

HABITAT QUALITY AND REPRODUCTION OF RED-COCKADED WOODPECKER GROUPS IN FLORIDA

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Abstract: Current foraging habitat guidelines for management of the red-cockaded woodpecker (*Picoides borealis* [RCW]) are based on the hypotheses that reproductive success, number of adults per family group, and occupancy of a cluster of cavity trees by a group are related to the amount of foraging habitat available to each group. We tested these hypotheses in a population in the Apalachicola National Forest (ANF) in Florida. Guidelines mandate providing ≥ 6350 pine trees ≥ 25 -cm diameter at breast height (dbh) within 800 m of each cluster of cavity trees; occupied clusters we studied had 1,200–13,176 available pines. We detected no association between number of young fledged and the availability of pine trees or degree of habitat fragmentation. We found a weak association between number of young fledged and demographic isolation surrounding cavity tree clusters. No differences were detected in the amount of available foraging habitat or degree of habitat fragmentation surrounding cavity tree clusters occupied by groups of different sizes. However, unoccupied clusters had fewer occupied clusters within 2 km than did occupied clusters. We could not reject the null hypotheses that reproductive attainment and group size were the same for groups with different amounts of available foraging habitat. Our results are consistent with the majority of earlier studies. We suggest that foraging guidelines should not categorically prohibit actions designed to benefit RCW long-term when these actions reduce available foraging habitat below guideline levels in the short-term.

J. WILDL. MANAGE. 60(4):826–835

Key words: Florida, foraging habitat, fragmentation, group size, *Picoides borealis*, red-cockaded woodpecker, reproduction.

According to the recovery plan (U. S. Fish and Wildl. Serv. 1985), providing 51 ha of preferred foraging habitat per family group would ensure recovery of RCW populations if other criteria were also met. The recovery plan further specified that foraging habitat must be within 800 m of the cavity tree cluster, with 40% of trees ≥ 60 years old, and provide at least 6,350 pine stems ≥ 25.4 -cm dbh and 789 m² of pine basal area. In 1985, the U. S. Forest Service (USFS) adopted these guidelines as the minimum amount of foraging habitat that would be provided for each family group of RCWs in populations on National Forests (U. S. For. Serv. 1985). Before any trees can be cut within 800 m of a cavity tree cluster, an analysis must show that the guidelines will be met if the proposed removal of trees occurs.

Conflicts sometimes arise when trying to satisfy the foraging habitat guidelines and meet other desirable, sometimes essential, management activities related to recovery of the species and the ecosystem upon which it ultimately depends. For example, thinning of pine stands is sometimes necessary for restoration of the understory plant community. Understory plants contain most of the biodiversity in the longleaf pine (*Pinus palustris*) ecosystem (Walker and Peet 1983, Peet and Allard 1993) and provide much of the fuel for the fires that drive the ecosystem (Myers 1990). Southern pine beetles (*Dendroctonus frontalis*) are a major threat to RCW habitat in some areas, particularly where loblolly (*P. taeda*) and shortleaf pine (*P. echinata*) occur (Conner et al. 1991, Conner and Rudolph 1995, Rudolph and Conner 1995). Thinning of pine stands is a prophylaxis for this pest (Thatcher et al. 1986), and the emergency removal of buffers of live pines is sometimes the best method of stopping epidemic level ad-

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vances of the beetle (Billings and Varner 1986). Most designated RCW recovery populations are in high-risk hurricane areas (Hooper and McAdie 1995). The ability of RCW populations in forests comprised of even-aged stands to survive hurricanes is enhanced by a balance of tree age classes (Watson et al. 1995) and the growing of wind firm trees. Regeneration is necessary to achieve a balance of age classes (Walker 1995), and periodic thinning is necessary for the growth of wind-firm trees (Hooper and McAdie 1995). In the past, slash (*Pinus elliottii*) and loblolly pine have been planted in areas that historically grew and are better suited to longleaf and shortleaf pines. The sooner these areas are converted back to longleaf or shortleaf pine, the sooner they will grow into more suitable RCW habitat. Implementation of these management activities involves the cutting of trees that would sometimes result in failure to meet prescribed foraging habitat guidelines. Even though the RCW would benefit from these management activities in the long-term, they would be subjected to a potential reduction of foraging habitat for up to 30 years.

Foraging guidelines in the recovery plan were intended to provide ample habitat for population recovery. Red-cockaded woodpecker groups can survive and successfully reproduce with less habitat than that provided by the guidelines (U. S. Fish and Wildl. Serv. 1985). A criticism of the current guidelines is that they were developed from a small dataset ($n = 18$) in a single population.

Although a minimum threshold of foraging habitat must exist, if this threshold is below USFS guidelines, RCWs may benefit in the long-term by management actions that initially reduce foraging habitat. Our objective was to evaluate the relation between RCW group size, reproductive success, and several measures of foraging habitat quality on the ANF, in north Florida. Specifically, we tested the following null hypotheses: (1) RCW groups with different amounts of foraging habitat available have equal levels of nesting success; (2) RCW groups with different amounts of foraging habitat have equal numbers of adults; (3) RCW groups exposed to different degrees of forest fragmentation have equal levels of nesting success; and (4) RCW groups exposed to different levels of isolation have equal levels of nesting success.

Funding was provided by the U. S. Forest Service. We thank the Apalachicola and Wak-

ulla Districts for support of field data collection. J. Caffin and G. Wood assisted with geographic information system analyses and E. Libby assisted with data compilation. S. R. Winterstein provided statistical advice. We thank R. N. Conner, R. S. DeLotelle, R. T. Engstrom, F. C. James, and D. C. Rudolph for comments on the manuscript.

STUDY AREA

Our study site, the ANF in north Florida, supported the largest RCW population in existence, with about 685 groups. The ANF encompassed 228,255 ha of flat to gently rolling terrain with 4 major vegetative types: pine, bay, bottomland, and savanna. Suitable RCW habitat was provided by 117,917 ha of pine and pine-hardwoods. Bays were found in poorly drained depressions dispersed throughout the pine flatwoods. Bays often surrounded cypress (*Taxodium distichum*) swamps. Bottomland consisted of hydric hardwood swamps, loblolly pine, and mixed hardwoods. Savannas included treeless areas dominated by grasses and sedges and pine flats that grade into pine flatwoods or high pine-land. Detailed descriptions of the physiography, geology, soils, vegetation, climate, and drainage are presented in U. S. Forest Service (1984).

METHODS

We followed Walters et al. (1988) RCW nomenclature where the term cluster (formerly called colony) refers to the aggregation of cavity trees used by a group (formerly called clan) of woodpeckers. We collected group size and reproductive data on 106 active clusters during 1990–93. These data were collected as part of ANF's RCW augmentation program. The augmentation program consists of identifying and translocating subadult RCWs from ANF to small declining populations. During the study, 19 females and 1 male were removed from groups that we studied. None of the groups we studied were augmented. The females removed from our study groups for augmentation would have dispersed naturally before nesting (Lennartz et al. 1987, Walters 1990). Because we measured group size for our study during the nesting period the removal of females did not affect our results. Groups monitored for the augmentation program were not selected at random but for logistical reasons. However, we had no prior knowledge of their size, reproductive performance, or the quality of habitat surrounding the

cluster. We compared the frequency distribution (Chi square goodness-of-fit test) of fledgling success in our sample to a dataset of 50 randomly selected clusters from the Apalachicola population (Hess, unpub. data). The randomly selected groups were part of a separate study, although 14 of the groups were also in our sample. The 2 samples did not differ ($P = 0.26$), which suggests that our sample was not biased.

Annually, during the breeding season, we counted the number of adult birds in each group as they left their roosts in the morning and before roosting in the evening. Beginning in late April of each year, we visited all clusters at least once every 10 days to determine if nesting had been initiated. Nestlings were banded when they were between 4 and 7 days old. We determined the number of young fledged by visiting each group 3 days after the expected fledging date. We followed birds in each group until we made a total count of the group.

We estimated the number of pine trees ≥ 25.4 -cm dbh and the amount of pine basal area available within 800 m of each cluster, as directed by USFS foraging habitat guidelines. We used a geographic information system to allocate resources among clusters that had overlapping 800-m radius circles. A given tree or area of habitat was allocated to only one cluster by the following convention. Resources within 400 m of a given cluster were allocated only to that cluster, even if that zone was overlapped by a 800-m radius circle from an adjacent cluster. Otherwise, the resources within the overlapping area of 800-m radius circles were allocated equally among the clusters.

Funding constraints prevented us from measuring numbers of pine trees and pine basal area around all 106 active clusters. Because we could only sample 60 of the 106 active clusters we wanted to ensure our sample included the entire range of available numbers of pine trees and pine basal area within that sample. However, numbers of trees and basal area were the subject of our estimations and therefore unknown. Thus, to approximate the range of habitat conditions we made the assumption that a high correlation existed between ha of foraging habitat and number of available trees (post-data collection analyses showed this to be a reasonable assumption—e.g., $R^2 = 0.91$ between ha of foraging habitat and no. of available trees). Foraging habitat is defined as pine or pine-hardwood stands ≥ 30 years old (U.S. Fish and Wildl. Ser. 1985).

Through geographic information system analyses, we determined the area of available foraging habitat for all 106 clusters. We then stratified our selection of clusters for study by area of foraging habitat. We estimated the number of pine trees ≥ 25.4 -cm dbh and amount of pine basal area within 800 m of all clusters that had < 40 ha ($n = 20$) or > 80 ha ($n = 9$) of available foraging habitat. Because of past management guidelines, most clusters ($n = 77$) had from 40 to 80 ha of foraging habitat available. We randomly selected 31 clusters from this category.

We also measured habitat quality around 10 randomly selected inactive clusters. Our sample population of inactive clusters was limited to those > 0.4 km but < 4.8 km from active clusters. We imposed these criteria in an attempt to avoid sampling inactive clusters that were the result of cluster drift (Hooper 1983) and those that became inactive because of extreme demographic isolation.

We determined the number of pine trees and amount of pine basal area for foraging habitat located within 800 m of each of the 70 clusters (60 active and 10 inactive) by sampling with 0.04-ha circular plots. At each sample point we tallied all pine trees ≥ 10 cm dbh by 5-cm dbh classes. We sampled most stands with a randomly located 60- \times 60-m grid that equated to 1 plot/0.4 ha. In stands > 32 ha, we sampled with a 80- \times 80-m grid that equated to 1 plot/0.6 ha.

For all 116 clusters we measured the degree of forest fragmentation with the angular sum index of fragmentation (Conner and Rudolph 1991). To assure comparable results we adopted Conner and Rudolph's use of pine stands < 20 years of age as the fragmenting feature to measure. We determined angular sum by measuring and summing the angles formed by drawing 2 lines from the geometric center of each cluster to the lateral edges of each fragmenting feature within 800 m of the cluster center. We also used the percent of non-foraging habitat within 800 m as an additional index of forest fragmentation. Following Hooper et al. (1982), DeLotelle et al. (1987), Conner and Rudolph (1991), and Hooper and Lennartz (1995) we assessed cluster isolation by determining the number of active clusters within 2 km of each study cluster center.

We used linear regression to analyze the relation between the number of young fledged and each independent variable. The independent variables used for the models were: number of pine trees ≥ 25.4 -cm dbh within 400 and 800

m, ha of foraging habitat within 400 and 800 m, number of active clusters within 2 km, angular sum, and percent non-foraging habitat within 800 m. We dropped basal area from the analyses because of its high correlation with number of pine trees ($R^2 = 0.96$). Because we sampled the number of young fledged for 4 years we included 3 indicator variables in each model, coded as zero or 1, to assess the variability of these relations among years (Neter et al. 1985:329–330). We tested for interactions between year and each independent variable. We made a more direct comparison with the results presented in the recovery plan (U. S. Fish and Wildl. Serv. 1985). Like the recovery plan, we divided groups into 3 categories based on the amount of available foraging habitat: <40 ha, 40–60 ha, and >60 ha. We compared the mean number of young fledged in these groups with the Kruskal-Wallis test (Siegal 1956:184).

To examine the relation between RCW group size and habitat quality we compared number of pine trees ≥ 25.4 -cm dbh within 400 and 800 m, ha of foraging habitat within 400 and 800 m, number of active clusters within 2 km, and angular sum among 5 categories of group size: no birds; pairs that did not have helpers any year; pairs that had at least 1 helper 1 of 4 years; pairs that had at least 1 helper 2 of 4 years; and pairs that had at least 1 helper 3 or 4 of 4 years. We used ANOVA (Steel and Torrie 1980:137) to make comparisons among groups and Tukey's procedure (Steel and Torrie 1980:185) to separate the means. We also compared the mean number of young fledged among the same categories of group size, except the no bird group. We considered results significant if $P < 0.05$.

RESULTS

Habitat Measurements

The mean number of pine trees ≥ 25.4 -cm dbh available within 800 m was 5,312 ($n = 60$, $SE = 336$). Sixty-seven percent of the clusters sampled had <6,350 trees specified by USFS guidelines. The mean number of pine trees within 400 m was 2,693 ($n = 60$, $SE = 157$). Pine basal area available within 800 m averaged 631 m^2 ($n = 60$, $SE = 40 m^2$), with 73% of the clusters having less than the 789 m^2 specified by the guidelines. Pine basal area within 400 m averaged 311 m^2 ($n = 60$, $SE = 16 m^2$).

Our indices of habitat fragmentation, angular sum and percent non-foraging habitat within

800 m, averaged 129 ($n = 106$, $SE = 8.0$) and 48.5 ($n = 106$, $SE = 1.5$), respectively. On average, 8.1 clusters were found within 2 km of each study cluster ($n = 106$, $SE = 0.3$).

Number of Young

Inspection of bivariate scatter plots suggests that the number of young fledged was not associated with the number of available pine trees (Fig. 1). Regression analyses, taking into account the effects of possible yearly variation, confirmed our observations; we found no associations between the number of young fledged and the number of available pine trees ≥ 25.4 -cm dbh within 400 or 800 m (Table 1). Nor did the data suggest that the relation between number of young fledged and number of pine trees varied among years (e.g., probability of overall model including no. of pine trees within 800 m, indicator variables, and interaction terms = 0.16).

By substituting ha of foraging habitat within 400 and 800 m in place of number of pine trees, we increased our sample sizes substantially (i.e., from 60 to 106 clusters). Again, there were no discernible patterns in the bivariate scatter plots (Fig. 2). Regression analyses confirmed that no significant associations between number of young fledged and ha of foraging habitat within 400 and 800 m existed in the dataset (Table 1). Inclusion of interaction terms in the models indicated that the relation did not vary by year.

Similarly, we found no association between number of young fledged and either of our fragmentation indices (Fig. 2, Table 1). Inclusion of the interaction terms did suggest that number of young fledged in 1991 was negatively associated with angular sum (overall model $P = 0.03$, angular sum:Y2 (yr) interaction $P = 0.03$). However, the association was weak ($R^2 = 0.04$). The number of young fledged was positively associated with the number of active clusters within 2 km (Table 1). However, the association was weak and not discernible in the scatter plots (Fig. 2). Two other models were significant, but the independent variables of interest did not contribute significantly, and the amount of variation in number of young fledged accounted for by the models was trivial (Table 1).

The regression models and a separate ANOVA ($P = 0.01$) did suggest that there were differences in the number of young produced in individual years. The mean number of young fledged in 1991 ($\bar{x} = 0.92$, $SE = 0.09$, $n = 98$)

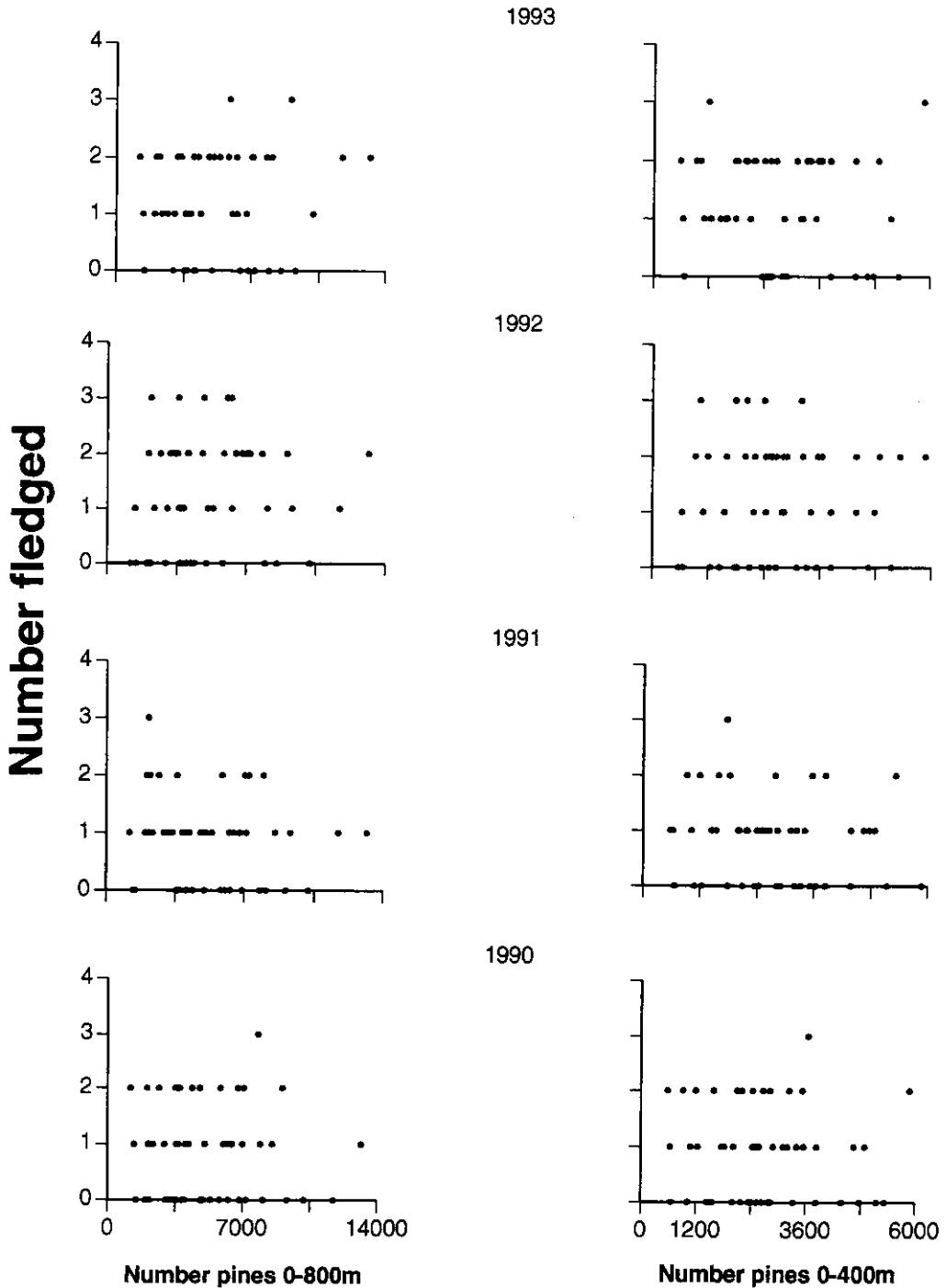


Fig. 1. Relation between the number of red-cockaded woodpecker young fledged and the number of pine trees > 25.4-cm dbh within 400 and 800 m of the cavity tree clusters, Apalachicola National Forest, Florida, 1990-93.

was significantly lower than the mean number of young fledged in 1992 ($\bar{x} = 1.31$, SE = 0.10, $n = 97$). The mean number of young fledged in 1990 ($\bar{x} = 1.05$, SE = 0.09, $n = 104$) and 1993

($\bar{x} = 1.24$, SE = 0.10, $n = 96$) did not differ from the other years.

We found no differences in the mean number of young fledged among groups with <40 ha,

Table 1. Results of linear regressions between number of young fledged per red-cockaded woodpecker group and independent variables associated with habitat quality and cluster isolation in the Apalachicola National Forest, Florida, 1990-93.

Variable	Probability of overall model	R ²	Probability of independent variable	Probability of indicator variables ^a		
				Y1	Y2	Y3
No. of pines >25-cm dbh within 800 m	0.07	0.03	0.71	0.15	0.02	0.98
No. of pines >25-cm dbh within 400 m	0.06	0.04	0.49	0.15	0.02	0.98
Ha of foraging habitat ^b within 800 m	0.07	0.02	0.71	0.34	0.02	0.75
Ha of foraging habitat within 400 m	0.03	0.03	0.19	0.34	0.02	0.74
Angular sum ^c	0.04	0.02	0.23	0.33	0.02	0.75
% non-foraging habitat within 800 m	0.06	0.02	0.39	0.34	0.02	0.74
No. of active clusters within 2 km	0.002	0.04	0.005	0.34	0.02	0.72

^a Indicator variables are dummy variables coded as zero or 1 to represent 4 yr that no. of young fledged were determined.

^b Foraging habitat is defined as pine and pine-hardwood stands \geq 30 yr old.

^c Sum of angles defined by the edge of pine stands < 20 yr old and the center of each red-cockaded woodpecker group's cluster of cavity trees (see text).

40-60 ha, and >60 ha of foraging habitat available ($P = 0.85$).

Group Size

We detected no differences in the number of pine trees \geq 25.4-cm dbh or area of foraging habitat within 400 or 800 m among the different RCW group sizes (Table 2). Nor were there any differences in either fragmentation index among the different group sizes. The mean number of active clusters within 2 km was lower for inactive clusters than for active clusters regardless of group size (Table 2).

Red-cockaded woodpecker groups that had 1 or more helpers during the 4 year study fledged on average more young ($P < 0.05$) than groups that did not have helpers in any year (2 birds with no helpers: $\bar{x} = 0.85$; 2 birds plus helper for 1 yr: $\bar{x} = 1.24$; 2 birds plus helper for 2 yr: $\bar{x} = 1.26$; 2 birds plus helper for 3 or 4 yr: $\bar{x} = 1.41$).

DISCUSSION

We did not find an association between the number of RCW young fledged and the amount of foraging habitat within 800 m of cavity tree clusters. Our results are consistent with Wood et al. (1985), DeLotelle et al. (1992), and Hooper and Lennartz (1995). Wood et al. (1985) studied the effects of clearcutting up to 36% of foraging habitat from the home ranges of 6 RCW groups. Only 2 groups exceeded the USFS pine basal area guideline before the removal of foraging habitat. After treatment, only 1 group exceeded this guideline. No adverse effects on nestling production were noted in 3 years of study. DeLotelle and Epting (1992) found that the density of pines and their juxtaposition to the

cluster were not significantly related to RCW reproductive success. They did find that RCW reproductive success was related to territory size, but that conspecific intruders and breeder experience were more important factors. Hooper and Lennartz (1995) studied the effect of removing 43% of foraging habitat on RCW reproductive success and group size. This removal reduced the average number of pine trees \geq 25.4-cm dbh available to groups from about 5,400 to 2,500 over 5 years. One year of post-harvest data showed no significant changes in group size or reproductive success. In addition, the number of active groups increased from 10 to 13 as foraging habitat was being removed. These studies used different approaches in different populations to test the same hypothesis, and they reached the same conclusion: within the range of habitat area studied, reproductive success of RCW groups is not strongly related to variation in available foraging habitat. Our study is the largest to date and we directly tested the assumption of the USFS guidelines that number of young fledged was correlated with available habitat within 800 m of clusters. However, we too failed to find a relation between foraging habitat and reproductive output.

Current guidelines are based on the average conditions in 18 year-round home ranges (U. S. Fish and Wildl. Serv. 1985). The recovery plan reported that groups with average home ranges fledged more young than groups with below average home ranges but less than groups with above average home ranges. We did not determine RCW home ranges. Instead our study was based on USFS guidelines that assume most foraging takes place within 800 m of the cluster and that the availability of foraging habitat in

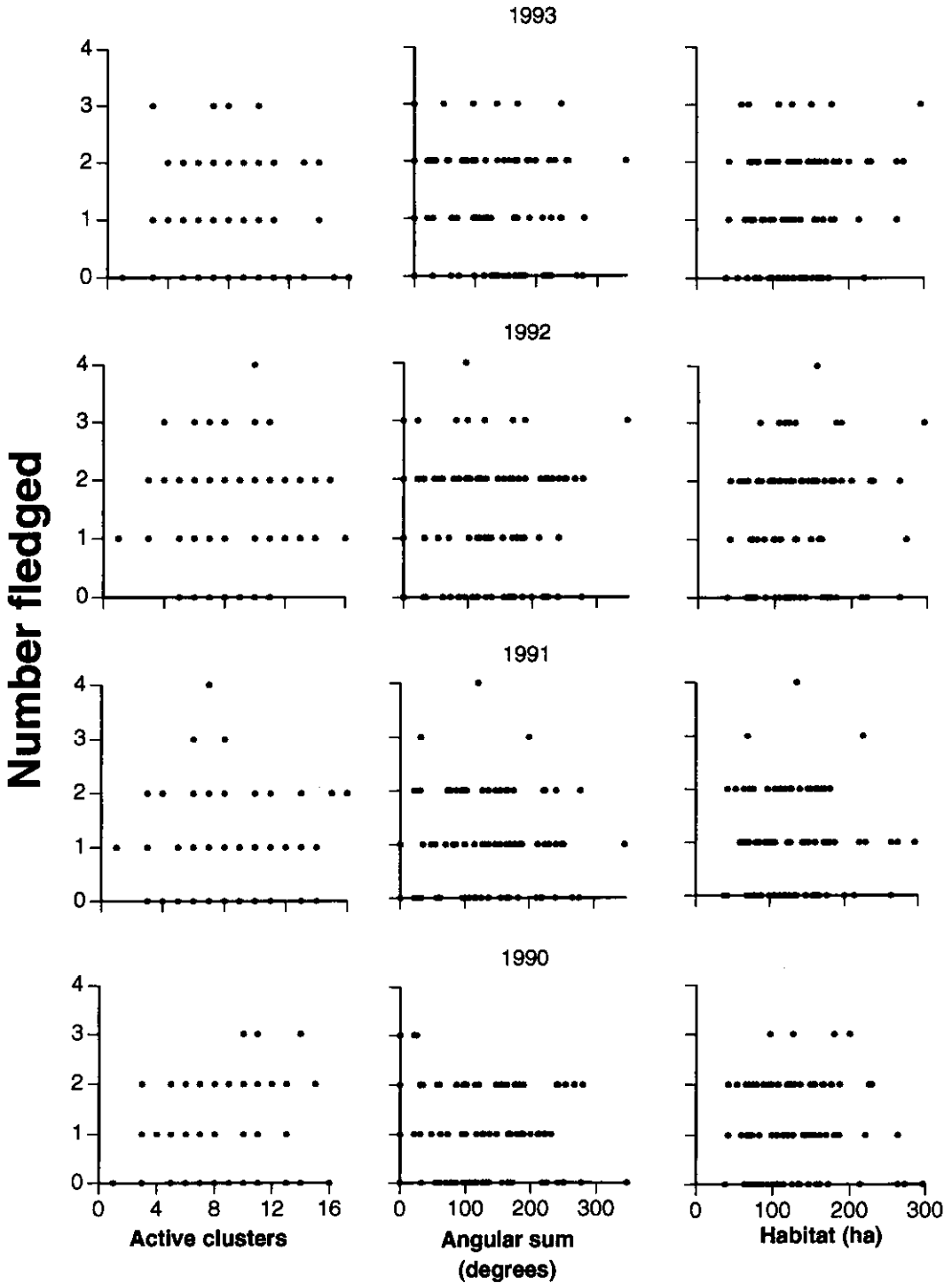


Fig. 2. Relation between number of red-cockaded woodpecker young fledged and the number of active clusters within 2 km, angular sum fragmentation index, and area of foraging habitat available within 800 m, Apalachicola National Forest, 1990-93.

that zone is the most critical to the well-being of groups. This is a reasonable assumption given that most foraging in relatively dense populations occurs within 800 m of clusters (Hooper et al. 1982, Porter and Labisky 1986). However, it does not necessarily follow that the number of young fledged are related to the amount of habitat within 800 m of a cluster. Some groups may forage beyond 800 m and some may not use all the habitat available to them within 800 m. Thus, even though our results suggest that number of young fledged is not related to the amount of foraging habitat within 800 m of clusters, the number of young fledged may still be related to the actual amount of habitat used by groups.

Reproduction in other birds has been associated with variation in annual food supply (Stacey and Koenig 1990). The lack of association between number of young fledged and amount of foraging habitat might be related to annual variation in the limiting factor. One could hypothesize that in years of good insect production most RCW groups reproduce successfully. Conversely, in years of poor insect production, groups with access to more foraging habitat may be able to obtain the resources they need to successfully fledge young. Groups with less foraging habitat available may be unable to obtain the resources necessary to be successful. Results presented in the recovery plan show a significant positive association ($R^2 = 0.39$) between the amount of foraging habitat used and number of young fledged in one year but not the following year (U.S. Fish and Wildl. Ser. 1985). Our results did suggest that the number of young fledged did vary in at least 1 of the 4 years. However, the variability in the number of young fledged was not associated with the habitat variables we measured. Possibly foraging resources were not limiting throughout the entire study, but may become limiting in the future.

Conner and Rudolph (1991) found a negative association between RCW group size and the amount of forest fragmentation in sparse RCW populations (1 active cluster/2,300 ha of forest area). They found no association in a denser population (1 active cluster/389 ha of forest area) subjected to even greater habitat loss. Conner and Rudolph (1991) cautioned that it may have been too early to observe the effects of fragmentation in the denser population. In comparison, population density in the ANF (1 cluster/352 ha of total forest area) was much greater

Table 2. Comparison of the amount of foraging habitat, degree of forest fragmentation (angular sum), and degree of isolation (active clusters within 2 km) surrounding red-cockaded woodpecker groups of different size categories in 1990-93 on the Apalachicola National Forest in Florida.

Variable	No birds			2 birds each yr			2 birds + helper 1 yr			2 birds + helper 2 yr			2 birds + helper 3-4 yr		
	n	z ^a	SE ^b	n	z	SE	n	z	SE	n	z	SE	n	z	SE
Foraging habitat															
No. of pines >25-cm dbh in 400 m	10	2,430a	432	20	2,542a	306	14	3,207a	366	7	2,024a	517	7	3,099a	517
No. of pines >25-cm dbh in 800 m	10	5,326a	1,000	20	4,641a	707	14	5,977a	845	7	4,565a	1,195	7	6,072a	1,195
Ha foraging habitat in 400 m	10	24a	3	31	27a	2	27	29a	2	16	26a	2	17	29a	2
Ha foraging habitat in 800 m	10	54a	8	31	50a	4	27	53a	5	16	56a	6	17	56a	6
Habitat fragmentation															
Angular sum	10	160a	25	31	118a	14	27	105a	15	16	136a	20	17	158a	19
% non-foraging habitat in 800 m	10	58.9a	5.5	31	45.7a	2.9	27	48.5a	3.4	16	43.6a	4.3	17	48.4	1.8
No. of active clusters in 2 km	10	3.1a	0.9	31	8.6b	0.5	27	7.7b	0.5	16	8.7b	0.7	17	9.4b	0.7

^a For a given variable, means followed by different letters are significantly different ($P < 0.05$) based on ANOVA and Tukey's tests.
^b SE = standard error.

than the sparse populations studied by Conner and Rudolph (1991). Also, the average angular sum measurement in the ANF population (\bar{x} = 129) was lower than in Conner and Rudolph's (1991) sparse (\bar{x} angular sum = 206) or dense (\bar{x} angular sum = 287) populations.

Hooper and Lennartz (1995) suggested that populations with <4.7 active clusters within 2 km on average, had critically low densities that inhibited population expansion. In our study, inactive clusters averaged only 3.1 clusters within 2 km. Perhaps the location of currently inactive clusters in the landscape relative to other groups contributed to their failure in maintaining active status.

Our results suggest a positive association between group size and the number of young fledged. Results in the literature are not consistent and suggest an interaction between breeder experience and the effect of helpers (Lennartz et al. 1987, Walters 1990). For example, Lennartz et al. (1987) found a positive association between reproductive success and breeder experience in pairs without helpers. In pairs with helpers, a negative association was found.

MANAGEMENT IMPLICATIONS

We envision future resource management conflicts with implementation of the foraging guidelines as population densities increase. Population growth of RCW will make it more difficult to meet current foraging guidelines as foraging habitat must be divided among more clusters. Some minimum habitat thresholds must surely exist, but our study does not provide the definitive results needed to redefine foraging requirements for RCWs. However, the preponderance of studies suggests that the quantity of foraging habitat provided to individual groups could, in some cases (e.g. larger populations), be reduced below those prescribed in the guidelines without adversely affecting group size or reproductive success. Although we are not proposing widespread reduction in foraging habitat for any population, adherence to existing guidelines does not in and of itself appear to be a valid reason to limit management activities (in moderation) that would otherwise benefit RCWs, other resources, or ecosystem restoration. Clearly, additional research is needed to identify which habitat components affect reproductive success and if those components can be manipulated through management.

LITERATURE CITED

- BILLINGS, R. F., AND F. E. VARNER. 1986. Why control southern pine beetle infestations in wilderness areas? The Four Notch and Huntsville State Park experience. Pages 129-134 in D. L. Kulhavy and R. N. Conner, eds. Wilderness and natural areas in the eastern United States: a management challenge. Stephen F. Austin State Univ., Nacogdoches, Tex.
- CONNER, R. N., AND D. C. RUDOLPH. 1991. Forest habitat loss, fragmentation, and red-cockaded woodpecker populations. *Wilson Bull.* 103:446-457.
- , AND ———. 1995. Losses of red-cockaded woodpecker cavity trees to southern pine beetles. *Wilson Bull.* 107:81-92.
- , ———, D. L. KULHAVY, AND A. E. SNOW. 1991. Causes of mortality of red-cockaded woodpecker cavity trees. *J. Wildl. Manage.* 55: 531-537.
- DELOTELLE, R. S., AND R. J. EPTING. 1992. Reproduction of the red-cockaded woodpecker in central Florida. *Wilson Bull.* 104:285-294.
- , ———, AND J. R. NEWMAN. 1987. Habitat use and territory characteristics of red-cockaded woodpeckers in central Florida. *Wilson Bull.* 99: 202-217.
- 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 symposium II. Florida Game and Fresh Water Fish Comm., Tallahassee, Fla.
- , AND M. L. LENNARTZ. 1995. Short-term response of a high density population of red-cockaded woodpeckers to loss of foraging habitat. Pages 283-302 in D. L. Kulhavy, R.G. Hooper and R. Costa, eds. Red-cockaded woodpecker: species recovery, ecology, and management. Stephen F. Austin State Univ., Nacogdoches, Tex.
- , AND C. J. MCADIE. 1995. Hurricanes and the long-term management of the red-cockaded woodpecker. Pages 148-166 in D. L. Kulhavy, R.G. Hooper and R. Costa, eds. Red-cockaded woodpecker: species recovery, ecology, and management. Stephen F. Austin State Univ., Nacogdoches, Tex.
- , L. J. NILES, R. F. HARLOW, AND G. W. WOOD. 1982. Home ranges of red-cockaded woodpeckers in coastal South Carolina. *Auk* 99:675-682.
- LENNARTZ, M. R., R. G. HOOPER, AND R. F. HARLOW. 1987. Sociality and cooperative breeding of red-cockaded woodpeckers, *Picoides borealis*. *Behav. Ecol. Sociobiol.* 20:77-88.
- NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1985. Applied linear statistical models. Richard D. Irwin, Homewood, Ill. 1127pp.
- MYERS, R. L. 1990. Scrub and high pine. Pages 150-193 in R. L. Myers and J. J. Ewel, eds. Ecosystems of Florida. Univ. Central Florida Press, Orlando. 765 pp.
- PEET, R. K., AND D. J. ALLARD. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast Regions. Tall Timbers Fire Ecol. Conf. 18:45-81.

- PORTER, M. L., AND R. F. LABISKY. 1986. Home range and foraging habitat of red-cockaded woodpeckers in northern Florida. *J. Wildl. Manage.* 50:239-247.
- RUDOLPH, D. C., AND R. N. CONNER. 1995. The impact of southern beetle induced mortality on red-cockaded woodpecker cavity trees. Pages 208-213 in D. L. Kulhavy, R.G. Hooper and R. Costa, eds. Red-cockaded woodpecker: species recovery, ecology, and management. Stephen F. Austin State Univ., Nacogdoches, Tex.
- SIEGAL, S. 1956. Non-parametric statistics. McGraw-Hill Book Co., New York, N. Y. 312pp.
- STACEY, P. B., AND W. D. KOENIG, EDITORS. 1990. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge Univ. Press. New York, N.Y. 615 pp.
- STEEL, R. G. D., AND J. H. TORRIE. 1980. Principals and procedures of statistics a biometrical approach. McGraw-Hill Book Co., New York, N. Y. 633pp.
- THATCHER, R. C., G. N. MASON, AND G. D. HERTEL. 1986. Integrated pest management in southern pine forests. USDA For. Ser. Agric. Handb. 650. Washington D. C. 38pp.
- U. S. FOREST SERVICE. 1984. Soils and vegetation of the Apalachicola National Forest. Southern Reg., Atlanta, Ga. 165pp.
- . 1985. Red-cockaded woodpecker. Chapter 420 in Wildlife management handbook. For. Serv. Handb. 2609.23R. Southern Reg., Atlanta, Ga. 19pp.
- . 1993. Draft environmental impact statement for the management of the red-cockaded woodpecker and its habitat on national forests in the southern region. Southern Reg., Atlanta, Ga. 460pp.
- U. S. FISH AND WILDLIFE SERVICE. 1985. Red-cockaded woodpecker recovery plan. U. S. Fish and Wildl. Ser., Atlanta, Ga. 88pp.
- WALKER, J. L., AND R. K. PEET. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55:163-179.
- WALKER, J. S. 1995. Potential red-cockaded woodpecker habitat produced on a sustained basis under different silvicultural systems. Pages 112-130 in D. L. Kulhavy, R.G. Hooper and R. Costa, eds. Red-cockaded woodpecker: species recovery, ecology, and management. Stephen F. Austin State Univ., Nacogdoches, Tex.
- WALTERS, J. R. 1990. Red-cockaded woodpeckers: a 'primitive' cooperative breeder. Pages 69-101 in P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge Univ. Press, New York, N.Y.
- , P. D. DOERR, AND J. H. CARTER, III. 1988. The cooperative breeding system of the red-cockaded woodpecker. *Ethology* 78:275-305.
- WATSON, J. C., R. G. HOOPER, D. L. CARLSON, W. E. TAYLOR, AND T. E. MILLINGS. 1995. Restoration of the red-cockaded woodpecker population on the Francis Marion National Forest: three years post Hugo. Pages 172-182 in D. L. Kulhavy, R.G. Hooper and R. Costa, eds. Red-cockaded woodpecker: species recovery, ecology, and management. Stephen F. Austin State Univ., Nacogdoches, Tex.
- WOOD, G. W., L. J. NILES, R. M. HENDRICKS, J. R. DAVIS, AND T. L. GRIMES. 1985. Compatibility of even-aged timber management and red-cockaded woodpecker conservation. *Wildl. Soc. Bull.* 13:5-17.

Received 15 May 1995.

Accepted 15 April 1996.

Associate Editor: Noon.