

## COMPETITION FOR RED-COCKADED WOODPECKER ROOST AND NEST CAVITIES: EFFECTS OF RESIN AGE AND ENTRANCE DIAMETER

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**ABSTRACT.**—Competition for roost and nest cavities was investigated in a Texas population of Red-cockaded Woodpeckers (*Picoides borealis*) in longleaf pine (*Pinus palustris*) habitat. Twenty-two percent of all examined cavities were occupied by Red-cockaded Woodpeckers, and 46% were occupied by other species. Red-cockaded Woodpeckers did not roost in the open or in sub-optimum cavities due to the presence of other species, with one temporary exception. Southern flying squirrels (*Glaucomys volans*) were a potential competitor. Similar to Red-cockaded Woodpeckers, flying squirrels preferred cavities with small entrance diameters, and their use of cavities was not hampered by the presence of a resin barrier or woodpecker cluster status (active vs inactive). Other potentially competing species were either rare or restricted to enlarged cavities no longer used by Red-cockaded Woodpeckers. These data suggest that competition for cavities is not an important factor in this particular population of Texas Red-cockaded Woodpeckers during the period prior to breeding. *Received 3 Nov. 1988, accepted 1 May 1989.*

The Red-cockaded Woodpecker (*Picoides borealis*) inhabits mature pine forests in the southeastern United States. Red-cockaded Woodpecker population structure is complex, consisting of parent-offspring groups termed clans (Ligon 1970). A Red-cockaded Woodpecker clan typically consists of a breeding pair and some male offspring of previous years (Ligon 1970, Gowaty and Lennartz 1985). Non-breeding male clan members, called helpers, assist the breeding pair in maintaining cavities, feeding young, and other activities (Baker 1971, Ligon 1970, Lennartz and Harlow 1979). Female offspring disperse prior to the breeding season following fledging (Gowaty and Lennartz 1985, J. A. Jackson pers. comm.). Clans occupy clusters consisting of one to many cavity trees that provide roosting and nesting sites (Ligon 1970, 1971; Hooper and Lennartz 1983).

Due to climate and the historical importance of fire, southeastern pine forests provide minimal numbers of dead trees and limbs for cavity construction by woodpeckers (Ligon 1970, 1971). But Red-cockaded Woodpeckers are unique among woodpeckers in their nearly exclusive use of living pines for cavity sites (Ligon 1970, Short 1979). Red-cockaded Woodpecker cavities are typically excavated in the trunks of pines, often below the lowest branches (Ligon 1970, Wood 1983). Entrance tunnels that pass through living, resin-transporting tissue, slope upward to the

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interior, which directs resin flow toward the exterior and away from the cavity chamber (Dennis 197 1 a, Jackson 1978a).

Red-cockaded Woodpeckers also construct small ancillary holes, termed resin wells, in the immediate vicinity of the cavity entrance (Steirly 1957, Ligon 1970, Dennis 197 1 a). Because these resin wells are worked regularly by the birds, resin flow persists. The eventual result is a copious coating of resin around the cavity entrance and several meters below. In addition, the woodpeckers persistently scale loose bark from the trunk of the cavity tree resulting in a smoother surface and a more even and complete resin coating (Ligon 1970, Dennis 197 1 a, Jackson 1978b).

Several hypotheses have been suggested to explain the evolution of Red-cockaded Woodpecker behavior involving this scaling of bark and the constructing and maintaining of resin wells. Lay and Russell (1970) proposed a social context for these behaviors, suggesting that the changed appearance of the trunks of cavity trees might advertise the birds' location and status. Reduction of predation, especially by snakes, has been hypothesized by Pearson et al. (1942), Dennis (197 1 a), and Ligon (1970).

Ligon (1970) and Dennis (197 1 a) have also proposed that the smooth resin-coated trunks reduce interspecific competition for cavities. Definitions and theoretical formulations of interspecific competition require that population size be negatively affected by the interaction. In practice, detrimental effects of potential competitors on survival or reproduction are considered evidence of competitive interaction. In the case of Red-cockaded Woodpeckers, cavity use by other species would not necessarily represent competition. However, if Red-cockaded Woodpeckers were roosting in the open due to other species occupying suitable cavities, then detrimental effects due to competition could be inferred. More subtle effects of competition, due to attempted cavity usurpation and cavity enlargement, resulting in increased energy demands for defense and construction of additional cavities, might also occur.

Testing and evaluation of these hypotheses, which are not mutually exclusive, has been minimal. Jackson (1974) and Rudolph et al. (1990) have presented data demonstrating the effectiveness of resin in preventing access to Red-cockaded Woodpecker cavities by rat snakes (*Elaphe* spp.). Baker (197 1), Dennis (197 1 a), Harlow and Lennartz (1983), Hopkins and Lynn (197 1), and Jackson (1978a) have documented extensive use of Red-cockaded Woodpecker cavities by other species. Previous studies have not, however, examined the use of cavities by species other than Red-cockaded Woodpeckers in relation to the cavity requirements of the Red-cockaded Woodpeckers and the status of the potential resin barrier.

This paper presents data specifically collected to evaluate the impact of potential cavity competitors on Red-cockaded Woodpeckers. Complete

cavity surveys were conducted in active and inactive clusters. Data were obtained on cavity use by Red-cockaded Woodpeckers and other species, cavity availability, and status of the resin barrier. The resulting data base was used to examine specific questions relating to cavity use by Red-cockaded Woodpeckers and potentially competing species.

#### STUDY AREA AND METHODS

This study included all known Red-cockaded Woodpecker clusters in the portion of the Angelina National Forest located south and west of Lake Sam Rayburn, Angelina and San Augustine counties, Texas. The population contained 16 currently active clusters, and 30-50 individuals, during our study. The population has been declining during the past 20 years (D. W. Lay pers. comm.). Vegetation here is a pine-hardwood mosaic with longleaf pine (*Pinus palustris*) dominating the uplands occupied by Red-cockaded Woodpeckers. The area is managed for timber production with longleaf pine typically managed on an 80-year rotation. Red-cockaded Woodpecker cluster sites are managed as separate stands. Prescribed burning has been conducted at irregular intervals. Locke et al. (1983) provide detailed information about the study area and cavity-tree characteristics.

Red-cockaded Woodpecker cavities were surveyed diurnally in active and inactive clusters between 19 March and 22 May 1986. Surveys in active clusters were completed by 25 April, prior to the initiation of egg laying by the Red-cockaded Woodpeckers. Sectional climbing ladders were used to climb cavity trees. Mirrors and a headlamp were used to determine cavity contents. All cavities located in trees exhibiting signs of current Red-cockaded Woodpecker use were surveyed. Cavities in inactive trees were omitted occasionally due to excessive height or obstructing limbs.

The interiors of all cavities, including occasional vertical extensions above the cavity entrance (Beckett 1971), were examined visually. All vertebrate species and active wasp nests were recorded. Nest material was noted and a brief description recorded. In active Red-cockaded Woodpecker clusters, the number of clan members and their roost sites were determined. Visual observations were conducted in the morning and evening as the birds exited and entered their roost cavities. Strategic positioning of 1-2 observers allowed the roost sites of all clan members to be determined in 1-5 observation periods per cluster.

Cavity entrance diameter was measured at the point of narrowest constriction using a drafting compass and rule. A 5-category classification of resin age was established, and the resin surrounding each cavity was assigned to the appropriate category. The categories and definitions were: (1) very fresh-copious amounts of clear, semi-fluid, actively flowing resin, (2) fresh-resin solidified and yellowed, but sticky to touch, (3) old-resin dried, not sticky to touch, (4) very old-resin very dry, large areas free of resin due to growth of tree and progressive loss of bark, and (5) absent-most resin lost due to continued growth of tree. These categories are clearly subjective to some extent, but in this study were sufficient to characterize the basic pattern of resin age.

#### RESULTS

A total of 123 cavities in 89 trees (87 *P. palustris*, 2 *P. taeda*) were examined. The 89 trees comprised 16 active and 15 inactive clusters, plus six isolated inactive trees that were not associated with a specific cluster. Diurnally active tree squirrels (*Sciurus* spp.) were potentially absent from cavities at the times of individual surveys. Cavities known to be used by

TABLE 1  
CAVITY CONTENTS IN ACTIVE AND INACTIVE RED-CKOADED WOODPECKER CLUSTERS

Contents		Active clusters	Inactive clusters
Red-cockaded Woodpecker	<i>Picoides borealis</i>	27	0
Southern flying squirrel	<i>Glaucomys volans</i>	15	12
Tree squirrels	<i>Sciurus</i> spp.	8	4
Eastern Screech-Owl	<i>Otus asio</i>	2	3
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	1	2
Tufted Titmouse	<i>Parus bicolor</i>	0	3
American Kestrel	<i>Falco sparverius</i>	0	1
Evening bat	<i>Nycticeius humeralis</i>	0	1
	Wasps (3 spp.)	2	2
	Water	0	1
	Empty	25	14
	Total	80	43

tree squirrels contained abundant pine needles, typically filling the entire cavity. Cavities containing typical tree squirrel nests were recorded as being occupied by tree squirrels even if squirrels were not observed. Seven of 12 tree squirrel records (Table 1) refer to nests only. Avian records in Table 1 all consist of active nests. Breeding activity of cavity-nesting birds exhibits an April-May maximum in east Texas (pers. obs.). Thus the one-time survey does not cover yearlong cavity use by nesting birds but should approximate the maximum possible at any one time. Roosting in cavities by avian species other than Red-cockaded Woodpeckers was not observed during morning and evening observation periods and apparently was minimal.

A total of 83 (68%) cavities were occupied, and one other cavity contained water. Eight vertebrate species and three wasp species were recorded in cavities in addition to Red-cockaded Woodpeckers. A ninth vertebrate species, the Wood Duck (*Aix sponsa*), nested in a cavity subsequent to the initial survey. Red-cockaded Woodpeckers roosted in 22% of the available cavities. Flying squirrels and tree squirrels were the most frequent of the remaining species (22% and 10%, respectively). All other species occupied a total of 14% of all available cavities. No significant difference was indicated between occupancy rates of all species in active and inactive clusters (G-test,  $P > 0.05$ ).

Red-cockaded Woodpeckers occupied cavities ranging from 40-58 mm in entrance diameter (Table 2). Of the nine other vertebrate species recorded, five (fox squirrel [*S. niger*], eastern gray squirrel [*S. carolinensis*],

TABLE 2  
RANGES OF CAVITY ENTRANCE DIAMETERS (MM) OF CAVITIES OCCUPIED BY VERTEBRATE SPECIES

Species		Cavity entrance diameter		sample size
		Mean	(Range)	
Red-cockaded Woodpecker	<i>Picoides borealis</i>	49	(40-58)	27
Southern flying squirrel	<i>Glaucomys volans</i>	66	(4 1-89)	27
Tree squirrels	<i>Sciurus</i> spp.	93	(73-1 15)	12
Eastern Screech-owl	<i>Otus asio</i>	96	(72-125)	5
American Kestrel	<i>Falco sparverius</i>	90	(90)	1
Wood Duck	<i>Aix sponsa</i>	108	(108)	1
Tufted Titmouse	<i>Parus bicolor</i>	61	(56-7 1)	3
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	70	(46-85)	3
Evening bat	<i>Nycticeius humeralis</i>	51	(51)	1

Eastern Screech-Owl [*Otus asio*], American Kestrel [*Falco sparverius*], and Wood Duck) were restricted to cavities with larger entrance diameters (72-125 mm) than those occupied by Red-cockaded Woodpeckers. Three uncommonly occurring species (Tufted Titmouse [*Parus bicolor*], Great Crested Flycatcher [*Myiarchus crinitus*], and evening bat [*Nycticeius humeralis*]) occupied cavities with entrance diameters (5 1-85 mm) overlapping the range of diameters of cavities occupied by Red-cockaded Woodpeckers. The remaining species, flying squirrels, used cavities with a range of entrance diameters (41-89 mm) that completely overlapped the entrance diameter range of cavities used by Red-cockaded Woodpeckers.

Red-cockaded Woodpeckers used a restricted range of available cavities in relation to entrance diameter and resin age (Fig. 1). The 27 Red-cockaded Woodpeckers observed roosted in cavities of the two smallest entrance diameter classes and the two freshest resin age categories, with two exceptions. The two exceptions were birds roosting in cavities with old resin (category 3). One was a single bird reoccupying an abandoned cluster site; four weeks later resin wells were active and the cavity would have been classified in category 1. The second was a bird in a large cluster with available category 1 and 2 cavities. Ten days after the survey, this bird was roosting in one of these cavities and was present there four weeks later. Cavities of the two smallest entrance diameter classes and the two freshest resin age classes are hereafter termed "optimal" Red-cockaded Woodpecker cavities.

Thirty-five optimal Red-cockaded Woodpecker cavities were recorded

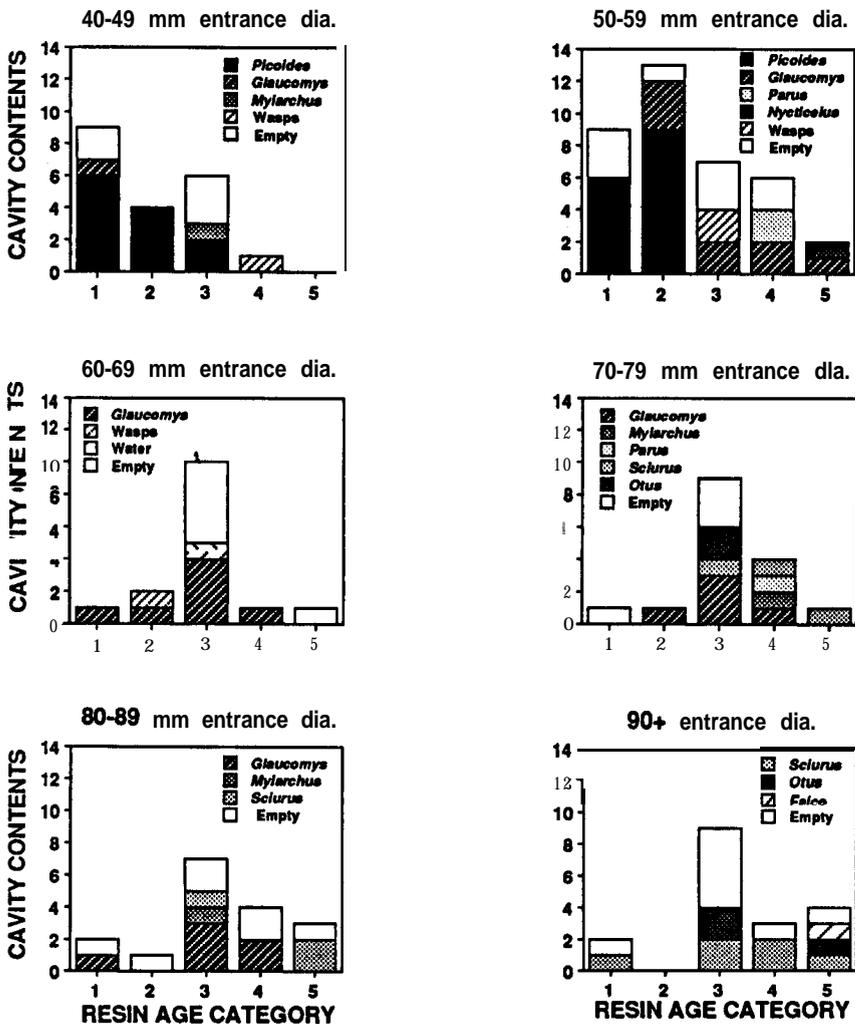


FIG. 1. Cavity contents in relation to entrance diameter and resin age category.

in 16 active clusters. Twenty-five of these cavities were used by Red-cockaded Woodpeckers as roost cavities at the time of the survey. In five clusters, the number of optimal cavities equaled the number of birds present in the clan. Nine clusters contained optimal cavities in excess of the number of clan members (eight clusters with one excess cavity, one cluster with two excess cavities). The two remaining clusters contained one and two fewer optimal cavities than clan members. These two clusters

lacked non-optimal cavities and the three additional birds roosted in the open in the crowns of cavity trees. The ten additional optimal cavities were empty (6) or occupied by flying squirrels (4). In no instance during the survey was a Red-cockaded Woodpecker roosting in the open, or in a non-optimal cavity, due to the presence of other species in optimal cavities.

However, some additional observations are pertinent. After the cavity survey, an optimal cavity previously used as a roost site by a Red-cockaded Woodpecker, was occupied by a flying squirrel. This particular cluster contained three optimal cavities and one old cavity showing no recent activity. The clan was comprised of three birds that had previously used the three optimal cavities as roost sites. The flying squirrel occupied the optimal cavity for at least one week. During this period, evening roosting behavior of the Red-cockaded Woodpeckers was observed three times. In each instance, one of the Red-cockaded Woodpeckers approached the cavity entrance at the normal roost time, peered in once or twice, and flew to an adjacent tree. No direct interaction between the flying squirrel within the cavity and the Red-cockaded Woodpecker was observed. On each occasion, the Red-cockaded Woodpecker eventually roosted in the crown of an adjacent cavity tree. One week later, the flying squirrel was absent, and a Red-cockaded Woodpecker was roosting in the cavity again.

Following the initial cavity survey, a number of cavities previously occupied by either Red-cockaded Woodpeckers or flying squirrels were resurveyed. These observations were made at various times 7-31 days after the original survey. Twenty-one cavities used as roosts by Red-cockaded Woodpeckers during the initial survey were resurveyed. Nineteen were still occupied by woodpeckers, one contained the flying squirrels discussed above and was subsequently re-occupied by the Red-cockaded Woodpecker, and one was a sub-optimum cavity abandoned in favor of an optimum cavity. Fifteen cavities occupied by flying squirrels during the initial survey were resurveyed. Six were still occupied by flying squirrels and nine were empty.

Flying squirrels occupied a wide range of cavities in relation to resin age and entrance diameter (Fig. 1). Cavities ranging in entrance diameter from essentially the smallest available up to 89 mm and of all resin age categories were used. To provide a more detailed understanding of flying squirrels' cavity use, it is necessary to compare cavity use with availability. **Accepting** the argument that Red-cockaded Woodpeckers can maintain possession of cavities against the challenge of potential flying squirrel competition, and assuming that at least some of the remaining species, especially the larger ones, do also, the best measure of cavity availability for flying squirrels is the number of empty cavities. Observation of flying

squirrels displaced from cavities confirms that they have detailed knowledge of the location of additional cavities within their activity ranges (Sawyer and Rose 1985, pers. obs.).

The number of cavities occupied by flying squirrels was compared to the number of empty cavities in relation to three factors: cluster status, resin age, and cavity entrance diameter. In active clusters 15 of 40 cavities were occupied vs 12 of 26 in inactive clusters. A G-test indicated no significant difference ( $G = 0.109$ ,  $P > 0.05$ ). A comparison of flying squirrel occupancy vs resin age revealed eight of 18 cavities of resin age categories 1 or 2 occupied compared to 19 of 48 cavities of resin age categories 3, 4, and 5. No significant difference was indicated ( $G = 0.385$ ,  $P > 0.05$ ). A comparison of flying squirrel occupancy vs cavity entrance diameter revealed 27 of 58 cavities with entrance diameters  $<90$  mm occupied vs 0 of 8 with entrance diameters  $>90$  mm. This difference was highly significant ( $G = 15.597$ ,  $P < 0.01$ ). Due to small sample sizes, Yates' correction was used in all tests.

The remaining species comprise the group (tree squirrels, Eastern Screech-Owl, American Kestrel, Wood Duck) restricted to cavities with entrance diameters larger than those typically occupied by Red-cockaded Woodpeckers. This diverse assemblage undoubtedly responded to cavity characteristics in various ways. Sample sizes are too small to conclude much beyond the obvious limitations of entrance diameters. This is especially true because cavities with larger entrance diameters and fresher resin are rare. Two observations are worth noting, however. A fox squirrel and a Wood Duck were each able to raise young in a cavity with extremely fresh, copious resin. This was actually the same cavity used sequentially, and was also in the tree that contained the current nest cavity of the Red-cockaded Woodpeckers. Neither species exhibited any obvious difficulty with the resin.

The smaller species (Tufted Titmouse, Great Crested Flycatcher, evening bat, wasps) used cavities of smaller entrance diameters, but, except for one cavity occupied by wasps, were restricted to cavities with resin of the three older age categories. However, the sample size is small and not too much should be made of this. The literature suggests that various small and medium-sized avian species are able to use cavities with fresh, well-developed resin barriers (Jackson 1978a, Harlow and Lennartz 1983, Ligon 1971).

#### DISCUSSION

Surveys and incidental observations have identified more than 20 species of birds and mammals using Red-cockaded Woodpecker cavities as roost and/or nest sites (Baker 1971, Dennis 1971a, Harlow and Lennartz 1983,

Hopkins and Lynn 1971, Jackson 1978a, this study). Reported occupancy rates for vertebrate species other than Red-cockaded Woodpeckers are 35% (Dennis 1971a), 46% (this study), and 56% (Harlow and Lennartz 1983) of available cavities. The potential for significant competition for cavities between Red-cockaded Woodpeckers and other species therefore exists. Determining if competition actually occurs is difficult. Many of the occupied cavities are presumably unsuitable for Red-cockaded Woodpeckers. Also, quantitative data are usually lacking on the cavity requirements of individual Red-cockaded Woodpecker clans and the availability of cavities in the clusters. Dennis (1971a), however, comments that many woodpecker cavities occupied by other species are enlarged and/or long abandoned.

A number of possible instances of competition involving cavities have been documented. Ligon (1971) observed a Red-bellied Woodpecker (*Melanerpes carolinus*) physically removing a Red-cockaded Woodpecker from a cavity, and found cavity defense against Red-bellied Woodpeckers an important part of Red-cockaded Woodpecker behavior. Baker (1971) reported sequential use of a cavity by Red-bellied Woodpeckers and Red-cockaded Woodpeckers. Jackson (1978a) reported the abandonment of two Red-cockaded Woodpecker colonies presumably due to the usurping of all active cavities by Red-bellied Woodpeckers. Harlow and Lennartz (1983) reported the failure of two clans to breed during four of twelve years due to the occupancy of potential nest cavities by Eastern Bluebirds (*Sialia sialis*) and flying squirrels.

Cavity characteristics and differences among species in types of cavities used must be considered to evaluate cavity use in the woodpecker clusters. Cavities constructed by Red-cockaded Woodpeckers are suitable as roost and nest cavities at the time of completion. These cavities are characterized by small entrance diameters and active resin wells. Cavities may remain suitable for use by Red-cockaded Woodpeckers for many years (Lay and Russell 1971, Jackson 1978a). Over a period of years, barring death of the tree, cavities evolve into having larger entrance diameters and inactive resin wells. Cavity entrance enlargement by other woodpeckers, squirrels, and fire (Beckett 1971, Jackson 1978a, Conner and Locke 1979) eventually results in a cavity unsuitable for Red-cockaded Woodpeckers. Enlargement may occur before or after abandonment of a cavity by Red-cockaded Woodpeckers. After abandonment by Red-cockaded Woodpeckers, resin flow declines to a very low level, and progressive drying and loss of the once well-developed resin coating occurs. Inactive cavities with inactive resin wells can be reactivated by Red-cockaded Woodpeckers if entrance diameters are still acceptable.

The data reported here quantified the cavity requirements of individual

Red-cockaded Woodpecker clans and the availability of cavities in the respective clusters. In no instance, during the initial survey, was a Red-cockaded Woodpecker roosting in the open, or in a sub-optimal cavity, due to the occupancy of cavities by other species. Red-cockaded Woodpeckers roosting in the open ( $N = 3$ ) or in sub-optimal cavities ( $N = 2$ ) were in clusters with insufficient cavities, except for the bird in a sub-optimum cavity from which it later moved to an optimal cavity. The observation of a flying squirrel temporarily displacing a Red-cockaded Woodpecker to an open roost site was the only example in this study of cavity loss due to another species. Thus, competition for available roost cavities appears minimal during the period prior to the breeding season in this Red-cockaded Woodpecker population.

Five of the species using Red-cockaded Woodpecker cavities were restricted to cavities with entrance diameters larger than those used by Red-cockaded Woodpeckers. These species and others reported in the literature (Dennis 1971 a) are substantially larger than Red-cockaded Woodpeckers and cannot use optimal Red-cockaded Woodpecker cavities. Interactions between these species and Red-cockaded Woodpeckers occur in the context of the historical aspects of cavity enlargement. In this population, cavity enlargement by Pileated Woodpeckers (*Dryocopus pileatus*) is common. These interactions may be important but have not been examined.

The remaining species are smaller and can use optimal Red-cockaded Woodpecker cavities. Flying squirrels are the most abundant of these species. The data from this study support two general conclusions relevant to competition between these two species. First, flying squirrels are not displacing Red-cockaded Woodpeckers from optimal cavities in this population during the period prior to the breeding season. This conclusion is supported by the lack of examples of displacement (see below for a discussion of the one exception) and the lower flying squirrel occupancy rate of optimal cavities compared to non-optimal cavities. Second, flying squirrels are not prevented from using cavities protected by a copious and fresh resin barrier. No significant difference was found in flying squirrel occupancy rates of cavities with fresher resin (categories 1 and 2) compared to those with older resin (categories 3 to 5). Observations of flying squirrels occupying cavities with a fresh resin barrier indicated no obvious difficulty with the resin accumulations. Beckett (in Dennis 1971 a) reported only small amounts of resin on the feet of flying squirrels occupying similar cavities.

The observation of a Red-cockaded Woodpecker roosting in the open while its previous roost cavity was occupied by a flying squirrel is of interest. The Red-cockaded Woodpecker maintained an interest in the cavity at roost time, but made no direct attempt to displace the squirrel.

The bird subsequently re-occupied the cavity. This is the only published account of interaction between these two species other than data on sequential cavity occupation. How is this observation to be reconciled with the pattern of cavity occupation indicating that flying squirrels are not displacing Red-cockaded Woodpeckers from optimal cavities?

We hypothesize that both Red-cockaded Woodpeckers and flying squirrels may be unable to evict the other species when the other species is already in a cavity. Red-cockaded Woodpeckers are diurnal (roost times in Baker 1971) and flying squirrels are nocturnal (Sonenshine and Levy 1981), and their normal activity periods do not overlap. Consequently, either species searching for a cavity at the conclusion of its normal activity period would probably encounter the other species already occupying cavities in presumably invincible positions. If, as the limited data reported above suggest, Red-cockaded Woodpeckers are consistent in their use of a specific cavity, and flying squirrels much less so, the observed pattern of cavity occupancy would rapidly develop. Red-cockaded Woodpeckers would relatively quickly encounter the optimal cavities vacant, and once occupied, they would hold them for extended periods. This obviously begs the question of how the flying squirrel referred to above obtained the Red-cockaded Woodpecker's roost cavity, but exceptions always occur. Also, if the cluster areas contain a lower ratio of optimal to **sub-optimal** cavities, the level of competition might be increased because of reduced availability of diurnal roosting sites for flying squirrels.

The data reported support the conclusion that interspecific competition for cavities is minimal in this Red-cockaded Woodpecker population prior to the breeding season. Competition may vary temporarily, and the existence of significant competition at other times should not be discounted. In particular, the limited availability of excess cavities may result in intense competition at the time of woodpecker fledging when cavity requirements of clans increase. In addition, the potential exists for predation by flying squirrels on eggs and nestlings and other detrimental interactions. Data are currently lacking on these aspects of the flying squirrel-Red-cockaded Woodpecker interaction.

Variation in population levels of competitors, especially flying squirrels, could also alter the level of competition for cavities. Other studies, in particular Harlow and Lennartz (1983), Jackson (1978a), and Ligon (1971) suggest the possibility of significant competition from other woodpeckers, especially Red-bellied Woodpeckers. Cavity usurpation, ejection of Red-cockaded Woodpecker nestlings, and frequent agonistic encounters were reported. Two considerations may be involved in the apparent discrepancies between these studies and the present study. First, methods and sample sizes differ. The cited studies examined more clusters and also

included extensive observations of behavior. The instances of interaction were thus obtained from a larger pool of possibilities. Second, the level of competition and other interactions may vary with location. Although Red-bellied Woodpeckers were moderately common at our study site, ample lightning and beetle-killed pines appeared to be available for the Red-bellied Woodpecker population. We also suspect that competition with Red-bellied Woodpeckers would be higher in habitats with more hardwoods. Thus, the availability of alternatives may be a major influence on the extent of competition for cavities between species of woodpeckers.

There is no evidence that the resin barrier significantly reduced competition for cavities. Red-cockaded Woodpeckers apparently have no specific behavioral adaptations to avoid problems with resin, so it is not unexpected that other vertebrate species, at least those with limbs, have little difficulty occupying resin-protected cavities.

Five instances of birds entrapped in the resin of Red-cockaded Woodpecker cavities have been reported. These examples, two Red-cockaded Woodpeckers (Locke et al. 1979, pers. obs.), a Red-bellied Woodpecker (Barnett et al. 1983), a bluebird (Dennis 1971a), and a warbler (Dennis 1971b) possibly represent mortality directly attributable to the resin barrier. Despite these examples, cavity-nesting species can successfully use Red-cockaded Woodpecker cavities with well-developed resin barriers, and the benefits of a cavity protected from predatory snakes may more than compensate for some resin-induced mortality. Additional data comparing occupancy rates of cavities with fresh resin to those with older resin, similar to the data reported here for flying squirrels, would be informative.

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