

STUDIES ON THE VERTICAL DISTRIBUTION OF
BREEDING BIRDS WITH REFERENCE TO THE VEGETATION

by

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Detroit, Michigan

1944

A report of an original field study conducted
as a requirement for Advanced Ornithology (Zoology 119)
and Advanced Zoological Studies (Zoology 231),
University of Michigan Biological Station

INTRODUCTION

The term distribution is commonly used to indicate the geographical range of any taxonomic group of organisms and implies parallelism to the surface of the earth. Vertical distribution refers to the location of organisms with respect to a plane perpendicular to the earth's surface. Conceivably this plane may pass through any medium such as air, water, or soil, and any object such as a tree, rock or mountain. Ecologists recognize a vertical habitat gradation in vegetation and have attempted to place animal life on a vertical as well as horizontal plane. The outstanding studies of this nature are by W. C. Allee,¹ and A. A. Allen.²

Dr. Allee has divided a tropical jungle of a rain-forest type into vegetational zones as follows.

- "1. The air above the forest.
2. Tree tops above the main forest roof, 125 or more feet high.
3. Upper forest canopy, 75-100 feet high.
4. Lower tree tops (second story or mid-forest) 40-60 feet up.
5. Small trees, 20-30 feet high.
6. Higher shrubs, 10 feet high.
7. Forest floor.
8. Subterranean."

It is seen that an area of this nature presents a type of vertical habitat gradation.

Dr. Allen takes a wooded area and gives a rather general classification of the bird habitats as follows.

"Birds of the Woodland and Woodland Borders

- a. ground-hesting birds
- b. birds of the undergrowth and low bushes
- c. birds of the higher bushes and lower branches
- d. birds of the higher branches and tree tops
- e. birds that nest in holes."

Dr. Allen's arrangement is certainly vertical but refers to birds of the woodland and woodland borders only.

J. C. Dunlavy⁵ made a study of the vertical distribution of birds in a chaparral type of vegetation in California but did not state the seasons in which he worked. He divided this region into zones based upon the vegetational levels and established definite criteria by which the birds could be assigned to these zones. The criteria used in his observations were the place chosen by the bird for refuge in time of danger, and the "altitude of the nesting site."⁵ He found a close degree of agreement between the zones chosen for nesting and those chosen for refuge by the species studied. This, he believes, gives a clue to the true habitat zone of the studied species, and gives a foundation for the vertical distribution of birds.

I have adopted certain of his methods and made application of them to the areas around the University of Michigan Biological Station.

ACKNOWLEDGMENTS

I wish to express my gratitude for the interest and assistance shown me by Dr. O. S. Pettengill, Jr. and for the help and numerous suggestions given to me by certain of the students working at the Biological Station.

METHODS

Three areas were chosen for observations. They were not set off by natural boundaries the first being one mile and a half long by one quarter of a mile wide, the second a mile long by 400 yards wide, and the third about a square mile.

The first area was along the shore of Douglas Lake (between South Fishtail Bay and North Fishtail Bay) and the adjoining woodland. The shore itself is composed of sand for the most part until Pine Point is reached. The vegetation bordering the shore is white pine (Pinus Strobus), aspens (Populus grandidentata and P. tremuloides) and a few Norway pines (Pinus resinosa). Pine Point, that is, the beach has several species of Equisetum, ^{Scirpus} ~~Sarbus~~, Potentilla, Lobelia, Vaccinium, and a number of grasses. The beach gives away to a growth of white and red pines. Farther up the beach is found a sandy outgrowth called East Point. The beach itself is covered with Scirpus and bordered by a growth of maple (Acer)

and willow (Salix) saplings; this gives way to the woods itself which is made up of red maple (Acer rubrum), white pine, red oak (Overcus boreales), and birch (Betula alba).

The woodland area from the Station to East Point is made up of two definite sub-climax areas leading to a climax area of Beech-Maple. The main association is of the Aspen-Birch nature which develops into a small but well defined association of conifers. The natural course of succession has, of course, been interrupted by logging and fire resulting in a mixture of the dominant life forms of these sub-climax areas.

The second area was a hill south of the Station. This area may be divided into the hillside and the top of the hill. The hillside consists of american beech, birch, red oak, moosewood (Acer pennsylvanicum), red maple, mountain maple (Acer specatum), basswood (Tilia americana), arrow-wood (Viburnum acerfolium), locust (Robinia Pseudo-Acacia), and sumac (Rhus typhina). The top of the hill is of a more open nature and consists of small aspens, birch, red oaks, red pines, and jack pine (Pinus banksiana).

The third area, located a mile and a half south by a half a mile east of the Station, was used mainly for cattle grazing. It is divided into four areas each with a different dominant lifeform: the first area was made up of Populus, Betula and Abies balsamea, the second area was rather low

and swampy and made up of Salix, the third area was of mixed conifers and the last an open wood lot of Populus, Acer and a few Betula.

In accordance with the methods of Dunlavy, the above areas were divided into certain vertical zones based upon the various vegetational levels. These zones are represented by the distance from the ground.

1. Ground zone - Ground surface to one foot above the ground.
2. Low-bush zone - One to five feet in altitude.
3. High-bush zone - Five to ten feet in altitude.
4. Low-tree zone - Ten to thirty-five feet in altitude.
5. High-tree zone - Above thirty-five feet.
6. Aerial zone - Above the substratum, in the air.

There are very few high trees in the Station area and no observations were made in this zone. The lower branches of trees and the higher branches of the high-bush zone, when found overlapping, were regarded as being in the zone according to their altitude. For instance, if some of the branches of an aspen tree were but eight feet from the ground they were regarded as being in the high-bush zone.

The criteria used to determine the zone in which a bird belonged were four.

Feeding:

The place where a bird feeds is dependent upon a number of food requirements: quantity and quality of the food,

type of food, and so on. During the study, data was kept on where certain species were found eating and conclusions were drawn to the effect that the activity was too variable to be a good index of zone.

Singing:

A bird sings to proclaim and protect its territory, with this in mind it seems logical that, during the breeding season, bird song, that is, the place or spot where a bird sings, should be a good indicator of vertical distribution. I also attempted to gain information about the singing perch in relation to the nest and place of refuge.

Refuge Zone:

The level in the vegetational formation which a bird selects as a place of refuge when frightened may be considered a good indicator of the vertical ecological niche of the bird.

Nesting Site:

The place in the vegetational formation where a bird places its nest may be a good indicator of the place at which the species attains greatest security from predators. Thus it may be considered a good index to the habitat of the species. I did not have enough data about the height of the nests of the birds I studied to make much of a correlation. Material drawn from literature was much too vague and variable to be of any use. It is suggested that a paper be published giving

the nest heights of birds in the different types of trees.

The procedure used was to walk as quietly as possible through the various areas taking notes as to where a bird was singing, feeding, and where it would fly when frightened. The ideal situation would be to observe the bird when chased by some enemy such as a hawk. The results are given in Table One.

It will be noticed that most of the birds listed were found in the low-tree zone. This is due to the fact that the majority of vegetation in this area is of a low-tree nature. In fact, out of the 15 most abundant birds, 345 observations were made and 260 of them were in the low-tree zone, 60 in high-bush zone and 28 in low-bush zone. There are some birds that fly from danger, that is, they do not dive into any certain vegetational level when frightened. Such birds as sea-gulls, swifts, swallows, hawks, eagles and certain shore birds must be assigned to the aerial zone, a zone with no known levels.

Altogether 31 species were under observation, some, of course, being observed more than others due to relative abundance. From the results summarized in Table I, I have drawn graphs, using graph paper of the semi-logarithmic type, for certain of the birds. Their purpose is to show comparatively the most and least used zones, and the relation of feeding, singing and the refuge zones to each other, see Graph I.

It is worthwhile to discuss here the results of four of the 31 birds that seem to represent the various types of actions peculiar to the other species.

Least Flycatcher:

The Least Flycatcher was observed 20 times and 16 of these times was found in the low-tree zone. Nesting information given to me by Peggy Muirhead, student assistant in Ornithology at the Station, showed that out of 19 nests, 18 were in the low-tree zone. Thus it may be said that the true vertical habitat of the Least Flycatcher in the Aspen-Birch sub-climax association is in the low-tree zone.

Robin:

The Robin was observed 35 times and was found in the low-tree zone 19 times, high-bush zone 10 times and low-bush zone six times. It is known to nest from the ground up showing no preference for a particular zone. It is also known to be very adaptable to all types of habitat and displays no preference to life-zone or biome. I suggest calling the bird a ranging vertical zone type. Examination of the graph shows that the bird is not so variable in its choice of singing perch.

Purple Finch:

The Purple Finch was observed 32 times and each time was found in the low-tree zone. This is another good example of a bird with a limited vertical distribution

although no accurate nesting material was available.

Song Sparrow:

The Song Sparrow proved to be very interesting. It was observed 28 times and was found in the low-tree zone nine times, high-bush zone nine times and low-bush zone 10 times. The data shows the bird has no zonal preference in this region. The graph shows that the bird sang in the low-tree high-bush zones more than in the low-bush zone.

DISCUSSION

In making a study of this nature one finds himself confronted with a number of problems that are definite obstacles to the continuation of the study. Some of these problems will be presented and discussed with the hope that some of the information presented will solve them; it must be realized that this is all supposition.

As Pitelka⁸ (p. 130) points out each bird is a unit expressing itself physiologically and functionally and dependent upon another unit just as complex and making the same type of expression: vegetation. As a result of one dependent upon the other there develops a maze of intricate interrelations and interdependence which can only be worked out in a manner suitable for the survival and reproduction of both, there must be harmony and this harmony, as expressed

in nature, is distribution of one in the other. The distribution seems to be the animal within the vegetation and is of two types: horizontal and vertical. The horizontal distribution of animals is a complex thing, great interdependence being developed between animal, vegetation, climate, soil and so on, whereas vertical distribution is again complex but the bird begins to express itself as more than something physiological or functional, it becomes a beast possessing certain psychical characteristics. Within the bird possessing both functional and psychical characteristics there tends to develop a conflict between the two with the result that the bird becomes not a mere machine stuck in its niche and not moving from it, but a beast possessing cunning and wit in its choice of place of activity; it realizes that it must not only get food, which is of a functional nature, but it must depend upon certain physical types of vegetation to provide it with safety, not only for itself, but for its young.

In its choice of habitat the bird depends not upon the environment but upon what it, as a unit, possesses. Then it attempts to correlate its own characteristics with those of the total environment which is, of course, impossible so it ends up in a habitat which offers it the greatest security or offers it a good quantity or quality of food. Which of these, food or security dominates, the choice of habitat?

This question, I believe, can be answered by saying neither or both, that is, during the nesting cycle and at night (roosting) the psychical element is strongest (which, I believe, is manifested almost completely in the desire for self-preservation) but when the nesting cycle passes, when the bird no longer has nestlings to feed, the psychical element begins to die out.

This presents an interesting situation: with the young out of the nest and able to fly a bit, will the parent take them to the food or leave them in a place of safety? I believe that, as the young get older, they will tend to follow the feeding parent so they will end up in the area with the greatest abundance of food. Now the parent bird realizes that the young are not protected as they used to be so she begins to make herself more conspicuous upon being approached by an intruder, this being offered in preference to a zone of refuge. When the nesting and upbringing is over the safety element is very much reduced, when in such a state a bird, when frightened, will attempt to get to what is the safest habitat but, of course, will not always make it so it hides in the nearest thing to its true habitat. Thus when a bird is found in its true vertical habitat it tends to function in a definite manner but when removed from this habitat its functions fluctuate according to the habitat in which it finds itself.

The physical characteristics (a tree, shrub, vine; the food contained within; the amount of cover offered, and so on) of the vegetation seem to be of prime importance in the study of how birds are distributed vertically. You must recognize the various types of vegetation based not upon some type area in your locality (an area that possesses all of the zones) but upon some assumption that is applicable to an area as the continent of North America. Of what use is a study of this nature if every woods and field in the country has to be studied individually? It's a foolish thing to think of, there must be some method of study that can be applied to the country as a whole.

The plant ecologist has divided the continent of North America into certain biomes which is a natural unity of landscape aspect such as tundra, grassland and so on. Each of these is divided into stages as climax, sub-climax, and seral; the climax stage being that stage which is capable of self-perpetuating itself and is characterized by a dominant life-form. The climax stage is developed by a series of successions from seral stages to sub-climax to climax. Here, I believe, lies the key to vertical distribution.

It is a well recognized fact that birds are found in certain forest types, that is, in the different climax formations. Group these together and you have a picture of the horizontal distribution of American bird life. I suggest

making a study of each type of climax area (including steps of succession). With reference to the physical characteristics of the vegetation rather than to the height of the vegetation. Then divide the physical characteristics of the vegetation into vertical zones and study these zones for bird-life contained within them; in this manner you would not have to study every woods in the country, only the various types of climax areas; the assumption being that if certain birds are distributed vertically in one type of climax area they will be found to be the same in another climax area of the same type.

The next question raised is that a Maple-Beech of Maine will contain different types of plants than one of Michigan. It must be realized that I am dealing with physical characteristics and not the plant itself. Pitelka⁸ (p. 130) points this out with the following sentence "Birds apparently do not respond to any specific differences among the dominant plants of a climax or any of its seral stages" and on p. 131, "More importantly, then, life-form as a differentiating feature of a climax, seems to be a controlling factor in distribution."

Saunders⁹ and Hicks⁷ have made studies somewhat to the effect of what I'm discussing. Hicks (p. 174) discusses the succession of a forest in the following manner. "When from one to ten feet high the tree growth consists mostly of sprouts and seedlings of a temporary species and these have

large open spaces between the crowns.....five birds species predominate, the Indigo Bunting, the Field Sparrow, the Blue-winged Warbler, the Chestnut-sided Warbler, the Towhee and in moist areas, the Northern Yellow-throat, When from ten to eighteen or twenty feet high, the forest crown converges and slowly closes over and soil humus begins to accumulate.

The species named begin to disappear and are replaced by the Robin, Red-eyed Vireo, Oven-bird, Rose-breasted Grosbeak, Goldfinch and Least Flycatcher. When from twenty to thirty-five or forty feet the temporary species disappear, herbacious plants develop on the forest floor and in certain localities young hemlocks begin to develop. The last named species continue and several new ones come in, including the Ruffled Grouse, Scarlet Tanager, Junco, Black-capped Chickadee and Blue Jay" and so on.

Saunders (pp. 126-131) describes the same process for a Maple-Beech-Hemlock forest and offers the summation in the form of a chart reproduced on next page.

From these two illustrations I think it is clear what I mean. My study here was done in this manner as much as possible, and I think my data accurate.

I could not make a very good connection between nesting and refuge zones. Let me offer the information on three common species of birds as to their nests that I have taken from two good books.

Redstart: Barrows³ - rarely more than 20 feet,
majority not even 10.

Forbush⁶ - three to 35 or more feet.

Pewee: Barrows - 10 to 40 feet.

Forbush - 20 to 60 feet.

Purple Finch: Barrows - 12 to 50 feet.

Forbush - five to 60 feet.

From this type of information I found it impossible to make a correlation. Again the plea for a paper giving complete information as to nests.

The question of escape in a bird is of interest. How does escape differ from mere movement? I have made birds fly from me by shouting and throwing objects at them but are they escaping? I have information that when a Least Flycatcher is frightened by some animal it will dive into low bushes instead of going into the low trees as it did when I frightened it, perhaps birds react differently toward human beings than toward other enemies.

From my observations I conclude that birds are distributed fairly logically in a vertical plane, and they will tend to be found in this plane if found in the locality. Of course, birds may be seen elsewhere due to feeding or mating, but they seem to display a preference for a particular zone which, ecologically, may be called its true habitat.

SUMMARY

1. A study was made of the vertical distribution of breeding birds with reference to the vegetation.

2. The vegetation of the area was divided into definite vertical zones, and the birds were placed in these zones by watching where they fed, sang, and escaped.

3. A supposition was proposed as a basis for birds being in vertical zones and for their actions within these zones.

a. Horizontal distribution dependent, for the most part, upon physiological and functional activities of the bird; vertical distribution dependent upon, for the most part, psychical activities of the bird.

b. Actions during breeding cycle dependent upon psychical activities, after the breeding cycle dependent upon physiological and functional activities of the bird.

4. A method of study was suggested and several examples of it shown.

a. Study of the various climax areas (including steps of succession) with reference to the physical characteristics of the vegetation.

b. Division of these physical characteristics into vertical zones and study the zones for the bird-life contained within.

5. The conclusion was reached that there are definite vertical zones and certain birds within these zones, this being an indication of the true habitat of the bird.

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EXPLANATION OF GRAPH I

An arbitrary number was given to each of the zones as follows:

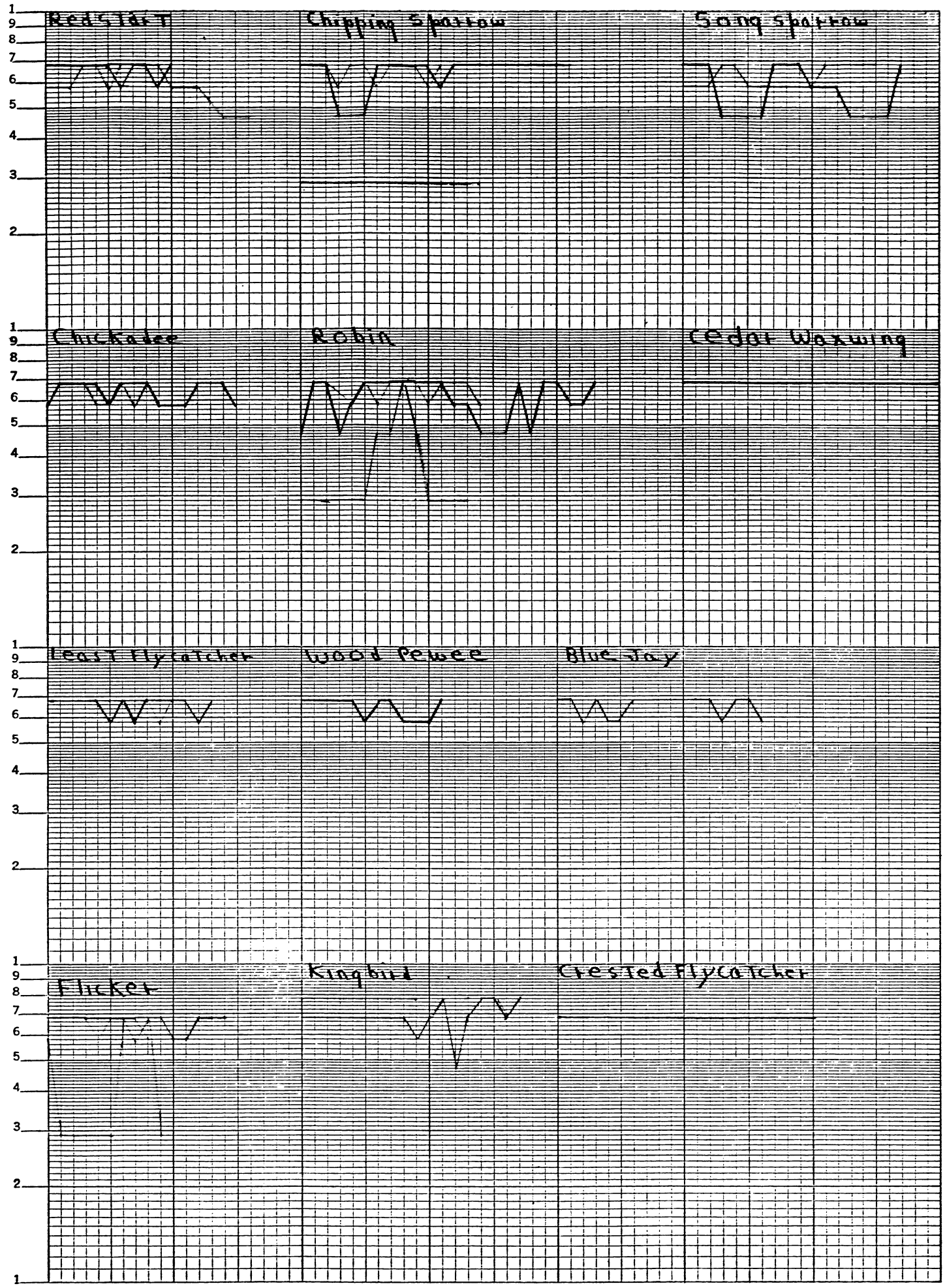
1. Ground zone - 195 log. of is 2.90
2. Low-bush zone - 295 log. of is 4.71
3. High-bush zone - 395 log. of is 5.96
4. Low-tree zone - 495 log. of is 6.94
5. Aerial zone - 595 log. of is 7.74

The blue line represents the singing zone, the red line represents the refuge zone, the green line represents the feeding zone, the ink is where two or more lines run together. The number of times observed is plotted against the zone.

Graph I

Semi-Logarithmic
4 Cycles X 10 to the inch
MADE IN U.S.A.

NO. 5784



AIR ABOVE FOREST

Chimney Swift Feeds

Broad-leaf Trees			Hemlock Trees		
Red-eyed Vireo	Nest and Feed		Black burnian warbler	nest and feed	
Blue-headed Vireo	" " "		Magnolia Warbler	" " "	
Scarlet Tanager	" " "		Black throated Green	" " "	
Warblers	Feed		Warbler	" " "	
Black throated					
Green Warbler	" " "				

Trunks and Large Limbs			Old Stubs - Dead Trees - Limbs		
White-breasted Nuthatch			Hairy Woodpecker - Nest and Feed		
	Nest and Feed		Flicker	" " "	
Brown Creeper	" " "		Chestnut sided		
Black and White			Warbler probably nests		
Warbler	Feed				

Undergrowth			Stumps, Logs, Upturned Roots in Mounds		
Wood Thrush	Nest and Feed		Winter Wren	Nests and Feeds	
Olive-backed			Black and White		
Thrush	" " "		Warbler	Nests	
Black-throated			Junco	Nests	
Blue Warbler	" " "				
Hooded Warbler	" " "				
Vireos	" " "				
Warblers	Feed				

Forest Floor, Litter of Dead Leaves - Twigs
 Thrushes Feed, Oven bird - Junco Nest and Feed

HUMUS

SOIL

From A. A. Saunders⁹

TABLE I

	# Times Observed	Feeding	Refuge	Nesting Site	Singing Height	Variations
<i>Actitis macularia</i> Spotted Sandpiper	40			aerial	ground	2
<i>Larus argentatus</i> Herring Gull	39	water		aerial	ground	
<i>Larus delawarensis</i> Ring-Billed Gull	35	water		aerial	ground	
<i>Zenaidura macroura</i> Mourning Dove	10	ground	low tree	low tree		3
<i>Coccyzus lerythroptthalmus</i> Black-Billed Cuckoo	5	high bush	high bush		low tree	1
<i>Megasceryle a. alcyon</i> E. Belted Kingfisher	11	water		aerial	bank	0
<i>Colaptes auratus</i> Flicker	27	ground	low tree	low tree		5
<i>Dryobates villosus</i> Hairy Woodpecker	11	tree	low tree			7
<i>Dryobates pubescens</i> Downy Woodpecker	10	tree	low tree			5
<i>Tyrannus tyrannus</i> E. King bird	33	aerial	low tree			8
<i>Myiarchus crinitus</i> Crested Flycatcher	20	low tree	low tree		low tree	0
<i>Empidonax minimus</i> Least Flycatcher	20	low tree	low tree	low tree	low tree	4
<i>Myiochanes virens</i> E. Wood Pewee	22	low tree	low tree	low tree		7

TABLE I (Cont.)

	# Times Observed	Feeding	Refuge	Nesting Site	Singing Height	Variations
<i>Progne S. subis</i> Purple Martin	30	aerial	aerial	box		0
<i>Cyanocitta cristata</i> Blue Jay	16	low tree	low tree		low tree	5
<i>Penthestes atricapillus</i> Black-capped Chickadee	25	low tree high bush	low tree		low tree high bush	10
<i>Nannus h. hiemalis</i> E. Winter Wren	10	low bush	low bush		low bush	1
<i>Dumetella carolinensis</i> Cat bird	6	high bush	low bush		high bush	2
<i>Turdus migratorius</i> Robin	35	all zones	low tree high bush		low tree	16
<i>Bombycilla cedrorum</i> Cedar Waxwing	31	low tree	low tree	low tree		7
<i>Vireo olivaceus</i> Red-eyed Vireo	27	low tree	low tree		low tree	3
<i>Dendroica pinus</i> Pine Warbler	17	low tree	low tree		low tree	0
<i>Seiurus aurocapillus</i> Ovenbird	9	ground	low bush	ground	high bush	4
<i>Setophaga ruticilla</i> American Red start	26	high bush	low tree		low tree	5
<i>Sturnella magna</i> Meadowlark	10	ground	ground	ground	high bush	3
<i>Agelaius phoeniceus</i> Red-wing	8	low bush	high bush	low bush	high bush	3

TABLE I (Cont.)

	Time Observed	Feeding	Refuge	Nesting Site	Singing Height	Variations
<i>Passerina cyanea</i> Indigo Bunting	12	high bush	high bush		low tree	4
<i>Carpodacus p. purpureus</i> E. Purple Finch	32	low tree	low tree		low tree	0
<i>Pipilo erythrophthalmus</i> Towhee	8	ground	high bush	ground	high bush	3
<i>Spizella p. passerina</i> E. Chipping Sparrow	56	ground	low tree		low tree	13
<i>Melospiza melodia</i> Song Sparrow	32	low bush high bush	high bush low tree	high bush	high low tree bush high bush	16