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# REGIONAL DIFFERENCES IN HABITAT OCCUPANCY BY BACHMAN'S SPARROW

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ABSTRACT.—Bachman's Sparrow (*Aimophila aestivalis*) has declined over much of its range in the last fifty years. To understand the role of habitat loss in this decline, we examined patterns of habitat occupancy by this species in two areas of South Carolina. At both sites we recorded relatively high densities of breeding sparrows in mature (>80 yr old) pine stands, and relatively low densities in young pine stands. Habitat occupancy varied between sites in clearcuts and middle-aged pine stands. Sparrows used areas with open understories and dense ground covers of grasses and forbs. Habitat occupancy differed between the two main study areas because these preferred vegetation characteristics were found in different habitats in the two areas. Timber management practices (especially burning rotations, site-preparation techniques, and thinning) have a strong effect on understory vegetation and, therefore, habitat suitability for the sparrow. Management practices that produce suitable habitat for Red-cockaded Woodpeckers (*Picoides borealis*) also provide habitat for Bachman's Sparrow. We believe that, even though the sparrow may use open habitats that appear to be relatively common, its habitat requirements are relatively strict, and that habitat loss may be an important factor in this species' population decline. *Received 5 September 1989, accepted 17 February 1990.*

BACHMAN'S Sparrow (*Aimophila aestivalis*) is an enigmatic resident of the pinelands of the southeastern United States. Traditionally the species was associated with mature longleaf pine (*Pinus palustris*) forests, where it was found in grassy openings among the pines (Brooks 1938, Stoddard 1978, Haggerty 1986). At the turn of the 20th century, Bachman's Sparrow underwent a large range expansion, with breeding populations reported for the first time from Illinois, Ohio, West Virginia, and Pennsylvania (Ridgway 1879, Eifrig 1915, Brooks 1938). Northern breeding populations were reported from a variety of open habitats, including agricultural fields, abandoned pastures, and clearcuts (Gainer 1921, Brooks 1938, Clayton 1969, Dorsey 1976). Since the early 1930s, this range expansion has apparently been reversed, as the sparrow has disappeared from much of the northern part of its range. Current patterns of habitat usage are less clear. Some sources continue to describe local habitat as mature pine forest (Allaire and Fisher 1975, Buckner and Landers 1979, Meanley 1988), whereas other sources emphasize more open habitats (Hardin and Probasco 1983).

Concern for Bachman's Sparrow mounted in the 1970s and 1980s as the population decline became more evident. In addition to the contraction of the species' range at its northern edge, large populations in the southern portion of Bachman's Sparrow's range have declined (e.g. southern Mississippi [Jackson 1985] and southwestern Missouri [Peterjohn 1987]). Bachman's Sparrow is considered a potentially threatened species. It has been on the National Audubon Society's Blue List every year the list has been compiled (1972–1986; Tate 1986). The U.S. Fish and Wildlife Service classifies the sparrow as a Category 2 species, indicating that classification as threatened or endangered is possibly warranted, but that too little data currently exists to evaluate the species' status.

Loss of habitat has been suggested to play a large role in population declines of other southeastern pinewoods residents, especially the Red-cockaded Woodpecker (*Picoides borealis;* Jackson 1986, Ligon et al. 1986). The use of open habitats by Bachman's Sparrow makes habitat loss a more uncertain factor in this species' population decline. If the sparrow is dependent on mature longleaf pine forests, then habitat loss is potentially very important, because approximately 90% of such forests in the southeast has been logged (Platt et al. 1988). If, on the other hand, the sparrow can also breed in clearcuts, old fields, and agricultural edges, it is hard to see how loss of habitat could contribute to the population decline, because these habitats remain relatively common throughout its range. Determining patterns of habitat occupancy and the factors that affect habitat selection are important steps in determining the potential threats that face Bachman's Sparrow.

In 1988 we initiated a study of habitat usage by this species in two areas of South Carolina. Both areas supported sparrow populations, but the sites differ in forest management histories and in the relative proportions of available habitat types. We report the patterns of habitat usage at the two sites, and examine the habitat factors that may help to explain the similarities and differences in habitat occupancy between the sites.

## METHODS

We examined habitat occupancy by Bachman's Sparrow at the Savannah River Site, a U.S. Department of Energy facility in Aiken and Barnwell counties, South Carolina, and at the Francis Marion National Forest near Charleston, South Carolina. These areas are approximately 165 km apart. Both contain large numbers of pine stands ranging from newly planted clearcuts to old-growth forest. In addition, both sites have well-documented management histories. They are managed by the U.S. Forest Service, which keeps extensive records on stand treatment.

In the 1950s, most of the upland areas of the Savannah River Site (hereafter, Savannah River) were planted in longleaf and loblolly (*Pinus taeda*) pines. Small areas of the 777 $km^2$ were already forested. Savannah River is now covered by a mosaic of forest stands, a majority of which are 30-40 yr old. Forest Service stands usually range from 5 to 150 ha, and are organized into compartments of up to 100 stands each. A significant portion of Savannah River has been logged in the past decade, consequently a portion of the study area consists of clearcuts and young pine stands (4-12 yr old). Approximately 200 ha of mature (>80 yr old) longleaf pine stands remain scattered across the site. In the Forest Service compartments in which our work was concentrated, middle-aged (20-79 yr old) pine stands covered 72.5% of the areas dominated by pine. Clearcuts and young stands each covered 11.5% of the area, while mature pine stands were found on 4.5% of the pine acreage. (Although parts of both study areas are covered with deciduous woodlands, Bachman's Sparrows are not found in such habitat.) Compartments at Savannah River are burned infrequently, and many of the stands of all ages contain thick understories of oaks, blueberries, and other shrubs. Several small mature stands are managed as Red-cockaded Woodpecker management areas by cutting understory shrubs and saplings, and poisoning deciduous trees to maintain clear understories.

Francis Marion National Forest (hereafter, Francis Marion) is also a mix of pine stands of various ages, clearcuts, and other managed stands. The majority of pine stands are much older (many ranging from 80-120 yr old) than those at Savannah River. In the compartments we studied, mature pine forest constituted 48% of the pine-dominated acreage, while only 32% of the stands we studied were middle-aged. Study compartments were 7% clearcuts and 13% young stands.

At Francis Marion, the Forest Service burns all forest compartments on a 3-5 yr rotation. Only a few tall saplings are present in the understory, especially in years immediately following burns. Most stands contain dense layers of ground vegetation, such as ferns, grasses, forbs, and blueberries and other low shrubs. Much of the western portion of Francis Marion (where our study plots were located) is managed in a condition suitable for Red-cockaded Woodpecker colonies.

We selected 24 study plots at each site. We attempted to locate six plots 10-20 ha in size in each of the following categories: clearcuts (1-3 yr since planting); young stands (6-12 yr); middle-aged stands (22-50 yr); and mature stands (80 yr or older). The rarity of some stand types at each site forced us to modify our final selections from this proposed design (Table 1). For example, we were limited to four mature stands at Savannah River because no other accessible mature stands existed in a condition potentially usable by the sparrow.

We searched each plot for singing male sparrows four times between May and June 1988. On two occasions (once early in the summer and once later), both of us walked over each plot and counted singing birds. Bachman's Sparrows sing throughout the summer and at all times of the day (Stoddard 1978), which aided in the location of males. In addition, we cen-

TABLE 1. Number and mean size of plots used at each study site. Range is in parentheses.

| | $n$ | Plot size (ha) |
|---|---|---|
| Savannah River | | |
| Clearcut | 6 | 13.5 (9.7–21.9) |
| Young stand | 8 | 18.3 (11.2–23.5) |
| Middle-aged stand | 6 | 12.3 (10.3–15.4) |
| Mature stand | 4 | 19.1 (17.4–20.6) |
| Francis Marion | | |
| Clearcut | 6 | 15.1 (13.0–20.2) |
| Young stand | 4 | 14.2 (10.5–19.7) |
| Middle-aged stand | 4 | 14.2 (10.5–19.7) |
| Mature stand | 10 | 14.6 (8.3–23.0) |

sused birds twice on each plot by recording all birds heard and seen during 3-min censuses at six marked locations within each plot. Each census was conducted by one observer within 4 h of sunrise. To reduce any bias caused by variation between our censusing abilities, each plot was censused once by each of us.

All sightings of singing males were located on maps of the stands. Many of the males could be heard from several census points, which facilitated the task of determining the total number of males present. In addition, many plots had discrete natural boundaries and were adjacent to forest stands that were different in age or tree composition from the focal stand. In these plots, sparrow territories rarely crossed plot boundaries; thus, sparrow territories could be assigned unequivocally to plots. We also recorded the number of silent, secretive adults (presumably females) and of nests. We spent an average of 7 h in each of the 48 study plots. The summer of 1988 was extremely dry; however, we have no evidence that habitat usage by the sparrow was affected by the drought. Patterns of habitat use reported here were similar to those found in a subsequent field season in 1989 at Savannah River (Watts, Dunning, and Danielson unpubl. data).

We used two-way Analysis of Variance (ANOVA) to determine if the number of singing males/ha (hereafter, "sparrow densities") differed between the two areas, and among the four categories of stand types. Variances among our samples were not homogeneous (Bartlett's test for homogeneity, $F = 2.18$, df $= 7$, $P = 0.034$), which implies that ANOVA analysis might be inappropriate. Unfortunately, most nonparametric equivalents to ANOVA do not determine if interactions between variables are significant, which was of particular interest in our study. We followed the suggestions of Conover and Iman (1976) in determining the impact of violation of assumptions in ANOVA interpretation. First, we ran ANOVA using the original data, then we recalculated the analysis using the ranks of the original data. By comparing the results of the two analyses, we determined that rank-transforming the data did not change any of the results. If the results of the ANOVA using rank-transformed data are nearly identical to the original ANOVA results (as was true in our case), then "the rank transform confirms that the original analysis is likely to be accurate" (Conover and Iman 1976: 1358). The rank transformation is not a nonparametric version of ANOVA, but it does transform the original data into numbers that better fit the assumptions of a parametric model. The lack of any substantial changes between the two ANOVAs suggests that the violation of the assumption of equal variances was relatively minor, and that the significance estimates reported for the original ANOVA were reasonably accurate. We therefore include the results of the ANOVA using untransformed data. This procedure has been used recently by Bros (1987), and the general approach is described further in Conover and Iman (1981).

As with all analyses described below, ANOVAs were also run on the data from Savannah River plots and Francis Marion plots separately, to help distinguish differences between the sites that might be obscured in the combined data set. No differences were noted between the analyses using the combined data sets and those using a subset of the data, and only the results of the combined analyses will be reported here.

We quantified the vegetation characteristics of each study plot by measuring vegetation volumes at 200 points within each plot. Since previous studies of habitat use by Bachman's Sparrow emphasize the importance of understory vegetation (Haggerty 1986, Wan A. Kadir 1987), we measured the vegetation in the first four meter layers above the ground. We measured vegetation volumes using the pole method as described by Mills et al. (1989). This method records all vegetation within a series of 0.1-m radius cylindrical volumes centered around a pole marked into 0.1- and 1.0-m sections. At each of 200 points, we recorded the number of 0.1-m volumes that contained vegetation in each meter layer above ground, and in each case identified the plant. We recorded the species of all tree saplings and shrubs that entered the space being sampled. All other plants were grouped into the following categories: fern, grass, forb, and vine. Dead vegetation was noted separately. For analysis, all tree and shrub species except pines were lumped into a single shrub category. Data collected in this manner can be used to generate indices of total vegetation volume, volume in each meter layer, and volumes of each plant species or category.

To reduce the number of vegetation variables, we performed Principle Components Analysis (PCA) on 12 original variables: volume of grass, forb, fern, pine, shrub, vine, dead shrub, dead grass, total vegetation volume in the first meter-layer, volume in the second, volume in the third, and volume in the fourth meter-layer. We used PCA instead of factor analysis because all of our vegetation variables were similar in nature. Factors with an eigenvalue of <1.0 were excluded

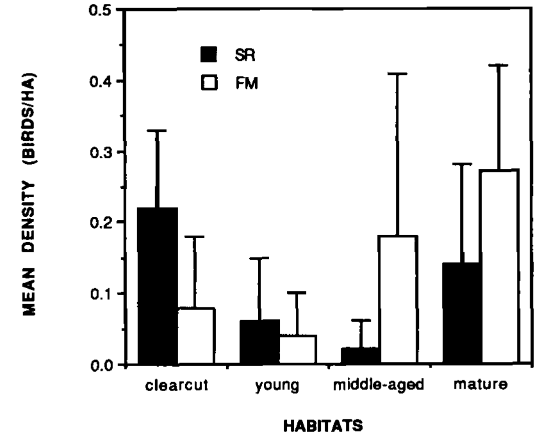


Fig. 1. Mean densities of Bachman's Sparrows in different stand types at Savannah River (SR) and Francis Marion (FM). Vertical lines = standard deviations.

from subsequent analyses. The remaining three factors were interpreted through the component weights associated with the original vegetation variables.

To determine which habitat variables best differentiated between plots that had Bachman's Sparrows and those plots that did not, we performed Discriminant Function Analysis (DFA), using the presence or absence of the sparrow as the dependent variable. We ran DFAs using the following sets of variables: (1) the principal component factors, (2) the vegetation volumes in each meter layer, (3) vegetation volumes of the original vegetation categories, and (4) the age and size of the plot.

Finally, we used stepwise multiple regression analysis to examine variation in bird density in occupied plots. The purpose of these analyses was to determine if any of the vegetation characteristics accounted for the variation in sparrow density found between occupied plots. These analyses used sparrow density as the dependent variable, and various combinations of the principal component factors, the original vegetation variables, and age and size of the plots as independent variables.

Mean values of sparrow density and vegetation volumes were compared using Student's $t$-tests. All analyses were run on the Stratgraphics statistical program.

## RESULTS

*Distribution of birds among stand types.*—Densities of Bachman's Sparrows varied from 0 to 0.48 birds/ha. The ranges of sparrow densities across all plots at both sites were virtually identical (Savannah River: 0.0–0.41 birds/ha; Francis Marion: 0.00–0.48 birds/ha). This resulted in a nonsignificant effect of location (Savannah River or Francis Marion) on sparrow density in the two-way ANOVA ($F = 0.80$, df = 1, $P = 0.39$ NS).

Sparrows were not distributed evenly among habitat types at either study site (Fig. 1), as reflected by a significant effect of stand type on sparrow density (ANOVA $F = 5.11$, df = 3, $P = 0.004$). Densities were highest at Savannah River in clearcuts and mature stands, with few birds found in either young or middle-aged stands. Both Savannah River clearcuts and mature stands had significantly more birds than Savannah River middle-aged stands ($t = 4.23$, $P = 0.002$; and $t = 2.70$, $P = 0.027$, respectively). Savannah River young stands had significantly fewer birds than Savannah River clearcuts ($t = 2.91$, $P = 0.013$), and marginally fewer birds than mature stands there ($t = 2.14$, $P = 0.054$).

Like Savannah River, Francis Marion mature stands contained high densities of sparrows, while young stands had fewer birds. Unlike Savannah River, middle-aged stands at Francis Marion had relatively high sparrow densities, while clearcuts had low densities. Francis Marion mature stands had significantly more birds than either clearcuts ($t = 2.67$, $P = 0.02$) or young stands ($t = 2.86$, $P = 0.01$) at this site. All other differences between stands were not significant. The differences between the two study areas in sparrow use of clearcuts and middle-aged stands may be reflected by a significant interaction effect between stand type and location (ANOVA $F = 3.74$, df = 3, $P = 0.019$).

*Vegetation analysis.*—Clearcuts and young stands at the two sites did not differ significantly in the volumes of most vegetation parameters we measured (Table 2, Fig. 2). Savannah River clearcuts had more vegetation in the second meter, and less bracken fern than Francis Marion clearcuts. Savannah River young stands had less grass and bracken fern (resulting in less vegetation in the first meter) than did Francis Marion young stands. These differences were relatively minor.

Mature and middle-aged stands were substantially different at the two sites. Savannah River middle-aged stands had much less vegetation in the first meter, less total vegetation volume, less forb and shrub volume, but more pine and dead grass, compared with Francis Marion middle-aged stands. Savannah River mature stands had less vegetation volume in the first meter, but more in the third and fourth meters than did Francis Marion mature stands.

TABLE 2. Vegetation variables that differed significantly between sites. Means (±SD) are vegetation volumes ($m^3/m^2$). All means were compared using Student's $t$-tests.

| | Vegetation volumes | | | |
|---|---|---|---|---|
| | Savannah River | Francis Marion | $t$ | $P$ |
| Clearcuts | | | | |
| Meter2[a] | 0.03 ± 0.18 | 0.007 ± 0.004 | 2.85 | 0.02 |
| Bracken | 0.003 ± 0.005 | 0.04 ± 0.03 | 2.73 | 0.02 |
| Young stands | | | | |
| Meter1 | 0.41 ± 0.05 | 0.58 ± 0.09 | 3.66 | 0.004 |
| Grass | 0.08 ± 0.02 | 0.13 ± 0.05 | 2.46 | 0.03 |
| Bracken | 0.003 ± 0.007 | 0.02 ± 0.01 | 2.60 | 0.03 |
| Middle-aged stands | | | | |
| Meter1 | 0.18 ± 0.04 | 0.51 ± 0.09 | 6.05 | 0.0001 |
| TVV[b] | 0.26 ± 0.06 | 0.55 ± 0.08 | 5.31 | 0.0003 |
| Forb | 0.05 ± 0.03 | 0.11 ± 0.04 | 2.75 | 0.02 |
| Pine | 0.04 ± 0.01 | 0.004 ± 0.002 | 4.50 | 0.001 |
| Shrub | 0.11 ± 0.04 | 0.29 ± 0.04 | 3.63 | 0.005 |
| Dead grass | 0.02 ± 0.01 | 0.002 ± 0.004 | 2.38 | 0.04 |
| Mature stands | | | | |
| Meter1 | 0.25 ± 0.06 | 0.54 ± 0.10 | 5.78 | 0.0002 |
| Meter3 | 0.02 ± 0.01 | 0.003 ± 0.003 | 3.62 | 0.005 |
| Meter4 | 0.02 ± 0.01 | 0.002 ± 0.002 | 2.90 | 0.02 |
| TVV | 0.33 ± 0.06 | 0.57 ± 0.12 | 3.87 | 0.003 |
| Bracken | 0.001 ± 0.002 | 0.08 ± 0.06 | 3.28 | 0.008 |
| Shrub | 0.16 ± 0.05 | 0.29 ± 0.12 | 2.27 | 0.046 |
| Vine | 0.06 ± 0.01 | 0.007 ± 0.006 | 10.13 | 0.000001 |
| Dead shrub | 0.04 ± 0.02 | 0.02 ± 0.02 | 2.89 | 0.02 |

[a] Meter$x$ = vegetation volume in the $x$ meter layer above ground.

[b] Total vegetation volume summed over first four meter layers above ground.

Total vegetation volume at Savannah River mature stands was less than that at Francis Marion. In addition, Francis Marion mature stands had more bracken fern and shrubs, and less vine and dead shrubs, than did mature stands at Savannah River.

We used PCA on the original set of 12 vegetation variables to reduce the vegetation data set to a smaller set of orthogonal variables. Three factors accounted for 76% of the variation in the original variables (Table 3), and had eigenvalues of >1.0. Factor I (hereafter, the young-stand factor) accounted for 42% of the original variance and had high positive loadings with four of the original variables: vegetation volumes in the second, third, and fourth meter layers, and volume of pine. This factor contrasted stands with a large amount of tall understory vegetation, especially pine, from stands with open understories. At both sites, young stands scored high on this factor.

Factor II (hereafter, the meter1 factor) had high positive loadings of forb, grass, and vegetation volume in the first meter layer. Sites with high scores of this factor had dense ground layers of grass and forbs. Factor III (the bracken factor) had high positive loadings of bracken fern and shrubs, and a high negative loading of dead grass. Dense carpets of bracken ferns were especially typical of some Francis Marion mature and middle-aged stands.

*Factors associated with sparrow presence.*—We ran DFA using the factors generated in the PCA, and also using subsets of the original vegetation variables. Because the discriminant function using the PCA factors was the most significant, and readily interpretable, we present those results here. With data from all 48 plots, the DFA model significantly discriminated between plots with and without sparrows ($\chi^2$ = 14.01, $P$ = 0.003). Plots with birds were characterized by a high amount of vegetation in the ground layer (high positive loadings of the meter1 factor). Plots without birds were characterized by high amounts of understory vegetation (high negative loadings of the young-stand factor). The discriminant function therefore created an axis contrasting occupied plots (dense ground cover

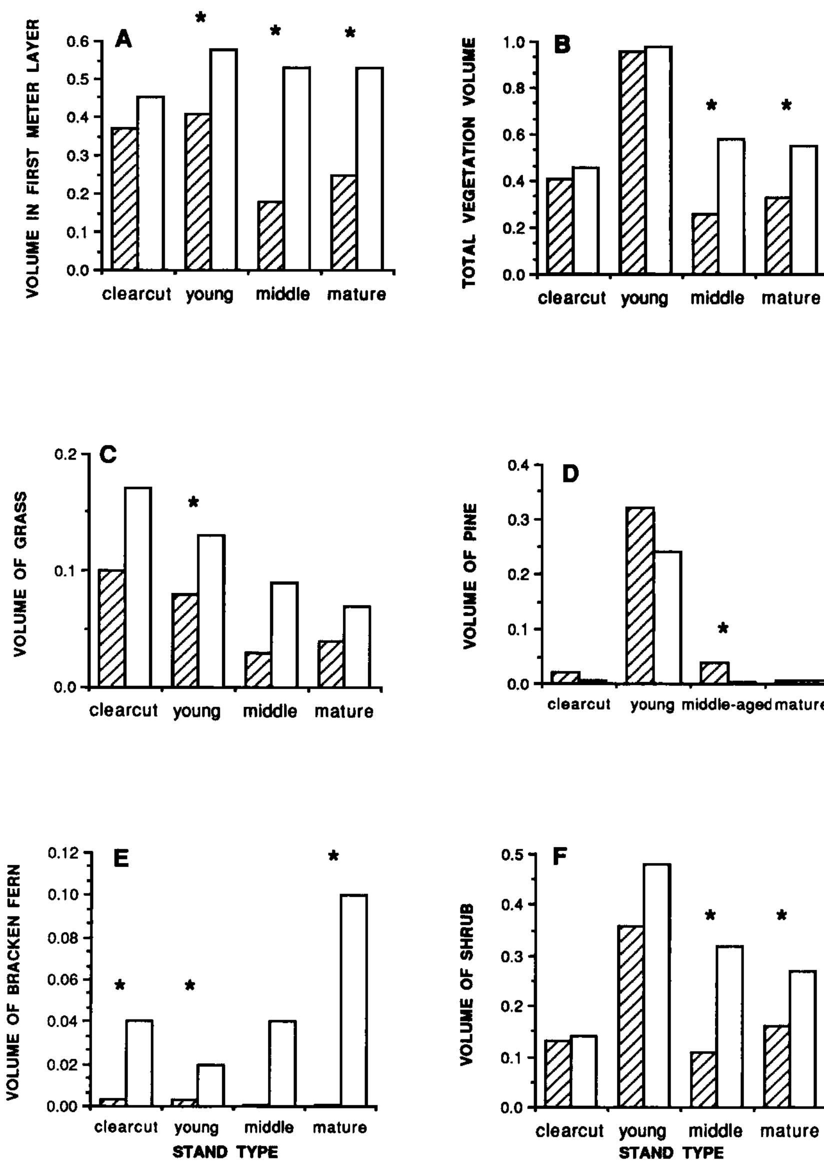


Fig. 2. Volumes of selected vegetation variables in different stand types at Savannah River (hatched bars) and Francis Marion (open bars). Asterisk indicates significant difference between sites.

and open understories) with unoccupied plots (dense understories or bare ground layers). Discriminant functions built using the data sets from Savannah River and Francis Marion separately emphasized the same variables.

*Factors associated with sparrow density at occupied sites.*—To determine if the variables we measured explained a significant amount of the variance in sparrow density at occupied plots, we performed stepwise multiple regression analyses on the subset of 30 occupied plots. Significant models were built using PCA factors and several different subsets of the original variables. Almost all of the models explained a similar amount of variance in sparrow density ($r^2$ ranged from 0.31 to 0.35 for four of the five models).

The PCA factors that loaded into a significant model were the bracken factor (strong positive coefficients) and the young-stand factor (marginally significant negative coefficients). Sparrow densities were correlated positively with fern and shrub volumes, and negatively with tall pine sapling volume. All of the regression models explained only a third of the variance in sparrow density at the occupied plots, so other factors undoubtedly played important roles in determining sparrow numbers on our plots.

## Discussion

Bachman's Sparrows occupied different habitats at the two study sites. However, the plots that were occupied fit a single set of descriptive parameters. We conclude that the sparrows occupied different habitats at Savannah River and Francis Marion not because their preferences changed, but rather because the site characteristics they prefer were found in different habitats at the two sites.

The sparrows consistently occupied plots that had a high volume of vegetation, especially grasses and forbs, in the first meter layer above ground; and low volumes of understory vegetation in the second through fourth meters above ground. Previous quantitative work on habitat characteristics in this species have emphasized similar variables (Haggerty 1986, Wan A. Kadir 1987). At Savannah River, clearcuts and the few mature stands being managed as Red-cockaded Woodpecker colonies met these criteria. Savannah River middle-aged stands had too little ground vegetation, while young stands had too much pine understory to be used consistently by the sparrows. At Francis Marion, most mature and middle-aged stands met the criteria, while young stands did not. Like Savannah River, most young stands at Francis Marion contained a large volume of understory vegetation.

Francis Marion clearcuts appeared to fit the criteria, but supported few birds. The clearcuts contained the same amount of ground vegetation as Savannah River clearcuts, and had virtually no vegetation in the understory layer. There were a few apparent differences in vegetation structure between clearcuts at the two sites that may have been important to the birds. Francis Marion clearcuts were mostly drumchopped, a site-preparation technique that reduces the levels of above-ground vegetation and debris before planting (see below). The shrubs that resprouted in Francis Marion clearcuts were low and dense, with little deadwood projecting above the surface of the field. Savannah River clearcuts had a larger amount of tall shrubs and dead standing timber, resulting in a significantly greater vegetation volume in the second meter layer at Savannah River compared with Francis Marion clearcuts (Table 2). Sparrows often sang from these exposed perches. Francis Marion clearcuts may have fewer sparrows because of the lack of such perches or other structural components.

TABLE 3. Component weights and percent variance explained by the first three Principal Components Analysis factors.

| | Factors | | |
|---|---|---|---|
| | I | II | III |
| Meter1[a] | 0.05 | 0.5 | 0.35 |
| Meter2 | 0.42 | 0.11 | 0.00 |
| Meter3 | 0.44 | −0.01 | 0.00 |
| Meter4 | 0.42 | −0.10 | 0.09 |
| Grass | −0.01 | 0.41 | −0.33 |
| Forb | 0.00 | 0.43 | −0.10 |
| Pine | 0.40 | 0.11 | −0.14 |
| Bracken | −0.16 | 0.21 | 0.54 |
| Shrub | 0.26 | 0.16 | 0.48 |
| Vine | 0.31 | −0.21 | −0.09 |
| Dead shrub | 0.29 | −0.24 | 0.16 |
| Dead grass | 0.15 | 0.37 | −0.41 |
| Total variance explained (%) | 42.1 | 19.8 | 14.3 |

[a] Meter$x$ = vegetation volume in the $x$ meter layer above ground.

*Effect of management practices.*—These differences in habitat structure, and subsequent sparrow occupancy, appear to be related to Forest Service management practices. At Francis Marion, forest compartments are burned on a 3–5 yr rotation schedule. Frequent burning such as this results in a dense carpet of bracken fern, grasses, and blueberries in the ground layer, and an open understory. Sparrows were common in stands that provided these conditions. The same stands also provided suitable habitat for Red-cockaded Woodpeckers, which are very common at Francis Marion. Management for the woodpecker is likely to provide suitable conditions for the sparrow.

Clearcuts at Francis Marion are drumchopped before planting (U.S. Forest Service personnel pers. comm.). *Drumchopping* is a process in which debris and shrubs are crushed and mixed into the soil. The drumchopped clearcuts we surveyed had low ground cover, little standing dead vegetation, and no sparrows. The single clearcut we surveyed at Francis Marion that had not been drumchopped had three singing male sparrows, and appeared similar in vegetative structure to clearcuts at Savannah River that had not been drumchopped.

Although some burning takes place at Savannah River each year, individual compartments are not burned as regularly as Francis Marion compartments. Many older Savannah River stands had not been burned recently, and had dense understories in 1988. One mature stand with a dense understory was included in our survey, and had no sparrows. The only forested stands with sparrow populations at Savannah River that we located were the few stands being managed for Red-cockaded Woodpeckers. In these stands, open understories are maintained by cutting of saplings, girdling of older deciduous trees, and infrequent burning.

Some Savannah River clearcuts were not drumchopped. These clearcuts were filled with low shrubs and standing debris, and tended to have high sparrow densities. Many clearcuts showed evidence of being burned before planting; however, burning retains more standing debris than does drumchopping.

Young stands at both sites had a low number of sparrows. We found that birds present in young stands tended to be in the most open sections of the stands. Young stands usually had dense carpets of grass, blackberries, and vines. They also had a substantial pine understory, a combination that was apparently less attractive to the sparrow.

Most individual stands are apparently suitable for Bachman's Sparrows only for a short period of time. We estimate that the understory in forested stands at Francis Marion becomes too dense for the sparrows by the fourth or fifth year of the burning rotation. In the absence of a frequent burn policy, most forested stands would rapidly lose suitable Bachman's Sparrow habitat. Similarly, undisturbed clearcut habitats become overgrown with understory shrubs and pines within 7–8 yr of clearing (and within much shorter periods if fast growing pines such as loblolly are planted immediately after clearing). Although some sparrows were found in 6–20 yr old pine stands, fewer birds were present there than in adjacent clearcuts.

Few pine stands older than 20 yr have a dense enough layer of grasses and other ground vegetation to be used by the sparrows, at least up to stand ages approaching mature pinewoods. This is especially true of stands that have not been thinned, because dense pine canopies restrict light access to ground layers.

It is apparent that Bachman's Sparrows can be found in a variety of habitat types. However, it is also apparent that management practices have a strong effect on the availability of suitable habitat. In areas where timber production management emphasizes drumchopping, suppression of fire, and harvesting of pine woodlands before they reach maturity, our study suggests that stands will be suitable for sparrow occupancy during only a fraction of the harvest cycle. On the other hand, management schedules that call for frequent burning, retention of some mature woodland, and less destructive methods of clearcut preparation will provide suitable habitat for the sparrow for a much longer period.

*Population decline.*—The recent decline of Bachman's Sparrow throughout much of its range has been perplexing, because some suitable habitat types still appear to be abundant. We believe that the sparrow's habitat requirements are relatively strict, however; and that habitat loss may play a role in the species' decline.

The loss of sparrow populations from the northern edge of its range has been pronounced (e.g. Hall 1985, Peterjohn 1985, Armistead 1986), but must be viewed from the perspective of its historical population trends. The species underwent a large-scale range expansion to the north at the turn of the 20th century, peaking probably in the 1920s. Reports from this period usually described Bachman's Sparrow habitat as abandoned farmland or pastures. Northern populations began to decline in the late 1930s (Brooks 1938, Haggerty 1986). By the 1970s this decline was pronounced enough that concern about the species' status was widespread. It is important to realize, though, that the current rarity of the sparrow along the northern edge of its range may be part of a population fluctuation occurring on a time scale longer than that usually considered in ecological studies. The factors that allowed the sparrow to expand its range so dramatically in the 1900s and 1910s may have changed sufficiently in the past seven decades that populations can no longer be supported there. To understand the long-term fluctuations of the sparrow in the northern part of its range, it may be necessary to examine regional changes in human land-use. Haggerty (1986) believed that the population decline was related to successional changes on abandoned farmland across wide regions. This factor may be important throughout the species' range, because Odum (1987) showed that abandoned agricultural land has declined drastically on a regionwide basis across the South since the 1930s.

Several arguments suggest that habitat may be limiting in spite of the sparrow's apparent ability to use divergent habitat types. First, the sparrow is capable of reaching high densities in mature pine forests with open understories. However, virtually all of these forests in the southeast have been logged in the last several decades (Platt et al. 1988). Secondly, as argued above, much of the younger forested land currently used for timber production is probably too overgrown with deciduous understory shrubs to support the dense ground cover of grasses and forbs with which the sparrow is usually associated. In the absence of a short burning rotation or other management practice that keeps the understory layer open, only a small fraction of the extensive acreage of land devoted to pine production in the southeast will support healthy populations of sparrows.

Finally, several factors probably limit the suitability of open habitats. Clearcuts that are replanted with fast-growing pines become too overgrown within 5 yr of planting. Clearcuts that are not planted with pine may be suitable for a few more years. Thus, each individual patch of open habitat is suitable only for a relatively short period of time. In a landscape that consists of open habitat patches embedded in a larger matrix of unsuitable habitat, a population will be able to sustain itself only if it can effectively disperse to find available patches. If each patch exists for a relatively short time, species that can disperse easily between patches will be able to survive, while poor dispersers will be eliminated as occupied patches become unsuitable. The ability of a species to maintain itself thus becomes dependent on its dispersal ability, and the dispersion of habitat patches across the landscape (Pulliam and Danielson 1990). It is possible that, over much of the range of Bachman's Sparrow, current land-use patterns have created a regional landscape where poor dispersal ability may have led to local extinctions. We are currently investigating dispersal in this species to examine this idea. The effect of patch isolation, coupled with the short-lived nature of open habitats and loss of mature woodlands, implies that many patches of apparently suitable habitat may be too isolated on a spatial or temporal scale to support Bachman's Sparrow populations. Investigations at these larger spatial and temporal scales will be necessary to understand the factors that underlie the decline in this species.

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