Breeding Bird Censuses in Old-Growth Deciduous Forests

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Abstract

Thirty-nine bird censuses from climax or near-climax forest stands in the central part of the Eastern North American deciduous forests are compared, including six by the authors in Indiana. Thirty-eight forest-interior bird species are tabulated by area and forest type. Total densities are greater in lowland forest than in other forest types. Species number and bird species diversity are significantly highest in western lowland and lowest in oak-chestnut.

Introduction

Censuses of North American breeding birds made on measured plots and published chiefly in *American Birds* (including its predecessors, *Bird Lore*, *Audubon Magazine*, and *Audubon Field Notes*) have been analyzed by several ecologists. Kendeigh (19) compared the results on the eight best deciduous forest plots studied up to that time. Udvardy (49) analyzed 300 censuses, including 130 in temperate deciduous forests. Tramer (48), Ricklefs (41), and others have compared many of these published censuses by means of various mathematical measures of species diversity.

Our results of five censuses during 1971 (1, 2, 51, 52, 53), made in some of the finest old-growth forests of the Midwest, invited comparison. In this analysis, we have been very selective, reducing the 300 available from deciduous forest to 39 on the following basis:

1) Only censuses from the Oak-pine, Oak-chestnut, Mixed mesophytic, Western mesophytic, and Beech-maple forest regions of Braun (7) of the eastern deciduous forest were used. The Northern hardwoods forest type of the high Appalachians was also excluded.

2) Only censuses from old-growth forests were used. Most were described as "Virgin," "Climax," or "Mature." All included many trees over 2 feet dbh; most included many trees over 3 feet dbh. In the 21 census areas in which tree height was stated, the trees ranged up to more than 80 feet in every case and to 150 feet in 3 cases; the average height of canopy trees was over 90 feet in nearly all areas.

3) Censuses accompanied by a good description of the plants, or at least of the trees, were preferred. This criterion could not be held to in every case, and some of the tree "analyses" were absurdly oversimplified. In fact, only 12 censuses included reasonably thorough quantitative tree studies; 9 more gave the relative density of tree species; 18 gave the commonest kinds of trees, or the species of trees in order of density, or relative densities with unfortunate lumpings such as "maples."

4) Censuses of areas including two or more major types of forest, for instance oak-hickory and beech-maple, were omitted, as were those

including considerable amounts of "edge." Every forest is more or less patchy, of course, and so this criterion is difficult to assess from written reports. Notice that three of the eight areas utilized by Kendeigh (19) were omitted here, because of more exacting standards of edge and type.

5) Censuses of areas including more than 5% of coniferous trees were usually omitted. Exceptions were census #18, which included 10% hemlock, and #5, which included 20% hemlock.

Methods

The method of making a breeding bird census is well described by Hall (12). Bird censuses published in early years—before 1944—were not very uniform, but those utilized here were of high quality except, in some cases, for the plant descriptions. Names of trees follow Little (26), where their scientific names are listed. Nomenclature of birds follows the A. O. U. checklist (4).

Results

Table 1 summarizes the data from the 39 census areas, classified into 5 forest types on the basis of their trees, and some geographic subdivisions. Each entry gives the density in males per 100 acres, followed by the percentage of censuses recording that species. The first 38 species are those which are most typical of middle-latitude deciduous forest interiors. The lowest 5 species are simply examples from the 65 other species which were counted as breeding on one or more censuses. Of these latter, some are rather generally distributed, but rare, and the sharp-shinned hawk is an example. Some are localized; the black-throated blue warbler is an example. Some are clearly forest-edge species whose presence betrays the "edgy" impurity of some of the forest areas; the catbird is an example. A few of these other species, such as the flicker and the parula warbler, are difficult to classify.

The main list of 38 forest-interior species deserves further comment. It was derived from a similar list of 34 species by Kendeigh (19). Two species were removed from the Kendeigh list due to their rarity. (Woodcock and saw-whet owl; one occurrence each in 39 censuses.) The cowbird was added on the basis of clearer data since 1944. The chuckwill's widow was added as a result of the more southern censuses. The hummingbird, cardinal, indigo bunting, and towhee were transferred from edge to interior species in disagreement with Kendeigh. Each of these species is rather consistent in these old-growth censuses; in fact, the cardinal occurred in 32 of the 39 censuses, making it the fifth most consistent of all species. We found all four of these species far in the interior of Kramer Woods, for instance, in what is probably the largest, least disturbed natural forest stand in the Midwest (*cf.* 24). Of course, Kendeigh is correct in that they require a single windfallen tree or a patch of brush. But every natural forest has such "wounds" if it is natural.

TABLE 1. *Bird censuses in old growth forests. Densities of forest interior species. Each entry gives the density in males (or females) per 100 acres, followed by the percentage of censuses recording the species. The asterisk before two species indicates that densities are computed for females; densities are computed for males for all other species. A "+" indicates that the species is present, but in a density less than 1 per 100 acres.*

Species	Mesophytic			Oak-	Lowland		Beech-	Oak-
	Ind.-Ohio	West Va.	Md.-Conn.	Chestnut	West	East	Maple	Hickory
Ruffed Grouse	—	+(44)	1(33)	3(100)	—	—	+(33)	—
Yellow-billed Cuckoo	3(100)	1(22)	+(67)	—	12(100)	4(100)	2(67)	3(43)
Great Horned Owl	—	—	+(33)	—	—	+(33)	+(44)	—
Barred Owl	2(67)	+(33)	—	—	1(100)	1(33)	1(56)	+(14)
Chuck-will's-widow	—	—	—	—	+(100)	—	—	+(14)
Whip-poor-will	1(33)	+(11)	—	—	—	+(33)	1(22)	3(29)
*Ruby-throated Hummingbird	5(100)	2(33)	—	1(33)	5(100)	5(100)	3(44)	2(57)
Pileated Woodpecker	1(67)	1(89)	2(33)	2(33)	1(100)	1(33)	1(78)	+(29)
Red-bellied Woodpecker	9(100)	1(44)	6(67)	—	16(100)	9(67)	5(78)	5(43)
Hairy Woodpecker	2(67)	2(44)	1(100)	2(67)	3(100)	2(67)	3(89)	3(86)
Downy Woodpecker	9(100)	3(44)	8(100)	5(100)	19(100)	13(100)	9(100)	7(86)
Crested Flycatcher	7(100)	3(44)	4(100)	2(33)	9(100)	10(100)	7(100)	6(71)
Acadian Flycatcher	36(100)	35(100)	13(67)	20(33)	20(100)	34(67)	23(100)	11(71)
Wood Pewee	18(100)	8(78)	6(100)	2(67)	17(100)	26(67)	16(100)	12(100)
Blue Jay	3(67)	+(22)	9(100)	3(33)	6(100)	10(67)	3(100)	3(43)
Chickadee species	15(100)	4(56)	13(100)	8(67)	16(100)	19(100)	8(78)	6(71)
Tufted Titmouse	29(100)	10(78)	9(100)	10(67)	26(100)	20(100)	14(89)	12(86)
White-breasted Nuthatch	7(67)	3(44)	4(67)	4(100)	8(100)	6(67)	8(100)	6(86)
Carolina Wren	6(67)	1(22)	2(33)	2(33)	16(100)	36(100)	3(33)	4(71)
Wood Thrush	24(100)	13(100)	15(100)	23(100)	20(100)	30(67)	19(100)	30(100)
Veery	—	—	2(33)	5(67)	—	—	+(11)	—
Blue-gray Gnatcatcher	27(100)	9(78)	+(33)	—	26(100)	11(67)	8(67)	6(57)
Yellow-throated Vireo	14(100)	3(33)	1(33)	3(33)	20(100)	3(33)	4(67)	7(71)
Red-eyed Vireo	36(100)	33(100)	19(100)	52(100)	29(100)	71(100)	30(100)	48(100)
Black & White Warbler	—	13(78)	2(33)	12(67)	1(50)	3(33)	+(11)	8(86)
Worm-eating Warbler	4(33)	17(78)	6(67)	12(33)	—	—	—	+(14)
Cerulean Warbler	50(100)	19(56)	3(33)	—	37(100)	+(33)	14(89)	24(43)
Ovenbird	4(33)	8(56)	26(100)	21(100)	—	13(33)	17(67)	23(71)
Louisiana Waterthrush	10(67)	5(56)	1(33)	2(33)	—	2(33)	3(78)	1(14)
Kentucky Warbler	22(100)	9(89)	6(67)	1(33)	19(100)	12(67)	6(56)	7(57)
Hooded Warbler	2(33)	6(56)	8(67)	19(33)	7(100)	12(100)	7(67)	14(86)
American Redstart	1(33)	12(56)	1(67)	—	+(50)	52(100)	11(56)	14(43)
*Brown-headed Cowbird	13(100)	1(44)	4(67)	—	10(100)	9(100)	4(100)	3(43)
Scarlet Tanager	7(67)	11(89)	4(67)	14(67)	2(50)	10(67)	7(89)	14(71)
Summer Tanager	10(100)	1(11)	—	—	7(100)	—	2(22)	4(43)
Cardinal	32(100)	6(67)	19(100)	11(33)	26(100)	37(100)	14(89)	14(86)
Indigo Bunting	5(67)	2(67)	+(33)	—	14(100)	1(33)	5(56)	+(29)
Rufous-sided Towhee	8(100)	6(67)	19(100)	2(33)	9(100)	17(67)	10(89)	5(71)
Sharp-shinned Hawk	—	—	—	—	—	—	—	+(14)
Yellow-shafted Flicker	2(100)	2(33)	5(100)	3(33)	6(100)	8(100)	2(78)	1(29)
Catbird	—	—	4(100)	—	—	10(67)	1(44)	+(29)
Parula Warbler	—	12(56)	2(33)	—	—	32(67)	—	1(29)
Black-throated Blue Warbler	—	—	—	36(67)	—	—	—	—
# of censuses	3	9	3	3	2	3	9	7
Ave. total density (males/100 acres)	469	307	257	331	483	565	288	316

TABLE 2. *Census areas utilized in this paper.*

State	Stand	Reference	Years censused	Area (acres)	3 most dominant trees in order
Mesophytic, Western					
1. Indiana	Donaldson Woods	(2)	1	23	White Oak, Beech, Sugar Maple
2. Ohio	Cincinnati	(15)	3	35	Tuliptree, Beech, Sycamore
3. Indiana	S. Officer's Woods	(51)	1	25	Beech, Tuliptree, Black Gum
Mesophytic, Mixed					
4. West Va.	Pendleton Co.	(11)	1	15	Tuliptree, Basswood, Sugar Maple
5. West Va.	Cat Rock Run	(10)	1	15	Basswood, Hemlock, Tuliptree
6. West Va.	New Martinsville	(17)	1	15	White Ash, Sugar Maple, White Oak
7. West Va.	Cedar Creek	(18)	1	15	Tuliptree, Sugar Maple, Northern Red Oak
8. West Va.	Cedar Cr. Campground	(20)	1	15	Tuliptree, Northern Red Oak, Sugar Maple
9. West Va.	Huntington	(21)	1	15	Beech, Northern Red Oak, Tuliptree
10. West Va.	Summersville	(37)	1	15	Tuliptree, Beech, Red Maple
11. West Va.	Bethany	(8)	1	30	Sugar Maple, White Oak, Beech
12. West Va.	Smoke Hole	(45)	1	15	Sugar Maple, Basswood, Hickory
Mesophytic, Eastern					
13. Maryland	Columbia	(42)	1	30	Tuliptree, Red Maple, White Oak
14. Conn.	Greenwich	(38)	2	20	Sugar Maple, Beech, Northern Red Oak
15. Delaware	Wilmington	(54)	2	20	Tuliptree, Black Oak, Northern Red Oak
Oak-Chestnut					
16. North Car.	Highlands	(34)	1	25	Chestnut, Chestnut Oak, White Oak (7)
17. Georgia	Clayton	(29)	2	15	Chestnut Oak, Red Maple, Northern Red Oak
18. Tenn.	Great Smokies	(3)	1	23	Sugar Maple, Tuliptree, Silverbell
Lowland, Western					
19. Indiana	Hemmer Woods	(53)	1	18	Sweet Gum, Tuliptree, Red Maple
20. Indiana	Kramer Woods	(52)	1	23	Shumard Oak, Shellbark Hickory, Pin Oak
Lowland, Eastern					
21. Maryland	Cabin John I.	(5)	10	19	Sycamore, Am. Elm, Black Walnut
22. N. Jersey	Monmouth Co.	(6)	6	16	Red Maple, Sweet Gum, Beech
23. Virginia	Richmond	(44)	1	16	Sycamore, Sweet Gum, Bitternut
Beech-Maple					
24. Ohio	Cleveland	(55)	18	65	Beech, Sugar Maple, Red Maple (56)
25. Ohio	Wellington	(9)	4	14	Beech, Sugar Maple, not given
26. Ohio	Youngstown	(28)	8	55	Beech, Sugar Maple, Red Maple
27. Ohio	S. Dysart Woods	(39)	1	23	Sugar Maple, Beech, White Oak (22)
28. Ohio	N. Dysart Woods	(40)	1	19	Beech, Sugar Maple, White Oak (22)
29. Indiana	Connersville	(50)	3	20	Sugar Maple, Beech, Pignut Hickory
30. Indiana	Versailles	(1)	1	15	Beech, Sugar Maple, Tuliptree
31. Ohio	Cleveland	(32)	3	30	Beech, Sugar Maple, Black Oak
32. Ontario	Aylmer	(46)	1	25	Beech, Red Maple, Northern Red Oak
Oak-Hickory					
33. Georgia	Athens	(33)	1	20	White Oak, Northern Red Oak, Post Oak
34. N. Carolina	Durham	(35)	1	28	Southern Red Oak, Post Oak, White Oak
35. Virginia	Pamplin	(27)	3	20	White Oak, Black Oak, Northern Red Oak
36. Maryland	Upper Marlboro	(47)	1	36	Tuliptree, White Oak, Pignut Hickory
37. West Va.	Batt Picnic	(13)	1	15	Chestnut Oak, Scarlet Oak, Northern Red Oak
38. West Va.	Little Jug	(14)	1	15	Northern Red Oak, White Oak, Chestnut Oak
39. West Va.	Brier Creek	(16)	1	15	Chestnut Oak, Black Oak, Scarlet Oak

The names which we have used for forest types and areas follow Braun (7). Braun's description of the eastern mesophytic type is diffuse (7, p. 244-256). Notice that the eastern mesophytic stands are in the Oak-chestnut region; the western lowland stands are in the Western mesophytic region; the eastern lowland stands are in the Oak-chestnut and Oak-pine regions; one of the beech-maple stands (#30) is in the Western mesophytic region and two (#'s 27 and 28) are in the Mixed mesophytic region; the oak-hickory stands are variously in the Oak-pine, Oak-chestnut, and Mixed mesophytic regions. Several of the titles under which the censuses were published are at variance with this terminology. Where tree data were adequate, we calculated the stand type by the criteria of Lindsey and Schmelz (23) and Schmelz and Lindsey (43). Fortunately, in most of the 18 censuses with inadequate tree data, placement was obvious. The census areas are all listed in Table 2. In calculating the data for Tables 1 and 3, all census areas were treated uniformly, regardless of how many annual censuses had been taken, by first averaging the data for all census years at that place.

The average number of species per census area per year was: Western mesophytic 32, mixed mesophytic 23; eastern mesophytic 29; oak-chestnut 18, western lowland 44, eastern lowland 25; beech-maple 30; oak-hickory 25. Bird species diversities ($\overline{H}_2$), calculated by the Shannon-Wiener formula ($\overline{H}_2 = -\Sigma Pi \log_2 Pi$ where Pi=density of males of species i/total density of males), are given in Table 3.

TABLE 3. *Bird species diversity in forest types of the Eastern Deciduous Forest. (The numbers of census areas by type appear in parenthesis.)*

Forest Type	Bird Species Diversity		
	Highest	Lowest	Mean
Western Lowland (2)	5.14	4.71	4.92
Western Mesophytic (3)	4.64	4.43	4.51
Beech-maple (9)	4.93	3.88	4.30
Eastern Mesophytic (3)	4.45	4.09	4.26
Eastern Lowland (3)	4.37	4.06	4.18
Oak Hickory (7)	4.60	3.46	3.95
Mixed Mesophytic (9)	4.25	3.39	3.87
Oak-chestnut (3)	4.00	3.12	3.55

Discussion

The species of birds present and their densities are not the same throughout the middle part of the eastern deciduous forest. However, the data in Table 1 are too coarse to show much detail. Some species are consistent in every kind of forest; for instance the red-eyed vireo is found in every census (the only species so reported) and in moderate to high densities throughout. Some species are inconstant for what appear to be geographical reasons; for instance the cerulean warbler is in high density in the west, moderate in West Virginia, low in the east, and absent in the Southern Appalachians. Density of other species appears clearly to depend on forest type; for instance the Carolina wren

is in low density in every kind of forest but lowland, where it is in moderate numbers from Indiana to New Jersey.

It is difficult to see a pattern in total densities. Mesophytic census areas totaled 160 to 601 males per 100 acres, with a mean of 304. Oak-chestnut censuses ranged from 160 to 500, with a mean of 327. Lowland censuses ranged from 376 to 633, with a mean of 533. Beech-maple censuses ranged from 140 to 471, with a mean of 292. Oak-hickory censuses ranged from 210 to 450, with a mean of 321. From these figures we may conclude only that bottomland forests support significantly higher breeding bird populations than other deciduous forests—a point made years ago by Udvardy (49). According to Oelke (36) and Linehan (25) total densities in similar habitat decrease as the size of the census area increases. In the present study, the data from beech-maple forests do show this tendency. The data from mesophytic forests (all three regions combined, or two of the three separately) show the opposite trend—the larger the census area the denser the bird population. (The largest area was only 35 acres, however.) Data from other forest types are equivocal. Another possibility is that the individuality of the census-taker determines the density, but the data do not support this. Censuses taken by E. O. Mellinger have densities from 226 to 500, for instance.

We had anticipated that bird species number and bird species diversity would be highest in the mixed mesophytic forest, corresponding to high number of tree species (7) and high tree species diversity (31), and the demonstration that this was the ancestral deciduous forest type. Our data do not support this assumption. Bird species diversity and number of species are highest in western lowland and lowest in oak-chestnut forest types. Probably the recent extirpation of the chestnut has reduced the diversity of birds of oak-chestnut forests. When classified by forest region rather than by forest type, no significant trends appear. Future comparisons with census data on old growth forests in eastern Kentucky, in the heart of the mixed mesophytic region, and with more outlying parts of the deciduous forest will be needed. No thorough breeding bird censuses in old growth forests in Kentucky have been made (*cf.* 30:25); those from outlying regions are few, except from mixed deciduous-coniferous forest. Perhaps the rate of range expansion and of species evolution in birds is so much faster than in trees that no distinct trends in geographical distribution of bird species diversity exist within climax eastern deciduous forest.

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