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ECOSYSTEM MANAGEMENT AND THE NICHE GESTALT OF THE RED-COCKADED WOODPECKER IN LONGLEAF PINE FORESTS

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Abstract. We use the term ''optimal niche gestalt'' to refer to the concept that there are structural features of the environment that allow a species to thrive over and above those that allow it to persist. Analyses of the covariation between demographic and habitat features can reveal a trajectory toward this optimal state. To help identify new criteria for foraging-habitat guidelines for the Red-cockaded Woodpecker (*Picoides borealis*) in the Apalachicola National Forest, we examine seven years of demographic data for the woodpecker population and habitat in core stands, the naturally regenerated prime habitat in the centers of their territories. For both districts of the forest, two compound habitat variables are highly related to the average number of adult birds per social group, the average number of young fledged per group, and the density of groups. These variables are, first, the difference between the density of trees >35 cm dbh and that of trees 15–25 cm dbh and, second, the difference, in the ground cover, between the percentage of wiregrass and that of woody-plus-palmetto vegetation. Although the birds require a few old relict trees for their cavities, a regression analysis shows that including data for variation in the availability of relict trees in this forest does not improve the power of the above habitat variables to account for variation in the demography of the birds.

Because covariation between demographic variables and the recommendations in the current federal guidelines for the management of foraging habitat of the Red-cockaded Woodpecker is low, we conclude that experimental tests of whether causal mechanisms underlie the much higher correlative relationships we have found are warranted. Such tests should use differing levels of prescribed fire, which has dramatic effects on the ground cover. Smaller size classes of trees in closed-canopy stands should be thinned, creating patchy openings in the forest that will promote natural pine regeneration. Traditional uneven-aged silvicultural management could adopt a target tree distribution similar to that on the Apalachicola Ranger District, which supports a population of woodpeckers that is deemed to have recovered. We think that in addition to being beneficial for the birds the proposed program of habitat management is more likely to promote the long-term restoration of the longleaf pine/wiregrass ecosystem within Red-cockaded Woodpecker habitat than are alternative scenarios.

Key words: Apalachicola National Forest (Florida, USA); ecosystem management; endangered species; Florida, northern; foraging guidelines; habitat; longleaf pine; niche gestalt; Picoides borealis; Pinus palustris; *Red-cockaded Woodpecker.*

INTRODUCTION

Although much progress has been made in the last decade toward formulating plans for ecosystem management of coniferous forests on public lands in the Pacific Northwest (U.S. Forest Service et al. 1993*a, b*, 1994), no similar coordinated effort has yet been made for the management of the coniferous forests in the southeastern United States. Another major difference is that, although substantial old-growth forest remains in the Pacific Northwest, before 1920 virtually all of the virgin old-growth forests in the southeast were cut (Frost 1993). Even so, some regenerated longleaf pine (*Pinus palustris*) forests still contain a few relict trees, and they support >180 rare vascular plant taxa. Some areas are as rich in endemic plants as any other habitat in North America (Walker 1993).

The species in the longleaf pine ecosystem for which the ecology is best understood is the endangered Red-cockaded Woodpecker (*Picoides borealis*; Jackson 1994, Conner et al. 2001). It occurs also in loblolly (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) forests (Epting et al. 1995, Doster and James 1998), but researchers agree that it is most closely adapted to the longleaf pine ecosystem (Conner et al. 2001). As with the Northern Spotted Owl (*Strix occidentalis caurina*) in the Pacific Northwest, the legal power of the Endangered Species Act has been used to constrain timber harvest on public land to promote recovery of this endangered species (U.S. Forest Service 1995, Conner et al. 2001). In response, there are newly published guide-

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lines for the management of habitat of the Red-cockaded Woodpecker on Forest Service land (U.S. Forest Service 1995) and unpublished guidelines for wildlife refuges, military bases, and private land. All of them retain some criteria similar to those in the latest recovery plan (U.S. Fish and Wildlife Service 1985), which is currently under revision.

In the present paper, we examine the current federal guidelines in relation to data for Red-cockaded Woodpeckers in the Apalachicola National Forest in northern Florida. We then propose a new model for habitat management based on the concept of the niche gestalt. This concept is based on early ideas about the perceptual world of animals (the ''Umwelt'' of von Uexkull [1909]) and their species-specific requirements (Grinnell 1917*a*, *b*, Hutchinson 1958, 1968). The unit of interest is not the habitat of the focal species but rather that subset of the structure of its environment that is relevant to its reproduction and survival (James 1971, Dueser and Shugart 1978, James et al. 1984, Reinert 1984, Morrison et al. 1992:32; see also the autecological paradigm of Hengeveld and Walter [1999]). Because we cannot understand the perceptual world of the animal, we assume here only that predictable relationships exist between a species and the structure of its environment. If there is covariation between the fitness of the population and the structure of its habitat in the many places where it exists, that covariation should lead to a hypothetical optimal niche gestalt. Although it sounds esoteric, wildlife habitat management can be viewed as tests of hypotheses about whether correlative relationships between the habitat and the fitness of a focal species are based on causal relationships. One result of such work should be the ability to develop target criteria for improved habitat for the focal species. It should allow managers to estimate quantitatively whether changes in habitat are associated with improvement in the status of the species. Experimental trials and planned comparisons would constitute quasi-experimental tests of the predictions based on the concept (Everhardt and Thomas 1991, James and McCulloch 1995).

In the particular example used here, we analyze covariation between demographic data for the Red-cockaded Woodpecker and habitat data in a way that allows identification of the structure of the habitat that is associated with the healthiest population as opposed to a structure that may be less satisfactory. Similar work for other species could lead to an integrated program for the restoration of the longleaf pine ecosystem. These objectives are consistent with those in the FEMAT report for the management of forests on federal land in the Pacific Northwest and its associated documents (U.S. Forest Service and cooperating agencies 1993*a*, *b*, 1994), which used population viability analysis but not the concept of the niche gestalt.

Most current longleaf pine forests are aging without replacement (Landers et al. 1995). They lack the open canopies that are required for regeneration. One specific objective in this study was to ask whether there is evidence that the Red-cockaded Woodpecker in this ecosystem is being harmed because so many current forests have closed canopies.

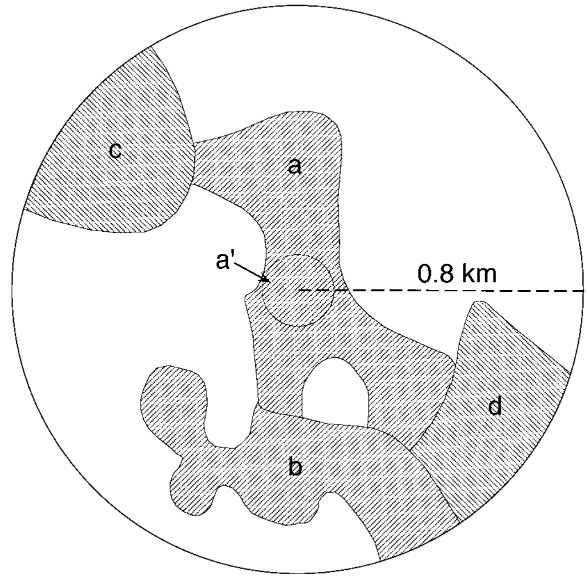

FIG. 1. Diagram of a sample Red-cockaded Woodpecker management circle in the Apalachicola National Forest showing (a) the core stand, (a′) the 4-ha cluster site within it that contains the cluster of cavity trees, (b) one other stand that is also longleaf pine forest >60 yr old, and (c and d) two thinned slash pine plantations that have trees >25 cm dbh. Some of the foraging habitat (a–d) of the group occupying these stands may be assigned to other groups, if circles overlap. The blank areas do not qualify as Red-cockaded Woodpecker habitat because they do not have pine trees ≥25 cm dbh. They consist of either dense younger pine plantations or hardwoods.

Current federal guidelines

For management purposes, Red-cockaded Woodpecker habitat is usually defined as consisting of a central 4-ha nesting area, which contains the cluster of relict cavity trees where a social group of 1–5 birds roosts and nests, plus foraging habitat. This central area, which we will call the cluster site, is usually part of a substantially larger stand of similar habitat, which we refer to here as the core stand. Except in rare cases of remaining old-growth forest, core stands are pine and mixed pine–hardwood stands that regenerated naturally after their initial cut. Both the current recovery plan (U.S. Fish and Wildlife Service 1985) and subsequent government documents (Henry 1989, U.S. Forest Service 1995) recommend that foraging habitat for the Red-cockaded Woodpecker include a combination of pine and pine–hardwood stands summing to ≥51 ha within a 200-ha area (a circle of 0.8-km radius) centered on the cluster site (Fig. 1). The recommendations say that these qualifying stands in the 200-ha management circles should have ≥6350 pine trees ≥25 cm in diameter at breast height (dbh) and a cross-sectional area of wood (basal area) of 789 m^2. Forty percent of the trees should be ≥60 yr old.

Apalachicola National Forest

The Apalachicola National Forest in northern Florida, which consists of two districts divided by the Ochlockonee River, includes 118 000 ha of managed pine and pine–hardwood forest. The Apalachicola Ranger District (ARD), encompassing approximately half of the managed pine forest, is estimated to harbor ∼500 territorial groups of birds, and its population is deemed to have recovered (U.S. Forest Service 1995). The Wakulla Ranger District (WRD) was estimated in 1990 to have 90 pairs of territorial birds plus an estimated 18 more single birds defending territories (James 1991, 1995). This high proportion of single birds indicates a declining population (Conner et al. 2001), a situation that has continued through the late 1990s. In a random sample of 23 territories with pairs of birds in the WRD in 1996, two had been abandoned and two reduced to single birds by 1999 (17% without pairs). Some abandoned territories have been reactivated and some new territories established in the northeastern section of the WRD during this period (J. Ruhl, *personal communication*). In a 1996 random sample of 32 territories with pairs in the ARD, one had been abandoned and one had a single bird in 1999 (6%).

The study by Beyer and colleagues

Beyer et al. (1996) showed that many of the 0.8-km-radius management circles around Red-cockaded Woodpecker groups in the Apalachicola National Forest are not in compliance with the current federal guidelines for minimum number of trees >25 cm dbh and total basal area in the foraging habitat. They found no relationship between the variables used in the guidelines and either the number of adults per group or the average number of young fledged per group. Their analysis was for a combination of both the stable ARD and the declining WRD populations, but Hovis and Labisky (1985) had shown previously that, even for the healthy population in the ARD alone, many management circles were not in compliance with the guidelines. Beyer et al. concluded that allowing limited reductions of the minimal criteria in the guidelines could be justified, if such reductions allowed other management procedures beneficial to the birds in the long term. Reductions from these standards have been approved recently by the U.S. Fish and Wildlife Service for the ARD (U.S. Forest Service 1999*a*, *b*: 3–27; ≥4100 pine trees ≥25 cm dbh and ≥30 yr old and a total basal area of ≥511 m^2 of trees >13 cm dbh within the management circle; 14–25 m^2/ha basal area in stands not managed as uneven-aged).

Our view is that Red-cockaded Woodpeckers are indeed responsive to the amount and quality of their habitat, but that the variables used in the current guidelines and by Beyer et al. (1996) do not measure them. Like Beyer et al. (1996), we investigated bird–habitat relationships, using the average number of adults per group (group size 1–4 adults, according to whether the territory is being defended by a single bird, a pair, or a pair with one or two male "helpers," which are sons from previous years) and the average number of fledglings per year from the first successful nest in a given year (productivity 0–3 fledglings).

We extended the analysis of Beyer et al. (1996) by estimating the relationship between the bird variables (group size and productivity) and the variables in the current federal guidelines separately by district. These two bird variables are known to be related (Lennartz et al. 1987, Walters 1990, James et al. 1997). Two of the habitat variables in the guidelines (total number of trees over a specified diameter in an undefined area of stands within the management circle and their basal area) seemed unlikely to us to be relevant to woodpecker habitat, so we considered new variables expressing the density of trees by size class and the composition of the ground cover. We knew from previous work that although Red-cockaded Woodpeckers rarely go to the ground, there is substantial covariation across the forest as a whole between the bird variables and the percentage of herbaceous vegetation in the ground cover, an indirect indicator of fire history and perhaps more subtle ecosystem processes (James et al. 1997).

Core stands

Next, we analyzed bird–habitat relationships in core stands. Core stands include the cluster site with its cavity trees but are larger and have fairly uniform habitat characteristics. They are typical of stands that regenerated after the initial harvest, which occurred in this forest between 1900 and 1920. The current cavity trees are living, mostly flat-topped, trees that were spared when the old-growth forest was cut. These cavity trees, which now average >95 yr old, are usually within stands dominated by 60- to 70-yr-old trees that have regenerated naturally. There may be slash pines (*Pinus elliotti*) in wetter areas and a few scattered hardwoods, mostly oaks (*Quercus* spp.). Other stands qualifying as foraging habitat within the management circle may have a similar history, or they may have been cut, plowed, fertilized, and planted in even-aged timber. Red-cockaded Woodpeckers do forage in these pine plantations, especially those that have been thinned. The core stands and other stands that regenerated naturally after the initial cut are the most important areas of the territory of a Red-cockaded Woodpecker group. They are the ones from which most of the food is procured when the group is feeding nestlings. The particular areas that are defended by the group or constitute its home range extend beyond the core stand, but home ranges of Red-cockaded Woodpeckers are smallest

TABLE 1. Summary of bird data and habitat data for appropriate stands in 55 circles of 0.8-km radius centered on clusters of cavity trees in the two districts of the Apalachicola National Forest (Wakulla Ranger District, WRD; Apalachicola Ranger District, ARD) in Florida, USA.

Measure	Abbreviation	WRD average (SD)	ARD average (SD)	(WRD − ARD)	*P* (*t* test)
Woodpeckers					
Sample size		18	37		
Group size (average no. adults), 1990–1997	ADUL	1.62 (0.81)	2.23 (0.22)	−0.61	<0.01
Productivity (average no. fledged per group), 1990–1997	FLEG	0.67 (0.54)	1.12 (0.4)	−0.45	<0.01
Density of groups (no. groups within 1.6 km in 1994)	DENS	4 (2.8)	9 (3.1)	−5	<0.01
Habitat					
Area of stands with trees >25 cm dbh†‡	AREA	65 (22)	55 (23)	+10	NS
Number of trees >25 cm dbh within the 0.8-km circle‡	*T*>25	5810 (2170)	4540 (2190)	+1270	0.05
Fragmentation of stands within the 0.8-km circle‡		180 (84)	150 (75)	+30	NS
Total basal area of stands with trees >25 cm dbh‡§	TOBA	720 (286)	527 (242)	+193	0.02
Percentage of wiregrass in ground cover	WIGR	17 (10)	35 (15)	−18	<0.01
Percentage of gallberry in ground cover	GALB	18 (9)	19 (11)	−1	NS

Notes: Standard deviations (SD) are given in parentheses. Only 10 groups on the WRD had an average of >1.5 adults per group for 1990–1997. WRD − ARD is the average difference between districts. See Fig. 1 for a diagram of a sample circle.

† The area of a circle with a radius of 0.8 km is ~200 ha. The number of trees divided by the area of their stands (AREA) gives a general estimate of tree density in the appropriate stands.

‡ Data provided by R. Beyer. Five of Beyer et al.'s (1996) territories were omitted because they had been altered by subsequent management or they no longer harbored Red-cockaded Woodpeckers.

§ In m^2/ha of trees >10 cm dbh in stands with trees ≥25 cm dbh.

where the habitat is apparently of the highest quality (Engstrom and Sanders 1997).

We do not contend that habitat improvement alone will be sufficient to reverse declines in Red-cockaded Woodpecker populations. Even in the ARD, birds rarely establish new territories. The two most important additional considerations are cavity limitation (Walters et al. 1992, Kappes and Harris 1995) and habitat fragmentation (Conner and Rudolph 1991, Haig et al. 1993, Heppell et al. 1994, Rudolph and Conner 1994, Walters 1991, 1998, Thomlinson 1995, 1996). Current management to address the first need emphasizes the provision of artificial cavities and the translocation of birds among populations to establish new social groups (Hess and Costa 1995, Carrie et al. 1999); the second is addressed by plans to manage habitat in multiterritory units (Habitat Management Units, U.S. Forest Service 1995). Nevertheless, more attention is needed to long-term habitat quantity and quality.

METHODS

The habitat analysis is based on two sets of data. The first is for stands with trees >25 cm dbh within management circles, for 55 groups of woodpeckers in 32 management compartments in the two districts (Table 1, Fig. 1a–d). Each pine stand has been managed for timber harvest as a unit, and the prescribed burning program has been conducted by compartments, which can include several woodpecker management circles (Fig. 1). A stand was assigned to only one group of birds, and several groups in the ARD had overlapping circles. Other areas within the circle were unsuitable because they either were dense plantations of small slash or longleaf pines or were wetter areas dominated by deciduous vegetation. Beyer et al. (1996) reported bird and habitat variables in the federal guidelines for these groups for 1990–1993 plus data for the angular-sum index of fragmentation and contributed that information to this analysis. The angular-sum index (ASIN) is based on sums of angles formed by drawing pairs of lines from the geometric center of each cluster of cavity trees to the lateral edges of each fragmenting feature within the management circle. The habitat data were collected as directed by the U.S. Fish and Wildlife Service on the basis of one 0.04-ha circular plot per 0.4 ha or 0.6 ha. For each stand, we determined the percentage composition of the ground cover by taking 60 readings through an ocular tube on alternate steps along three transects that were representative of the stand (James and Shugart 1970). Averages of ground-cover percentages of wiregrass (*Aristida stricta*) and gallberry (*Ilex glabra*) were weighted by the size of that stand relative to the sizes of other qualifying stands. We have added bird data for 1994–1997.

The second set of data is for birds (1992–1998) and habitat (1996) in both districts in 55 core stands (Fig. 1a), each of which is in a separate management compartment (Table 2). One group of birds was chosen for inclusion from each of a random sample of the 200 management compartments in the entire forest. Each group had an average of >1.5 adults for the period 1992–1998. The core stands ranged in size from 9 to 60 ha for the WRD and from 9 to 62 ha for the ARD. Densities of trees by size class were estimated from counts in three representative 0.04-ha circular plots (James and Shugart 1970). Ground-cover data were obtained using an ocular tube as above for >20 species of plants.[3] Only five of the woodpecker groups in this data set were in the first data set.

[3] URL: ⟨http://bio.fsu.edu/htmls/fjindex.html⟩

TABLE 2. Summary of bird data and habitat data for 55 core stands by district (Wakulla Ranger District, WRD; Apalachicola Ranger District, ARD).

Measure	Abbreviation	WRD (n = 22 core stands)	ARD (n = 33 core stands)
Group size (average no. adults), 1992–1998†	ADUL	2.15 (0.30)	2.57 (0.50)
Productivity (average no. fledged per group), 1992–1998	FLEG	0.91 (0.40)	1.44 (0.50)
Density of groups within 1.6 km	DENS	3.5 (1–7)‡	6 (2–12)‡
Area of the core stand (ha)		32 (15)	30 (15)
Relict trees within a circle of 50-m radius	RLCT	93 (0–6)‡	5 (0–21)‡
Small trees (15–25 cm dbh) per hectare	SMTR	93 (50)	47 (30)
Medium trees (25–35 cm dbh) per hectare	METR	90 (40)	81 (45)
Large trees (>35 cm dbh) per hectare	LATR	14 (13)	41 (20)
Trees >25 cm dbh per hectare		104 (35)	123 (45)
Large minus small trees	LATR−SMTR	−79 (50)	−6 (43)
Basal area (m^2/ha)		7.5 (2.5)	10.3 (3.5)
Percentage wiregrass in ground cover	WIGR	15 (11)	43 (20)
Percentage gallberry in ground cover	GALB	14 (10)	14 (11)
Percentage woody vegetation in ground cover		46 (13)	29 (18)
Percentage palmetto		25 (13)	12 (8)
Percentage woody + palmetto	WDPM	71 (18)	40 (23)
Wiregrass − (woody + palmetto)	WIGR−WDPM	−56 (26)	3 (40)
Median no. trees <25 cm dbh in 0.8 ha, pine regeneration	NPRE	3.5 (0–30)‡	9 (0–80)†

Notes: Data are averages with standard deviations (SD) given in parentheses except where noted otherwise. Habitat data were obtained in 1996. See area ''a'' in Fig. 1 for a sample core stand. Multiply square meters per hectare by 10.76 to get square feet per hectare. Multiply square feet per hectare by 2.47 to get square feet per acre.
† All groups averaged >1.5 adults.
‡ Median and range.

We visited all woodpecker groups reported here once every 10 d in the breeding season to determine whether nesting had been initiated. Nestlings were banded when they were 5–8 d old. We determined the number fledged by visiting each group 3 d after the expected fledging date. The bird data are averages for the number of adults (breeding pair plus helper males) per group and the average number of fledglings produced per year (productivity).

Statistical analyses consist of Pearson correlations, simple and multiple regressions, and Kruskal-Wallis tests. These and the more exploratory box plots and graphs that give locally weighted regression (LOESS) lines (Cleveland and Devlin 1988) were performed in SYSTAT (Wilkinson et al. 1992).

RESULTS

Habitat in the management circle and compliance with current federal guidelines

Although the ARD has fewer trees >25 cm dbh (T>25) and lower total basal area (TOBA) within qualifying stands in woodpecker management circles, group size (ADUL), productivity (FLEG), and the density of nearby active groups (DENS) are higher in the ARD than in the WRD (Table 1). The ARD also has more wiregrass (WIGR) in the ground cover (Table 1). Eight groups of birds in the WRD sample disappeared between 1990 and 1997. Some of the remaining 47 areas were occupied by single birds or no birds in some years, but the averages were all >1.5 adults. The density of social groups is negatively related to all of the habitat variables in the federal guidelines (AREA, T>25, TOBA) but strongly positively related to the percentage of wiregrass in the ground cover (Table 3A). Some of the low correlations may be at least partly due to some weak but interesting nonlinear relationships. For example, group size and productivity are larger when the area of stands with trees >25 cm dbh (AREA) within the management circle is 40–75 ha than below and above those values (Fig. 2a, b). The same pattern is apparent with the percentage of wiregrass in the appropriate stands in the management circle. Note that all 10 of the WRD values fall below the LOESS fit through the data as a whole (Fig. 2c). The percentage of gallberry (GALB) tends to increase with area of appropriate stands in both districts (Fig. 2d). Birds do better in smaller territories where there is less gallberry in the understory (Table 3A). Note in Fig. 2d that the largest areas of foraging habitat have the highest percentage of gallberry in the ground cover and in Fig. 2b that these areas are not the most productive. Group size and productivity do not increase with area >75 ha. Thus, with high gallberry, the birds require exceptionally large areas of foraging habitat, but even then they are less productive than groups with smaller territories that have more wiregrass and less gallberry (Fig. 2b–d).

In both districts of the forest, the average number of trees >25 cm dbh and the total basal area of the stands with such trees within 0.8 km of the cluster of cavity trees are estimated to be lower than required by the current federal guidelines (4540 trees for the ARD, 5810 trees for the WRD, 6350 trees in the guidelines; 527 m^2 basal area for the ARD, 720 m^2 for the WRD, 789 m^2 in the guidelines) (Table 1). By these criteria, habitat of the healthier ARD population falls farther short of the guidelines than does that in the WRD. Only

TABLE 3. Two sets of Pearson correlations between woodpecker and habitat variables, one for habitat within 0.8 km of the cluster of cavity trees (Table 1) and one for habitat in the core stand (Table 2).

Variables	ADUL	FLEG	DENS
A) Habitat within 0.8 km (n = 47 groups)†			
AREA	0.09	−0.06	−0.19
T>25	0.06	−0.13	−0.24
TOBA	0.02	−0.11	−0.25
T>25 + TOBA	0.04	−0.12	−0.25
ASIN	0.11	−0.06	−0.01
WIGR	0.16	0.12	0.51
GALB	−0.23	−0.17	−0.08
B) Habitat in core stand (n = 55 groups)			
SMTR	−0.48	−0.29	−0.23
METR	−0.08	−0.15	−0.04
LATR	0.37	0.29	0.11
LATR−SMTR	0.52	0.34	0.22
WIGR	0.47	0.36	0.48
GALB	−0.11	−0.07	−0.07
WOOD	−0.47	−0.49	−0.34
WDPM	−0.52	−0.51	−0.38
WIGR−WDPM	0.51	0.45	0.44
SQR(RLCT)‡	0.41	0.26	0.36
NPRE	0.17	0.14	0.37

Notes: All groups had an average of ≥ 1.5 adults. ASIN is the angular sum index. Tables 1 and 2 give definitions of the variables.

† Only 10 groups were in the Wakulla Ranger District. Correlations by district were also below ±0.25 except that r = −0.35 for percentage of gallberry vs. productivity on WRD (Table 1).

‡ Square root of the number of relict trees.

44% of the territories on the WRD and 15% of those on the ARD are estimated to be in full compliance with all three major criteria of the guidelines. All Kruskal-Wallis tests among groups within districts showed that groups whose habitat meets the guidelines do not have significantly larger group size or higher productivity of fledglings than do groups in habitat that does not meet the guidelines. Apparently, the recommendations for total tree number and basal area in the current guidelines are inappropriate for this forest (Table 4).

Habitat in core stands

In the second data set (Table 2), the vegetation data include densities of trees by size class and percentages of 21 species of plants in the ground cover of the core stand of each territory. The Pearson correlation between adult group size (ADUL) and productivity of fledglings (FLEG) was r = 0.59 for this second data set of 55 groups. Only five species of plants each comprised >4% of the ground cover in one district. In the ARD, the dominant species were wiregrass (WIGR) (43%), gallberry (GALB) (14%), palmetto (*Serenoa repens*) (12%), and bluestem grass (*Andropogon* spp.) (6%). In the WRD, they were palmetto (25%), wiregrass (15%), runner oak (*Quercus* spp.) (16%), gallberry (14%), and shiny blueberry (*Vaccinium myrsinites* and *V. darrowi*) (5%). We report data for wiregrass, gallberry, total woody vegetation, and palmetto vegetation in the ground cover (Table 2).

By examining data for the distribution of pine trees organized by all 5-cm size classes, we were able to identify size classes and combinations of size classes that were associated with high values of the woodpecker variables. For simplicity, we refer to trees 15–25 cm dbh as ''small,'' trees 25–35 cm dbh as ''medium,'' and trees >35 dbh as ''large.''

The first striking relationship is the difference between districts in the relative densities of large and small trees, expressed as the density of large trees minus the density of small ones (LATR − SMTR) (−79 for WRD, −6 for ARD; Table 2) and its high positive correlations with the bird variables (Table 3B). A second major difference between districts is the relative percentages of wiregrass and woody vegetation plus palmetto vegetation in the ground cover, expressed as the percentage of wiregrass minus the percentage of (woody + palmetto) vegetation (−56% for WRD, 3% for ARD; Table 2). This composite variable (WIGR − WDPM) is also highly correlated with the bird variables (Table 3B). The Pearson correlations between woodpecker variables and these composite habitat variables for core stands are higher than those for any of the habitat variables considered in data for habitat within 0.8 km, except for wiregrass (Table 3).

Next we explored relationships in the 55 core stands by making graphic comparisons between districts (Figs. 3–5). The Pearson correlation between the densities of small and large trees for these 55 core stands in the two districts is r = −0.44, higher than correlations among other potential combinations of tree-density variables. In a graphic habitat space for these two variables, 60% concentration ellipses for the two districts show that this negative relationship is largely due to the differences between districts (Fig. 3). Within the WRD, variation in the density of small trees is high. Stands in the ARD tend to have high ratios of large to small trees. Because the graph presents the position of the habitat in the core stand of each group of birds in this space, it shows how densities of the two size classes of trees would have to change to make the WRD territories more like the ARD ones (Fig. 3). The values for the average ARD site, which might be taken to be a conservative management objective, are close to 40 large and 50 small pine trees per hectare (Table 2), whereas those for the average WRD site are closer to 15 large and 90 small trees/ha, respectively.

Both the percentage of wiregrass and that of (woody + palmetto) vegetation in this data set for core stands are related to the density of social groups (WIGR vs. DENS r = 0.48, WDPM vs. DENS r = −0.38). In a graphic habitat space, 60% concentration ellipses show that their negative relationship occurs independently on each district (Fig. 4). To make the ground cover of the WRD more like that of the ARD, management would have to move it along this axis of increasing

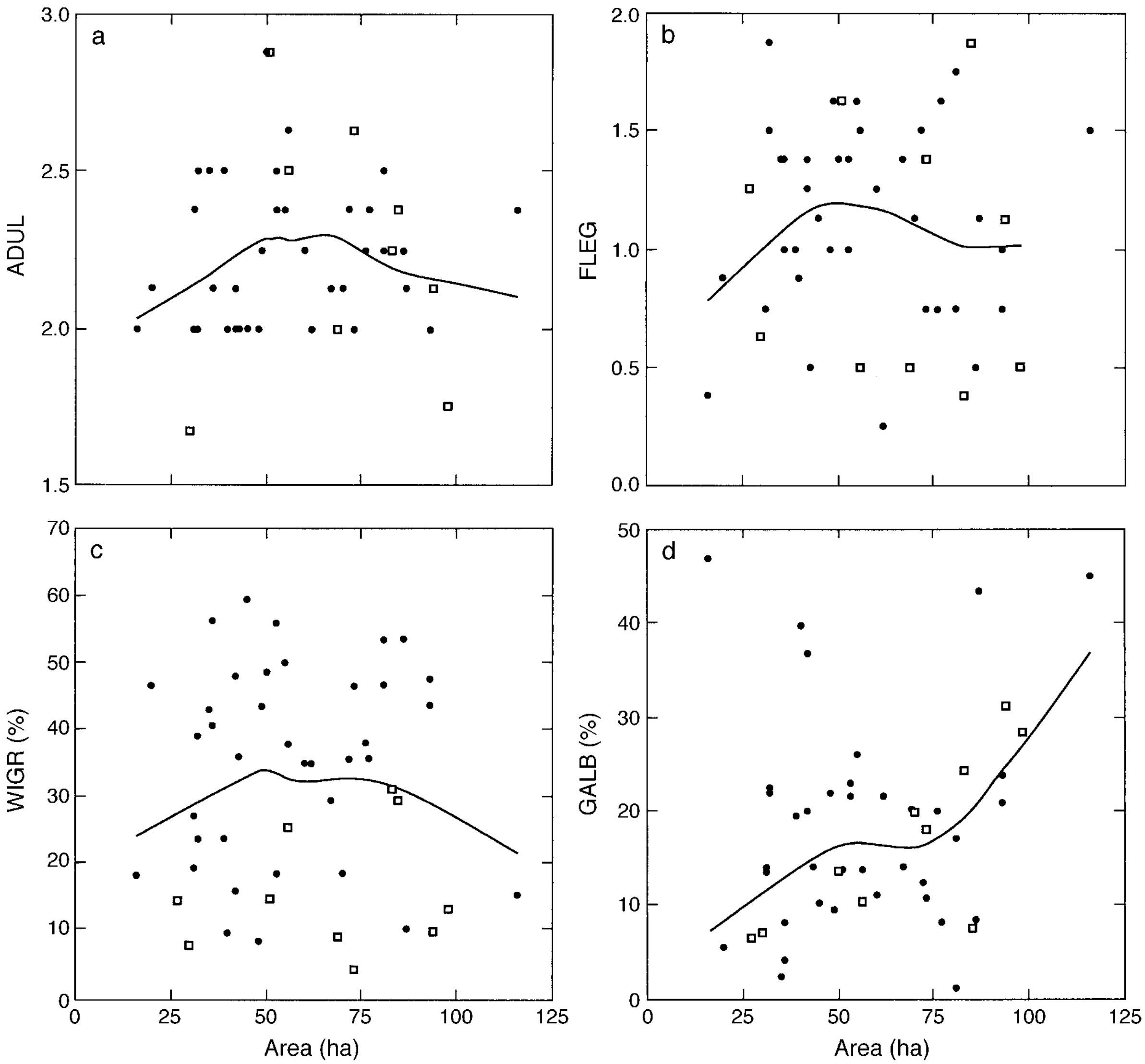

FIG. 2. Relationships between area of foraging habitat within the management circle (AREA) and (a) average group size (ADUL), (b) average productivity of fledglings (FLEG), and (c) percentage wiregrass (WIGR) and (d) gallberry (GALB) in the ground cover. The data are for the 47 groups of Red-cockaded Woodpeckers that had an average of >1.5 adults per group from 1990 through 1997 in the data set reported in Table 1. LOESS lines use $f = 0.7$. Dots are ARD sites; open squares are WRD sites.

wiregrass and other herbaceous vegetation and decreasing (woody + palmetto) vegetation. The average values for the ARD, which again might be taken as a conservative objective, imply that wiregrass, or at least herbaceous vegetation, should constitute ≥40% of the ground cover (Table 2). Alternatively, (woody + palmetto) vegetation should not be >40% of ground cover.

In summary, the health of the woodpecker population is related, however indirectly, to the density and size-class distribution of pine trees and also to the composition of the ground cover. These relationships were not apparent when only the total number of trees >25 cm dbh in an undefined area of qualifying stands within the management circle was considered, as in the first data set (Table 3). That total does not give the density of trees because the area of such stands within 0.8 km of the cluster of cavity trees is variable. In the core stand, the lowest percentage of (woody + palmetto) vegetation combined with the highest density of large trees and the lowest density of small trees tends to be where the group size and productivity of woodpeckers are largest (Table 3).

The difference between density of large trees and density of small ones is more highly correlated with the bird variables than is the density of either class alone, and areas with positive differences have the most vigorous woodpecker groups (Table 3B), suggesting that the structure of the pine forest is at least as im-

TABLE 4. Status of Red-cockaded Woodpecker groups and longleaf pine forest in northern Florida in relation to U.S. federal guidelines for management of the woodpecker population.

Measures	WRD (n = 18 groups) Yes	WRD No	ARD (n = 37 groups) Yes	ARD No
Area of foraging habitat within management circle ≥51 ha				
Percentage in compliance	78	22	51	49
Group size	1.62	1.51	2.26	2.20
Productivity	0.67	0.66	1.13	1.11
At least 6350 medium or large pine stems within management circle				
Percentage in compliance	50	50	19	81
Group size	1.60	1.65	2.27	2.22
Productivity	0.52	0.82	1.09	1.13
Basal area of pines in foraging habitat ≥789 m²†				
Percentage in compliance	44	56	15	85
Group size	1.46	1.76	2.23	2.23
Productivity	0.53	0.78	1.15	1.12

Notes: Shown are values for 55 woodpecker management circles (circles of 0.8-km radius centered on the cluster of cavity trees; see Table 1) in the two districts (WRD, ARD) of the Apalachicola National Forest that are (''Yes'') and are not (''No'') in compliance with current federal guidelines.

† Does not say in what size area, which is variable according to the area of stands that qualify (have trees >25 cm dbh).

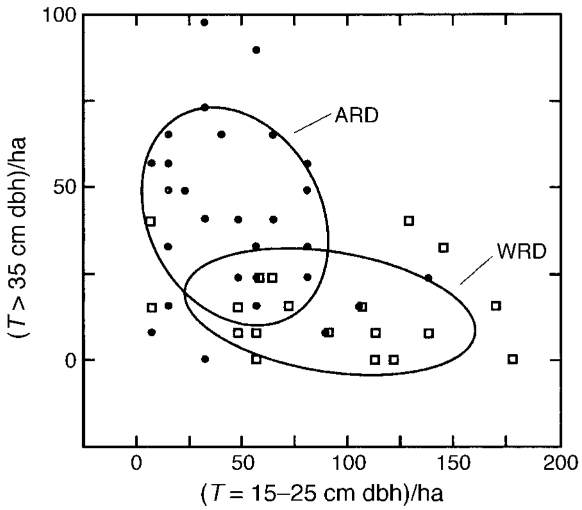

FIG. 3. The structure of the pine forest expressed as numbers of large (>35 cm dbh) and small (15–25 cm dbh) trees per hectare in 55 core stands in the Apalachicola National Forest. A 60% concentration ellipse is given for each district. See Table 2 for a data summary and the region marked ''a'' in Fig. 1 for an example of a core stand. Dots are ARD sites; open squares are WRD sites.

portant as the densities of individual size classes of trees.

There is substantial covariation between tree structure and the proportion of herbaceous vegetation in the ground cover (Fig. 5a). Both of these major structural variables are related to group size both within and between districts. Even so, note that the relationship is most pronounced in the ARD (Fig. 5b, c).

Regression analysis and the importance of relict trees

Some of the above relationships may be happenstance correlations with other variables. For example, we know that Red-cockaded Woodpeckers require relict trees for cavity excavation. The Pearson correlation of the square root of the number of relict trees (SQR(RLCT)) with LATR − SMTR is r = 0.45 and with WIGR − WDPM r = 0.43. A comparison of the explanatory power of various simple and multiple linear regressions can help clarify the nature of this covariation (Table 5). First, the square root of the number of relict trees, SQR(RLCT), alone accounts for 17% of the variance in group size (ADUL), whereas LATR − SMTR and WIGR − WDPM alone each account for >25%. Also, a combination of all three variables accounts for 31% of the variation in group size (R^2 = 0.31), but this is not higher than the percentage accounted for without SQR(RLCT). Similarly, when group density (DENS) is the dependent variable, a combination of SQR(RLCT) and WIGR accounts for 23% of the variance, but WIGR alone accounts for 22% and SQR(RLCT) for only 13%. Thus, although a few relict trees are required by Red-cockaded Woodpeckers, in this data set group size and density are more closely related to general structural features of the forest. Information about the number of additional relict trees does not improve the explanatory power of the tree density and ground cover variables.

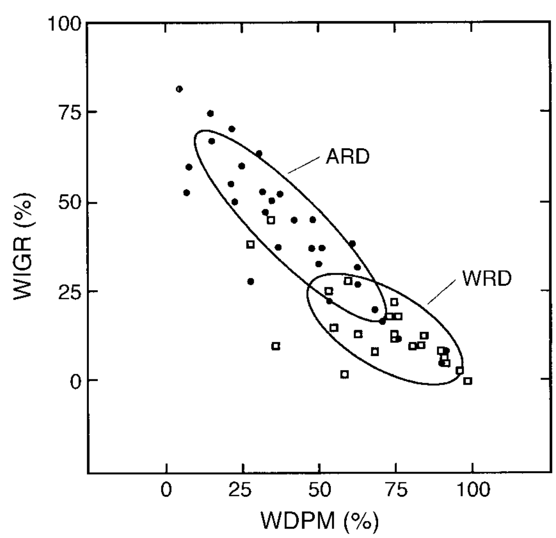

FIG. 4. The composition of the ground cover in 55 core stands in the Apalachicola National Forest (Table 2). The variables are percentage wiregrass (WIGR) and percentage (woody + palmetto) vegetation (WDPM). A 60% concentration ellipse is given for each district. Dots are ARD sites; open squares are WRD sites.

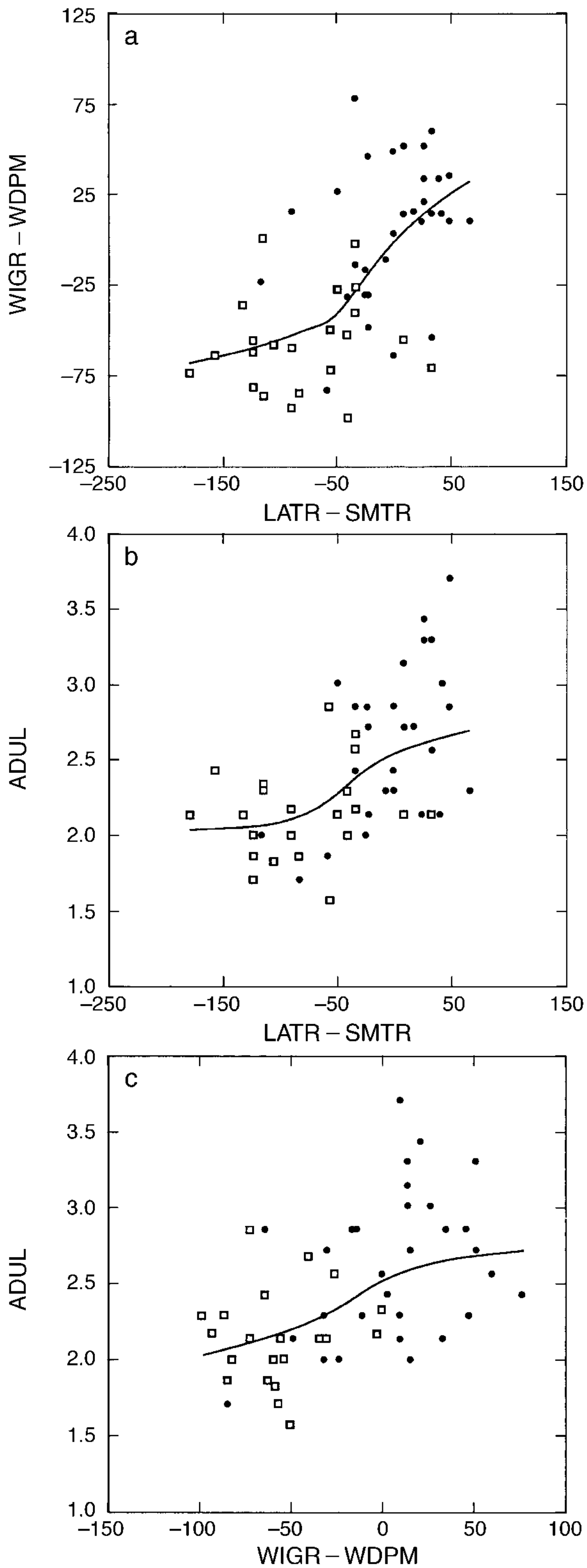

FIG. 5. (a) The relationship between ground cover (WIGR − WDPM) and tree structure (LATR − SMTR) in core stands. (b) The relationship between group size (ADUL) and tree structure. (c) The relationship between group size and ground cover. Dots are ARD sites; open squares are WRD sites.

Could the habitat within the ARD be improved?

Yes. For the 33 woodpecker groups in the ARD, Pearson correlations between group size and core-stand tree structure and between group size and ground cover are $r = 0.46$ and $r = 0.40$, respectively. With this relationship and the substantial variation among groups, it might be possible to increase average group size and productivity of fledglings, which are highly related to one another ($r = 0.60$) in the district. For the 22 groups in the WRD, these correlations are weaker (group size and tree structure $r = 0.18$, group size and ground cover $r = 0.11$), and variation among groups is lower (see standard deviations in Table 2). Note the difference in slopes between districts in both Fig. 5b and c. It is only when the ARD groups are included that the strong relationships become apparent (for combined data, group size and tree structure $r = 0.52$; group size and ground cover $r = 0.51$; Table 3).

Thinning to change the structure of the forest

The difference between adequate and good habitat for the Red-cockaded Woodpecker in the Apalachicola National Forest is shown diagramatically in Fig. 6a and b, which represent average differences between the WRD and the ARD. The good habitat has small patches of pine regeneration and an open canopy. Its more herbaceous ground cover readily carries prescribed fire. More detail about the differences in tree structure is apparent from examination of smoothed values for average differences in the estimated number of trees per 4 ha by size class between the two districts of the forest (columns 3 and 4 in Table 6; squares in Fig. 7a, b). Again it is clear that thinning trees in size classes $<$35 cm would alter the structure of the WRD forest toward that of the ARD forest.

The bulge in the size distribution of ARD trees at 35 cm dbh (Fig. 7a) is attributable to the pulse of regeneration that followed the initial cut. Data from cores of 23 ARD trees in flatwoods habitat provided by A. Clark indicate that the average 80-yr-old tree is 35 cm dbh. Suppression in tree growth in the WRD relative to the ARD is indicated by the larger number of trees in lower size classes (Fig. 7b) and from the estimate, from 70 cores of trees from flatwoods sites on the WRD, that the average 80-yr-old tree is 31 cm dbh.

In spite of the bulge in 70- to 80-yr-old trees, an important characteristic of the densities of trees by size class in the ARD is its nearly linear pattern for dbh $>$10 cm (Fig. 7a). Thus, a reasonable general target distribution that would mimic the distribution of trees by size class in the ARD, where the Red-cockaded Woodpecker population has recovered, might be described by the equation

$$\text{(number of trees in 4 ha in a 5-cm size class)} = \text{intercept} - 3.4\text{(average size for that class)}.$$

If site differences in soil, soil moisture, and tree density

TABLE 5. Regression analysis for predictions of group size (ADUL) and group density (DENS) from habitat variables for core stands (Table 2) in 55 territories of Red-cockaded Woodpeckers.

Prediction equations	R^2	F	P
Group size =			
2.6 + 0.003 (LATR − SMTR) + 0.003 (WIGR − WDPM)	0.31	13.1	<0.001
2.4 + 0.002 (LATR − SMTR) + 0.003 (WIGR − WDPM) + 0.07 SQR(RLCT)	0.31	8.9	<0.001
2.5 − 0.004 (LATR − SMTR)	0.27	19.2	<0.001
2.5 + 0.005 (WIGR − WDPM)	0.26	19.0	<0.001
2.0 + 0.19 SQR(RLCT)	0.17	10.1	0.003
Group density =			
2.7 + 0.05 WIGR + 0.48 SQR(RLCT)	0.23	8.6	<0.001
3.3 + 0.06 WIGR	0.22	15.7	<0.001
5.7 + 0.02 (WIGR − WDPM)	0.19	12.4	<0.001
3.4 + 0.93 SQR(RLCT)	0.13	7.7	0.008

Note: Variables are defined in Table 1.

varied so much that 80-yr-old trees were substantially smaller or larger than 35 cm dbh, the target distribution could be shifted, changing the maximum tree size for the target distribution but keeping the slope (Fig. 7a).

The second column in Table 6 gives an example of a theoretical distribution proposed by Farrar (1996) for a program of uneven-aged management (UEAM). This distribution is calculated by selection of a maximum tree diameter (in this case, 56 cm) and a size distribution determined by multiplication of successively smaller 2.54-cm size classes by 1.2. The result is a reverse-J size distribution, a negative exponential probability density function. Note that this distribution is more nonlinear than the current WRD distribution and quite different from our target distribution (columns 5–7 in Table 6).

DISCUSSION

The longleaf pine ecosystem, which initially covered $\sim 37 \times 10^6$ ha of the southeastern United States, has been displaced from most of the vast uplands it once occupied (Frost 1993). Opportunities for its restoration are best in the 1×10^6 ha of forest that now occurs in stands that regenerated naturally after the initial cut and have never been plowed, but of that forest Frost (1993) estimated that <300 000 ha remain in good condition, not heavily invaded by hardwoods, with some herbaceous vegetation remaining in the ground cover, and being managed with prescribed fire. New habitat-management areas for the Red-cockaded Woodpecker in longleaf pine forests in national forests (U.S. Forest Service 1995) and similar areas on wildlife refuges and military bases are likely to be among the best examples of what remains and should have high priority as sites for restoration, not just as foraging habitat for the Red-cockaded Woodpecker but for the ecosystem as a whole. That this longleaf pine ecosystem requires an open canopy and frequently burned forests to be healthy is well known (Hermann 1993). What our results show is that even within a population of the Red-cockaded Woodpecker deemed to have recovered, there is substantial room for improvement in this direction.

Others have already complained about the minimal criteria in the current federal guidelines for the management of foraging habitat of Red-cockaded Woodpeckers (Beyer et al. [1996], using the first four of the eight years of data reported here; Wigley et al. [1999], using data from industrial land in Louisiana; Hardesty et al. [1997], using data from Eglin Air Force Base in the Florida panhandle) but not about the choice of variables. Even in South Carolina, where the guidelines were developed, subsequent work showed that group size and reproductive success of the birds did not necessarily decline when timber harvest reduced habitat below the recommended standards (Hooper and Lennartz 1995). New guidelines are being developed for a new recovery plan, which is now in draft form.

We found, for both districts in the Apalachicola National Forest, not only that the current guidelines are using inappropriate levels of variables but that some of the variables themselves are inappropriate. The first example is basal area, a measure of the cross-sectional area of wood in a forest stand, and the second is the total number of trees >25 cm dbh. Both variables are used as minimal criteria in the current guidelines for undefined sizes of areas of qualifying stands within management circles.

We introduced the concept of the niche gestalt and proposed that management to mimic the structure of the habitat of a species where it has an especially healthy population might provide the species-specific resources that allow it to thrive. Even though it may be impossible to know the optimal niche gestalt or to understand all the mechanisms at work, comparisons among many places can be used to develop target values of habitat characteristics that can be useful to managers. This part of species-centered environmental analysis (James et al. 1997) could be repeated for other target species to evaluate the likelihood of trade-offs whereby management might harm some species while favoring others. Of course if the threat to the focal species is not ecosystem-related, as for example competition with an invading species (Kappes and Harris 1995), the method will fail.

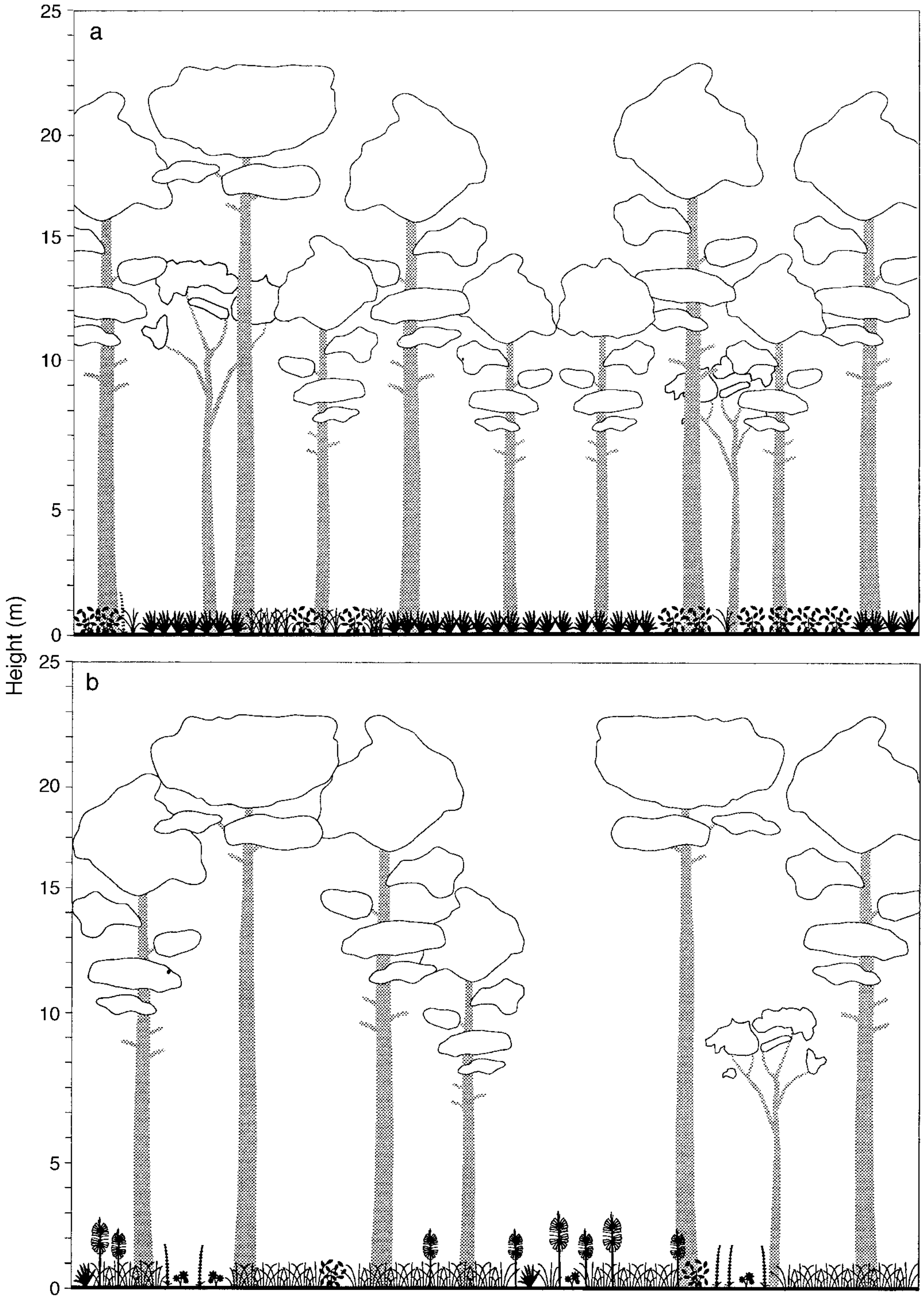

FIG. 6. Diagrams of (a) adequate and (b) good habitat. The latter has a more open canopy, more large than small trees, and more herbaceous than woody ground cover. It can be achieved by more burning plus thinning of trees and creation of small open patches. The burning reduces the woody shrubs and palmetto, promotes the growth of wiregrass and forbs, and provides a substrate for pine regeneration. Thinning releases the remaining trees from competition and allows more sun to reach the ground cover.

TABLE 6. Theoretical target numbers of trees by size class per 4 ha after several decades of uneven-aged management (UEAM) compared with smoothed estimates of current numbers in core stands in the two districts (WRD and ARD) of the Apalachicola National Forest.

Size class (cm dbh)	No. trees/4 ha† Theoretical no. trees (UEAM)	Current no. trees WRD	Current no. trees ARD	Target no. trees, average size at 80 yr 25 cm	35 cm‡	45 cm
>55	10	0	0	0	0	15
50–55	25	0	0	0	15	20
45–50	40	0	0	20	30	50
40–45	50	0	30	35	50	65
35–40	80	35	132	50	65	85
30–35	110	130	170	70	85	100
25–30	160	130	100	85	100	115
20–25	230	200	80	105	115	135
15–20	340	230	70	120	135	150
10–15	480	230	160	135	150	170
>25 (rounded)	475	300	430	260	345	450

Notes: The theoretical numbers in column 2 are calculated from Farrar (1996) for uneven-aged management. Columns 3 and 4 give current estimates for the average core stand for WRD and ARD. Column 6 gives our recommended target distribution. It is a smoothed and extended version of column 4 for the ARD, where the Red-cockaded Woodpecker population is large and healthy and the average tree of size 35 cm dbh is estimated to be 80 yr old. Columns 5 and 7 show how this target could be adjusted for site differences in estimates of the average diameter of 80-yr-old trees.

† To get trees per acre, divide by 10.

‡ Basal area is 11.1 m^2/ha or 48.4 ft^2/acre; ft^2/acre = (m^2/ha × 10.76)/2.47.

We suggest that revised guidelines include targets for the percentage of herbaceous vegetation in the ground cover and for the densities of trees by diameter size classes. They should be tried not only in the core stand but in all naturally regenerated longleaf pine stands in designated restoration circles in Red-cockaded Woodpecker habitat. Red-cockaded Woodpeckers prefer to forage on older trees (Engstrom and Sanders 1997, Moranz and Hardesty 1998, Zwicker and Walters 1999), and their spatial arrangement is an important component of the niche gestalt.

The trajectory of change in restoration circles would move stands toward the target tree structure in Table 6 and from the lower right to the upper left quadrants of Figs. 3 and 4. This management would require a more aggressive program of prescribed burning plus the harvest of smaller pine trees where there is a closed canopy. A longer term objective of developing old-growth conditions might be feasible but is not necessary for recovery of the species and is not compatible with another objective in most Red-cockaded Woodpecker habitat—that of providing timber for harvest.

Caveats and possible objections

First, we are not discussing the management of habitat that is in stands of loblolly or shortleaf pine. Such areas are likely to require different strategies (Rudolph and Conner 1996). Also, we are not discussing methods for the removal of hardwood midstory, a successional problem in many other areas (Conner et al. 1999) and an issue under investigation by Hardesty et al. (1999).

Second, why did we find tree structure to be so important when neither James et al. (1997) nor others have done so in composite analyses of the various stand structures in management circles? One reason is that averaging the characteristics of a set of stands, some of which are plantations, as in James et al. (1997), obscures some of the explanatory power of the relationships in naturally regenerated stands. Note, however, that both James et al. (1997) and Hardesty et al. (1997) found that the number of trees in all stands of current Red-cockaded Woodpecker habitat is negatively related to the productivity of the birds.

Third, is tree structure more important than ground cover? No, these aspects must be managed together, and achievement of target conditions may take several decades. With an open canopy, the pine trees grow better (Boyer 1993), more light gets to the ground, herbaceous vegetation flourishes in the ground cover and then carries a fire well (Platt et al. 1988).

Fourth, is it only the core stand that is important to Red-cockaded Woodpeckers? No. Defended areas in all populations of Red-cockaded Woodpeckers cover ≥40 ha (Engstrom and Sanders 1997; Conner et al. 2001), and home ranges are much larger (Porter and Labisky 1986). The density of social groups is highest in habitat that has a high percentage of herbaceous vegetation in the ground cover (James et al. 1997) and that most

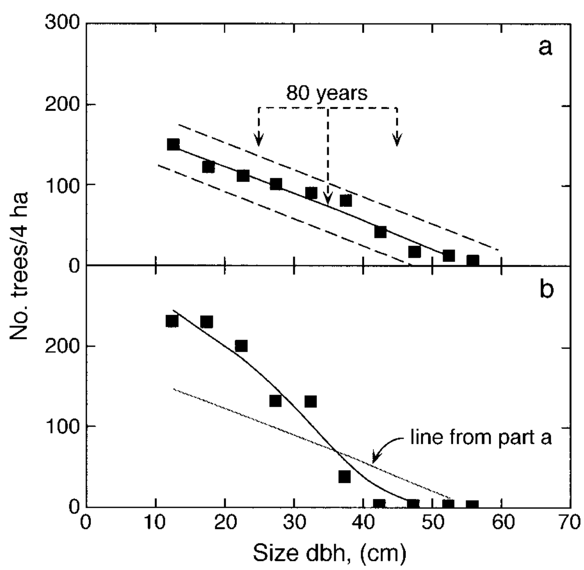

FIG. 7. (a) Target distribution of trees by size class (see Table 6, column 6). If a 25-cm-dbh tree is estimated to be <80 yr old, distribution can be shifted to the left. If a 45-cm-dbh tree is estimated to be 80 yr old, distribution can be shifted to the right. (b) Current distribution of trees by size class in the Wakulla Ranger District, compared with the target distribution.

closely resembles old-growth forest (Engstrom and Sanders 1997). In the WRD, where the average area of habitat available to a group for foraging is 65 ha, the woodpecker population is declining and habitat quality is low. This population and others may already have declined to the point that habitat fragmentation is limiting dispersal, causing a shortage of mates and a demographic collapse (Heppell et al. 1994, Thomlinson 1996, Conner et al. 2001). That particular concern is being addressed in a large experimental project at Eglin Air Force Base in western Florida (Moranz et al. 1998) and elsewhere with programs for the insertion of artificial cavities and the translocation of birds (U.S. Forest Service 1995, Walters et al. 1995, Conner et al. 2001). It is also being addressed in the new plans to manage multiple territories in national forests in habitat-management areas (U.S. Forest Service 1995).

Fifth, are there inherent site-quality differences, like properties of the soil, that are also correlates of the habitat variables, so that management toward the habitat of the recovered population might not work? Certainly there are. Our data do not include sites in the sandhills area in the northeastern part of the forest. Across most of the remainder of the forest, soils are similar, but the soil of the savannas in the westernmost 10% of the Apalachicola Ranger District has clayey subsoil and a higher water-retention power than the soils elsewhere (U.S. Forest Service 1984). Because the entire forest was originally cut at about the same time, the current habitat differences are due to an unknown combination of site differences, past burning history, past harvest, and suppression due to crowding. Nevertheless, opening up the structure of the habitat of closed-canopy stands should be beneficial for the ecosystem regardless of initial conditions. Guidelines could allow for assessments of initial conditions and then give scales along which quantitative improvements could be measured.

Sixth, do we expect the correlations found here within the ARD and between the WRD and the ARD and by Hardesty et al. (1997) to be apparent within populations elsewhere? Not unless there is substantial variation in habitat and bird variables within those study populations. The variation in habitat and birds in the Apalachicola National Forest and the fairly large number of groups available for study made it possible for us to analyze their covariation.

The Florida plan

For longleaf and slash pine forests in the three national forests in Florida, the National Forests of Florida (U.S. Forest Service 1999*b*) recommend prescribed burning plus a combination of uneven-aged and even-aged silviculture. With uneven-aged management, thinning would occur in size classes of trees deemed to be in excess of a specific distribution of trees by size class, and at least 15 trees/ha larger than 46 cm dbh would be retained. With uneven-aged management (group selection, U.S. Forest Service 1999*b*), patches of 0.1 to 0.8 ha would be cut to encourage natural pine regeneration. An even-aged method, called irregular shelterwood harvest, which is a clearcutting method that leaves ≥15 trees/ha over 46 cm, is also available. It is beyond the scope of this paper to evaluate the arguments for and against different methods of silviculture (Walker 1995). Hedrick et al. (1998) prefer even-aged management; Engstrom et al. (1996) prefer uneven-aged management. Note, however, that the recommendations in the new Florida plan (U.S. Forest Service 1999*b*) are for a combination of strategies for achieving a self-perpetuating all-aged forest. If implemented carefully they could improve the composition of the ground cover, release overcrowded pine crowns, open up the canopy, facilitate regeneration, and maintain a healthy size and age distribution of pine trees. That would require substantial thinning of current stands, burning, and opening up of new patches of the forest floor. It could be entirely compatible with our recommendations.

The large area of current Red-cockaded Woodpecker habitat that was plowed and is now in thinned plantations of slash pine >25 cm dbh (Fig. 1, stand d) will require conversion. Managers agree that conversion back to longleaf pine would be beneficial (U.S. Forest Service 1995). The objective of changing a plantation into good Red-cockaded Woodpecker habitat could be accomplished gradually, without plowing, by creation of openings, planting of longleaf pine seedlings, and management toward the target niche gestalt.

In national forests and elsewhere, the question should not be limited to how timber harvest should be restricted so that Red-cockaded Woodpeckers can fulfill their foraging requirements. It is really how the long-term health of the longleaf pine ecosystem, including the Red-cockaded Woodpecker population, can be promoted, even as the production of saw timber is allowed (Landers et al. 1995). The management proposed in the plan for the national forests of Florida (U.S. Forest Service 1999*b*) is compatible with management toward a target niche gestalt for the Red-cockaded Woodpecker, but that result is unlikely without more specific guidelines for changes in the ground cover and structure of the forest.

Extension to multiple-species analysis

Extension from single- to multiple-species analysis that spans the scales considered here is clearly possible (e.g., Morrison et al. 1992:246, Plentivich et al. 1998), although it might involve trade-offs in objectives. An analysis for the gopher tortoise (*Gopherus polyphemus*) would show the extent to which its demography covaries with environmental features like deep dry soil, a pine forest with an open canopy, minimal midstory, and a thick herbaceous ground cover. Aresco and Guyer (1999) showed that, in slash pine plantations in the Conecuh National Forest, tortoises abandon burrows when the canopy closes. An analysis for the flatwoods salamander (*Ambystoma cingulatum*) would show the extent of dependence on both the open pine woods and cypress ponds. Like the Red-cockaded Woodpecker and the longleaf pine ecosystem itself, these species now occupy only a small fraction of their original geographic ranges, and it is almost entirely on federal land. Most if not all of the rare plants associated with longleaf pine forests in Florida would be expected to benefit from being released from the shade of a closed-canopy forest (S. M. Hermann, *personal communication*). More burning in both the growing and the dormant seasons for plant growth and opening up the canopy of the pine forests could promote restoration of this ecosystem in places that have not been plowed.

Other models

There are several other ways to model habitat relationships of focal species of animals, to make predictions about where they occur, and to develop management recommendations. For the Red-cockaded Woodpecker, Heppell et al. (1994) used a deterministic stage-based matrix model to show that the best way to increase the number of breeding groups is to control the understory vegetation and to provide artificial drilled cavities. However, they admitted that the main problem for managers is the lack of suitable territories. Another approach is the analytic model advocated by the U.S. Fish and Wildlife Service (1980), which uses an index to a combination of species-specific habitat variables (Habitat Suitability Index models of Schamberger et al. [1982]; Habitat Evaluation Procedures of the U.S. Fish And Wildlife Service [1980]). The history of the success of predictions made by these analytic models has been disappointing (Stauffer and Best 1986). A third method combines simulations of forest succession in land cover types (Boyce 1980, 1985, Benson and Laudenslayer 1986) to predict the population density of a focal species (Kirkman et al. 1986). By far the most complex method combines demographic simulation modeling with a habitat classification system into a spatially explicit model that allows for interacting subpopulations (Noon and McKelvey 1996, Letcher et al. 1998). Such individual-based models require more precise demographic data than are usually available, so their reliability can be uncertain (Green and Hirons 1991, Murdoch 1992, Heppell et al. 1994, NRC 1995, Caughley and Gunn 1996, Groom and Pascual 1998, Walters 1998). We think that simpler models that emphasize covariation between environmental variables and selected demographic variables might have higher predictive power and be more efficient as tools for developing hypotheses to be tested with various restoration measures (see Hardesty et al. 1997).

Recommendations

Although we have data for only two populations, there is substantial covariation between habitat and demography within each. On the basis of these results, and those of prior results elsewhere, we recommend that the new guidelines being developed by the U.S. Fish and Wildlife Service for foraging habitat of the Red-cockaded Woodpecker include a long-term program for the restoration of the longleaf pine ecosystem in all longleaf pine habitat. The first phase of this program should be applied to selected 0.8-km-radius circles in current foraging habitat and in recently active sites. Interspersed circles with standard management should be monitored to provide comparative data. In restoration circles, naturally regenerated stands would be managed over several decades to approach the tree structure in current circles in the Apalachicola Ranger District. Closed-canopy stands would be thinned, and patchy openings in the forest would be created. The midstory and ground cover would be managed to promote the growth of herbaceous vegetation, primarily with prescribed fire. Plantations would be managed toward the same target structure. The program would be a form of adaptive management that uses both a long-term strategy and planned comparisons based on quantitative data before subsequent expansion in scale.

The current management of Red-cockaded Woodpecker habitat is based on inappropriate foraging guidelines. These guidelines should be replaced with a long-term program for the restoration of the longleaf pine ecosystem, one that allows for some ongoing harvest of timber.

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