FINAL REPORT

As Required By

THE ENDANGERED SPECIES PROGRAM

TEXAS

Grant No. E-1-11

Endangered and Threatened Species Conservation

Project Number WER13(62): Southern Pine Beetle Infestation of Red-cockaded Woodpecker Cavity Trees

Project Coordinator: Ricky W. Maxey

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FINAL REPORT

STATE: Texas **GRANT NUMBER:** E-1-11

PROGRAM TITLE: Endangered and Threatened Species Conservation

PERIOD COVERED: September 1, 1995 through August 31, 1998

PROJECT NUMBER: WER13(62)

PROJECT TITLE: Southern Pine Beetle Infestation of Red-cockaded Woodpecker Cavity Trees

OBJECTIVES:

To examine Southern Pine Beetle (SPB) infestation of single Red-cockaded Woodpecker cavity trees. Specifically we propose to:

(a) Examine cavity tree infestation rates in loblolly-shortleaf pine and longleaf pine habitats,

(b) Determine concurrent levels of management activities that potentially serve as site disturbances,

(c) Determine the effect of cavity status (active vs. inactive) and tree type (natural vs. cavity insert) on infestation rates,

(d) Determine the season and process of cavity tree infestation, and

(e) Compare infestation rates of single cavity trees with ambient SPB population levels on adjacent forest habitat.

ACTUAL SEGMENT COSTS: $132.04

PREPARED BY: Ricky W. Maxey **DATE:** January 1, 2000

APPROVED BY: [signature] **DATE:** 1/13/2000

Neil E. Carter
Federal Aid Coordinator

FINAL SECTION 6 REPORT

SOUTHERN PINE BEETLE INFESTATION OF RED-COCKADED WOODPECKER CAVITY TREES:

FINAL REPORT OF THREE-YEAR STUDY

TPWD Contract No. 335-0239
Year 3 Collection Agreement # 33-CC-98-403

Investigators: Richard N. Conner, Southern Research Station
D. Craig Rudolph, Southern Research Station
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Robert N. Coulson, Texas A&M University

Substantial new information was discovered during this three-year investigation of relationships between southern Pine beetles *(Dendroctonus frontalis)* and Red-cockaded Woodpeckers *(Picoides borealis)*. But the basic cause for elevated infestation rates of active woodpecker cavity trees and their apparent attractiveness to southern pine beetles was not discovered.

Previously declining woodpecker populations in Texas National Forests (Conner and Rudolph 1989) stabilized during the mid 1990s. During 1997, all Red-cockaded Woodpecker populations in Texas national forests declined slightly after several years of small increases (Conner et al. 1995), but only the Angelina and Sabine National Forests have continued to decline in 1998. These declines appear to be in part a result of the return of encroaching hardwood midstory and understory vegetation between 1995 and early 1998. This encroaching hardwood vegetation was eliminated during late summer - early fall, 1998. However, losses of active cavity trees to infestation by southern pine beetles continue to impact woodpecker cavity trees and populations, but not as severely during 1997 and 1998 because southern pine beetle populations are very low. Management's ability to use artificial cavity inserts continues to aid Red-cockaded Woodpecker populations impacted by southern pine beetle activity (Conner and Rudolph 1995, Rudolph and Conner 1995, Conner et al. 1997, Conner et al. 1998), particularly those populations located in loblolly and shortleaf pine habitat.

Angelina National Forest

Between September 1995 and August 1996 we checked all active and inactive cavity trees in the Angelina National Forest during late fall 1995 and spring 1996. During the field work, approximately 121 loblolly pines, 52 shortleaf pines, 17 slash pines, 360 longleaf pines, and 18 pines of undetermined species (a total of 568 pines each season) were examined for status and possible southern pine beetle activity. Six cavity trees were infested and killed by southern pine beetles (two loblolly pines, three shortleaf pines, and one longleaf pine) in the Angelina National Forest during FY 1996. One additional cavity tree was killed by wind-snap.

Between September 1996 and August 1997 we checked all active and inactive cavity trees in Angelina National Forest and Huntsville State Fish Hatchery for southern pine beetle activity during late summer 1996, winter 1996-1997, and spring 1997. Six cavity trees were infested and killed by southern pine beetles (two loblolly pine, three shortleaf pines, and one longleaf pine) in the entire Angelina National Forest during FY 1996. One additional cavity tree was killed by wind-snap. During FY 1997 nine cavity trees died in the Angelina National Forest: five killed by bark beetles, two killed by lightning, one killed by wind snap, and one death by unknown causes.

Between September 1997 and August 1998 we checked all active and inactive cavity trees at Angelina National Forest and Huntsville State Fish Hatchery for southern pine beetle activity during late summer 1997, winter 1997-1998, and spring 1998. Four cavity trees were infested and killed by pine bark beetles (all loblolly pines) in the entire Angelina National Forest during FY 1998. Only two of these four trees were killed by southern pine beetles; *Ips* beetles infested and killed the other two cavity trees. Eight additional cavity trees were killed by wind-snap, 10 killed by wind throw, and one killed by lightning. During FY 1998, fifty-seven southern pine beetle spots were detected, and 915 pines were infested by southern pine beetles according to the Southern Pine Beetle Information System (SPBIS) data set.

Data on southern pine beetle activity for 1984-1997 in the forest compartments on the north end of the Angelina National Forest (compartments 1-20 plus the Turkey Hill Wilderness Area) were obtained from the Forest Pest Management section of the U.S. Forest Service in Pineville, Louisiana. There are currently 14 years of complete data available to explore relationships between southern pine beetle infestation of single cavity trees and "ambient" population levels of southern pine beetles (Table 1).

Table 1

Annual Red-cockaded Woodpecker cavity tree mortality resulting from southern pine beetle (SPB) infestation and measures of beetle activity in surrounding forest compartments (1-20) on the northern portion of the Angelina National Forest.

YEAR	CAVITY TREE DEATHS	NUMBER SPB SPOTS	NUMBER PINES INFESTED
1984	1	20	247
1985	2	133	10,111
1986	1	90	3,262
1987	2	12	208
1988	3	24	470
1989	4	149	2,215
1990	2	58	470
1991	1	145	2,004
1992	7	110	1,672
1993	14	327	21,353
1994	5	140	2,871
1995	8	66	1,620
1996	5	27	263
1997	2	57	915
1998	2	*	*

* Data for 1998 not yet available.

The additional year of data provided by the continuation of our study (FY 1998) has strengthened our understanding of the relationship between southern pine beetle activity in the forest habitat that surrounds active Red-cockaded Woodpecker cavity-tree clusters and the impact these beetles have on active cavity trees. We have determined that southern pine beetle population levels are significantly correlated with the infestation and mortality of Red-cockaded Woodpecker cavity trees (see Conner et al. 1998). We do not know why southern pine beetles appear to single out active cavity trees for infestation at a higher rate than infest inactive cavity trees. We also do not know why southern pine beetles appear to prefer the active cavity tree that was used as the nest tree during the preceding breeding season (Conner et al. 1998).

Several publications have resulted from this Section 6 study (see Attachments).

Huntsville State Fish Hatchery

During spring 1996 cavity trees at the Huntsville State Fish Hatchery were inventoried as a base line check for status (active vs. inactive) and past mortality. Eight live cavity trees and three dead cavity trees were found. Seven of the eight live trees were active and had fresh resin flowing from active resin wells. Three artificial cavity starts had been drilled, two into existing cavity trees. Three restrictor plates have been added to cavity trees to prevent/reconstruct damage done by Pileated Woodpeckers *(Dryocopus pileatus)*. Based on the distribution of active cavity trees, there appeared to be two groups of Red-cockaded Woodpeckers present at the hatchery. Subsequent roosting efforts suggested that five woodpeckers may be present in one group, and possibly two woodpeckers in the second group. The actual number of groups and woodpeckers still needs to be precisely determined. Cavity trees will again be monitored in the fall to determine if infestation by southern pine beetles or other forms of mortality have occurred.

During FY 1997, fourteen cavity trees at the Huntsville State Fish Hatchery were inventoried as a base line check for status (active vs. inactive) and past mortality. Twelve live cavity trees and two dead cavity trees were found. Six of the 12 live trees were active and had fresh resin flowing from active resin wells. During summer 1997 a deep active cavity start was discovered near the nest tree of the 1997 breeding season. Three artificial cavity starts had been drilled, two into existing cavity trees. Based on the behavior of the woodpeckers, there appears to be one group of Red-cockaded Woodpeckers present at the hatchery. During the spring nesting season check, four woodpeckers were present, with seven woodpeckers present post-nesting. Cavity trees will again be monitored in the fall to determine if infestation by southern pine beetles or other forms of mortality have occurred. No cavity trees died during this past FY. Texas Department of Correction has accomplished significant midstory reduction with the Red-cockaded Woodpecker habitat at the hatchery.

During FY 1998, eighteen cavity trees at the Huntsville State Fish Hatchery were inventoried as a base line check for status (active vs. inactive) and past mortality. Four new artificial insert cavities were added during FY 1998. Sixteen live cavity trees and two dead cavity trees were found. Six of the 16 live trees were active and had fresh resin flowing from active resin wells. During summer 1998 a second deep active cavity start was discovered near the nest tree of the 1998 breeding season, but the active start found last year was now inactive. Based on the behavior of the woodpeckers, there appears to be one group of Red-cockaded Woodpeckers present at the hatchery. During the spring nesting season check, four woodpeckers were present, with six woodpeckers present post-nesting. No cavity trees died during FY 1998. Texas Department of Correction has accomplished significant midstory reduction within the Red-cockaded Woodpecker habitat at the hatchery.

General Conclusion from This Study and Our Previous Research

Southern pine beetle infestation was the major cause of mortality for Red-cockaded Woodpecker cavity trees in loblolly *(Pinus taeda)* and shortleaf *(P. echinata)* pines. We examined southern pine beetle infestation rates of pines with natural vs. artificial cavities in loblolly and shortleaf pine habitat on the northern portion of the Angelina National Forest. No significant difference existed in the rate at which southern pine beetles infested and killed pines with natural cavities vs. those with artificial cavity inserts ($x^2 = 0.84$, $P = 0.36$). Southern pine beetles infested and killed 20 natural cavity trees (25.6%) during the five-year study (78 cavity-tree years) and 19 artificial cavity trees (18.8%; 101 cavity-tree years). Data for the entire Angelina National Forest indicate that 40% (25 of 62) of the cavity trees killed by southern pine beetles between 1984 and 1996 had been the nest tree during the preceding breeding season. The annual infestation rate of cavity trees appears to be related to southern pine beetle population levels of the surrounding forest. Use of artificial cavities is essential to maintain sufficient numbers of usable cavities for Red-cockaded Woodpeckers in Texas. Why southern pine beetles appear to preferentially infest active Red-cockaded Woodpecker cavity trees is still unknown, but may be related to southern pine beetle attraction to resin volatiles produced when woodpeckers excavate resin wells and/or changes in the levels of infestation-inhibiting tree volatiles as a result of cavity and resin well excavation.

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Wilson Bulletin, 110(1), 1998, pp. 100–109

SOUTHERN PINE BEETLE-INDUCED MORTALITY OF PINES WITH NATURAL AND ARTIFICIAL RED-COCKADED WOODPECKER CAVITIES IN TEXAS

RICHARD N. CONNER,[1,3] DANIEL SAENZ,[1] D. CRAIG RUDOLPH,[1] AND ROBERT N. COULSON[2]

ABSTRACT.—Southern pine beetle (*Dendroctonus frontalis*) infestation is the major cause of mortality for Red-cockaded Woodpecker (*Picoides borealis*) cavity trees in loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines. Recent intensive management for Red-cockaded Woodpeckers includes the use of artificial cavity inserts. Between 1991 and 1996 we examined southern pine beetle infestation rates of pines with natural vs artificial cavities in loblolly and shortleaf pine habitat on the northern portion of the Angelina National Forest. No significant difference existed in the rate at which southern pine beetles infested and killed pines with natural cavities vs those with artificial cavity inserts ($\chi^2 = 0.84$, $P > 0.05$). Southern pine beetles infested and killed 20 natural cavity trees (25.6%) during the 5-year study (78 cavity-tree years) and 19 artificial cavity trees (18.8%; 101 cavity-tree years). Data for the entire Angelina National Forest indicate that 40% (25 of 62) of the cavity trees killed by southern pine beetles between 1984 and 1996 had been the nest tree during the preceding breeding season. The annual infestation rate of cavity trees appears to be related to southern pine beetle population levels of the surrounding forest. Use of artificial cavities is essential to maintain sufficient numbers of usable cavities for Red-cockaded Woodpeckers in Texas. Why southern pine beetles appear to preferentially infest active Red-cockaded Woodpecker cavity trees is still unknown, but may be related to southern pine beetle attraction to resin volatiles produced when woodpeckers excavate resin wells and/or changes in the levels of infestation-inhibiting tree volatiles as a result of cavity and resin well excavation. *Received 8 April 1997, accepted 23 Sept. 1997.*

Cavity trees are a critical resource for Red-cockaded Woodpeckers (*Picoides borealis*) (Ligon 1970; Lennartz et al. 1987; Walters et al. 1988, 1992). They are essential for reproduction and roosting, require a long period of time to excavate (Conner and Rudolph 1995a), and are often limited in availability (Conner and Rudolph 1989, Costa and Escano 1989, Walters et al. 1992). During the past decade, several studies attributed severe Red-cockaded Woodpecker population declines to several factors, among which was limited availability of cavity trees (Conner and Rudolph 1989; Costa and Escano 1989). Cavity tree mortality, which may further reduce cavity tree availability, may be of great importance for management and recovery of Red-cockaded Woodpecker populations.

The development and use of artificial Red-cockaded Woodpecker cavities to reduce shortages of cavities and facilitate population expansion through the formation of new woodpecker groups has greatly enhanced the forest manager's ability to recover dwindling populations (Copeyon 1990, Copeyon et al. 1991, Allen 1991). Use of artificial cavities has contributed to Red-cockaded Woodpecker population increases in Texas (Conner et al. 1995), Mississippi (Richardson and Stockie 1995), North Carolina and Georgia (Carter et al. 1995), and South Carolina (Gaines et al. 1995, Watson et al. 1995).

The major cause of Red-cockaded Woodpecker cavity tree mortality in loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines is pine bark beetle infestation (Conner et al. 1991, Ross et al. 1995). Of 26 Red-cockaded Woodpecker populations on U.S. Forest Service lands, 19 are primarily associated with loblolly or shortleaf pine habitat (Costa and Escano 1989). Thus, pine bark beetle-induced mortality of cavity trees is a significant potential problem throughout the range of the woodpecker. The majority of bark beetle infestations are primarily composed of southern pine beetles (*Dendroctonus frontalis*). Four other pine bark beetles often occur in association with southern pine beetle infestation in

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varying proportions. These include three species of engraver beetles (*Ips avulsus, I. grandicollis,* and *I. calligraphus*) and, occasionally, black turpentine beetles (*Dendroctonus terebrans*). In this paper, we focus on cavity-tree mortality induced primarily by southern pine beetles.

In Texas, artificial cavities, primarily cavity inserts, have been used regularly to provide sufficient cavities for woodpecker groups that have lost active cavity trees to southern pine beetle infestation (Conner et al. 1995, Rudolph and Conner 1995). However, when Red-cockaded Woodpeckers begin to use artificial cavity inserts and peck resin wells, southern pine beetles infest and kill pines containing cavity inserts, apparently finding them as attractive for infestation as natural cavity trees (Conner and Rudolph 1995b).

We compared the beetle infestation rates of pines containing natural Red-cockaded Woodpecker cavities with pines containing artificial cavities over a 5-year period on the Angelina National Forest. We evaluated instances where only a single Red-cockaded Woodpecker cavity tree was infested and killed. Cavity trees can also be infested and killed as the result of the "growth" of an expanding beetle spot (multiple tree infestation; Billings and Varner 1985, Conner et al. 1995b); no cavity tree deaths resulting from beetle spot growth were observed on the Angelina National Forest during our study.

Red-cockaded Woodpeckers create a resin barrier on the pine's bole that serves as a barrier against rat snakes (*Elaphe* spp.; Jackson 1974, Rudolph et al. 1990). The resin system of pine trees serves as their primary defense against southern pine beetles and some pines with superior resin output can survive beetle attack (Lorio 1986). Pines that are able to produce more resin might be preferentially selected by woodpeckers because they would provide better resin barriers against rat snakes and potentially be more resistant to southern pine beetle infestation. Nebeker and coworkers (1992) observed that wound-induced resin flow rate, total resin flow, and viscosity in loblolly pines were genetically controlled. Red-cockaded Woodpeckers may be able to detect the ability of a pine to produce resin when they begin to excavate a cavity start. In contrast, a cavity tree is selected for a cavity insert based on the openness of its bole and a sufficient diameter (38 cm) at the height of installation to physically contain the cavity insert. No consideration is made for the potential resin production of the trees. This suggests that pines with cavity inserts may be more susceptible to mortality following southern pine beetle infestation, since on the average, they might produce less resin than trees selected by woodpeckers. We hypothesized that pines selected by biologists for installation of cavity inserts were more likely to be infested by southern pine beetles than pines selected by woodpeckers for natural cavity excavation.

We also compared the number of Red-cockaded Woodpecker cavity trees killed by southern pine beetle infestation per year (only single tree infestations, not cavity-tree mortality resulting from beetle spot growth) with beetle population levels in forest stands surrounding woodpecker cavity-tree clusters, and determined the number of active cavity trees killed each year by bark-beetle infestation relative to the total number available.

STUDY AREA AND METHODS

We studied southern pine beetle infestation of Red-cockaded Woodpecker cavity trees on the Angelina National Forest (62,423 ha; 31° 15′ N, 94° 15′ W) in eastern Texas. The northern portion of the Angelina National Forest is predominantly covered by loblolly and shortleaf pines, whereas longleaf pine (*Pinus palustris*) is the dominant tree species on the southern portion of the forest in the areas where Red-cockaded Woodpeckers are found (Conner and Rudolph 1989). The loblolly-shortleaf pine habitat where Red-cockaded Woodpecker clusters occur on the northern portion of the Angelina National Forest is located primarily on mesic, shrink-swell clays (Woodtel and LaCerda soil types), which readily support growth of hardwood vegetation (Fuchs 1980, Conner and Rudolph 1995). Varying moisture conditions throughout the year produce the shrink-swell characteristics of the soils, which can strip root hairs off lateral pine roots, increasing stress and pine susceptibility to southern pine beetle infestation (Lorio et al. 1982, Mitchell et al. 1991, Conner and Rudolph 1995). The longleaf pine habitat where Red-cockaded Woodpeckers occur on the southern portion of the Angelina National Forest is located primarily on deep loamy sands (Tehran and Letney soil types) containing materials of volcanic origin (Neitsch 1982). These soils contain very little organic material resulting in a low water holding capacity. High soil temperatures during summer reduce the water holding capacity in these soils, retarding the growth of hardwoods on these sites and stressing pines, but do not usually affect longleaf pine resin production or increase the susceptibility of these longleaf pines to southern pine beetle infestation. Historically, southern pine beetle infestation of cavity trees in the longleaf pine habitats of the Angelina National Forest has been minimal (Conner et al. 1991).

We made annual spring visits to all Red-cockaded Woodpecker cavity trees on the Angelina National Forest (1983 through 1996) to evaluate cavity tree status and condition using the indicators described by Jackson (1977, 1978). Cavity tree clusters occupied by woodpeckers were visited several times per year. We determined the occurrence and causes of all cavity tree mortality (Conner et al. 1991, Conner and Rudolph 1995). Cavity trees infested by southern pine beetles typically had numerous white "popcorn-like" pitch tubes of crystallized pine resin around wounds on the bole where individual beetles had chewed through the bark and into the cambium. Dead cavity trees with signs of bark beetle infestation were examined to determine whether lightning strike was also associated with tree death or if the infestation was caused by other species of bark beetles. Cavity-tree mortality caused by lightning, wind action, and fire have been reported previously (Conner et al. 1991, Conner and Rudolph 1995c).

As part of intensive efforts to recover Red-cockaded Woodpecker populations, a program of cavity insert installation (Allen 1991) began on the Angelina National Forest during 1990 (see Conner et al. 1995). A total of 399 cavity inserts was installed on the northern and southern portions of the forest between January 1990 and spring 1996: 57 between early 1990 and spring 1991, 50 between summer 1991 and spring 1992, 59 during 1992–1993, 31 during 1993–1994, 139 during 1994–1995, and 63 during 1995–1996. Cavity inserts were installed primarily within active woodpecker clusters, but also within inactive clusters and recruitment stands near active clusters.

We used χ^2 analysis to compare southern pine beetle infestation rates of artificial and natural cavity trees in 11 active woodpecker clusters on the northern portion of the Angelina National Forest over a 5-year period between October 1991 and May 1996. We also used χ^2 analysis to evaluate the effect of recency of natural cavity completion or artificial insert activation on likelihood of beetle infestation, as well as the likelihood of beetle infestation of active cavity trees used for nesting and roosting.

To compare southern pine beetle population levels with annual losses of cavity trees, we obtained records of the annual number of southern pine beetle infestations (beetle spots) and the number of pines infested on the northern portion of the Angelina National Forest from the USDA Forest Service Pest Management Office in Pineville, Louisiana, and Atlanta, Georgia (SPBIS—Southern Pine Beetle Information System data base). Pearson correlations were calculated to examine relationships between annual, beetle-induced cavity-tree mortality in 11 cavity-tree clusters on the northern portion of the Angelina National Forest and yearly measures of southern pine beetle population levels in the surrounding forest stands.

RESULTS

Southern pine beetle infestation of Red-cockaded Woodpecker cavity trees has occurred regularly in loblolly and shortleaf pines on the Angelina National Forest over the past 14 years, killing 2–40% of the active cavity trees annually (Fig. 1). Bark beetle-induced mortality of active cavity trees increased after the intensity of woodpecker management increased in the early 1990s following the detection of severe population declines and litigation (Conner and Rudolph 1995b, Conner et al. 1995). Since 1983 on the entire Angelina National Forest, 25 of 62 southern pine beetle-killed cavity trees (40%) had been nest trees during the preceding breeding season. Over a 14-year period an average of 23.1% of the active cavity trees were nest trees in a given year [376 active cavity-tree years (number of active cavity trees each year summed over the 14 years) vs 87 nest tree years in loblolly and shortleaf pines on the Angelina National Forest]. The 40% infestation rate of nest trees is significantly greater than what would be expected based on the ratio of active cavity trees to nest trees on the average (40% vs 23%, $\chi^2 = 13.85$, $P = 0.001$).

Between 1990 and 1996, 399 cavity inserts were installed on the Angelina National Forest. Eighty-seven of these artificial cavities were installed in the 11 active woodpecker clusters we examined closely in loblolly and shortleaf pines on the northern portion of the forest. As a result of cavity-tree losses to southern pine beetles and cavity enlargement by Pileated Woodpeckers (*Dryocopus pileatus*; Conner et al. 1991), most active cavity trees used by Red-cockaded Woodpeckers since 1991 have contained artificial cavities (Fig. 2). During 1992 52% of active cavity trees contained artificial cavities, 63% in 1993, 49% in 1994, 56% in 1995, and 61% in 1996, averaging 56.4% over a 5-year period.

Southern pine beetles infested and killed 39 natural and artificial cavity trees in loblolly and shortleaf pines in the 11 active clusters examined between 1991 and 1996. Of the 39 cavity trees killed by beetles between the fall of 1991 and the summer of 1996, 32 were active and 7 were inactive. Eleven of the 32

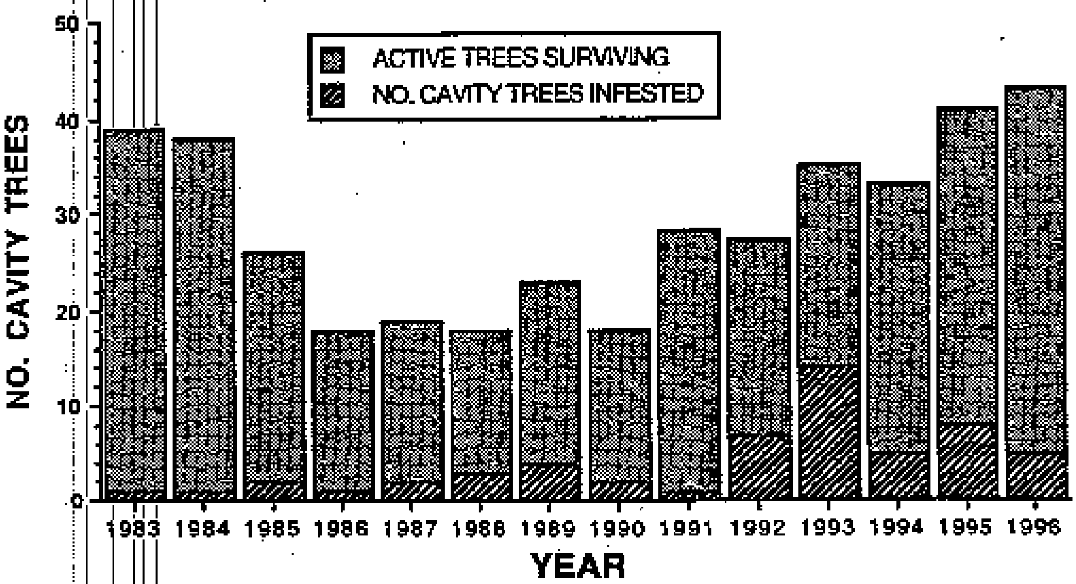


FIG. 1. Number of active Red-cockaded Woodpecker cavity trees and the number of cavity trees infested and killed by southern pine beetles on the northern portion of the Angelina National Forest from 1983 through 1996.

active cavity trees (34%) had been nest trees during the preceding breeding season, 15 (47%) had been roost trees for several years, and in 6 (19%) cavity trees, cavities had been completed just prior to infestation. Relative to their availability, nest trees on the northern portion of the Angelina National Forest were infested at a higher rate than active cavity trees used only for roosting ($\chi^2 = 4.6$, $P = 0.032$).

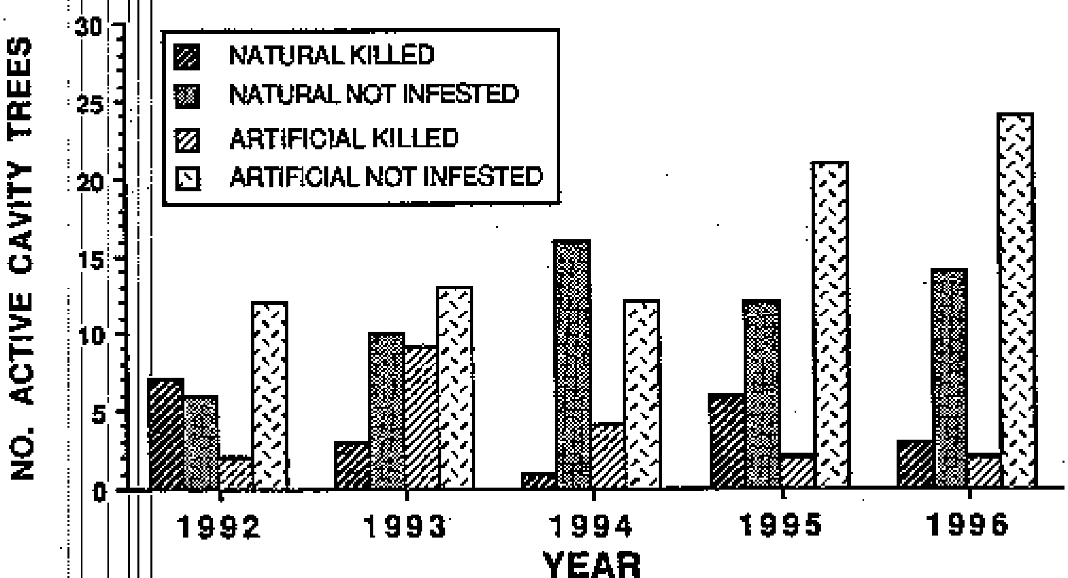


FIG. 2. The number of active Red-cockaded Woodpecker cavity trees with artificial and natural cavities in loblolly and shortleaf pines compared to the number infested and killed by southern pine beetles in eleven cavity-tree clusters on the northern portion of the Angelina National Forest between 1992 and 1996.

During the 5-year study, 20 (25.6%) natural cavity trees (78 cavity-tree years) were killed by southern pine beetles whereas 19 (18.8%) artificial cavity trees (101 cavity-tree years) were killed. Pines with natural cavities and pines with artificial cavities did not differ in the rate at which they were infested by southern pine beetles (Fig. 2; 25.6% vs 18.8%, $\chi^2 = 0.84$, adjusted for continuity, $P > 0.05$).

The recency of natural cavity completion and occupation of artificial inserts by woodpeckers, both of which included the excavation of a series of resin wells around the cavity entrances, affected the likelihood of bark beetle infestation. Over the 5-year period between 1992 and 1996, 24.5% of active cavity trees (24 of 98) were infested and killed within one year of natural cavity completion or use of cavity inserts, whereas only 7.9% of active cavity trees (13 of 164 cavity-tree years) were killed after the first year of their completion or use, respectively ($\chi^2 = 13.9$, $P = 0.001$).

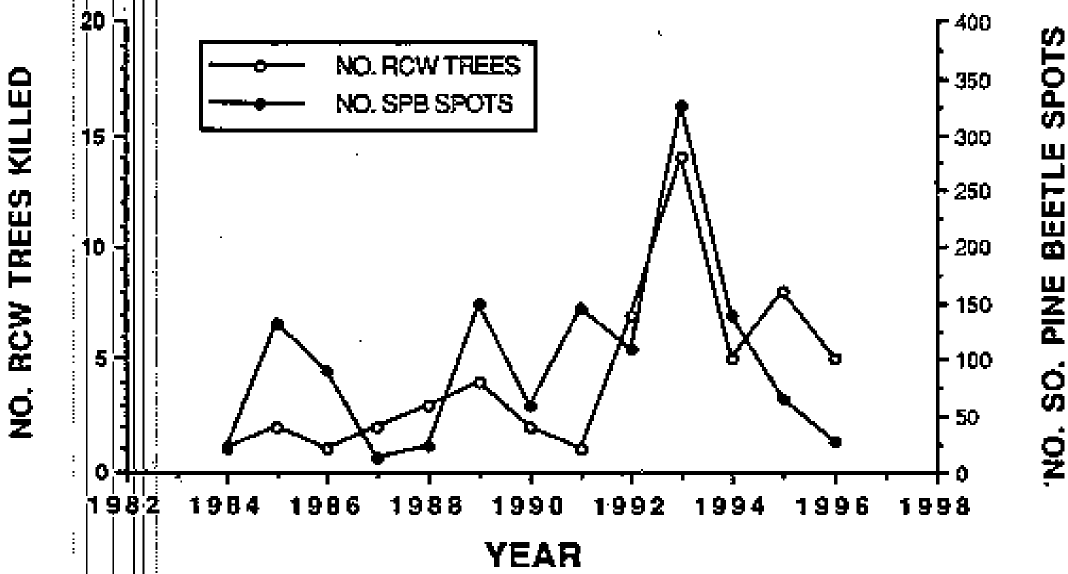
Cavity-tree mortality occurring in pines with artificial cavity inserts (31.1%) during the first year of occupation was not significantly greater than mortality in newly completed natural cavity trees (18.9%; $\chi^2 = 1.97$, $P > 0.05$). However, during the four years following insert occupation or natural cavity completion, only 1.39% of the cavity trees with artificial inserts (1 of 72 cavity-tree years) were killed by bark beetles compared to 13.04% of natural cavity trees (12 of 92 cavity-tree years; $\chi^2 = 7.52$, $P = 0.006$). This suggests that active cavity trees with inserts that survive their first year have a high probability of surviving at least four more years.

Southern pine beetle-induced mortality of Red-cockaded Woodpecker cavity trees on the northern portion of the Angelina National Forest was positively correlated with outbreaks of southern pine beetles in the surrounding forest stands (Fig. 3). Cavity tree mortality was correlated with both the number of southern pine beetle spots ($r = 0.667$, $P = 0.013$) and the number of pines infested ($r = 0.673$, $P = 0.012$) in forest stands surrounding woodpecker cluster areas.

DISCUSSION

Southern pine beetle-induced mortality of Red-cockaded Woodpecker cavity trees in loblolly and shortleaf pine habitat on the Angelina National Forest and many other forests in the South has a substantial impact on the availability of woodpecker cavity trees (Conner and Rudolph 1995, Rudolph and Conner 1995). Between 1983 and 1988 the infestation of single Red-cockaded Woodpecker cavity trees by southern pine beetles averaged about 1.7 cavity trees per year on the Angelina National Forest. Subsequent to intensification of management activities during the late 1980s to halt severe woodpecker population declines, the mean number of single cavity trees infested and killed by southern pine beetles increased significantly, more than tripling that observed previously (5.7/y; see Conner and Rudolph 1995b). As suspected by Conner and Rudolph (1995b), cavity tree infestation rates are significantly correlated with outbreaks of southern pine beetles in surrounding forest stands. However, the apparent preference of southern pine beetles for active as opposed to inactive cavity trees is still not fully understood (Conner and Rudolph 1995b, Rudolph and Conner 1995). Because of these substantial cavity-tree losses to bark beetles and the extensive use of artificial cavities by Red-cockaded Woodpeckers, most cavity trees currently used by the woodpeckers on the northern portion of the Angelina National Forest contain artificial cavities. Fortunately, Red-cockaded Woodpeckers roosted and nested readily in artificial cavities relative to natural cavities during our study and other previous studies (Copeyon 1990, Allen 1991). The importance of this management technique for Red-cockaded Woodpecker recovery in areas where bark beetles are abundant is obvious.

Our hypothesis that pines with artificial cavity inserts would be more susceptible to southern pine beetle infestation than natural cavity trees was incorrect. Artificial cavity trees were not infested and killed by southern pine beetles more or less often than natural cavity trees. This suggests that characteristics used by forest biologists on the Angelina National Forest to select pines for cavity insert installation (open boles and at least 38 cm diameter at 6 m above the ground) may not have been substantially different from those used by Red-cockaded Woodpeckers during their selection of natural cavity trees. Clearly, forest management is not creating a biological sink for Red-cockaded Woodpeckers by installing cavity inserts to re-



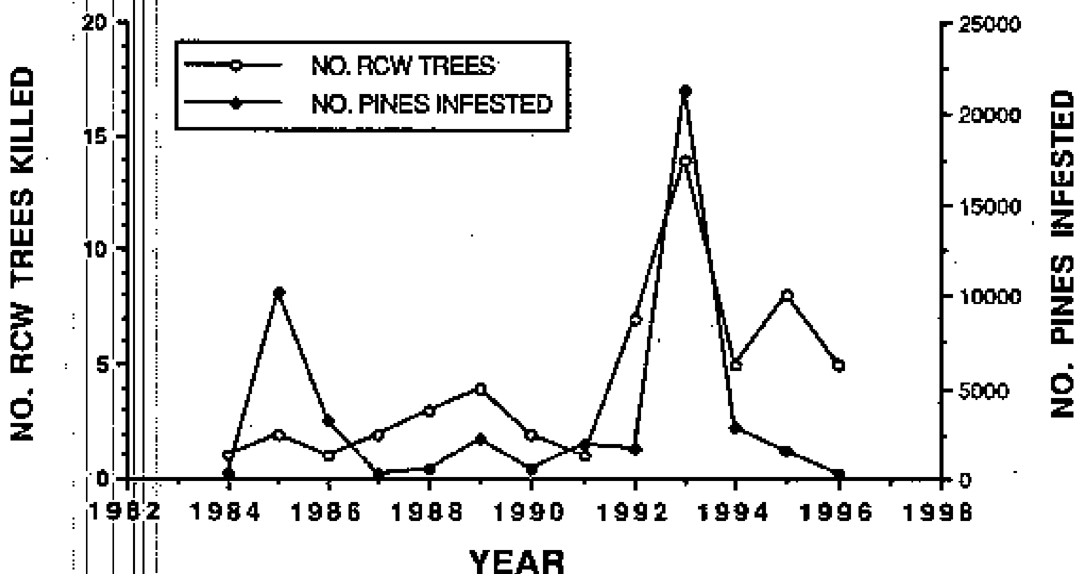


FIG. 3. The number of single Red-cockaded Woodpecker cavity trees that were infested and killed by southern pine beetles (SPB) versus the number of beetle infestations (top) and the number of pines infested by beetles (bottom) on the northern portion of the Angelina National Forest from 1983 through 1996.

place lost natural cavity trees and provide sites for woodpecker population expansion. In fact, loblolly and shortleaf pines chosen by biologists to be artificial insert trees that survived the first year of use by Red-cockaded Woodpeckers had a lower probability of being infested by bark beetles than occupied natural cavity trees. The reason for the lower infestation rate of occupied, insert cavity trees after the first year remains unknown.

Newly completed natural cavities and recently activated artificial cavities were infested at a greater frequency than cavity trees that had been active for more than one year. This was particularly true for trees with cavity inserts, suggesting that effective use of southern pine beetle repellents such as the pheromone verbenone (Payne and Billings 1989, Billings and Upton 1993) and the host tree volatile phenylpropanoid 4-allylanisole (Strom et al. 1995, Hayes et al. 1996) during the first year of insert use by Red-cockaded Woodpeckers may substantially reduce bark beetle-induced mortality to cavity trees containing artificial inserts.

There are several possible reasons why recently activated insert trees had a higher mortality rate than newly completed natural cavity trees. Excavation of natural cavities can take an extended period of time, often as much as 2 to 6 years (Conner and Rudolph 1995a). During cavity excavation and the gradual inclusion of resin wells around the cavity entrance the pine tree may have time to respond to the wounding by adding radial traumatic resin ducts and increasing resin production (Gerry 1922, Hodges et al. 1979, Nebeker et al. 1988, Ross et al. 1997). When installed cavity inserts are used by Red-cockaded Woodpeckers, the process of installation and resin well excavation often occurs in a fairly short period of time (less than a week to several months). Resin produced over a short period of time following an initial wounding is thought to be preformed resin (Nebeker et al. 1988) and not elevated production resulting from a wounding response (Gerry 1922, Harper and Wyman 1936). This sudden wounding of pines with cavity inserts followed by immediate use and resin well excavation by Red-cockaded Woodpeckers may increase their relative susceptibility to bark beetle infestation by reducing the pine's preformed resin. Excessive wounding of pines during turpentining for naval stores weakened pines and occasionally precipitated attack by bark beetles (Wyman 1932).

A significantly higher percentage of cavity trees (artificial and natural) killed by southern pine beetles had been nest trees within one year of beetle infestation. Cavity trees used for nesting are probably the most important trees for woodpecker groups and typically have numerous resin wells that produce copious amounts of fresh pine resin (R. Conner, C. Rudolph, and D. Saenz, pers. obs.). Previous research has demonstrated that active cavity trees are killed at a higher rate than inactive cavity trees (Conner and Rudolph 1995b, Rudolph and Conner 1995). The amount of resin produced by loblolly and shortleaf pines is highly variable depending in part on tree growth form, soil factors, moisture, and season of year (Schopmeyer and Larson 1955; Lorio 1986; Ross et al. 1993, 1995). The apparent attractiveness of active cavity trees with copious resin flow to southern pine beetles suggests that some component of resin volatiles, the amount of resin volatiles produced, or stress exerted on the pines by extensive resin well excavation may increase the preference/vulnerability of such cavity trees to southern pine beetle attack.

Southern pine beetles are attracted to and aggregate on pines where the resin volatile alpha-pinene (a major component of pine resin) and the beetle pheromone frontalin are present. The combination of these two chemicals serves as a strong attractant for southern pine beetles (Thatcher et al. 1980). Alpha-pinene, alone, does not appear to serve as a primary attractant to southern pine beetles (Thatcher et al. 1980, Billings 1985). Thus, it is somewhat perplexing why southern pine beetles are attracted to active loblolly and shortleaf pine cavity trees at a higher rate than to inactive cavity trees.

Site disturbance (Coulson et al. 1986, Flamm et al. 1993) and lightning strikes (Coulson et al. 1983, Lovelady et al. 1991) have been shown to be associated with the infestation of pines by southern pine beetles. Such disturbances apparently increase the attractiveness of pines for an initial attack by southern pine beetles. Woodpecker excavation of resin wells on cavity trees may sufficiently stress loblolly and shortleaf pines that they take on characteristics of pines suffering other types of stress.

The mechanism by which southern pine beetles select Red-cockaded Woodpecker cavity trees for initial attack may relate in part to the pine's production of allylanisole. This host volatile, produced by healthy pines, is known to inhibit infestation by southern pine beetles and other bark beetles (Hayes and Strom

1994, Hayes et al. 1994). Reduced levels of allylanisole have been associated with southern pine beetle attack and successful infestation of pines. Research is needed to evaluate the relative contributions of allylanisole reduction and alpha-pinene elevation resulting from Red-cockaded Woodpecker activity at resin wells toward increasing the attractiveness of pines to southern pine beetles.

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LOSSES OF RED-COCKADED WOODPECKER CAVITY TREES TO SOUTHERN PINE BEETLES

RICHARD N. CONNER AND D. CRAIG RUDOLPH[1]

ABSTRACT.—Over an 11-year period (1983–1993), we examined the southern pine beetle (*Dendroctonus frontalis*) infestation rate of single Red-cockaded Woodpecker (*Picoides borealis*) cavity trees on the Angelina National Forest in Texas. Southern pine beetles infested and killed 38 cavity trees during this period. Typically, within each cavity tree cluster, beetles infested only a single tree (usually the nest tree of the previous spring) during autumn and used the cavity tree as an over-wintering site for brood development. Seven (4 active and 3 inactive) cavity trees (out of 346 cavity tree years) died as a result of beetle infestation during the first five years of the study (1983–1987). In 1988, an intensive habitat management program was initiated on the forest to halt a severe population decline of the woodpecker. During the next six years (1988–1993), a much higher mortality rate was observed; 31 single cavity trees (out of 486 cavity tree years) were infested and killed ($\chi^2 = 8.8$, $P < 0.003$). Southern pine beetle-caused mortality of cavity trees also was high on other Texas national and state forests during this period. This marked increase of beetle-caused cavity tree mortality during a period of increased intensity of necessary management is of extreme concern. As a result of high beetle-caused mortality of active cavity trees, 64% of active cavity trees being used by Red-cockaded Woodpeckers on the northern portion of the Angelina National Forest during 1993 were artificial cavities. Pines selected by biologists for cavity inserts may produce less resin than those selected by woodpeckers and not provide an adequate barrier against snakes. The relationship between infestation of single active cavity trees and the number of beetle infestations (spots) on the northern portion of the Angelina National Forest from 1984 to 1993 was inconclusive ($r = 0.56$, $P > 0.09$, $N = 10$); further research is needed for a definitive conclusion. *Received 13 Apr. 1994, accepted 14 Sept. 1994.*

In the southeastern United States, old pines required for Red-cockaded Woodpecker (*Picoides borealis*) cavity excavation (Conner and O'Halloran 1987, Rudolph and Conner 1991) are rare, and the current age structure of pines on most national forests indicates that this shortage is likely to continue for at least 20 years (Conner and Rudolph 1989, Costa and Escano 1989). Provision of adequate old growth pines as potential cavity sites for this endangered woodpecker is a key element for its recovery.

Southern pine beetles (*Dendroctonus frontalis*) are the major cause of cavity tree death on Texas national forests (Conner et al. 1991). Growth of multiple-tree infestations (beetle spots) normally occurs from early spring to late summer (Coulson et al. 1972, Belanger et al. 1993), is facilitated by attractant pheromones (Thatcher et al. 1980), and can rap–

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idly eliminate entire cavity tree clusters. More than 350 cavity trees, which included more than 50 entire cavity tree clusters, were killed by southern pine beetles during a major infestation in the Four-Notch area of the Sam Houston National Forest between 1983 to 1985 (Billings and Varner 1986, Conner et al. 1991).

Although less catastrophic, annual losses of single cavity trees to southern pine beetle infestations appear to be persistent and cumulative. Bark beetle infestation of single cavity trees primarily affects active woodpecker cavity trees. Such trees are typically infested during the fall and serve as over-wintering sites for beetle brood development, with southern pine beetles emerging prior to summer of the following year (Conner et al. 1991, Rudolph and Conner 1995). Regular annual losses of cavity trees by single tree infestations have the potential to impact woodpecker groups significantly over the long term by limiting sufficient numbers of cavities for roosting and nesting. Cavity excavation by woodpeckers for replacement of dead cavity trees can require from one to four years ($\bar{x}$ = 2.4 years for shortleaf pine and 1.8 years for loblolly pines, Conner and Rudolph 1995).

Southern pine beetle infestation is not normally a problem in longleaf pines (*Pinus palustris*) because of this species' copious production of pine resin which serves as the pine's first line of defense against beetle infestation (Wahlenberg 1946, Hodges et al. 1977). Loblolly (*P. taeda*) and shortleaf (*P. echinata*) pines produce less resin, and generally are more susceptible to southern pine beetle infestation.

Following reports of severe woodpecker population declines (Conner and Rudolph 1989, Costa and Escano 1989) and a 1988 federal court case (Bigony 1991, MacFarlane 1992), the National Forest System intensified cluster area management on National Forests in Texas, and on nearly all other national forests in the south between 1988 and 1993, in an urgently needed effort to reverse the severe population declines. This intensified management included complete removal of hardwood tree species and substantial reduction of pine basal area to bring clusters into the 14 to 16 m^2/ha basal area range ordered by the federal court. Typically, the entire hardwood and pine midstory was removed by mechanical equipment (Conner and Rudolph 1991). Starting in 1990, an aggressive program was initiated to install artificially drilled cavities and cavity inserts using the techniques of Copeyon (1990) and Allen (1991) to give woodpecker groups sufficient cavities for nesting and roosting. As a response to events on national forests, management efforts for Red-cockaded Woodpeckers also were intensified on the W. Goodrich Jones and I. D. Fairchild State Forests in Texas during the late 1980s.

In this paper, we examine past baseline and recent increases in beetle caused mortality on the northern portion of the Angelina National Forest, which is primarily a loblolly-shortleaf pine forest. Southern pine beetle infestations of single cavity trees on the Sam Houston and Davy Crockett National Forests and two state forests in Texas also are examined. We explore the hypothesis that southern pine beetle caused mortality of Red-cockaded Woodpecker cavity trees on the Angelina National Forest is a function of ambient beetle population levels in the surrounding forest habitat.

STUDY AREAS AND METHODS

The Angelina National Forest (62,423 ha; 31°15'N, 94°15'W) is located in eastern Texas. The northern portion of the Angelina National Forest is predominantly covered by loblolly and shortleaf pines, whereas longleaf pine is the dominant tree species on the southern portion of the forest in the areas where Red-cockaded Woodpeckers are found (Conner and Rudolph 1989). The Davy Crockett (65,329 ha; 31°21'N, 95°07'W) and Sam Houston (65,218 ha; 30°30'N, 95°22'W) National Forests are both predominantly loblolly and shortleaf pine. The I. D. Fairchild (648 ha; 31°47'N, 95°22'W) and W. Goodrich Jones (688 ha; 30°13'N, 95°29'W) State Forests are primarily shortleaf and loblolly pine.

The loblolly-shortleaf pine habitat where Red-cockaded Woodpecker clusters are located occurs mainly on mesic, shrink-swell clays (Woodtel and LaCerda soil types), which readily support growth of hardwood vegetation (Fuchs 1980). Varying moisture conditions throughout the year produce the shrink-swell characteristics of the soils, which can strip root hairs off lateral roots of both pines and hardwood vegetation. Such soils place considerable stress on the plant communities they support and can increase the hazard of southern pine beetle infestation (Lorio et al. 1982, Mitchell et al. 1991). Longleaf pines occur primarily on deep loamy sands (Tehran and Letney soil types) containing materials of volcanic origin (Neitsch 1982). These soils contain very little organic material, resulting in a low water holding capacity. High soil temperatures during summer and limited water in these soils limit the growth of hardwoods on these sites but do not negatively affect longleaf pine resin production. Historically, southern pine beetle infestation of cavity trees in the longleaf pine habitats of the Angelina National Forest has been minimal (Conner et al. 1991).

The woodpecker population on the Angelina National Forest is comprised of widely separated isolated subpopulations (Conner and Rudolph 1989). Woodpeckers on the northern side of the Angelina National Forest (12 active clusters) are 34 km (including the 4–6 km wide Sam Rayburn reservoir) from 15 active clusters in the two southern subpopulations.

We made annual spring visits to all Red-cockaded Woodpecker cavity trees on the Angelina National Forest in eastern Texas (1983 through 1993) to evaluate cavity tree status and condition, using the indicators described by Jackson (1977, 1978). Active cavity tree clusters were visited several times per year. We examined each cavity tree to ascertain activity at resin wells (number of active wells and a subjective estimate of volume of resin flowing from the wounds), amount of scaling of bark, and condition of the cavity entrance. We determined the occurrence and causes of cavity tree mortality (Conner et al. 1991). Cavity trees infested by southern pine beetles typically had numerous white "popcorn-like" pitch tubes of crystallized pine resin around wounds where individual beetles had chewed through the bark and into the cambium of the bole. Dead cavity trees with signs of bark beetle infestation were examined to determine whether lightning strikes were also associated with tree deaths. Records of southern pine beetle infestation of Red-cockaded Woodpecker cavity trees and cavity tree activity status on the Davy Crockett and Sam Houston National

Forests and the I. D. Fairchild and W. Goodrich Jones State Forests were obtained from respective forest biologists.

In order to compare ambient southern pine beetle population levels with annual losses of cavity trees, we obtained records of the annual number of southern pine beetle infestations (beetle spots) and the number of pines infested on the northern portion of the Angelina National Forest from the USDA Forest Service Pest Management Office in Pineville, Louisiana, and Atlanta, Georgia (SPBIS—Southern Pine Beetle Information System data base). The National Forest and Grasslands in Texas provided data on areas affected by midstory removal within Red-cockaded Woodpecker clusters between 1988 and 1993.

RESULTS

Southern pine beetles infested and killed 38 single Red-cockaded Woodpecker cavity trees (active and inactive combined) on the northern portion of the Angelina National Forest from fall 1983 through spring 1993. The number of woodpecker groups on the northern portion of the Angelina National Forest ranged between seven and 10 over this 11 year time span. Southern pine beetles typically infested cavity trees during the fall (October and November), and trees appeared dead (dropped all needles and some bark pecked off by woodpeckers at mid bole height) by the following spring (March through June). Seven cavity trees (out of 346 cavity tree years) were killed by single-tree beetle infestation during the five-year period (1983–1987) immediately prior to initiation of intensive management for Red-cockaded Woodpeckers (Table 1). During the next six years, when intensive management occurred (1988–1993, Table 2), 31 cavity trees (out of 486 cavity tree years) were killed. This was a much higher mortality rate (6.3% vs 2.0%) than during the previous five-year period ($\chi^2 = 8.8$, $P = 0.003$). Seven of these 31 cavity trees were killed between fall 1991 and spring 1992 and 14 during the same time period the following year (Fig. 1).

Active cavity trees on three national and two state forests (Table 1) were infested at a higher average annual rate per year ($\bar{x} = 10.9 \pm 10.7\%$) than inactive trees ($\bar{x} = 0.8 \pm 1.3\%$, $t = 4.31$, $P = 0.0003$) (also see Rudolph and Conner 1995). This was particularly apparent during the 1988–1992 five-year period on the Angelina National Forest (Fig. 2). The majority of cavity tree mortality on the Angelina National Forest occurred within active cavity tree clusters (Fig. 3).

Fifty-five percent (21 of 38) of the beetle-caused cavity tree mortality occurred during the last two years of the 11-year period ($\chi^2 = 38.7$, $P < 0.001$). Thirty-three and 44 active cavity trees were present on the northern portion of the Angelina National Forest during 1991–1992 and 1992–1993, respectively. Thus, the loss of seven active cavity trees in 1991–1992 represents a 21% loss of active cavity trees, and the 14 active cavity trees killed in 1992–1993 represents a 32% loss (Table 1). Rates of single

TABLE 1

SOUTHERN PINE BEETLE INDUCED MORTALITY OF LOBLOLLY AND SHORTLEAF PINE, RED-COCKADED WOODPECKER CAVITY TREES ON NATIONAL AND STATE FORESTS IN EASTERN TEXAS

Forest	Year	No. active cavity trees	No. inactive cavity trees	Active SPB killed N	Active SPB killed %	Inactive SPB killed N	Inactive SPB killed %
Angelina N. F.	1993	44	63	14	32	0	0
	1992	33	39	7	21	0	0
	1991	33	44	0	0	1	2
	1990	29	44	2	7	0	0
	1989	34	45	3	9	1	2
	1988	29	49	3	10	0	0
	1987	28	46	0	0	2	4
	1986	28	44	1	4	0	0
	1985	27	44	2	7	0	0
	1984	46	24	0	0	1	4
	1983	34	25	1	3	0	0
Davy Crockett N. F.	1993	192	429	11	6	8	2
	1992	184	405	24	13	4	<1
	1991	117	406	4	3	2	<1
	1990	90	372	5	6	2	<1
Sam Houston N. F.	1993	438	1303	35	8	7	<1
	1992	425	1184	29	7	10	<1
I. D. Fairchild State Forest	1993	16	48	6	38	0	0
	1992	17	45	5	29	0	0
Jones State Forest	1993	40	73	4	10	0	0
	1992	36	70	6	17	1	1

TABLE 2

AREA WITH MIDSTORY REMOVAL COMPLETED WITHIN RED-COCKADED WOODPECKER CLUSTERS ON NATIONAL FORESTS IN TEXAS BETWEEN 1988 AND 1993

	Year of management activity				
	1988–1989	1989–1990	1990–1991	1991–1992	1992–1993
Midstory removal (ha)					
Angelina N. F.	0	127	170	102	75
Davy Crockett N. F.	273	163	90	153	101
Sam Houston N. F.	139	174	1023	331	86
Total	598	522	1444	796	314

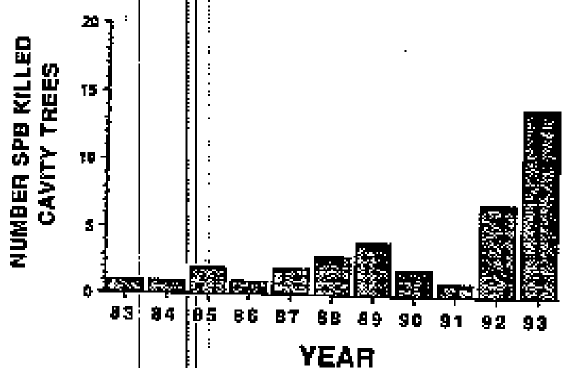

FIG. 1. Number of single Red-cockaded Woodpecker cavity trees infested and killed by southern pine beetles on the northern side of the Angelina National Forest before (1983–1987) and after (1988–1992) intensive woodpecker management was initiated.

cavity tree losses to southern pine beetles also were high on state forests; during 1991–1992 and 1992–1993 a total of 11 and 10 active cavity trees, respectively, were killed by southern pine beetles on the W. Goodrich Jones and I. D. Fairchild State Forests. The highest loss rates of any forest (29% and 38%) were observed on the I. D. Fairchild State Forest (Table 1). Although not as high as loss rates on the Angelina National Forest, losses on the Davy Crockett and Sam Houston National Forests during 1991–1992 and 1992–1993 were substantial (Table 1).

On the northern portion of the Angelina National Forest the number of detected southern pine beetle infestations (spots) and the number of pines infested within these spots varied considerably from 1984 through 1993 (Fig. 4A, B). The annual number of single cavity trees infested by

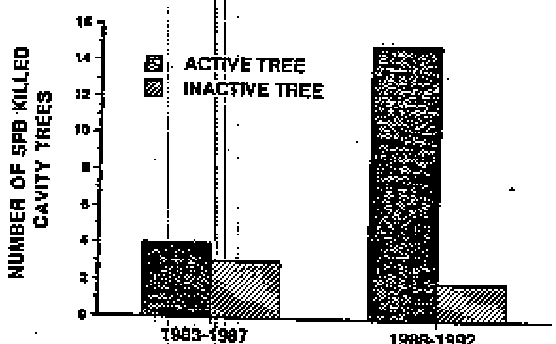

FIG. 2. Number of active and inactive Red-cockaded Woodpecker cavity trees killed by southern pine beetles before (1983–1987) and after (1988–1992) intensive woodpecker management was initiated on the Angelina National Forest.

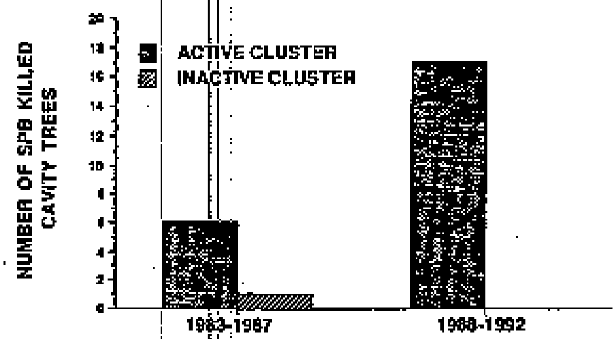

FIG. 3. Number of Red-cockaded Woodpecker cavity trees killed by southern pine beetles within active and inactive clusters during 1983–1987 and 1988–1992 on the Angelina National Forest.

southern pine beetles was marginally correlated with the number of southern pine beetle infestations (r = 0.56, N = 10, P = 0.09) but not correlated with the total number of pines infested within the general area (r = 0.27, P = 0.44) of the cavity tree clusters. However, the sample sizes for these correlations were small, and thus the biological significance of the results remains inconclusive.

DISCUSSION

The increase in southern pine beetle-caused mortality of Red-cockaded Woodpecker cavity trees beginning in 1988 is of extreme concern. The coincidental timing of increased cavity tree losses with initiation of intensive management suggests that efforts to correct habitat problems may be associated with increases in southern pine beetle infestation of active cavity trees. Physical disturbance of soils and root systems of trees during thinning and midstory removal operations is known to increase the risk of beetle infestation and the susceptibility of pines to attack (Nebeker and Hodges 1985, Hicks et al. 1987, Mitchell et al. 1991). Infestation of cavity trees occurred primarily within active woodpecker clusters. Intensive management activities were focused primarily on active cavity tree clusters when they were first initiated, again suggesting the possibility of a relationship between cluster management activities and beetle infestation of cavity trees. The most aggressive midstory and thinning work was completed between 1989 and 1991 on the Angelina National Forest; but the mortality rates of cavity trees were highest during 1992 and 1993 when southern pine beetle populations were at high levels. Midstory removal and thinning of pines was restricted to woodpecker cluster areas and did not include the surrounding general forest. Thus, present man-

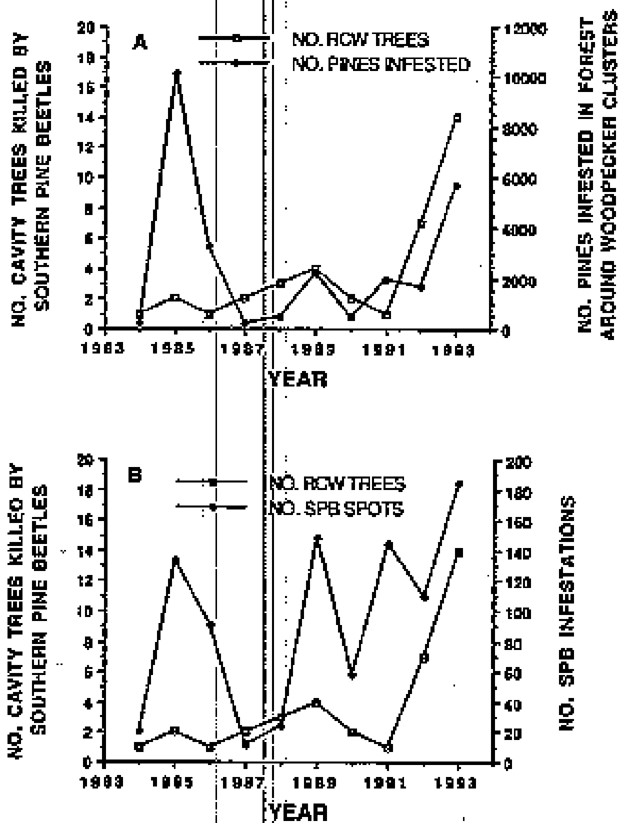

FIG. 4. Number of single Red-cockaded Woodpecker cavity trees killed by southern pine beetles versus the number of pines infested by southern pine beetles (A) and the number of southern pine beetle infestations (B) on the northern portion of the Angelina National Forest from 1983 through 1993.

agement produces a pocket of relatively open pine forest surrounded by a sea of pines and dense hardwood midstory. Southern pine beetles have a search image for vertically oriented dark objects—e.g., pine boles, and hardwood foliage is known to interfere with beetle movements (Showalter and Turchin 1993). Green leaf volatiles from deciduous foliage also interrupt bark beetle aggregation response to attractant pheromones when infesting southern pines (Dickens et al. 1992). Management's creation of islands of open pine forest within a sea of forest with midstory may serve as "magnets" to increase southern pine beetle numbers within Red-cockaded Woodpecker cluster areas.

In addition, woodpecker pecking at resin wells may elevate susceptibility of cavity trees to infestation either by decreasing tree vigor or by creating a wick of resin volatiles that serves as an attractant for southern pine beetles. When Red-cockaded Woodpeckers initially excavate resin wells in a pine around a newly completed cavity, resin flow from the wound is typically high because the pine actively transports oleoresins to the wound site (Ross et al. 1991, 1993). As woodpecker excavation of resin wells continues through time, resin flow to excavated wells in loblolly and shortleaf pine often decreases, perhaps to levels below what is adequate for defense against southern pine beetles (Ross et al. 1993). This would account for the fact that active cavity trees were infested at a higher rate than inactive trees (Table 1).

Resin flow to wound sites serves as the pine's primary defense against infesting southern pine beetles (Schmitt et al. 1988), but it is influenced by periods of active tree growth, moisture, temperature, and season of the year (Lorio 1986). Trees infested by southern pine beetles during the fall are often those that have been recently hit by lightning and serve as overwintering sites for beetle brood development (Coulson et al. 1983, Blanche et al. 1985). Lightning strikes impair the pine's ability to transport oleoresins (Blanche et al. 1985), perhaps similar to decreased resin flow resulting from continued Red-cockaded Woodpecker excavation of resin wells in loblolly and shortleaf pines. There are similarities between lightning-struck pines and loblolly and shortleaf pine cavity trees that may increase their susceptibility to successful infestation by southern pine beetles.

Fortunately, the severe losses of cavity trees to southern pine beetle infestation can be offset by the new technology of artificial cavity installation (Copeyon 1990, Allen 1991). As cavity trees are killed by southern pine beetles, new cavity inserts are installed to replace the lost trees. Over 100 cavity inserts were installed on the Angelina National Forest during 1992 alone (pers. commun., Alfredo Sanchez, District Biologist, Angelina National Forest). As a result of the cavity tree mortality and the insert program to offset it, 28 of 44 (64%) active cavity trees being used by Red-cockaded Woodpeckers on the northern Angelina National Forest during 1993 had artificial cavities. This percentage is likely to increase as beetles kill more natural cavity trees and more cavity inserts are installed. However, pines with artificial cavities are also susceptible to southern pine beetle infestation, particularly when Red-cockaded Woodpeckers begin to use them. Ninety-three percent (13 of 14) of cavity trees killed by southern pine beetles between fall 1992 and spring 1993 contained artificial cavities.

Southern pine beetle populations in the general forest area around woodpecker cavity tree clusters would likely have an influence on infestation of cavity trees. However, on the northern portion of the Angelina National Forest, we failed to detect a significant relationship between infestation of single Red-cockaded Woodpecker cavity trees and measures of the ambient southern pine beetle population. Our sample size was quite low (N = 10), which limited statistical power. The lack of a clear relationship between ambient beetle populations and cavity tree mortality suggests that factors such as management of cluster areas or individual cavity tree characteristics (pine tree volatiles in resins) may be associated with the infestation of single Red-cockaded Woodpecker cavity trees.

Long-term effects of woodpecker use of primarily artificial cavities are unknown. When excavating natural cavities, woodpeckers may select pines that produce desired amounts of pine resin (Conner and O'Halloran 1987). Pines selected by biologists for cavity installation may have different resin characteristics than those selected by woodpeckers. If such pines are unable to produce sufficient resin to repel southern pine beetles, they also may not be able to produce enough resin at resin wells for barriers to adequately protect cavity trees from climbing rat snakes (*Elaphe obsoleta*) (Rudolph et al. 1990).

Additional research is needed to explore relationships among woodpecker management, southern pine beetle infestation of single cavity trees, and ambient beetle population levels. Information is needed to determine if woodpecker cluster area management accumulates beetles around cavity trees by creating open patches of mature pines within otherwise dense vegetation. Although there is experimental evidence that southern pine beetles are not attracted to certain host volatiles (alpha pinene) (Billings 1985, Thatcher et al. 1980), production of all host volatiles at resin wells also needs examination as a possible attractant for southern pine beetles.

Southern pine beetles are a problem pest in southern pines throughout the southeastern United States (Thatcher et al. 1980). Verbal reports from Arkansas, Louisiana, and Mississippi suggest that beetles are infesting active cavity trees at higher than expected rates (F. L. Oliveria, pers. commun.). Thus, there is a likelihood that the phenomenon we have observed is a south-wide problem in areas where Red-cockaded Woodpeckers use loblolly and shortleaf pines for cavity trees.

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THE RED-COCKADED WOODPECKER'S ROLE IN THE SOUTHERN PINE ECOSYSTEM, POPULATION TRENDS AND RELATIONSHIPS WITH SOUTHERN PINE BEETLES

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Abstract.—This study reviews the overall ecological role of the Red-cockaded Woodpecker (*Picoides borealis*) in the southern pine ecosystem. It is the only North American woodpecker species to become well adapted to a landscape that was relatively devoid of the substrate typically used by woodpeckers for cavity excavation (i.e. snags and decayed, living hardwoods). Its adaptation to use living pines for cavity excavation has expanded the use of this fire-disclimax ecosystem for numerous other cavity-using species. As such, the Red-cockaded Woodpecker represents an important keystone species of fire-disclimax pine ecosystems of the South. Historically, populations of this woodpecker and other cavity dependent species decreased dramatically with the logging of the southern pine forests between 1870 and 1930. Woodpecker populations continued to decline into the 1980s as a result of inadequate old-growth pine habitat, and suppression of fire which permitted encroachment of hardwoods into the previously pine-dominated ecosystem. Management practices initiated after 1988 have resulted in woodpecker population increases on Texas national forests. Cavity-tree mortality and southern pine beetle (*Dendroctonus frontalis*) infestation of cavity trees on the Angelina National Forest in eastern Texas were studied from 1983 through 1996. The intensive management activities initiated to stabilize severely declining woodpecker populations in 1989 may have increased beetle infestation rates of cavity trees in loblolly (*Pinus taeda*) and shortleaf (*Pinus echinata*) pine habitat resulting in a net loss of cavity trees over the past seven years. Initial results suggest that beetle-caused mortality of cavity trees may be related in part to ambient southern pine beetle population levels in surrounding forest stands.

As a cooperative breeder (Ligon 1970), the Red-cockaded Woodpecker (*Picoides borealis*) lives in family groups composed of a breeding pair and one to several helpers (Walters et al. 1988; Walters 1990). The woodpecker excavates cavities into the heartwood of old pines that typically are infected with red heart fungus (*Phellinus pini*), have relatively thin sapwood, and a large diameter of heartwood (Conner & Locke 1982; Conner et al. 1994; Hooper 1988; Hooper et al. 1991b; Rudolph et al. 1995). Red-cockaded Woodpeckers peck shallow excavations, termed resin wells, around their cavity entrances (Jackson 1978b).

Daily pecking at these sites causes a copious flow of pine resin from resin wells down the bole of the pine (Ligon 1970). Bark scaling and resin flow serve as a deterrent by creating a barrier against climbing rat snakes (*Elaphe obsoleta*) (Jackson 1974; Rudolph et al. 1990b), but have little deterrent effect against southern flying squirrels (*Glaucomys volans*), which frequently use unenlarged cavities (Rudolph et al. 1990a; Loeb 1993).

Pileated Woodpeckers (*Dryocopus pileatus*) enlarge many cavities (expand the cavity entrance tube and cavity chamber by excavation) and occasionally nest in Red-cockaded Woodpecker cavities (Conner et al. 1991). Over a nine year period Pileated Woodpeckers enlarged 55 Red-cockaded Woodpecker cavities on the Angelina National Forest in eastern Texas (Conner & Rudolph 1995a). An average of 6.1 cavities was enlarged per year, representing 2.4 percent of the cavity trees present each year on the forest. The enlarged cavities created by Pileated Woodpeckers provide cavity sites for many other relatively large secondary cavity users, such as fox squirrels (*Sciurus niger*), American Kestrels (*Falco sparverius*), Wood Ducks (*Aix sponsa*), and Eastern Screech-Owls (*Otis asio*).

THE ROLE OF RED-COCKADED WOODPECKERS AS A KEYSTONE SPECIES

Although the Red-cockaded Woodpecker is often singled out as an example of single species management, it is in fact a keystone species of fire-disclimax, pine ecosystems of the South, and is the primary species to excavate cavities in what can be an otherwise cavity-barren environment (Conner 1995). Cavity excavation by Red-cockaded Woodpeckers in live pines requires a relatively long period of time, averaging 1.8 yr in loblolly pines (*Pinus taeda*), 2.4 yr in shortleaf pines (*P. echinata*), and 6.3 yr in longleaf pines (*P. palustris*) (Conner & Rudolph 1995a). Thus, the cavities they create tend to be in high demand by other species (Dennis 1971; Rudolph et al. 1990a; Loeb 1993; Conner et al. 1996).

Approximately 24 species of vertebrates are known to use Red-cockaded Woodpecker cavities (Dennis 1971; Baker 1971; Beckett 1971; Hopkins & Lynn 1971; Jackson 1978a; Harlow & Lennartz 1983; Rudolph et al. 1990a; Loeb 1993; Kappes & Harris 1995). Although the majority of these vertebrates use either enlarged or abandoned cavities, several species, such as Red-bellied (*Melanerpes carolinus*) and

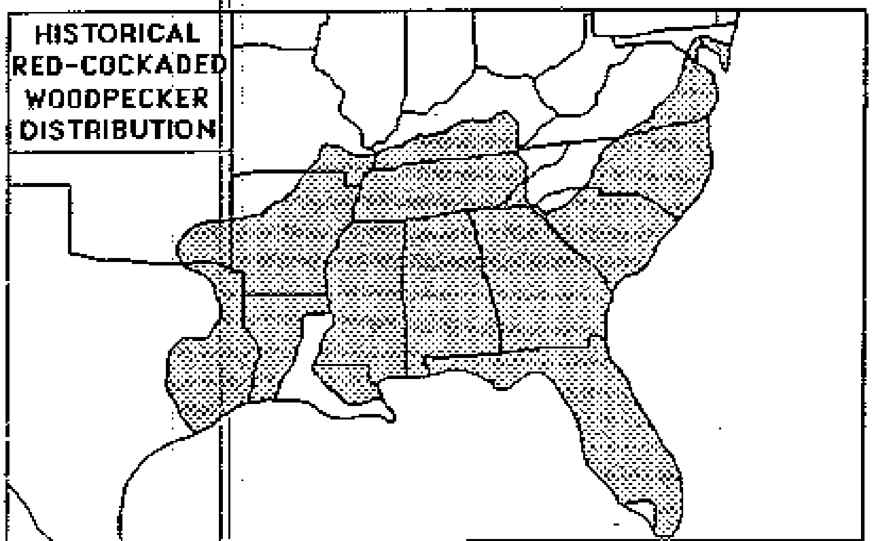
Red-headed (*M. erythrocephalus*) woodpeckers and southern flying squirrels, appear to actively compete with Red-cockaded Woodpeckers for normal, unenlarged cavities. Because of the dependence of many other cavity nesters on Red-cockaded Woodpecker cavities, forest biodiversity would suffer substantially in the absence of this endangered woodpecker in southern pine ecosystems.

Red-cockaded Woodpecker Population Status, Trends and Essential Management

Two major factors are associated with the historic declines of Red-cockaded Woodpeckers throughout the southeastern United States (Fig. 1). Loss of old-growth pine forest initially caused severe population losses (USFWS 1985). In the coastal plain of Texas, "bonanza era" harvesting occurred between 1890 and 1930 (Maxwell & Baker 1983; McWilliams & Lord 1988). Subsequent to the loss of old-growth pines and fragmentation of southern pine forests through harvesting, the suppression of natural fires and development of artificial fire breaks, such as roads, reservoirs and agricultural lands across the landscape, permitted a gradual encroachment of hardwoods into what had been the open-pine savannahs of the South.

Because of continuing loss and fragmentation of pine forest habitat and exclusion of fire, the Red-cockaded Woodpecker continued to decline throughout its range during the 1970s, 1980s and early 1990s (Jackson 1980; Baker 1982; 1983; Carter et al. 1983; Eddleman & Clawson 1987; Ortego & Lay 1988; Conner & Rudolph 1989; Costa & Escano 1989; Masters et al. 1989) despite more than two decades of protection under the Endangered Species Act and two recovery plans. Of the 26 Red-cockaded Woodpecker populations on national forests in the South, 11 were still declining between 1990 and 1992 and 15 appeared to be stable (USDA 1995). South-wide, only the Francis Marion National Forest population in South Carolina (prior to Hurricane Hugo) increased without the aid of artificial cavities and woodpecker translocations (Hooper et al. 1991a). The largest remaining woodpecker population (nearly 700 woodpecker groups on the Apalachicola National Forest in Florida) has recently exhibited signs of population declines within the smaller subpopulations on the eastern portion of the forest (James 1991).

Small Red-cockaded Woodpecker populations (<50 woodpecker groups) are highly vulnerable to demographic problems resulting from



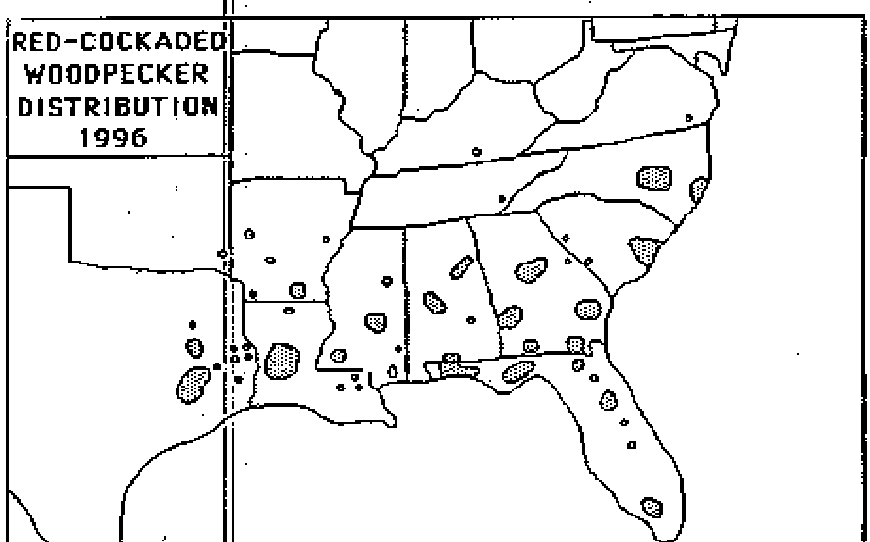


Figure 1. Historical and present distribution of Red-cockaded Woodpeckers in the southeastern United States.

cluster isolation and habitat fragmentation, and thus, are more likely to suffer population declines than larger populations (Walters et al. 1988; Conner & Rudolph 1989; 1991a; Costa & Escano 1989; Hooper & Lennartz 1995; Rudolph & Conner 1994). Populations or subpopulations composed of < 10 groups with large distances between clusters are

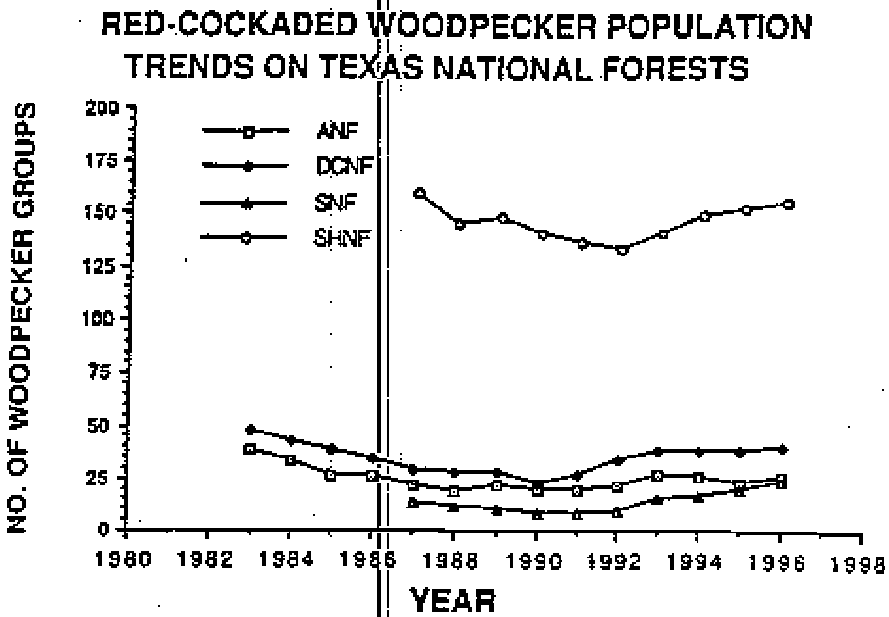


Figure 2. Population trends of Red-cockaded Woodpeckers on the Angelina, Davy Crockett, Sabine and Sam Houston National Forests between 1983 and 1996.

in critical danger of extirpation (Conner & Rudolph 1989; 1991a).

In Texas, Red-cockaded Woodpecker populations declined during the 1960s (Lay 1969; Lay & Russell 1970), 1970s (Jackson et al. 1978), and 1980s (Ortego & Lay 1988; Conner & Rudolph 1989; Rudolph & Conner 1994). Populations continued to decline on the Angelina and Davy Crockett National Forests between 1983 and 1988, appeared to stabilize between 1988 and 1991, and increased in 1992 and 1993 (Fig. 2, also see Conner et al. 1995). Populations on the Sabine National Forest decreased between 1987 and 1990, but increased in 1992 and 1993. Woodpecker populations on the Sam Houston National Forest decreased between 1989 and 1992, but increased in 1993 (Conner et al. 1995). Populations on the Davy Crockett, Sabine and Sam Houston National Forests have continued to increase through 1996 and the Angelina National Forest appears to be stable (Fig. 2).

As of spring 1996, approximately 316 groups of Red-cockaded Woodpeckers were present in Texas. The Sam Houston National Forest had 156 groups present, with 40 on the Davy Crockett National Forest, 26 on the Angelina National Forest, and 24 on the Sabine National Forest. The W. Goodrich Jones and I. D. Fairchild State Forests had

14 and six groups, respectively, with two groups present on the Huntsville State Fish Hatchery. The Alabama-Coushatta Indian Reservation had two groups and the Big Thicket National Preserve one group. Approximately 45 groups occurred on private lands, primarily lands belonging to private industrial timber companies.

Several significant problems have affected small, isolated Red-cockaded Woodpecker populations in Texas and elsewhere in the South. Encroachment of hardwood vegetation is a primary cause of cluster abandonment (Conner & Rudolph 1989; Locke et al. 1983; Van Balen & Doerr 1978). On the Angelina and Davy Crockett National Forests between 1981 and 1987 the woodpeckers abandoned cavity-tree clusters with abundant hardwood vegetation at a significantly higher rate than clusters with little or no hardwood vegetation (Conner & Rudolph 1989). Although Conner & Rudolph (1989) identified hardwood midstory encroachment in clusters as the major probable cause of population declines in Texas, they later identified a lack of suitable cavity trees, cluster isolation, and forest fragmentation as contributing factors (Conner & Rudolph 1991b). Midstory reduction within cluster areas on national forests was aggressively pursued by mechanical means during the late 1980s and early 1990s (Conner & Rudolph 1991a; Conner et al. 1995). Efforts to thin pine stands within and around cavity-tree cluster areas were also intensified. Beginning in late 1989, use of artificial cavities (Allen 1991; Copeyon 1990) and cavity restrictors to prevent cavity enlargement (Carter et al. 1989) became widespread on all Texas national forests. In the early 1990s Red-cockaded Woodpeckers were translocated to augment single woodpecker clusters (DeFazio et al. 1987), temporarily solving problems created by cluster isolation and demographic dysfunction (Conner et al. 1995). In several instances pairs of Red-cockaded Woodpeckers were reintroduced to sites of previous extirpation (Rudolph et al. 1992).

The 1988 court-ordered management plan in Texas enjoined clear-cutting within 1200 m of Red-cockaded Woodpecker cavity-tree clusters in an effort to prevent habitat fragmentation and provide sufficient older growth pines for nesting, roosting and foraging. Any possible beneficial effects of this component of the court order have not had sufficient time to come to fruition. Thus, the court-ordered change in timber harvesting techniques (single tree selection rather than clear-cutting) can not account for the observed favorable Red-cockaded Woodpecker population response (Conner et al. 1995).

Collectively, an aggressive management program that included hardwood midstory control through mechanical means and fire, cavity restrictors and thinning within cluster areas stabilized some Red-cockaded Woodpecker populations (1989-1991, Fig. 2). Red-cockaded Woodpecker population increases on the Texas national forests occurred only after the beginning of aggressive installation of artificial cavities and translocation of woodpeckers which began in 1991 (Conner et al. 1995).

SOUTHERN PINE BEETLES AND RED-COCKADED WOODPECKER CAVITY TREE MORTALITY

Southern pine beetles (*Dendroctonus frontalis*) are the major cause of cavity tree death on Texas national forests (Conner et al. 1991). Growth of multiple-tree infestations (beetle spots) normally occurs from early spring to late summer (Coulson et al. 1972; Belanger et al. 1993), is facilitated by attractant pheromones (Thatcher et al. 1980), and can rapidly eliminate entire cavity tree clusters (Billings & Varner 1986). Southern pine beetles killed more than 350 cavity trees, including more than 50 entire clusters, during a major infestation on the Sam Houston National Forest between 1983 and 1985 (Billings & Varner 1986; Conner et al. 1991). During major epidemics, southern pine beetles account for more than 75% of cavity tree mortality, whereas losses to these bark beetles during endemic population levels are about 53% (Fig. 3).

Although less catastrophic, losses of single cavity trees to southern pine beetle infestations are persistent and cumulative. Bark beetle infestation of single cavity trees affects primarily active woodpecker cavity trees. Such trees are typically infested during the fall, serve as over-wintering sites for beetle brood development, and southern pine beetles emerge prior to summer of the following year (Conner et al. 1991; Conner & Rudolph 1995b; Rudolph & Conner 1995). Regular annual losses of cavity trees by single tree infestations have the potential to significantly impact woodpecker groups over the long term by reducing the number of suitable cavities for roosting and nesting (Conner & Rudolph 1995b).

From fall 1983 through summer 1996, southern pine beetles infested and killed 62 single Red-cockaded Woodpecker cavity trees (active and inactive combined) on the northern portion of the Angelina National Forest, where loblolly and shortleaf pine predominate (Fig. 4). The number of woodpecker groups on this portion of the Angelina National Forest ranged between seven and 11 over this 13-year period. Southern pine beetles typically infested cavity trees during the fall (October and

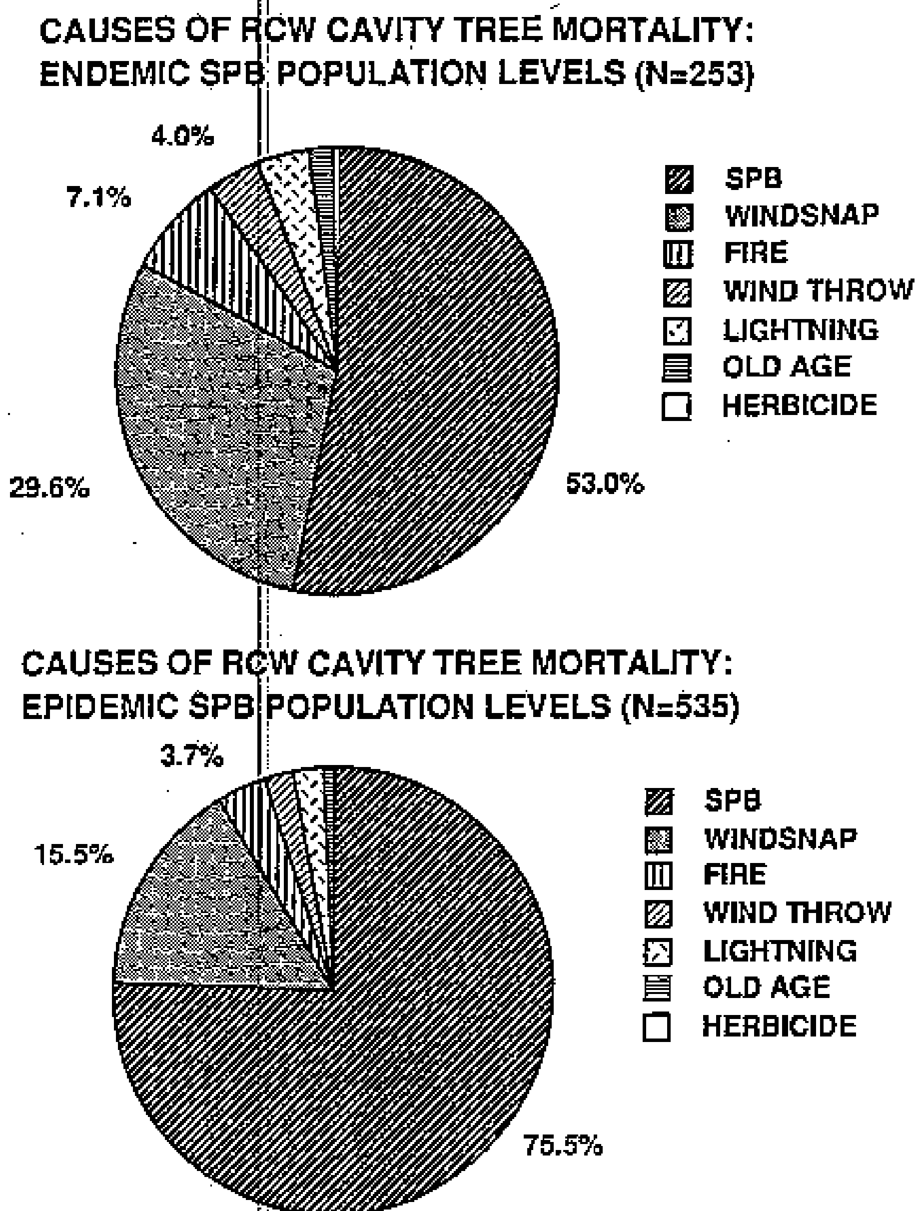


Figure 3. Causes of Red-cockaded Woodpecker cavity tree mortality during periods of endemic and epidemic southern pine beetle population levels in eastern Texas between 1983 and 1988.

November) and trees appeared dead (dropped all needles and some bark pecked off by woodpeckers at mid bole height) by the following spring

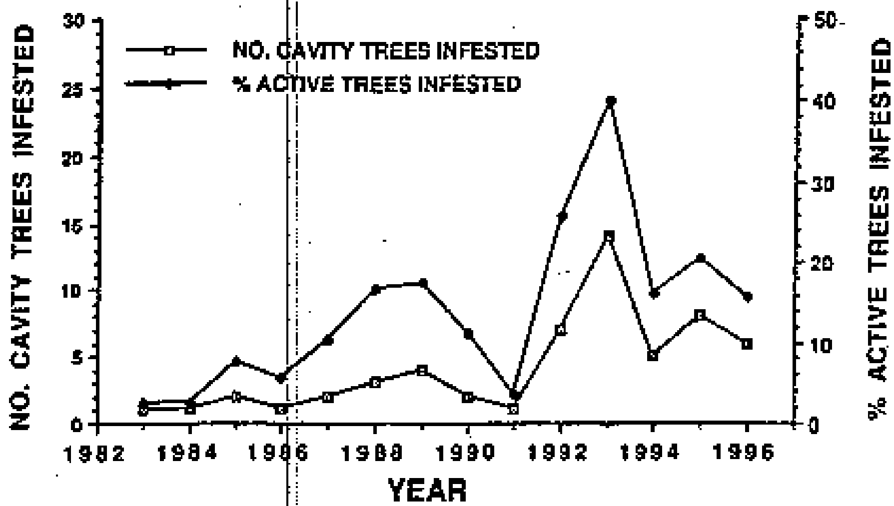


Figure 4. The number of Red-cockaded Woodpecker cavity trees (loblolly and shortleaf pines only) and percentage of active cavity trees infested and killed by southern pine beetles on the northern portion of the Angelina National Forest from 1983 to 1996.

(March through June) (Conner & Rudolph 1995b). In about 40% of the cases (25 of 62), the cavity tree killed had been the nest tree of the preceding breeding season. Typically, bark beetles infest active cavity trees at a much higher average annual rate than inactive trees (Conner & Rudolph 1995b; Rudolph & Conner 1995).

The intensified forest management that occurred following the development of the 1988 court-ordered management plan included complete removal of hardwood tree species and substantial reduction of pine basal area to bring clusters into a 14 to 16 m^2/ha basal area range. Typically, the entire hardwood and pine midstory was removed by mechanical equipment, as mentioned above, and caused substantial site disturbance to woodpecker cluster areas (Conner & Rudolph 1991a). Seven cavity trees (out of 346 cavity tree years) were killed by single-tree beetle infestation during the five-year period (1983-1987) immediately prior to initiation of intensive management for Red-cockaded Woodpeckers on the northern portion of the Angelina National Forest. Over the next nine years during intensified management (1988-1996), 49 cavity trees (out of 729 cavity tree years) were killed. This was a much higher mortality rate (6.7% vs 2.0%) than the previous five-year period ($\chi^2 = 9.6$, $P < 0.002$).

From 1984 through 1996, the number of detected southern pine beetle infestations (spots) and the number of pines infested within these spots varied considerably on the northern portion of the Angelina National Forest (Fig. 5). The annual number of single cavity trees infested by southern pine beetles (1984-1995) was correlated with the number of southern pine beetle infestations ($r = 0.71$, $N = 11$, $P = 0.02$), but not correlated with the total number of pines infested within the general area ($r = 0.49$, $P = 0.13$) of the cavity tree clusters. However, because of the small sample sizes for these correlations, the biological significance of the results remains inconclusive.

Southern pine beetle infestation is not typically a problem in longleaf pine because of this species' copious production of pine resin, which serves as the pine's first line of defense against beetle infestation (Wahlenberg 1946; Hodges et al. 1977). Loblolly and shortleaf pines produce less pine resin and they are generally more susceptible to southern pine beetle infestation (Hodges et al. 1977). The coincidental timing of increased cavity tree losses with initiation of intensive management in loblolly and shortleaf pine habitat on the Angelina National Forest is of considerable concern and suggests that efforts to correct habitat problems may be associated with increases in southern pine beetle infestation of active cavity trees. Physical disturbance of soils and root systems of trees during thinning and midstory removal operations increases the risk of beetle infestation and the susceptibility of pines to attack (Nebeker & Hodges 1985; Hicks et al. 1987; Mitchell et al. 1991). Infestation of cavity trees occurred primarily within active woodpecker clusters. Intensive management activities focused primarily on active cavity tree clusters when they were first initiated, again suggesting the possibility of a relationship between cluster management activities and beetle infestation of cavity trees. Midstory removal and thinning of pines was restricted to woodpecker cluster areas and did not include the surrounding general forest. Thus, present management produces a pocket of relatively open pine forest surrounded by a sea of pines and dense hardwood midstory. Southern pine beetles have a search image for vertically oriented dark objects (e.g., pine boles) and hardwood foliage can interfere with beetle movements (Schowalter & Turchin 1993). Green leaf volatiles from deciduous foliage also interrupt bark beetle aggregation response to attractant pheromones (Dickens et al. 1992). Management's creation of islands of open pine forest within a sea of forest with midstory may accumulate southern pine beetles within Red-cockaded Woodpecker cluster areas. Additional research is needed to determine if management essential for woodpecker recovery is increasing the frequency of southern pine beetle infestation of cavity trees. Fortunately, the severe losses of cavity trees to southern

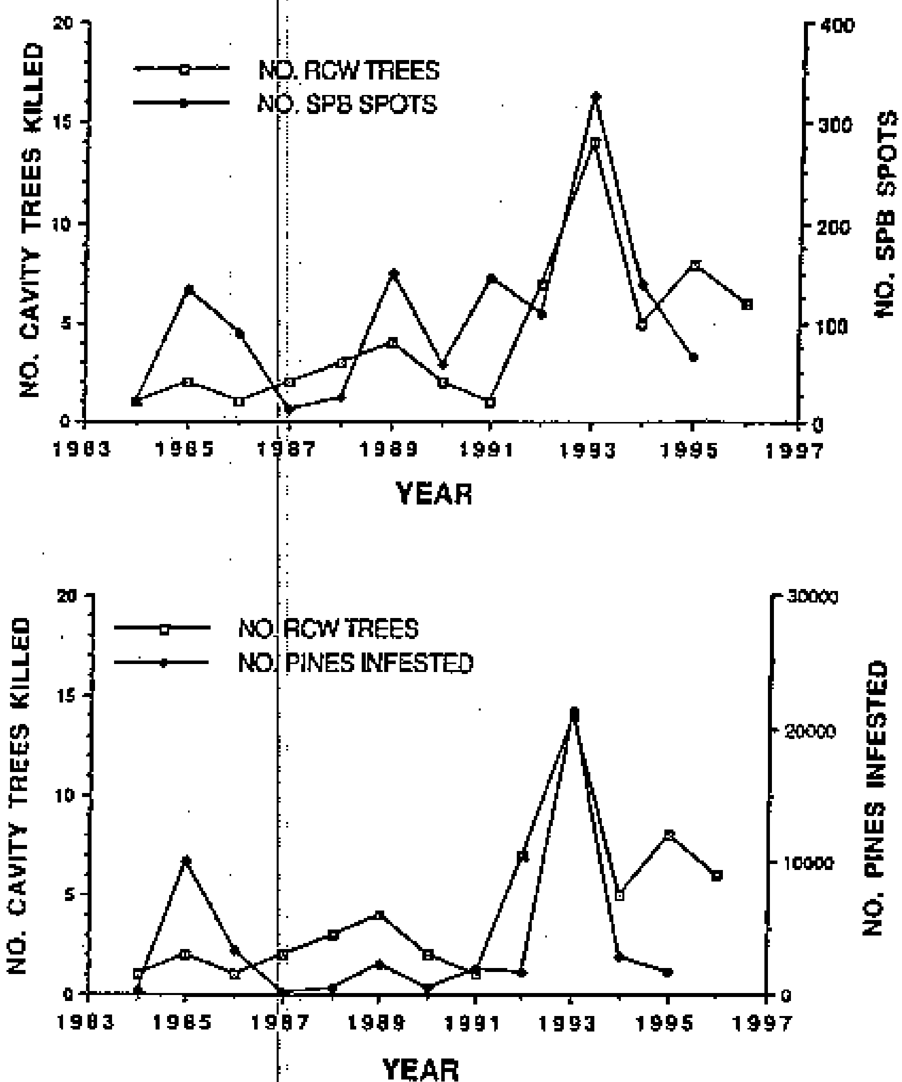


Figure 5. Southern pine beetle induced mortality of Red-cockaded Woodpecker cavity trees on the northern portion of the Angelina National Forest versus the number of southern pine beetle spots and the number of pines infested in loblolly-shortleaf pine forest habitat surrounding Red-cockaded Woodpecker cavity-tree clusters between 1984 and 1995.

pine beetle infestation can be offset by the new technology of artificial cavity installation (Copeyon 1990; Allen 1991).

Southern pine beetles are a problem pest in southern pines throughout the southeastern United States (Thatcher et al. 1980). Verbal reports from Arkansas, Louisiana, and Mississippi suggest that beetles are infesting active cavity trees at higher than expected rates (Oliveria, pers. comm.). Thus, observations made here in Texas likely represent a southwide problem in areas where Red-cockaded Woodpeckers use loblolly and shortleaf pines for cavity trees.

THE FUTURE OUTLOOK FOR RED-COCKADED WOODPECKERS IN TEXAS

The biological diversity of southern pine ecosystems in Texas is closely tied to management of the Red-cockaded Woodpecker because of the dependence of many birds, mammals, amphibians, reptiles and arthropods on woodpecker cavities. Some problems such as the high loss rates of cavity trees to southern pine beetle infestation in loblolly and shortleaf pine habitat still need solutions. However, intensive management and subsequent favorable population responses observed on Texas national forests indicate that recovery of the Red-cockaded Woodpecker is possible. The outlook for Red-cockaded Woodpeckers in Texas and the rest of the South is good; the ecological need exists and scientific technology is available to recover this endangered woodpecker and the ecosystem in which it thrives. The final outcome rests on the management priorities of federal and state agencies, and private land managers.

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