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Author(s): David G. Krementz and Jeffrey S. Christie

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SCRUB-SUCCESSIONAL BIRD COMMUNITY DYNAMICS IN YOUNG AND MATURE LONGLEAF PINE–WIREGRASS SAVANNAHS

DAVID G. KREMENTZ,¹ U.S. Geological Survey, Patuxent Wildlife Research Center, Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, USA

JEFFREY S. CHRISTIE, Institute of Ecology, University of Georgia, Athens, GA 30602, USA

Abstract: Public agencies are required to manage for threatened and endangered species and for biodiversity. However, at times, management for threatened and endangered species precludes consideration of other species. We investigated how managing for red-cockaded woodpeckers (*Picoides borealis*) and biodiversity at the Savannah River Site (SRS), South Carolina, affected communities of bird species that use early-successional scrub habitat (hereafter, scrub-successional species). Management for red-cockaded woodpeckers at the SRS involved both (1) manipulating mature longleaf pine (*Pinus palustris*)–wiregrass (*Andropogon* spp.) stands via canopy thinning, removal of midstory trees, and prescribed burning; and (2) even-aged timber harvesting. The former management practice encouraged red-cockaded woodpeckers to establish new colonies in previously unoccupied stands (hereafter, “recruitment” stands). The latter management practice is used to remove off-site planted pines and replant with preferred longleaf pines. We conducted a constant-effort mist net study in recruitment and regenerating stands (stands clearcut and planted with longleaf pine) during the breeding seasons of 1995–96. We hypothesized that the scrub-successional bird community in recruitment stands would have greater species richness and higher survival and reproductive rates per species than in regenerating stands. However, recruitment stands always had fewer scrub-successional species (1995: 36 species; 1996: 31 species) than regenerating stands (1995: 54 species; 1996: 55 species), and all species that occurred in recruitment stands also occurred in regenerating stands. Species which commonly occurred in both recruitment and regenerating stands had similar adult:juvenile ratios ($P > 0.15$) and relative proportion of adults in breeding condition ($P > 0.05$). We detected no difference in survival rates of Bachman’s sparrows (*Aimophila aestivalis*), indigo buntings (*Passerina cyanea*), and of “combined” scrub-successional birds between stand types ($P > 0.05$). We found that even-aged forestry is an important management practice for maintaining and increasing avian biodiversity on public lands, as well as an acceptable management practice for red-cockaded woodpeckers.

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Key words: COMDYN4, community dynamics, forest management, longleaf pine–wiregrass, *Picoides borealis*, red-cockaded woodpecker, scrub-successional birds, South Carolina, species richness, survival rate.

Long-term population trends of scrub-successional birds (Peterjohn and Sauer 1993) in eastern North America indicate about 65% either have steady or declining population trends (Sauer et al. 1997). Further evidence of a possible decline in scrub-successional birds in southeastern North America are the Partners in Flight concern scores, which consistently place some scrub-successional birds among the species of “very high concern” (scores >23 of possible 35; Hunter et al. 1992). Askins (1993) hypothesized that species of the scrub-successional group were adapted to specific habitat types and components within those habitats. So specialized were these species that Askins (1993) proposed that natural resource agencies consider management actions to include both scrub-successional birds and forest interior birds because the current trend in land use in the east-

ern United States is toward proportionately more forest lands (Odum and Turner 1990).

The need to manage for scrub-successional birds results from 2 facts. First, scrub-successional habitat is short-lived: <15 years in most cases (Meyers and Johnson 1978, Johnson and Landers 1982). Second, many scrub-successional birds are highly specialized on specific components of these habitats (Perkins 1973, Johnson and Landers 1982, Askins 1993). For example, at SRS in South Carolina, Dunning and Watts (1990) demonstrated that stands which were drum-chopped or had fires suppressed retarded colonization rates and lowered relative abundances of Bachman’s sparrows. Additionally, Askins (1993) hypothesized that many scrub-successional birds require large continuous blocks of scrub-successional habitat to maintain stable population levels.

Whereas active management for scrub-successional birds seems warranted (Dunning

¹ E-mail: krem@uga.cc.uga.edu

1993), the competing needs of rare and endangered species must also be considered. In the southeastern United States, the red-cockaded woodpecker is actively managed via intensive and extensive forestry practices (James 1995). Management practices used to promote red-cockaded woodpeckers include 2 basic approaches. Usually, pine stands of established colonies are intensively treated via thinning, removal of midstory vegetation, and burning to maintain these stands in a seral state that red-cockaded woodpeckers prefer (Gaines et al. 1995). Additionally, these same practices are implemented in pine stands that are presently unoccupied by red-cockaded woodpeckers (so called "recruitment" stands), but which have potential to receive dispersing or transplanted red-cockaded woodpeckers. Another practice is to use even-aged forestry to remove less desirable pine species (e.g., loblolly [*Pinus taeda*] or slash [*P. ellioti*]) and plant the stand ("regeneration" stands) with longleaf pine. Both practices result in stands that are attractive to scrub-successional birds because grasses, forbs, and shrubs flourish under the more open canopies of longleaf pine (Lewis and Harshbarger 1976). However, land managers have to consider the benefits of managing for red-cockaded woodpeckers against potentially negative effects on other bird groups (e.g., scrub-successional birds; Salwasser et al. 1996, Plentovich et al. 1998). We investigated the effects of both even-aged and recruitment stand management on the species richness and community dynamics of scrub-successional birds.

In addition to simply attracting scrub-successional birds to a particular site, it is important that birds survive and produce enough young to maintain a viable population (Pulliam 1988, Pulliam and Danielson 1991, Hanski and Simberloff 1997). Therefore, we estimated survival rates and measured indices of reproduction for scrub-successional birds in both regenerating and recruitment longleaf pine-wiregrass stands.

In forming hypotheses to test, we knew that regenerating stands mimicked natural disturbances in being short-lived and unpredictable in space. Also, we knew the Southeast historically had extensive tracts of mature longleaf pine stands with well-developed understories (Jackson 1988) in which scrub-successional bird species likely evolved. Therefore, we hypothesized that the scrub-successional bird community would have more species in the recruit-

ment than regenerating stands, and that survival and reproductive rates would be lower in regenerating stands.

STUDY AREA

We conducted our research at the SRS, a U.S. Department of Energy facility in Aiken, Barnwell, and Allendale counties, South Carolina. The SRS is 770 km² and managed as a research park by the Savannah River Natural Resource Management and Research Institute. The site was located on the Upper Coastal Plain in western South Carolina and was 65% forested with longleaf pine, loblolly pine, and other pine species (Workman and McLeod 1990). The U.S. Forest Service uses even- and uneven-aged stand rotations to extensively manage these pine forests for timber production and conservation of native plant and animal communities. We studied 2 stand age categories: regeneration and recruitment. Regeneration stands were stands that had been clearcut and site prepared; site preparation usually involved herbiciding, burning and, infrequently, seedbed preparation. All regeneration stands, except 1, were planted with longleaf pine seedlings. The 1 exception was planted in alternating double rows of loblolly and longleaf, and also in a single, large longleaf block. We located our net grids (see below) in the longleaf block. Recruitment stands were >32 years old (most >60 yr) and were typically old abandoned crop fields. The predominant pine type in these mature stands was longleaf pine. These stands were treated by thinning the canopy, removing the hardwood midstory, and prescribed summer burning. All recruitment stands had received at least 1 summer burn.

In 1995, we studied population dynamics of scrub-successional birds in 8 longleaf pine regeneration stands and 8 recruitment longleaf pine stands. Regeneration stands ranged from 2 to 5 years old, with 2 stands selected in each of the 4 age classes, and ranged from 2.8 to 25.9 ha. In 1996, we used 12 longleaf pine regeneration stands and 4 recruitment longleaf pine stands. Regeneration stands ranged from 3 to 6 years old, with the following distribution: 3 3-year-old stands, 3 4-year-old stands, 4 5-year-old stands, and 2 6-year-old stands. Five of the 8 regeneration stands in 1996 were repeats from 1995; the remaining 3 stands from 1995 were burned between field seasons. The regeneration stands in 1996 spanned a greater range in size:

2.8–56.7 ha. Although stands ranged considerably in size, Rudnický and Hunter (1993) found no effect of sample plot size on bird species richness.

METHODS

We placed mist nets in each stand in a 5×5 array (4 ha) in 1995 or a 5×4 array (3 ha) in 1996, with 50 m between nets. In only a single stand (Compartment 54, Stand 47) was the 4-ha minimum area not met, but we still placed 25 nets in this stand. We reduced the number of nets used in 1996 because, during days on which we captured many birds in 1995, we were unable to attend to captured birds as quickly as our protocol required (see below). Birds were captured during 3 rounds: 1995—Round 1 (25 Apr–24 May), Round 2 (25 May–23 Jun), Round 3 (26 Jun–21 Jul); 1996—Round 1 (1–30 May), Round 2 (1–28 Jun), Round 3 (1–30 Jul). In 1995, during Round 1, we netted in 1 recruitment stand and 1 regeneration stand for 2 days, after which we moved nets to the next 2 stands. This netting cycle continued until we sampled all 16 stands. The netting cycle was then repeated 2 more times, which ensured each stand was sampled during 3 different 2-day rounds. Each stand was randomly selected for sampling within a round, and visits to each stand averaged 28 days apart. For the purpose of data analysis, the first time a 1995-banded bird was recaptured in 1996, we treated that individual as a first-time capture for 1996. Also, we treated recaptures at different stands within the year as new individuals.

Each day, beginning 30 min before sunrise, we opened 12-m, 4-panel mist nets (30-mm mesh) for 4 hr, and did not close the nets unless precipitation exceeded 0.5 cm/hr or temperatures exceeded 30°C. We checked nets at 30–45-min intervals, more often when weather conditions threatened health of netted birds. For each captured bird, we recorded species, age, sex, reproductive status, and banded each bird with a National Biological Service leg band. We categorized each male as nonbreeding, partial-breeding, or full-breeding (Codes 1–3), based on the development of the cloacal protuberance, and females were placed into 4 categories based on development of the brood patch (Pyle et al. 1987). Males with scores 2 and 3 and females with scores 3 and 4 were classified as breeding; all other sex \times score combinations were classified as nonbreeding.

Although we initiated our netting operation after the bulk of spring migration had occurred, we captured birds during both years that apparently were migrating through the study area. To reduce the confounding effects of including migrants in our data, we excluded potential migrant species based on 2 criteria. If the mapped breeding range covered <5% of the combined area of Georgia and South Carolina (Sauer et al. 1997), and the edge of the mapped breeding range was >150 km from the SRS boundary, we excluded data from this species.

We investigated the community dynamics of birds for recruitment and regeneration stands via program COMDYN4 (Nichols et al. 1998). This program produces estimates of community characteristics that can be used to compare communities. The program is based on the general applicability of model M_h (Otis et al. 1978) for species richness estimation from species presence–absence data for recruitment (REC) and regenerating (REG) stands. First, we estimated the detection probability in each stand type (\hat{p}_{REC} , \hat{p}_{REG}). If the average species detection probabilities were different between the 2 stand types, then we estimated relative species richness for the 2 stand types, REC and REG, as

$$\hat{\lambda}_i^{\text{REC/REG}} = \frac{\hat{N}_i^{\text{REG}}}{\hat{N}_i^{\text{REC}}},$$

where \hat{N}_i^{REG} denotes estimated species richness in regeneration in time i , and \hat{N}_i^{REC} denotes estimated species richness in recruitment at time i . Time in this case represents year. If the average species detection probabilities were the same for the 2 stand types, then we estimated relative species richness for the 2 stand types as

$$\hat{\lambda}_i^{\text{REC/REG}} = \frac{\hat{R}_i^{\text{REG}}}{\hat{R}_i^{\text{REC}}},$$

where \hat{R}_i^{REG} denotes the number of species actually observed in regeneration stands during sampling efforts in period i , and \hat{R}_i^{REC} denotes the number of species actually observed in recruitment stands during sampling efforts in period i . We used a contingency table analysis based on the frequencies of species detected on exactly 1, 2, and 3 rounds in each stand type to test the null hypothesis of equal species detection probabilities for the 2 stand types. Also, we estimated the proportion of species found in regeneration stands that were also found in recruitment stands. Define $\phi_i^{\text{REC/REG}}$ as the prob-

ability that a species present in regeneration stands in time i was also present in recruitment stands at that time. We estimated this probability as

$$\hat{\phi}_i^{\text{REGREC}} = \frac{\hat{M}_i^{\text{REC}(\hat{R}_i^{\text{REC}})}}{\hat{R}_i^{\text{REC}}},$$

where $\hat{M}_i^{\text{REC}(\hat{R}_i^{\text{REC}})}$ denotes the number of species observed in regeneration stands at time i that were also present in recruitment stands at that time. Finally, we estimated the number of species ($\hat{B}_i^{\text{REGREC}}$) present in regeneration stands at time i , but not present in recruitment stands at that time as

$$\hat{B}_i^{\text{REGREC}} = \hat{N}_i^{\text{REC}} - \phi^{\text{REGREC}} \hat{N}_i^{\text{REC}}.$$

Program COMDYN4 uses the total number of species per treatment type, the number of species observed in recruitment stands that also were observed in regeneration stands by round, the number of species observed in regeneration stands that also were observed in recruitment stands by round, the number of species observed in only 1 round, in exactly 2 rounds, and in all 3 rounds, and the number of species observed at round i (Nichols et al. 1998). All of the estimators in program COMDYN4 are based on the jackknife estimators of Burnham and Overton (1978, 1979). For each of the estimated parameters, bootstrap 95% confidence intervals were calculated based on 1,000 iterations using a random seed (Nichols et al. 1998: Appendix). We used a bootstrapped confidence interval, rather than an asymptotic normal confidence interval, because the distributions of the parameters were not well known (Nichols et al. 1998). Fit of the detection frequency data to model M_h was tested via a goodness-of-fit (GOF) test, which tested the null hypothesis that the 2 sets of detection frequency data were produced by the same average detection probability. Equality of species detection probabilities was tested with a chi-square test. These analyses were conducted by year because of the unequal sampling effort between years. Finally, to corroborate Rudnický and Hunter's (1993) finding that plot size was independent of bird species richness, we analyzed variation in species richness with clearcut stand size by using generalized linear models (PROC GLM; SAS Institute 1990). Species richness was the response variable, with clearcut stand size, clearcut age, and the interaction of the 2 factors as predictive variables.

We compared 2 indices of reproductive effort between stand types. One index was the relative proportion of adults in breeding condition. We compared the relative proportion of adults in breeding condition in regeneration and recruitment stands by using log-likelihood ratio tests. Small sample sizes forced us to pool scores by sexes and species. The relative proportion of adults in breeding condition appeared to be species specific (D. G. Krementz and J. S. Christie, unpublished data), with most individuals being active (many zeros in the nonreproductive column). Combining across species eliminated the zeros and resulted in 8 separate 2×2 log-likelihood ratio tests. We combined species into 2 groups: (1) the Nearctic–Neotropical migrant group was composed of blue grosbeak (all scientific names of birds can be found in Table 1), indigo bunting, prairie warbler, and summer tanager; and (2) the resident–short distance migrant group was composed of northern cardinal, Bachman's sparrow, eastern bluebird, and eastern towhee. Thus, the 8 tests were composed of 2 groups \times 2 sexes \times 2 years.

Another index of reproductive effort was the ratio of adults to juveniles for each species. We calculated ratios for regeneration and recruitment stands and compared them via Mann-Whitney Wilcoxon rank sum tests. Only bird species that occurred in both stand types and produced young in at least 1 stand type were compared. We ran tests for Round 2 captures and Round 2 and 3 captures combined. We did not use Round 1 data, because few juveniles had fledged. Because we sampled fewer recruitment stands, we calculated adult:juvenile ratios for species with >20 individuals captured in 1995 and >8 individuals in 1996.

We estimated survival rates and capture probabilities with program SURVIV (White 1983). Estimates were based on the time interval between rounds, so they represent monthly survival rates (95% CI). We pooled data from both sexes for these analyses because sample sizes were small. We estimated survival for Bachman's sparrows and indigo buntings. Also, we combined data from several species, including Bachman's sparrows, prairie warblers, indigo buntings, blue grosbeaks, and yellow-breasted chats, and estimated survival. Because these species have similar life histories (Ehrlich et al. 1988), we believed the combined data were representative of a "typical" scrub-successional bird and would allow more precise survival and

Table 1. Summaries of captured birds categorized by breeding habitat groups (Sauer et al. 1997). Numbers represent birds captured (Caps), and banded, and number of birds recaptured (Recaps) in regeneration and recruitment longleaf pine stands during the breeding seasons of 1995 and 1996 at the Savannah River Site, South Carolina. Birds banded and recaptured on the same day are not included in recapture totals. Birds originally banded in 1995 and recaptured in 1996 are noted in parentheses. All birds in parentheses were treated as new birds in 1996. Species-specific capture–recapture records are available from D. G. Krementz (U.S. Geological Survey–Patuxent Wildlife Research Center, Laurel, Maryland, USA).

Species	Regeneration stands				Recruitment stands			
	1995		1996		1995		1996	
	Caps	Recaps	Caps	Recaps	Caps	Recaps	Caps	Recaps
Grassland species ^a	3	0	5	0 (1)	4	0	0	0
Scrub-successional species ^{a,b}	443	101	503	91 (33)	295	56	77	25 (9)
Woodland species ^{a,b}	275	37	237	19 (23)	376	65	105	10 (10)
Urban species	42	9	26	4 (3)	48	11	9	2 (0)
Totals	763	147	771	114 (60)	723	132	191	37 (19)

Grassland species: Brown-headed cowbird (*Molothrus ater*); Scrub-successional species: northern bobwhite (*Colinus virginianus*), common ground-dove (*Columbina passerina*), eastern kingbird (*Tyrannus tyrannus*), carolina wren (*Thryothorus ludovicianus*), eastern bluebird (*Sialia sialis*), gray catbird (*Dumetella carolinensis*), brown thrasher (*Toxostoma rufum*), loggerhead shrike (*Lanius ludovicianus*), white-eyed vireo (*Vireo griseus*), yellow warbler (*Dendroica petechia*), prairie warbler (*Dendroica discolor*), common yellowthroat (*Geothlypis trichas*), yellow-breasted chat (*Icteria virens*), northern cardinal (*Cardinalis cardinalis*), blue grosbeak (*Guiraca caerulea*), indigo bunting (*Passerina cyanea*), painted bunting (*Passerina ciris*), eastern towhee (*Pipilo erythrophthalmus*), field sparrow (*Spizella pusilla*), orchard oriole (*Icterus spurius*), and american goldfinch (*Carduelis tristis*).

Woodland species: yellow-billed cuckoo (*Coccyzus americanus*), eastern screech-owl (*Otus asio*), whip-poor-will (*Caprimulgus vociferus*), ruby-throated hummingbird (*Archilochus colubris*), red-headed woodpecker (*Melanerpes erythrocephalus*), red-bellied woodpecker (*Melanerpes carolinus*), downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), eastern wood-pewee (*Contopus virens*), Acadian flycatcher (*Empidonax virens*), great-crested flycatcher (*Myiarchus cinerascens*), Carolina chickadee (*Parus carolinensis*), tufted titmouse (*Baeolophus bicolor*), brown-headed nuthatch (*Sitta pusilla*), blue-gray gnatcatcher (*Poliophtila caerulea*), wood thrush (*Hylocichla mustelina*), cedar waxwing (*Bombicilla cedrorum*), yellow-throated vireo (*Vireo flavifrons*), red-eyed vireo (*Vireo olivaceus*), northern parula (*Parula americana*), yellow-throated warbler (*Dendroica dominica*), pine warbler (*Dendroica pinus*), black-and-white warbler (*Mniotilta varia*), American redstart (*Setophaga ruticilla*), ovenbird (*Seiurus aurocapillus*), Kentucky warbler (*Oporornis formosus*), hooded warbler (*Wilsonia citrina*), summer tanager (*Piranga rubra*), and Bachman's sparrow (*Aimophila aestivalis*); Urban species: mourning dove (*Zenaidura macroura*), blue jay (*Cyanocitta cristata*), northern mockingbird (*Mimus polyglottos*), and chipping sparrow (*Spizella passerina*).

^a The brown-headed cowbird, eastern kingbird, eastern bluebird, loggerhead shrike, orchard oriole, and cedar waxwing were not categorized by Sauer et al. (1997); hence, we placed these species in a group we thought appropriate.

^b Northern bobwhites, eastern screech-owls, and ruby-throated hummingbirds were captured and released unbanded.

recapture-rate estimates because of increased sample size. For each analysis, we created 4 model structures based on the Cormack-Jolly-Seber open population design (Pollock et al. 1990, Nichols 1992). Each model produced parameter estimates for each treatment type for each year. The most general model estimated 16 time- and habitat-specific survival and capture rates, (i.e., 2 years \times 2 stand types \times 2 time periods for each parameter). The most restricted model estimated 1 survival rate and 1 capture probability. We used Akaike's information criterion (AIC) to select the most parsimonious model (Lebreton et al. 1992).

We sampled vegetation at 10 random points in each stand in 1995. At each point, a 10-m transect was mapped in each cardinal direction. Twenty measurements were taken at 2-m intervals along each transect for a total of 400 measurements/point and 4,000 measurements/stand. We used the pole method (Mills et al. 1989) to record the frequency of all plant parts encountered in each of 20 0.1-m cylinders above ground level, as well as the ground litter cover at each point. We identified trees and shrubs to species as they were encountered within the cylinder. All other plants occurring

within the cylinder were tallied by category (i.e., grasses, forbs, ferns, vines, dead vegetation). In 1996, we followed the same sampling procedure with the exception that only 5 random points were sampled within each stand.

From these data, we calculated total vegetation frequency, frequency in each meter layer of habitat, and frequencies of each plant species or category. We compared the frequencies of vegetation by height between stand types via *t*-tests. All values are presented as mean \pm standard error.

RESULTS

During 1995, mist nets were open for 11,200 net-hr (700 net-hr/stand), and 1,486 birds were captured during the 3 capture rounds (Table 1). Of these, 1,480 birds representing 48 species were banded (species-specific capture–recapture records are available from David G. Krementz, U.S. Geological Survey–Patuxent Wildlife Research Center). Overall, 279 birds of the 1,480 originally banded were recaptured (18.9%); 24 of the 48 species banded were recaptured. The greatest number of captures in regeneration stands was of indigo buntings, whereas in recruitment stands it was pine war-

blers. Bachman's Sparrow was the most frequently recaptured bird species (49 recaptures of 111 captures). Five species were classified as migrants and were excluded from the analysis. We captured ≤ 5 individuals for each of the 5 migrant species.

During 1996, mist nets were open for 7,680 net-hr (480 net-hr/stand), and 962 birds were captured, of which 956 birds representing 49 species were banded (Table 1). Overall, 151 birds of the 956 originally banded were recaptured (15.8%); 22 of the 49 species banded were recaptured. The greatest number of captures in regeneration stands was prairie warblers, whereas in recruitment stands it was pine warblers. Indigo bunting was the most frequently recaptured bird species (28 recaptures of 91 captures). We excluded data from 5 species we classified as migrants, in which ≤ 3 birds were captured for each species. In addition, 79 individuals banded in 1995, representing 19 species, were recaptured in 1996. The most commonly recaptured bird species between years was Bachman's sparrow (12 recaptures).

We documented movements by banded individuals among capture sites within the breeding season. In 1995, 1 male indigo bunting and 3 male prairie warblers were banded and recaptured at stands 1.0–3.2 km apart. In 1996, 2 male prairie warblers, 1 female prairie warbler, 1 female Bachman's sparrow, 1 female painted bunting, 1 male indigo bunting, 1 female eastern towhee, and 1 loggerhead shrike of unknown sex were banded and recaptured at different stands 0.6–14.7 km apart. One individual was banded at a netting site in Round 1, recaptured at another site later in Round 1, and recaptured again in Round 2 at the site in which it was originally banded.

In 1995, estimated species richness (R) was 36 (95% CI = 33.0–40.0) in recruitment stands versus the raw count of 33, and the GOF test indicated the data fit the heterogeneity model ($\chi^2_2 = 1.17$, $P = 0.56$). For the regeneration stands, estimated species richness (R) was 54 (95% CI = 48.0–63.4) versus the raw count of 48, and the GOF test indicated the data fit the heterogeneity model ($\chi^2_2 = 3.22$, $P = 0.20$). The 95% confidence intervals for R did not overlap, indicating more species were present in regeneration stands than in recruitment stands. The probability of detecting a species (\hat{p}) in both the regenerating and recruitment

stands was high: $\hat{p}_{\text{regeneration}} = 0.88$ (95% CI = 0.756–1.00), and $\hat{p}_{\text{recruitment}} = 0.91$ (95% CI = 0.825–1.00), which is why R and the raw species counts were similar. Thus, the mist nets were effective in detecting those species susceptible to nets (i.e., we were sampling the same scrub-successional bird community in both areas). The probability of detecting a species was not different between stand types ($\chi^2_2 = 4.12$, $P = 0.13$). Consequently, we used the raw species counts to compute the relative richness of regenerating stands compared to recruitment stands. Doing so, we found that there were 45% (45/33) more species in regenerating stands than in recruitment stands. The estimated probability of species in regeneration stands also occurring in recruitment stands was moderate ($\hat{\phi}_{1995}^{\text{REG,REC}} = 0.67$, 95% CI = 0.541–0.844), but the estimated probability of birds in recruitment stands occurring in regeneration stands was high ($\hat{\phi}_{1995}^{\text{REC,REG}} = 1.00$, 95% CI = 0.812–1.00). The number of species found in regenerating stands that did not occur in recruitment stands was high ($\hat{B}_{1995}^{\text{REG,REC}} = 30$), whereas the number of species found in recruitment stands that did not occur in regeneration stands was low ($\hat{B}_{1995}^{\text{REC,REG}} = 0.0$). Commonly captured species unique to regenerating stands were field sparrow, gray catbird, northern mockingbird, orchard oriole, and yellow-breasted chat (Table 1). Another 12 species were infrequently captured (< 5 captures/yr) in regenerating stands, and never captured in recruitment stands. Examples of the 12 such species included painted bunting, eastern kingbird, and loggerhead shrike (Table 1).

In 1996, estimated species richness (R) was 31 (95% CI = 27.0–39.9) in recruitment stands versus the raw count of 27, and the GOF test indicated the data did not fit the heterogeneity model ($\chi^2_2 = 13.00$, $P = 0.002$). Estimates for model M_h are quite robust to departures of assumptions and usually constitute the best of all models possible (J. D. Nichols, U.S. Geological Survey, personal communication). Consequently, we used these estimates but warn readers of potential problems in interpretation. For regenerating stands, estimated species richness (R) was 55 (95% CI = 48.0–64.8) versus the raw count of 48, and the GOF test indicated the data fit the model ($\chi^2_2 = 1.39$, $P = 0.50$). The 95% confidence intervals of R did not overlap, indicating more species were present in regen-

Table 2. Adult:juvenile age ratios in regeneration and recruitment pine stands for scrub-successional bird species captured April–July 1995–96 at the Savannah River Site, South Carolina. Only data for species represented by ≥20 captured individuals/regeneration stand in 1995 or ≥8 captured individuals/recruitment stand in 1996 are included.

Species	Regeneration				Recruitment			
	1995		1996		1995		1996	
	Round 2 ^a	Round 3 ^b	Round 2 ^c	Round 3 ^d	Round 2 ^a	Round 3 ^b	Round 2 ^c	Round 3 ^d
Eastern wood-pewee					6:3	2:1	2:0	3:0
Tufted titmouse			5:0	4:8	3:7	1:5		
Carolina wren	4:3	4:18	6:2	4:3	10:8	0:17	7:1	3:1
Pine warbler	4:30	0:11	7:9	0:15	10:67	10:61	2:33	1:2
Prairie warbler	9:7	1:2	15:2	7:8	12:1	7:25	4:4	1:0
Northern cardinal	6:0	6:8	13:2	7:4	4:0	6:13	5:0	1:0
Blue grosbeak	8:1	10:0	12:1	16:9			4:4	4:0
Indigo bunting	14:0	9:2	23:2	10:4	8:2	6:2	1:0	0:0
Eastern towhee	7:4	5:9	14:5	4:10	7:8	3:5	0:1	0:3
Bachman's sparrow	10:7	7:5	7:1	10:2	10:4	8:4	6:3	3:1
Chipping sparrow			3:0	1:1	3:5	2:5		

^a 25 May–23 June 1995.

^b 26 June–21 July 1995.

^c 1 June–28 June 1996.

^d 1 July–30 July 1996.

erating stands than in recruitment stands. Capture probabilities were high for regeneration stands ($\hat{p}_{\text{regeneration}} = 0.87$, 95% CI = 0.74–1.00) and recruitment stands ($\hat{p}_{\text{recruitment}} = 0.85$, 95% CI = 0.68–1.00). We found no difference between treatments in the probability of detecting a species ($\chi^2_2 = 2.47$, $P = 0.29$); thus, we computed relative richness directly from the raw species counts. There were 78% (48/27) more species in regenerating stands than in recruitment stands, which was greater than the difference in 1995. The estimated probability that all species found in recruitment stands also occurred in regenerating stands was great ($\hat{\phi}_{1996}^{\text{REG,REG}} = 1.00$, 95% CI = 0.83–1.00), but the estimated probability that all species found in regenerating stands were also found in recruitment stands was moderate ($\hat{\phi}_{1996}^{\text{REG,REG}} = 0.57$, 95% CI = 0.45–0.76). Again, the number of species present in recruitment stands that did not occur in regeneration stands was small ($\hat{B}_{1996}^{\text{REG,REG}} = 0.0$), but there were many species found in regenerating stands that did not occur in recruitment stands ($\hat{B}_{1996}^{\text{REG,REG}} = 37$). As in 1995, there were 2 groups of birds (17 species), based on relative numbers of captures (e.g., many, few), that were detected only in the regenerating stands (Table 1).

Because we found no evidence of a year effect on species richness by stand size ($F_{4,6} = 0.47$, $P > 0.50$), we combined data across years. We found that both main factors, stand size and stand age, as well as the interaction of the main

factors, were all important in explaining species richness ($P < 0.001$). Oddly, however, the slope of the species richness–stand size relation was negative. The primary reason for the negative slope was 2 large stands that were 5 and 6 years old each. Removing these 2 points from the regression resulted in a slope that was not different from zero ($F_{1,16} = 0.88$, $P = 0.36$). We found a weak, negative relation between species richness and stand age ($F_{1,18} = 3.07$, $P = 0.10$).

We found proportionately more resident and short-distance females in 1995. In 1996 Nearctic–Neotropical migrant males from regeneration stands were reproductively active versus individuals from recruitment stands ($P < 0.05$). All other comparisons indicated individuals from recruitment stands were as likely to be reproductively active as individuals from regeneration stands.

In general, few juveniles were captured (Table 2); hence, small sample sizes, along with annual variability, reduced the statistical power of our tests to detect differences in reproductive effort. In addition, there were species-specific year differences in reproductive effort by stand type, and these differences were not in the same direction (Table 2). Of those species meeting our minimum number of captures by stand type, only great-crowned flycatchers and summer tanagers were captured in both stand types, but juveniles were never captured in either stand type. Adult:juvenile ratios for all species did not differ by stand type or year ($P >$

0.15). The number of young for all species captured during Rounds 2 and 3 combined was not consistent: more young were captured in recruitment stands in 1995, but not in 1996.

For both the Bachman's sparrow and the combined scrub-successional bird species, the model with the lowest AIC value was the model with a single constant survival rate for both treatments and time-specific capture probabilities. The monthly survival rate was high in both cases (Bachman's sparrow: $\hat{\phi} = 0.94$, SE $[\hat{\phi}] = 0.2674$; combined: $\hat{\phi} = 0.93$, SE $[\hat{\phi}] = 0.1799$). The model with the smallest AIC value for the indigo bunting had a single constant survival rate ($\hat{\phi} = 0.64$, SE $[\hat{\phi}] = 0.1746$) and capture probability ($\hat{p} = 0.23$, SE $[\hat{p}] = 0.0897$). The monthly survival rate was noticeably lower for indigo buntings than for Bachman's sparrows or the combined scrub-successional species. In all cases, the capture probabilities were low (range = 0.11–0.32). Capture probabilities between Rounds 2 and 3 (range = 0.11–0.18) were lower than between Rounds 1 and 2 (range = 0.18–0.32), which indicated avoidance of mist nets.

The mean vegetation frequencies (first and second meters, and total) in regeneration stands increased as stand age increased ($F_{1,6} = 47.15$, $P < 0.001$) from 2 to 5 years old (1995) and from 3 to 6 years old ($F_{1,10} = 34.27$, $P < 0.001$ 1996; Table 3). The frequency of vegetation in the first meter, second meter, and first 2 meters combined was lower in recruitment stands than that in regeneration stands during both years ($P < 0.05$; Table 3). Thus, the ground cover component in the recruitment stands was less well developed than in all but the youngest regeneration sites.

DISCUSSION

Not only are all scrub-successional species of the recruitment stands found in regeneration stands, but an entirely separate subset of scrub-successional birds occurs in the regeneration stands. These latter scrub-successional birds appear in the regeneration stands when the early-successional vegetation community develops about 2 years following clearcutting and planting. The understory vegetation in recruitment stands never equaled or exceeded the abundance of vegetation found in regeneration stands during years 2–6. Also, we observed that understory vegetation in recruitment stands coincided with gaps in the canopy (D. G. Kre-

Table 3. Mean total vegetation frequencies for regeneration stands (ages 2–6 yr) and recruitment stands (mature) by height (m) aboveground (<1 m, 1–2 m, <2 m), and year, Savannah River Site, South Carolina.

Year	Height (m)	Stand age (yr)														
		2		3		4		5		6		Mature				
		\bar{x}	SE	n^a	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE	n
1995	<1	19.9	1.31	2	26.0	1.77	2	25.3	0.64	2	29.3	0.96	2	17.2	0.74	8
	1–2	3.4	0.78	2	3.6	0.23	2	5.9	0.53	2	10.0	0.30	2	2.5	0.66	8
	<2	23.3	2.09	2	29.6	1.54	2	31.2	0.11	2	39.3	1.26	2	19.8	1.01	8
1996	<1				19.1	0.96	3	20.6	1.17	3	23.3	1.66	4	24.2	0.93	2
	1–2				2.3	0.26	3	5.0	0.97	3	6.8	1.11	4	8.9	0.23	2
	<2				21.5	1.06	3	25.7	1.25	3	30.1	1.84	4	33.2	1.15	2
														14.1	2.62	4

^a Number of stands used to calculate mean and standard error.

mentz and J. S. Christie, unpublished data). Vegetation in regeneration stands was less patchily distributed because there was no overstory vegetation to intercept incoming light. We suspect the greater biomass of grass, forb, and shrub vegetation created unique niches occupied by this subset of scrub-successional birds. Further, we hypothesize that the mechanism responsible for the increased frequency of vegetation to operate is positively related to food resource abundance (Childers et al. 1986). Childers et al. (1986) worked in successional stages of loblolly pine plantations in Virginia and found that early-successional stages were preferred by a variety of bird species and attributed these preferences to both vegetation structure and the greater availability of various food types found there. Likewise, the absence of certain bird species from older pine plantations was attributed by Johnston and Odum (1956) to the absence of mid- and understory vegetation and the vertical homogeneity of these stands. In addition to the scrub-successional guild, species that occupy the overstory in recruitment stands also frequented regeneration stands. These regeneration stands were used by overstory birds for feeding, especially once their young had fledged. We often captured adults and young of overstory species in the same net, which suggested overstory bird families were traveling together. Apparently regeneration stands not only provided food resources for scrub-successional species, but also for adjacent forest interior species.

Current forest management practices used to improve and maintain red-cockaded woodpecker habitat at the SRS produce vegetation stands that are attractive to scrub-successional birds in both regeneration and recruitment stands (Gaines et al. 1995). Whereas managing recruitment stands for red-cockaded woodpeckers is compatible with the resource needs of some scrub-successional species, there is a suite of scrub-successional species that prefers early-successional stands. If maintenance of biodiversity is a goal of the U.S. Forest Service at the SRS, then at the level of a compartment, and certainly at the level of the forest, even-aged forest management should be maintained both from the standpoint of the red-cockaded woodpecker and scrub-successional birds.

Neither measurement that we used to index reproductive activity, proportion of reproductively active adults, and adult:juvenile ratios was

ideal for investigating reproductive effort because of small sample sizes, annual variability, and species- and age-specific net-avoidance effects (DeSante et al. 1996). We assumed net avoidance was not stand-type specific. Most adults were reproductively active regardless of the stand type. Given that the average annual survival rate of 36 species of eastern North American terrestrial land birds is 0.529 (DeSante et al. 1996), and therefore the mean life span is 1.57 years (Anderson 1975), we believe most adults would try to reproduce every year. Thus, any inherent habitat quality differences might not be reflected in adult reproductive effort, because songbirds do not have the luxury of delaying reproduction.

Adult:juvenile ratios varied among species by stand type. Not only did some species not produce young in 1 stand type (eastern wood pewee produced young only in recruitment stands, and brown thrashers and eastern bluebirds produced young only in regeneration stands), but some species produced young in alternate stand types during the study (tufted titmouse, chipping sparrow). Such year- and stand-specific species responses suggest that combining data across species may mask true patterns, but the typically small number of juveniles captured in mist net projects (DeSante et al. 1996) forced us to do so. We concluded that scrub-successional birds were putting constant effort into reproduction, regardless of the stand type. This conclusion does not support our hypothesis that scrub-successional birds in recruitment stands had a greater reproductive effort.

Estimating survival rates of passerines is difficult because few birds are recaptured (DeSante et al. 1996). Of the 54 species captured, we obtained enough data to estimate survival rates for only 2 species. We estimated a "combined" survival rate for 5 species to estimate survival rate with greater precision. Although this approach may seem unusual, we believe it warrants further research because mist net studies of passerines will always have few recaptures.

Survival rates for Bachman's sparrows, indigo buntings, and our combined scrub-successional group did not differ between regeneration and recruitment stands. We recognize that our failure to detect differences in survival rates may be because of small sample sizes and low statistical power. However, independent support for

our findings exist. Stober (1996), who used radiotelemetry to estimate breeding season survival rates for Bachman's sparrows at the same study site, found no difference in survival rates between these same treatments. The similarity in survival-rate patterns between treatment types at the SRS did not support our hypothesis that survival rates of scrub-successional bird species were higher in recruitment stands than in regeneration stands.

The tendency for capture probabilities to decline over time could have resulted from net avoidance, adults dispersing from stands after breeding (as evidenced by the among-stand movements within years), or a change in behavior after breeding (e.g., becoming sedentary). Stober (1996) observed that radiomarked Bachman's sparrows at the SRS avoided mist nets.

In oak-hickory forests, Thompson and Fritzell (1990) found that scrub-successional birds occupied newly created habitat and produced young in response to clearcutting. Similar to our findings, Thompson and Fritzell (1990) identified a group of scrub-successional species common and unique to clearcuts (eastern towhees, yellow-breasted chats). However, in contrast to our study, they reported that northern cardinals and indigo buntings were common in clearcuts but rare in mature forests. Not only did Thompson and Fritzell (1990) find scrub-successional birds productive in young stands, but they also found area-sensitive forest interior species reproducing in young stands (e.g., blue-gray gnatcatchers, black-and-white warblers, Kentucky warblers). Similar to our findings, Thompson and Fritzell (1990) found species richness in young stands was equivalent to mature stands, and they noted species composition varied among young stands.

Raivio and Haila (1990) studied bird assemblages in pine-spruce (*Picea abies*) systems under forest management in Finland. They found species richness was greater (42 species) in areas under management compared to old-growth forests (34 species). However, upon correcting richness values by using rarefaction (James and Rathbun 1981), Raivio and Haila (1990) concluded there were no differences in species richness between habitat types. Similar to our findings, Raivio and Haila (1990) identified 2 groups of birds using regenerating stands: (1) those common and unique to regenerating stands, and (2) those common in regenerating stands but also sometimes observed in mature

stands. Raivio and Haila (1990) concluded that avian diversity and abundance increased with horizontal habitat heterogeneity, and that if biodiversity is a management objective, then small-scale habitat heterogeneity will be a necessary component of the landscape.

Based on Thompson and Fritzell (1990), Raivio and Haila (1990), and our results, it seems there exists a similar set of bird assemblages among different habitat types (southern hardwoods, northern conifers, southern conifers). These assemblages depend to varying degrees on either the earlier or later successional stages, but not always to the exclusion of either stage. While extreme specialists do exist, they make up a relatively small proportion of the entire community. We hypothesize that the generally greater use of the early-successional stage by both early- and late-successional bird species results from the greater abundance and availability of food resources there. The availability of food resources in early-successional stages is especially important to recently fledged young of species that use late-successional habitat that may be less efficient at collecting food compared to adults, as well as having high total energy needs. We agree with Raivio and Haila (1990) that local bird biodiversity is, in part, maintained through habitat diversity. The complexity and scale of habitat heterogeneity needed to meet management needs will vary with the specific goals and the disturbance history of the ecosystem (Pearson et al. 1996).

Intensively managed clearcuts probably do not mimic early-successional sites produced through natural means (e.g., fire, disease, weather). Thus, future research should focus on the role of coarse woody debris removal and site preparation techniques in even-aged management systems on early-successional bird communities. Also, because some early-successional bird species (e.g., Bachman's sparrows) have difficulty locating newly created early-successional habitat (Dunning 1993, Stober 1996), another area of future research should be the positioning of clearcuts within forests.

MANAGEMENT IMPLICATIONS

Early-successional bird species should be considered in management schemes on public lands, especially in eastern North America where many populations of these birds are declining (Askins 1993, Sauer et al. 1997). For these shrub-successional species, land managers

should develop management plans to provide both early- and late-successional habitat scattered throughout the landholding. These plans should also consider habitats available on private lands bordering public lands, where early-successional stands resultant from even-aged forestry are more common.

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