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CLEARCUT STAND SIZE AND SCRUB-SUCCESSIONAL BIRD ASSEMBLAGES

DAVID G. KREMENTZ[1,3] AND JEFFREY S. CHRISTIE[2]
[1]*U.S. Geological Survey, Patuxent Wildlife Research Center, Warnell School of Forest Resources, University of Georgia, Athens, Georgia 30602, USA; and*
[2]*Institute of Ecology, University of Georgia, Athens, Georgia 30602, USA*

ABSTRACT.—We investigated the effects of clearcut stand size on species richness, reproductive effort, and relative abundance of scrub-successional birds and the entire bird assemblage at the Savannah River Site in South Carolina. We used standardized mist-net grids to mark and recapture birds in clearcuts replanted with longleaf pine (*Pinus palustris*) in stands of 2 to 57 ha that were two to six years old. Species richness for the entire bird assemblage was not explained by stand size ($P = 0.67$), stand age ($P = 0.95$), or the interaction of these two variables ($P = 0.90$). Similarly, species richness of scrub-successional birds was not explained by stand size ($P = 0.63$), stand age ($P = 0.55$), or the interaction of stand size and stand age ($P = 0.35$). Regressing species richness on clearcut stand size, we found a significant negative relationship between these variables for the entire bird assemblage ($P = 0.01$) and for scrub-successional birds ($P = 0.02$). The ratio of juveniles to adults in mist-net samples varied by year ($P = 0.04$), but neither clearcut size ($P = 0.23$) nor the interaction of clearcut size and year ($P = 0.25$) was related to the ratio of juveniles to adults in the sample. We found no relationship between the frequency of capture of any category of birds and stand size (scrub-successional, $P = 0.52$; woodland, $P = 0.77$; combined sample, $P = 0.55$). Neither bird-species richness, reproductive effort, nor relative abundance differed across clearcut stand sizes. Clearcut stand size does not appear to be an important management variable if variation in species richness, reproductive effort, or relative abundance are objectives. We suggest that even-aged forestry is a useful tool for managing birds in the southeastern United States. *Received 8 March 1999, accepted 16 April 2000.*

EARLY SUCCESSIONAL bird assemblages contain many species that are experiencing declines. Long-term data on scrub-successional birds in eastern North America indicate that about 65% of the species have steady or declining population trends (Sauer et al. 1997). Further evidence of a possible decline in scrub-successional birds in southeastern North America is the *Partners in Flight* "concern scores" that consistently place some scrub-successional birds among the species of "very high concern" (scores >22 of possible 35; Hunter et al. 1992). Askins (1993, 1994) hypothesized that scrub-successional species are adapted to specific habitat types and to components within those habitats. These species are so specialized that Askins proposed that resource agencies gear their management actions toward scrub-successional birds before management for forest-interior birds because the current trend in land use in the southeastern United States is toward proportionately more forest lands (Odum and Turner 1990).

The need to target scrub-successional birds for management results from three facts. First, scrub-successional habitat is short lived, less than 15 years in most cases (Meyers and Johnson 1978, Johnson and Landers 1982, Askins 1993). Second, many scrub-successional birds are highly specialized on specific components of these habitats (Perkins 1973, Johnson and Landers 1982, Confer 1992, Askins 1993). For example, at the Savannah River Site (SRS) in South Carolina, stands that were "drumchopped" or had fire suppression had slower colonization rates and lower relative abundances of Bachman's Sparrows (*Aimophila aestivalis*), which occupy scrub-successional habitats (Dunning and Watts 1990). Third, some scrub-successional birds are thought to be area sensitive (Confer 1992, Askins 1994, Bay 1994).

Rudnicky and Hunter (1993) found that rel-

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[3] Present address: United States Geological Survey, Arkansas Cooperative Fish and Wildlife Research Unit, Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701, USA. E-mail: krementz@comp.uark.edu

ative abundances of scrub-successional birds were independent of clearcut stand size in Maine, and we were curious to determine whether this pattern occurred in the Southeast. In addition to 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, Hanski and Simberloff 1997). The effects of land-management practices on survival and reproductive success are probably more important than the relative abundance of the animals under consideration (Thompson 1993).

One way to manage for scrub-successional species is through clearcutting. Clearcutting produces early scrub-successional vegetation that is used by scrub-successional as well as by forest-interior birds (Krementz and Christie 1999). Although many questions remain concerning the management of clearcuts for birds, one tactic, manipulation of stand size, has received surprisingly little research (Rudnicky and Hunter 1993). At the SRS, most clearcuts range in size from 2 to 30 ha. Managers have been concerned with how clearcut size affects native birds, in particular scrub-successional species. Consequently, the focus of our study was to determine how clearcut stand size influences species richness, relative abundance, and reproductive effort of scrub-successional birds.

STUDY AREA AND METHODS

Study site.—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 a 770-km^2 area that is managed as a research park by the Savannah River Natural Resource Management and Research Institute. The site is located on the upper coastal plain in western South Carolina and is 65% forested with longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), and other pine species (USDA 1995). Both even-aged and uneven-aged stand rotations are used at the SRS to manage for Red-cockaded Woodpeckers (*Picoides borealis*; Gaines et al. 1995), timber production, and conservation of native communities. We studied regeneration stands on sandy sites that had been clearcut, site-prepared, and planted. Usually, site preparation involved the application of herbicides, burning, and sometimes seed-bed preparation. All regeneration stands except one were planted with longleaf pine seedlings. The exception was planted in alternating double rows of loblolly and longleaf pines, and also in a single large block of longleaf pines. We located our mist-net grids (see below) in the longleaf pine block.

In 1995, we monitored birds in eight longleaf pine regeneration stands that varied from two to five years old and from 2.8 to 25.9 ha in size (Table 1). In 1996, we monitored birds in 12 longleaf pine regeneration stands that were three to six years old and 2.8 to 56.7 ha (Table 1). Six of the stands were used in both years. Regeneration stands were located primarily across the northern half of the SRS and ranged from 0.5 to 26.7 km apart.

Capture methods.—We placed mist nets in each stand in a 5 × 5 (4 ha, 1995) or a 5 × 4 (3 ha, 1996) array, with 50 m between nets. In one stand in 1995, the 4-ha minimum area was not met (we placed 25 nests in this stand, but not in a 5 × 5 array). We reduced the number of nets in 1996 because on days in which we captured many birds in 1995, we were unable to attend to them as quickly as our protocol required. Birds were captured during three rounds: 25 April to 24 May (round 1), 25 May to 23 June (round 2), and 26 June to 21 July (round 3) in 1995; and 1 to 30 May (round 1), 1 to 28 June (round 2), and 1 to 30 July (round 3) in 1996. In both years we netted each stand for two days during round 1, after which nets were moved to the next stand. This netting cycle continued until all stands were sampled and then was repeated two more times. This netting schedule ensured that each stand was sampled during three different two-day rounds.

Each day, we opened four-panel mist nets (12 m long, 30-mm mesh) for 4 h beginning 30 min before sunrise. Nets were closed if precipitation exceeded 0.5 cm/h or temperatures exceeded 30°C. Nets were checked every 30 to 45 min or sooner when weather conditions threatened the health of birds. We recorded the species, age, sex, and reproductive status of captured birds and banded each one with a numbered metal leg band. Males were categorized as nonbreeding or full breeding based on the development of the cloacal protuberance, and females were categorized as nonbreeding or breeding based on scores for the incubation patch (Pyle et al. 1987).

We also documented movements of banded individuals among capture sites. Any bird captured during one round at a particular site that was recaptured during another round at a different site was treated as a new individual, as were marked birds that were recaptured between years. Banded birds that moved among sites were only recorded on their first capture when we estimated species richness.

During both years, we captured birds that were migrating through the study area. To reduce the confounding effects of including migrants in our data, we excluded data from potential migrant species based on two criteria. If the mapped breeding range covered less than 5% of the combined area of Georgia and South Carolina (Sauer et al. 1997), or the edge of the mapped breeding range was more than 150 km from the SRS boundary, we excluded data for that species.

TABLE 1. Stand attributes, number of species captured, and species-richness estimates for each clearcut stand sampled from April to July 1995 and 1996, Savannah River Site, South Carolina. Dispersion statistics are SE.

Stand	Age (years)	Size (ha)	No. species caught	Overall species-richness estimate[a]	No. scrub-successional species caught	Scrub-successional species-richness estimate	Adj. scrub-successional species-richness estimate
1995							
08/10	2	19	22	29 ± 3.98	9	11 ± 1.86	10.13
19/19	4	24	29	41 ± 4.80	11	13 ± 1.86	12.38
23/47	2	5	29	47 ± 4.95	12	14 ± 1.85	13.51
25/27	4	15	19	41 ± 4.49	11	15 ± 3.18	12.38
53/12	5	10	27	30 ± 2.94	11	11 ± 0.15	12.38
53/51	5	15	25	43 ± 4.33	10	11 ± 1.52	11.26
54/47	3	3	21	28 ± 3.98	9	11 ± 1.86	10.13
58/12	3	26	26	48 ± 4.80	10	12 ± 2.59	11.26
1996							
19/19	5	24	24	31 ± 3.98	10	12 ± 1.86	11.54
23/45	3	30	23	27 ± 3.71	10	10 ± 2.15	11.54
23/47	3	5	25	40 ± 4.49	11	11 ± 2.19	12.70
23/53	5	33	16	26 ± 3.60	9	11 ± 1.86	10.39
25/27	5	15	19	32 ± 3.80	9	9 ± 1.06	10.39
53/12	6	10	25	35 ± 4.33	10	11 ± 1.51	11.54
54/47	4	3	20	34 ± 4.33	8	9 ± 2.19	9.23
57/25	3	17	22	41 ± 4.33	10	15 ± 3.45	11.54
58/12	4	26	21	29 ± 4.16	7	7 ± 1.86	8.08
58/24	5	57	19	26 ± 3.79	8	10 ± 2.18	9.23
58/26	4	20	20	39 ± 4.49	7	12 ± 2.76	8.08
84/09	6	53	18	23 ± 3.73	6	9 ± 1.51	6.93

[a] Estimated using program SPECRICH2.

Analyses.—We captured a variety of bird species and decided to categorize them into three groups based on their habitat affinities and life-history characteristics: (1) scrub-successional (sensu Sauer et al. 1997), (2) woodland (sensu Sauer et al. 1997), and (3) the entire assemblage.

We used SPECRICH2 (White et al. 1978, Rexstad and Burnham 1991) to estimate species richness and COMDYN4 (Nichols et al. 1998) to estimate capture probabilities of selected subsets of birds. SPECRICH2 implements the jackknife estimator for model M_h (White et al. 1978). This model permits estimation of species richness where detection probabilities vary among species. This procedure uses mark-recapture methodology and treats the species encountered as if they were individuals in the traditional mark-recapture setting. Most important, this estimator does not assume that all species are detected (i.e. that $p = 1$), which is a significant shortcoming of ad hoc methods (J. D. Nichols pers. comm.). Using the list of scrub-successional species developed by Sauer et al. (1997), we found that only small numbers of such species were present in the SRS (15 in 1995, 17 in 1996). With relatively few species and only three capture occasions, the efficiency of SPECRICH2 is reduced (J. D. Nichols pers. comm.). To circumvent this problem, we compared the number of species captured during one, two, or all three rounds of mist netting for scrub-successional versus non-scrub-successional birds. If the capture probabilities between these two groups did not differ significantly, we could use the capture probabilities estimated using COMDYN4 based on the entire data set to correct the raw counts of species captured by site (i.e. raw counts of species captured by site divided by p for entire bird data set; J. D. Nichols pers. comm.). The species-richness counts corrected for capture probability are unbiased estimates of the true number of scrub-successional species present at each site.

We were unable to use repeated measures to analyze variation in species richness with clearcut size because only six stands were sampled in both seasons. For the stands that we sampled twice, we used the average species richness of the two estimates and the average stand age for the two years. We investigated whether stand size and stand age explained variation in species richness using the following general linear model (PROC GLM; SAS 1990):

$$\text{species richness} = \text{stand size} + \text{stand age} + \text{stand size} \times \text{stand age}, \quad (1)$$

where species richness is the estimated species richness for the entire bird assemblage or the adjusted scrub-successional bird assemblage, stand size is in ha, stand age is the number of growing seasons since the stand was replanted with longleaf pine, and stand size × stand age is the interaction between the two variables. We incorporated stand age in the model because species richness can be related to stand age, especially for stands younger than 10 years (Johnston and Odum 1956, Meyers and Johnson 1978). We used type III sum of squares to determine significance of the factors. Type III sum of squares gives the sum of squares that would be obtained for each variable if it were entered last into the model (i.e. the effect of each variable is evaluated after all other factors have been accounted for). Because of small sample sizes, we used $\alpha = 0.10$. We also investigated relative abundance of scrub-successional and woodland species (based on Sauer et al. 1997) across stand sizes. We examined the relationship between frequency of capture of scrub-successional, woodland, and combined groups and clearcut stand size using a contingency analysis. We lumped stand sizes into five categories because it resulted in an even distribution of stands per category except for the absence of the largest category (>26 ha) in 1995. We lumped the frequency of captures into three classes: absent (no captures), rare (one or two captures), and common (three or more captures) and combined capture data across years.

We compared two indices of reproductive effort among clearcut stand sizes: (1) the relative proportion of adults in breeding condition, and (2) the relative proportion of juveniles:adults captured. Because the former data set was larger than the latter (see below), we categorized species according to their migration status (resident, short-distance migrant, Nearctic-Neotropical migrant) in an attempt to determine if reproductive activity was sensitive to life-history characteristics across stand sizes (Sauer et al. 1996). We first tested whether the proportion of adults in reproductive condition differed between years using a chi-square test. Depending on that outcome, we either lumped data across years or conducted likelihood-ratio chi-square tests by year to examine the difference in the proportion of reproductively active adults by migration status across three stand-size categories. Next, we analyzed the ratio of juveniles to adults using a two-step analysis. First, we used only species with 20 or more captures and used all three netting rounds to increase the numbers of juveniles in the sample (because we were confronted with small sample sizes and low numbers of juveniles captured). We tested for a year effect on the ratio of juveniles to adults by species group using a heterogeneity chi-square test (Zar 1974). Depending on that outcome, we then analyzed (either by year or across years) the relative proportion of adults in breeding condition between different-sized stands using a likelihood-ratio chi-square test. We investigated whether stand size and year explained variation in the ratio of juveniles to adults using the following general linear model (PROC GLM; SAS 1990):

$$\text{juvenile} : \text{adult} = \text{stand size} + \text{year} + \text{stand size} \times \text{year}, \qquad (2)$$

where juvenile:adult is the ratio of juveniles captured divided by adults captured across species by stand, year is year of study (1995 or 1996), and stand size × year is the interaction of the two predictor variables. To assess whether combining the ratio of juveniles to adults across species was in some way masking a true species-specific relationship, we examined this same general linear model for just those species for which (1) 20 or more individuals were captured per year, and (2) juveniles were captured at most sites.

Finally, to assess if productivity across clearcuts was sufficient to maintain bird populations, we compared our observed ratio of juveniles to adults against an expected age ratio. As an expected age ratio, we used the average ratio of captures of juveniles to adults for the Southeast region MAPS stations (35%; DeSante et al. 1996), under the assumption that region-wide age ratios equaled or exceeded local mortality.

To investigate whether the relationships among species richness, reproductive effort, and relative abundance and clearcut stand size resulted from changes in vegetation coincident with stand size, we examined variation in vegetation across stand size. 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 per point and 4,000 measurements per 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 height increments 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 each height increment. All other plants occurring within the height increment were tallied by category (i.e. grass, forb, fern, vine, and dead vegetation). In 1996, we followed the same sampling procedure except that only five random points were sampled in 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. To investigate whether vegetation characteristics were related to clearcut stand size, we conducted a series of regressions between vegetation measurements and stand size.

TABLE 2. Summary of captured birds categorized by breeding habitat (sensu Sauer et al. 1997) in regeneration stands of longleaf pine during the breeding seasons of 1995 and 1996, 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 in parentheses. All birds in parentheses were treated as new birds in 1996. Species-specific capture-recapture records are available from the senior author. See Krementz and Christie (1999: table 1) for a list of bird species in each habitat group.

	1995		1996	
Habitat group	Captured	Recaptured	Captured	Recaptured
Grassland species	3	0	5	0 (1)
Scrub-successional species	443	101	503	91 (33)
Woodland species	275	37	237	19 (23)
Urban species	42	9	26	4 (3)
Totals	763	147	771	114 (60)

RESULTS

During 1995, mist nets were opened for 5,600 h (700 h per stand), and 763 birds from 47 species were banded (Table 2). Overall, 147 individuals of the original 763 (19.3%) were recaptured; 22 of the 47 species were recaptured at least once. The most frequently captured bird was the Indigo Bunting (*Passerina cyanea*). Bachman's Sparrows and Indigo Buntings were the most frequently recaptured species, with 19 recaptures each. Five species of migrants were eliminated from the analyses, none of which was captured more than five times. Species-richness estimates in clearcut stands ranged from 28 to 48 ($\bar{x}$ = 38.4 ± SE of 2.89; Table 1).

During 1996, mist nets were opened for 5,760 h (480 h per stand), and 771 birds from 47 species were captured (Table 2), of which 763 were banded. Overall, 114 individuals of the original 771 (14.7%) were recaptured; 20 of the 47 species banded were recaptured at least once. Again, the most frequently captured bird was the Indigo Bunting, which also was the most frequently recaptured (22 recaptures). Five species of migrants were eliminated from the analyses, none of which was captured more than three times. Species-richness estimates in clearcut stands ranged from 23 to 41 ($\bar{x}$ = 31.9 ± 1.73; Table 1). Sixty individuals that were banded in 1995, representing 18 species, were recaptured in 1996. Blue Grosbeaks (*Guiraca caerulea*) were recaptured the most frequently between years (eight occasions).

In 1995, we caught one Indigo Bunting and three Prairie Warblers (*Dendroica discolor*) at different stands. In 1996, we caught two Prairie Warblers, one Bachman's Sparrow, one Painted Bunting (*Passerina ciris*), one Indigo Bunting, one Eastern Towhee (*Pipilo erythrophthalmus*), and one Loggerhead Shrike (*Lanius ludovicianus*) at different stands. Both sexes and only adults were represented. Distances between captures averaged 4.4 km and ranged from 0.6 to 14.7 km.

The distribution of capture frequencies for scrub-successional and non-scrub-successional species did not differ significantly in either year (1995, $\chi^2 = 3.95$, df = 2, $P = 0.13$; 1995, $\chi^2 = 4.67$, df = 2, $P = 0.09$). Because capture probabilities did not differ between these groups, we lumped the groups to increase sample sizes and to estimate more precisely the year-specific capture probabilities. We used year-specific capture probabilities (1995 = 0.8884; 1996 = 0.8663) to correct the raw richness measurements for scrub-successional species by site (Table 1).

Species richness for the entire assemblage was not explained by stand size ($F = 0.18$, df = 1 and 13, $P = 0.67$), stand age ($F = 0.00$, df = 1 and 13, $P = 0.95$), or the interaction of the two variables ($F = 0.51$, df = 1 and 13, $P = 0.90$). Similarly, species richness for scrub-successional birds was not explained by stand size ($F = 0.24$, df = 1 and 13, $P = 0.63$), stand age ($F = 0.38$, df = 1 and 13, $P = 0.55$), or the interaction of the two ($F = 0.95$, df = 1 and 13, $P = 0.35$).

When we regressed species richness against clearcut size, a negative relationship occurred for both groups of birds (Fig. 1). Testing this specific hypothesis (i.e. by dropping stand age and the interaction of stand size and stand age in a regression) revealed a significant negative relationship between species richness and stand size for the entire bird assemblage ($F =$

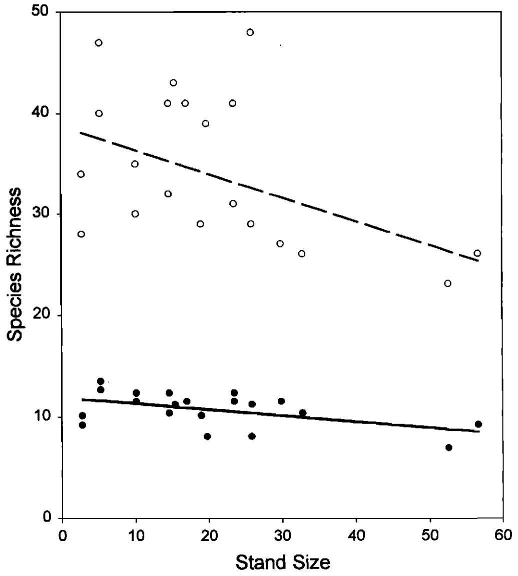

FIG. 1. Linear regression of clearcut stand size (ha) and species richness for the entire bird assemblage (open circles) and for scrub-successional birds (closed circles) in 1995 and 1996, Savannah River Site, South Carolina.

9.09, df = 1 and 13, $P = 0.01$, $r^2 = 0.43$; species richness = 40.3 − 0.28[stand size]) and for the scrub-successional birds ($F = 6.42$, df = 1 and 13, $P = 0.02$, $r^2 = 0.348$; species richness = 11.9 − 0.06[stand size]; Fig. 1). The influence of the two largest clearcut stands in driving the negative slope was large (Fig. 1); removing these two points resulted in a slope that was not significantly different from zero for the entire bird assemblage ($T = -1.42$, $P = 0.18$) and for the scrub-successional birds ($T = -0.72$, $P = 0.48$).

For either group or for all species combined, we found no relationship between the frequency of capture of any category of bird and stand size (scrub-successional, $\chi^2 = 7.09$, df = 8, $P = 0.52$; woodland, $\chi^2 = 4.84$, df = 8, $P = 0.77$; combined, $\chi^2 = 6.90$, df = 8, $P = 0.55$; Table 3). This suggests that rare birds were no more likely to be captured in large stands than in small stands.

Only male Nearctic-Neotropical migrants exhibited a difference in the proportion of individuals in reproductive condition between years ($\chi^2 = 4.33$, df = 1, $P = 0.03$). In 1995, there were significantly fewer reproductively active male Nearctic-Neotropical migrants in larger stands than in smaller stands ($\chi^2 = 4.46$, df = 1, $P = 0.03$). No significant relationship existed for female Nearctic-Neotropical migrants lumped across years ($\chi^2 = 0.87$, df = 1, $P = 0.35$), or for males in 1996 ($\chi^2 = 0.92$, df = 1, $P = 0.34$). After lumping residents and short-distance migrants across years, we found no significant relationship between stand size and reproductive condition of males ($\chi^2 = 1.28$, df = 1, $P = 0.26$) or females ($\chi^2 = 0.04$, df = 1, $P = 0.83$).

The ratio of juveniles to adults varied by year ($F = 4.58$, df = 1 and 19, $P = 0.04$; Fig. 2), but neither clearcut size ($F = 1.54$, df = 1 and 19, $P = 0.23$) nor the interaction of clearcut size and year ($F = 1.39$, df = 1 and 19, $P = 0.25$) was related to the age ratio of captures. Examining individual species, only four species in 1995 (Eastern Towhee, Prairie Warbler, Bachman's Sparrow, and Carolina Wren [*Thryothorus ludovicianus*]) and one species in 1996 (Eastern Towhee) met our criteria for in-depth analyses. In 1995, only Eastern Towhees had a significant negative relationship between the ratio of juveniles to adults and stand size ($F = 16.6$, df = 1 and 7, $P = 0.006$; juvenile:adult = 51.5 − 2.13[stand size]). In 1996, the ratio of juvenile to adult Eastern Towhees was not related to stand size ($F = 0.27$, df = 1 and 11, $P = 0.61$).

In both years, the distribution of observed age ratios differed significantly from the expected age ratio of 35% (1995, $\chi^2 = 38.80$, df = 7, $P = 0.001$; 1996, $\chi^2 = 51.67$, df = 11, $P = 0.001$). Age ratios were higher than the expected in 1995 and lower than the expected in 1996 (Fig. 2).

Of the 11 vegetation variables, "all shrubs" (a combination of shrubs and broadleaf trees; $F = 4.80$, df = 1 and 18, $P = 0.04$) and "broadleaf trees" ($F = 7.12$, df = 1 and 18, $P = 0.02$) decreased in frequency as stand size increased. These two variables were highly correlated ($r^2 = 0.83$). In 1995, total vegetation frequency increased as stand age increased from two to five years ($F = 47.15$, df = 1 and 6, $P < 0.001$), as did vegetation frequency in the first ($F = 16.21$, df = 1 and 6, $P = 0.007$) and second meter ($F = 30.72$, df = 1 and 6, $P = 0.002$) above ground. As clearcuts aged, broadleaf tree vegetation and shrubs were replaced or shaded out by coniferous trees. In 1996, total vegetation frequency increased as stand age increased from three to six years ($F = 34.27$, df = 1 and 10, $P < 0.001$), as did vegetation frequency in the

TABLE 3. Distribution of capture frequencies of species by clearcut size class, 1995 and 1996, Savannah River Site, South Carolina. C = common (captured three or more times in two years); R = rare (captured one or two times in two years); A = not captured. Two stands were sampled per size class per year except for >26 ha (no stands in 1995, four in 1996).

	Size class (ha)				
Species	0 to 8	9 to 15	15 to 20	21 to 26	>26
Northern Bobwhite (*Colinus virginianus*)	R	R	A	A	A
Mourning Dove (*Zenaida macroura*)	A	A	R	A	A
Common Ground-Dove (*Columbina passerina*)	A	A	A	R	A
Yellow-billed Cuckoo (*Coccyzus americanus*)	A	A	A	R	A
Whip-poor-will (*Caprimulgus vociferus*)	R	A	R	A	R
Ruby-throated Hummingbird (*Archilochus colubris*)	R	R	R	R	R
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	A	C	C	C	R
Red-bellied Woodpecker (*Melanerpes carolinus*)	C	C	R	R	R
Downy Woodpecker (*Picoides pubescens*)	R	R	C	C	R
Hairy Woodpecker (*Picoides villosus*)	A	A	R	A	A
Northern Flicker (*Colaptes auratus*)	R	A	A	R	A
Eastern Wood-Pewee (*Contopus virens*)	R	R	R	C	R
Acadian Flycatcher (*Empidonax virescens*)	A	A	A	A	R
Eastern Kingbird (*Tyrannus tyrannus*)	R	A	C	A	A
Great Crested Flycatcher (*Myiarchus crinitus*)	C	C	C	C	C
Loggerhead Shrike (*Lanius ludovicianus*)	A	A	C	C	R
White-eyed Vireo (*Vireo griseus*)	R	R	A	C	R
Yellow-throated Vireo (*Vireo flavifrons*)	A	A	A	R	A
Red-eyed Vireo (*Vireo olivaceus*)	R	R	A	C	A
Blue Jay (*Cyanocitta cristata*)	R	R	A	A	A
Carolina Chickadee (*Poecile carolinensis*)	C	C	C	C	C
Tufted Titmouse (*Baeolophus bicolor*)	C	C	C	C	R
Brown-headed Nuthatch (*Sitta pusilla*)	R	C	R	R	C
Carolina Wren (*Thryothorus ludovicianus*)	C	C	C	C	C
Blue-gray Gnatcatcher (*Polioptila caerulea*)	C	C	R	C	R
Eastern Bluebird (*Sialia sialis*)	C	C	C	C	C
Wood Thrush (*Hylocichla mustelina*)	R	A	A	A	A
Gray Catbird (*Dumetella carolinensis*)	C	C	C	C	R
Northern Mockingbird (*Mimus polyglottos*)	R	A	C	C	C
Brown Thrasher (*Toxostoma rufum*)	C	C	C	C	R
Cedar Waxwing (*Bombycilla cedrorum*)	A	A	A	R	A
Northern Parula (*Parula americana*)	R	A	R	A	A
Yellow Warbler (*Dendroica petechia*)	A	A	R	A	A
Pine Warbler (*Dendroica pinus*)	A	C	C	C	C
Prairie Warbler (*Dendroica discolor*)	C	C	C	C	C
Black-and-white Warbler (*Mniotilta varia*)	A	A	R	R	A
American Redstart (*Setophaga ruticilla*)	C	C	A	R	A
Ovenbird (*Seiurus aurocapillus*)	R	R	R	R	R
Kentucky Warbler (*Oporornis formosus*)	R	A	A	A	A
Common Yellowthroat (*Geothlypis trichas*)	C	C	C	C	R
Hooded Warbler (*Wilsonia citrina*)	A	A	A	A	R
Yellow-breasted Chat (*Icteria virens*)	C	C	C	C	C
Summer Tanager (*Piranga rubra*)	C	C	C	C	C
Eastern Towhee (*Pipilo erythrophthalmus*)	C	C	C	C	C
Bachman's Sparrow (*Aimophila aestivalis*)	C	C	C	C	C
Chipping Sparrow (*Spizella passerina*)	C	C	C	C	C
Field Sparrow (*Spizella pusilla*)	R	C	R	C	C
Northern Cardinal (*Cardinalis cardinalis*)	C	C	C	C	C
Blue Grosbeak (*Guiraca caerulea*)	C	C	C	C	C
Indigo Bunting (*Passerina cyanea*)	C	C	C	C	C
Painted Bunting (*Passerina ciris*)	C	A	R	A	R
Brown-headed Cowbird (*Molothrus ater*)	C	A	A	C	A
Orchard Oriole (*Icterus spurius*)	R	R	C	C	C
American Goldfinch (*Carduelis tristis*)	C	A	C	R	R

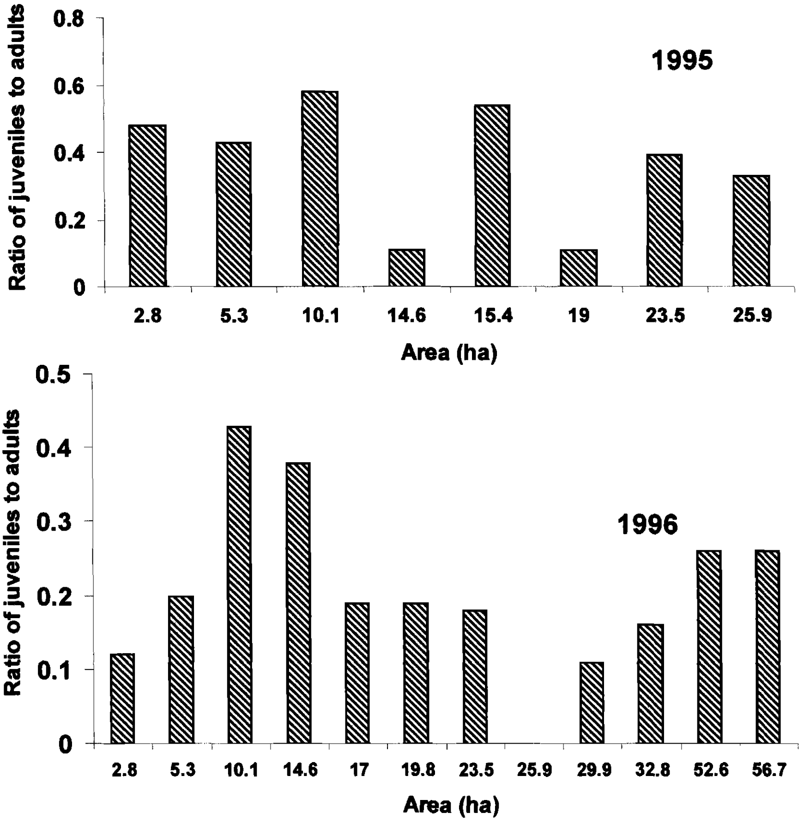

FIG. 2. Ratio of captures of juveniles to adults summed across all species and capture periods by clearcut stand size in 1995 and 1996, Savannah River Site, South Carolina. No juveniles were captured in the 25.9-ha site in 1996.

first ($F = 8.84$, df = 1 and 10, $P = 0.01$) and second meter ($F = 28.36$, df = 1 and 10, $P < 0.001$) above ground. As in 1995, broadleaf tree and shrubs were replaced by coniferous trees as stands became older.

DISCUSSION

Species richness did not increase with increasing clearcut size for scrub-successional birds or for the entire bird assemblage. Within the typical size range of clearcuts at SRS (ca. 5 to 25 ha), which also is typical for clearcuts on public lands in the Southeast (J. Blake pers. comm.), we found no relationship between stand size and species richness (Fig. 1). Only when larger stands were included did we find a negative relationship between stand size and species richness.

One possible reason why we did not find a positive species-area relationship is that in many studies, sampling effort usually increases with stand size. We believe that increasing sampling effort with stand size confounds interpretations of species-area results because capture probabilities are directly related to sampling effort. We are not aware of a similar study in which capture probabilities have been estimated and used accordingly to correct estimates of species richness. In our study, we addressed the issue of sampling and therefore capture probability from two standpoints. First, we sampled on a constant basis, both in terms of area sampled per stand and net hours sampled per plot. Second, we used mark-recapture methods to estimate capture probabilities and correct our species-richness measurements. We believe that this is the first case of doing the latter when dealing with the species-area relationship.

A second possible reason why we did not find the typical positive species-area relationship is that as we sampled larger and larger clearcuts, by chance our grids may have fallen in a habitat type that was not different across clearcut stand sizes. One explanation of the species-area relationship is that with increasing stand size, the number of habitat types increases. With a greater number of habitats (niches) available, the number of species that could occupy the site can increase. Again, this argument is confounded. One of the original arguments MacArthur and Wilson (1967) used to explain the species-area curve involved the relationship between the probability of encountering a larger island versus a smaller island, based solely on area and not on the number of habitats contained therein. By bringing in the notion of an increasing number of habitat types in association with patch size, the species-area relationship is confounded between area and habitat type. Our sampling protocol specifically addressed the issue of the number of habitat types. We selected stands with sandy soils that had been clearcut, site-prepared, and replanted with longleaf pine seedlings. These stands were homogeneous regardless of stand size. Thus, our data reflected sampling area alone versus the combination of habitat types and area.

Across a larger range of clearcut sizes (2 to 112 ha) in Maine, Rudnicky and Hunter (1993) found that the number of bird species per plot did not differ significantly with stand size; when sampling effort increased with stand size, species richness increased. As we noted above, the latter finding can result from an interaction of sampling effort and stand size.

Another explanation for the species-area curve relates to the quality of habitat available in a fragment. Several authors have noted that with increasing age of clearcuts, relative abundance and species diversity of birds decline (e.g. Johnston and Odum 1956, Titterington et al. 1979, Childers et al. 1986), apparently in concert with a reduction in the amount and complexity of vegetation in the midstory and understory layers (Harris et al. 1974). Indirectly, we examined this through our measurements of vegetation. We observed a reduction in volume of shrub and hardwood vegetation with increasing clearcut size, but the reduction in volume of shrubs and broadleaf trees with increasing clearcut size was driven by the two largest clearcuts we monitored. These two clearcuts were not only the largest, they were at least five years old. Because broadleaf trees declined significantly with increasing clearcut age, concomitant with an increase in volume of coniferous foliage (Christie 1997), the relationship between broadleaf tree volume and clearcut size was confounded by clearcut age. This precluded a clear relationship between species richness and vegetation at our study site. Nevertheless, vegetation volume is thought to be related to the density and richness of breeding bird species (Mills et al. 1989), probably through a direct relationship with resource abundance (Brunswig and Johnson 1972, Johnson and Landers 1982, Mills et al. 1989).

In addition to the absence of a species-area relationship, we determined that neither the relative proportion of adults in breeding condition nor the ratio of juveniles to adults captured varied across clearcut stand sizes in a systematic pattern, with the exception of Eastern Towhees in 1995. This suggests that reproductive effort was constant across stand sizes. Thus, larger clearcuts are not needed to produce relatively more young birds per unit area. Krementz and Christie (1999) examined reproductive effort of scrub-successional birds at this same site in clearcuts and in mature longleaf pine stands. They found no difference in the proportion of juveniles captured by species or habitat type. If reproductive effort was not different between early scrub-successional and mature longleaf pine stands where large differences in vegetation existed (Stober 1996, Christie 1997, Krementz and Christie 1999), we see no reason why reproductive effort should vary across clearcut size in a systematic fashion (but see Bay 1994).

Without an apparent relationship between age ratios and stand size, the question remains whether production in clearcuts was sufficient to offset losses (sensu source-sink dynamics; Pulliam 1988). The only comparison that we could devise to address this notion was the distribution of age ratios against the region-wide age ratio of 35%. We do not assume that the 35% value is necessarily the proportion needed to insure replacement of adult losses, only that it is the value found across a large geographic area and therefore should represent the fraction of juveniles captured in most situations where population stability exists. Our results indicated that production exceeded the expected age ratio during the first year of study but was lower than the expected age ratio during the second year of study. It is not surprising that we found strong annual effects on productivity because abiotic and biotic factors can vary greatly over time. Longer-term data will be needed to adequately address this question.

The absence of a strong relationship between species richness and clearcut age counters the findings of Meyers and Johnson (1978) that in loblolly-shortleaf (*P. echinata*) pine forests in the southeastern United States, bird-species richness generally increased with stand age. In contrast, Johnson and Landers (1982) noted that bird-species richness in a Georgia slash pine (*P. elliottii*) flatwoods was lowest in the first growing season after planting, but from then through 16 to 28 years (i.e. mid-rotation), species richness was roughly constant. In loblolly pine clearcuts (2 to 24 years old) in the Virginia Piedmont, Childers et al. (1986) found no trend in bird-species richness and stand age. Thus, the relationship between stand age and bird-species richness in pine plantations in the Southeast appears to be equivocal.

Our regeneration stands were used by more than just early scrub-successional birds. Not only did they harbor species unique to early scrub-successional stands (e.g. Gray Catbird [*Dumetella carolinensis*], Yellow-breasted Chat [*Icteria virens*], and Field Sparrow [*Spizella pusilla*]; Krementz and Christie 1999), they also provided nesting (e.g. Bachman's Sparrow, Prairie Warbler, and Carolina Wren) and foraging (e.g. Red-bellied Woodpecker [*Melanerpes carolinus*], Great Crested Flycatcher [*Myiarchus crinitus*], and Pine Warbler [*Dendroica pinus*]) habitat for birds that frequent early and late scrub-successional stands (S. F. Pearson pers. comm.). Thus, it would be incorrect to think of early scrub-successional stands as being used only by species that breed in that habitat type.

We found no overwhelming evidence for a species-area relationship in scrub-successional birds or for the entire assemblage. The use of early successional stands by forest-interior birds remains unclear, but a suite of scrub-successional birds at SRS occurs only in such stands (Krementz and Christie 1999). Managing mature pine stands for Red-cockaded Woodpeckers benefits some early successional species, but the need for truly early successional habitat remains if beta diversity is an objective. Because the complexity and scale of habitat heterogeneity needed to meet management needs will vary with specific goals (Thomas et al. 1975, Childers et al. 1986, Pearson et al. 1996), and because maintenance of biodiversity is a goal of the Savannah River Institute at SRS, at the landscape level even-aged forest management should be maintained both from the standpoint of Red-cockaded Woodpeckers (Hedrick et al. 1998) and of scrub-successional birds.

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