

HABITAT AND AVIAN DIVERSITY ON STRIP-MINED LAND IN EAST-CENTRAL ILLINOIS

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In the past many studies of bird populations have concentrated on describing species composition and population sizes of avian aggregations. These studies usually included brief descriptions of the vegetation type in the areas under study. Recently, new analyses of population studies have been made in an effort to increase our understanding of the relationships between avian diversity and habitat structure and how these are related to latitudinal gradients in diversity (MacArthur and MacArthur 1961; MacArthur *et al.* 1966).

Another area of intensive research has been in ecological energetics. Most studies concerned with this have been conducted using caged birds. There have been few attempts to integrate these two approaches. Margalef (1961) has stated that there are two approaches to the study of ecosystems, including one concerned with biomass, production, and energy, and another concerned with community structure. I contend that an integration of the two approaches can be both rewarding and informative. Although structural analyses are emphasized in this report, some relationships between the two approaches are explored.

METHODS

During the spring and summer of 1966 a study of bird populations on four areas of different vegetation types was conducted on strip-mined lands in and near Kickapoo State Park, six miles west of Danville, Illinois. Concurrent studies of vegetation were made so changes in bird populations could be correlated with redevelopment of vegetation following strip-mining. A fifth study area, William Trelease Woods, a 55-acre upland near-climax forest about five miles northeast of Urbana, Illinois, is also discussed. The bird censuses in these woods were conducted by Barnett and Balda (1966).

Bird activity was plotted on 8½ × 11 inch dittoed maps by the spot-map method of Williams (1936). Enemar (1959) presents an extensive discussion of the assets and limitations of this technique. Surveys were con-

ducted between 15 March and 11 July, totaling approximately 8, 40, 42, and 39 hours on the bare ground, early shrub, late shrub, and bottomland forest areas, respectively. A total of 45 hours was spent censusing the 55-acre Trelease Woods area.

Vegetation was sampled along two transects established at random on each study area between 30 August and 3 September 1966. The presence or absence of vegetation was recorded at points one meter apart for each of the three strata: herbaceous (< 2 feet), shrub (2–20 feet), and tree (> 20 feet). If vegetation was present, the species was noted for the shrub and tree layers and the genus or species was noted in the herbaceous layer. A technique similar to this has recently been presented by Emlen (1967).

HISTORY AND DESCRIPTION OF STUDY AREAS

Old mining records of the Illinois Geological Survey, unpublished sources, and growth rings on borings from trees indicate that the bare ground study area was mined about 1963. The oldest tree present on this area has two growth rings and is about 15 feet tall. This area shows the pronounced ridge-and-valley topography characteristic of strip-mined land. Due to the high rate of erosion on exposed steep banks, no vegetation was present except in some of the more deeply cut erosion channels. In basins, where no water was present, cocklebur, aster, and barnyard grass had colonized and a few cottonwoods were present (table 1). In shallow depression areas that contained more permanent water, broad-leaved cattail was developing rapidly. On the northeast corner of this study area bulldozers had been used to level the ridges, and introduced sweet clover had developed a fairly dense stand.

Some parts of the early shrub area, mined in 1954, show extreme relief, up to 60 feet, while other parts are fairly level. The oldest tree on this area has 10 growth rings. There are a few small ponds present but no drainage streams. The only parts of the early shrub

TABLE 1. Habitat and vegetation analysis in percentage of points in each category and species.

	Bare ground	Early shrub	Late shrub	Bottomland forest
<i>Herbaceous layer</i>				
Bare ground	76.0	15.4	10.7	1.7
Water	15.8	3.4	6.5	-
Dead vegetation	-	9.3	4.4	15.9
Vegetation	8.1	71.9	78.3	82.5
Cocklebur (<i>Xanthium</i> sp.)	23.3			
Barnyard grass (<i>Echinochloa crusgalli</i>)	11.6			
Sweet clover (<i>Melilotus alba</i>)	20.9	36.8	11.5	
Aster (<i>Aster ericoides</i>)	9.3	8.0		
Broad leaved cattail (<i>Typha latifolia</i>)	9.3			
Goldenrod (<i>Solidago</i> sp.)		11.0		
Poison Ivy (<i>Rhus radicans</i>)			30.1	
Bluegrass (<i>Poa pratensis</i>)			9.9	
Nettle (<i>Laportea canadensis</i>)				61.5
Jewelweed (<i>Impatiens</i> spp.)				6.6
Other	25.6(7) ^a	44.2(21)	48.5(32)	31.9(16)
<i>Shrub layer</i>				
Without shrub	100.0	64.2	42.6	48.8
With shrub	-	35.8	57.4	51.2
Black Locust (<i>Robinia Pseudo-Acacia</i>)		27.6		
Cottonwood (<i>Populus deltoides</i>)		21.5		
Smooth Sumac (<i>Rhus glabra</i>)		17.1	9.5	
Sycamore (<i>Platanus occidentalis</i>)		12.2		
Willow (<i>Salix nigra</i>)		8.8	23.0	
Slippery Elm (<i>Ulmus fulva</i>)			30.3	51.4
Honey Locust (<i>Gleditsia triacanthos</i>)			13.5	
Silver Maple (<i>Acer saccharinum</i>)				29.6
Other		12.8(6) ^a	23.7(12)	19.0(10)
<i>Tree layer</i>				
Without tree	100.0	94.1	91.2	8.3
With tree	-	5.9	8.8	91.7
Cottonwood (<i>Populus deltoides</i>)		90.0	30.0	52.5
Black Locust (<i>Robinia Pseudo-Acacia</i>)		10.0		
Honey Locust (<i>Gleditsia triacanthos</i>)			34.0	
Willow (<i>Salix nigra</i>)			18.0	
Slippery Elm (<i>Ulmus fulva</i>)			16.0	
Silver Maple (<i>Acer saccharinum</i>)				29.2
Sycamore (<i>Platanus occidentalis</i>)				14.7
Other			2.0(1) ^a	3.6(2)
Number of points	530	506	568	422

^a Number of "other" species in parentheses.

area that lacked a vegetative cover were steep slopes. Three permanent and two semi-permanent ponds were present. This area had been seeded with sweet clover and planted with various species of trees, primarily black locust (*Robinia*), juniper (*Juniperus*), and a few baldcypress (*Taxodium distichum*).

The late shrub study area was mined between 1920 and 1925. The oldest tree present on the area has 37 growth rings. This area has much less relief (10-12 feet) than the bare ground or early shrub areas. The vegetation is also more abundant and diverse than in the earlier successional stages. Although undersampled in the transect data as a result of being overtopped by other herbaceous species, bluegrass was common in the herbaceous layer. The high percentage of willow

in the data for the shrub layer reflects the presence of a large, open, moist area in the northeast corner of the study area.

The bottomland forest area was mined between 1900 and 1910. The oldest tree now on the area shows 49 growth rings. This area has almost lost the ridge-and-valley topography characteristic of strip-mined lands; the relief between ridges and valleys is less than 5 to 6 feet. This has probably occurred as a result of (1) early mining equipment not leaving as great a relief as that of modern equipment, (2) deposition of silt during annual floods, and (3) erosion of ridges. The reduction in number of species in the herbaceous layer and the presence of the early successional trees, cottonwood and sycamore, as the dominant tree species is characteristic.

In summary, the redevelopment of vegeta-

tion on strip-mined land, excluding the introduction of species and other reclamation activities of man, begins with the colonization of herbaceous species and the pioneer trees with windblown seeds. Noteworthy was the lack of grasses in the early stages, followed by their invasion only after establishment of broad-leaved herbaceous species and pioneer trees and shrubs.

Trelease Woods is an upland maple-oak forest with large numbers of fallen logs and dead trees as a result of the death of elms from Dutch elm disease (Bogges 1964).

Although criticism might be made on the basis of apparent heterogeneity of the study areas, I do not believe the problem is worse than in most forest-edge habitats. Ideally, as many factors as possible should be controlled; but, on the other hand, it is necessary to determine what occurs in more complex habitats. It is felt that strip-mining activities on the study areas have resulted in a more equal distribution and interdigitation of habitat types (grassland, shrub, tree, and water) than could be expected in natural situations; that is, structural heterogeneity is reasonably uniform throughout each study area. The only major exception to this is a large open area in one corner of the late shrub study area. This area was not included in the diversity analyses.

BREEDING BIRD POPULATIONS

On the bare ground study area (table 2), Redwinged Blackbirds were associated with the several small beds of cattail. The Song Sparrow and Spotted Sandpiper used areas that had well-developed stands of sweet clover. Horned Larks and Killdeer occurred on barren areas.

Although 70 Common Grackle nests were located in junipers that had been planted in the southwest corner of the early shrub study area, it is estimated that nine-tenths of the feeding and other activities took place outside the area, so the equivalent of only seven pairs were counted as resident population. Catbird nests were generally located in either rose or blackberry thickets. Yellow Warblers always occurred in dense stands of moderately tall black locust. Traill's Flycatcher territories were generally associated with low areas that contained willow thickets and were near water. Early Mourning Dove nests were located on the ground while later nests were in shrubs and trees. Redwinged Blackbirds, of course, were near the small ponds.

Both Red-headed and Red-bellied Wood-

peckers were observed in the late shrub study area in the early spring, but only the Red-headed Woodpecker remained through 21 June and fledged young. The Bluebird nested in a poison-ivy-covered elm stump. Wood Thrush territories were in areas where the shrub layer was the densest. Warbling Vireos, Baltimore Orioles, and Great Crested Flycatchers used primarily trees greater than 30 to 40 feet in height. Starling and most woodpecker nests were located in tall dead trees. Wood Pewees used the intermediate heights of tall trees as perches. The Spotted Sandpiper pair nested in an open, stream-bed area in the northeast corner of the area.

Of the six species of wood warblers in the bottomland forest, Cerulean and Parula Warblers used the tree canopy, American Redstarts used areas just below the tree canopy, Kentucky Warblers and Yellowthroats were found near the ground, and Prothonotary Warblers were at intermediate heights (5 to 25 feet) near open water areas. Warbling Vireos, Red-eyed Vireos, and Blue-gray Gnatcatchers foraged and sang in the tree canopy. Great Crested Flycatchers foraged in the areas just below the upper canopy. Wood Pewees and Acadian Flycatchers foraged at lower heights. Acadian Flycatchers were found in areas with fairly dense shrub or sapling understory, and Wood Pewees used areas with little or no understory. The Ruby-throated Hummingbird territory was adjacent to the river.

To obtain an area in Trelease Woods comparable in size to the others censused and to minimize the effect of the surrounding open farmlands, only the birds nesting in a 16-acre rectangular plot in the center of the woods were counted. No species was found on this area that was not represented on the strip-mined areas.

It is apparent from table 2 that there is a general increase in the species composition and size of the bird population from the bare ground to the bottomland forest areas and a decrease in Trelease Woods. Bird populations on the strip-land areas are higher than populations on similar habitats in eastern North America (Odum 1950; Case 1964). The ridge-and-valley topography might allow increased abundance by decreasing the frequency of interactions between adjacent pairs as a result of intervening ridges. In addition, actual increase in land surface per unit area might permit some decrease in horizontal territory size in some species through increased productivity per unit area. The effect of water on the avian aggregations is discussed later.

TABLE 2. Breeding bird populations of the strip-mined areas and Trelease Woods.

Species	Bare ground	Early shrub	Late shrub	Bottomland forest	Trelease woods
Killdeer (<i>Charadrius vociferus</i>)	6				
Horned Lark (<i>Eremophila alpestris</i>)	6				
Spotted Sandpiper (<i>Actitis macularia</i>)	6		2		
Redwinged Blackbird (<i>Agelaius phoeniceus</i>)	8	19	19		
Song Sparrow (<i>Melospiza melodia</i>)	2	26	14		
Common Grackle (<i>Quiscalus quiscula</i>)		33			
Trail's Flycatcher (<i>Empidonax traillii</i>)		19			
Yellow-breasted Chat (<i>Icteria virens</i>)		9			
Bell's Vireo (<i>Vireo bellii</i>)		9			
Yellow Warbler (<i>Dendroica petechia</i>)		36	9		
Field Sparrow (<i>Spizella pusilla</i>)		28	21		
Bobwhite (<i>Colinus virginianus</i>)		12	5		
Catbird (<i>Dumetella carolinensis</i>)		36	16		
Brown Thrasher (<i>Toxostoma rufum</i>)		12	14		
American Goldfinch (<i>Spinus tristis</i>)		19	9	6	
Mourning Dove (<i>Zenaidura macroura</i>)		19	16		9
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)		9	14		6
Cardinal (<i>Richmondia cardinalis</i>)		5	16		9
Indigo Bunting (<i>Passerina cyanea</i>)		31	14	13	16
Cowbird (<i>Molothrus ater</i>)		14	9	13	6
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)		5	2	6	3
Eastern Bluebird (<i>Sialia sialis</i>)			5		
Eastern Kingbird (<i>Tyrannus tyrannus</i>)			2		
Warbling Vireo (<i>Vireo gilvus</i>)			12	26	
Carolina Chickadee (<i>Parus carolinensis</i>)			9	29	
Tufted Titmouse (<i>Parus bicolor</i>)			9	26	
Baltimore Oriole (<i>Icterus galbula</i>)			7	6	
Yellowthroat (<i>Geothlypis trichas</i>)			5	6	
House Wren (<i>Troglodytes aedon</i>)			30		37
Starling (<i>Sturnus vulgaris</i>)			37	32	74
Yellow-shafted Flicker (<i>Colaptes auratus</i>)			16	23	22
Blue Jay (<i>Cyanocitta cristata</i>)			16	13	28
American Robin (<i>Turdus migratorius</i>)			14	6	9
Downy Woodpecker (<i>Dendrocopos pubescens</i>)			9	23	9
Wood Thrush (<i>Hylocichla mustelina</i>)			7	10	12
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)			7	13	6
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)			5	16	46
Eastern Wood Pewee (<i>Contopus virens</i>)			5	19	16
American Redstart (<i>Setophaga ruticilla</i>)				32	
Kentucky Warbler (<i>Oporornis formosus</i>)				26	
Wood Duck (<i>Aix sponsa</i>)				13	
Blue-gray Gnatcatcher (<i>Poliptila caerulea</i>)				13	
Prothonotary Warbler (<i>Protonotaria citrea</i>)				13	
Parula Warbler (<i>Parula americana</i>)				13	
Cerulean Warbler (<i>Dendroica cerulea</i>)				13	
White-breasted Nuthatch (<i>Sitta carolinensis</i>)				6	
Carolina Wren (<i>Thryothorus ludovicianus</i>)				3	
Acadian Flycatcher (<i>Empidonax virescens</i>)				23	
Hairy Woodpecker (<i>Dendrocopos villosus</i>)				13	
Red-bellied Woodpecker (<i>Centurus carolinus</i>)				19	6
Red-eyed Vireo (<i>Vireo olivaceus</i>)				13	12
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)				3	3
Size of study area (acres)	25.0	21.5	21.5	15.3	16.0
Number of species	5	18	32	32	19
Number of pairs/100 acres	28	341	375	489	329
Standing crop biomass (g/100 acres) ^a	3,220	31,282	36,738	48,412	39,280
Consuming biomass (g/100 acres) ^a	715	6,929	8,187	9,613	8,312
Existence energy (kcal/day per 100 acres) ^a	1,446	14,017	16,562	19,448	16,816

^a Bird weights for these calculations were obtained from the following papers: Stewart (1937), Baldwin and Kendeigh (1938), Poole (1938), Roberts (1955), and Stegeman (1955).

TABLE 3. Comparison of diversity indexes and variations in diversity indexes with changes in size of populations or study area.

Study area and subset number	Number of species	Number of individuals	Area (acres)	Diversity index ^a		
				λ	H	H'
BG1	3	2.5	6.8	0.3000	0.1597	0.9503
BG2	4	5.5	13.9	0.2000	1.0133	1.3421
BG3	5	7.0	25.0	0.1648	1.1099	1.5367
BG4	5	28.0	100.0 ^b	0.1958	1.3162	1.5367
ES1	17	24.5	6.2	0.0536	2.2374	2.7178
ES2	18	49.0	12.9	0.0614	2.4610	2.7486
ES3	18	74.0	21.5	0.0656	2.5300	2.7378
ES4	18	341.0	100.0 ^b	0.0692	2.6313	2.7420
LS1	24	22.0	6.8	0.0254	2.3610	3.1065
LS2	29	60.0	14.3	0.0434	2.8242	3.1824
LS3	32	81.0	21.5	0.0385	2.9551	3.2721
LS4	32	375.0	100.0 ^b	0.0419	3.1068	3.2715
BF1	24	19.5	4.3	0.0256	2.2053	3.0814
BF2	30	48.5	9.1	0.0320	2.7996	3.2660
BF3	32	76.0	15.3	0.0338	2.9896	3.3215
BF4	32	489.0	100.0 ^b	0.0385	3.1790	3.3149
Bottomland						
Forest, Fawver (1947)	24	144.0	100.0 ^b	0.0567	2.6586	2.9166
Trelease Woods	19	329.0	100.0 ^b	0.1037	2.4410	2.5542

^a Computation based on natural logarithm.

^b Populations computed for a 100-acre area to permit rapid comparison of areas (for example, BG-25 acres; to convert to 100 acres-population $\times 4$).

DISCUSSION

BIRD-SPECIES DIVERSITY

In recent years the use of information theory (Shannon and Weaver 1949) as a measure of biotic diversity has been common (Margalef 1958; MacArthur 1965; and many others). In addition, several other models for determining diversity have been discussed (Simpson 1949; Williams 1964). At this time the most promising seem to be λ (Simpson 1949), and two measures (H and H') based on information theory (MacArthur 1965; Pielou 1966a, b, c; Lloyd, Zar, and Karr 1968). All three measures of diversity gave the same relative ranks for the study areas. Since H' varies least with changes in sample size, only H' will be used in further discussions. The index H' has, in the past, been calculated from the equation $H' = -\sum_{i=1}^s p_i \log p_i$ where p_i is the proportion of the i th species in the population composed of s species. This index can be calculated more easily with the equation $H' = I/N$ ($N \log_e N - \sum_{i=1}^s n_i \log_e n_i$) where N = total population, n_i = number of pairs of species i , and s = number of species in the aggregation (Lloyd, Zar, and Karr 1968).

Species diversity increases from bare ground through the shrub stages to bottomland forest and then decreases to the climax Trelease Woods (table 3). The greater diversity of

shrub over climax habitats is a result of the interdigitation of grassland, shrubs, and trees. The lower diversity of the bottomland forest at White Heath (Fawver 1947) when compared with the strip-mined bottomland forest is correlated with the more advanced forest development, including the presence of bitter-nut hickory (*Carya cordiformes*) and bur oak (*Quercus macrocarpa*). Bird-species diversities (H') reported in this study are higher than those elsewhere in the eastern part of the United States reported by MacArthur and MacArthur (1961). They also exceed those from Puerto Rico and all but the mature and young tropical forests in Panamá (MacArthur *et al.* 1966).

In recent years much effort has been expended to determine the factors causing increased diversity in tropical areas (Klopfer and MacArthur 1961; Pianka 1966; and many others). Analysis of my data with respect to the censuses of MacArthur *et al.* (1966) of Neotropical populations lends support to the hypothesis of increased micro-spatial heterogeneity.

In MacArthur's study (MacArthur *et al.* 1966), as the size of the area was decreased there was a significant decrease in the value of H' . The mature tropical rain forests on Barro Colorado Island (MacArthur *et al.* 1966) had 66.5 pairs of 40 species and a diversity of 3.39. However, when a subarea of this was

censused, only 21.8 pairs of 17 species were present, with a diversity of 2.66 (a decrease of 21 per cent). The same reduction in diversity was found with decrease in area size in a young tropical forest on the mainland of Panamá. Reduction of populations by reducing area size in my late shrub and bottomland forest stages to areas containing about 20 to 25 pairs reduces diversities by only seven and five per cent, respectively (table 3). On the strip-mined areas, study-area size was reduced by using concentrically smaller areas around the approximate geographic center of each study area. In MacArthur's forest areas these changes reduce the number of species considered by 57 and 61 per cent; similar changes on my late shrub and bottomland forest areas decrease the number of species only 25 per cent. MacArthur does not give the size of his study areas. Thus it is impossible to make comparisons on an area basis.

Richards (1964) has shown that tropical forests are very heterogeneous in tree-species composition. The great diversity of dominant tree species in the mixed-mesophytic forests of eastern North America (Braun 1950) might be a step toward the apparent patchiness of a tropical forest. In fact, calculation of H' for a moderately disturbed mixed mesophytic forest in Pike County, Kentucky (Mengel 1965) yields a high diversity index, 2.977, for a temperate area without water. Thus, great patchiness of the vegetation may be responsible for the great decrease in avian diversity when study area size is reduced in tropical forests. If it is not patchiness in vegetation, as such, it may be a result of patchiness of bird distributions in tropical areas. This problem should be investigated further.

BIOMASS AND ENERGY RELATIONS

Most previous studies of bird populations have discussed only the number of pairs per unit area or, at most, the total weight (standing crop biomass) on the area. However, recent laboratory studies on the energetics of birds have made it possible to estimate the existence energy requirements of birds as functions of bird weight and environmental temperature. It is well known that the amount of energy required by large birds does not increase in direct proportion to the increase in their weight. Salt (1957) and Crowell (1962) adjusted the weight of their birds to the 0.7 power to obtain comparable consuming biomasses for different populations. Recent studies (Kendeigh, unpublished data) have shown this value to be somewhat high. For this study, consuming biomass is calculated

by adjusting the weight of each bird to the 0.633 power, *i.e.*, $W^{0.633}$ (see below). An even more important measure of the importance of a population in a community is its energy requirements. Existence energy is the energy required by a caged bird to maintain a constant weight and is determined with calorimetric methods by subtracting energy excreted in feces from energy consumed. Existence energy increases with a drop in temperature. In this study the mean daily temperature for the main breeding season, 15 April to 15 July, was 19°C. The following regression equation for existence energy at 19°C was calculated by interpolation between equations for 0° and 30°C given by Kendeigh (unpublished data):

$$\log M = 0.306 + 0.633 \log W$$

where M = kcal consumed per bird per day (existence energy) and W = weight in grams (individual).

These calculations do not include the energy metabolized by young birds or extra energy needed by the adults for such activities as nesting and flight, or does it include that portion of the food consumed that is not metabolized but excreted. With these additions the total energy consumed may be about two times the existence energy values shown in table 2 (see Uramoto 1961; El-Wailly 1966).

Standing crop biomass, consuming biomass, and existence energy increase from the bare ground to the bottomland forest and decrease in the climax forest (Trelease Woods).

AVIAN DIVERSITY VS. HABITAT DIVERSITY

Bird-species diversity (BSD) was analyzed with respect to several measures of habitat diversity—foliage-height diversity (FHD), category diversity (CD), plant-species diversity (PSD), physiognomic and physiographic diversity (PPD), and per cent vegetation cover (PCC). To calculate FHD the total number of points in each of the three strata with vegetation present is determined, and the sum of the three is used to calculate the proportion (p) contributed by each stratum. The equation for H' is used to calculate FHD from these data. CD, PSD, and PPD were computed with the same equation, except an H' value was calculated for each stratum and the sum of the three H' s was used as the diversity index. With CD, each plant species, water, bare ground, and dead vegetation (or "no vegetation present" for the shrub and tree strata) were used as categories, and p was calculated for each category. PSD was calculated similarly but without including non-

TABLE 4. Avian diversity and habitat diversity (see text).

Study area	Bird-species diversity, H'	Standing-crop-biomass diversity	Consuming-biomass diversity	Existence-energy diversity	Plant-species diversity	Category diversity	Physiognomic-physiographic diversity	Foliage-height diversity	Log per cent vegetation cover
Bare ground	1.5367	1.4061	1.4644	1.4644	2.1797	0.8809	0.7502	0.0000	0.9085
Early shrub	2.7420	2.4079	2.6206	2.6206	4.5963	4.1260	2.5047	0.8071	2.0554
Late shrub	3.1824 ^a	2.8549 ^a	3.0163 ^a	3.0163 ^a	6.2201	5.1361	3.2510	0.9199 ^a	2.2159 ^a
Bottomland forest	3.3149	2.5815	3.0588	3.0588	4.1374	4.5802	2.1907	1.0703	2.3716

^a Excluding data collected on the northeast corner of the study area.

vegetation categories. PPD was calculated similarly, but the following physiognomic classifications were used for each stratum:

Herbaceous layer: forbs, grasses and grass-like plants, vines and briars, woody plants, water, bare ground, dead vegetation.

Shrub layer: vines, dead trees, shrubby plants, sapling trees, gymnosperms, no vegetation present.

Tree layer: trees, vines, no vegetation present.

Per cent vegetation cover was determined by summing over the three strata the percentages of points with vegetation present in each stratum.

CD, PSD, and PPD show no significant relationship with BSD (table 4). These data show in all cases that habitat diversity is greater in the third rather than the fourth successional "stage" while BSD increased throughout the four areas. These data support the notion that "forest-edge" habitats may have increased diversity as a result of interdigitation of two habitats (forest and grassland).

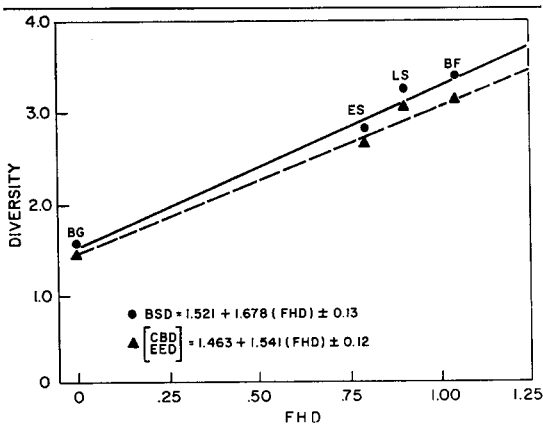


FIGURE 1. Correlation of bird-species diversity (BSD), consuming-biomass diversity (CBD), and existence-energy diversity (EED) with foliage-height diversity (FHD).

On the other hand, when FHD is plotted against BSD, a linear relationship is found. If the large stream-bed area in the northeast corner of the late shrub area is excluded in both vegetation data and bird data, a significant fit to a straight line is obtained at the 5 per cent level (fig. 1). MacArthur and MacArthur (1961) and MacArthur *et al.* (1966) found a similar relationship between BSD and FHD (measured in a different way), but their Y-intercept is about 0.7 units below mine.

Calculations of H' indexes using standing crop biomass (SCD), consuming biomass (CBD), and existence energy requirements (EED) were also made (table 4). All were calculated using the biomass or energy requirements for the individual species. As expected, the values for CBD and EED are identical.

SCD increases through the first three stages and then decreases in the bottomland forest while CBD increases throughout the four areas. Linear regression analysis showed that SCD was not linearly related at the 5 per cent level with either FHD or PCC. On the other hand, CBD was significantly linearly correlated with FHD and PCC at the 5 per cent level (figs. 1 and 3) as was EED. This supports the notion that energy, biomass, and productivity are related to ecosystem structure. Furthermore, it is not the total biomass (standing crop) that is important in the ecosystem; the energetics requirements of the aggregation are the most important.

Also of interest, I believe, is that the slopes of the lines for BSD and CBD on FHD are statistically indistinguishable. Analysis of the relationship of these two factors to the ecosystem should be investigated more fully. Apparently BSD and CBD (or EED) are equally good measures in avian communities. Perhaps avian aggregations generally have the same distribution of sizes and the importance of size differences is thereby negated.

Conversion of BSD and FHD to number of equally common species and layers makes it possible to determine the number of equally

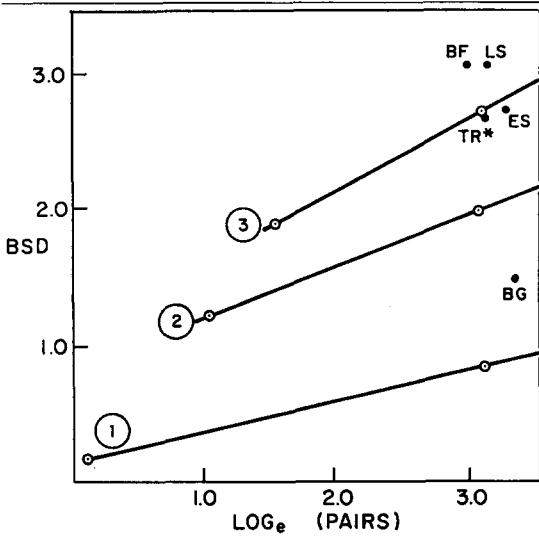


FIGURE 2. Correlation of bird-species diversity (BSD) with \log_e (number of pairs) for point (left-hand \odot) and 20–25 pair (right-hand \odot) censuses in habitats with one (1), two (2), and three (3) vegetation strata (dimensions). (From MacArthur 1964). TR* = Trelease Woods, diversity for entire 16-acre area used (53 pairs).

common species (or BSD) for areas with one, two, or three equally important layers of vegetation (MacArthur 1964). The conversion is made with the equation E (equally common species) = $e^{H'}$. This measure tells us how many species would be present with the present diversity index if all species were equally abundant.

Figure 2, taken from MacArthur, makes it possible to determine the number of equally important dimensions in the environment. This is done by plotting BSD vs. \log_e of the number of pairs and studying the position of the resultant points relative to the three lines. It is important to note that we are not determining the number of dimensions in the environment but the number of dimensions of equal importance to the predesignated vegetation layers (MacArthur 1964). MacArthur (1964) discusses more fully the theoretical implications of this procedure and the assumptions necessary for this analysis.

When diversities from this study are plotted on MacArthur's graph (fig. 2), it is found that BSD averages 0.5 to 0.9 dimensions higher than MacArthur's data for habitats with similar vegetation. This is also the case when BSD values for two other bottomland forests are plotted (Fawver 1947; Case 1964). MacArthur (1964) found that a similar situation existed with the diversity of a diked-wet meadow censused by Robbins and

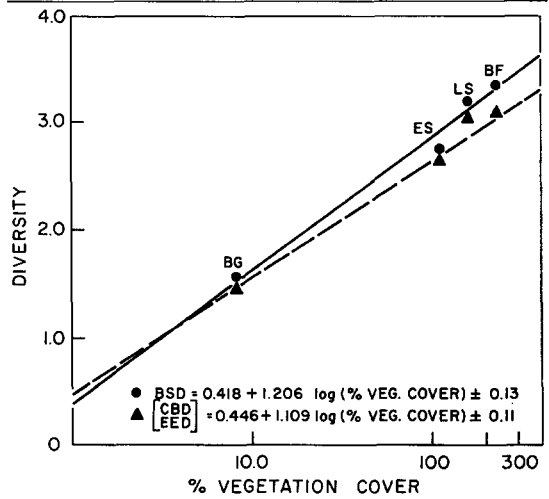


FIGURE 3. Correlation of bird-species diversity (BSD), consuming-biomass diversity (CBD), and existence-energy diversity (EED) with per cent vegetation cover.

Boyer (1953). Conversely, plotting diversity of Trelease Woods, an area without water, indicates that only three equally important dimensions are present (fig. 2).

I suspect that the increased diversity and apparent increase in number of environmental dimensions of the strip-mined areas is due to the presence of permanent and semipermanent ponds. The addition of ponds interspersed throughout the study areas may add another component to the environment and thereby increase its patchiness.

A straight-line relationship also exists between BSD and the logarithm of per cent vegetation cover (fig. 3). A regression analysis of the data indicates that they are linearly correlated at the 5 per cent level of significance. This indicates that addition of equal increments of vegetation to the habitat gives smaller and smaller increases to BSD. Again, use of this measure of habitat diversity and study of its relation to BSD deserves further investigation.

SUCCESSION AND AVIAN POPULATIONS

Margalef (1958, 1963) suggested the following changes as characteristics of biotic succession: (1) increased stability, (2) increased structural complexity, (3) increase in average size of organisms, (4) increased biomass accumulation, and (5) decrease in flow of energy per unit biomass. He also suggested (6) that diversity initially increases rapidly, reaches a maximum, and then decreases in later stages. In general these suggestions are supported by this study.

Two measures of structural complexity, FHD and PCC, increase throughout the successional stages. With the exception of the bare-ground study area, there is an increase in average individual size through this successional series as indicated by the following figures (average bird weight in grams): BG = 57.5, ES = 45.9, LS = 49.0, BF = 49.5, TR = 59.7. There is also an increase in biomass accumulation throughout the sere. Diversity of both avian species and plant species increases in early stages, reaches a maximum, and then decreases. The suggestion of increased stability cannot easily be tested with these data, but there does not seem to be a trend in flow of energy per unit biomass when measured with the ratio of standing crop biomass to existence energy.

SUMMARY

Bird populations were studied on four successional stages following strip-mining from bare-ground to bottomland forest. Quantitative data are presented to show the present development of vegetation on each study area. The rate of revegetation was affected by the manner in which the area was mined and the amount of reclamation work done after mining, in addition to time since mining.

Bird-species diversity increased throughout the strip-mined sere and was linearly correlated with foliage-height diversity and the logarithm of per cent vegetation cover. Analysis of relationships between energy requirements expressed as consuming biomass or as existence energy requirements indicated a linear relationship between these factors and habitat structure as measured by either foliage-height diversity or the logarithm of per cent vegetation cover. These data indicate that avian-species diversity and energy requirements of the avian population are related to habitat structure.

Greater avian diversity on strip-mined land when compared with other areas with similar vegetation is probably due to the presence of water, and to a lesser extent to the ridge-and-valley topography. Data presented here indicate that micro-spatial heterogeneity may account for a portion of the increased avian diversity in tropical areas.

Estimated daily existence requirements for bird populations varied from 1446 to 19,488 kcal per day per 100 acres, and it is suggested that inclusion of energy requirements for all activities might double these figures.

Future studies of this type should be attempted to determine the effects of such structural factors as relief and water on avian diversity. In addition, relationships between avian diversity and per cent vegetation cover should be investigated. Most importantly, attempts to integrate structural and energetics approaches to ecosystem study should be emphasized.

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