VERTICAL DISTRIBUTION OF BIRDS IN A LOUISIANA BOTTOMLAND HARDWOOD FOREST

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Resources used by avian species are probably in limited supply in forest ecosystems resulting in interspecific competition, in resource partitioning, and in the segregation of species on habitat gradients (Koplin and Hoffman 1968, Cody 1974, Schoener 1974). Resource partitioning has been accomplished through various "coexistence mechanisms" (Cody 1974). Schoener (1974) hypothesized that habitat dimensions are important more often than food-type dimensions which are more important than temporal dimensions in resource partitioning. One of these mechanisms or dimensions is a spatial segregation of birds into vertical strata. Vertical height distribution is one dimension of niche definition. MacArthur and MacArthur (1961) correlated vegetative height diversity and bird species diversity showing how bird communities responded to vegetative profiles. Tramer (1969) also noted the response of bird populations to vegetative layering. Cody (1968) observed vertical feeding height selectivity in tall vegetation, and Pearson (1971) and Karr (1971) documented vertical stratification in tropical birds.

How does maturity of an ecosystem affect bird populations and resource use? Odum (1969) predicted an increase in potential niches and interspecific competition resulting from increased biomass stratification with the advance of vegetative succession.

Another question that remains essentially unanswered is what are the seasonal patterns of resource partitioning in communities. Bird energy budgets fluctuate seasonally (King 1974) as do behavior patterns. Deciduous forests present seasonally changing vegetative profiles and habitat structures. These seasonal phenomena result in changes in bird spatial distributions.

The objective of our investigation was to ascertain vertical distributions of certain avian species and to analyze the seasonal changes in these distributions in a mature Louisiana bottomland hardwood forest.

STUDY AREA AND METHODS

This investigation was conducted on the Thistlethwaite Wildlife Management Area between Washington and Labeau, St. Landry Parish, Louisiana. The area is an old floodplain of the Mississippi and Red rivers. It is described as a south central Louisiana mature bottomland hardwood forest, and classified as hardwood bottom (Braun 1950:293). Vegetation on the area was measured on variable radii plots. The mature bottomland hardwood forest was fully stocked (28.2 m^2 basal area/ha). Oaks (*Quercus* spp.) were dominant overstory vegetation. Cane (*Arundinaria gigantea*), palmetto (*Sabal minor*), and ironwood (*Carpinus caroliniana*) were primary understory species.

Vertical height data from 4103 sightings of 26 species of birds were analyzed. Height data were collected approximately 5 mornings per month from January 1972 to February 1974 while censusing birds from a 1.6 km transect. Sightings were made from sunrise to 4 h after sunrise; therefore, no data on daily patterns in heights were gathered. Vertical strata categories (MacArthur and MacArthur 1961) were: ground–0.6 m, 0.6–7.6 m, 7.6 m–canopy top (approximately 25.9 m), and above-canopy. These zones probably corresponded, as well as any, to the vegetation profile, although no distinct layers of vegetation were observable. No corrections were applied to compensate for differences in sighting distances in foliage profile throughout the year, although there were decided seasonal changes. In summer the vegetation appeared to be almost equally distributed at different heights. In winter after the deciduous leaves had fallen, the ground and mid-story vegetation, mainly palmetto and cane (both evergreen), was denser than the mostly leafless canopy.

Singing birds were omitted in this study. Sightings were not restricted to any particular behavioral category, although most birds were foraging when detected. There may have been some height differences corresponding to different bird behavior, but we did not attempt to distinguish behavior when recording heights. A behavioral division of height classes would have reduced our sample sizes significantly. We do not believe this lumping significantly affected results.

Birds were categorized into 1 of the 4 strata at the time of initial sighting with a few minor exceptions (Table 1). Ground occupants were often first seen in mid-air after having been flushed from the ground. These instances of flushing were regarded as ground sightings.

Height diversities were calculated from the information theory of Shannon (1948). Using this formula, dispersal among classes, or diversity, was calculated, based on equality of distribution of observations among the 3 classes (above-canopy stratum excluded). Height diversity $= -\sum P_i \log_e P_i$, where $P_i =$ proportion of observations in the *i*th category. For the 3 height categories used, 1.099 would represent maximum diversity or equal dispersal among all categories, and conversely, a complete distribution in only 1 category would have zero diversity.

Birds in the "above-canopy" stratum were divided into 2 groups: those carrying on their "normal" activities at that height and those merely relocating themselves. We included the above-canopy stratum for Black Vultures and Common Crows (Table 1) because they appeared to regularly use that height while carrying on their "normal" activities. Those relocating themselves in the "above-canopy" stratum were omitted from further consideration.

Bird vertical stratifications were compared on a seasonal, species, and family basis. The 3 strata comparisons within the forest were used for all species except the Black Vulture and Common Crow. Comparisons were tested by means of the chi square test for independent samples at the .01 level of significance unless otherwise specified. There were 2 degrees of freedom in each chi square test of 3 vertical strata. The basic assumption of this test is that all observations were independent of all other observations. We felt that data on Common Grackles and Cedar Waxwings did not meet the basic assumption, due to their occurrence in flocks and to our influence on their vertical distribution. As a result, they were excluded from further consideration. Flocking was observed to a lesser degree in other bird groups but not to the extent to invalidate the assumption of independence. The criterion for sufficient samples for reliability was taken from Siegel (1956). In comparing the 3 vertical strata within the forest, no expected

TABLE 1

VERTICAL STRATAL INDEX OF COMMON THISTLETHWAITE BIRDS BASED ON FREQUENCY OF OCCURRENCE IN 3 STRATA[1]

Common name	Scientific name	Index[2]
Black Vulture	(*Coragyps atratus*)	3.50
Common Crow	(*Corvus brachyrhynchos*)	3.04
Red-headed Woodpecker	(*Melanerpes erythrocephalus*)	2.80
Blue Jay	(*Cyanocitta cristata*)	2.75
Pileated Woodpecker	(*Dryocopus pileatus*)	2.74
Carolina Chickadee	(*Parus carolinensis*)	2.67
Red-bellied Woodpecker	(*Melanerpes carolinus*)	2.66
Tufted Titmouse	(*Parus bicolor*)	2.51
Yellow-bellied Sapsucker	(*Sphyrapicus varius*)	2.39
Yellow-rumped Warbler	(*Dendroica coronata*)	2.34
Brown-headed Cowbird	(*Molothrus ater*)	2.30
Hooded Warbler	(*Wilsonia citrina*)	2.24
Mockingbird	(*Mimus polyglottos*)	2.24
Common Flicker	(*Colaptes auratus*)	2.23
Ruby-crowned Kinglet	(*Regulus calendula*)	2.14
White-eyed Vireo	(*Vireo griseus*)	2.13
American Goldfinch	(*Spinus tristis*)	2.10
Brown Thrasher	(*Toxostoma rufum*)	2.08
Carolina Wren	(*Thryothorus ludovicianus*)	2.01
Cardinal	(*Cardinalis cardinalis*)	2.00
American Robin	(*Turdus migratorius*)	1.94
Kentucky Warbler	(*Oporornis formosus*)	1.88
Hermit Thrush	(*Catharus guttatus*)	1.77
Rusty Blackbird	(*Euphagus carolinus*)	1.74
Rufous-sided Towhee	(*Pipilo erythrophthalmus*)	1.41
White-throated Sparrow	(*Zonotrichia albicollis*)	1.27
		$\sum$ 58.88
		$\bar{X}$ 2.26

[1] Fourth stratum (above canopy) used only for Black Vulture and Common Crow.
[2] Index was computed by multiplying number of sightings in each stratum by: 1 for stratum 1 (ground–0.6 m), 2 for stratum 2 (0.6–7.6 m), and 3 for stratum 3 (7.6 m–canopy top). The sum of these products for each species was then divided by total sightings, giving relative mean height.

values of less than 1 were tolerable, and no more than 20% of the expected values could be less than 5. In the few instances of a low value in 1 stratum, strata were combined for purposes of comparison.

For comparative purposes, the strata were assigned the following values: ground, 1; mid-story, 2; canopy, 3; and above-canopy, 4. Stratal index was calculated by multiplying these values in each stratum by the frequency in each stratum. The sum of these products divided by total frequency defined stratal index, based on frequency of observations in each of the strata.

TABLE 2

VERTICAL HEIGHT DIVERSTIY OF COMMON BIRDS IN 3 HEIGHT CATEGORIES

Species	Diversity[1]	Species	Diversity
Maximum Diversity[2]	1.099	Yellow-bellied Sapsucker	.762
American Robin	1.075	Red-bellied Woodpecker	.682
Common Flicker	1.056	Ruby-crowned Kinglet	.678
Rusty Blackbird	1.051	White-throated Sparrow	.650
American Goldfinch	1.014	Carolina Chickadee	.634
Brown Thrasher	1.006	Pileated Woodpecker	.622
Hermit Thrush	.980	Kentucky Warbler	.616
Cardinal	.950	Blue Jay	.604
Brown-headed Cowbird	.924	Carolina Wren	.571
Mockingbird	.898	Hooded Warbler	.551
Yellow-rumped Warbler	.868	White-eyed Vireo	.534
Tufted Titmouse	.801	Red-headed Woodpecker	.513
Rufous-sided Towhee	.792		
			Σ 18.832
			$\bar{X}$ .785

[1] Computed by information theory (height diversity $= -\sum P_i \log_e P_i$, where P_i = proportion of observations in the *i*th height category).

[2] Equal distribution in all height categories, height diversity = 1.099; distribution in only 1 height category, height diversity = 0.

RESULTS AND DISCUSSION

Species and families.—Black Vultures had the highest mean vertical distribution (Table 1). Over ⅔ of the sightings were of soaring birds above the canopy.

Woodpeckers were predominately canopy dwellers, but different niche breadths in vertical distributions were evident. Of all sightings, 68% were above 7.6 m and less than 3% were found near the ground (Fig. 1). Pileated and Red-bellied woodpeckers were similar in vertical distribution to the aggregate of woodpeckers. Distributions of 3 species differed from the 2 above species. Common Flickers were more ground oriented (21% of sightings), and were exceeded in vertical dispersion (diversity index (DI) = 1.056, Table 2) by only one bird. Yellow-bellied Sapsuckers were primarily mid-story occupants (58%), and secondarily canopy occupants (41% of sightings) during their winter presence (DI = 0.762). Red-headed Woodpeckers were the most canopy dependent Picidae (82%) with the most restrictive vertical height dimension of niche breadth of all birds (DI = 0.513, Table 2).

The corvids were located high in the Thistlethwaite woods (Table 1). Blue Jays were closely associated with the canopy level (stratal index = 2.75, DI =

0.604). They were even more strongly canopy oriented than were the Picidae ($\chi^2 = 12.6$, $P < .01$). Common Crows were located even higher; 40% above the tree tops.

The similarly distributed ($P > .01$) Tufted Titmouse and Carolina Chickadee were common canopy occupants. Fifty-four % of the Tufted Titmice and 67% of the Carolina Chickadees were observed in the canopy. They were less frequently observed in the mid-story (43% titmice, 33% chickadees). The Paridae, along with the Picidae, were the least frequent ground level occupants (titmice 3%; chickadees, none).

We sighted 83% of the Carolina Wrens in the mid-story. The chi square value for the comparison of wrens to the aggregate of all birds (which was also most numerous in mid-story sightings) was 128.6 ($P < .01$). Supporting this idea of mid-story association is the low height diversity of .571.

The Mimidae, Northern Mockingbirds and Brown Thrashers, were a vertically diverse group (DI = 0.898, Northern Mockingbirds; DI = 1.006, Brown Thrashers), tending toward the mid-story level. Over 50% of the sightings of each were in this level.

The turdidae exhibited an unusual pattern of height distributions. Although we assumed that intrusion into the woods had no influence on bird heights, we may have had some effect on the heights at which Hermit Thrushes and American Robins were observed. Half of the Hermit Thrush sightings were in the mid-story and over ⅓ on the ground (Fig. 1). Perhaps a small portion of the mid-story sightings were of birds that flew there from the ground after being flushed. The robin was the most uniformly distributed bird in the 3 strata (DI = 1.075): ground (41%), canopy (35%), and mid-story (24%).

Ruby-crowned Kinglets were common mid-story winter residents. Of 73 sight tallies, 76% were within the 0.6–7.6 m level. The ground stratum was of little importance (5%) and the canopy stratum was of medium importance (19%). Their dispersal among the 3 strata was 0.678, near the mean of all species (0.785).

White-eyed Vireos were the only breeding vireo commonly seen. These birds were closely associated with the mid-story. This is shown by the proportion of mid-story sightings (82%) and the low height diversity (0.534, second lowest of all birds). Although there were insufficient sightings of Red-eyed and Yellow-throated vireos (*V. olivaceus* and *V. flavifrons*) for valid conclusions, the few that were sighted, and those heard, showed a canopy preference.

Yellow-rumped Warblers, 1 of 2 common winter warblers, were located mainly in mid-story (54%) and canopy (40%). The 2 commonly seen breeding season warblers, Kentucky Warbler and Hooded Warbler were selective

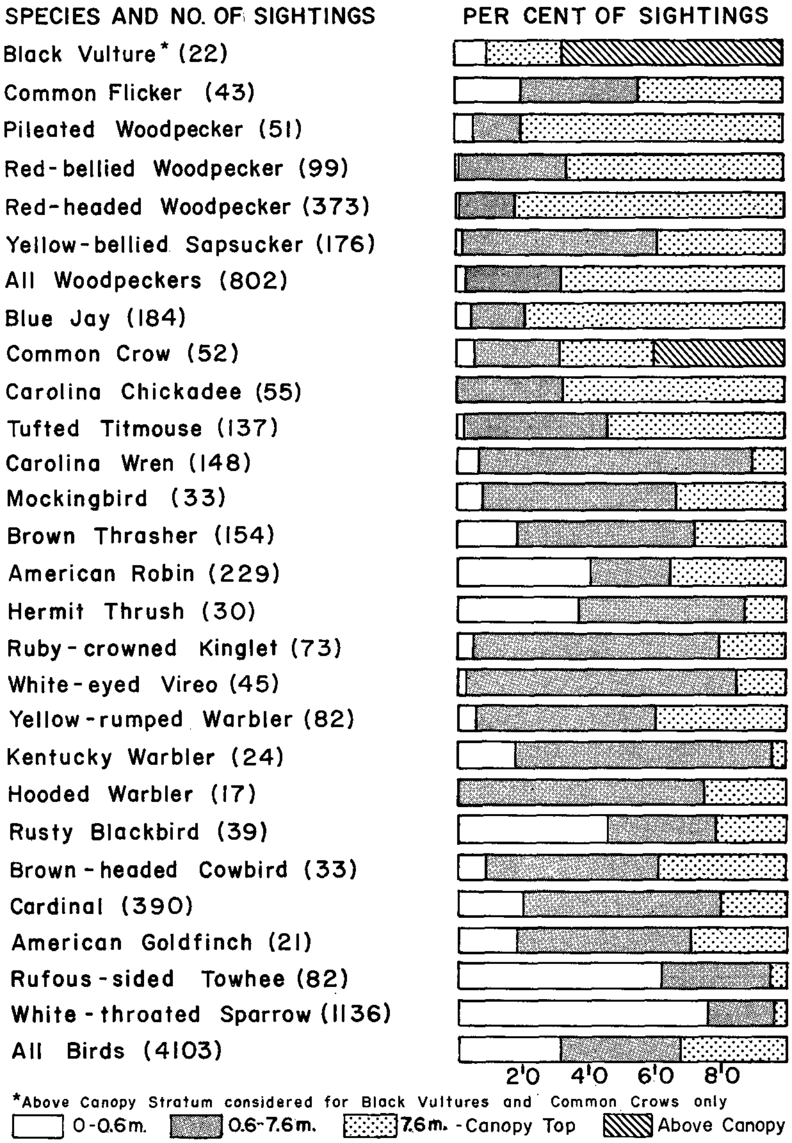

FIG. 1. Vertical height distributions of common birds.

in their forest profile use. Over 75% of sightings of Kentucky and Hooded warblers were in the 0.6–7.6 m stratum and the height diversity of each was less than the mean of all birds by more than 25%. They appeared to differ in use of the ground stratum (4 of 24 sightings—Kentucky Warblers, 0 of 17 sightings—Hooded Warblers), although there were insufficient data for a valid statistical test.

Brown-headed Cowbirds were mainly a mid-story, and secondarily a canopy occupant (DI = 0.924). Rusty Blackbirds were diversely distributed (DI = 1.051, 34% higher than the mean for all birds); they were found on the ground, mid-story, and canopy in decreasing order of occurrence.

The seed-eating fringillids, as expected, tended to be close to the ground. The 2 species (White-throated Sparrow and Rufous-sided Towhee) found most frequently near the ground were in this family. Over 75% of the White-throated Sparrows and 62% of the Rufous-sided Towhees were detected within 0.6 m of the ground. Conversely, only 3% of the sparrows and 4% of the towhees were detected in the tree canopies. The Northern Cardinal and the less common American Goldfinch differed ($P < .01$) from other fringillids. Both were mainly located in mid-story (60%, cardinal; 52%, goldfinch), and both showed high dispersal within the 3 strata (DI > 20% higher than the mean of all species).

Most individual species were more specialized than the aggregate of all birds. Of the different species investigated, only Brown-headed Cowbirds, American Goldfinches, Hermit Thrushes, and Northern Mockingbirds did not differ significantly ($P > .05$) in height distribution from sightings of all birds. These species were commonly found in all strata and as a result, exhibited a greater than average height diversity.

Vertical resource partitioning.—Different vertical resource use strategies were evident in birds in this mature ecosystem. Some species were specialists in using 1 of the 3 strata; some used 2 strata exclusively, or nearly so; some were found in all strata, but preferred 1 or 2 strata; and some species used all strata almost equally. Specialist species (i.e., those with lowest DI and >78% of sightings in 1 stratum) in the 7.6 m–canopy top stratum were Pileated Woodpecker, Red-headed Woodpecker, and Blue Jay. Carolina Wrens, White-eyed Vireos, and Kentucky Warblers were mid-story associated species, and no species were predominantly ground dwellers.

Other species concentrated their activities in 2 strata (>94% of sightings). Those found predominantly in the mid-story/canopy were: Red-bellied Woodpecker, Yellow-bellied Sapsucker, Carolina Chickadee, Tufted Titmouse, Ruby-crowned Kinglet, and Hooded Warbler. White-throated Sparrows and Rufous-sided Towhees were the ground/mid-story dwellers.

Northern Mockingbird, Brown Thrasher, Hermit Thrush, Yellow-rumped

Warbler, Brown-headed Cowbird, and Northern Cardinal were basically generalists in vertical selectivity, but showed slight preferences for 1 or 2 strata.

Common Flicker, American Robin, American Goldfinch, and Rusty Blackbird were generalists in vertical distribution, displaying optimum height dispersal among the 3 strata, and maximum niche breadth.

The aggregate heights of all birds revealed a fairly uniform use of the 3 strata (Fig. 2). Each stratum was of approximate equal value as an avian resource unit. This substantiated the height units selected, and pointed out the scaling differential of birds in vertical distribution (Cody 1974:70). Although the canopy stratum represented 71% of the total forest height, only 33% of bird sighings were within this stratum. Conversely, the 0–0.6 m ground stratum represented 2% of the total height and contained 31% of the birds. Plant detritus, particularly mast, accumulated on the ground and this provided direct and indirect food sources for the ground foraging birds. Additionally, the solid substrate probably rendered the ground more accessible to foraging birds.

The mid-story contained proportionately more birds than the canopy, but fewer than the ground stratum. The continuous cover of evergreen cane and palmetto of the mid-story, may have influenced vertical distribution. Flying birds also appeared to prefer this height.

Seasonal vertical distribution.—Seasonal shifts in vertical distribution were evident in Thistlethwaite birds. Due to the seasonal occurrence of some species, and the small number of samples of many others when categorized into seasons, we usually grouped individual species into higher taxa or on a residency status basis.

There was a gradual shift in distribution of birds upward in height through the 3 strata from the winter season through spring to summer and a pronounced downward movement from fall to winter. The comparison of winter to summer showed decided differences. Spring brought a slight, but nonsignificant ($P > .05$), shift upward in height for the aggregate of all birds, and for permanent residents when considered separately (Fig. 2). For all birds, ground detections fell from 38 to 36% and canopy detections rose from 29 to 32% from winter to spring. In the permanent resident group, ground detections fell from 27 to 20% and canopy sightings increased from 22 to 27% from winter to spring. Common fringillids (White-throated Sparrows, Rufous-sided Towhees, and Northern Cardinals), which were, in part, included in the 2 previous groupings, showed a significant ($P < .05$) shift upward in distribution from winter to spring. Ground detections fell from 70 to 65%, and canopy detections increased from 4 to 7%, as the birds responded to the seasonal spring flourish of primary production of trees and the corresponding shift of available food. Birds were attracted to new vegetation

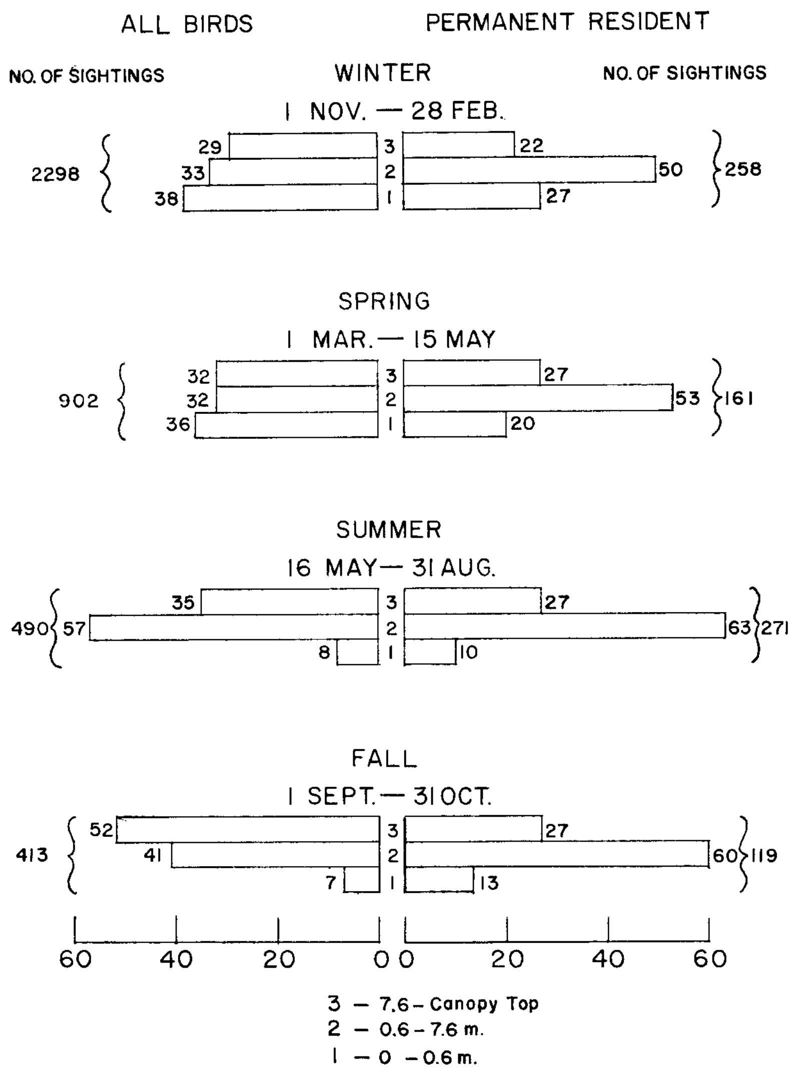

FIG. 2. Seasonal vertical distribution of Thistlethwaite birds, expressed as % of sightings in 3 height categories.

growth of the deciduous forest. White-throated Sparrows and Northern Cardinals were commonly observed feeding on new buds and samaras of American elm (*Ulmus americana*) in March. This winter to spring height distribution shift of the common fringillids was partially responsible for the change in height distribution of other bird groupings in which the fringillids may have been included (permanent residents and all birds).

The movement from ground to mid-story, and from mid-story to canopy, was more pronounced from spring to summer. In comparing the spring to summer distributions of all birds combined, a chi square value of 143.81 ($P < .01$) was noted. Ground sightings declined to 8%, mid-story sightings increased to 57%, and canopy sightings increased to 35%. The increase in stratal index of birds substantiated this upward movement. This was partially due to a species change between seasons. The departure of White-throated Sparrows from February to April lessened the lower strata detections. But the permanent residents also exhibited a significant ($\chi^2 = 8.98$, $P < .05$) shift upward in response to the vegetation profile change.

A highly significant difference ($P < .01$) was noted between winter and summer vertical height distributions for common permanent residents ($\chi^2 = 26.11$) and the aggregate of all birds ($\chi^2 = 178.78$). There was a slight change in height distribution from winter to spring, and a more pronounced change from spring to summer. The winter to summer comparison embodied these 2 lesser seasonal height distribution changes.

The summer to fall comparison showed no discernible shift in vertical distribution of Thistlethwaite birds. Ground detection percentages remained virtually unchanged for all birds and permanent residents. Figure 2 reveals a shift of about 16% of sightings of all birds from mid-story to canopy. We believe this was misleading due to the autumn arrival of numerous Red-headed Woodpeckers. This conspicuous canopy dweller inflated the number of canopy detections. A check of the common permanent residents revealed no notable change in vertical distribution from summer to fall ($\chi^2 = 0.66$, $P > .05$).

With the accumulation of plant detritus, particularly mast, on the ground in fall and early winter, the birds redistributed themselves at lower levels in the profile. There was a highly significant difference ($P < .01$) between fall and winter for all birds ($\chi^2 = 156.25$) and for permanent residents ($\chi^2 = 9.84$).

This seasonal height distribution change resulted in a corresponding change in height diversity. A Least Squares Analysis of Variance showed a highly significant difference ($F = 8.37$; d.f. $= 2, 3$; $P < .01$) between seasons. Height diversity approached maximum during winter (1.092) and spring (1.097). During summer and fall diversity was lower (0.890, 0.894), with birds favoring the mid-story and canopy.

SUMMARY

Vertical height data from 4103 sightings of 26 species of birds were analyzed in order to better understand height segregations and resource use. Height categories used were:

ground to 0.6 m, 0.6 m to 7.6 m, and 7.6 m to canopy top (approximately 25.9 m). Bird height distributions were compared by means of the chi square test for 2 independent samples. Height diversities were computed by the information theory. The most ubiquitous species in height dispersion were: American Robin, Common Flicker, Rusty Blackbird, and American Goldfinch. The species most restricted in the forest profile and the zones they inhabited were: Red-headed Woodpecker, Pileated Woodpecker and Blue Jay—canopy; White-eyed Vireo, Kentucky Warbler, and Carolina Wren—mid-story. There was a gradual upward shift in distribution of all birds from winter through spring to the summer breeding season. There was a highly significant winter to summer height distribution change from a nearly equal distributon at all levels in winter to a predominantly mid-story and canopy distribution in summer. Corresponding with this was a reduction in height diversty of the aggregate of all birds. These shifts were presumably a response of the birds to the seasonal change in foliage profile and food supply of a deciduous forest.

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REQUESTS FOR ASSISTANCE

International shorebird surveys 1978.—A cooperative International Shorebird Survey scheme has been organized by the Canadian Wildlife Service and the Manomet Bird Observatory since 1974 to obtain information on shorebird migration and to identify and document areas of major importance. This scheme has been highly successful, with much very valuable information on shorebird distribution and migration coming from contributors throughout eastern Canada and the U.S.A., the Caribbean Islands, and Central and South America. Information from the scheme will be valuable in assessing requirements for the future protection and conservation of the birds and their habitat. It is planned to make 1978 the fifth and final year of the project. Any observer who may be able to participate in regular counts of shorebirds during spring and autumn migration periods, as well as during the winter in shorebird wintering areas, is asked to contact one of the undersigned. Occasional counts from observers visiting shorebird areas on an irregular basis would also be most welcome. For areas in Canada: Dr. R. I. G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada K1G 3Z7. For areas in U.S.A., Caribbean Islands, Central and South America: Brian A. Harrington, Manomet Bird Observatory, Manomet, MA 02345.

Shorebird color-marking.—In 1978, the Canadian Wildlife Service will be continuing a large-scale program of banding and color-marking shorebirds in James Bay. During the past 3 years, over 30,000 shorebirds have been captured, resulting in more than 1200 "bird days" of sightings of dyed birds ranging from eastern Canada to South America. Much valuable information on migration routes and strategies is being obtained and observers are again asked to look out for and report any color-dyed *or* color-banded shorebirds that they may see. Reports should include details of species (with age if possible), place, date, color-marks and, if possible, notes on the numbers of other shorebirds present. For color-dyed birds, please record the color and area of the bird that was dyed. For color bands and standard metal leg bands, please record which leg the bands were on, whether they were above or below the "knee," the colors involved (yellow or light blue), and the relative position of the bands if more than one was on a leg (e.g. right lower leg, blue over metal, etc.). All reports will be acknowledged and should be sent to: Dr. R. I. G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada K1G 3Z7.