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FOREST FRAGMENTATION AND RED-COCKADED WOODPECKER POPULATION: AN ANALYSIS AT INTERMEDIATE SCALE

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Abstract.—The Red-cockaded Woodpecker population on the Sam Houston National Forest in Texas was surveyed during 1988. The 128 active clusters present make this population one of the largest in existence. Pine stand ages varied considerably across the forest. Correlation analysis indicated that stand area in excess of 60 yr of age is positively correlated with measures of woodpecker density. This relationship is present across a range of areas from individual compartments (= 520 ha) to blocks of 10–15 compartments. A positive correlation of area in pines of 60 yr of age and number of woodpeckers per group suggests that the causes of these relationships are still operating. It is hypothesized that the fragmentation of forest in excess of 60 yr of age by younger stands is impacting the demographics of this population.

EFECTO DE LA FRAGMENTACIÓN DE BOSQUE EN UNA POBLACIÓN DE *PICOIDES BOREALIS*: UN ANÁLISIS A ESCALA INTERMEDIA

Sinopsis.—Durante el 1988, se estudió la población del carpintero *Picoides borealis* en el Bosque Nacional Sam Houston, Texas. Esta población, representada por 128 grupos activos, es una de las mayores en existencia. A todo lo largo del bosque hay rodales de pinos de diferentes edades. Se encontró una correlación positiva entre los rodales con edades superiores a los 60 años y altas densidades de carpinteros. Esta relación está presente a través de una variedad de áreas que van desde compartimientos individuales (= 520 ha) hasta bloques de 10–15 compartimientos. La correlación positiva entre áreas (rodales) de pinos de 60 años y el número de individuos de carpinteros por grupos, sugieren que las causas de esta relación se encuentran aún operando. Se presenta como hipótesis, que la fragmentación de bosques de 60 años con rodales más jóvenes, está impactando negativamente la demografía de esta población de aves.

Since the publication of "The Theory of Island Biogeography" by MacArthur and Wilson (1967) there has been a rapid increase in the study of habitat fragmentation in relation to species diversity patterns and single species survival (Brown 1971, Case 1975, Culver et al. 1973, Diamond 1975, Diamond and Mayr 1976, Heaney 1986, Lynch and Whigham 1984, Soulé et al. 1988, Whitcomb et al. 1981, Wilcove et al. 1986, Wilcox 1978). Two general conclusions are evident from this work: habitat fragmentation influences species diversity and probability of individual species survival, and the biology of individual species influences probability of survival in fragmented habitats.

Habitat fragmentation can affect biotic communities in many ways, such as rates of colonization and extinction, and metapopulation structure (Brown 1971; Diamond 1972, 1984; Hanski and Gilpin 1991; Karr 1982; Lawlor 1986; MacArthur and Wilson 1967; Soulé et al. 1988). Alteration of species interactions (e.g., competition, predation) determined by varying degrees of habitat fragmentation also influence biotic communities. Colonization of fragmented forests by Brown-headed Cowbirds, *Molothrus* *ater* (Brittingham and Temple 1983), increased predation in habitat patches of reduced size (Eisenberg et al. 1979, Glanz 1982, Soulé et al. 1988), and access of competitors to previously unavailable habitat have all been implicated in changes in community structure with varying degrees of habitat fragmentation. In extreme cases habitat fragmentation might eventually result in isolated populations that are too small to retain genetic diversity and avoid detrimental effects due to loss of heterozygosity and inbreeding (Gilpin and Soulé 1986, Lande and Barrowclough 1987).

Most studies to date have been concerned with habitat islands embedded in a matrix of unsuitable habitat. This traditional type of habitat fragmentation has important implications due to reductions in gene flow and recolonization following extinction. Habitat fragmentation also exists, however, when a matrix of suitable habitat has islands of unsuitable habitat embedded within. Fragmentation of this type has been hypothesized to have detrimental effects on Red-cockaded Woodpecker (*Picoides borealis*) demographics (Conner and Rudolph 1991). Obviously a continuum can exist between these two extremes. Perhaps due to the difficulties of quantifying fragmentation in the latter case, the effects of this type of fragmentation have received little attention.

The Red-cockaded Woodpecker currently exists in a forest habitat that is highly fragmented in the traditional sense. Populations currently consist of one to a few hundred breeding pairs typically separated by tens to hundreds of kilometers from other populations (Lennartz et al. 1983). The probabilities of significant genetic exchange and recolonization following local extinction are therefore very low. The low probability of recolonization exhibited by Red-cockaded Woodpeckers, due in large measure to the difficulties of excavation of cavities (Walters et al. 1992), effectively prevent the species from functioning as a metapopulation (Hanski and Gilpin 1991).

Within populations additional forest fragmentation is present due to removal of patches of forest habitat. Demographic effects of forest fragmentation (removal) within 400 and 800 m of cavity tree clusters have been documented for Red-cockaded Woodpecker populations in Texas (Conner and Rudolph 1991). In this paper we examine the relationships between Red-cockaded Woodpecker population parameters and forest fragmentation at an intermediate scale between the forest fragmentation surrounding individual clusters (Conner and Rudolph 1991) and the fragmentation of surviving populations throughout the species range.

STUDY AREA

The Sam Houston National Forest (SHNF) consists of two districts, the Raven (41,170 ha) and the San Jacinto (24,048 ha). Federal ownership is fragmented. Adjacent private land is variously managed, typically pasture or short rotation pine plantations, and in general not suitable Red-cockaded Woodpecker habitat, although significant exceptions occur.

Loblolly pine (*Pinus tadea*) is the dominant pine species on the SHNF.

Shortleaf pine (*P. echinata*) is present in most older stands and dominates on some drier sites. Longleaf pine (*P. palustris*) occurs rarely in mixed stands in the eastern portion of the SHNF. Pine sites have a variable mixture of canopy hardwoods, and a well developed hardwood midstory is characteristic of most sites. Mixed hardwood forest occurs adjacent to most drainages.

Even-aged forest regeneration methods (primarily clearcutting) have been used on the forest since the mid 1960s. Approximately 35% of the forest is occupied either by pine plantations less than 20 yr of age or recent clearcuts. A significant portion of recent cutting has resulted from southern pine beetle (*Dendroctonus frontalis*) infestations and subsequent control measures. A major beetle epidemic occurred during 1984–1985.

METHODS

Data analyzed in this paper were obtained during a status survey of all known Red-cockaded Woodpecker cavity tree clusters (termed "colonies" in part of literature, see Walters et al. 1988) located on the SHNF. The initial survey was conducted between Nov. 1987 and Jun. 1988. All known cavity trees were surveyed and their status, active or inactive, determined visually (Jackson 1977, 1978). Active clusters, containing at least one active cavity tree, and those of questionable status were subject to dawn or dusk roost surveys to verify status and provide data on the number of Red-cockaded Woodpeckers present. Roost surveys were conducted between 1 February and 15 June and in all cases prior to fledging. Detailed survey methods are available in Conner and Rudolph (1989).

Additional data on clusters discovered after the survey period were obtained from National Forest System (NFS) District records updated as of February 1989 and July 1989. Data on number of birds per cluster were not available for clusters discovered after the initial survey. Data on stand age (age of dominant trees) were obtained from a map provided by the Raven District, SHNF.

Detailed analysis of fragmentation data was restricted to compartments 1–54 of the Raven District. A compartment is an administrative unit which on the SHNF average approximately 520 ha in area. The 1–54 compartment area, approximately 27 × 16 km in size, is over 90% in USFS ownership and contains approximately 75% of the total SHNF Red-cockaded Woodpecker population.

Pearson correlation analyses were based on forest area greater than 60 yr of age or less than 60 yr of age obtained for each of the 54 compartments from the map of stand age. These two measures of habitat are not reciprocal variables due to differences in compartment area. A tracing of each compartment was cut in appropriate age classes and the area measured using a digital area meter.

A variety of block sizes were used for the correlation analyses. Each of the 54 compartments were used for one set of comparisons. In a second set of comparisons, the 54 compartments were grouped into eight contiguous blocks of approximately equal size based on percent of forest area greater than 60 yr of age. This grouping was performed independently by two individuals unfamiliar with the distribution of cavity tree clusters or woodpeckers in the compartments. Initially the two groupings were slightly different and a consensus grouping was easily determined by consultation.

An opposing approach was also used. The 54 compartments were grouped into larger contiguous blocks based on the known distribution of active clusters. Two groupings, one of 15 blocks and one of four blocks, were performed and analyzed separately.

RESULTS

A total of 282 Red-cockaded Woodpecker clusters was reported on the SHNF, 221 on the Raven District and 61 on the San Jacinto District. One hundred twelve of these clusters were confirmed active (roosting birds present), 90 on the Raven District and 22 on the San Jacinto District during the 1988 survey. The number of active clusters on the Raven District included two clusters in which the active cavity tree(s) were located on private land adjacent to the SHNF. In both cases the majority of potential foraging habitat was on the SHNF. A total of 103 clusters were inactive, roosting birds absent; 73 on the Raven District and 30 on the San Jacinto District. Fifty-four reported clusters had no surviving cavity trees, 47 on the Raven District and seven on the San Jacinto District. These losses were primarily due to the Southern Pine Beetle epidemic of 1984–1985. An additional 13 clusters were either unconfirmed during the survey (nine) or not Red-cockaded Woodpecker cavity trees (four).

The dawn and dusk roosting surveys provided data on the number of roosting Red-cockaded Woodpeckers per cluster prior to the 1988 breeding season. Of the 112 active clusters 24 (21.4%) were occupied by a single bird. Seventy-eight (69.6%) were occupied by 2–3 roosting birds, and 10 (8.9%) were occupied by 4–7 roosting birds. A total of 264 individual Red-cockaded Woodpeckers (2.36/group) were found; 215 (2.4/group) were on the Raven District, and 49 (2.2/group) were on the San Jacinto District.

Since the completion of the 1988 survey, additional clusters have been located by NFS district personnel. An additional 16 active clusters have been located as of July 1989, 14 on the Raven District and two on the San Jacinto District. Most newly discovered clusters show evidence, primarily in the form of old abandoned cavities, of having been in existence for at least several years. Few consist only of recently excavated cavity trees, and those that do are often adjacent to Southern Pine Beetle infestations that may have eliminated existing cavity trees.

The distribution of active clusters is non-random on the SHNF. Several areas with a relatively high density of active clusters occur interspersed with areas of lower density. Many sizable areas, especially the more fragmented tracts of National Forest, lack active clusters entirely. Questions relating to this pattern for a subset of the forest are addressed more fully below.

The initial 1988 survey detected 79 active Red-cockaded Woodpecker clusters in compartments 1–54 of the Raven District. The February 1989 update listed an additional nine active clusters discovered in the interim. This update provided data used in the analysis below. A total of 85 inactive clusters were also detected within the 54 compartment area. Figure 1 shows the distribution of active and inactive clusters within the area. The July 1989 update listed an additional five active clusters. Due to lack of specific data on these groups they are not included in the current analysis. Active clusters discovered since the 1988 survey and the February 1989 update have been predominately in areas with prior concentrations of known active clusters. Consequently, clusters discovered since the February 1989 field work and those yet to be discovered should not substantially alter the results reported below.

The distribution of active clusters is also non-random within the 54 compartments considered. Two blocks of contiguous compartments (15 total compartments) comprising approximately 33% of the total area contain a majority of the active clusters (64.6% based on the 1988 survey, 67.8% based on the July 1989 update).

Results of Pearson correlation analyses comparing measures of Red-cockaded Woodpecker population with forest area greater than 60 yr of age and forest area less than 60 yr of age by compartment are presented in Table 1. Number of active clusters, number of woodpeckers, and number of woodpeckers per cluster are all significantly correlated with forest area greater than 60 yr of age. The correlation between number of inactive clusters and forest area greater than 60 yr of age is not significant. No significant correlations between woodpecker population measures and forest area less than 60 yr of age were detected.

Similar analyses for the eight contiguous blocks (6–9 compartments each) based on forest area greater than 60 yr of age are similar (Table 1). Significant correlations exist between number of active clusters, number of woodpeckers, and number of woodpeckers per cluster, and forest area greater than 60 yr of age for the eight blocks. The number of inactive clusters per block is not significantly correlated with forest area greater than 60 yr of age.

The results of the opposing approach were complementary. Significant correlations were found between number of active clusters, number of woodpeckers, and number of woodpeckers per cluster and the area of forest greater than 60 yr of age, for both the four-block and 15-block groupings of the 54 compartments based on number of active clusters per compartment ($P < 0.001$ in all six cases). The number of inactive clusters was not significantly correlated with forest area greater than 60 yr of age in either grouping ($P > 0.05$).

The data presented in Conner and Rudolph (1991) were also examined after regrouping to fit the present analysis. The amount of nonforest habitat (defined to include pine plantations <20 yr of age) within 400 and 800 m of each cluster was available for analysis. The 54 compartments were split into two groups based on the amount of forest >60 yr of age

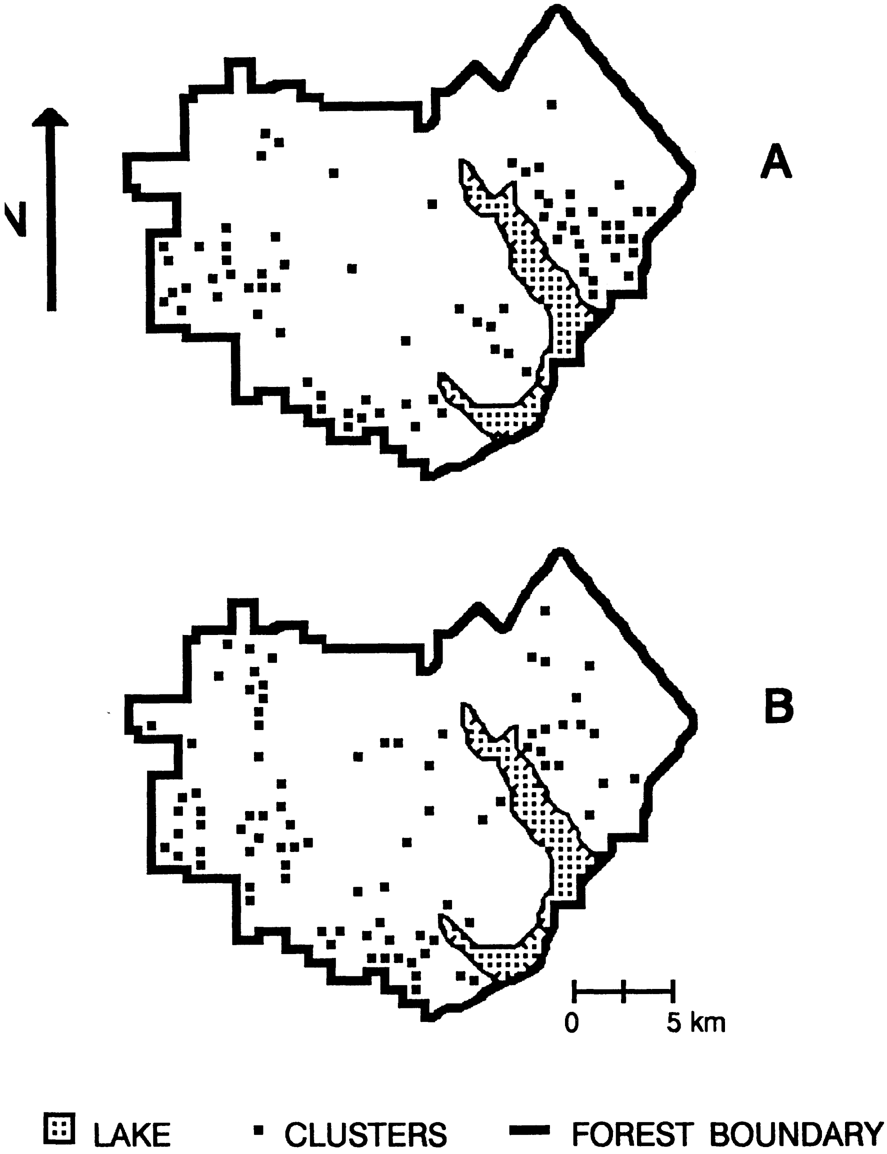

FIGURE 1. Distribution of active (A) and inactive (B) Red-cockaded Woodpecker clusters in compartments 1–54 on the Sam Houston National Forest.

(group 1 <20%, group 2 >20%). The overall average of nonforest habitat within 400 and 800 m of all clusters in each compartment were then calculated. The compartments with <20% forest cover >60 yr of age (group 1) had an average of 36.0% and 39.4% of non-forest habitat within

TABLE 1. Pearson correlation analyses of forest area greater than or less than 60 yr of age compared to selected Red-Cockaded Woodpecker population measures.

Woodpecker population (54 compartments)	Forest area >60 yr (54 compartments)	Forest area <60 yr	8 block[a]
# active clusters[b]	0.4145**	−0.0651	0.3280**
# Red-cockaded Woodpeckers[c]	0.4805***	−0.1183	0.3261**
# Red-cockaded Woodpeckers/cluster[c]	0.2325*	0.0019	0.2988
# inactive clusters[b]	0.1976	0.2031	0.915

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[a] Eight contiguous blocks of forest based on percent of area greater than 60 yr of age.

[b] 1988 survey data plus Feb. 1989 update.

[c] 1988 survey data only.

400 and 800 m of clusters, respectively. The respective averages for group 2 compartments were 37.8% and 37.4%. The minimal differences in these figures, and the opposite trends at the two distances suggest that foraging availability and fragmentation within 800 m of clusters are not contributing to the above correlations.

DISCUSSION

The SHNF, with 128 known active Red-cockaded Woodpecker clusters, is one of the largest concentrations of this endangered species in existence (Costa and Escano 1989, Jackson 1978, Lennartz et al. 1983). Survey data for 1987–1992 for the SHNF Red-cockaded Woodpecker population provide some indication of recent population trends (NFS, unpub. data). On the San Jacinto District the number of woodpecker groups increased from 22 to 25. On the Raven District the number of known groups has increased from 90 in 1988 to 107 in 1992. The increase on the Raven District is due to the discovery of additional groups of woodpeckers during this period, especially in the 1988–1990 period. Most of these groups were in cavity tree clusters that appeared to have been in existence for several years based on number of cavity trees and cavity characteristics. Assuming that these groups were in existence in 1988 the number of groups has been declining at approximately 3% per year during the 1988–1992 period. This decline is similar to that for the subset of groups known in 1988.

Red-cockaded Woodpecker populations on the three other National Forests in Texas are small (<30 active clusters) and were also declining until recent intensification of management. Encroaching midstory and isolation from other active clusters, and fragmentation of forest habitat within 400 m of clusters have been demonstrated to have a negative effect on the probability of clusters remaining active and on group size (Conner and Rudolph 1991). Extensive tree age data also suggest that lack of optimum cavity trees may be a contributing factor (Rudolph and Conner 1991). Similar measures of these factors on the SHNF indicate that they are of similar magnitude on the SHNF as on the three other National Forests in Texas (Conner and Rudolph 1991). This is true even for cluster isolation exclusive of the areas of concentration.

The correlation analyses of number of active clusters and number of Red-cockaded Woodpeckers per cluster with area of forest greater than 60 yr of age and less than 60 yr of age are instructive. The significant positive correlations of these woodpecker population measures with area of forest greater than 60 yr of age demonstrates that woodpecker population density is greater in areas with more mature forest. This relationship is consistently present across a range of areas from individual compartments (= 520 ha) to blocks of 10–15 compartments. This relationship is not simply due to limited area of available habitat. The average density of woodpecker groups is low and much of the area is currently unoccupied.

The possible cause(s) of this pattern can be grouped into four categories: (1) past distribution, (2) reduced foraging habitat, (3) cluster removal and (4) differential attrition due to changes in extent of forest fragmentation. The possibility that the current distribution reflects the past distribution is unlikely. The forested habitats are generally similar throughout the study area in species composition, soil types, etc. The primary differences are in stand ages and extent of fragmentation of older stands. The currently existing correlation of number of woodpeckers per group and area of forest greater than 60 yr of age suggests that the cause of the existing pattern is still operating and is reflected in demographic patterns in existing groups.

A reduction in group size could result from reduced foraging habitat rather than the effects of fragmentation. Walters et al. (1988) have demonstrated a positive correlation between reproductive success and group size. In a previous study (Conner and Rudolph 1991), based in part on the SHNF data, group size in sparse populations was found to decline with an increase in forest removal. In dense populations, however, the relationship was much weaker. This suggests that reduced foraging habitat is not the primary cause of the observed patterns.

The possibility that past harvesting of timber has eliminated clusters thereby contributing to the present pattern is difficult to evaluate. Prior to 1968 there were no prohibitions against cutting of Red-cockaded Woodpecker cavity trees. In 1968 the species was identified as rare and endangered (United States Department of Interior 1968) and was afforded Federal protection with the passage of the Endangered Species Act in 1973. Loss of clusters due to timber harvesting should have ceased at this time. Consequently, the current distribution pattern is undoubtedly due in part to harvesting practices prior to 1968–1973. The data relating to group size and proportion of clusters currently active, however, suggest that the correlations observed are, at least in part, due to ongoing causes.

The fourth possibility, differential attrition of active clusters related to extent of forest fragmentation, is supported by the above data. The positive correlation between number of woodpeckers per group and area of forest greater than 60 yr of age is strong evidence that the species is sensitive to this parameter. These data also support the conclusion that the effect is still influencing the demographics of the individual groups and the population. The absence of a significant correlation between number of inactive clusters and area of forest greater than 60 yr of age provides additional support for this interpretation.

We have argued elsewhere (Conner and Rudolph 1991) that reduced dispersal efficiency rather than loss of foraging habitat is the primary cause of the relationship between forest fragmentation and Red-cockaded Woodpecker population parameters in small populations with isolated clusters. The persistence of a similar relationship at an intermediate scale supports this interpretation. The habitat occupied by this population is a mosaic of mature forest habitat and non-forest or young pine plantation habitats. The relative proportions of these habitats and their distributions result in a landscape consisting of a mature forest matrix highly fragmented by islands of unsuitable Red-cockaded Woodpecker habitat. The suitable habitat is not fragmented in the sense of complete isolation between patches. Broad connections and corridors typically remain between most areas of suitable habitat. It is difficult in such situations to differentiate between effects due to habitat loss and those due to habitat fragmentation.

We hypothesize that the levels of fragmentation observed may be sufficient to reduce the efficiency with which dispersing juvenile females locate groups lacking females (Walters et al. 1988). The result is a population with an increased proportion of groups failing to breed in a given year due to absence of potentially breeding females. The observed result is a reduction in average group size due to absence of breeding females and lost reproductive potential correlated with the level of habitat fragmentation.

It is also possible that differential attrition is due to the reduced availability of potential cavity trees in areas with less forest >60 yr of age. The rapid turnover in the cavity tree population due to tree mortality and cavity enlargement in loblolly and shortleaf pine habitat (Conner et al. 1991) would exacerbate this problem.

Additional research is necessary to determine if sensitivity to fragmentation is a factor in Red-cockaded Woodpecker demographics and the specific nature of the proximal causes.

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18TH STATED MEETING OF THE COLONIAL WATERBIRD SOCIETY

The Colonial Waterbird Society will hold its 18th annual meeting on 9–12 Nov. 1994 at the Shell Island Resort Hotel in Wrightsville Beach, North Carolina. For information regarding the program, contact Scientific Program Chair, James Kushlan, Department of Biology, University of Mississippi, University, MS 38677. For information on other matters, contact Local Committee Chair James Parnell, Department of Biological Sciences, University of North Carolina at Wilmington, College Road, Wilmington, NC 28403.