Wilson Bull., 107(1), 1995, pp. 81–92

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

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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 (χ^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

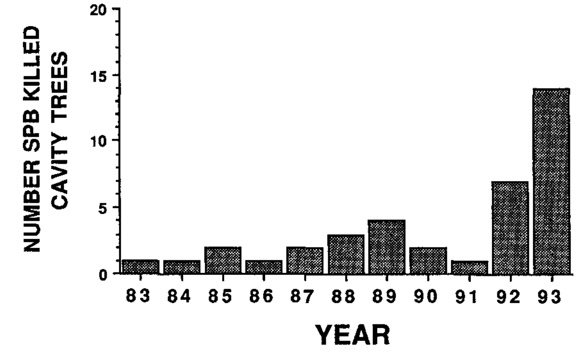

FIG. 1. Number of single Red-cockaded Woodpecker cavity trees infested and killed by southern pine beetles on the northern side of the Angelina National Forest before (1983–1987) and after (1988–1992) intensive woodpecker management was initiated.

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

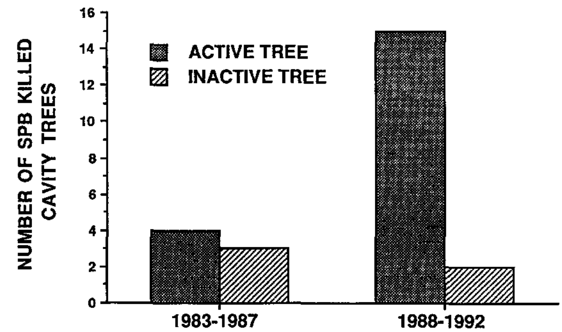

FIG. 2. Number of active and inactive Red-cockaded Woodpecker cavity trees killed by southern pine beetles before (1983–1987) and after (1988–1992) intensive woodpecker management was initiated on the Angelina National Forest.

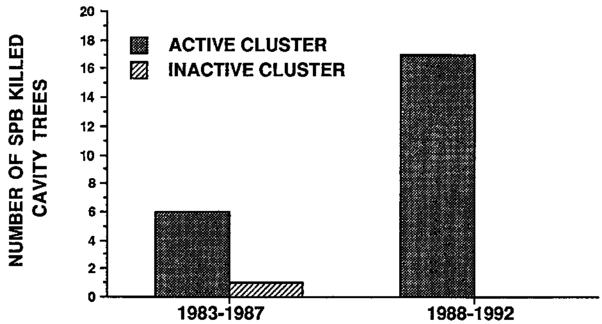

FIG. 3. Number of Red-cockaded Woodpecker cavity trees killed by southern pine beetles within active and inactive clusters during 1983–1987 and 1988–1992 on the Angelina National Forest.

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-

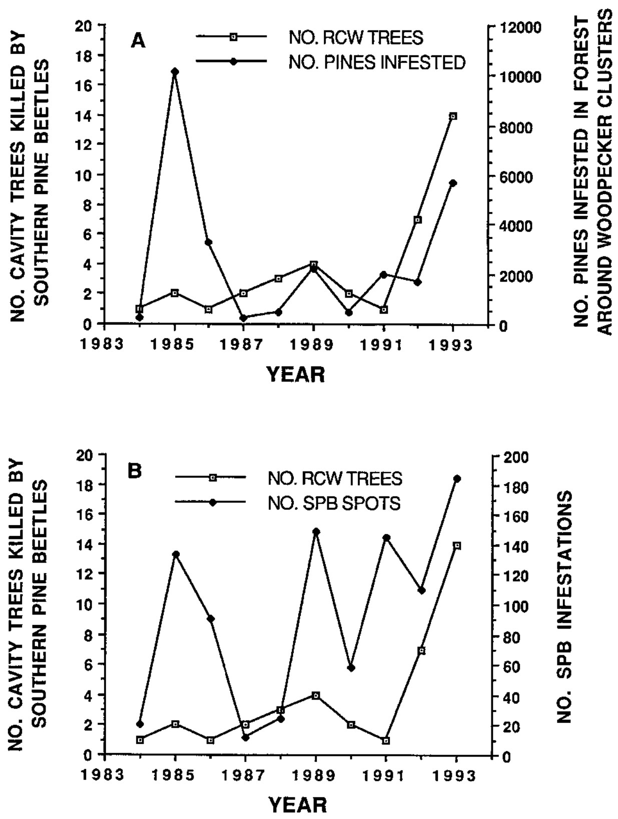

FIG. 4. Number of single Red-cockaded Woodpecker cavity trees killed by southern pine beetles versus the number of pines infested by southern pine beetles (A) and the number of southern pine beetle infestations (B) on the northern portion of the Angelina National Forest from 1983 through 1993.

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.

ACKNOWLEDGMENTS

We thank S. Best, D. Bieber, D. Carrie, R. Mize, and R. Sandal, for records from the Davy Crockett and Sam Houston National Forests and The I. D. Fairchild and W. Goodrich Jones State Forests, and V. Peacher, W. Nettleton, and F. Oliveria for assistance with SPBIS records for the Angelina National Forest. We thank R. F. Billings, J. L. Hayes, J. A. Jackson, F. C. James, and B. R. Parresol for constructive comments leading to the improvement of an early draft of the manuscript.

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