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AN INCREASE IN A POPULATION OF RED-COCKADED WOODPECKERS

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Once abundant in pine forests of the southern United States, the red-cockaded woodpecker (*Picoides borealis*) was identified as endangered in 1968 (U.S. Fish and Wildlife

Service 1968), and was officially listed as such in 1970 (U.S. Fish and Wildlife Service 1970). The species received full protection of the law with passage of the Endangered Species Act in 1973. Attempts at managing the bird to improve its status began in the mid-1960's (Beland 1971) and have increased steadily. De-

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spite 2 decades of effort, however, significant declines and even extirpations of red-cockaded woodpecker populations have continued (Baker 1983, Carter et al. 1983, Jackson 1987, Ortego and Lay 1988, Conner and Rudolph 1989, Costa and Escano 1989, Walters 1990). Until now no red-cockaded woodpecker population has been observed to increase. Indeed, only 3 new clans (breeding pair, and frequently, helpers and young of the year) using new colony sites (aggregate of cavity trees used by a clan) have been reported (Lennartz and Heckel 1987, Jackson 1987).

Our objective was to monitor population change, if any, in a large and apparently healthy population of red-cockaded woodpeckers existing in what was thought to be a good habitat. In addition, we wanted to verify colonization (a new clan using a new colony site) if it was occurring. Finally, we wanted to describe the habitat conditions and management history associated with the population.

STUDY AREA

The 101,209-ha Francis Marion National Forest (FMNF) is on the lower coastal plain of South Carolina. The forested area (96,970 ha) is 51% loblolly pine (*Pinus taeda*), 19% longleaf pine (*P. palustris*), 2% pond pine (*P. serotina*), 25% hardwood, and 3% mixed pine and hardwood forest types (U.S. Forest Service 1985a).

Old-growth timber was harvested between 1885 and 1930 (U.S. Forest Service 1985a), before FMNF was established. After establishment of FMNF in 1936 and until 1950, timber was managed by single-tree selection. In 1950 even-age management with an 80-year rotation for pine was initiated. Rotation age for loblolly was lowered to 70 years in 1964 and to 60 years in 1971. In 1985, rotation age for loblolly pine was increased to 70 years, except on wet sites (6% of pine type), where rotations were lowered to 40 years. Longleaf pine rotations have been 80 years since 1950 (U.S. Forest Service 1977, 1985b).

Volume of pine sawtimber increased from 853,000 m³ in 1936 to 3,052,000 m³ in 1986. Five-year averages of annual harvests of pine sawtimber volumes were 15,000 m³ in 1937–1941 and 115,000 m³ in 1983–1987. During the past 10 and 30 years, respectively, 15% and 36% of pine acres were harvested and regenerated. After prescribed burning began in 1944, pine stands typically were burned in winter every 3–5 years. About 18,000 ha have been burned annually (U.S. Forest Service 1977, 1985b).

The first directive not to cut red-cockaded wood-

pecker cavity trees in FMNF came in 1966 or 1967, and by 1968 a 60-m uncut buffer was left around cavity trees during regeneration cuts. Prior to that time, cavity trees were cut as culls during thinnings and regeneration cuts (C. von Herrmann, National Forests in South Carolina, Columbia, S.C., pers. commun.). During timber harvests after 1974, at least 16 ha of pine >20 years old were left adjacent to each colony with the intent of providing foraging areas. Pine stands with colonies were thinned to reduce loss of cavity trees to pine beetles. The control of hardwood and pine mid-stories around cavity trees also was ordered (U.S. Forest Service 1975). Starting in 1980, colonies were adjacent to foraging areas, but no amount of foraging habitat was specified as was done formerly (U.S. Forest Service 1980). After lengthy consultation with the U.S. Fish and Wildlife Service, major changes in management occurred in 1985 (U.S. Forest Service 1985c). These changes had little, if any, impact on the condition of the forest or woodpecker population prior to completion of our study.

METHODS

Design

We determined population trend by comparing the results of 2 surveys, made 7 years apart, on the same random sample of plots. A plot was composed of 1–3 management compartments. To reduce sample variation, we excluded from the sampled population 10 of the 216 management compartments because they lacked pine forests and thus would not be used by red-cockaded woodpeckers. Also excluded was the 2,450-ha Santee Experimental Forest within FMNF. The remaining 205 compartments were grouped into 161 plots, each with 400–600 ha of pine forest. Ten plots then were selected randomly from each of the 2 FMNF ranger districts.

Surveys

Searches for Cavity Trees.—In 1979 and again in 1987–1988 the 20 plots, totalling 10,245 ha of pine stands, were thoroughly searched for red-cockaded woodpecker cavity trees. An observer walked parallel compass lines through forest stands with potential for presence of cavity trees and visually inspected all pine trees >30 cm diameter at breast height. The distance between compass lines and their orientation varied according to light conditions and density of the forest to ensure that no cavity trees were overlooked.

Determination of Clans.—One to 14 cavity trees tend to be aggregated into a cluster referred to as a colony. If a colony is not used by red-cockaded woodpeckers, it is considered abandoned. A colony used by red-cockaded woodpeckers is considered active, but could represent 0–2 clans. Thus, the number of active colonies in a sample plot does not necessarily equal the number of clans.

To determine the number of clans that active colonies in each sample plot represented, we found nests or watched the behavior of birds after they left their cavities in the morning in 1980–1981 and 1987–1988. We assumed that 2 or more birds using a colony and peacefully foraging together represented a clan. Colonies that were close together were watched simultaneously by several workers to determine the number of clans using them. Birds from adjacent colonies that either avoided each other or fought were considered 2 clans: those that foraged together peacefully were considered 1 clan. Our assumptions are supported by long-term intensive studies of marked birds in the FMNF (Hooper and Lennartz 1981, 1983; Hooper et al. 1982; Hooper and Harlow 1986; Lennartz et al. 1987).

Finding nests and observing behavior produced equivalent results. However, nest finding is limited to the nesting season, not all clans nest every year, and nest attempts can fail before they are discovered. In the initial survey we concentrated on finding nests by repeatedly climbing cavity trees throughout the 1980 and 1981 breeding seasons and examining cavity contents, but still had to observe behavior to determine clan status of 3 clans that did not nest. In 1988 we used a combination of nest searches and behavioral observations to determine the number of clans: if a nest was not readily found, we observed the behavior of the birds after they left their roost cavities.

Adjustment for Plot Boundary.—Colonies frequently occurred on the common boundary between surveyed and nonsurveyed plots. If the clan occupying that colony was tallied as 1 clan, the number of clans would have been overestimated. We assigned the value of 0.5 clan to any clan occupying a colony with cavity trees in both a surveyed plot and an adjacent nonsurveyed plot.

Adjustment for Colony Drift.—Colonies expand in geographic extent as new cavity trees are added. They also shift location, either rapidly when a clan establishes a new colony site disjunct from its original site, or gradually as new cavity trees extend 1 side of the colony and dying trees contract the other side (Hooper 1983, Walters et al. 1988, Walters 1990). Thus, apparent gains and losses within a plot are caused by colonies drifting into and out of surveyed plots, even when the number of clans in the population has not changed. When colony drift caused a clan using a colony astride a plot boundary to have a greater or lesser plot value in 1987–1988, its 1980–1981 clan value was assigned to the 1987–1988 resurvey. Therefore, any recorded change in number of clans in a surveyed plot represented either an addition or loss to the population, and not just the expansion of an existing colony into or out of a survey plot. Had we not made this adjustment, an inflated population increase would have resulted.

Forestwide Estimates

We used a stratified random ratio estimator (Cochran 1977:150–167) to estimate the total number of clans

in FMNF in 1980–1981 and 1987–1988. Each ranger district was a stratum. The auxiliary variate for the ratio estimator was the area of pine forest in each plot. We used a Wilcoxon's signed-ranked test (Conover 1980: 278–292) to test the null hypothesis of no increase in clans between 1980–1981 and 1987–1988.

Tests of Assumptions for Permanent Plots

Use of permanent plots is a more sensitive way to detect population change than use of a new random sample each time a survey is made (Cochran 1977: 345). Also, a population increase, if it occurred, would indicate that colonization had taken place. Given no prior increase in other populations and the rarity of colonizations reported in the literature, we felt it was critical to document colonization rather than rely on inference. Verification of colonization is dependent upon complete knowledge of clan and colony locations surrounding a suspected colonization. Such complete information would not be obtained from a new random sample each time a survey was repeated.

Use of permanent plots assumes surveyed and non-surveyed plots received similar treatment between surveys. The area of pine stands harvested during 1979–1988 and the area of mature pine remaining in 1988 were compared between the surveyed and nonsurveyed plots with *t*-tests. Rejection of the null hypothesis would tend to invalidate our assumption that surveyed and nonsurveyed plots had been managed the same. We also compared the ratio of active : inactive colonies from a 20% random sample of colony sites shown in Forest Service records for nonsurveyed plots to the ratio of active : inactive colonies in the surveyed plots with a *G*-test of independence. Rejection of the hypothesis of no difference would tend to invalidate our assumption that the permanent plots were representative of the FMNF.

Abandoned Colonies

We sampled the midstory basal area in the 9 inactive colonies in the surveyed plots and in 20 randomly selected active colonies in the surveyed plots with a 10-factor prism at 5 systematically located points in each colony. Midstory was considered pine and hardwood trees that had less than crown dominance or codominance within the stand. We used a *t*-test to test the null hypothesis that midstory basal area was similar in active and inactive colonies.

RESULTS

Trend in Survey Plots

In the 20 surveyed plots, we determined there were 82 clans present in 1980–1981 and

Table 1. Status of red-cockaded woodpecker clans in surveyed plots in 1980–1981 and 1987–1988 in Francis Marion National Forest, South Carolina. Changes in clans caused by colony drift are not accounted for (see Table 2).

Status		Number of occurrences
1980–1981	1987–1988	
Colony and clan	Colony and clan	71
No colony and no clan	Colony and clan	10
Colony and clan	Colony but no clan	5
Colony but no clan	Colony but no clan	4
Colony but no clan	No colony and no clan	2
Colony and clan	Colony and 2 clans	2
Colony but no clan	Colony and clan	1

91 clans in 1987–1988. The change in the number of clans between the 2 surveys was caused by demographics (Table 1) and colony drift (Table 2). As outlined in the methods, 2 adjustments were needed in the gross number of clans before a comparison could be made between the 2 surveys.

In 1980–1981, 28 clans occupied colonies astride the boundary between a surveyed and nonsurveyed plot. These 28 clans were assigned the value of 0.5, thus reducing the 82 clans to 68 clans. In 1987–1988, 28 clans again occupied colonies astride the boundary between a surveyed and nonsurveyed plot. As in the initial survey, the clans were given half value, thus reducing the 91 clans to 77 clans. The 1987–1988 data then were adjusted for colony drift (Table 2). We used the 1980–1981 value of each of the colonies in Table 2 rather than their 1987–1988 values. This adjustment for colony drift reduced the 1987–1988 results from 77 clans to 75 clans. All comparisons between the 1980–1981 and the 1987–1988 surveys were based on these 68 and 75 clans, respectively.

The increase of 68 to 75 clans was based on enumeration of clans in the survey plots, and no statistical inference was involved. Thus, the 10.3% increase represented an actual net increase in the number of clans in the surveyed plots.

Table 2. Changes in status of clans of red-cockaded woodpeckers caused by drifting of their colonies across survey plot boundaries between 1980–1981 and 1987–1988 in Francis Marion National Forest, South Carolina. The assigned values for 1980–1981 were used in analyses because changes caused by colony drift did not represent true population changes.

Assigned values		Number of occurrences
1980–1981	1987–1988	
0.5 ^a	1.0 ^b	3
0.0 ^c	0.5	2
0.5	0.0	1

^a A clan associated with a colony split by the survey plot boundary.

^b A clan associated with a colony entirely in a survey plot.

^c A clan associated with a colony entirely outside a survey plot.

Thirteen new clans were found in the surveyed plots in 1987–1988 (Table 1). One of these new clans resulted from a colony that was inactive in 1980–1981 becoming occupied by a clan by 1987–1988. Two of the 13 new clans were formed when 2 colonies that existed in 1980–1981 and supported 1 clan each were occupied by 2 clans each in 1987–1988 (Table 1). Ten of the 13 new clans were in new colonies disjunct from the adjacent colonies and represented colonization. In all 13 cases, the colonies adjacent to these new clans were still occupied by other clans.

Seven inactive colonies were found in the 1980–1981 survey. One of these colonies was reactivated by 1987–1988; in 2 others all the cavity trees had died. Five colonies that supported a clan in 1980–1981 were inactive in 1987–1988. With the 4 remaining colonies that were inactive in 1980–1981 and the 5 newly abandoned colonies, there were 9 inactive colonies in 1987–1988 (Table 1). Basal area of midstory pine and hardwoods was greater in the 9 inactive colony sites in the survey than in the 20 randomly selected active colony sites in the survey (9.3 vs. 3.3 m²/ha; $t = 2.7$, 9 df, $P = 0.022$).

Estimated Forestwide Trend

In 1980–1981, the estimated number of clans in the sampled population was 427 (95% CI =

249–605). The estimated number of clans in the 1987–1988 resurvey was 470 (95% CI = 263–676). This net increase of 10.1% was statistically significant ($T = 1.7$, 19 df, $P = 0.045$).

Comparability of Surveyed and Nonsurveyed Plots

The proportion of pine stands ≤ 10 years old did not differ among surveyed and nonsurveyed plots in 1988 (14.3% vs. 15.1%, respectively; $t = 0.3$, 199 df, $P = 0.746$). Neither was the proportion of pine stands ≥ 60 years old different among surveyed and nonsurveyed plots (18.7% vs. 18.8%, respectively; $t = 0.02$, 199 df, $P = 0.982$). Also, the proportion of inactive colonies was not significantly different between surveyed and nonsurveyed plots (10.5% vs. 11.1%; $\chi^2 = 0.5$, 1 df, $P = 0.250$). Thus, we did not reject the assumption that surveyed and nonsurveyed plots were similar.

DISCUSSION

Validity of Results

Did a population increase occur or were our results an artifact of our methods? We think the evidence overwhelmingly supports our conclusion of a population increase: (1) permanent plots allowed us to validate the occurrence of new colonies; (2) we determined the number of clans, not active colony sites; (3) the condition of the habitat in surveyed and nonsurveyed plots was similar; (4) people doing the field work were experienced with red-cockaded woodpeckers; (5) the same people searched for cavity trees in both surveys; (6) the method of finding colonies was highly accurate; (7) new colonies did not have the characteristics of old colonies; and (8) information independent of the surveys supported the hypothesis of a population increase. The first 3 factors were presented in the methods and results, but the others deserve further discussion.

Two people found cavity trees in the first survey, and 1 of these same people found the trees in the resurvey. A test of their accuracy

is provided by use of our tree-finding techniques by these same people in timber sale activities not related to the surveys. Collectively they have used our survey technique to locate colonies prior to timber sales in about 240 management compartments during 24 man-years. Assuming on average 2 colonies were involved in each compartment, they found 480 colonies during timber sale activities. Their searches prior to timber sales were followed by timber markers that examined for cavities and marked (either to leave or to cut) virtually every tree in timber sale areas that would potentially have a red-cockaded woodpecker cavity. The timber markers found only 2 colonies that the survey people had missed (1 each), giving an error of 0.42% in finding colonies associated with the timber sale work. Using the percent error derived from the timber sale searches gives an expected error of 0.4 colony for the initial survey if all 99 colonies found in the resurvey existed during the initial survey. If performance of these surveyors is treated as a binomial distribution (Zar 1984: 375–378), the estimated number of colonies missed in the initial survey would fall within 0.1–1.8 colonies ($P = 0.010$). Thus, it's unlikely that the 10 new colonies found in the resurvey were missed in the initial survey.

From past experience and because they have few or no resin wells, we believe for certain that some incomplete cavities were not located by the surveys. Colonies with completed cavities would have been found by virtue of their completed cavities, even if the uncompleted cavities were missed. Incomplete cavities that were isolated from a colony would not have represented a clan (no cavity and probably only 1 bird). Thus, failure to find all incomplete cavities had no bearing on the study.

New colonies in the resurvey ($n = 10$) differed in number of cavities and appearance from colonies found in both surveys ($n = 85$). New colonies averaged 1.8 cavities, compared to 5.0 cavities in the old colonies ($t = 8.9$, 35 df, $P = 0.001$). All cavities in new colonies

were active, but in old colonies, 32% of the cavities (139/435) were inactive. The appearance of cavities changes with age, and newly excavated cavities are strikingly different from cavities that have been excavated for a long time (Hooper et al. 1980). None of the cavities in new colonies had the characteristics of old cavities (weathered sapwood in the entrance tunnel and a large area of bark removed from around the entrance tunnel).

The inferred forestwide increase in the number of clans in FMNF between 1980–1981 and 1987–1988 was supported by additional evidence. First, the number of clans in the survey plots increased by actual count. Second, 2 major premises from the forestwide inference were partially verified: colonization and an increase in number of clans also occurred in at least some of the nonsurveyed plots. Research and management activities not related to the survey verified 4 colonizations, and 2 new clans not involving a new colony had occurred in nonsurveyed plots since 1981. We also found evidence that the population had increased in a cluster of nonsurveyed plots from which Beckett (1974) reported 13 active clans. We determined the area had 17 clans in 1989.

Factors Affecting an Increase in Clans

Why did the FMNF population increase when the majority of other populations are decreasing? At least 5 factors were involved: (1) a large inventory of pine sawtimber, (2) availability of old trees for cavity excavation, (3) control of hardwood midstory with prescribed fire, (4) protection of cavity trees, and (5) provision of foraging habitat.

After increasing steadily since 1936, the inventory of pine sawtimber remained stable between 1978 and 1986, the approximate period covered by our study. Pine sawtimber is the basic resource for red-cockaded woodpecker cavity trees and foraging habitat. The birds forage almost exclusively on pine when it is

available (Hooper and Lennartz 1981). Their cavities are put exclusively in live pines. They prefer trees with decayed heartwood (Hooper et al. 1991), and frequency of decay is a function of tree age. Thus, maintenance of large pine sawtimber volumes, accompanied by continued aging of the forest, provided improved habitat. However, these factors alone were not adequate to explain the population increase in FMNF. Pine sawtimber volumes have increased and forests are, on average, getting older on all southern national forests, but many are believed to have declining red-cockaded woodpecker populations (Costa and Escano 1989).

Two other factors, frequently lacking individually or in combination in other national forests (Costa and Escano 1989), appeared to have played a critical role in the population increase in FMNF. The first was the intensive prescribed burning program that retarded hardwood midstory development; populations lacking such programs at their colony sites have declined even though old trees were available for activities where some of these populations were located (Costa and Escano 1989, Conner and Rudolph 1989). The second factor was that old trees were available for cavity excavation. Hooper (1988) thought the availability of old trees in FMNF was the major factor accounting for its higher population density compared to 2 other national forests that lacked old trees for cavities. All 3 forests had equivalent burning programs.

Protection of cavity trees and foraging habitat played a role in the increase by reducing the rate of clan loss. Prior to about 1967, cavity trees were intentionally cut as cull trees during thinnings, and both cavity trees and foraging habitat were destroyed in timber harvests. Although the volume of pine sawtimber increased between 1936 and 1967, cutting of cavity trees may have slowed or prevented population growth. Initial attempts at protecting colonies were only partially successful because foraging habitat was provided only by

chance. The policy that began in 1975 of not isolating colonies from foraging habitat also was a major factor in reducing colony abandonment. Although adopted in 1985, the policy of providing 50 ha of foraging habitat for each clan had no effect on timber harvested until about 1988 and thus had no influence on the population changes we measured.

A reduction in timber harvesting could not have caused the population increase. The FMNF had more pine timber cut during the monitoring period than during the preceding period of equal length (88,475 m³ in 1981–1987 vs. 66,542 m³ in 1974–1980). Between 1979 and 1989, 1.5% of the pine acreage was regenerated annually, compared to 1.1% annually in the preceding 20 years.

Colonization

Walters et al. (1988) and Walters (1990) suggested that most red-cockaded woodpeckers compete to occupy territories with existing cavity trees rather than establish a new colony and territory. Their hypothesis is empirically supported by all studies of red-cockaded woodpeckers with relevant data. However, Walters et al. (1988) further suggested that under some conditions new clans with new colonies might occur. Walters' (1990) population was declining, and abandoned colony sites were relatively common and frequently reoccupied by new clans. Apparently, there was little pressure to form new colony sites in their population. In contrast, we found that 14 of 19 new clans in FMNF (13 in surveyed plots and 6 in non-surveyed plots) were occupying new colony sites. Most abandoned colonies in FMNF were not suitable for reoccupancy because of mid-story development or because adequate foraging habitat was not near to the colony. But potential cavity trees and large amounts of foraging habitat did provide opportunities for colonization.

Clearly red-cockaded woodpeckers do create new colony sites, and the rate at which we

observed their formation indicates populations can increase given suitable habitat. Nevertheless, only about 1% of males pursued this option in FMNF.

Hooper (1983) hypothesized that new clans could be added to a population by: (1) splitting a colony site and territory into 2 ownerships (budding), and (2) a male claiming a territory and excavating cavity trees to form a new colony (pioneering). Both processes have been observed (Walters 1990, this study). A third way a population could increase is for new clans to reoccupy abandoned colony sites, a common process in some populations (Walters 1990). Walters (1990) used the term "colonization" in the sense Hooper (1983) used "pioneering." We suggest that "pioneering" be retained because it has been observed as a distinct process and that "colonization" be expanded to include any new colony site, however created, if occupied by a new clan. Pioneering would always create a new colony site, but budding also has that potential when new cavity trees are disjunct from the original colony (see Hooper 1983).

Of the 14 colonizations we found, 2 clearly were formed by pioneering. In these 2 cases, a banded male excavated an isolated incomplete cavity into a completed cavity, obtained a mate, and nested successfully. Prior to completing their cavities, the males roosted in the open, either on the tree with the incomplete cavity or on an adjacent tree. One had been banded as a nestling in a colony that was 2 territories and 1,340 m from the new cavity tree. He was 25 months old when discovered excavating the cavity. The other male was captured in an artificial cavity erected briefly for that purpose. Neither male was associated with an adjacent clan while the new colonies were being constructed. In 1 case the closest colony was 520 m and in the other 1,530 m from the respective new cavity trees.

Four of the 14 colonizations we found in FMNF were <400 m, 4 were 401–800 m, 2 were 801–1,200 m, and 4 were 1,201–2,440 m

from the nearest colony. The 2 colonizations we saw formed by pioneering were >400 m from the nearest established colony. Therefore, it seems likely that some of the other colonizations were formed by pioneering. Although the budding process was not observed, some colonizations, especially those <400 m from another colony, probably occurred that way.

Abandonment of Colonies

Although we observed a net increase in the number of clans, colonies were being abandoned at a rate of 1.1% per year. Beckett (1971), Van Balen and Doerr (1978), Locke et al. (1983), and Conner and Rudolph (1989) thought hardwood midstory was associated with colony abandonment. Recently M. R. Lennartz (U.S. Forest Service, Washington, D.C., pers. commun.) found that pine or hardwood midstory encroachment had similar effects on colony abandonment. The greater midstory development in the abandoned colonies in the surveyed plots suggests that midstory encroachment was a primary cause of colony abandonment in FMNF. Indeed, of the 5 colonies abandoned since the initial survey, we think 4 were related to midstory. The fifth colony did not have a midstory problem and appeared to have ample foraging habitat.

SUMMARY

Using a repeated survey of randomly selected management compartments in FMNF, we estimated there were 427 clans of red-cockaded woodpeckers in 1980–1981 and 470 clans in 1987–1988. We inferred from the repeated surveys that this population increase of 10.1% over a 7-year period was significant ($P < 0.05$). Our inference was supported by (1) documentation of colonization (new clans using new colony sites) in both surveyed and nonsurveyed compartments; (2) an actual increase in number of clans in surveyed compartments; and (3) an actual increase in the number of clans in a group of nonsurveyed compartments.

Fourteen of 19 new clans were occupying new colony sites <400 m to 2,440 m from an adjacent colony. Two of these 14 colonizations were observed to be formed by pioneering, and were 520 m and 1,530 m from another colony. Either pioneering or budding was suspected in the formation of the 12 remaining new colonies, depending upon the distance the new colony was from another colony. Although only 1% of males were estimated to have colonized, colonization appears to be an important factor in the population biology of the species.

The population increase was attributable to: (1) a large inventory of pine sawtimber, (2) availability of old trees for cavity excavation, (3) control of hardwood midstory with prescribed fire, (4) protection of cavity trees, and (5) provision of adequate foraging habitat. The lack of any of these factors probably would have prevented a population increase.

Despite a net increase in number of clans, colonies were being abandoned at a rate of 1.1% annually. This loss was thought to be caused by encroachment of hardwood and pine midstories around cavity trees.

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ADDENDUM

On 21–22 September 1989, Hurricane Hugo hit FMNF killing an estimated 63% of the red-cockaded woodpeckers. In addition, 87% of their cavity trees and >50% of their foraging habitat were destroyed (Hooper et al. 1990). During the breeding season in 1990, the FMNF was estimated to have 236 potential clans (colonies with ≥ 2 adults) and an additional 79 colonies occupied by single birds (R. G. Hooper and J. C. Watson, FMNF, Moncks Corner, S.C., unpubl. data). Many of these birds were roost-

ing and nesting in the 550 manmade cavities that were excavated following the storm. The population could continue to decline until such time as it adjusts to the remaining habitat. Following regeneration of the forest, the population should begin to recover. The post-Hugo population and the remaining amount of habitat may be similar to the suspected population and habitat conditions following cutting of the old-growth forest prior to purchase of FMNF by the federal government in 1936 (R. G. Hooper, unpubl. data). The birds increased from those conditions to their 1988 level. Thus, we have some optimism that the population can recover to that level over the next 7 decades. Major obstacles to such a recovery are other hurricanes and possible restrictions on prescribed burning in the future.

LITERATURE CITED

- BAKER, W. W. 1983. Decline and extirpation of a population of red-cockaded woodpeckers in north-west Florida. Pages 44-55 in D. A. Wood, ed. Proc. red-cockaded woodpecker symp. II. Fla. Game and Fresh Water Fish Comm., Tallahassee.
- BECKETT, T. A. 1971. A summary of red-cockaded woodpecker observations in South Carolina. Pages 87-95 in R. L. Thompson, ed. The ecology and management of the red-cockaded woodpecker. U.S. Bur. of Sport Fish. and Wildl., and Tall Timbers Res. Stn., Tallahassee, Fla.
- . 1974. Habitat acreage requirements of the red-cockaded woodpecker. East. Bird Banding Assoc. News 37:3-7.
- BELAND, J. M. 1971. Timber management practices for red-cockaded woodpeckers on federal lands. Pages 125-127 in R. L. Thompson, ed. The ecology and management of the red-cockaded woodpecker. U.S. Bur. of Sport Fish. and Wildl., and Tall Timbers Res. Stn., Tallahassee, Fla.
- CARTER, J. H., R. T. STAMPS, AND P. D. DOERR. 1983. Status of the red-cockaded woodpecker in the North Carolina Sandhills. Pages 24-29 in D. A. Wood, ed. Red-cockaded woodpecker symp. II. Fla. Game and Fresh Water Fish Comm., Tallahassee.
- COCHRAN, W. G. 1977. Sampling techniques. John Wiley and Sons, New York, N.Y. 428pp.
- CONNER, R. N., 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. SO-250. 15pp.
- CONOVER, W. J. 1980. Practical nonparametric statistics. John Wiley and Sons, New York, N.Y. 494pp.
- COSTA, R., AND R. E. F. ESCANO. 1989. Red-cockaded woodpecker status and management in the southern national forests. U.S. For. Serv., Tech. Publ. R8-TP 12. 71pp.
- HOOPER, R. G. 1983. Colony formation by red-cockaded woodpeckers: hypotheses and management implications. Pages 72-77 in D. A. Wood, ed. Red-cockaded woodpecker symp. II. Fla. Game and Fresh Water Fish Comm., Tallahassee.
- . 1988. Longleaf pines used for cavities by red-cockaded woodpeckers. J. Wildl. Manage. 52: 392-398.
- , AND R. F. HARLOW. 1986. Forest stands selected by foraging red-cockaded woodpeckers. U.S. For. Serv. Res. Pap. SE-259. 10pp.
- , L. J. NILES, AND G. W. WOOD. 1982. Home ranges of red-cockaded woodpeckers in coastal South Carolina. Auk 99:675-682.
- , AND M. R. LENNARTZ. 1981. Foraging behavior of the red-cockaded woodpecker in South Carolina. Auk 98:321-334.
- , AND ———. 1983. Roosting behavior of red-cockaded woodpeckers with insufficient cavities. J. Field Ornithol. 54:72-76.
- , ———, AND H. D. MUSE. 1991. Heart rot and cavity selection by red-cockaded woodpeckers. J. Wildl. Manage. 55:323-327.
- , A. F. ROBINSON, AND J. A. JACKSON. 1980. The red-cockaded woodpecker: notes on life history and management. U.S. For. Serv. Gen. Rep. SA-GR 9. 8pp.
- , J. C. WATSON, AND R. E. F. ESCANO. 1990. Hurricane Hugo's initial effects on red-cockaded woodpeckers in the Francis Marion National Forest. Trans. North Am. Wildl. and Nat. Resour. Conf. 55:220-224.
- JACKSON, J. A. 1987. The red-cockaded woodpecker. Pages 479-493 in R. L. Di Silvestro, ed. Audubon Wildl. Rep. 1987. Academic Press Inc., Orlando, Fla.
- LENNARTZ, M. R., AND D. G. HECKEL. 1987. Population dynamics of a red-cockaded woodpecker population in Georgia Piedmont loblolly pine habitat. Proc. Southeast. Nongame and Endangered Wildl. Symp. 3:48-55.
- , R. G. HOOPER, AND R. F. HARLOW. 1987. Sociality and cooperative breeding of red-cockaded woodpeckers, *Picoides borealis*. Behav. Ecol. and Sociobiol. 20:77-88.
- LOCKE, B. A., R. N. CONNER, AND J. C. KROLL. 1983. Factors influencing colony site selection by red-cockaded woodpeckers. Pages 46-50 in D. A. Wood, ed. Red-cockaded woodpecker symp. II. Fla. Game and Fresh Water Fish Comm., Tallahassee.
- ORTEGO, B., AND D. LAY. 1988. Status of red-cockaded woodpecker colonies on private land in east Texas. Wildl. Soc. Bull. 16:403-405.
- U.S. FISH AND WILDLIFE SERVICE. 1968. Rare and endangered fish and wildlife of the United States. Resour. Publ. 34. 143pp.
- . 1970. Conservation of endangered species

- and other fish and wildlife. *Fed. Regist.* 35:16047-16048.
- U.S. FOREST SERVICE. 1975. Red-cockaded woodpecker. *In* Wildlife management handbook. For. Serv. Handb. 2609.23R, Southern Region, Atlanta, Ga.
- . 1977. Francis Marion National Forest land management plan: final environmental impact statement. Francis Marion and Sumter National Forests, Columbia, S.C. 288pp.
- . 1980. Red-cockaded woodpecker. *In* Wildlife management handbook. For. Serv. Handb. 2609.23R, Southern Region, Atlanta, Ga.
- . 1985a. Final environmental impact statement land and resources management plan. Francis Marion and Sumter National Forests, Columbia, S.C. 560pp.
- . 1985b. Francis Marion National Forest land resources management plan. Francis Marion and Sumter National Forests, Columbia, S.C. 286pp.
- . 1985c. Red-cockaded woodpecker. *In* Wildlife management handbook. For. Serv. Handb. 2609.23R, Southern Region, Atlanta, Ga.
- VAN BALEN, J. B., AND P. D. DOERR. 1978. The relationship of understory to red-cockaded woodpecker activity. *Proc. Southeast. Assoc. of Fish and Wildl. Agencies* 32:82-92.
- WALTERS, J. R. 1990. The red-cockaded woodpecker. Pages 69-101 *in* W. D. Koenig and P. B. Stacey, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge Univ. Press, Cambridge, England.
- , P. D. DOERR, AND J. H. CARTER. 1988. The cooperative breeding system of the red-cockaded woodpecker. *Ethology* 78:275-305.
- ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J. 718pp.

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