity was not correlated with flying squirrel use of woodpecker cavities within clusters. In addition, we observed six instances where Red-cockaded Woodpeckers successfully nested while flying squirrels occupied other cavities in the same tree. Our results suggest that complete removal of hardwoods from woodpecker cluster areas in loblolly and shortleaf pine habitat may not provide benefits to the woodpeckers through reduction of flying squirrel numbers. Reduction of hardwood midstory around cavity trees, however, is still essential because of the woodpecker's apparent innate intolerance of hardwood midstory foliage. *Received 3 Nov. 1995, accepted 21 Mar. 1996.*

The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperative breeder that lives in family groups composed of a breeding pair and frequently one to several helpers (Ligon 1970, Walters et al. 1988, Walters 1990). The activities of the group center around a cluster of cavity trees composed of living pines that contain one to several cavities and cavity starts. Cavities are excavated into the heartwood of pines that typically are infected with red heart fungus (*Phellinus pini*) (Conner and Locke 1982, Hooper 1988, Hooper et al. 1991, Rudolph et al. 1995). Cavity excavation in Texas requires an average of 1.8 y in loblolly pines (*Pinus taeda*), 2.4 y in shortleaf pines (*P. echinata*), and 6.3 y in longleaf pines (*P. palustris*) (Conner and Rudolph 1995). Pines selected for cavities in Texas usually exceeded 90 years of age (Conner and O'Halloran 1987,

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Rudolph and Conner 1991). The Red-cockaded Woodpecker is a keystone species of the fire-climax, southern pine ecosystems in that they are the primary species to excavate cavities in an otherwise cavity-barren environment relative to hardwood ecosystems (Conner and Rudolph 1995). Thus, the cavities that take Red-cockaded Woodpeckers a long time to create tend to be in relatively high demand by other cavity-using species (Dennis 1971, Rudolph et al. 1990b, Loeb 1993).

As cavities near completion, Red-cockaded Woodpeckers peck shallow excavations, termed resin wells, around their cavity entrances. Continued pecking at resin wells causes a copious flow of resin down the bole of the pine (Ligon 1970). Woodpeckers also scale loose bark from the bole of the cavity tree and nearby pines. Although bark scaling and resin flow usually deters climbing by rat snakes (*Elaphe obsoleta*) (Jackson 1974, Rudolph et al. 1990a), the resin barrier does not deter southern flying squirrels (*Glaucomys volans*) which are frequent users of cavities with unenlarged entrances that are also preferred by Red-cockaded Woodpeckers (Rudolph et al. 1990b, Loeb 1993).

Past studies have indicated a negative association between Red-cockaded Woodpeckers and the density of hardwood midstory and understory (Hopkins and Lynn 1971, Van Balen and Doerr 1978, Hovis and Labisky 1985, Conner and Rudolph 1989, Loeb et al. 1992). This has lead to widespread management programs that remove all hardwood vegetation from Red-cockaded Woodpecker cavity tree cluster areas (Conner and Rudolph 1991b). Although the negative effect of hardwood vegetation on Red-cockaded Woodpeckers is well documented, the mechanism that causes this negative relationship is poorly understood. One proposed mechanism for the hardwood effect is that southern flying squirrels, a potential competitor for Red-cockaded Woodpecker cavities, are dependent on hardwood midstory foliage. However, flying squirrels appear to prefer hardwood vegetation primarily as understory cover and as a food source (Bendel and Gates 1987). Contrary to popular belief, southern flying squirrels may avoid areas with dense midstory foliage because it interferes with flight paths between boles of larger pines (Bendel and Gates 1987). The influence of plant species composition and midstory and understory foliage densities in pine forests on southern flying squirrel abundance is not fully understood. To date, no published studies have demonstrated that southern flying squirrels have a negative effect on Red-cockaded Woodpecker populations, yet management programs that include removal of southern flying squirrels from cavities and euthanasia (Gaines et al. 1995) are becoming more widespread.

Several species of woodpeckers enlarge Red-cockaded Woodpecker cavity entrance tunnels by excavation and use the cavities (Conner et al.

1991, Neal et al. 1992). Some of these species, e.g., Pileated (*Dryocopus pileatus*) and Red-bellied (*Melanerpes carolinus*) woodpeckers, are considered to be primarily associated with hardwood forests (Reller 1972, Conner et al. 1975). Metal plates that restrict the entrance diameter of Red-cockaded Woodpecker cavities (Carter et al. 1989) have been developed for placement over enlarged cavities in hopes that some currently unsuitable cavities can be rehabilitated and on unenlarged cavities to prevent enlargement. Although these plates may prevent further damage by larger species of woodpeckers, they will not deter the use of cavities by southern flying squirrels or other small species of woodpeckers which prefer smaller entrances.

The competitive impact of southern flying squirrels on Red-cockaded Woodpeckers is largely hypothetical. If a detrimental impact is occurring, it may be exacerbated in small declining Red-cockaded Woodpecker populations such as those in eastern Texas that are also stressed by other factors such as isolation and forest fragmentation (Conner and Rudolph 1989, 1991a).

Our objectives were to (1) determine the availability and use of Red-cockaded Woodpecker cavities during the nesting, late-summer, and winter seasons, (2) evaluate southern flying squirrel use of cavities in relation to species composition and structure of vegetation, and (3) explore possible negative effects of southern flying squirrels on Red-cockaded Woodpecker breeding success.

STUDY AREAS AND METHODS

The study was conducted on the Angelina (62,423 ha; 31°15′N, 94°15′W) and Davy Crockett (65,329 ha; 31°21′N, 95°07′W) National Forests from March 1990 to October 1991. We examined 11 Red-cockaded Woodpecker cavity clusters in open longleaf pine habitat, 10 clusters in loblolly-shortleaf pine habitat with all hardwood vegetation removed in the cluster area, and seven clusters in loblolly–shortleaf pine habitat with extensive hardwood vegetation present during 1990. We suspected that different seasons of the year may impose varying levels of competition for cavities. The breeding season (spring) is likely to be a season of potentially elevated competition, and competition at that time can decrease breeding success. The late summer season may also be a critical period because new young have fledged and are searching for cavities for nocturnal roost sites. We sampled cavity occupants during winter to examine the possibility that thermal stress during the colder months may lead to increased demand for cavities.

We climbed approximately 230 cavity trees using Swedish climbing ladders and examined them for occupancy during spring (April to May) of 1990 and 1991, late summer (August to October) of 1990 and 1991, and winter of 1990–1991 (December 1990 to February 1991). Only a few cavity trees were not climbed because of safety factors during each climbing season. Such trees were typically small-diameter, old, inactive cavity trees that were primarily hollow shells and whose cavities were of no use to Red-cockaded Woodpeckers for cavities. We lowered a small, high intensity light into each cavity chamber, examined contents with an oval mechanics mirror mounted on an extendable handle, and identified and counted cavity occupants. Often more than one southern flying squirrel was present in a cavity. When this occurred, a coat hanger wire (with the end bent around to prevent injury) was placed into the cavity and flying squirrels lifted out for counting. We used presence of chewed pine needles and fresh flying squirrel feces as an indicator of flying squirrel use. Unchewed pine needles in an enlarged cavity indicated use by fox squirrels (*Sciurus niger*). Cavity trees that were being simultaneously used by both southern flying squirrels and Red-cockaded Woodpeckers (in two different cavities) were examined closely during the woodpecker nesting season to determine woodpecker fledging success and during other seasons to detect cavity usurpation by flying squirrels. We measured the entrance diameters of cavities and monitored cavities with restrictors in each cluster studied. Based on previous studies (Rudolph et al. 1990b), cavities were divided into those suitable for Red-cockaded Woodpecker use (entrance diameters <7 cm in diameter) and those too enlarged to be acceptable to Red-cockaded Woodpeckers (entrances >7 cm in diameter).

We measured reproductive success of Red-cockaded Woodpeckers in each cluster by determining the number of young fledged from nest cavities. Young were counted at 8, 20, and 23 days of age in each nest tree. Clusters were visited within a week of fledging to determine how many of the nestlings observed on day 23 successfully fledged. We also visited each cluster during August and September to determine number of surviving young. We made dawn and dusk visits to each woodpecker group to verify roost locations, band woodpeckers, and determine number of members in each family group during each climbing season. We also determined the number of Red-cockaded Woodpeckers roosting outside of cavities in the open.

Vegetation measured in each cavity tree cluster (six points per cluster) included basal area of overstory and midstory pines and hardwoods using a one-factor metric prism, height of midstory and understory vegetation using a clinometer, canopy closure using a 4-cm diameter by 12 cm hollow tube, and foliage density of vegetation from the ground to 1 m, and 1 m to 2 m using a density board as described by MacArthur and MacArthur (1961). By spring 1991, the seven clusters which had a well-developed hardwood midstory during the first year of the study had received midstory treatment. All hardwood vegetation was removed from these seven clusters during the 1990–1991 winter giving them the same structural appearance as the 10 clusters in loblolly–shortleaf habitat that were initially without hardwoods.

For each cavity tree cluster during each season we calculated the percentage of unenlarged cavities occupied by southern flying squirrels and those occupied by Red-cockaded Woodpeckers. Analysis of variance and Duncan's multiple range test were used to test for differences in flying squirrel and Red-cockaded Woodpecker use of cavities among habitat treatments during each season (P = 0.05). We related fledging success with the proportion of unenlarged cavities (all unenlarged and available unenlarged cavities) occupied by flying squirrels with Spearman correlations (r_s, P = 0.05).

RESULTS

Vegetation characteristics of cavity tree clusters.—Vegetation within the three treatments differed distinctly during the first year of the study (1990). Red-cockaded Woodpecker cavity tree clusters in longleaf pine habitat were nearly devoid of any hardwood vegetation or understory and midstory foliage except for grasses and forbs (Table 1), and the absence of hardwoods extended well beyond the boundaries of cluster areas. This was not the case in clusters located in loblolly–shortleaf pine habitat.

TABLE 1

VEGETATIVE CHARACTERISTICS (MEAN ± SD) OF RED-COCKADED WOODPECKER CLUSTER AREAS WHERE CAVITY OCCUPANTS WERE MONITORED IN LONGLEAF PINE, LOBLOLLY-SHORTLEAF PINE WITH NO MIDSTORY, LOBLOLLY-SHORTLEAF PINE WITH MIDSTORY PRESENT (PRE-TREATMENT 1990) AND MIDSTORY REMOVED (POST-TREATMENT 1991) ON THE ANGELINA AND DAVY CROCKETT NATIONAL FORESTS IN EASTERN TEXAS

Habitat variable	Longleaf pine (N = 11)	Loblolly-shortleaf no midstory (N = 10)	Loblolly-shortleaf with midstory (N = 7)	Loblolly-shortleaf midstory removed (N = 7)
Overstory pine basal area[a] (m²/ha)	14.0 (6.6)[b]	12.7 (3.5)[b]	10.9 (4.1)[c]	13.6 (3.7)[b]
Overstory hardwood basal area (m²/ha)	0.1 (0.2)[b]	0.0 (0.0)[b]	1.0 (4.3)[c]	0.0 (0.3)[b]
Midstory pine basal area (m²/ha)	0.2 (0.5)[b]	0.5 (1.2)[b]	1.8 (3.0)[c]	0.3 (0.9)[b]
Midstory hardwood basal area (m²/ha)	0.0 (0.0)[b]	0.1 (0.3)[b]	1.7 (1.7)[c]	0.2 (0.6)[b]
Canopy closure (%)	46.3 (26.1)[b]	51.5 (16.9)[bc]	55.8 (19.8)[c]	53.5 (15.8)[bc]
Overstory height (m)	23.1 (2.0)[b]	24.8 (2.8)[c]	27.0 (3.7)[d]	25.3 (1.5)[c]
Midstory height (m)	6.7 (5.4)[b]	3.3 (5.4)[c]	12.4 (4.5)[d]	3.3 (7.3)[c]
Understory height (m)	1.9 (0.9)[b]	1.6 (0.6)[c]	2.0 (0.8)[b]	1.5 (0.5)[c]
Foliage density 0–1 m (cm²/m³)	0.2 (0.2)[b]	0.3 (0.1)[b]	0.3 (0.2)[b]	0.5 (0.7)[c]
Foliage density 1–2 m (cm²/m³)	0.1 (0.1)[bc]	0.1 (0.1)[b]	0.2 (0.1)[d]	0.1 (0.2)[cd]

[a] Common letters indicate nonsignificant differences (ANOVA, Duncan's multiple range test [$P = 0.05$]).

Clusters in habitat where hardwoods had recently been removed were quite similar to longleaf habitat in the actual cluster area (Table 1), however, a virtual wall of hardwood midstory foliage was encountered at the edges of each cluster where midstory removal and thinning of overstory pines had ceased. Clusters that had not yet received hardwood removal treatment still had substantial hardwoods in the overstory, midstory, and understory (Table 1). During the winter of 1990–1991, hardwoods and midstory trees in the seven untreated clusters were removed, changing those clusters into a vegetative condition similar to the loblolly–shortleaf clusters that had received midstory treatment prior to the study (Table 1).

Faunal use of Red-cockaded Woodpecker cavities.—A variety of vertebrates and invertebrates were observed using Red-cockaded Woodpecker cavities during the study. Although observed in cavities infrequently, American Kestrels (*Falco sparverius*), Eastern Screech-Owls (*Otus asio*), Pileated Woodpeckers, Wood Ducks (*Aix sponsa*), and fox squirrels typically used cavities which had both the entrance and cavity chamber enlarged. Eastern Screech-Owls were observed in three cavities with entrances <7 cm in diameter, but the entrances of these three cavities had been slightly enlarged and were between 6.5 and 7 cm in diameter. Red-bellied Woodpeckers are known to conflict with Red-cockaded Woodpeckers over cavities (Neal et al. 1992, Kappes and Harris 1995) but were observed using unenlarged cavities only once during spring 1991 and on four occasions during winter.

Mud-daubers (Sphecidae) were typically found in inactive cavities. Their mud chambers were tolerated or pecked off when Red-cockaded Woodpeckers began to use a cavity containing mud-dauber nests. The presence of mud-daubers or their nests did not appear to interfere with Red-cockaded Woodpecker use of cavities. However, the presence of paper wasps (Vespidae), particularly large nests, and honey bees (*Apis mellifera*) did prevent Red-cockaded Woodpecker use of cavities. Broad-headed skinks (*Eumeces laticeps*), five-lined skinks (*E. fasciatus*), and gray tree frogs (*Hyla versicolor\chrysoscelis*) were observed occasionally within inactive enlarged and unenlarged cavities.

Southern flying squirrel use of woodpecker cavities.—Red-cockaded Woodpeckers preferred unenlarged cavities (Table 2); they used cavities with greatly enlarged entrances ($\geq$7 cm) in only two instances, both during late summer 1990. As previously noted by Rudolph et al. (1990b) and Loeb (1993), southern flying squirrels also prefer entrance diameters $<$7 cm. Thus, the southern flying squirrel exhibited extensive overlap in cavity use with Red-cockaded Woodpeckers; it was observed in relatively high numbers and also used primarily unenlarged cavities (Table 2). In most clusters, however, empty unenlarged and enlarged cavities were available throughout the year for either Red-cockaded Woodpeckers or flying squirrels to use (Tables 2, 3).

Southern flying squirrel use of Red-cockaded Woodpecker cavities during the woodpecker breeding season (spring) was high, but dwindled greatly by late summer during both 1990 and 1991 (Table 2). The number of cavities used by Red-cockaded Woodpeckers was somewhat higher during late summer than during the breeding season. Red-cockaded Woodpeckers were present in greater numbers in the late summer because young woodpeckers had recently fledged from nest cavities and many were now roosting in cavities.

We detected very few significant differences in the percentage of unenlarged cavities used by Red-cockaded Woodpeckers and southern flying squirrels among habitat treatments (Table 3). During spring 1990 southern flying squirrels used unenlarged Red-cockaded Woodpecker cavities at a higher frequency in longleaf pine habitat than in loblolly–shortleaf habitat where hardwood midstory vegetation was absent (Table 3). During spring 1991 the percentage of empty unenlarged cavities in loblolly–shortleaf pine habitat without midstory was significantly lower than in longleaf

TABLE 2

NUMBER OF UNENLARGED (ENTRANCE <7 CM DIAMETER) AND ENLARGED (ENTRANCE ≥7 CM DIAMETER) RED-COCKADED WOODPECKER CAVITIES OCCUPIED BY RED-COCKADED WOODPECKERS AND SOUTHERN FLYING SQUIRRELS IN THREE HABITAT TREATMENTS ON THE ANGELINA AND DAVY CROCKETT NATIONAL FORESTS IN EASTERN TEXAS

	Loblolly-shortleaf pine					
	With midstory pre-removal		Without midstory		Longleaf pine	
Cavity occupant	<7 cm	≥7 cm	<7 cm	≥7 cm	<7 cm	≥7 cm
Spring 1990 sample sizes	(N = 49)	(N = 15)	(N = 31)	(N = 20)	(N = 52)	(N = 21)
Red-cockaded Woodpecker	21	0	22	0	18	0
Flying squirrel/no. of squirrels	18/55	1/2	9/25	2/8	28/77	2/3
Empty cavities	7	4	8	13	2	7
Summer 1990 sample sizes	(N = 52)	(N = 11)	(N = 45)	(N = 18)	(N = 56)	(N = 23)
Red-cockaded Woodpecker	28	0	23	1	23	1
Flying squirrel/no. of squirrels	6/8	1/1	4/5	0	4/7	0
Empty cavities	14	7	15	15	24	18
Spring 1991 sample sizes	(N = 49)	(N = 13)	(N = 65)	(N = 12)	(N = 69)	(N = 23)
Red-cockaded Woodpecker	13	0	27	0	22	0
Flying squirrel/no. of squirrels	15/45	1/4	24/65	2/4	22/77	4/15
Empty cavities	13	4	10	5	17	11
Summer 1991 sample sizes	(N = 49)	(N = 13)	(N = 65)	(N = 13)	(N = 67)	(N = 26)
Red-cockaded Woodpecker	23	0	37	0	37	0
Flying squirrel/no. of squirrels	10/16	1/1	5/7	0	11/24	5/11
Empty cavities	11	6	15	10	19	18
Winter 1990-1991 sample sizes	(N = 51)	(N = 14)	(N = 55)	(N = 18)	(N = 52)	(N = 21)
Red-cockaded Woodpecker	17	0	30	0	26	0
Flying squirrel/no. of squirrels	13/31	1/2	7/22	1/2	10/30	1/5
Empty cavities	16	10	9	9	21	15

TABLE 3

PERCENTAGE OF UNENLARGED CAVITIES WITHIN EACH CLUSTER OCCUPIED BY RED-COCKADED WOODPECKERS BY SOUTHERN FLYING SQUIRRELS, OR EMPTY (MEAN ± SD) IN LOBLOLLY-SHORTLEAF PINE HABITAT WITHOUT HARDWOOD MIDSTORY VEGETATION (N = 10), LOBLOLLY-SHORTLEAF PINE HABITAT WITH HARDWOOD MIDSTORY VEGETATION (PRE- AND POST-REMOVAL, N = 7), AND LONGLEAF PINE HABITAT (N = 11) IN EASTERN TEXAS

	Habitat treatment							
	Loblolly-shortleaf without midstory		Loblolly-shortleaf with midstory (pre-removal)		Loblolly-shortleaf post midstory removal		Longleaf	
Variable	$\bar{x}$[a]	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Spring 1990								
Red-cockaded (%)	56.4[b]	26.3	43.5[b]	24.6			50.3[b]	33.7
Flying squirrel (%)	16.9[b]	18.8	38.8[bc]	28.0			44.8[c]	31.0
Empty (%)	14.7[b]	16.6	14.6[b]	18.3			3.8[b]	8.6
Spring 1991								
Red-cockaded (%)	48.2[b]	17.2			29.5[b]	14.7	35.5[b]	26.3
Flying squirrel (%)	41.6[b]	14.8			38.4[b]	15.0	28.5[b]	20.9
Empty (%)	7.2[b]	13.0			27.2[c]	15.1	30.9[c]	14.7
Summer 1990								
Red-cockaded (%)	64.0[b]	34.8	60.8[b]	25.8			46.9[b]	30.7
Flying squirrel (%)	7.0[b]	9.5	14.4[b]	14.1			6.1[b]	11.2
Empty (%)	25.0[b]	23.8	21.4[b]	24.5			46.3[b]	28.4
Summer 1991								
Red-cockaded (%)	60.4[b]	17.5			49.7[b]	24.9	58.8[b]	20.1
Flying squirrel (%)	7.8[b]	10.4			23.0[b]	23.2	19.6[b]	13.2
Empty (%)	26.2[b]	15.1			25.0[b]	10.3	21.6[b]	21.3
Winter 1990–1991								
Red-cockaded (%)	62.8[b]	25.2			38.2[c]	12.6	47.1[bc]	26.3
Flying squirrel (%)	16.3[b]	19.3			25.7[b]	12.5	19.4[b]	15.2
Empty (%)	18.9[b]	21.2			27.8[b]	11.4	28.1[b]	22.9

[a] Common superscript letters following means indicate nonsignificant differences among habitat treatments (ANOVA, Duncan's multiple range test, $P = 0.05$).

pine or loblolly–shortleaf pine from which midstory had been recently removed (Table 3). Southern flying squirrel use of Red-cockaded Woodpecker cavities was not related to the presence or absence of hardwood midstory (Table 3). Thus, treatment specific and annual use of cavities by flying squirrels appears to be minimally affected by hardwood midstory abundance.

Southern flying squirrel use of cavities in the loblolly–shortleaf habitat with midstory was greater than their use of loblolly–shortleaf habitat without hardwood vegetation during spring 1990, although not significantly

TABLE 4

NUMBER OF RED-COCKADED WOODPECKERS ROOSTING IN THE OPEN DURING SPRING AND LATE SUMMER 1990 AND 1991 IN LOBLOLLY-SHORTLEAF PINE HABITAT WITHOUT HARDWOOD MIDSTORY VEGETATION (N = 10 CLUSTERS), WITH HARDWOOD MIDSTORY VEGETATION (PRE- AND POST-HARDWOOD REMOVAL, N = 7 CLUSTERS), AND LONGLEAF PINE HABITAT (N = 11 CLUSTERS) IN EASTERN TEXAS

	Habitat treatment		
	Loblolly-shortleaf without midstory	Loblolly-shortleaf with midstory	Longleaf
Season	No. woodpeckers	No. woodpeckers	No. woodpeckers
Spring 1990	1	1[a]	6
Summer 1990	3	5[a]	4
Spring 1991	1	3[b]	0
Summer 1991	2	2[b]	2

[a] Pre-midstory removal treatment within these clusters.
[b] Post-midstory removal treatment within cluster areas completed during winter 1990–1991.

so (Table 3). However, the percentage of unenlarged cavities used by flying squirrels remained the same during spring 1991 even though hardwood midstory vegetation had been removed (Table 3). Flying squirrel use of unenlarged cavities increased in the loblolly–shortleaf area without midstory even though no habitat alteration occurred (Table 3). Both the percentage of cavities used by flying squirrels and the abundance of flying squirrels counted in Red-cockaded Woodpecker cavities decreased between spring and late summer in 1990 and 1991 (Table 2, 3). We did not make a detailed survey of the crowns of nearby pines and hardwoods in the woodpecker cluster areas, but strongly suspect that flying squirrels were spending the hot, late summers in leaf nests rather than woodpecker cavities, as also observed by Muul (1974).

During winter, the percentage of unenlarged cavities and available unenlarged cavities used by southern flying squirrels was relatively similar in all habitat treatments (Table 3). Empty unenlarged cavities were readily available in clusters in all habitat treatments during winter, suggesting that cavity availability did not create a competitive problem for Red-cockaded Woodpeckers during winter.

Extra-cavity roosting by woodpeckers.—Extra-cavity roosting as described by Hooper and Lennartz (1983) is a possible indicator of insufficient cavity availability for Red-cockaded Woodpeckers. In general, very few Red-cockaded Woodpeckers were observed roosting in the open (Table 4). Typically, when Red-cockaded Woodpeckers roosted in the open, there were empty cavities available within their cluster areas. Spring 1990 in the longleaf pine habitat appeared to be exceptional in this regard.

With the exception of longleaf pine habitat in spring 1990, Red-cockaded Woodpeckers appeared to roost in the open more during late summer than during the breeding season (Table 4). Flying squirrels were very abundant during spring 1990 in the longleaf habitat (Table 2) and empty cavities were few, suggesting that a few Red-cockaded Woodpeckers may have been forced temporarily to roost in the open. Many recently fledged young Red-cockaded Woodpeckers did not roost in cavities during the late summer. Because many unenlarged empty cavities were available for these woodpeckers to use during late summer, roosting in the open appears to be voluntary and may have been in response to the typical high air temperatures during August and September.

Red-cockaded Woodpecker fledging success.—We examined Red-cockaded Woodpecker fledging success to explore the possibility that interactions with southern flying squirrels reduced woodpecker nest productivity. Because southern flying squirrel use of woodpecker cavities was uniformly high over all habitat treatments and years, our ability to evaluate the influence of squirrel use of cavities on fledging success through comparisons across habitats was limited.

Fledging success was slightly higher in loblolly–shortleaf habitat with hardwood vegetation (pre-hardwood removal) than in the loblolly–shortleaf habitat without hardwood vegetation during 1990 (Fig. 1). Fledging success remained somewhat higher in these cluster areas in 1991 (post-treatment) even though the hardwood vegetation had been removed prior to the 1991 breeding season. Longleaf pine habitat, relatively devoid of hardwood vegetation, and often considered the premiere habitat for the woodpecker, had a slightly lower fledging success than either loblolly–shortleaf habitats during both 1990 and 1991 (Fig. 1). Excluding nests where eggs failed to hatch, we failed to detect any significant differences in fledging success among habitat treatments (Kruskal-Wallis χ^2 approximation, $\chi^2 = 1.42$, $P = 0.49$).

We compared the proportion of all unenlarged cavities used by flying squirrels and the proportion of available unenlarged cavities (open cavities not used by Red-cockaded Woodpeckers) that contained flying squirrels with woodpecker fledging success (Fig. 1). During both 1990 and 1991 we observed no relationship between southern flying squirrel occupancy and habitat condition (abundance of hardwood midstory) or Red-cockaded Woodpecker fledging success. Red-cockaded Woodpecker fledging success per habitat treatment during the two breeding seasons (N = 6) was not correlated with the percentage of all unenlarged cavities occupied by southern flying squirrels ($r_s = -0.08$, $P = 0.87$) or the percentage of available unenlarged cavities (those not used by Red-cockaded Woodpeckers) occupied by southern flying squirrels ($r_s = -0.46$, $P = 0.35$). If

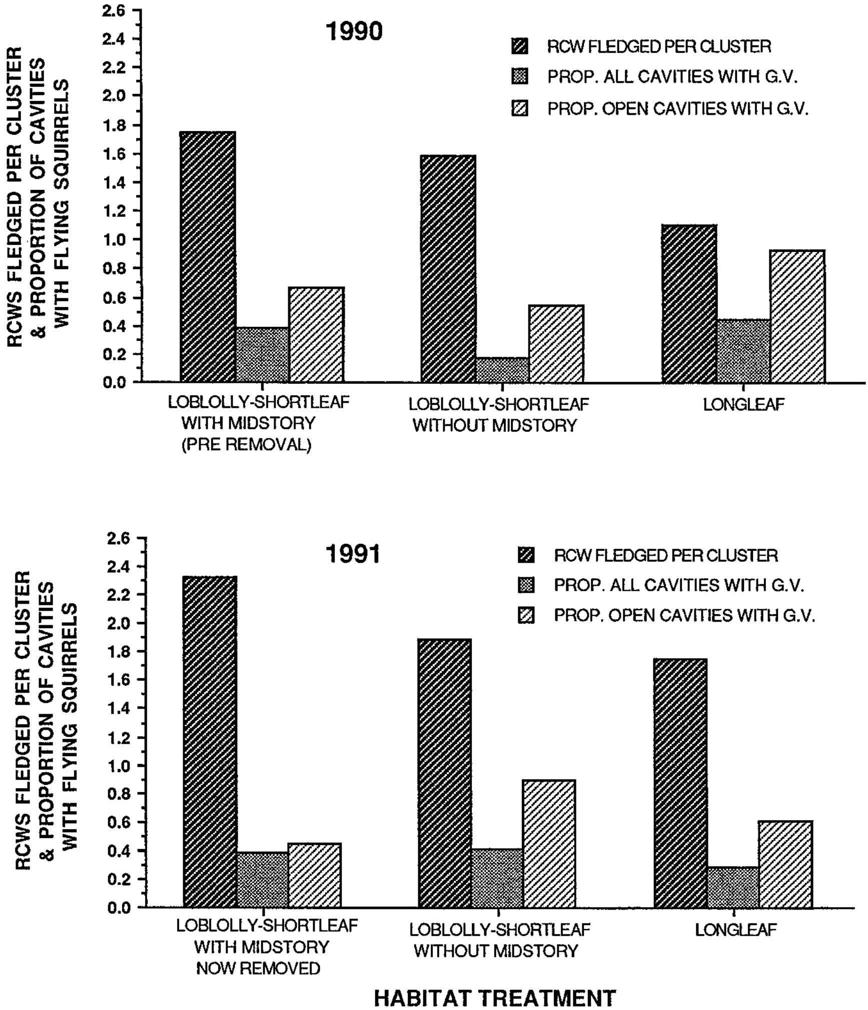

FIG. 1. Comparisons of Red-cockaded Woodpecker fledging success with the proportion of all unenlarged Red-cockaded Woodpecker cavities occupied by southern flying squirrels (*Glaucomys volans,* G. V.) and available unenlarged cavities (those not used by Red-cockaded Woodpeckers) occupied by southern flying squirrels in loblolly-shortleaf pine habitat with hardwood midstory present (pre- and post-hardwood removal), loblolly-shortleaf pine habitat without hardwood midstory throughout the study, and longleaf pine habitat during the 1990 and 1991 breeding seasons on the Angelina and Davy Crockett National Forests in eastern Texas.

clusters are treated as the sample unit (N = 44), fledging success is still not correlated with either the percentage of all unenlarged cavities occupied by flying squirrels ($r_s = -0.18$, $P = 0.23$), or the percentage of available unenlarged cavities occupied by flying squirrels ($r_s = -0.11$, $P = 0.48$).

Potential for flying squirrel predation on woodpeckers.—During our 2 year study we observed 6 instances where Red-cockaded Woodpeckers nested and produced young in cavities while southern flying squirrels were occupying other cavities in the same pine tree. In only one instance were eggs lost (to unknown causes), but the woodpeckers renested and successfully fledged young from the same cavity. Young fledged successfully from all five of the other nest cavities.

DISCUSSION

Competition between flying squirrels and woodpeckers.—Our observations in eastern Texas suggest a minimal competitive impact of southern flying squirrels on Red-cockaded Woodpeckers. Because we did not measure woodpecker fledging success over a wide range of flying squirrel abundance, however, our results may not be definitive. Competition from southern flying squirrels in Texas is likely transient and occurs as isolated events during ecological "bottle-necks." If such competition occurs at all in eastern Texas, the effects are subtle rather than overwhelming. The effect of southern flying squirrels on any healthy woodpecker population is probably minimal to non-existent.

Specifically, we have not seen (1) a relationship between woodpecker fledging success and flying squirrel use of cavities, (2) Red-cockaded Woodpeckers forced to roost in the open because of a squirrel-caused shortage of unenlarged cavities, or (3) regular squirrel predation on Red-cockaded Woodpecker eggs and young even when both woodpeckers and flying squirrels occupied the same cavity tree.

Relationships among woodpeckers, squirrels, and hardwood vegetation.—We did not observe a strong relationship between southern flying squirrel abundance and presence of hardwood vegetation. Flying squirrels were common in cavities in longleaf pine habitat with almost no hardwood vegetation. This finding, however, does not negate the necessity to reduce hardwood vegetation within woodpecker cluster areas. Past studies have clearly demonstrated the negative effects of excessive hardwood midstory on woodpecker populations (Van Balen and Doerr 1978, Hovis and Labisky 1985, Conner and Rudolph 1989, Loeb et al. 1992). Thus, we strongly urge that *reduction* (not elimination) of hardwood vegetation within Red-cockaded Woodpecker cluster areas be continued.

Our results indicate that complete or partial removal of all hardwoods will likely not affect the use of Red-cockaded Woodpecker cavities by southern flying squirrels. What our study suggests is that southern flying squirrels are not the cause of harmful effects on Red-cockaded Woodpeckers associated with the presence of hardwood vegetation within their cluster areas. As we have suggested before (Conner and Rudolph 1991b), Red-cockaded Woodpeckers may have an innate avoidance of areas with extensive hardwood vegetation as a result of their adaptation to the southern fire-climax pine ecosystem. A selective advantage may accrue for Red-cockaded Woodpecker pairs that avoid habitat with abundant hardwood vegetation because such areas may support greater numbers of other species of woodpeckers that can easily out-compete Red-cockaded Woodpeckers for cavities or destroy the cavities they excavate. Another possible reason why Red-cockaded Woodpeckers have an aversion to hardwoods is that they may provide predators access to cavities (Walters 1990).

We saw no negative effect of southern flying squirrels on Red-cockaded Woodpeckers, nor have any other studies demonstrated such an effect. We strongly discourage removal and euthanasia of southern flying squirrels in woodpecker clusters because of the complete lack of evidence that it would benefit Red-cockaded Woodpeckers. If removal of southern flying squirrels is deemed necessary, it should be based on site-specific data that statistically demonstrates a severe competitive problem. In such instances, control of flying squirrels should last only as long as the woodpecker population is small and vulnerable to sudden extirpation.

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