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Does Red-Cockaded Woodpecker Excavation of Resin Wells Increase Risk of Bark Beetle Infestation of Cavity Trees?

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The Red-cockaded Woodpecker (*Picoides borealis*) is unique among North American woodpeckers in that it nests and roosts nearly exclusively in living pines (*Pinus* spp.). Red-cockaded Woodpeckers make daily excavations at small wounds, termed "resin wells," around their cavity entrance and on the bole of their cavity tree, from which resin flows down the tree (Ligon 1970). The woodpeckers also flake off loose bark which results in a smoother surface on the pine tree's bole. Those behaviors result in a resin barrier that serves as an effective defense against rat snakes (*Elaphe* spp.; Jackson 1974, Rudolph et al. 1990). Rat snakes regularly attempt to climb active Red-cockaded Woodpecker cavity trees (cavity trees currently in use for nesting and roosting) and are known to prey on Red-cockaded Woodpeckers when the resin barrier is inadequate (Jackson 1978b, Neal et al. 1993). The resin barrier is believed to increase the probability of a breeding pair's nest success and survival of roosting woodpeckers (Conner et al. 1998).

Red-cockaded Woodpecker cavity trees in eastern Texas, especially active cavity trees, are regularly attacked and killed by southern pine beetles (*Dendroctonus frontalis*) and occasionally by various species of engraver beetles (*Ips* spp.; Conner et al. 1991, Conner and Rudolph 1995, Rudolph and Conner 1995). The pine tree's resin, which woodpeckers use to create a barrier against rat snakes, serves also as the pine tree's primary defense against bark beetle infestation (Wahlenberg 1946, Hodges et al. 1977, Conner et al. 1998). The resin's flow rate and total production (yield) influence the pine tree's ability to physically repel a bark beetle attack. However, daily maintenance of resin wells by woodpeckers may decrease the pine tree's resin yield, and thus, reduce its ability to repel attacks by bark beetles.

We examined resin yield and bark beetle infestation rates in Red-cockaded Woodpecker cavity trees in longleaf (*Pinus palustris*), loblolly (*P. taeda*), and shortleaf (*P. echinata*) pines. Longleaf pine is widely known to produce greater yields of resin than loblolly and shortleaf pines and, as a result, is much more resistant to bark-beetle infestation (Hodges et al. 1977). Thus, if Red-cockaded Woodpeckers affect the ability of cavity trees to produce resin, the effect would most likely occur in loblolly and shortleaf pines. Also, if woodpecker activity at resin wells does increase susceptibility to bark beetles, the increase in bark-beetle-induced mortality should be

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greater in loblolly and shortleaf pines than in longleaf pines.

Methods.—We determined causes of mortality of Red-cockaded Woodpecker cavity trees on the Angelina National Forest (62,423 ha; 31°N15′N, 94°N15′W) in eastern Texas. The northern portion of the forest is predominantly covered by a mixture of loblolly and shortleaf pines on shrink–swell soils, whereas, longleaf pine is the dominant tree species in the deep sandy soils in the southern portion of the forest. Only a few remnant longleaf pines still occur on the northern portion of the Angelina National Forest. Small subpopulations of Red-cockaded Woodpeckers occur on both portions of the national forest (Conner and Rudolph 1989).

We visited all active and inactive (cavity trees previously used but currently not being used by woodpeckers) Red-cockaded Woodpecker cavity-tree clusters (a cluster is the aggregation of cavity trees used by a group of woodpeckers) during March through June from 1983 through 1998 to evaluate cavity tree status and condition. We used woodpecker activity at resin wells, amount of bark scaling, and condition of the cavity entrance as indicators of tree status (see Jackson 1977, 1978a). Active cavity tree clusters were visited several times per year. The age of many cavities within particular trees was determined by the year (and month if possible) they were completed, not the year that excavation began (see Conner et al. 1998). During each visit, we determined occurrence and causes of cavity tree mortality, such as wind throw, wind snap, fire, bark beetles, and lightning (see Conner et al. 1991). Cavity trees infested by bark beetles typically had numerous white "popcorn-like" pitch tubes of crystallized pine resin around wounds where individual attacking beetles had chewed through the bark and into the cambium of the pine tree's bole, or many small "shotgun-pellet-like" holes from which brood beetles had emerged. Dead cavity trees with signs of bark beetle infestation were examined closely to determine whether a lightning strike had contributed to the tree's death. Here we report observations for cavity trees that were infested and killed singly by bark beetles and not those killed during the growth of a beetle spot where multiple trees die in an expanding infestation. During such large infestations and epidemics, any pine tree in close proximity can be overwhelmed by the sheer numbers of bark beetles, regardless of the pine tree's ability to produce pine resin (Billings and Varner 1986). As a measure of beetle population levels, we obtained records of annual number of southern pine beetle infestations (beetle spots) and number of pines infested on both northern and southern portions of the Angelina National Forest in forest compartments where Red-cockaded Woodpeckers occur from the United States Forest Service Pest Management Office in Pineville, Louisiana (SPBIS, Southern Pine Beetle Information System data base).

During the growing seasons, we collected resin-yield data monthly from Red-cockaded Woodpecker cavity trees in loblolly–shortleaf pine habitat (1987 through 1988) and in longleaf pine habitat (1988 through 1989) (see Ross et al. 1995, 1997). We collected resin data from active and inactive cavity trees with naturally excavated cavities. We measured resin yield on sunny days by driving a 2.54 cm diameter circular arch punch (after Lorio et al. 1990) into the interface of xylem and phloem tissue on the pine tree'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 24 h after wounding to obtain a complete sample of the pine tree's preformed resin (see Ross et al. 1995, 1997). Only one sample per tree was taken per sampling period to avoid placing undue stress on active cavity trees. Because of the co-occurrence of loblolly and shortleaf pine cavity trees in woodpecker clusters on the clayey shrink–swell soils, as well as the similarity of those pine species in susceptibility to bark beetle infestation and magnitudes of resin production (Hodges et al. 1977), loblolly and shortleaf pine trees were considered as a single group for measurements of resin production and bark beetle mortality.

We used a paired *t*-test to evaluate the relative abilities of (1) longleaf pine cavity trees and (2) loblolly and shortleaf pine cavity trees to sustain resin production by comparing differences in spring resin yields of the same active cavity trees during subsequent years. Active cavity trees selected for that comparison contained completed, single cavities during the first year of comparison and remained active through the second year. Inactive cavity trees, used as controls, were measured during the same month and year. We also used Pearson correlation analyses to examine the relationship between spring resin yield from active cavity trees and the number of years the active cavity trees had been continuously used by Red-cockaded Woodpeckers. Only forest interior pines were used in those analyses because pines on the edges of forest stands are known to produce significantly more resin than pines in the forest interior (Ross et al. 1997). We also compared resin yield of active and inactive cavity trees within tree species throughout the growing season using a general linear model procedure (two-way factorial ANOVA, cavity tree status × month).

We totaled data over the 15 year study and used a chi-square test (adjusted for continuity) to examine differences in bark beetle infestation rates of cavity trees in longleaf versus loblolly and shortleaf pines, and to compare rates between active and inactive cavity trees within species groups. We also used a general linear model procedure (two-way factorial

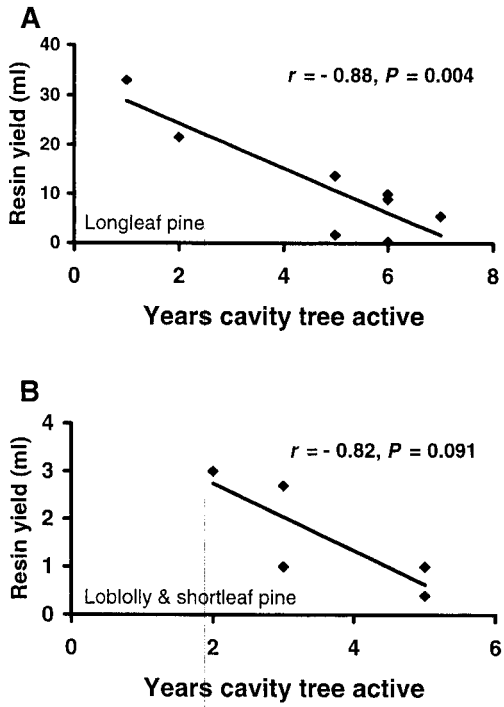

FIG. 1. Resin yield versus the number of years cavity trees have been actively used by Red-cockaded Woodpecker in longleaf (A) and loblolly and shortleaf pines (B) on the Angelina National Forest. Only data from forest interior cavity trees are used in these graphs, because pine trees on the edges of forest stands are known to produce greater resin yields than interior trees (Ross et al. 1997).

ANOVA) to examine differences in annual bark-beetle-induced cavity tree mortality rates among and within tree species throughout the 15 year study. All analyses were performed on SAS (release 6.12) for the PC (SAS Institute 1988).

Results.—Number of years that longleaf-pine cavity trees had been actively used by Red-cockaded Woodpeckers was negatively correlated with the pine tree's ability to produce spring resin ($r = -0.88$, $P = 0.004$; Fig. 1a). Although marginally significant, a similar relationship was observed in loblolly and shortleaf pines ($r = -0.82$, $P = 0.091$; Fig. 1b). Our comparisons of 24 h resin yield from cavity trees over a 1 year interval revealed that active loblolly and shortleaf pine cavity trees with single, completed cavities produced less spring resin in 1987 than they produced in 1988 (Table 1). During the same period, we detected no significant difference in spring resin yield from one year to the next among inactive loblolly and shortleaf pine cavity trees. We did not detect a significant difference in the yield of spring resin from active longleaf pine cavity trees in 1988 compared to spring resin yields from the same active cavity trees one year later (Table 1). Similar to inactive loblolly and shortleaf cavity trees, we detected no significant difference in spring resin yield from one year to the next among inactive longleaf pine cavity trees.

TABLE 1. Twenty-four-hour spring resin yield (mean ± SD) of active and inactive Red-cockaded Woodpecker cavity trees in longleaf and loblolly and shortleaf pines in eastern Texas between 1987 and 1989.

	Longleaf pine		Loblolly and shortleaf pines	
	Active (n = 16)	Inactive (n = 28)	Active (n = 14)	Inactive (n = 28)
	Spring resin yield (ml)			
1987	—	—	3.6 ± 1.6	5.3 ± 3.1
1988	10.1 ± 7.0	5.0 ± 3.7	2.2 ± 1.4	6.1 ± 5.3
1989	11.8 ± 10.9	4.4 ± 3.6	—	—
	Paired t-test[a]			
t	0.57	0.62	3.26	1.09
P	0.58	0.54	0.02	0.30

[a] Paired t-test results reflect differences between means within columns.

Two-way factorial ANOVA (cavity-tree status and month as factors) examining resin yield indicated that active longleaf pine cavity trees ($\bar{x}$ = 7.7 mL resin, error df = 368) produced more resin than inactive longleaf-pine cavity trees ($\bar{x}$ = 5.4 mL resin, $F = 15.29$, df = 1 and 7, $P = 0.0001$). We did not detect a difference in resin yield between active ($\bar{x}$ = 5.7 mL resin, error df = 635) and inactive loblolly and shortleaf pine cavity trees ($\bar{x}$ = 6.6 mL resin, $F = 3.32$, df = 1 and 8, $P = 0.07$). The interaction term in both ANOVAs was not significant ($F = 0.57$, $P = 0.7832$ and $F = 0.51$, $P = 0.85$, respectively).

A two-way factorial ANOVA (pine species and cavity-tree status as factors, df = 3 and 56) examining annual bark-beetle-induced mortality rates indicated that active cavity trees were killed at a higher rate than inactive cavity trees ($F = 15.99$, $P = 0.0002$) and loblolly and shortleaf pines were killed at a higher rate than longleaf pines ($F = 14.70$, $P = 0.0003$, Table 2). A significant interaction term ($F = 10.13$, $P = 0.0024$) indicated that the difference in mortality rates between active loblolly and shortleaf pines and active longleaf pines was greater than the difference between species for inactive cavity trees.

When standardized to deaths per 1,000 cavity-tree years, active loblolly and shortleaf pine cavity trees were killed by bark beetles at a rate of 81.8 per 1,000 cavity-tree years ($\chi^2 = 61.7$, $P < 0.001$), a 10.4-fold increase compared to the bark-beetle-induced mortality rate for inactive loblolly and shortleaf pine cavity trees (7.9 per 1,000 cavity-tree years, Table 2). Active longleaf pine cavity trees were killed at a rate of 10.4 per 1,000 cavity-tree years ($\chi^2 = 9.8$, $P = 0.002$),

TABLE 2. Bark-beetle-induced mortality of active and inactive loblolly, shortleaf, and longleaf pine Red-cockaded Woodpecker cavity trees in eastern Texas between 1983 and 1998.

Tree status and species	Cavity-tree years	Trees killed	Death rate per 1,000	Mean annual mortality rate %±SD
		Active		
Loblolly and shortleaf pine	489	40	81.8	8.17 ± 7.0
Longleaf pine	772	8	10.4	1.06 ± 1.2
		Inactive		
Loblolly and shortleaf pine	1,142	9	7.9	0.90 ± 1.4
Longleaf pine	2,757	5	1.8	0.24 ± 0.4

only a 5.7-fold increase relative to inactive longleaf pine cavity trees (1.8 per 1,000 cavity-tree years).

Bark-beetle induced-mortality rates differed between pine species. Active loblolly and shortleaf pine cavity trees were killed by bark beetles at 7.9 times the rate of active longleaf pine cavity trees, whereas inactive loblolly and shortleaf pine cavity trees were killed by bark beetles at 4.4 times the rate of inactive longleaf pine cavity trees. Although the difference is not statistically significant, it is important to note that active longleaf pine cavity trees were killed by bark beetles at 1.3 times the rate of inactive loblolly and shortleaf pine cavity trees ($\chi^2 = 0.322$, $P = 0.57$). Usually, longleaf pines are much more resistant to bark beetle infestation than loblolly and shortleaf pines (Hodges et al. 1977). Because of their greater vulnerability to bark beetle infestation, population levels of southern pine beetles were higher in loblolly shortleaf pine habitat ($\bar{x} = 97.0 \pm 82.6$ bark beetle spots) than in longleaf pine habitat ($\bar{x} = 16.2 \pm 20.2$) throughout the study ($t = 3.54$, df $= 24$, $P = 0.003$, see also Schaefer 1996).

Discussion.—We suggest that the observed higher rate of bark-beetle-induced mortality in active cavity trees is related to woodpecker excavation at resin wells. Regular, daily excavation at resin wells by Red-cockaded Woodpeckers may reduce the ability of active cavity trees to produce resin in response to beetle attack. Active Red-cockaded Woodpecker cavity trees were also more susceptible to bark-beetle-induced mortality than inactive cavity trees in all three species of pines (Conner and Rudolph 1995, Rudolph and Conner 1995, this study), which suggests that activity of woodpeckers at resin wells may increase the vulnerability of cavity trees to bark-beetle-induced mortality.

The rate of bark-beetle-induced mortality in active loblolly and shortleaf pine cavity trees was nearly 8 times greater than the rate of mortality in active longleaf pine cavity trees. When mortality rates were compared between active and inactive cavity trees within species groups, the increase in bark-beetle-induced mortality in loblolly and shortleaf pines was nearly double that in longleaf pines. That suggests that woodpecker activity on cavity trees is having a greater impact on susceptibility to bark beetles in loblolly and shortleaf pines than it is in longleaf pines.

Longleaf pines are known to produce larger amounts of resin than loblolly and shortleaf pines (Hodges et al. 1977), and are able to maintain a higher yield of resin when stressed by woodpecker excavation at resin wells than loblolly and shortleaf pines (Conner et al. 1998; Fig. 1). In spite of longleaf pine tree's known ability to produce higher yields of resin than loblolly and shortleaf pine trees, it appears that some active longleaf pine cavity trees still suffer bark-beetle-induced mortality. That may occur when longleaf pines are used continuously as cavity trees for 5 to 7+ years and their ability to produce resin drops to a point where they become vulnerable to bark beetles. Unfortunately, we do not have premortality resin data for the longleaf pines that were killed by bark beetles. The high resin production we observed in active longleaf pine cavity trees that we sampled relative to inactive cavity trees may represent the pine tree's response to repeated wounding by the woodpecker. In contrast, loblolly and shortleaf pines are known to generally produce less resin than longleaf pines. Because of their lower resin yields, when loblolly and shortleaf pines become active cavity trees, their ability to produce resin dwindles within the first year and they quickly incur an increased rate of bark-beetle-induced mortality.

The reduction in the ability of active cavity trees to produce sufficient resin—resin which serves as the pine trees' primary defense against bark beetles—appears to be a major factor affecting cavity tree mortality rates. When attacked by bark beetles, pine trees with a reduced capability to produce resin would be more vulnerable than pine trees with unimpaired resin production. The activity of Red-cockaded Woodpeckers at resin wells appears to reduce the cavity tree's resin production below what is necessary to "pitch-out" bark beetles, primarily in loblolly and shortleaf pines.

Daily excavation at resin wells coats Red-cockaded Woodpecker cavity trees with fresh pine resin, producing a constant "wick" of resin volatiles that evap-

orate and diffuse from trees. The presence of those resin volatiles around active cavity trees (volatiles that are known to be attractive to some bark beetles), may be a second factor explaining why bark-beetle-induced mortality is elevated in active cavity trees (see Payne and Coulson 1985, Coulson et al. 1995).

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