

# ECOLOGICAL SUCCESSION OF BREEDING BIRD POPULATIONS IN NORTHWESTERN ARKANSAS

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THIS study was designed to determine the species and densities of breeding birds in seral stages of upland subseral succession in the Ozark Highlands at Pea Ridge National Military Park in Benton County, Arkansas. Ecological succession of upland plants in the Ozark Highlands (Figure 1) varies regionally with the nature of the bedrock (Cozzens, 1940). Dale and Fullerton (1964) described the early stages of the upland subseral near the present study area.

The first stage of the secondary succession is highly variable depending on prior land use. Fields burned and abandoned often have horseweed (*Erigeron canadensis*); land heavily grazed before abandonment has much bitterweed (*Helenium tenuifolium*); land that was plowed and abandoned has hayfever weed (*Ambrosia artemisiifolia*) as a dominant plant species (scientific names of plants were taken from Fernald, 1950). Within 1–3 years this initial variable stage is followed predominantly by white heath aster (*Aster ericoides*). The aster stage is replaced after a year or two by broom sedge (*Andropogon virginicus*) grassland. Five or more years later the broom sedge dominance gradually begins to yield to an early tree stage characterized by persimmon (*Diospyros virginiana*), sassafras (*Sassafras albidum*), or winged elm (*Ulmus alata*) (Hite, 1960; Bullington, 1961). This stage can persist over 40 years (Hite, 1960). On favorable sites, the early tree stage develops into forest dominated by white oak (*Quercus alba*) and black oak (*Q. velutina*), the climax community in the region (Cozzens, 1940). On xeric sites the early tree stage becomes post oak (*Q. stellata*) forest, which ultimately transforms to climax forest as moisture conditions improve with soil buildup (Turner, 1935).

A glade with red cedar (*Juniperus virginiana*) develops on limestone (Steyermark, 1940; Quarterman, 1950), which is the pioneer woody stage on outcroppings (Beilman and Brenner, 1951). Cedar glades slowly transform to post oak subclimax (Kucera and Martin, 1957).

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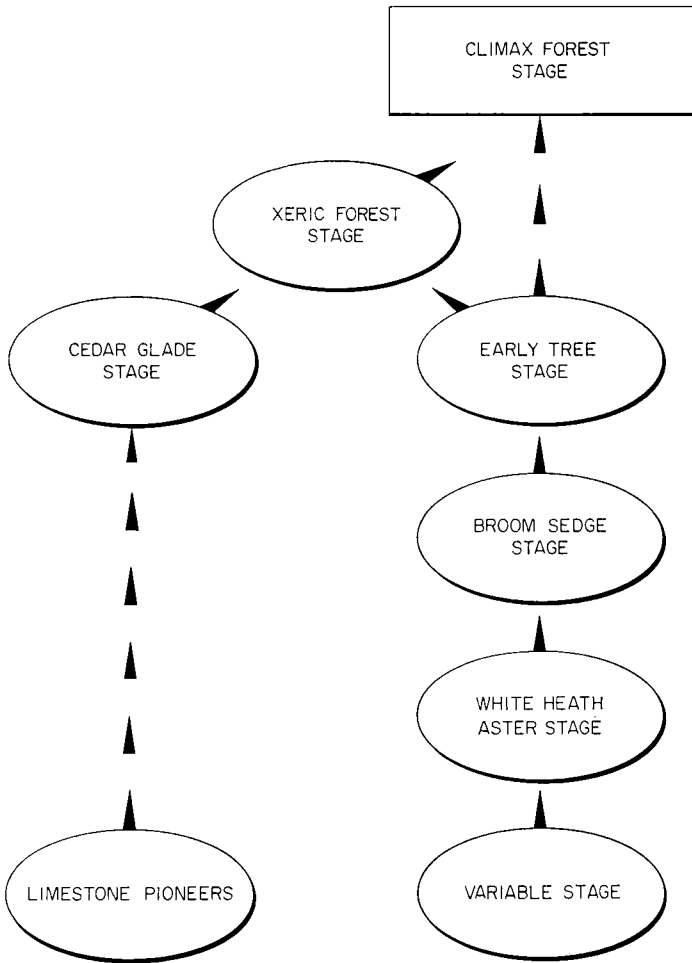


Figure 1. Ecological succession of upland plant communities in northwestern Arkansas.

METHODS

Ten plots ranging from 4 to 24 acres and averaging 16 acres were chosen for uniformity and for representativeness of upland subserere succession. Tree-ring data were obtained with increment borers to determine study plot ages since agricultural abandonment. Plots also were dated by Ivan Tolley and Alvin Seamster, who provided information about past cultivation and land abandonment.

As the plots varied in physiognomy, it was necessary to use several vegetation-sampling techniques depending on the life forms of the plants. A sighting tube (Winkworth and Goodall, 1962) sampled ground cover in the field plots. In forests the first 20 ground plants less than 4.5 feet tall were identified along a

line having a random starting point and a random direction (Baur, 1943). Understory stems ( $\leq 3$  inches DBH and  $\geq 4.5$  feet tall) were counted and identified in 0.01-acre, paced, arm-length rectangles (Rice and Penfound, 1955). Trees ( $\geq 3$  inches DBH) were counted and identified in 0.1-acre rectangular samples and were grouped into 3-inch size classes (Diameter Breast High). Canopy density in the forest plots was determined by noting if canopy cover was present or absent at 20 random points. In fact all sample sites in each habitat were located randomly.

The bird populations were censused using the territory mapping method of Williams (1936, 1947). At least six early morning censuses were taken on each plot during April and May 1967. Care was taken to enter each plot from different sides each time and to visit each plot at different times in the morning. Two night counts of nocturnal birds were made on all plots.

One-acre grids were used for territory mapping. Bird densities were converted to number of territorial males per 100 acres. Increased accuracy in determining population densities on the smaller plots was obtained by analyzing fractions of bird territories.

### THE STUDY PLOTS

The Ozark Highlands contain no large expanses of uniform habitat representing all stages of secondary succession. This is due in part to the fact that land abandonment practices are not random through time, but are influenced by climatic events such as droughts, governmental policies such as the soil bank program, and, in the case of the present study, historical events such as the Civil War, the Great Depression, and the coming of the railroads. Also the variability of succession according to the bedrock in the Ozarks (Cozzens, 1940) makes it impossible to search large regions for suitable study plots. These constraints limit any successional study in the Ozark Highlands to smaller study plots than one would use in other areas. We recognize the shortcomings of using small study plots, but feel that not conducting studies in areas that are difficult to sample is the less viable alternative.

Bird populations on land prior to abandonment were studied on a 16-acre mowed hayfield plot with no woody vegetation. This plot's dominant plant was blue grass (*Poa* sp.).

A 16-acre burned field plot represented the initial variable stage of succession. This former field of broom sedge and sassafras saplings had burned the winter before the study. Most broom sedge and sassafras was destroyed but some dead sassafras stems still stood 4–5 feet tall and were used as song perches.

A 16-acre plot in a broom sedge field was established for the next stage of succession. Blackberry (*Rubus* sp.) and persimmon were important woody plants on this grassland plot.

The early tree stage was represented by two study plots. The 16-acre clonal persimmon plot was an early phase of the early tree stage. Shade

intolerant species formed groups of small trees separated by expanses of broom sedge plus other herbaceous species. Tree density was 122 trees per acre, stem density 322 stems per acre. Within the clonal clumps of trees the ground cover was relatively sparse. Overall the canopy was 83 percent open.

A woody field plot represented a later phase in the early tree stage. This was a 4-acre plot in which the separated clonal clumps of shade intolerant trees, primarily sassafras, had expanded to the point of barely joining and thus were totally excluding the grasses. A well-developed understory with 4,550 stems per acre was composed primarily of winged sumac (*Rhus copallina*). The canopy was 75 percent open and there were 210 trees per acre.

The cedar glade stage of succession was studied on a 4-acre plot. The soil was shallow and on limestone. Red cedar predominated in both the tree and shrub layers, but the presence of post oak in both layers demonstrated the connection between this stage and the post oak forest. Broom sedge was the principal ground cover, but was accompanied by several other species. With 126 trees per acre the canopy was 53 percent open; the understory had 270 stems per acre.

A 7-acre forest edge plot was included in the study. This plot was bisected by the junction of a post oak forest and a broom sedge field. The junction included a dense understory of winged sumac and blackberry.

A xeric forest study plot covered 24 acres of post oak subclimax forest. Post oak predominated, but the presence of large and small white oaks and black oaks linked this stage to later successional stages. Ground cover was sparse and the understory layer was well-developed (730 stems per acre). The canopy was 36 percent open with 367 trees per acre.

A mesic forest plot of 7 acres represented the climax forest. There were no dominants in any of the three vegetation layers, but white oak and black oak were important trees. The plot had been in standing timber since the time of the Civil War. The understory layer was sparse (223 stems per acre). The canopy was 26 percent open with 193 trees per acre.

## RESULTS AND DISCUSSION

### UPLAND AVIAN SUBSERE AND SUCCESSION

Upland succession in the region of the study involved three general stages: fields dominated by grasses and forbs, fields dominated by shrubs and shade intolerant trees, and forests dominated by trees. These general stages each have distinctive breeding bird species (Table 1).

TABLE 1  
BIRD SPECIES AND COMMUNITY DIVERSITIES IN THE STUDY PLOTS<sup>1</sup>

Species	Territorial males per 100 acres in study plots										
	HF	BF	BS	CP	WF	CG	FE	XF	IF	MF	
Loggerhead Shrike ( <i>Lanius ludovicianus</i> )	3	-	-	-	-	-	-	-	-	-	-
Horned Lark ( <i>Eremophila alpestris</i> )	13	+	-	-	-	-	-	-	-	-	-
Grasshopper Sparrow ( <i>Ammodramus saviannarum</i> )	38	19	-	-	-	-	-	-	-	-	-
Eastern meadowlark ( <i>Sturnella magna</i> )	59	19	6	-	-	-	-	-	-	-	-
Common Nighthawk ( <i>Chordeiles minor</i> )	+	+	+	+	+	+	+	+	+	+	+
Mourning Dove ( <i>Zenaidura macroura</i> )	2	2	+	-	-	-	14	3	+	-	-
Bobwhite ( <i>Colinus virginianus</i> )	2	6	13	9	25	13	29	-	2	-	-
Marsh Hawk ( <i>Circus cyaneus</i> )	-	+	-	-	-	-	-	-	-	-	-
Ruby-throated Hummingbird ( <i>Archilochus colubris</i> )	-	+	-	-	-	-	-	-	-	-	-
Mockingbird ( <i>Mimus polyglottos</i> )	-	6	-	-	-	-	14	-	-	-	-
Eastern Bluebird ( <i>Sialia sialis</i> )	-	6	-	-	13	-	-	-	-	-	-
Bell's Vireo ( <i>Vireo bellii</i> )	-	6	2	-	-	-	-	-	-	-	-
Baltimore Oriole ( <i>Icterus galbula</i> )	-	2	-	6	-	-	-	-	-	-	-
Dickcissel ( <i>Spiza americana</i> )	-	21	-	-	+	-	-	-	-	-	-
Common Crow ( <i>Corvus brachyrhynchos</i> )	-	+	-	-	+	-	-	-	+	-	-
Brown Thrasher ( <i>Toxostoma rufum</i> )	-	6	-	3	25	-	-	-	-	-	-
American Goldfinch ( <i>Spinus tristis</i> )	-	6	-	13	25	-	-	-	-	-	-
Yellow-shafted Flicker ( <i>Colaptes auratus</i> )	-	2	-	-	6	-	-	2	6	-	-
Eastern Kingbird ( <i>Tyrannus tyrannus</i> )	-	6	6	6	+	-	-	-	-	-	-
Yellow-breasted Chat ( <i>Icteria virens</i> )	-	6	6	13	50	25	7	-	-	-	-
Rufous-sided Towhee ( <i>Pipilo erythrophthalmus</i> )	-	6	12	19	25	-	57	6	-	-	-
Field Sparrow ( <i>Spizella pusilla</i> )	-	19	44	69	50	25	21	-	-	-	-

<sup>1</sup> Numerals represent territorial males per 100 acres. A plus indicates that a bird was present on a plot, but it was not possible to determine actual density per 100 acres. HF indicates mowed hay field plot; BF, burned field plot; BS, broom sedge field plot; CP, clonal persimmon field plot; WF, woody field plot; CG, cedar glade plot; FE, forest edge plot; XF, xeric forest plot; IF, intermediate forest plot; MF, mesic forest plot. Common and scientific names of birds taken from the A.O.U. Check-list of North American Birds (1957).

TABLE 1. (CONTINUED)

Species	Territorial males per 100 acres in study plots										
	HF	BF	BS	CP	WF	CG	FE	XF	IF	MF	
Cardinal ( <i>Richmondia cardinalis</i> )	-	9	6	9	25	25	61	29	41	29	
Barn Owl ( <i>Tyto alba</i> )	-	+	-	-	-	-	-	-	-	-	
Prairie Warbler ( <i>Dendroica discolor</i> )	-	22	28	-	18	21	-	-	-	-	
Blue Grosbeak ( <i>Guiraca caerulea</i> )	-	-	-	3	-	-	-	-	-	-	
Painted Bunting ( <i>Passerina ciris</i> )	-	-	-	3	-	-	-	-	-	-	
Blue-winged Warbler ( <i>Vermivora pinus</i> )	-	-	-	6	-	-	14	-	-	-	
Indigo Bunting ( <i>Passerina cyanea</i> )	-	-	-	3	+	+	25	14	-	-	
Blue Jay ( <i>Cyanocitta cristata</i> )	-	-	-	9	12	-	14	-	13	14	
Robin ( <i>Turdus migratorius</i> )	-	-	-	-	25	-	-	-	-	-	
Red-winged Blackbird ( <i>Agelaius phoeniceus</i> )	-	-	-	-	+	-	-	-	-	-	
Turkey ( <i>Meleagris gallopavo</i> )	-	-	-	-	+	-	-	-	-	-	
Roadrunner ( <i>Geococcyx californianus</i> )	-	-	-	-	-	+	-	-	+	-	
Eastern Wood Pewee ( <i>Contopus virens</i> )	-	-	-	-	-	25	-	-	9	7	
Red-bellied Woodpecker ( <i>Centurus carolinus</i> )	-	-	-	-	-	-	-	7	6	4	
Tufted Titmouse ( <i>Parus bicolor</i> )	-	-	-	-	-	6	-	12	38	29	
Blue-gray Gnatcatcher ( <i>Poliophtila caerulea</i> )	-	-	-	-	-	25	14	8	9	43	
Summer Tanager ( <i>Piranga rubra</i> )	-	-	-	-	-	-	14	4	9	-	
Great Horned Owl ( <i>Bubo virginianus</i> )	-	-	-	-	-	-	+	+	+	+	
Chuck-will's-widow ( <i>Caprimulgus carolinensis</i> )	-	-	-	-	-	-	+	+	+	+	
Carolina Wren ( <i>Thryothorus ludovicianus</i> )	-	-	-	-	-	-	14	-	6	7	
Black-and-white Warbler ( <i>Mniotilta varia</i> )	-	-	-	-	-	-	14	6	14	29	
Hairy Woodpecker ( <i>Dendrocopus villosus</i> )	-	-	-	-	-	-	-	4	-	-	
Great Crested Flycatcher ( <i>Myiarchus crinitus</i> )	-	-	-	-	-	-	-	4	-	7	
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	-	-	-	-	-	-	-	4	-	50	
White-breasted Nuthatch ( <i>Sitta carolinensis</i> )	-	-	-	-	-	-	-	4	9	4	

TABLE 1 (CONTINUED)

Species	Territorial males per 100 acres in study plots										
	HF	BF	BS	CP	WF	CG	FE	XF	IF	MF	
Red-tailed Hawk ( <i>Buteo jamaicensis</i> )	-	-	-	-	-	-	-	-	+	-	
Downy Woodpecker ( <i>Dendrocoptes pubescens</i> )	-	-	-	-	-	-	-	-	6	-	
Pileated Woodpecker ( <i>Dryocopus pileatus</i> )	-	-	-	-	-	-	-	-	-	+	
Acadian Flycatcher ( <i>Empidonax virescens</i> )	-	-	-	-	-	-	-	-	-	14	
Catbird ( <i>Dumetella carolinensis</i> )	-	-	-	-	-	-	-	-	-	7	
Wood Thrush ( <i>Hylocichla mustelina</i> )	-	-	-	-	-	-	-	-	-	7	
White-eyed Vireo ( <i>Vireo griseus</i> )	-	-	-	-	-	-	-	-	-	14	
Worm-eating Warbler ( <i>Helminthos vermivorus</i> )	-	-	-	-	-	-	-	-	-	14	
Parula Warbler ( <i>Parula americana</i> )	-	-	-	-	-	-	-	-	-	14	
Cerulean Warbler ( <i>Dendroica cerulea</i> )	-	-	-	-	-	-	-	-	-	14	
Ovenbird ( <i>Seiurus aurocapillus</i> )	-	-	-	-	-	-	-	-	-	14	
Kentucky Warbler ( <i>Oporornis formosus</i> )	-	-	-	-	-	-	-	-	-	14	
American Redstart ( <i>Setophaga ruticilla</i> )	-	-	-	-	-	-	-	-	-	14	
Scarlet Tanager ( <i>Piranga olivacea</i> )	-	-	-	-	-	-	-	-	-	7	
TOTAL NUMBER OF SPECIES	7	22	12	17	18	13	18	18	22	27	
TOTAL MALES PER 100 ACRES	117	147	115	192	281	300	336	115	196	370	
DIVERSITY INDEX	1.19	2.73	1.87	2.22	2.25	1.79	2.53	2.41	2.32	2.86	
PLOT SIZE (ACRES)	16	16	16	16	4	4	7	24	16	7	

Grasshopper Sparrows and Eastern Meadowlarks, characteristic of grasslands, were found in both the mowed field and the burned field plots (Table 1). As the fields were invaded by shrubs and smaller trees in the broom sedge field plot and to a greater extent in the two plots representative of the early tree stage, the Field Sparrow became the typical bird (Table 1). Although not found at such high densities as the Field Sparrow, the Bell's Vireo also seemed to be typical of this later field habitat. The two plots in the early tree stage of succession had a large complement of species with the Field Sparrow, Yellow-breasted Chat, and American Goldfinch being the most abundant. The Blue-winged Warbler, Blue Grosbeak, Painted Bunting, and Mockingbird were less numerous but typical. The woody field plot that was late in the early tree stage also had the Rufous-sided Towhee and Brown Thrasher associated with the densest invading vegetation. Cardinals were common in this latter habitat too, but also occurred in large numbers in the forest plots and thus could not be considered exclusive to the field-to-forest transition (Table 1). The cedar glade had several of the bird species associated with the early tree stage of succession, but also had a good complement of forest birds (Table 1).

The forested plots supported two general groups of birds: species that occurred in all forested habitats and those that were confined to the mesic forest. The former were the Tufted Titmouse, Blue-gray Gnatcatcher, Carolina Chickadee, Eastern Wood Pewee, Red-bellied Woodpecker; the latter included Acadian Flycatcher, Wood Thrush, Worm-eating Warbler, Parula Warbler, Cerulean Warbler, Ovenbird, Kentucky Warbler, and American Redstart (Table 1). The restricted species generally were less plentiful in the mesic forest than the wide-ranging species also present there.

Certain species, including the Cardinal, Bobwhite, Mourning Dove, and Blue Jay, were not limited to any single major successional stage.

#### SUCCESSION AND BIRD POPULATION DENSITY

A general increase in avian species and density through progressive successional communities toward climax vegetation was found by Saunders (1936) in New York, Kendeigh (1948) in Michigan, Karr (1968) in Illinois, Odum (1950) in North Carolina, Johnston and Odum (1956) in Georgia, and Haapanen (1965) in Finland. This represents similar findings in diverse regions including both deciduous forest and coniferous forest climax. Even so, Kendeigh (1946) found in the deciduous-coniferous forest ecotone that the highest bird densities occurred in the shrubby seral stage rather than in climax forest and Karr (1968) noted a decline in bird species and density in the last forest stage.



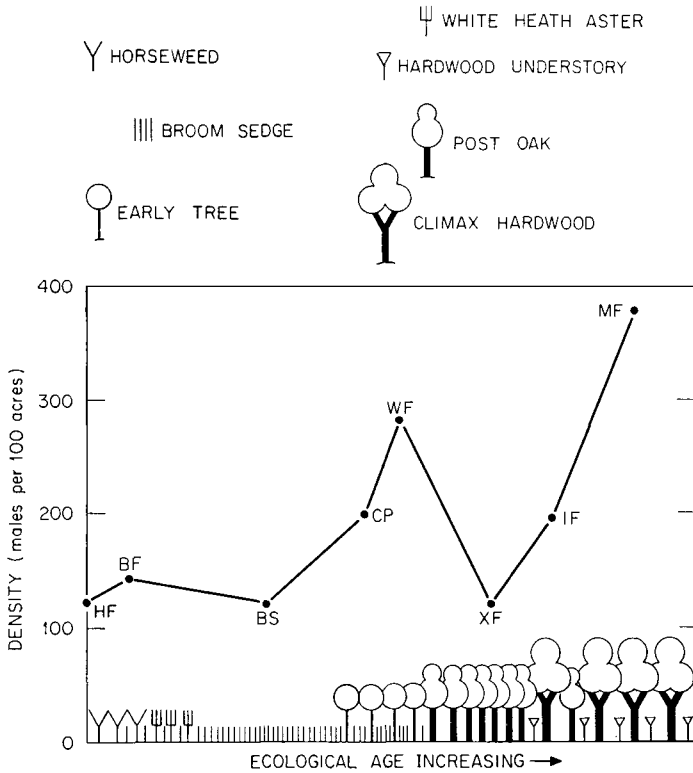


Figure 2. Density of birds expressed in territorial males per 100 acres in various stages of plant succession. Dots represent study plots. HF = mowed hay field plot; BF = burned field plot; BS = broom sedge field plot; CP = clonal persimmon field plot; WF = woody field plot; XF = xeric forest plot; IF = intermediate forest plot; MF = mesic forest plot.

In the region of the present study, bird population densities tended to increase with ecological age of the site (Figure 2). The study plots in the broom sedge field and the xeric post oak forest had relatively low avian densities if a uniform increase is expected, but both of these habitats are uniform in structure, and attract fewer birds than related habitats. The scarcity of birds in these two habitats is noted commonly throughout the region. Perhaps due in part to the small plot sizes, the woody field had high populations (Figure 2) and so did the forest edge and cedar glade (Table 1). These last two small study plots were omitted from Figure 2 because they were not in the direct line of ecological succession (Figure 1).

TABLE 2  
SIMILARITY INDICES FOR BIRD AND PLANT SPECIES<sup>1</sup>

Study plot	HF	BF	BS	CP	WF	CG	FE	XF	IF	MF
HF	—	.068	.235	.065	.099	.073	.118	.039	.000	.000
BF	.594	—	.415	.327	.475	.390	.666	.396	.288	.187
BS	.343	.642	—	.398	.313	.332	.391	.085	.076	.079
CP	.034	.680	.814	—	.417	.304	.688	.348	.291	.135
WF	.067	.679	.723	.836	—	.506	.815	.447	.356	.278
CG	.041	.402	.605	.665	.530	—	.587	.446	.468	.162
FE	.104	.529	.708	.753	.632	.567	—	.620	.479	.368
XF	.018	.230	.260	.205	.237	.486	.560	—	.744	.485
IF	.010	.198	.219	.179	.265	.625	.515	.823	—	.407
MF	.000	.071	.077	.113	.119	.402	.339	.532	.611	—

<sup>1</sup>Indices for birds in italics. HF indicates mowed hay field plot; BF, burned field plot; BS, broom sedge field plot; CP, clonal persimmon field plot; WF, woody field plot; CG, cedar glade plot; FE, forest edge plot; XF, xeric forest plot; IF, intermediate forest plot; MF, mesic forest plot.

#### CORRELATION OF AVIFAUNAL AND VEGETATIONAL SIMILARITIES

Several investigators (Bray and Curtis, 1957; Beals, 1960; Knight and Loucks, 1969; and others) evaluated the similarities between two communities using the similarity coefficient  $C = 2w/(a + b)$  where " $w$  is the sum of the lesser values of the species scores in the two stands compared,  $a$  and  $b$  are the sum of the scores in each stand" (Austin and Orloci, 1966). The coefficient loses precision when comparing greatly dissimilar communities such as those at different ends of a sere (Swan, 1970).

Using the data for species frequencies and densities in all three vegetational strata, the similarity coefficients were largest when comparing plant communities of similar ecological age. The same was true (Table 2) of similarity coefficients calculated from species-density values for avian populations in the same communities (Table 1). The breeding bird population and plant composition of the forest edge community was most similar to the early tree stage of succession.

Utilizing these coefficients (Table 2) it was possible to determine the correlation between the similarity of plants and the corresponding similarity of birds among the various plots. This is comparable to asking the question, "If there is a given degree of similarity in the vegetation of two areas to what extent is this associated with community similarity based on the composition and densities of the corresponding bird populations?" Because the data were indices the assumption of normality was

unrealistic and the nonparametric Spearman rank correlation coefficient ( $\rho$ ) was used to determine the association between the two variables (Siegel, 1956).  $\rho$  equalled 0.701 ( $n = 45$ ,  $P = 0.001$ ), which is a high correlation coefficient and is highly significant (at the 99.9 percent confidence level). As in the case of parametric statistics, a positive correlation of this type indicates a definite association between the two variables. Thus, the answer to the question asked is that when the vegetation between plots is very similar, the corresponding bird societies are also quite similar, and vice versa. Bond (1957) in a study of breeding birds on forest plots in southern Wisconsin used parametric statistics to determine a correlation between indices of bird and vegetative similarity and obtained similar results, finding a significant correlation in which  $r$  equalled 0.804.

#### BIRD POPULATION DIVERSITY AND SUCCESSION

The Shannon Function,  $H = -\sum p_i \log p_i$  where  $p_i$  is the sampling probability, has been used as a measure of diversity in connection with ecological studies (MacArthur and MacArthur, 1961; Patten, 1962; Lloyd and Ghelandi, 1964; Monk, 1967). Just which log base to use for these calculations has been debated, but diversity indices based on different logs can be converted to one another by multiplication by constants, so one suffers no loss of information regardless of the log base. We used natural logs because diversity indices are asymptotically normal in distribution when natural logs are used (Hutchinson, 1969). Comparable analyses have not been made using other log bases. The low density species represented by plus values in Table 1 were omitted from calculations. The indices were not affected because low density values contribute little to diversity indices (Buzas and Gibson, 1969).

In Arkansas we found a gradual trend toward increase in avian diversity with increased ecological age of the community (Table 1, Figure 3). The same pattern occurred in Georgia (Figure 3), which also is in the southeastern deciduous forest (Johnston and Odum, 1956). The precision of these comparisons is decreased by sample-size problems (Wilhm, 1970), the details of which are unknown in birds. In Georgia all the plots were nearly equal in size, meaning the Georgia indices could be compared with each other. If the small plots were below the critical asymptote size, difficulties could arise in comparing the Georgia plots and the small ones in Arkansas. As the small plots have lowered indices (Wilhm, 1970), this would make some actual diversities in Arkansas even higher than calculated (Figure 3). The inordinately high diversity in the burned field plot in Arkansas could have been due to the recent

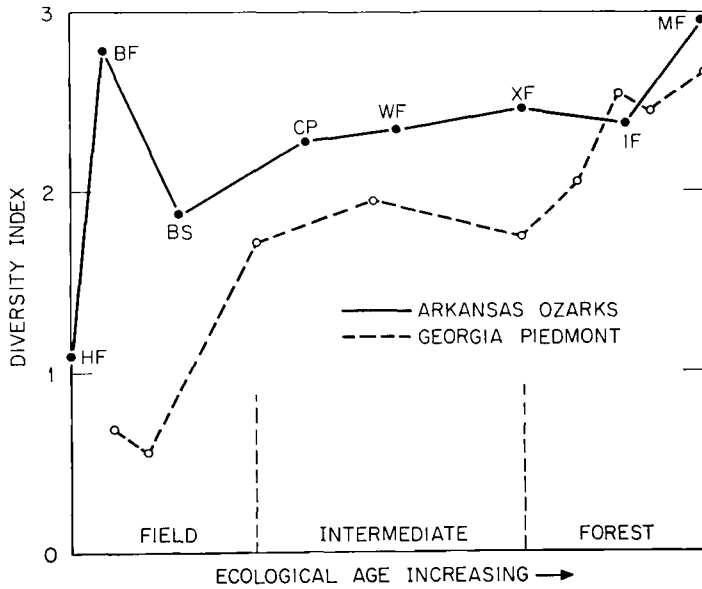


Figure 3. Comparison of avian diversity in the various stages of plant succession in the Arkansas Ozarks and in the Georgia Piedmont. Open circles = Georgia plots; closed circles = Arkansas plots. Linear sequence of the Arkansas plots as in Figure 2. Linear sequence of Georgia plots as given in original paper (Johnston and Odum, 1956).

burning of this former early tree and broom sedge field. Emlen (1970) found that despite destruction of habitat birds will occupy a burned area for months. Table 1 shows that the burned field still contained many birds of later successional stages plus many invading open-field birds. The overall similarity in the progressive seral increase in diversity in both Arkansas and Georgia suggests that this is a widespread phenomenon. This confirms the broader findings of Tramer (1969), who noted that the process is associated with the increase in foliage height during succession.

Adams (1908) discussed avian succession and listed characteristic species of successional stages from aquatic communities through bogs to climax forest on Isle Royale, Michigan. He did not measure density of the various species, but noted greater variety in bird life in the intermediate stages than in either the early or climax stages. Margalef (1958) stated that succession should feature rapidly increasing diversity with a decline at the end. Although Margalef generalized about community succession, Karr (1968) actually found this pattern in avian succession

in central Illinois. This finding was the same as in the study by Johnston and Odum (1956) and in the present study, except neither of these exhibited the decline at the climax end of the sere. This could have been due to sampling error, or possibly true climax was not found in Arkansas or Georgia.

Avian diversity was higher in Arkansas than in Georgia, especially during the early field stages. This high species diversity in fields in northwestern Arkansas could have been due to the original abundance of prairie and forest interdigitations in the region (Lesquereux, 1860; Steyermark, 1940; Allred and Mitchell, 1954). This would enable the shrub and forest birds in Arkansas to become better adapted to grasslands than farther east in Georgia where natural fields were uncommon. It would represent ecological geographic variation, which is well-documented in birds (Miller, 1942; Mayr, 1947; Svardson, 1949; Hilden, 1965). As behavioral phenomena commonly are implicated in habitat preference (Hilden, 1965; Johnston, 1947), this would require geographic changes in avian behavior of the kind Hilden (1965) and Kendeigh (1945) described with respect to habitat selection. Apparently forest edge birds in the Arkansas Ozarks utilize some of the grassier successional stages, having been conditioned by long contact with prairies there. In Georgia, Grasshopper Sparrows and Eastern Meadowlarks were the only bird species found in fields (Johnston and Odum, 1956). In Arkansas these two species plus a large number of species (Table 1) from adjoining habitats occupied fields. Most of the abundant species found in the fields in Arkansas were present in later successional stages in Georgia.

#### SUMMARY

Breeding bird populations in ten stages of the upland subsere succession were studied at Pea Ridge National Military Park, Benton County, Arkansas, during spring 1967. Bird populations were determined by the Williams' territory mapping technique.

The habitats of the birds could be classified as field, intermediate, and forest. Certain species of forest birds were confined to the climax forest habitat.

The density of bird populations increased with ecological age of the plots. The similarities in flora and avifauna on different plots were correlated significantly. The species diversity of birds increased with ecological age of the plots.

Comparison with a similar study in Georgia indicated that species diversity in field habitats was relatively high in Arkansas. The presence of prairie adjoining forest in northwestern Arkansas may have allowed

forest edge birds to become conditioned to grasslands so that they are now able to utilize grassier successional stages.

## LITERATURE CITED

- ADAMS, C. C. 1908. The ecological succession of birds. *Auk*, 25: 109-153.
- ALLRED, B. W., AND H. C. MITCHELL. 1954. Major plant types of Arkansas, Louisiana, Oklahoma, and Texas. Fort Worth, Texas, U. S. Dept. Agr., Soil Conserv. Serv.
- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, fifth ed. Baltimore, Maryland, Amer. Ornithol. Union.
- AUSTIN, M. P., AND L. ORLOCI. 1966. Geometric models in ecology. 2. An evaluation of some ordination techniques. *J. Ecol.*, 54: 217-227.
- BAUR, H. L. 1943. The statistical analysis of chaparral and other plant communities by means of transect samples. *Ecology*, 24: 45-60.
- BEALS, E. 1960. Forest bird communities in the Apostle Islands. *Wilson Bull.*, 72: 156-181.
- BEILMAN, A. P., AND L. G. BRENNER. 1951. The recent intrusion of forest in the Ozarks. *Ann. Missouri Bot. Garden*, 38: 261-282.
- BOND, R. R. 1957. Ecological distribution of breeding birds in the upland forest of southern Wisconsin. *Ecol. Monogr.*, 27: 351-384.
- BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.*, 27: 325-349.
- BULLINGTON, E. H. 1961. The vegetation of Devil's Den State Park, Washington County, Arkansas. Unpublished M.S. thesis, Fayetteville, Univ. Arkansas.
- BUZAS, M. A., AND T. G. GIBSON. 1969. Species diversity: Benthonic Foraminifera in western North Atlantic. *Science*, 163: 72-75.
- COZZENS, A. B. 1940. Physical profiles of the Ozark Province. *Amer. Midl. Naturalist*, 24: 477-489.
- DALE, E. E., JR., AND T. FULLERTON. 1964. Final report on ecological investigations on existing vegetation in the pre-impoundment and watershed area of Beaver Lake. Contract 14-16-008-626, Bur. Sport Fisheries and Wildlife and Univ. Arkansas.
- EMLEN, J. T. 1970. Habitat selection by birds following a forest fire. *Ecology*, 51: 343-345.
- FERNALD, M. L. 1950. *Gray's manual of botany*, eighth ed. New York, American Book Co.
- HAAPANEN, A. 1965. Bird fauna of the Finnish forests in relation to forest succession. *Ann. Zool. Fennica*, 2: 153-196.
- HILDEN, O. 1965. Habitat selection in birds. *Ann. Zool. Fennica*, 2: 53-57.
- HITE, J. M. R. 1960. The vegetation of Lowe Hollow, Washington County, Arkansas. Unpublished M.S. thesis, Fayetteville, Univ. Arkansas.
- HUTCHESON, K. 1969. The moments and distribution of the Shannon information measure and its application to ecology. Unpublished Ph.D. dissertation, Blacksburg, Virginia Polytechnic Inst.
- JOHNSTON, D. W., AND E. P. ODUM. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. *Ecology*, 37: 50-62.
- JOHNSTON, V. R. 1947. Breeding birds of the forest edge in east-central Illinois. *Condor*, 49: 45-53.
- KARR, J. R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. *Condor*, 70: 348-357.

- KENDEIGH, S. C. 1945. Community selection by birds on the Helderberg Plateau of New York. *Auk*, 62: 418-436.
- KENDEIGH, S. C. 1946. Breeding birds of the beech-maple-hemlock community. *Ecology*, 27: 226-245.
- KENDEIGH, S. C. 1948. Bird populations and biotic communities in northern lower Michigan. *Ecology*, 29: 101-114.
- KNIGHT, D. H., AND O. L. LOUCKS. 1969. A quantitative analysis of Wisconsin forest vegetation on the basis of plant function and gross morphology. *Ecology*, 50: 219-234.
- KUCERA, C. L., AND S. C. MARTIN. 1957. Vegetation and soil relationships in the Glade Region of the southwestern Missouri Ozarks. *Ecology*, 38: 285-291.
- LESQUEREUX, M. L. 1860. Botanical and palaeontological report on the geological state survey of Arkansas. Pp. 294-399 in "Second report of a geological reconnaissance of the middle and southern counties of Arkansas" (D. D. Owen, Ed.). Philadelphia, C. Sherman and Son.
- LLOYD, M., AND R. J. GHELANDI. 1964. A table for calculating the equitability component of species diversity. *J. Anim. Ecol.*, 33: 217-225.
- MACARTHUR, R. H., AND J. W. MACARTHUR. 1961. On bird species diversity. *Ecology*, 42: 594-598.
- MARGALEF, D. R. 1958. Information theory in ecology. *Gen. Syst.*, 3: 36-71.
- MAYR, E. 1947. Ecological factors in speciation. *Evolution*, 1: 263-288.
- MILLER, A. H. 1942. Habitat selection among higher vertebrates and its relation to intraspecific variation. *Amer. Naturalist*, 76: 25-35.
- MONK, C. D. 1967. Tree species diversity in the eastern deciduous forest with particular reference to north central Florida. *Amer. Naturalist*, 101: 173-188.
- ODUM, E. P. 1950. Bird populations of the Highlands (North Carolina) Plateau region in relation to plant succession and avian invasion. *Ecology*, 31: 587-605.
- PATTEN, B. C. 1962. Species diversity in net phytoplankton of Raritan Bay. *J. Marine Res.*, 20: 57-75.
- QUARTERMAN, E. 1950. Major plant communities of Tennessee cedar glades. *Ecology*, 31: 234-254.
- RICE, E. L., AND W. T. PENFOUND. 1955. An evaluation of the variable-radius and paired tree methods in the blackjack-post oak forest. *Ecology*, 36: 315-320.
- SAUNDERS, A. A. 1936. Ecology of the birds of Quaker Run Valley, Allegheny State Park, New York. State Mus., Albany, New York, Handbook No. 16.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. New York, McGraw-Hill.
- STEYERMARK, J. A. 1940. Studies of the vegetation of Missouri. 1. Natural plant associations and succession in the Ozarks of Missouri. *Bot. Ser., Field Mus. Nat. Hist.*, 9: 349-475.
- SVARDSON, G. 1949. Competition and habitat selection in birds. *Oikos*, 1: 157-172.
- SWAN, J. M. A. 1970. An examination of some ordination problems by use of simulated vegetational data. *Ecology*, 51: 89-102.
- TRAMER, E. J. 1969. Bird species diversity: components of Shannon's formula. *Ecology*, 50: 927-929.
- TURNER, L. M. 1935. Notes on forest types of northwestern Arkansas. *Amer. Midl. Naturalist*, 16: 417-421.
- WILHM, J. L. 1970. Effects of sample size on Shannon's formula. *Southwestern Naturalist*, 14: 441-445.

- WILLIAMS, A. B. 1936. The composition and dynamics of a beech-maple climax community. *Ecol. Monogr.*, 6: 318-408.
- WILLIAMS, A. B. 1947. Breeding bird populations of climax beech-maple forest with some hemlock. *Audubon Field Notes*, 1: 205-210.
- WINKWORTH, R. E., AND D. W. GOODALL. 1962. A crosswire sighting tube for point quadrat analysis. *Ecology*, 43: 342-343.

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