

CAUSES OF MORTALITY OF RED-COCKADED WOODPECKER CAVITY TREES

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Abstract: Over a 13-year period we examined the mortality of cavity trees ($n = 453$) used by red-cockaded woodpeckers (*Picoides borealis*) on national forests in eastern Texas. Bark beetles (53%), wind snap (30%), and fire (7%) were the major causes of cavity tree mortality. Bark beetles were the major cause of mortality in loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines, whereas fire was the major cause in longleaf pines (*P. palustris*). Cavity trees on the Angelina National Forest (NF) were dying at a higher rate than new, complete cavities were being excavated. Cavity enlargement by pileated woodpeckers (*Dryocopus pileatus*) on the Angelina NF was substantial, with 20% (49/249) of the cavity trees being enlarged over 7 years. To reduce cavity tree mortality, site disturbances in cluster areas (e.g., midstory control, prescribed burning, thinning) should be minimized during years when southern pine beetle (*Dendroctonus frontalis*) populations are elevated. Careful planning of timber cutting to avoid funneling wind into cluster areas might reduce wind damage to cavity trees.

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The red-cockaded woodpecker has been legally defined as an endangered species since 1970 (35 Fed. Register 16047, 13 Oct 1970). A habitat feature that is essential for the survival of this species is a constant supply of living, old pines with decayed heartwood (Jackson 1977, Conner and Locke 1982) and large crowns and open boles that have had some suppression in their growth history (Conner and O'Halloran 1987). The woodpecker excavates nest and roost cavities in these trees (U.S. Fish Wildl. Serv. 1985, Ligon et al. 1986). In the southern United States, old pines of this type are relatively rare. Costa and Escano (1989) indicated that sufficiently old pines for cavity excavation are in short supply on many national forests in the South and that the age structure of most forests is such that supply of old pines is likely to be low for >20 years. Recent declines in populations of red-cockaded woodpeckers (Conner and Rudolph 1989) might be caused in part by a lack of old-growth pines in southern pine forests.

Thus, to develop management options that reduce the loss of cavity trees, it is important to identify factors causing this loss. In our study, we evaluate mortality of cavity trees used by red-cockaded woodpeckers and suggest management options to reduce losses.

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METHODS

As part of annual visits to cavity trees on the Angelina NF from 1978 to 1990 and the Davy Crockett NF from 1987 to 1989, we observed cavity tree mortality and determined probable cause of death of 109 red-cockaded woodpecker cavity trees. In addition, we used our own observations and records from the Sam Houston

NF from 1983 to 1988 to evaluate causes of mortality of an additional 426 cavity trees. All cavity trees on all forests were cored with a 5-mm diameter increment borer and aged with the aid of a binocular dissecting microscope. To compare the relative vulnerability of pine species (longleaf vs. loblolly/shortleaf) to fire, we measured the distance between the lowest resin flow from resin wells and the ground on each cavity tree as an index of how vulnerable the trees were to fire. We also measured the lowest resin flow on 11 longleaf pine cavity trees, all >240 years old, at a small public park near Hemphill, Texas, to evaluate the vulnerability of old longleaf pine cavity trees to fire.

Annual visits to each red-cockaded woodpecker cluster (an aggregation of cavity trees used by a group of red-cockaded woodpeckers [see Walters et al. 1988]) on the Angelina NF included a search for new cavity trees. We searched areas around clusters by circling each cluster in a zig-zag path that extended about 300 m from the cluster center. Most new cavity trees were discovered as cavity starts (only a portion of the cavity entrance tube excavated) and were monitored annually until completion or abandonment. Although previously existing cavity trees (trees with large plates around the entrance and/or >1 cavity) were occasionally discovered, these cannot be considered true additions to the existing population of cavity trees. Only newly completed full cavities in new trees (single cavities with no plate or trees observed regularly by us after cavity starts were initiated) were considered to represent actual additions to the cavity tree population. New cavity starts cannot be counted because many of them are never completed.

Net annual cavity tree mortality was calculated based on the total cavity tree population, whereas red-cockaded woodpeckers were only excavating new cavity trees in active clusters, which contain only a portion of the total cavity tree population. To adjust for this bias, we determined the mortality of cavity trees in both active and inactive clusters on the Angelina NF from 1983 to 1990.

The presence of pitch tubes on the boles of pines indicated mortality caused by bark beetles, primarily the southern pine beetle. The after effect of mortality caused by wind was readily observable. Wind throw—trees blowing over from root decay—was distinguished from windsnap—trees breaking at a nest cavity leav-

ing a dead stub standing. Mortality caused by lightning and fire is often followed, and hence confounded, by bark beetle infestation. When we observed bark beetle attack on dead cavity trees with obvious signs of recent lightning or fire damage, beetles were not considered the mortality agent (see Conner and Locke 1979). The 4 trees that were considered to have died of old age and suppression were longleaf pines that were so old that fungal decay of the heartwood prevented age determination; growth increments (rings) in the outer 2 cm of xylem tissue were tightly packed, indicating very slow growth. Finally, if all the cavities in a tree were enlarged by other species of woodpeckers so that entrance diameters were >70 mm, we considered these cavity trees to have been lost. These losses were recorded on the Angelina NF from 1983 to 1990.

We used a *t*-test to compare heights of resin flow between tree species. A *G*-test (Sokal and Rohlf 1969:559–571) was used to compare cavity tree mortality within and between active and inactive clusters.

RESULTS

Bark Beetle Damage.—Bark beetles were the major direct cause (53.0%) of cavity tree death (Table 1). The primary bark beetle causing mortality was the southern pine beetle, which accounted for more than 98% of beetle-caused mortality. Bark engraver beetles (*Ips* spp.) and black turpentine beetles (*Dendroctonus terebrans*) were not a major problem. Most cavity tree loss occurred on the Sam Houston NF during the southern pine beetle epidemic from 1983 through 1986 following hurricane Alicia in 1983 (Table 1). During the peak of the southern pine beetle epidemic on the Raven Ranger District, active infestations were moving up to 16 m per day along a 5-km front (Billings and Varner 1986). Treatment to prevent additional beetle damage was delayed for 5 months due to administrative appeals because of the Four Notch area's Rare II classification (Billings and Varner 1986). In addition to 97 red-cockaded woodpecker cavity trees known to have been killed by bark beetles, up to 183 additional cavity trees (mortality cause unknown) and an additional 50 clusters may have been lost during this southern pine beetle epidemic (Table 1).

During endemic southern pine beetle population levels, bark beetles were still a major cause of mortality to cavity trees. Typically, only a

Table 1. Causes for mortality of red-cockaded woodpecker cavity trees on 3 national forests in eastern Texas.

Probable cause of death	No. cavity trees dying				% of all mortality factors
	Angelina (1978–90; n = 307 ^a)	Davy Crockett (1987–89; n = 390 ^a)	Sam Houston (1983–88 ^b ; n = 1,334 ^a)	Total of each mortality factor	
Bark beetles	30	7	97	134	53.0
Windsnapped	18	14	43	75	29.6
Fire	9	1	8	18	7.1
Wind throw (root rot)	1	1	8	10	4.0
Lightning	2	3	5	10	4.0
Old age/suppression	4	0	0	4	1.6
Herbicide	2	0	0	2	0.8
Subtotal	66	26	161	253	
Unknown	5	12	183 ^c	200	
Total	71	38	344 ^d	453	

^a n is the number of live cavity trees.
^b Exact years of deaths are unknown but are estimated to have occurred from 1983 to 1988.
^c Most of this mortality is most likely due to southern pine beetle infestation.
^d The total loss of an additional 50 clusters (≥82 cavity trees) that were killed most likely during the southern pine beetle infestation (by beetles or treatment cutting) is not listed in this table.

single cavity tree was infested by beetles, and adjacent trees in the cluster area were not affected. During the winter months (Nov–Mar), this same single tree mortality pattern is common at both endemic and epidemic southern pine beetle population levels (F. L. Oliveria, For. Pest Manage., U.S. For. Serv., pers. commun.). Mortality of this chronic nature is difficult to prevent once a cavity tree is infested. Bark beetle infestations during endemic populations are often dominated by *Ips* and black turpentine beetles with occasional southern pine beetle attacks (Bryant 1983).

Wind Damage.—High velocity winds caused many cavity trees (29.6% of mortality) to break at the cavity, leaving only a dead stub standing. Most of this mortality occurred in areas of continuous forest. However, there were >10 instances where cutting patterns appeared to increase wind associated mortality. Clear-cuts and beetle treatment cuts closer than 60 m to cavity trees, which is the Forest Service’s cluster protection zone, were often followed by breakage of ≥1 cavity tree.

Cutting that left 1 cluster area relatively isolated from other mature forest as a peninsula appeared to cause the loss of 2 cavity trees by windsnap in 2 years. In 1 instance a somewhat V-shaped cut, that was oriented so the tip of the V was near a cluster, appeared to funnel wind into a cluster area at higher forces than normal. Five cavity trees were snapped off in a 3-year period (1986–89) in this cluster.

Other Mortality Factors.—A variety of other

mortality factors also killed cavity trees. Prescribed fires caused 7.1% of the observed cavity tree mortality, which typically occurred when cavity trees were not adequately protected by removing flammable debris within 3 m of the base of the cavity tree (Conner and Locke 1979). Mortality caused by wind throw (4.0%) was typically associated with root rots (primarily *Heterobasidium annosum*) which decayed roots so extensively that even moderate wind velocities could blow the cavity tree over. Cavity trees wounded by lightning strikes (4.0%) were often subsequently infested and killed by bark beetles. During lightning strikes, the bark (down to xylem tissue) and often portions of the sapwood (xylem) were blown off the cavity trees in a spiraling vertical line down the bole, thus releasing terpenes attractive to the bark beetles (Coulson et al. 1983). Herbicide (2,4-D) injection of pine midstory trees during midstory control management accidentally killed 2 cavity trees. The herbicide apparently spread through the root systems of small injected pines that were 5 m from cavity trees (Conner 1989).

Pine Species Differences.—We examined mortality differences among tree species on the Angelina NF (Table 2). Bark beetles were the major cause of cavity tree mortality in loblolly and shortleaf pine, whereas fire was the major cause of mortality in longleaf pine cavity trees. The average height of the lowest resin flows on active longleaf pine cavity trees on the Angelina NF was 6.8 ± 3.6 (SD) m (n = 83), which was significantly lower than those on loblolly and

Table 2. Cavity tree mortality on the Angelina National Forest, Texas, by tree species, 1978–90.

Cause of death	No. pine trees dying			Total	%
	Loblolly	Shortleaf	Longleaf		
Bark beetles	18	6	6	30	42.3
Windsnapped	10	3	5	18	25.4
Prescribed fire	0	0	9	9	12.7
Old age/suppression	0	0	4	4	5.6
Lighting	1	0	1	2	2.8
Herbicide ^a	0	2	0	2	2.8
Wind throw (root rot)	0	0	1	1	1.4
Unknown	4	0	1	5	7.0
Total	33	11	27	71	

^a Killed by accident when adjacent pines were injected.

shortleaf pines ($\bar{x}$ = 9.0 ± 3.3 m, n = 47, t = 7.59, P < 0.001). Many of the longleaf pine cavity trees had resin flowing all the way to the ground. The average height of the lowest resin flow on old (>240 yr old) cavity trees in the Hemphill public park was 12.4 ± 3.5 m. Average cavity height in these old pines was 16.0 ± 6.7 m (n = 11), whereas cavity heights in longleaf pines on the Angelina NF averaged 8.9 ± 2.5 m (n = 64). Only longleaf pine cavity trees appeared to die of “old age” and suppression. The tops of a large proportion of loblolly pine cavity trees (30.3%) were snapped off by wind.

Active versus Inactive Clusters.—The observed rates of mortality of cavity trees differed between active and inactive clusters. Annual rates of mortality of cavity trees on the Angelina NF were 2.4% in active and 1.0% in inactive clusters (G = 4.21, P = 0.04). Comparable rates for the Davy Crockett NF were 4.6 and 2.5%, respectively. Although this difference was not statistically significant, mortality rates were higher in active clusters on both sites (G = 2.49, P = 0.14).

Within active clusters, we compared mortality rates for active and inactive cavity trees. No significant differences were detected for either forest or for the combined data for both forests (G -tests, P > 0.88), suggesting that cavity tree status (active vs. inactive) was not the cause of the observed difference in mortality rates between active and inactive clusters. Because inactive cavity trees tend to be older than active cavity trees (Conner and O’Halloran 1987), excessive tree age probably was not the cause of higher cavity tree mortality rates within active clusters.

Site Disturbance.—Bark beetle infestation or unknown causes were the primary causes of cav-

ity tree mortality in active clusters. Sixty percent of the total cavity tree mortality on the Angelina NF occurred during 2 (1988–89) of the 7 years (Table 3). This suggests that habitat disturbance within cluster areas might have increased the risk of bark beetle infestation. The higher priority given to essential management activities (e.g., midstory removal, basal area reduction, prescribed burns) in the vicinity of active clusters resulted in more disturbance in active than in inactive clusters; these disturbances could be associated with the observed differences in mortality rates.

Cavity Tree Dynamics.—Over the 7-year study period on the Angelina NF, red-cockaded woodpeckers were not excavating new cavity trees as rapidly as they were losing them. A comparison of newly completed cavities in new trees versus the number of cavity trees dying indicates a net loss of 28 trees for the entire cavity tree population over a 7-year period (Table 3). A comparison of the mortality of cavity trees in active and inactive clusters on the Angelina NF from 1983 to 1990 indicated that only 6 of the 28 cavity trees that died were in inactive clusters. This yields a net loss of 22 cavity trees for active clusters over the 7-year period. In addition, the loss of 49 useable cavities as a result of cavity enlargement by other woodpeckers over the 7-year period is a major concern (Table 3).

The population dynamics of cavity trees were different between tree species. Over a 7-year period on the Angelina NF, the average annual mortality of loblolly and shortleaf pine cavity trees was 5.3%, whereas annual longleaf pine cavity tree mortality averaged only 1.0% (paired t -test, t = 4.45, P = 0.004). Although red-cockaded woodpeckers replaced loblolly and shortleaf cavity trees at twice the rate of longleaf

Table 3. Gains and losses of red-cockaded woodpecker cavity/start trees on the Angelina National Forest, Texas.

	Yr							Total
	1984	1985	1986	1987	1988	1989	1990	
No. cavity/start trees ^a								
Loblolly/shortleaf	70	71	72	74	78	79	73	
Longleaf	164	169	170	173	175	187	187	
Subtotal	234	240	242	247	253	266	260	
No. new cavity/start trees ^b								
Loblolly/shortleaf								
New cavity	3	1	1	2	0	2	1	10
New start	4	2	1	4	6	4	0	21
Existing cavity/start tree	5	1	0	0	4	2	0	12
Longleaf								
New cavity	3	0	0	0	1	1	0	5
New start	1	2	0	4	3	3	3	16
Existing cavity/start tree	20	3	2	0	1	12	0	38
Subtotal	36	9	4	10	15	24	4	102
No. cavity trees dying								
Loblolly/shortleaf	1	3	1	4	6	7	7	29
Longleaf	2	0	1	1	3	4	3	14
Subtotal	3	3	2	5	9	11	10	43
Cavity enlargement ^c								
Loblolly/shortleaf	2	4	1	0	4	2	1	14
Longleaf	6	1	8	5	5	6	4	35
Subtotal	8	5	9	5	9	8	5	49
Net change in useable cavity trees ^d	+3	-2	-1	-3	-8	-8	-9	-28

^a Number reflects newly excavated trees and discovery of existing old cavity trees.
^b Trees found during spring surveys and preceding 11 months.
^c All cavities enlarged so extensively that the trees were unuseable for roosting and nesting.
^d Net change reflects the death of existing cavity trees versus newly excavated trees.

(1.4 vs. 0.7 newly completed cavity trees/yr), this difference was not statistically significant ($t = 1.99, P = 0.09$) (Table 3). The average age of loblolly and shortleaf pines at death was 87.8 years ($n = 29$), whereas dying longleaf pine cavity trees averaged 151.0 years old ($n = 14$), suggesting that longleaf may be of greater value to red-cockaded woodpeckers than other species of pine.

DISCUSSION AND MANAGEMENT IMPLICATIONS

Catastrophic disturbances such as hurricane Alicia in 1983 on the Sam Houston NF in Texas and hurricane Hugo in 1989 on the Frances Marion NF in South Carolina typically result in nonequilibrium forest landscapes (Shugart 1984). Nonequilibrium forest landscapes such as the Four Notch area of the Sam Houston NF can eventually become the focus of a massive disturbance such as a southern pine beetle epidemic (Coulson et al. 1986). Management cannot

prevent or anticipate the occurrence of catastrophic landscape disturbances. However, managers need to have the most effective methods available to prevent cavity tree loss during both epidemic and endemic levels of beetle populations.

We strongly advocate active management to reduce the loss of cavity trees. Direct treatments for southern pine beetle infestations include (1) cut and remove (salvage); (2) cut and leave; (3) cut and hand spray (chemical treatment); and (4) cut, pile, and burn (Billings 1980). Of these options, cut and remove provides the best opportunity to recover costs while removing material infested by bark beetles.

Currently, cut and leave or cut and hand spray are the only treatment options permitted during the red-cockaded woodpecker breeding season. The use of cut and leave during cooler months must be tempered with the potential risk that emerging bark beetles (Moser et al. 1987) may infest nearby cluster areas or cavity trees. Cut

and remove or cut and hand spray would greatly reduce or eliminate this risk. Cut and hand spray might be necessary during the breeding season, but only on trees cut during control operations. Cut, pile, and burn is prohibited in red-cockaded woodpecker clusters (U.S. Dep. Agric. 1987). These treatments are temporary at best and must be combined with long-term measures aimed at increasing stand vigor and an overall integrated pest management approach (Thatcher *et al.* 1986). Ideal treatment of beetles in red-cockaded woodpecker cluster areas might involve the use of bark beetle pheromones to inhibit infestation of cavity trees when such methods are perfected (e.g., Payne and Billings 1989). Cutting involved during direct treatment of southern pine beetle infestations needs to be implemented to prevent losses despite a possible increase in the chance of windsnap.

Site disturbance is known to be associated with beetle activity and hazard (Nebeker and Hodges 1985, Hicks *et al.* 1987). In view of this, management activities conducted in cluster areas (e.g., midstory control, fire lane plowing, and thinning operations) should be done when beetle activity in the general forest area is minimal and should minimize disturbance of root systems around and near cavity trees (Kulhavy *et al.* 1988).

Cavity tree loss caused by wind throw was probably unavoidable and will continue to occur. Minimizing root damage to pines and treating for annosus root rot during thinning in colony sites may help reduce such mortality (Froelich *et al.* 1977).

Cavity trees are quite vulnerable to fire because of the highly flammable resins that flow from the resin well wounds excavated daily by red-cockaded woodpeckers (Conner and Locke 1979). Of the 3 major causes of mortality, fire is the easiest to prevent by adequately protecting cavity trees (Conner and Locke 1979). Longleaf pine cavity trees are most vulnerable to fire because of the copious quantity of resin that seeps from resin wells and typically flows down close to the ground.

An obvious question arises as to how much damage natural fire did to cavity trees before the harvest of the virgin forest. Conner and O'Halloran (1987) suggested that cavities could be placed higher in the older pines of the virgin forest because sufficient heartwood would be present at greater heights in older pines. As a result, resin flows would not get as close to the

ground and the probability of ignition would be less. Examination of 11 virgin longleaf cavity trees at a small public park near Hemphill, Texas, lends support to this hypothesis. The average height of the lowest resin flow of these trees was 12.4 m, nearly twice as high as the 6.8-m average of longleaf pine on the Angelina NF that averaged 126 years old (Conner and O'Halloran 1987). Cavity entrance height (16.0 m) in the public park was also twice as high as cavity entrances (8.7 m) in longleaf pine on the Angelina NF.

Cavity tree mortality due to lightning is difficult to prevent. Mortality results from both mechanical injury to the bole and damage to the root system causing a loss of hydrostatic pressure (Taylor 1977). Prentice (1977) suggested that taller objects have a higher lightning strike frequency. Cutting patterns or methods that reduce the isolation of cluster areas from other mature forest might alleviate some of the potential for this type of mortality.

Cavity enlargement by pileated woodpeckers on national forest lands caused a major loss of cavities. Because cavity trees are not killed by enlargement, new cavities can be excavated in these trees. Enlarged cavities can be used by some cavity competitors (Rudolph *et al.* 1990), perhaps relieving some competitive pressure on unenlarged cavities. Enlargement damage, however, can either be prevented or repaired if not too extensive, with appropriate use of cavity restrictors (Carter *et al.* 1989).

LITERATURE CITED

- BILLINGS, R. F. 1980. Direct control. Pages 179–192 in R. C. Thatcher, J. L. Searcy, J. E. Coster, and G. D. Hertel, eds. *The southern pine beetle*. U.S. For. Serv. Sci. Educ. Adm. Tech. Bull. 1631.
- , AND F. E. VARNER. 1986. Why control southern pine beetle infestations in wilderness areas? The Four Notch and Huntsville State Park experience. Pages 129–134 in D. L. Kulhavy and R. N. Conner, eds. *Wilderness and natural areas in the eastern United States: a management challenge*. School of Forestry, Stephen F. Austin State Univ., Nacogdoches, Tex.
- BRYANT, C. M., V. 1983. Pine engraver and black turpentine beetles associated with endemic populations of southern pine beetles in east Texas. M.S. Thesis, Stephen F. Austin State Univ., Nacogdoches, Tex. 203pp.
- CARTER, J. H., III, J. R. WALTERS, S. H. EVERHART, AND P. D. DOERR. 1989. Restrictors for red-cockaded woodpecker cavities. *Wildl. Soc. Bull.* 17:68–72.
- CONNER, R. N. 1989. Injection of 2,4-D to remove

- hardwood midstory within red-cockaded woodpecker colony areas. U.S. For. Serv. Res. Pap. SOH-251. 4pp.
- , AND B. A. LOCKE. 1979. Effects of a prescribed burn on cavity trees of red-cockaded woodpeckers. *Wildl. Soc. Bull.* 7:291–293.
- , AND ———. 1982. Fungi and red-cockaded woodpecker cavity trees. *Wilson Bull.* 94:64–70.
- , AND K. A. O'HALLORAN. 1987. Cavity-tree selection by red-cockaded woodpeckers as related to growth dynamics of southern pines. *Wilson Bull.* 99:398–412.
- , AND D. C. RUDOLPH. 1989. Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine national forests. U.S. For. Serv. Res. Pap. SOH-250. 15pp.
- COSTA, R., AND R. E. F. ESCANO. 1989. Red-cockaded woodpecker status and management in the southern region. U.S. For. Serv. Reg. 8 Tech. Pap. R8-TP-12. 71pp.
- COULSON, R. N., P. B. HENNIER, R. O. FLAMM, E. J. RYKIEL, L. C. HU, AND T. L. PAYNE. 1983. The role of lightning in the epidemiology of the southern pine beetle. *Zeit. ang. Entomol.* 96:182–193.
- , E. J. RYKIEL, AND D. A. CROSSLEY, JR. 1986. Activities of insects in forests: implications for wilderness area management. Pages 115–119 in D. L. Kulhavy and R. N. Conner, eds. *Wilderness and natural areas in the eastern United States: a management challenge*. School of Forestry, Stephen F. Austin State Univ., Nacogdoches, Tex.
- FROELICH, R. C., E. G. KUHLMAN, C. S. HODGES, M. J. WEISS, AND J. D. NICHOLS. 1977. *Fomes annosus* root rot in the South, guidelines for prevention. U.S. For. Serv. Southeast. Area S & PF-4. 17pp.
- HICKS, R. R., JR., J. E. COSTER, AND G. N. MASON. 1987. Forest insect hazard rating. *J. For.* 85:20–26.
- JACKSON, J. A. 1977. Red-cockaded woodpeckers and pine red heart disease. *Auk* 94:160–163.
- KULHAVY, D. L., J. H. MITCHELL, AND R. N. CONNER. 1988. The southern pine beetle and the red-cockaded woodpecker: potential for interaction. Pages 337–343 in T. L. Payne and H. Saarenmaa, eds. *Integrated control of scolytid bark beetles*. Virginia Polytechnic Institute and State Univ., Blacksburg.
- LIGON, J. D., P. B. STACEY, R. N. CONNER, C. E. BOCK, AND C. S. ADKISSON. 1986. Report of the American Ornithologists' Union committee for the conservation of the red-cockaded woodpecker. *Auk* 103:848–855.
- MOSER, J. C., R. A. SOMMERS, P. L. LORIO, JR., J. R. BRIDGES, AND J. J. WITCOSKY. 1987. Southern pine beetles attack felled green timber. U.S. For. Serv. Res. Note SOH-342. 7pp.
- NEBEKER, T. E., AND J. P. HODGES. 1985. Thinning and harvesting practices to minimize site and stand disturbance and susceptibility to bark beetle and disease attacks. Pages 263–271 in S. J. Brannham and R. C. Thatcher, eds. *Proc. integrated pest management research symposium*. U.S. For. Serv. Gen. Tech. Rep. SOH-56.
- PAYNE, T. L., AND R. F. BILLINGS. 1989. Evaluation of (S)-verbenone applications for suppressing southern pine beetles (Coleoptera: Scolytidae) infestations. *J. Econ. Entomol.* 82:1702–1708.
- PRENTICE, S. A. 1977. Frequency of lightning discharges. Pages 465–496 in R. H. Golde, ed. *Lightning*. Vol. 1. Academic Press, New York, N.Y.
- RUDOLPH, D. C., R. N. CONNER, AND J. TURNER. 1990. Competition for red-cockaded woodpeckers roost and nest cavities: effects of resin age and entrance diameter. *Wilson Bull.* 102:23–36.
- SHUGART, H. H., JR. 1984. *A theory of forest dynamics*. Springer-Verlag, New York, N.Y. 278pp.
- SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman and Co., San Francisco, Calif. 776pp.
- TAYLOR, A. R. 1977. Lightning and trees. Pages 831–849 in R. H. Golde, ed. *Lightning*. Vol. 2. Academic Press, New York, N.Y.
- THATCHER, R. C., G. N. MASON, AND G. D. HERTEL. 1986. Integrated pest management in southern pine forests. U.S. For. Serv. Coop. State Res. Serv. Agric. Handb. 650. 38pp.
- U.S. DEPARTMENT OF AGRICULTURE. 1987. Final environmental impact statement—land and resource management plan national forests and grasslands Texas. U.S. For. Serv. Manage. Bull. R8-MB9. 626pp.
- U.S. FISH AND WILDLIFE SERVICE. 1985. Red-cockaded woodpecker recovery plan. U.S. Fish. Wildl. Serv., Atlanta, Ga. 88pp.
- WALTERS, J. R., P. D. DOERR, AND J. H. CARTER III. 1988. The cooperative breeding system of the red-cockaded woodpecker. *Ethology* 78:275–305.

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