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RED-COCKADED WOODPECKER NEST-CAVITY SELECTION: RELATIONSHIPS WITH CAVITY AGE AND RESIN PRODUCTION

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ABSTRACT.—We evaluated selection of nest sites by male Red-cockaded Woodpeckers (*Picoides borealis*) in Texas relative to the age of the cavity when only cavities excavated by the woodpeckers were available and when both naturally excavated cavities and artificial cavities were available. We also evaluated nest-cavity selection relative to the ability of naturally excavated cavity trees to produce resin, which is used by the woodpeckers to maintain a barrier against predation by rat snakes (*Elaphe* spp.). Longleaf pines (*Pinus palustris*) selected by breeding males as nest trees produced significantly greater resin yields at 2, 8, and 24 h post-wounding than cavity trees used for roosting by other group members. This preference was observed in loblolly pine (*P. taeda*) and shortleaf pine (*P. echinata*) cavity trees only at the 2-h resin-sampling period. When only naturally excavated cavities were available, Red-cockaded Woodpeckers in both longleaf pine and loblolly-shortleaf pine habitat selected the newest cavities available for their nest sites, possibly as a means to reduce parasite loads. When both naturally excavated and artificial cavity inserts were available, Red-cockaded Woodpeckers continued to select the newest cavity for nesting in loblolly-shortleaf pine habitat but not in longleaf pine habitat. Resin production in existing longleaf pine nest trees remained sufficient for continued use, whereas resin production in loblolly pine and shortleaf pine nest trees decreased through time, probably because of woodpecker activity at resin wells. For these latter tree species, breeding males switched to newer cavities and/or cavity trees with higher resin yields. *Received 7 July 1997, accepted 11 November 1997.*

THE RED-COCKADED WOODPECKER (*Picoides borealis*) is a cooperatively breeding species that lives in groups of two to seven members (Ligon 1970, Lennartz et al. 1987, Walters et al. 1988). Groups usually are composed of a single breeding pair and one to several adult helpers, typically males, from previous nestings. Each group member usually roosts singly at night in its own cavity (Ligon 1970). Group members occasionally roost in the open, in the fork of a tree or other natural tree crevice, when roost cavities are in limited supply or in late summer prior to acquisition of roost cavities by fledglings (Hooper and Lennartz 1983, Conner et al. 1996).

The breeding male typically is the dominant individual of the group (Walters 1990) and likely would have first choice when selecting a roost cavity. The quality of the cavity selected by the breeding male is important to all group members because the breeding male's roost cavity is used as the nest cavity during the breeding season. Breeding males often select the newest cavity in the cavity-tree cluster (Conner and Rudolph pers. obs.). A possible benefit of this behavior is a decreased parasite load for nestlings and incubating adults. Since 1990, artificial cavities (Allen 1991) have been used to provide roosting and nesting sites. The effect of the addition of artificial cavities on nest-site selection is unknown.

Roosting and nesting Red-cockaded Woodpeckers make daily excavations at small wounds, termed resin wells, around their cavity entrance, from which resin flows down the tree (Ligon 1970). The breeding male may select cavity trees with greater resin flow than other active cavity trees within the cluster. Such cavity trees would enhance the quality of the resin barrier against rat snakes (*Elaphe* spp.), thereby increasing the probability of nestling survival and the safety of the dominant, breeding male (Jackson 1974, Rudolph et al. 1990). Rat snakes regularly attempt to climb active

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Red-cockaded Woodpecker cavity trees (Neal et al. 1993).

We examined the age of cavities used by nesting and roosting Red-cockaded Woodpeckers over a 14-year period (1984 to 1997) in loblolly pine (*Pinus taeda*)-shortleaf pine (*P. echinata*) and longleaf pine (*P. palustris*) habitats in eastern Texas. We also examined how the use of artificial cavity inserts (Allen 1991) affected Red-cockaded Woodpecker selection of nest cavities. We compared the number of years that naturally excavated cavities and artificial insert cavities were used for nesting in both habitat types, and contrasted habitat types for the number of active cavity trees per group of woodpeckers. In addition, we compared resin yields from cavity trees used for nesting with those used for roosting in both habitat types, and evaluated the effect of cavity age on resin yield from cavity trees in loblolly-shortleaf pine and longleaf pine habitats. We measured cavity-tree moisture stress associated with resin yields to evaluate the influence of the physical environment on resin flow.

We predicted that: (1) because of their social dominance, breeding males would select the newest cavities available; and (2) breeding males would select cavity trees for roosting and nesting that produce greater resin yields, thereby giving better protection against rat snake predation.

STUDY AREA AND METHODS

The study area was on the Angelina National Forest (62,423 ha; 31°15'N, 94°15'W) in eastern Texas. The number of woodpecker groups present on the Angelina National Forest varied from 18 to 26 during the 14-year study. The northern portion of the forest is covered predominantly by a mixture of loblolly pine and shortleaf pine on shrink-swell clayey soils, whereas longleaf pine is the dominant tree species in the deep, sandy soils where Red-cockaded Woodpeckers occur in the southern portion of the forest (Conner and Rudolph 1989). Longleaf pines are virtually absent from the northern portion of the Angelina National Forest, and young slash pines (*Pinus elliottii*), an introduced species in this region, are not sufficiently old to be cavity trees where they occur near active woodpecker clusters.

We visited all active and inactive Red-cockaded Woodpecker cavity-tree clusters during March through June from 1983 through 1997, as well as other times throughout the year, and examined them closely for use by woodpeckers. Cavities where woodpeckers were observed incubating (peering out of the cavity during the middle of the day) were revisited weekly and checked visually using ladders, or from the ground by listening for vocalizing nestlings. A cavity was judged a nest cavity if we observed eggs or nestlings or heard nestlings vocalizing from the cavity.

We compared woodpecker selection of nest and roost cavities under two conditions: (1) clusters where only naturally excavated cavities (two or more) were available for selection (1984 to 1996), and (2) clusters where both naturally excavated and artificial cavity inserts were available (1990 to 1997). The age of a cavity was determined by the year (and month if possible) it was completed, not the year that excavation began. The age of a cavity insert was determined by the date it was installed. Cavity inserts were installed by National Forest personnel in active and inactive clusters as part of routine management activities; 57 were installed between summer 1990 and spring 1991, 50 during 1991 to 1992, 59 during 1992 to 1993, 31 during 1993 to 1994, 139 during 1994 to 1995, and 63 during 1995 to 1996. By spring 1997, some cavity-tree clusters still contained only naturally excavated cavities. Several cavity inserts were installed within a cluster at 6 m above the ground, a height lower than the mean heights of naturally excavated cavities in longleaf pines (8.9 ± SD of 2.5 m) and loblolly and shortleaf pines (11.0 ± 3.3 m) in Texas (Conner et al. 1991). The lower height was selected by National Forest personnel for ease of installation. Similar numbers of artificial cavities were installed within clusters in both loblolly pine-shortleaf pine and longleaf pine habitats.

We collected data on resin yield and xylem moisture potential (a measure of moisture stress) monthly from active cavity trees during the growing seasons of 1987 to 1989 in loblolly-shortleaf pine habitat and in longleaf pine habitat (see Ross et al. 1995, 1997). We collected resin data only from active (currently in use for nesting or roosting) and inactive (previously used, but currently not being used by woodpeckers) cavity trees with naturally excavated cavities prior to the time period when artificial cavities were installed. Unfortunately, our permit to collect resin samples from cavity trees was not renewed by the National Forests and Grasslands in Texas after 1989. Thus, we do not have data for resin yields from pines with artificial cavities.

We measured resin yield on sunny days by driving a 2.54-cm diameter circular arch punch (see Lorio et al. 1990) into the interface of xylem and phloem tissue on the pine's bole at approximately 1.4 m above ground. We punched holes on the south side of the bole between 0700 and 1000 h to minimize effects of diurnal variation in resin flow (Nebeker et al. 1988). We then placed triangular metal funnels directly under the wounds to channel exuded resin into clear plastic graduated tubes. Resin yield was recorded at 2 (1987 only), 8, and 24 h after wounding. Only one sample was taken per sampling period to avoid placing undue stress on cavity trees.

We determined xylem moisture potential (in megapascals) of cavity trees on sunny days using a pressure-chamber technique (Scholander et al. 1965). We sampled twigs from the upper crowns of cavity trees from among active cavity trees sampled for resin yield. We collected three twig samples from each cavity tree with a 12-gauge shotgun and evaluated tree moisture status within 60 s of collection between 1300 and 1500, at the same time resin sampling was conducted.

For time periods when two or more naturally excavated cavities were available within an active cavity-tree cluster, and when both naturally excavated and artificial cavities were available simultaneously, we used Chi-square analyses to test if Red-cockaded Woodpeckers used the newest cavity for a nest site within loblolly pine-shortleaf pine and longleaf pine habitat types. More than two active cavities were available for selection during most nestings (81.4%, 149 of 183 instances). We calculated Chi-square values, adjusting probabilities for variable numbers of active cavities within each cluster, to determine if the newest cavity was selected more often than expected.

Because Red-cockaded Woodpeckers sometimes used the same nest cavity in more than one year, we used Chi-square analysis to test whether woodpeckers selected the newest cavity available when they changed nest cavities in both habitat types, removing any bias from a possible lack of independence of observations. As before, we adjusted probabilities to account for variable numbers of active cavities within clusters. We also used a Wilcoxon signed-rank test to compare the mean age of nest cavities with the mean age of all available active roost cavities. We used a two-tailed t-test to compare the number of active cavity trees used by each woodpecker group between forest types from 1990 to 1997.

We used a Chi-square analysis to compare the frequency that woodpeckers used naturally excavated versus artificial cavities for nesting from 1992 through 1997, a period of time when adequate numbers of both cavity types were available for the woodpeckers to use. In addition, we used a two-way ANOVA (type III sum of squares) to compare the number of consecutive years that naturally excavated and artificial cavities were used as nest sites in loblolly-shortleaf and longleaf pine forest types during the six-year period.

We used a two-way factorial ANOVA (nest vs. roost cavity by month; type III sum of squares) within loblolly pine-shortleaf and longleaf pine habitats to compare resin yield and moisture stress of nest trees versus other active cavity trees. We used a Wilcoxon signed-rank test to compare mean resin yields from all active longleaf pine cavity trees with those from all active loblolly pine and shortleaf pine cavity trees. We used a paired t-test to evaluate the relative abilities of cavity trees to sustain resin production by comparing spring resin yields during subsequent years. All analyses were performed on SAS (release 6.11; SAS Institute 1988).

Results

Selection of nest cavities relative to age and recency of completion.—In clusters where only naturally excavated cavities were available (1984 to 1996), Red-cockaded Woodpeckers used the newest cavities for their nest site in longleaf pines (48 of 52 cases; $\chi^2 = 49.6$, $P < 0.0001$) and in loblolly pines and shortleaf pines (26 of 29 cases; $\chi^2 = 35.6$, $P < 0.0001$). Red-cockaded Woodpeckers also selected the newest naturally excavated cavity when they changed nest cavities in both longleaf pine (17 of 18 cases; $\chi^2 = 24.29$, $P < 0.0001$) and loblolly-shortleaf pine habitat (18 of 22 cases; $\chi^2 = 28.22$, $P = 0.0001$). The mean age of cavities selected for nesting was less than the mean age of other active cavities in both pine types (Table 1).

In clusters where both naturally excavated cavities and artificial cavity inserts were available for woodpeckers (1990 to 1997), Red-cockaded Woodpeckers selected the newest cavity for their nest site in loblolly pines and shortleaf pines (27 of 44 cases; $\chi^2 = 28.17$, $P < 0.0001$) but not in longleaf pines (21 of 53 cases; $\chi^2 = 5.74$, $P = 0.57$). When both naturally excavated and artificial cavities were available, Red-cockaded Woodpeckers again selected the newest cavity when they changed nest cavities in loblolly-shortleaf pine habitat (15 of 22 cases; $\chi^2 = 39.35$, $P < 0.0001$) but not in longleaf pines (12 of 24 cases; $\chi^2 = 9.15$, $P = 0.30$). We failed to detect a difference between mean age of nest cavities and mean age of other active cavities in either habitat type when both naturally excavated and artificial cavities were available (Table 1).

During the 14-year study, Red-cockaded Woodpeckers using loblolly pines and shortleaf pines for nest trees switched nest trees (0.355 switches per active cluster year) more often than woodpeckers nesting in longleaf pines (0.211 switches per active cluster year). The mean number of active cavities per cluster in loblolly-shortleaf pine habitat (3.83) was not significantly different from that in longleaf pine habitat (4.12; $t = 1.06$, df = 108, $P = 0.29$).

Use of artificial cavity inserts for nesting.—Combining data for both forest types from 1992

TABLE 1. Age in years ($\bar{x} \pm$ SD) of Red-cockaded Woodpecker nest cavities and of other active cavities within cavity-tree clusters in loblolly-shortleaf pine and longleaf pine habitats on the Angelina National Forest. Only naturally excavated cavities were available from 1984 to 1990; both naturally excavated and artificial cavities were available from 1990 to 1997.

Forest and cavity type	Nest-cavity age	Roost-cavity age per cluster	Z[a]	P
Only naturally excavated cavities available				
Loblolly-shortleaf (n = 164)	2.49 ± 2.0	4.58 ± 2.8	5.12	0.0001
Longleaf (n = 266)	3.68 ± 2.8	6.57 ± 3.4	6.65	0.0001
Naturally excavated and artificial cavities available				
Loblolly-shortleaf (n = 116)	2.32 ± 1.5	2.78 ± 1.7	1.21	0.226
Longleaf (n = 127)	2.85 ± 1.5	2.81 ± 1.6	0.30	0.762

[a] Wilcoxon signed-rank test.

through 1997, Red-cockaded Woodpeckers nested in artificial cavities 57.7% (64 of 111 nests) of the time; the remaining 47 nests were in naturally excavated cavities. During this six-year period, 180 active naturally excavated cavities and 230 active artificial inserts were available for use as nest sites. Neither artificial cavities nor naturally excavated cavities were used for nesting significantly more than they were available (χ^2 = 0.15, P = 0.70).

Individual naturally excavated cavities were used for nesting for more consecutive years than were artificial cavities (F = 5.88, df = 1 and 61, P = 0.018). The woodpeckers used naturally excavated cavities an average of 2.5 years and artificial cavities an average of 1.5 years in longleaf pine habitat and 1.5 and 1.3 years, respectively, in loblolly-shortleaf pine habitat. There was no significant interaction between the type of nest cavity used and forest type (F = 2.59, df = 1 and 61, P = 0.102). Longleaf pine cavities were used as nest sites for longer periods of time than were loblolly pine or shortleaf pine cavities (F = 6.41, df = 1 and 61, P = 0.011).

Resin production and nest tree selection.—In general, active longleaf pine cavity trees produced greater resin yields than active loblolly pine and shortleaf pine cavity trees (Table 2). Male Red-cockaded Woodpeckers in longleaf pine habitat selected cavity trees for roosting and subsequent nesting that produced significantly greater volumes of resin at 2, 8, and 24 h than other active cavity trees used by other group members for roosting (Table 3). Red-cockaded Woodpecker nest trees in longleaf pine habitat produced an average of 2.5, 8.1, and 11.7 mL of resin at 2, 8, and 24 h, respectively, whereas other active cavity trees produced 1.9, 4.7, and 7.1 mL, respectively, at similar time periods.

Only during the 2-h sampling period in loblolly pine-shortleaf pine habitat did nest trees produce more resin (P = 0.077) than active cavity trees used by other group members for roosting (Table 3). Red-cockaded Woodpecker nest trees in loblolly pine-shortleaf pine habitat produced an average of 2.0, 3.7, and 4.8 mL of resin at 2, 8, and 24 h, respectively, whereas active roost trees produced 1.3, 4.1, and 5.8 mL, respectively, at similar time periods.

Our measures of moisture stress on cavity trees, taken while conducting resin sampling, and subsequent two-way ANOVA (cavity tree type × month), failed to detect a difference in xylem moisture potential between Red-cockaded Woodpecker nest trees and active cavity trees used as roosting sites by other group

TABLE 2. Resin yields (mL) from active Red-cockaded Woodpecker cavity trees on the Angelina National Forest. Values are $\bar{x} \pm$ SD, with n in parentheses.

Sample period	Longleaf pine	Loblolly-shortleaf pine	Z[a]	P
After 2 hours	2.1 ± 3.2 (30)	1.4 ± 2.1 (171)	1.2	0.219
After 8 hours	5.2 ± 4.9 (144)	4.0 ± 4.0 (340)	2.4	0.015
After 24 hours	7.7 ± 7.6 (152)	5.7 ± 5.8 (338)	3.0	0.003

[a] Wilcoxon signed-rank test.

TABLE 3. Two-way ANOVA comparison of resin yields from Red-cockaded Woodpecker nest trees and other active cavity trees used by group members for roosting in loblolly-shortleaf pine and longleaf pine habitat on the Angelina National Forest, 1987 through 1989.

Source	df	2-hour yield		8-hour yield		24-hour yield	
		F	*P*	*F*	*P*	*F*	*P*
Loblolly-shortleaf pine							
Nest vs. active tree	1	3.2	0.077	1.7	0.189	2.8	0.095
Month	7	25.6	0.001	1.9	0.064	1.3	0.225
Cavity tree type × month	6	1.0	0.456	0.4	0.916	0.3	0.955
Error df		156		322		320	
Longleaf pine							
Nest vs. active tree	1	4.8	0.039	8.0	0.005	5.6	0.019
Month	4	37.9	0.001	2.1	0.049	1.4	0.228
Cavity tree type × month	2	1.5	0.246	0.4	0.930	0.4	0.909
Error df		22		128		136	

members (loblolly pines and shortleaf pines, $F = 0.51$, df = 1 and 114, $P = 0.48$; longleaf pine, $F = 0.33$, df = 1 and 26, $P = 0.57$). Thus, differences in resin production between nest and roost trees likely were not caused by nest trees being subjected to substantially different moisture stress regimes.

Cavity age affected the ability of trees to produce resin in loblolly pines and shortleaf pines but not in longleaf pines. We observed a significant drop in 24-h resin yields during April from active loblolly pine and shortleaf pine cavity trees between 1987 and 1988 (Table 4). Resin yields from inactive cavity trees did not decline during the same time period, suggesting that Red-cockaded Woodpecker activity at resin wells, rather than annual variation per se, caused the decreased resin production. There were no significant changes in resin yields from either active or inactive longleaf pine cavity trees between 1988 and 1989, suggesting that woodpecker activity at resin wells had no effect on resin production in longleaf pines (Table 4).

DISCUSSION

The differential ability of pines to produce resin appears to have a strong influence on the selection of nest cavities by Red-cockaded Woodpeckers. In longleaf pine habitat, breeding males selected nest cavities in trees that were better resin producers than cavity trees used for roosting by other group members. In loblolly pine-shortleaf pine habitat, the woodpeckers tended to nest in pines that were better resin producers (2-h resin yield only). The selection process likely was confounded by the inability of loblolly pines and shortleaf pines to provide a sustained yield of resin because woodpecker activity at resin wells decreased the ability of these tree species to produce resin. The presence of multiple cavities in a given tree and multiple-year use of trees with mul-

TABLE 4. Sequential spring resin yields (mL; $\bar{x} \pm$ SD) over 24-hour period from active and inactive Red-cockaded Woodpecker cavity trees in loblolly and shortleaf pines (1987 and 1988) and longleaf pines (1988 and 1989) over a two-year period.

Status	Yield (year 1)	Yield (year 2)	*t*	*P*
Loblolly and shortleaf pines				
Active cavity tree ($n = 14$)	3.6 ± 1.6	2.2 ± 1.4	3.26	0.02
Inactive cavity tree ($n = 28$)	5.3 ± 3.1	6.1 ± 5.3	1.09	0.30
Longleaf pine				
Active cavity tree ($n = 16$)	10.1 ± 7.0	11.8 ± 10.9	0.57	0.58
Inactive cavity tree ($n = 28$)	5.0 ± 3.7	4.4 ± 3.6	0.62	0.54

tiple cavities also may have confounded the results in loblolly pines and shortleaf pines. Longleaf pines are renowned for their ability to produce copious amounts of resin for extended periods of time, which was the basis for the naval stores industry during the first part of this century and earlier (Gerry 1922, Harper and Wyman 1936). When wounded, loblolly pines and shortleaf pines produce less resin and are not able to maintain a sustained flow for the extended periods of time achieved by longleaf pines (Hodges et al. 1979, Ross et al. 1993).

A sustained flow of copious amounts of resin is essential for Red-cockaded Woodpeckers to maintain adequate protection of nest cavities from rat snakes (Jackson 1974, Rudolph et al. 1990, Neal et al. 1993). Selection of cavity trees with sustained, high yields of resin results in a highly effective barrier against rat snakes (Rudolph et al. 1990), which enhances the survival of breeding males throughout the year and protects nests during the breeding season. Based on the longer life span of longleaf pines (Conner et al. 1991) and the greater resin production at resin wells, longleaf pines appear to be superior cavity trees compared with loblolly pines and shortleaf pines.

Cavity newness also was an important factor in Red-cockaded Woodpecker nest cavity selection. When only naturally excavated cavities were available, breeding males selected the newest cavities available for their roost and subsequent nest sites in both loblolly-shortleaf and longleaf pine habitat. In general, roost/nest cavities selected by breeding males were significantly younger than those used by other group members in both pine habitat types. However, when both naturally excavated and artificial cavities were available, Red-cockaded Woodpeckers still selected the newest cavity for their nest site in loblolly pine and shortleaf pine habitat but not in longleaf pine habitat. This suggests that resin production in existing longleaf pine nest trees remained sufficient for continued use, whereas resin production in loblolly pine and shortleaf pine nest trees was insufficient, requiring breeding males to switch to newer cavities and/or cavity trees that had higher resin yields.

Use of the newest cavity available might result in reduced parasite loads for both nestlings and incubating adults. A variety of parasites (lice, flies, and mites) occur on woodpeckers in the eastern United States (Emerson and Johnson 1961, Pence 1972, Price and Emerson 1975, Wilson and Bull 1977), but only lice (*Degeeriella* sp.) have been reported specifically on Red-cockaded Woodpeckers (Peters 1936). Although parasitic arthropods have the potential to affect avian reproductive success (Gold and Dahlsten 1983, Emlen 1986, Rendell and Verbeek 1996) and the fitness of adult breeders (Møller 1990), ectoparasites and their negative effects rarely have been observed in Red-cockaded Woodpeckers (LaBranche and Walters 1994, D. Carrie, J. A. Jackson, and J. R. Walters pers. comm., R. N. Conner et al. pers. obs.).

When cavities are excavated naturally by woodpeckers over the course of one to six years, the newest cavity usually has a well-developed resin-well system by the time of cavity completion (Conner and Rudolph 1995). The breeding male also has had an opportunity to monitor development of naturally excavated cavities in his cluster and to "assess" the ability of each cavity tree to produce resin. When woodpeckers first begin to occupy these cavities, the resin-well system is fully functional, and cavities are well protected from rat snake predation (Conner and Rudolph 1995). Artificial cavities are installed in about 30 min and have no functional resin-well system. Artificial cavities often are occupied within a week after installation, occasionally on the first day. Such artificial cavities do not have a well-developed resin barrier, usually are placed at lower heights than naturally excavated cavities, and are placed in trees that have not had their bark scaled smooth by woodpeckers (smooth bark decreases their accessibility to rat snakes; Rudolph et al. 1990). If the breeding male selected the newest cavity for nesting, and that cavity was an artificial insert, the survival of the breeding pair and success of their nesting effort likely would be affected because of the elevated susceptibility of new artificial cavities to rat snake predation. Based on observations that breeding males always seem to occupy cavity trees with the greatest amount of bark scaling and resin flow, we suspect that these males do not move into a new insert immediately. Instead, they appear to wait until they (or other group members) have scaled the bark and initiated resin wells. By waiting, breeding males might be able to monitor resin flow before choosing a cavity.

Resin production is likely to be affected by the combined and interacting influence of genetics, environment, and wound response. The moisture stress of pines, an environmental factor, has a major influence on their ability to produce resin (Lorio 1986). We failed to detect differences in moisture stress between nest trees and other active cavity trees. If moisture stress was not the primary cause of the differences we detected in resin production between cavity tree types, then the pines selected for nest trees may be genetically better resin producers than other pines selected for cavity trees. Further research is needed to explore this possibility in greater depth.

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