FINAL REPORT

SECTION 6

ENDANGERED SPECIES ACT

OKLAHOMA
DEPARTMENT OF WILDLIFE CONSERVATION

FEDERAL AID PROJECT E-3

BIOLOGY OF THREATENED AND ENDANGERED SPECIES IN OKLAHOMA

STATUS AND HABITAT RELATIONSHIP OF RED-COCKADED WOODPECKERS IN OKLAHOMA

APRIL 1, 1989 - MARCH 31, 1991

FINAL REPORT

STATE: OKLAHOMA **PROJECT NUMBER:** E-3

PROJECT TITLE: Biology of Threatened and Endangered Species in Oklahoma

STUDY TITLE: Status and Habitat Relationship of Red-cockaded Woodpeckers in Oklahoma

PERIOD COVERED: 1 April 1989 to 31 March 1991

ABSTRACT

We searched 4,600 ha of the McCurtain County Wilderness Area, Oklahoma, in 1989-90 and located 15 Red-cockaded Woodpecker (*Picoides borealis*) clans. In 1977, 83% (3,795 ha) of this area was searched, and 29 Red-cockaded Woodpecker clans were found (Wood 1977). There was a 62% decline (from 29 to 11) in the number of Red-cockaded Woodpecker clans and a 74-76% decline in the number of individuals (from 86-92 to 22) in the resurveyed area (3,795 ha) since 1977. Within the resurveyed area, we found only 3 of 22 clusters of cavity trees (active and abandoned) >400 m from a cluster that was active in 1977 (Wood, unpubl. data), which indicated a low rate of colonization of new areas. The productivity of the population was low during the study period; only 0.69 young per nesting attempt were fledged. Vegetation characteristics were measured in a 510-ha study area to assess quality of foraging habitat. Vegetation characteristics measured were basal area, DBH (diameter at 1.4 m above the ground), number of pines >25.4 cm DBH/ha, and number of midstory stems (<12.7 cm DBH). Linear regression was used to examine the relationship between foraging habitat quality and distance from the nearest active clusters. The distance from the sample points to the nearest active cluster did not explain a large portion of the variation in any of the vegetation variables for pines or hardwoods. Overall, foraging habitat in the McCurtain County Wilderness Area meets requirements established in the Red-cockaded Woodpecker Recovery Plan (USFWS 1985).

We compared habitat at 18 active Red-cockaded Woodpecker cavity trees (cluster sites) and 18 paired non-use sites. The area surrounding active cavity trees (0.04 ha) had significantly shorter hardwoods and less hardwood basal area than non-use sites. Within

cluster sites, the 0.01-ha quarter directly in front of the cavity opening also had significantly shorter hardwoods, hardwoods with smaller DBHs, and less hardwood basal area than the remainder of the area surrounding the cavity tree. In addition, basal areas of pines 31.3 m from cluster sites were significantly higher than randomly sampled habitats, but there was no significant difference in the density of hardwoods between these 2 samples. Hardwood density at cluster sites was greater than recommended by the Red-cockaded Woodpecker Recovery Plan but was comparable to hardwood densities documented elsewhere in the range of the Red-cockaded Woodpecker. Our observations suggest that Red-cockaded Woodpeckers selected habitat on at least 2 levels: (1) low hardwood densities were selected for cavity sites and (2) high pine densities were selected for foraging habitat.

REPORT CONTENT

I. OBJECTIVE NUMBER: 1

Determine the current status of the Red-cockaded Woodpecker (*Picoides borealis*) in southeastern Oklahoma by (1) intensively surveying the McCurtain County Wilderness Area to determine the locations of active and inactive colonies, and less intensively surveying areas where active colonies were known to exist off the wilderness area in 1977 (Wood 1977), and (2) determining size of clans and recruitment within currently active colonies on McCurtian County Wilderness Area.

Vegetative succession occurring on the wilderness area has been postulated as the reason for declining Red-cockaded Woodpecker numbers on the area. We will test the vegetative succession hypotheses by (3) comparing past and present forest characteristics (as established by Wood [1977]) of active and inactive colonies to see if a relationship exists between forest succession and colony location and productivity.

II. INTRODUCTION

The Red-cockaded Woodpecker is endemic to mature pine forests of the southeastern United States and has been listed as an endangered species since 1970. The decline of this species has been caused by loss and fragmentation of mature pine forests (USFWS 1985). Aside from documenting decreasing abundance, little research has been done on small (<25 clans) isolated populations of Red-cockaded Woodpeckers (Ortego and Lay 1988, Eddleman and Clawson 1987, Baker 1983, Thompson 1976). We have found no published instances where small isolated populations have maintained or increased in abundance.

The McCurtain County Wilderness Area in southeastern Oklahoma contains a small isolated population of Red-cockaded Woodpeckers (Wood 1977, Masters et al. 1989). Timber harvesting has never occurred in McCurtain County Wilderness Area; however, private timber lands managed on an even-age, short-rotation basis (<60 yrs) surround the wilderness area. The nearest population of Red-cockaded Woodpeckers from the wilderness area is in the Ouachita National Forest which is 40 km to the northeast (Burnside 1983).

A 1977 survey of 3,795 ha of the wilderness area located 29 clans and 86-92 individuals (Wood 1977). In 1985, the area within 400 m of those 29 active clusters was resurveyed for Red-cockaded Woodpecker activity; only 14 active clusters were found in this area (Masters et al. 1989). Fires in the wilderness area have been suppressed since 1926 (Carter 1967). Concern has been expressed that fire suppression in the wilderness area has or will preclude pine regeneration and result in a hardwood-dominated forest that is unsuitable for the Red-cockaded Woodpecker (Wood 1977, Masters et al. 1989).

Red-cockaded Woodpeckers excavate cavities exclusively in mature southern pines (e.g., *Pinus palustris, P. taeda, P. echinata*). Cavities are usually placed in trees >60 years old if they are available (USFWS 1985, Conner and O'Halloran 1987). Several studies have described characteristics of cavity trees and investigated causes of cavity abandonment (Hopkins and Lynn 1971, Teitelbaum and Smith 1985, Conner and O'Halloran 1987, Hooper 1988). Size and age of pines and density of hardwood midstory have been proposed as the primary factors that influence placement of cavities by Red-cockaded Woodpecker (Van Balen and Doerr 1978, Locke et al., 1983, USFWS 1985, Hovis and Labisky 1985, Conner and O'Halloran 1987, Conner and Rudolph 1989). Red-cockaded Woodpeckers select cavity trees that are surrounded by relatively open forests (within 200 m) (Hovis and Labisky 1985). Some evidence exists that Red-cockaded Woodpeckers select cavity trees that have sparse hardwood midstory within several meters and that the midstory nearest the cavity entrance differs from the remainder of the midstory in the vicinity of the cavity tree (Van Balen and Doerr 1978). However, the importance and differences in habitat selection at different levels (*e.g.*, distance from a prospective cavity tree) have not been investigated.

To examine habitat selection and the influence of hardwood encroachment on active cavities of Red-cockaded Woodpeckers in the wilderness area, we measured vegetative characteristics around cavity trees and compared them to the habitat around randomly chosen paired non-use sites (without cavities) and randomly placed sites.

III. STUDY AREA

The McCurtain County Wilderness area is a 5,700-ha shortleaf pine (*P. echinata*)-mixed hardwood forest located in southeastern Oklahoma. Pines are more abundant on upper south facing slopes (Carter 1967, Masters et al. 1989, pers. obs.); north facing slopes are dominated by hardwoods, primarily oaks (*Quercus* spp.) and hickories (*Carya* spp.). The terrain is rolling to steep, and elevations range from 183 m to 439 m (Masters et al. 1989). The wilderness area has been owned by the State of Oklahoma since 1918 and managed by the Oklahoma Department of Wildlife Conservation since 1926 (Carter 1967).

IV. METHODS

Clusters.--We used the term clan to refer to a group of Red-cockaded Woodpeckers that foraged together and used closely associated cavity trees: none of the cavity trees located were >300 m from the nearest cavity tree of the same cluster. Clan also referred to single birds that were not associated with other birds. A cavity tree was any tree that contained $\geq$1 Red-cockaded Woodpecker cavity. An active cluster referred to the cavity tree(s) currently used by a clan (Walters et al. 1988, Rudolph et al. 1990). A group of cavity trees that were not currently being used by a clan were termed an abandoned cluster.

In May-July 1989 and January-May 1990, 4,600 ha of the McCurtain County Wilderness Area were searched along transects placed at 60-m intervals. All pine trees within 30 m of the transects were examined for Red-cockaded Woodpecker cavities (Fig. 1). This technique was identical to the primary technique use by Wood (1977). All of the 3,795 ha searched by Wood in 1977 was resurveyed. An additional 120 ha in the McCurtain County Wilderness Area were assumed to contain no active clusters because infrared aerial photographs revealed that this area contained few pines, and therefore was not searched. Tape recordings of Red-cockaded Woodpecker calls were played intermittently throughout the searched area to attract birds.

When an active cluster was located, the number of birds in the clan was determined by watching the cavity trees at dawn, dusk, or during nesting (45-60 minutes/occasion) on $\geq$3 occasions in 1989 and $\geq$6 occasions in 1990. Clan size censuses were conducted in both years for clusters located in 1989. Nests were located by observing bird behavior and by listening for nestlings begging for food. Clans were observed weekly to determine the presence of a nest throughout the nesting season (15 April - 1 July). Nests were monitored on a weekly basis until young fledged or the nest failed. The number of fledglings was determined by monitoring each clan 2-3 times weekly after completion of nesting. After the number of adults known to be in the clan were located, they were followed for approximately 30 minutes to determine if fledglings were present. Fledglings were easily distinguished by their coloration, awkward bark-scaling, and begging behavior (Jackson 1983).

At each cavity tree we measured: (1) number of cavities; (2) diameter at 1.4 m above the ground (DBH); (3) tree height; (4) height of lowest limb; (5) cavity height; (6) cavity orientation; (7) slope; and (8) aspect. Aspect was defined as the orientation at which the slope was the greatest and was measured with a hand-held compass from 10 m upslope of the cavity tree. Heights and slopes were measured with a SUUNTO clinometer, and diameter was measured with a DBH tape. Active cavity trees were tagged with circular silver tags 1.4 m above the ground; each active cluster site was marked with orange-colored rebar stakes.

Vegetation surrounding 18 active cavity trees (cluster sites) and at 18 paired non-use sites was measured. At 15 active clusters, an active cavity tree (referred to as the base tree) was selected to be a plot center for habitat measurements if it had been used as a nest tree ($n = 2$). If the nesting history was unknown at a particular cluster, a base tree was chosen at random ($n = 13$). At 3 clusters, there was an active cavity tree >180 m from the initially selected base tree; these 3 trees were measured as independent base tree sites. Circular 0.04-ha plots were establish with the base tree at the center (Fig. 2). Within each base-tree plot, we measured height and DBH of all plants $\geq$1 m tall and $\geq$5.0 cm DBH and counted saplings (>1 m tall and <5.0 cm DBH). All species of deciduous trees were grouped as "hardwoods" for analysis. Each plot was divided into 4 quadrants; the direction of cavity orientation determined the midpoint of quadrant 1 (Fig. 2). Foliage cover was estimated using a forest densiometer at the point where each quadrant line intersected the 0.04-ha circular plot boundary. Basal area measurements were taken with a 10-factor prism at 31.3 m and 71.3 m from the center of the base tree along the quadrant boundary lines (Hovind and Rieck 1970).

Cluster and non-use sites were paired by the DBH of the base tree and slope and aspect of the site. Non-use sites were randomly located on a topographic map in areas that were: (1) within the 4,600 ha that had been searched for clusters; (2) >500 m from active clusters; and (3) >500 m from the boundary of the searched area. These criteria were used to eliminate the possibility that the non-use sites were being used by Red-cockaded Woodpeckers. We located these random points in the field and then found the site closest to the random point that had a pine within 5 cm DBH of the base tree and a slope within 3 degrees and aspect within 10 degrees of the paired cluster site. If no suitable base tree was found within 200 m of the random point, another random point was chosen. Tape recordings of Red-cockaded Woodpeckers were played intermittently over a 3-hour period at non-use sites to ensure that the area was not currently being used by Red-cockaded Woodpeckers. Orientation of quadrant directions at each non-use site base tree were the same as quadrant directions at the paired cluster site base tree. Comparisons were made among quadrants within cluster sites to identify habitat differences that were related to cavity orientation. Identical comparisons were made among quadrants of non-use sites to determine if site characteristics alone could account for differences found among quadrants in cluster sites. Cluster sites were compared to non-use sites by quadrant and overall.

Foraging Habitat Measurements.--Vegetation characteristics were measured at 127 points on 12 randomly located transects within a 510-ha study area (Fig. 1); these transects were not permanently marked. Points along transects were spaced at 80-m intervals; transects contained from 3-19 points. The sample points ranged from 50 to 1.650 m from the nearest active cluster ($\bar{x}$ = 560 $\pm$ 412 m, n = 127). At each point, we measured basal area and DBH of pines and hardwoods (>12.7 cm DBH) with a 10-factor prism (Grosenbaugh 1952, Hovind and Rieck 1970) and counted stems (<12.7 cm DBH) >1 m tall within 3.6 m of the point. Classification by DBH was used to separate trees that were potential foraging habitat (>12.7 cm DBH) from those that were too small to be important for foraging and may be selected against because of Red-cockaded Woodpeckers affinity for forests with an open midstory (USFWS 1985, Porter and Labisky 1986).

To assess overall quality of the foraging habitat, vegetation characteristics that we measured were compared to suitable foraging habitat parameters as defined in the Red-cockaded Woodpecker Recovery Plan (USFWS 1985). We also compared our observations to the habitat within the home range of 18 Red-cockaded Woodpecker clans in the Francis Marion National Forest (Hooper and Harlow 1986).

We hypothesized that if poor quality foraging habitat was responsible for the decline in the number of Red-cockaded Woodpeckers in the McCurtain County Wilderness Area, the remaining active clusters would be located near high quality foraging habitat and the quality of the habitat would decline further from colonies. We defined high quality foraging habitat by the following generalized model (USFWS 1985, Hooper and Harlow 1986, Porter and Labisky 1986): (1) more basal area of pines and less basal area of hardwoods; (2) pines with larger DBH and hardwoods with smaller DBH; (3) more large pines (>25.4 cm DBH); and (4) fewer midstory stems (<12.7 cm DBH) particularly hardwood stems.

Basal area point samples taken 31.3 m from the cluster site base trees along the quadrant boundary lines (Fig. 2) were compared to the 127 basal area samples used to evaluate foraging habitat. Trees <12.7 cm DBH were eliminated from the cluster site samples so that the techniques used in collecting the 2 samples were identical.

Statistical Analysis.--SYSTAT (version 2) was used to conduct all analyses (Wilkinson 1989). Linear regression analysis was used to determine relationships between the distribution of quality foraging habitat and the distance of the sample points from the nearest active cluster. Bartlett's test for homogeneity of variance was used to test for differences in variance in samples with $\geq$30 observations. T-tests were used to compare cavity tree characteristics when sample sizes were $\geq$30. When variances were unequal, a separate variance t-test was employed (Sokal and Rohlf 1981). Mann-Whitney U-tests were used for comparisons of samples with <30 observations. All deciduous tree species were grouped for analysis.

Cavity orientation and aspect data were analyzed by breaking down each angle (orientation) into its sine and cosine vectors. The mean sine and cosine vectors for all the orientations were calculated. The angle characterized by the mean sine and cosine was used as the mean orientation. The mean sine and cosine were squared and summed; the square root of the sum was a measure of distribution (r) of the data around the mean, which was tested against a random distribution (Batschelet 1981).

Comparison among quadrants within sites were made with Friedman's 2-way ANOVA (Conover and Iman 1981). Wilcoxon's signed ranks tests were used to make comparisons between cluster and non-use sites for each habitat variable (Sokal and Rohlf 1981). Because 5 Wilcoxon's tests were conducted for each habitat variable, a sequential Bonferroni correction was employed to control Type 1 error (Rice 1989). An initial critical P value of 0.01 (0.05/5 tests) was used to indicate significance. If none of the 5 tests had a P value <0.01 then none were significant. If 1 of the 5 tests had a P value <0.01 then it was significant and the critical P value was adjusted to 0.0125 (0.05/(5-1 tests)) and the remaining 4 P values were reexamined to determine if they were <0.0125. The critical P value was increased each time a test was significant (*i.e.*, for the 5th test the critical P value was 0.05 if the previous 4 tests were significant). Discriminant function analysis also was used to distinguish between cluster and non-use sites.

V. RESULTS

Population Status

Fifteen active Red-cockaded Woodpecker clans were located (Fig. 1); 11 of them (73%) within the 3,795 ha surveyed in 1977. This represented a 62% decline (29 to 11) in the number of clans in the 1977 survey area. Each of the 15 clans used one active cluster. Of the 11 active clusters in the resurveyed area, 10 were within 400 m of an active cluster located in 1977. In addition, 10 of 12 abandoned clusters (83%) located were within 400 m of an active cluster location reported by Wood (1977). This suggests that Red-cockaded Woodpeckers in the McCurtain County Wilderness Area have not frequently formed new clans or established clusters in new locations, and are restricted in the areas that they use.

The modal clan size was 2 (n = 15) with a range of 1-4 individuals. A total of 31 individuals was found. Of these, 22 individuals were within the resurveyed area, which represented a 74-76% decline. Birds were never located in areas without active cavity trees; however, a member of a clan had no known roost cavity in 2 cases. Cavity enlargement by competitors was examined as a possible contributing factor to population decline. Of all cavities that were located (active and abandoned; n = 64), 23% had been enlarged by other species. No Red-cockaded Woodpeckers were observed using enlarged cavities. Of the 32 cavities known to be active at some point during this study, 28% (n = 9) were later abandoned. Only 2 of these abandoned cavities were noticeably enlarged. It is not known if enlargement occurred prior or subsequent to abandonment.

During the 1989 nesting season, only 6 clans were located; 5 of these nested. A single young fledged at 1 nest; the other 4 nests did not fledge young that survived until the time of our next weekly census. Nests were located at 8 of 15 colonies in 1990, and all 8 nests produced a single fledgling. During both years, at least 10 of the 13 nests had >2 nestlings. However, brood reduction occurred in all successful nests; generally only 1 nestling remained in the nest 1 week prior to fledging. Nine fledglings were produced in these 13 nests, or an average of 0.69 young/nest.

We found clans with fewer individuals and clusters with fewer cavity trees than were reported by Wood (1977) (Table 1). Slope at the cluster was the only other characteristic that differed between 1977 and 1990 (Table 1). Cavity orientation ($\bar{x}$ = 254 degrees, n = 39, r = 0.55, $P < 0.001$) and aspect ($\bar{x}$ = 231.6 degrees, n = 32, r = 0.42, $P < 0.004$) found in

1990 had significantly directional distributions. The directional tendency of the aspect may be related to the higher abundance of pines on south facing slopes.

Habitat Characteristics

Within Site Comparisons.--No significant differences were found in the number of pine saplings, DBH of pine trees, basal area of pines, or height of pines among quadrants in either cluster or non-use sites. Quadrant 1 of cluster sites had shorter hardwoods than the other 3 quadrants (Friedman's statistic = 14.5, P = 0.002, df = 3: Sum of ranks: quadrant 1 = 28, quadrant 2 = 54, quadrant 3 = 53, quadrant 4 = 45). The difference in the height of hardwoods between quadrant 1 and the other 3 quadrants in cluster sites indicated that Red-cockaded Woodpeckers selected areas with shorter hardwoods in which to orient their cavity openings. At non-use sites, quadrant 1 also had shorter hardwoods (Friedman's statistic = 9.5, P = 0.023, df = 3; Sum of Ranks: quadrant 1 = 32, quadrant 2 = 44, quadrant 3 = 55, quadrant 4 = 49), which suggested that shorter hardwoods may be inherent to the cavity orientations and type of sites (*i.e.*, slope, aspect, and tree size) selected by Red-cockaded Woodpeckers. There were no significant differences in number of hardwood saplings, hardwood DBH, or hardwood basal area among quadrants within either cluster or non-use sites. Forest cover (measured with a densiometer) did not differ significantly among quadrants within sites. Basal area of pines and hardwoods 31.3 m and 71.3 m from the base tree did not differ significantly among quadrants within either cluster or non-use sites.

Between Site Comparisons.--Overall (*i.e.*, in all 4 quadrants combined), cluster sites had less hardwood basal area and shorter hardwoods than non-use sites. Quadrant 1 was the most disparate between the cluster and non-use sites (Table 2). Additionally, hardwoods in quadrant 3 were significantly shorter in cluster sites than in non-use sites. There was significantly less foliage cover in cluster sites (82.1 ± 4.1%, n = 18) than in non-use sites (84.2 ± 4.9%, n = 18) (Z = 2.44, P = 0.015). Because this difference was small, it is unclear if it is biologically significant; it may reflect smaller, sparser hardwoods at cluster sites than at non-use sites. The shorter, sparser hardwoods in quadrant 1 and cluster sites as a whole indicated selection against hardwoods near cavity trees by Red-cockaded Woodpeckers.

Overall and in quadrant 1, cluster sites had significantly more pine saplings than non-use sites (Table 3). There were no other significant differences in pines between cluster and non-use site, base-tree plots. The higher pine density in cluster sites compared to non-use sites, particularly the number of saplings in each quadrat, was probably due to the open (in terms of hardwoods) character of the forest selected for cluster sites.

Discriminant function analysis using basal area, average height, and average DBH of hardwoods in quadrant 1 correctly classified 28 of the 36 sites (78%) as either cluster or non-use ($X^2 = 48.4$, df = 4, $P < 0.001$), which further emphasized the importance of hardwoods in quadrant 1 in selection of cavity sites. Four cluster and 4 non-use sites were incorrectly classified.

Quadrant 3 at cluster sites had significantly more pine and less hardwood basal area 31.3 m and 71.3 m from the base tree than at non-use sites (Table 4). There was an overall trend toward more pine and less hardwood at cluster sites when compared to non-use sites at both 31.3 and 71.3 m from the base trees. There was significantly more pine basal area 31.3 m from cluster site base trees than at randomly selected sites (Table 5). These 2 samples did not differ significantly in the amount of hardwood basal area. Apparently, pine density is of greater importance than hardwood density in habitat selection 31.3 m from the cavity tree.

Foraging Habitat.--There were only 2 significant relationships between the distance from the nearest active cluster and 3 habitat variables, and only a small percentage of the variation was accounted for (Table 6). We believe that proximity of clusters to quality foraging habitat was not a primary influence on the specific locations of active clusters.

Overall, our study area met foraging habitat requirements stipulated by the Red-cockaded Woodpecker Recovery Plan (USFWS 1985) and contained comparable habitat characteristics to those in the home ranges of Red-cockaded Woodpeckers in the Francis Marion National Forest (Hooper and Harlow 1986) (Table 7). Average DBH and basal area were similar to those found to be preferred foraging habitat for Red-cockaded Woodpeckers in the Apalachicola National Forest (Porter and Labisky 1986). Despite the suitability of the foraging habitat, the number of clans declined in the sampled area, which suggested that the decline of the Red-cockaded Woodpecker in the McCurtain County Wilderness Area has not been exclusively due to a lack of foraging habitat.

VI. DISCUSSION

Population Status

Our data suggest that distribution of quality foraging habitat was not a primary factor determining the distribution or abundance of Red-cockaded Woodpeckers in the McCurtain County Wilderness Area. Other factors have the potential to limit the population; e.g., availability of suitable trees for cavity construction, which can be addressed indirectly. Characteristics of cavity trees in the McCurtain County Wilderness Area in 1990 were similar to those reported from the same area in 1977 (Table 1). Also, except for greater cavity height and tree age, cavity tree characteristics in 1977 and 1990 were similar to those reported elsewhere (Ligon 1970, Baker 1971, Hopkins and Lynn 1971, Hooper 1988). Between 1989 and 1990, 6 cavities were abandoned in 5 active clusters; however, we located 5 new cavity trees in these 5 clusters in 1990. In addition, 94% (29 of 31) of the birds that we located had known roost cavities. These factors suggested that availability of trees that could be used for cavities was probably not limiting in the areas where colonies were located. Also, the number of pines/ha $\geq$25.4 cm DBH throughout the 510-ha study area indicated that the number of trees of the size suitable for cavity construction was not detrimental to the Red-cockaded Woodpecker population (Table 2).

Productivity of Red-cockaded Woodpeckers in the McCurtain County Wilderness Area (0.69 fledglings/nest) was lower than has been reported elsewhere. Average productivity in coastal South Carolina was 1.8 fledglings/nest/year (USFWS 1985); in Florida the fledgling/nest average was 1.6 ($n = 9$ nests) (Ligon 1970). We found that the mean annual number of fledglings produced/breeder was 0.35 compared to the 0.74 reported by Reed et al. (1988) in the North Carolina Sandhills. Disparities may be caused by several factors, such as inbreeding due to the low number of individuals in the populations, low resource availability, competition, and/or predation.

The amount of gene flow from outside populations and its consequences for genetic fitness are important considerations in examining the decline of the Red-cockaded Woodpecker in the McCurtain County Wilderness Area. Theoretical estimates of minimal viable population size range from 500 to 1,018 individuals (USFWS 1985, Reed et al. 1988). Red-cockaded Woodpeckers dispersing into the wilderness area from the nearest population (the Ouachita National Forest) would have to travel 40 km, which is further than the maximum (31.5 km) and 3.4-8.8 times the mean dispersal distance (depending on the age, sex and status of the individual) reported by Walters et al. (1988). Lack of immigration and isolation were suggested as causes of the extirpation of a Red-cockaded Woodpecker population that was separated from a larger population by only 10 km (Baker 1983). Dispersal problems would be expected to increase as the distance between clans within a population and distance between populations increases.

The effect of population density on reproductive success of the population needs to be addressed. Most of the research that has been conducted on the Red-cockaded Woodpecker has focused on relatively large populations in forests managed for timber production. Factors that limit the abundance of large populations (*i.e.*, amount of suitable habitat) may not be as important in populations that have declined below a density where dispersing individuals can easily locate mates. Clan density probably influences ability of dispersing Red-cockaded Woodpeckers to locate mates or clans other than the natal clan. Low clan density could lead to increased mortality of dispersers and increased probability of inbreeding within clans of close proximity. Dispersing males have considerably lower survival than helpers in areas where populations are relatively large (Walters et al. 1988). A combination of low survival rate among dispersers, poor reproductive success, and few dispersing individuals (of both sexes due to population size) may limit the possibility of forming new colonies and explain why 10 of 11 colonies located in the resurveyed area were within 400 m of colonies sites identified in 1977.

Cavity competition from Pileated Woodpeckers (*Dryocopus pileatus*), Red-bellied Woodpeckers (*Melanerpes carolinus*) and Flying Squirrels (*Glaucomys volans*) also may contribute to the population decline of Red-cockaded Woodpeckers in McCurtain County Wilderness Area. Previous research has not found cavity competition from Pileated Woodpeckers to be important (Rudolph et al. 1990, Harlow and Lennartz 1983); however, McCurtain County Wilderness Area is predominantly a mixed forest and Pileated Woodpeckers are abundant (pers. obs.). The influence of cavity competition on individual clans may be significant. The frequency and overall impact of enlargement of active Red-cockaded Woodpecker cavities in McCurtain County Wilderness Area is unknown.

Habitat

The trend of forest succession in the wilderness area could not be assessed directly because comparable vegetation measurements from 1977 were not available. However, our habitat measurments demonstrate a dense midstory that is dominated by hardwoods (Table

2). The dominance of hardwoods in the midstory probably indicates a successional shift from pine dominance to hardwood dominance due to fire suppression in the wilderness area (Cain 1987). Previous research has indicated that high hardwood density decreases the suitability of forests for Red-cockaded Woodpeckers (Lennartz et al., 1983, USFWS 1985, Hooper and Harlow 1986). Unfortunately, the specific level at which hardwood density becomes problematic for Red-cockaded Woodpeckers is unknown (USFWS 1985).

Hardwood Encroachment.--Dense hardwood midstory has been proposed as a cause of abandonment of Red-cockaded Woodpecker cavities (Hopkins and Lynn 1971, Hovis and Labisky 1985, Kalisz and Boettcher 1991). There is some evidence that clusters in areas with high hardwood densities are more likely to be abandoned (Conner 1989). However, the reason why high hardwood density leads to abandonment is unclear. Possible explanations include: (1) hardwood encroachment on the cavity entrance obstructs the entrance making the cavity unsuitable to Red-cockaded Woodpeckers; (2) hardwood encroachment makes the cavity accessible to competitors and/or predators by allowing them to avoid the resin barrier; (3) dense midstory hardwoods decrease foraging habitat quality resulting in low productivity; and (4) forests with dense midstory hardwoods have denser populations of species that compete with or prey upon Red-cockaded Woodpeckers.

Hardwood density in the McCurtain County Wilderness Area was within the range of densities that have been reported elsewhere within the species' range (Van Balen and Doerr 1978, Conner 1989, Kalisz and Boettcher 1991). However, hardwoods surrounding Red-cockaded Woodpecker cavity trees in the wilderness area were generally denser (Table 2) than recommended in the Red-cockaded Woodpecker Recovery Plan (4.6 m^2/ha, USFWS 1985). Nevertheless, we do not think that hardwood encroachment on existing cavity entrances is an imminent threat to the remaining Red-cockaded Woodpeckers in McCurtain County Wilderness Area. While it is true that heights of Red-cockaded Woodpecker cavities in McCurtain County Wilderness Area were greater (12-13 m, Table 1) than have been reported elsewhere (Wood 1977, 1983), gaps between the cavity openings and the height of hardwoods (>5 m) were similar to those reported elsewhere (Van Balen and Doerr 1978, Kalisz and Boettcher 1991). This suggests that the remaining Red-cockaded Woodpeckers have placed their cavities in areas where hardwood encroachment will not cause imminent abandonment.

McCurtain County Wilderness Area is one of the few forests that has never been logged and contains Red-cockaded Woodpeckers. Wood (1977) found that average age of cavity trees in the wilderness area was 149 years and average cavity tree age from other forests was 81 years. Cavity trees in the wilderness area may be used for short periods of time because they are old and have high mortality rates and low resin flow. Cavities that are used for shorter periods of time are less likely to be encroached upon by hardwoods. However, if decreased resin flow of old trees causes cavity abandonment on a relatively short-term basis **and** suitable cavity trees are limited in availability due to densities of hardwoods elsewhere in the wilderness area, the remaining population of Red-cockaded Woodpeckers would have difficulty colonizing new areas. Such conditions would decrease the overall productivity of the population. During the 2 years of our study, 28% of the active cavities were abandoned for an approximate abandonment rate of 14% per year. This means that individual Red-cockaded Woodpeckers must be able to find a new tree that is suitable for cavity construction about every 7 years.

We suspect that the primary negative impact of hardwood density on this population of Red-cockaded Woodpeckers is a reduction in productivity and potential for expansion caused by (1) limitation of the number of suitable cluster sites, (2) degradation of foraging habitat as a result of succession from a pine to hardwood dominated forest, and/or (3) competition from Red-bellied and Pileated Woodpeckers, which are more abundant in dense hardwood than in open pine forests (USFWS 1985, Renken and Wiggers 1989).

Habitat Selection.--We suggest that Red-cockaded Woodpeckers in McCurtain County Wilderness Area select habitat at cluster sites on at least 2 levels and use different selection criteria at each of these levels. We found that structure of the hardwood midstory was most important within 11.3 m of the cavity tree and that pine density was more important than hardwood density at 31.3 m from the cavity tree. In general, cavities were constructed in areas where hardwoods were shorter and less dense. Specifically, hardwoods in quadrant 1 were less dense and smaller than in the rest of the quadrants; and overall, habitat in the 0.04 ha surrounding cluster sites had smaller hardwoods than were found at paired non-use sites. This indicated that selection against hardwoods was occurring in the immediate vicinity (within 11.3 m) of the cavity tree. The difference in the size and amount of hardwoods (particularly height) between quadrant 1 and the other 3 quadrants indicated that the hardwood density immediately in front of the cavity may be more important than overall forest composition in selection of a specific cavity site (Van Balen and Doerr 1978).

Basal area samples taken at 31.3 m from cluster site base trees did not differ from randomly placed basal area samples in the amount of hardwood basal area, suggesting that selection against hardwoods may cease to be important at that distance (Table 7). The area 31.3 m from the cavity tree is probably important foraging habitat for Red-cockaded Woodpeckers during the breeding season; the high density of pine at these sample points may reflect selection of foraging habitat by the resident clan. In addition, the trend of higher pine basal area at cluster sites when compared to non-use sites is consistent with prior observations that Red-cockaded Woodpeckers prefer to forage in areas with relatively high pine densities (Hooper and Harlow 1986, Porter and Labisky 1986).

VII. MANAGEMENT SUGGESTIONS

Our study indicates that the quality of the foraging habitat in the McCurtain County Wilderness Area is adequate for Red-cockaded Woodpeckers. However, it is apparent that succession towards a hardwood-dominated forest will be a long-term problem. Prescribed burning, particularly of ridgetops, south facing slopes, and abandoned cluster sites, should be used to maintain the pine-dominated character of these sites and to provide habitat for Red-cockaded Woodpeckers.

Successful recovery of the McCurtain County Wilderness Area's Red-cockaded Woodpecker population will require more than habitat management. This belief is supported by failure of habitat management alone in producing increasing trends in the number of Red-cockaded Woodpeckers elsewhere in the species' range (Conner and Rudolph 1989). Recently developed techniques that allow for artificial cavity construction have shown positive results for population expansion (Copeyon et. al in press). However, for these techniques to be used efficiently, the demography of the population must be known (R.N. Conner, pers. commun.). Clan members must be sexed and banded, and reproductive success of clans also must be followed closely. Another possible benefit of monitoring marked individuals is that augmenting clans that are all male with female fledglings from other clans could allow for an increase in the productivity of Red-cockaded Woodpeckers in the wilderness area. We suggest marking and monitoring the population immediately so that augmentation of clans and creation of cluster sites can be begun as soon as possible.

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IX. **DATE** 15 May 1991

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Table 1. Comparison of Red-cockaded Woodpecker clans, clusters, active cavity trees, and active cavity tree sites located in 1990 with those located in 1977. Sample sizes are in parentheses.

	1990	1977[a]		
	$\bar{X} \pm$ SD	$\bar{X} \pm$ SD	Test statistic	P
CLAN				
Number of birds	2.1 ± 0.8 (15)	3.1 ± 1.2 (29)	U = 112	0.008
CLUSTER				
Number of trees/cluster	1.9 ± 0.7 (15)	4.4 ± 2.0 (29)	U = 57	0.001
CAVITY TREE				
Height(m)	25.7 ± 4.8 (33)	24.9 ± 4.1 (154)	t = 0.98	0.329
Diameter(cm)	43.9 ± 6.3 (32)	44.6 ± 8.2 (154)	t = 0.39	0.693
Low limb height(m)	9.6 ± 3.6 (32)	10.7 --[b] (154)	--	--
Cavities/tree	1.3 ± 0.6 (32)	1.2 -- (155)	--	--
CAVITIES				
Height(m)	12.0 ± 3.0 (32)	13.1 -- (224)	--	--
Orientation(degrees)	260.0 ± 55.0 (32)	251.1 ± 56.7 (205)	--	--
SITE				
Slope(percent)	12.0 ± 4.9 (31)	26.0 ± 12.8 (153)	t = 5.27	0.001
Aspect(degrees)	232.0 ± 62.0 (32)		--	--

[a] Data from Wood (1977).

[b] Data as collected in 1977 precluded analysis.

Table 2. Comparisons of hardwood characteristics between cluster and non-use site base tree plots by quadrant and overall using Wilcoxon's paired signed ranks test. Variables compared were: (1) number of hardwood saplings; (2) DBH of hardwoods (cm); (3) total basal area of hardwoods (m^2/ha); and (4) height of hardwoods (m). All sample sizes = 18.

Hardwood Variable	Cluster Median(range)	Non-use Median(range)	P	Cluster Median(range)	Non-use Median(range)	P
	Quadrant 1			Quadrant 2		
Saplings	3.0 (0.0-17.0)	2.0 (0.0-26.0)	0.777	4.0 (0.0-15.0)	3.0 (0.0-26.0)	0.593
DBH	8.9 (0.0-13.7)	11.2 (7.7-16.3)	0.004[a]	10.3 (7.8-15.5)	12.5 (7.2-30.2)	0.085
Basal area	5.9 (0.0-14.8)	11.2 (5.4-19.1)	0.001[a]	8.8 (2.0-16.0)	12.6 (3.6-28.5)	0.058
Height	6.9 (0.0- 9.9)	8.6 (3.4-14.6)	0.003[a]	8.5 (6.9-12.0)	9.9 (7.1-14.5)	0.028
	Quadrant 3			Quadrant 4		
Saplings	3.5 (0.0-10.0)	1.0 (0.0-17.0)	0.678	3.0 (0.0- 8.0)	3.0 (0.0-12.0)	0.757
DBH	9.8 (7.1-21.9)	12.7 (7.4-19.4)	0.170	9.6 (8.3-18.5)	10.6 (8.1-24.4)	0.446
Basal area	7.0 (3.8-22.9)	12.9 (1.8-32.5)	0.199	7.2 (1.8-28.2)	9.7 (4.2-31.1)	0.184
Height	8.6 (7.3-12.7)	11.5 (6.2-17.8)	0.011[a]	7.8 (6.2-15.5)	9.3 (6.6-18.2)	0.035
	Overall					
Saplings	13.5 (1.0-44.0)	13.5 (0.0-79.0)	0.913			
DBH	10.3 (7.9-12.6)	12.0 (9.1-16.7)	0.018			
Basal area	8.6 (3.4-14.6)	11.3 (7.9-14.5)	0.008[a]			
Height	7.8 (6.7-10.7)	9.5 (7.5-12.8)	0.002[a]			

[a] P value is significant when using the sequential Bonferroni technique to control type 1 error for each variable; initial critical value = 0.01 (0.05/5 tests).

Table 3. Comparisons of pine characteristics between cluster and non-use site base tree plots by quadrant and overall using Wilcoxon's paired signed ranks test. Variables compared were: (1) number of pine saplings; (2) DBH of pines (cm); (3) total basal area of pines (m^2/ha); and (4) height of pines (m). All sample sizes = 18.

	Cluster	Non-use		Cluster	Non-use	
Pine Variable	Median(range)	Median(range)	P	Median(range)	Median(range)	P
	Quadrant 1			Quadrant 2		
Saplings	0.0 (0.0-59.0)	0.0 (0.0- 2.0)	0.012[a]	0.0 (0.0-42.0)	0.0 (0.0- 5.0)	0.161
DBH	24.5 (0.0-53.2)	22.3 (0.0-58.4)	0.984	22.2 (0.0-49.3)	18.1 (0.0-37.2)	0.744
Basal area	18.4 (0.0-45.9)	11.9 (0.0-26.8)	0.030	17.1 (0.0-67.4)	9.1 (0.0-37.3)	0.647
Height	14.3 (0.0-33.5)	14.9 (0.0-21.5)	0.679	14.2 (0.0-31.6)	14.7 (7.1-14.5)	0.744
	Quadrant 3			Quadrant 4		
Saplings	0.0 (0.0- 27.0)	0.0 (0.0- 1.0)	0.034	0.0 (0.0-91.0)	0.0 (0.0- 1.0)	0.161
DBH	19.8 (0.0- 42.9)	23.2 (0.0-39.6)	0.356	21.7 (0.0-46.0)	19.5 (0.0-43.6)	0.948
Basal area	13.5 (0.0- 56.1)	7.8 (0.0-26.8)	0.177	13.4 (0.0-36.8)	13.1 (0.0-57.8)	0.679
Height	14.1 (0.0- 31.0)	13.2 (0.0-23.3)	0.463	12.9 (0.0-30.8)	15.7 (0.0-22.4)	0.327
	Overall					
Saplings	3.5 (0.0-219.0)	0.0 (0.0- 5.0)	0.006[a]			
DBH	21.6 (7.9- 42.6)	19.6 (12.0-27.7)	0.372			
Basal area	17.8 (8.0- 31.8)	12.0 (1.3-19.8)	0.028			
Height	12.9 (7.3- 25.1)	13.5 (3.1-22.2)	0.879			

[a] P value is significant when using the sequential Bonferroni technique to control type 1 error for each variable; initial critical value = 0.01 (0.05/5 tests).

Table 4. Comparisons of basal area (m^2/ha) of pines and hardwoods sampled at 31.3 and 71.3 m from the base tree between cluster and non-use sites by quadrant and overall using Wilcoxon's paired signed ranks test. All sample sizes = 18.

	Hardwood basal area			Pine basal area		
	Cluster	Non-use		Cluster	Non-use	
Quadrant	Median(range)	Median(range)	P	Median(range)	Median(range)	P
			31.3 m from base tree			
1	10.3 (0.0-25.3)	11.5 (0.0-23.0)	0.297	16.1 (0.0-27.5)	16.1 (0.0-34.4)	0.553
2	11.5 (2.3-23.0)	11.5 (4.6-23.0)	0.568	12.6 (0.0-32.1)	14.9 (0.0-39.0)	0.717
3	9.2 (2.3-20.7)	12.6 (4.6-20.7)	0.008[a]	20.7 (6.9-32.1)	13.8 (0.0-27.5)	0.004[a]
4	10.3 (2.3-23.0)	11.5 (4.6-29.8)	0.121	17.2 (6.9-32.1)	11.5 (2.3-29.8)	0.161
Overall	11.2 (4.0-17.2)	11.8 (8.6-21.8)	0.013	16.4 (9.2-25.2)	13.8 (4.6-25.8)	0.472
			71.3 m from base tree			
1	11.5 (0.0-23.0)	14.9 (0.0-28.8)	0.312	16.1 (0.0-27.5)	18.4 (0.0-34.4)	0.337
2	13.8 (4.6-29.8)	13.8 (6.9-23.0)	0.421	17.2 (0.0-36.7)	6.9 (0.0-23.0)	0.019
3	11.5 (4.6-20.7)	13.8 (4.6-27.5)	0.263	16.1 (2.3-48.2)	12.6 (2.3-32.1)	0.162
4	11.5 (4.6-16.1)	14.9 (4.6-27.5)	0.041	16.1 (2.3-48.2)	6.9 (0.0-43.6)	0.041
Overall	12.1 (8.0-22.2)	14.1 (9.2-21.8)	0.016	15.2 (5.2-32.1)	12.3 (4.0-19.5)	0.020

[a] P value is significant when using the sequential Bonferroni technique to control type 1 error for each variable at each distance (31.3 and 71.3 m); initial critical value = 0.01 (0.05/5 tests).

Table 5. Comparison of pine and hardwood basal area (m^2/ha) between 127 randomly placed sample points and 72 cluster site sample points (4 at each base tree). Cluster site samples were taken 31.3 m from the base tree on the quadrant boundary lines.

Tree Type/Site	$\bar{X} \pm SD$	t-statistic	P
PINE			
Cluster	15.3 ± 7.3	4.07	>0.001
Random	10.8 ± 7.6		
HARDWOOD			
Cluster	7.8 ± 4.2	0.53	0.595
Random	7.4 ± 4.8		

Table 6. Habitat characteristics in a 510-ha area of McCurtain County Wilderness Area and the relationship (r^2) of each variable to the distance from the nearest active cluster. All sample sizes = 127.

Habitat variable	$\bar{X} \pm SD$	r^2	P
Basal Area (m^2/ha)			
Pine	10.8 ± 7.6	0.006	0.37
Hardwood	7.4 ± 4.8	0.028	0.06
DBH (cm)			
Pine	29.9 ± 15.1	0.018	0.13
Hardwood	24.0 ± 12.3	0.008	0.33
Number/ha >25.4 cm DBH			
Pine	58.8 ± 47.6	0.010	0.25
Number /ha <12.7 cm DBH			
Pine	281.7 ± 867.2	0.033	0.04
Hardwood	1487.0 ± 1194.4	0.079	0.01

Table 7. Comparison of a 510-ha study area in McCurtain County Wilderness Area (MCWA) with home ranges of 18 clans in the Francis Marion National Forest (FMNF) and the foraging habitat requirements stipulated in the Red-cockaded Woodpecker Recovery Plan (RCWRP) (Hooper and Harlow 1986, USFWS 1985). Sample sizes are in parentheses.

	MCWA		FMNF		
	$\bar{X} \pm$ SD		$\bar{X} \pm$ SD		RCWP
Pine					
Basal area (m^2/ha)	10.8 ± 7.6	(127)	11.5 ± 7.7	(276)	6.7-20.7
Percent	59.0 ---	---	67.3 ---	---	>50.0
Number/ha >25.4 cm DBH	58.8 ± 47.6	(127)	93.4 ± 72.1	(276)	≥59.3[a]
Hardwood					
Basal area (m^2/ha)	7.5 ± 4.9	(127)	5.6 ± 9.4	(276)	0.0-10.4
Percent	41.0 ---	---	32.7 ---	---	<50.0
Total					
Basal area (m^2/ha)	18.3 ± 7.6	(127)	17.1 ---	(276)	13.8-20.7

[a] Red-cockaded Woodpecker Recovery Plan stipulates 59.3 Pines/ha >24.0 cm DBH rather than 25.4 cm DBH.

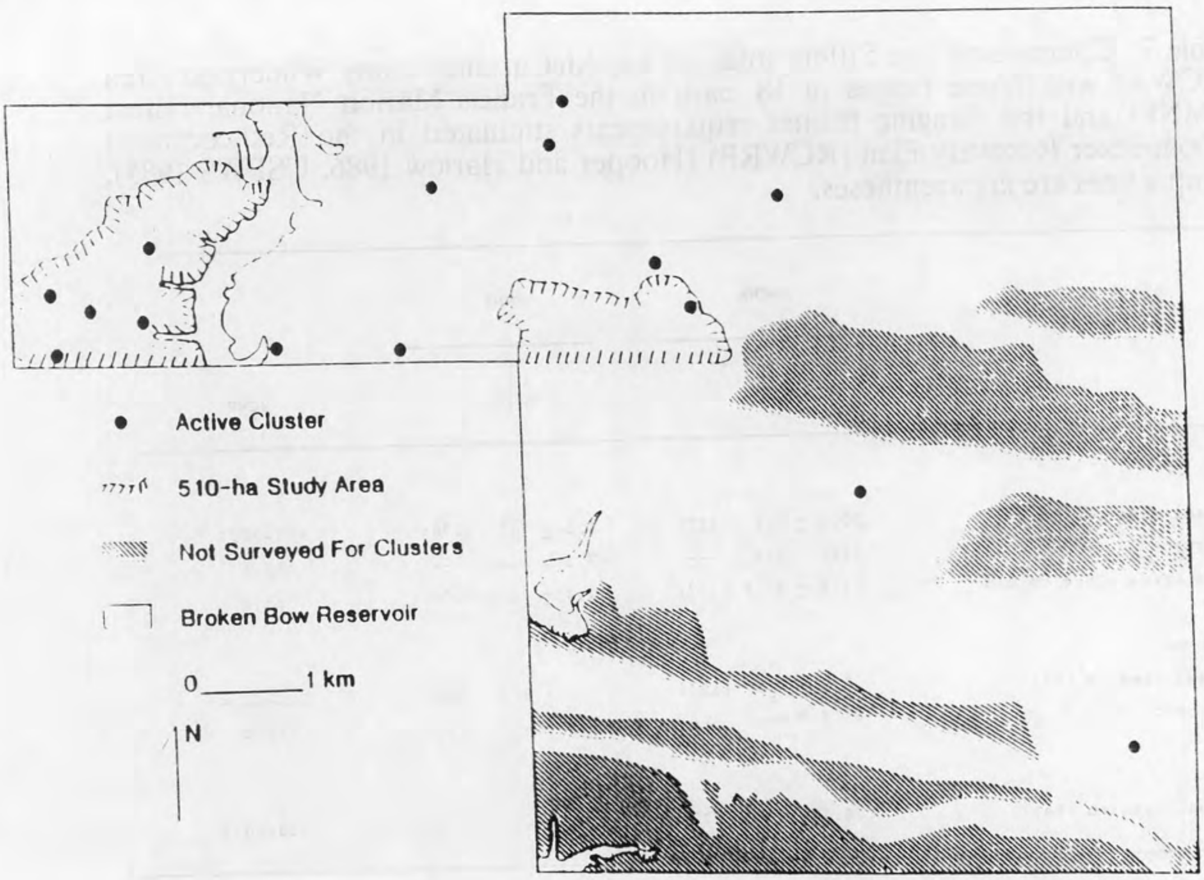

Fig. 1. Location of active clusters, the area used to measure foraging habitat, and the area surveyed for active clusters in the McCurtain County Wilderness Area, Oklahoma.

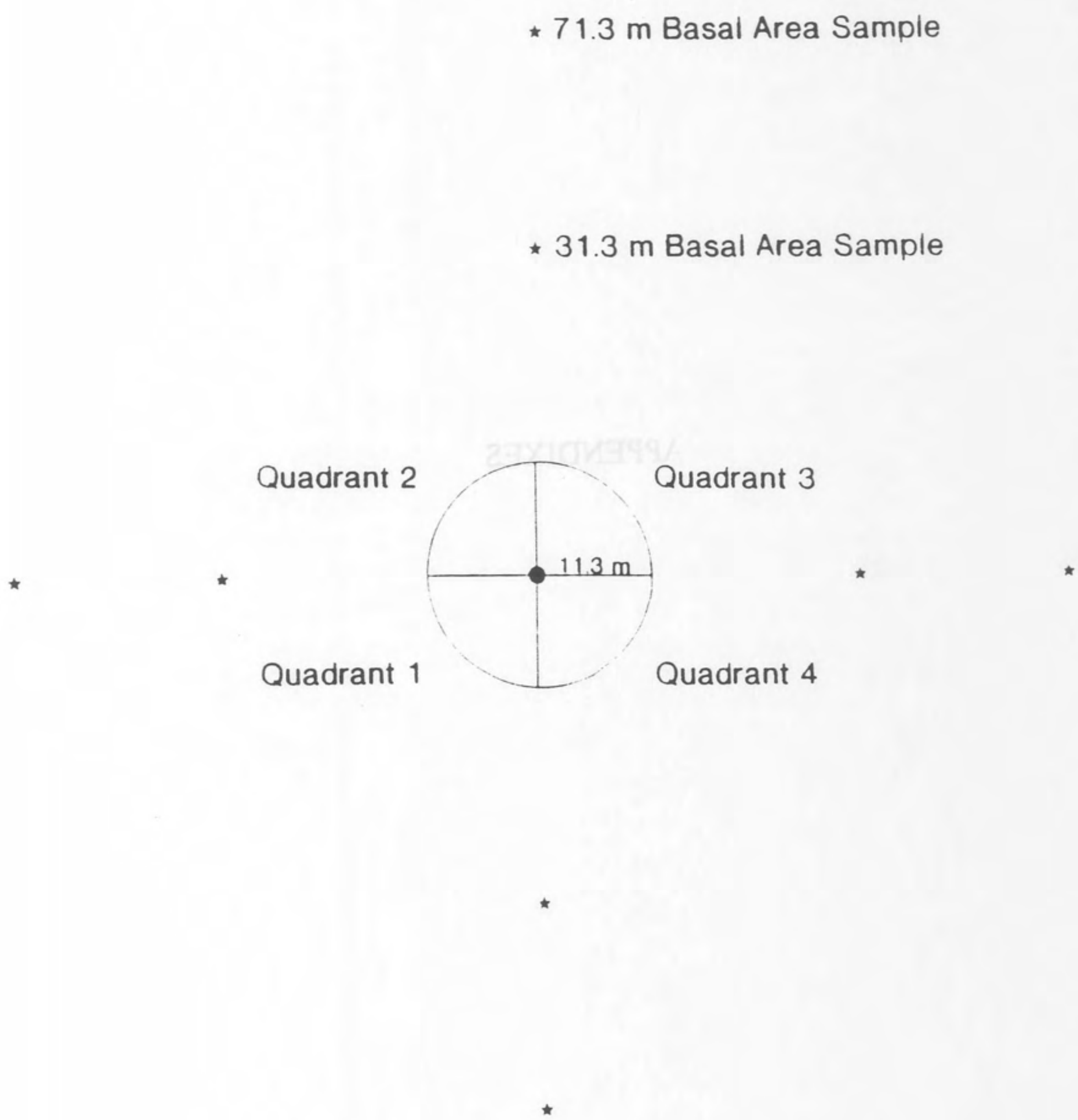

Fig. 2. Sampling design used at cluster and non-use site base-tree plots.

APPENDIXES

Appendix A. Means and standard deviations for data in Table 2. Variables were: (1) number of hardwood saplings; (2) DBH of hardwoods (cm); (3) total basal area of hardwoods ($cm^2/100m^2$); and (4) height of hardwoods (m). All sample sizes = 18.

Hardwood Variable	Cluster Mean (SD)	Non-use Mean (SD)	Cluster Mean (SD)	Non-use Mean (SD)
	Quadrant 1		Quadrant 2	
Saplings	3.5 (3.77)	4.2 (6.3)	4.5 (3.97)	5.8 (6.4)
DBH	8.7 (3.0)	11.7 (2.9)	10.8 (2.2)	13.2 (5.1)
Basal area	627 (421)	1114 (366)	859 (460)	1265 (661)
Height	6.8 (2.23)	8.8 (1.33)	8.5 (1.45)	10.0 (2.06)
	Quadrant 3		Quadrant 4	
Saplings	4.2 (3.17)	3.8 (4.8)	3.6 (2.9)	3.6 (3.3)
DBH	11.2 (3.6)	12.6 (2.9)	10.9 (3.1)	11.9 (3.7)
Basal area	936 (551)	1253 (697)	933 (720)	1161 (649)
Height	8.7 (1.4)	11.1 (2.9)	8.0 (2.0)	10.4 (3.08)
	Overall			
Saplings	15.8 (11.3)	17.4 (18.65)		
DBH	10.4 (1.36)	12.4 (2.24)		
Basal area[a]	3355 (1146)	4794 (1481)		
Height	8.0 (1.0)	10.0 (1.7)		

[a] Overall basal area is $cm^2/400m^2$.

Appendix B. Mean and standard deviations for data in Table 3. Variables were: (1) number of pine saplings; (2) DBH of pines (cm); (3) total basal area of pines ($cm^2/100m^2$); and (4) height of pines (m). All sample sizes = 18.

Pine Variable	Cluster Mean (SD)	Non-use Mean (SD)	Cluster Mean (SD)	Non-use Mean (SD)
	Quadrant 1		Quadrant 2	
Saplings	9.2 (19.0)	0.1 (0.5)	4.3 (10.5)	0.4 (1.2)
DBH	22.8 (14.8)	21.5 (13.7)	22.6 (16.4)	19.2 (10.1)
Basal area	1874 (1466)	1154 (889)	1408 (1822)	1058 (1000)
Height	14.9 (8.4)	13.8 (7.2)	14.0 (9.2)	14.2 (6.5)
	Quadrant 3		Quadrant 4	
Saplings	3.6 (7.8)	3.8 (4.8)	6.3 (21.2)	2.6 (3.3)
DBH	20.8 (14.3)	16.2 (11.5)	21.0 (13.8)	20.9 (11.9)
Basal area	1697 (1665)	977 (917)	1335 (1070)	1526 (1331)
Height	14.5 (8.7)	12.3 (7.8)	12.5 (7.7)	15.1 (6.7)
	Overall			
Saplings	23.3 (51.97)	0.7 (1.33)		
DBH	21.7 (7.8)	19.5 (4.8)		
Basal area[a]	6816 (2969)	4716 (2258)		
Height	14.0 (5.27)	13.8 (4.53)		

[a] Overall basal area is $cm^2/400m^2$.

Appendix C. Mean and standard deviations for data in Table 4. All sample sizes = 18.

	Hardwood basal area[a]		Pine basal area[a]	
	Cluster	Non-use	Cluster	Non-use
Quadrant	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
		31.3 m from base tree		
1	10.5 (6.6)	12.1 (6.4)	15.4 (8.3)	17.6 (10.6)
2	12.1 (5.7)	13.3 (5.7)	14.0 (7.5)	15.7 (10.5)
3	10.2 (4.7)	14.0 (4.5)	10.2 (4.7)	13.8 (8.3)
4	11.0 (4.6)	12.9 (6.9)	16.7 (7.9)	13.8 (8.4)
Overall	10.9 (3.5)	13.1 (3.8)	16.5 (4.3)	15.2 (6.2)
		71.3 m from base tree		
1	12.4 (5.7)	14.7 (7.6)	14.2 (7.3)	16.8 (10.0)
2	13.4 (6.6)	14.8 (5.1)	16.1 (9.5)	9.2 (8.1)
3	11.4 (4.4)	14.3 (7.5)	18.9 (16.1)	12.6 (7.8)
4	11.0 (3.9)	15.9 (7.1)	17.0 (11.4)	11.6 (11.6)
Overall	12.0 (2.8)	14.9 (3.6)	16.5 (6.2)	12.6 (4.7)

[a] m^2/ha.