AVIAN DISTRIBUTION PATTERNS IN FOREST ISLANDS OF DIFFERENT SIZES IN CENTRAL NEW JERSEY

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THE number of species present in a particular habitat is strongly influenced by the size of that habitat. Early ecological study of the relationship between species number and habitat area dates to Arrenhius (1921) and Gleason (1922). A large volume of literature on the theory and practical applications of the species-area concept has been developed since and is reviewed by Cain and Castro (1959) and Greig-Smith (1969). Hopkins (1955), Preston (1960), and MacArthur and Wilson (1967) give examples of species-area curves for both plant and animal communities, and the shapes of the curves are characteristic of the communities under study (Cain and Castro 1959). Usually there is a direct linear relationship between species number and the logarithm of area.

The use of islands of habitat for establishing species-area relationships differs from the use of parcels within the habitat, as enrichment of a parcel by species from adjoining terrain is minimized when islands are used. Also, islands of habitat provide an edge effect, discussed below. In central New Jersey patches of forest habitat surrounded by open fields exist in relative abundance. Because of their relatively discrete nature, these habitat patches may be considered terrestrial islands. They vary in size from less than a hectare to over 30 ha.

The purpose of this study was to determine (1) the relationship between size of a habitat patch and bird species richness in the mixed oak forests on the New Jersey piedmont, (2) the forest size requirements of different bird species, and (3) the importance of forest edge and forest interior as distinct zones for birds.

METHODS

Forest islands ranging from 0.01 to 24.0 ha were available in the study region and ten size classes were chosen (0.01, 0.2, 0.8, 1.2, 2.0, 3.0, 4.0, 7.5, 10.0, 24.0 ha). For statistical analysis the study region was divided into three geographic sections: northern, central, and southern. Each section contained 10 study islands, one of each size class. Forest islands in the northern and southern sections were censused three times and those of the central section were censused twice. The first census of 30 islands was done 5–29 June, the second census 30 June–23 July, and the third census of the northern and southern sections 24 July–8 August 1972. Woods within a section were censused in random order. The northern section was censused first followed by the southern and central sections. All censuses were made from 0630 to 0900, and none was conducted on days of heavy rain or fog.

To assure comparable sampling of each forest, the following procedure was employed.

A series of transect lines, located 30 m (100 feet) apart, throughout the island was marked with surveyor's flagging tied to trees. Guided by the flagging the investigator maintained a prescribed course through the forest and walked in the same direction in each census. All bird contacts, visual and auditory, within a 15-m (50-foot) strip on either side of the transect line were recorded and all birds encountered during a census, except those flying over the study site, were included. Most of the species encountered used the forest islands for both nesting and feeding, but no species was excluded if it was not dependent on the island for both needs. Scientific names of the bird species are given in the appendix.

In agreement with general usage, bird species richness refers simply to species number. It is important to realize that the number of species present can very adequately represent the breeding bird *diversity* (the BSD of the literature), as reported by Tramer (1969). Further, Kricher (1972) concluded that the effect of the equitability factor on species diversity of birds in mixed oak forests on the New Jersey Piedmont was minimal during the summer.

To assay for differences in internal heterogeneity of islands, foliage height diversity (FHD) was calculated using a 35-mm camera with a 200-mm lens to determine the number of leaves per 2 m thick layer over 100 regularly distributed points in each forest (after the methods of MacArthur and Horn 1969). Based on a plot of the average foliage profile of all islands we defined five horizontal layers: canopy, subcanopy, understory, shrub, and herb respectively.

In an effort to find the effect of even larger forest sizes and to estimate the size at which the increase in species richness might become minimal, we censused a 44-ha portion of the extensively forested Sourland Mountain in early August. The forest section chosen for study was adjacent to our other sites, and located in Hunterdon County. Specifically we chose the level portion of the northern side of Sourland Mountain, north and west of Mountain Road and Runyon Mill Road, respectively. The plot for census was 400 $\times$ 1100 m and was gridded into 100 $\times$ 400 m blocks. Each block was further divided by transect lines 33 m apart. The censusing procedure was the same as the one used in censusing the forest islands. Every bird encountered within 16.5 m of the transect line was recorded on the census.

Description of Study Sites

The forest islands are on the Piedmont of New Jersey, in an area bounded by New Brunswick, Princeton, Flemington, and Somerville. The region is composed of the relatively uniform soils of the Brunswick formation developed from Triassic red shale. The soil is characteristically shallow, well drained, and loamy. Detailed descriptions and locations of each site are given in Galli (1974) and Forman and Elfstrom (1975).

The study region is approximately 25 km in diameter and is surrounded by the igneous hills of the First Watchung Mountains, Cushetunk and Round Mountains, Sourland Mountain and the Kingston Ridge, all rising a few hundred feet above the Piedmont plain.

The forests are mixed oak dominated by *Quercus alba*, *Q. velutina*, and *Q. borealis.* Less abundant canopy species include: *Fagus grandifolia*, *Liriodendron tulipifera*, *Acer rubrum*, *Carya ovalis*, and *Fraxinus americana*. *Prunus serotina* and *P. avium* are associated with the forest edge. The understory is dominated by *Cornus florida* and includes saplings of canopy species and *Nyssa sylvatica*, *Amelanchier arborea*, and *Carpinus caroliniana*. *Viburnum acerifolium*, *V. prunifolium*, *V. dentatum*, and *Lindera benzoin* are the major shrub-layer species.

The following criteria were used in selecting the study sites: (1) slope less than

TABLE 1

ANALYSIS OF VARIANCE RELATING FOREST SIZE, GEOGRAPHIC SECTION, AND CENSUS PERIOD TO BIRD SPECIES RICHNESS[1]

Source	df	F value	Probability
Total	59	–	–
Size	9	88.24	$P <<< 0.001$
Section	2	2.49	n.s.
Time	1	0.08	n.s.[2]
Size × section	18	3.30	$P < 0.01$
Section × time	2	1.89	n.s.
Size × time	9	0.98	n.s.
Size × section × time	18	–	–

[1] As two geographic sections were censused three times and the other section only twice, this ANOVA was performed using only the two complete censuses.
[2] $P >> 0.75$.

10°; (2) well-drained silt or clay loam of the Penn series; (3) mature trees over the entire site; (4) presence of all vegetational strata; (5) not recently burned; (6) absence of streams; (7) distant from towns, air pollution sources, and other forests; (8) minimal internal environmental heterogeneity; (9) presence of a mature forest edge; and (10) surrounded by fields. There were a few exceptions for some of these criteria, but their effects were believed negligible. The criteria for selection of the Sourland Mountain study site were the same as those used for the forest islands, but the former site was on a different soil type and obviously was not surrounded by fields (and thus no mature forest edge). The Sourland Mountain site is characterized by mature oaks (including *Quercus alba*), *Liriodendron tulipifera*, various hickories (*Carya* spp.) and *Fraxinus americana*. The Monalto soil is typically deep and well drained.

RESULTS AND DISCUSSION

The census data were subjected to an analysis of variance, the main factors being forest size, geographic section, and census period. The effect of forest size on bird species number is highly significant, with $P << 0.001$ (Tables 1 and 2). Differences in geographic section made no significant effect. A size by section interaction is significant and indicates that the differences in species numbers from one forest size to another are not the same from section to section, but this has no obvious ecological significance.

TABLE 2

ANALYSIS OF VARIANCE RELATING FOREST SIZE AND GEOGRAPHIC SECTION TO BIRD SPECIES RICHNESS[1]

Source	df	F value	Probability
Total	79	–	–
Size	9	109.61	$P << 0.001$
Section	2	2.97	n.s.
Size × section	18	3.57	$P << 0.001$

[1] All three census periods are included and treated as replicates based on the lack of significance of the time factor in the Table 1 ANOVA.

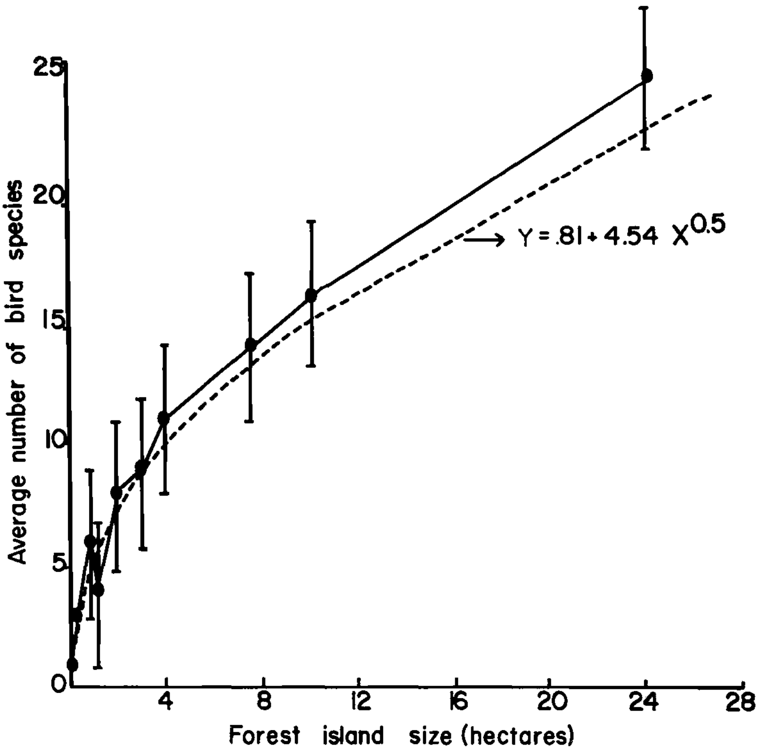

Fig. 1. Number of bird species in summer censuses vs. island size. The solid line is the average number of bird species based on eight censuses with 95% confidence intervals ($LSI_{0.05}$). The dashed line is the best fit curve for the species-area relationship with its regression equation.

Rather it is due mainly to the chance difference from one section to another in islands with high deviations in species number from the average, either above or below. (The northern section islands of 4.0 and 7.5 ha are below, the central 24 ha island is above, and the southern 7.5 ha island is above average.) The evidence shows that only the effect of forest size is ecologically important.

Species richness in the forest islands continues to increase curvilinearly with increase in forest size to 24 ha, the largest size (Fig. 1). The best regression equation for species richness is:

$$Y = 0.81 + 4.54\ X^{0.5}$$

where Y is species richness and X is forest size or area in hectares. The correlation coefficient is high, $R = 0.92$.

TABLE 3
ANALYSIS OF VARIANCE RELATING FOLIAGE HEIGHT DIVERSITY OF EACH FOREST LAYER TO FOREST SIZE

Forest layer[1]	F value[2]	Probability
Canopy (>14.5 m)	1.88	n.s.
Subcanopy (8.5–14.5 m)	1.293	n.s.
Understory (2.5–8.5 m)	2.024	n.s.
Shrub (0.5–2.5 m)	1.23	n.s.
Herb (0–0.5 m)	2.406	$0.025 < P < 0.05$[3]

[1] Using the method of average number of leaves over a point for each forest layer (MacArthur and Horn 1969).
[2] df = 9, 20.
[3] $P > 0.10$ (not significant) if 0.01-ha woods are omitted.

We recorded 23 species in the 44-ha plot within an extensive forest. This is clearly lower than the regression prediction for a 44-ha forest (31 species), and is even less than the number recorded in the 24-ha forest (25 species). This was caused by the virtual absence of edge species from the 44 ha as a habitat subplot. A 44-ha forest island with true edge can certainly be expected to have many more than 23 species, and we can safely infer that bird species richness continues to increase significantly at forest sizes above 24 ha.

MacArthur and co-workers (MacArthur et al. 1962, MacArthur 1964) have shown that heterogeneity of the habitat, which can be measured by foliage height diversity (FHD), strongly affects bird species diversity. In fact the number of species was found to increase proportionally with FHD. In light of this it was necessary to determine whether or not internal ecosystem heterogeneity increased with increasing forest size.

To assay for internal heterogeneity, FHD was calculated for each island. An analysis of variance showed no significant change in the amount of foliage in the canopy, subcanopy, understory, and shrub layers, and a barely significant change at the 0.05 probability level in the herb layer foliage with island size (Table 3). Overall, FHD and therefore internal environmental heterogeneity is clearly not considered to be a significant factor in explaining the observed change in bird species richness.

Wales (1972) determined the edge of a mixed oak forest on the New Jersey Piedmont to be the territory ending approximately 10 m within the forest on the north side and within 20 m on the south side. Based on these values we concluded that a forest of less than or equal to approximately 0.2 ha is entirely an edge habitat. Consequently birds occurring in these woods are considered edge species and include: House Wren, Starling, Song Sparrow, Gray Catbird, Common Grackle, American Robin, Rufous-sided Towhee, Common Flicker, Indigo Bunting, Mourning Dove, Northern Oriole, Common Crow, and Yellow Warbler.

TABLE 4
FREQUENCY OF OCCURRENCE OF BIRD SPECIES IN EIGHT CENSUSES[1]

	Forest size (ha)									
	0.01	0.2	0.8	1.2	2	3	4	7.5	10	24
Common species: Independent of forest size										
House Wren (I)	2	1	1	0	8	2	3	5	7	8
Starling (O)	1	0	6	2	3	2	5	3	3	4
Gray Catbird (I)	0	5	6	3	3	2	6	6	6	8
Common Grackle (O)	0	4	4	3	8	5	7	6	7	8
American Robin (I)	0	5	5	3	2	8	5	4	6	8
Rufous-sided Towhee (O)	0	3	2	3	3	6	6	7	6	8
* Common Flicker (I)	0	1	1	3	4	4	7	6	5	8
Tufted Titmouse (I)	0	1	1	1	4	4	7	6	8	8
Indigo Bunting (O)	0	1	0	1	2	0	2	2	5	3
Common species: Size-dependent										
Blue Jay (O)	0	0	5	5	6	8	8	8	8	8
Great Crested Flycatcher (I)	0	0	1	1	2	2	2	3	6	7
Cardinal (O)	0	0	2	0	1	2	3	1	3	5
Wood Thrush (I)	0	0	2	0	2	2	4	7	8	8
Red-eyed Vireo (I)	0	0	1	0	0	2	1	2	3	4
Brown Thrasher (I)	0	0	1	0	0	0	2	2	3	6
* Downy Woodpecker (I)	0	0	0	4	4	4	3	6	5	8
Eastern Wood Pewee (I)	0	0	0	0	3	7	4	6	6	8
White-breasted Nuthatch (I)	0	0	0	0	2	1	2	2	4	7
Ovenbird (I)	0	0	0	0	0	0	3	6	6	7
Uncommon species: Independent of forest size										
Song Sparrow (O)	1	1	0	0	0	0	0	0	1	2
* Mourning Dove (S)	0	1	1	0	0	1	1	0	1	3
Northern Oriole (I)	0	1	0	0	1	0	1	1	2	2
Common Crow (O)	0	1	1	0	0	0	1	2	1	5
Red-winged Blackbird (O)	0	0	1	0	0	0	0	1	0	3
Rose-breasted Grosbeak (I)	0	0	0	1	1	0	0	0	3	3
Blue-winged Warbler (I)	0	0	0	2	0	0	0	1	0	1
* Ring-necked Pheasant (S)	0	0	0	0	0	1	0	0	0	2
Uncommon species: Size-dependent										
* Hairy Woodpecker (I)	0	0	0	0	1	1	1	1	2	6
Black-capped Chickadee (I)	0	0	0	0	1	1	0	3	3	7
* Red-bellied Woodpecker (I)	0	0	0	0	0	2	0	4	2	7
Scarlet Tanager (I)	0	0	0	0	0	1	0	0	1	5
* Yellow-billed Cuckoo (I)	0	0	0	0	0	0	1	2	0	3
Black-and-white Warbler (I)	0	0	0	0	0	0	0	1	1	2
* Black-billed Cuckoo (I)	0	0	0	0	0	0	0	1	0	2
* Red-shouldered Hawk (P)	0	0	0	0	0	0	0	0	2	2

[1] Letters after the species names indicate general summer diet classes: I = insectivores, O = omnivores, S = seed eaters, and P = vertebrate predator. Also, * = nonpasserine. Other rare species for which there were insufficient data to describe forest size effects are listed below with the number recorded and the size of the forest: Eastern Phoebe (1/24), Swainson's Thrush (1/24), Eastern Bluebird (2/24), Field Sparrow (2/24), * Ruffed Grouse (2/10), Eastern Kingbird (2/10), Vireo sp. (1/10), * American Woodcock (1/4), Chestnut-sided Warbler (1/1.2), House Sparrow (1/1.2), and Yellow Warbler (1/0.2).

The frequency of occurrence, or the number of censuses per size class in which a particular species was recorded, is presented in Table 4. Maximum number of censuses for any size class is eight. For general ecological discussion the bird species were separated into four broad feeding classes:

(1) carnivorous, insects, (2) carnivorous, flesh, (3) herbivorous including granivorous, and (4) omnivorous. The increase in species diversity above 1.5–2.0 ha was due almost entirely to an increase in insect-eating carnivores. Herbivores and omnivores increased negligibly above the small island sizes.

The range of forest sizes and the minimum forest size in which a species is likely to occur can be determined from Table 4. Of the 46 total species, 17 were found over the entire range of forest sizes greater than 0.01 ha and these 17 species are considered size-independent. Eighteen other birds are considered size-dependent species, limited to a particular range of forest sizes from the largest down to a specific minimum size. The minimum areas vary from 0.8 to 10.0 ha and are characteristic of each species.

Nonpasserines in general required larger minimum sized forests than passerines. Eight of 11 nonpasserines occurred in forests greater than 1.2 ha (Table 4). The Red-shouldered Hawk, the only raptor censused, had a minimum area of 10 ha. On the other hand, only half of the passerines required a minimum area of greater than 1.2 ha. All size dependent species except the omnivorous Blue Jay and Cardinal are categorized as primarily carnivorous. Of these carnivores only the hawk is not chiefly an insect feeder.

As the habitat size increases new species appear when their minimum habitat size requirements are fulfilled. We therefore conclude that the increase in bird species richness can be due to the progressive encountering of different minimum areas. For example, the Red-bellied Woodpecker and Red-shouldered Hawk may require large territories in order to obtain their specific foods. Such findings would also be predicted by a knowledge of the sizes of breeding and feeding territories among birds (Schoener 1968). Other factors can also determine the minimum areas of various species. Some, such as the Hairy Woodpecker, Black-capped Chickadee, and White-breasted Nuthatch, may be limited by the number of standing dead trees available for nesting cavities, which, in all probability, would be more abundant in larger forests. And certain breeding species with small territories may require "deep woods" or forest interior environment not found in a small forest. For example, the ground nesting Black-and-white Warbler and Ovenbird both depend on undisturbed accumulations of dead leaves for their successful nest building on the forest floor (Harrison 1975). Thus multiple factors allow additional bird species to appear with larger woods.

SUMMARY AND CONCLUSIONS

We studied 30 forest islands varying in size from 0.01 to 24 ha in central New Jersey to determine the relationship between forest size and bird species richness, the importance of the forest edge, and the minimum habitat requirements of bird species. We made the following conclusions:

(1) Forest size has a significant effect on number of bird species, and a parabolic regression equation describes the relationship with $R = 0.92$.

(2) Size of the forest had no significant effect on foliage height diversity, so the bird species richness pattern here is likely a result of area itself, not internal environmental heterogeneity.

(3) Bird species richness increases significantly through an island size of 24 ha and is likely to continue increasing significantly at forest sizes beyond 24 ha.

(4) Woods of 0.2 ha contained forest edge birds only, while forest interior species began appearing at 0.8 ha. Almost half of the bird species were considered size-dependent, requiring a large area and/or forest interior. Carnivores, including insectivores, were mostly size-dependent.

(5) For land use considerations, larger forest patches are essential to maintain a complete regional avian community.

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APPENDIX

SCIENTIFIC NAMES OF BIRDS MENTIONED IN TEXT

Red-shouldered Hawk (*Buteo lineatus*)
Ruffed Grouse (*Bonasa umbellus*)
Ring-necked Pheasant (*Phasianus colchicus*)
American Woodcock (*Philohela minor*)
Mourning Dove (*Zenaida macroura*)[1]
Yellow-billed Cuckoo (*Coccyzus americanus*)[1]
Black-billed Cuckoo (*C. erythropthalmus*)[1]
Common Flicker (*Colaptes auratus*)[1]
Red-bellied Woodpecker (*Centurus carolinus*)[1]
Hairy Woodpecker (*Dendrocopos villosus*)[1]
Downy Woodpecker (*D. pubescens*)[1]
Eastern Kingbird (*Tyrannus tyrannus*)
Great Crested Flycatcher (*Myiarchus crinitus*)[1]
Eastern Phoebe (*Sayornis phoebe*)
Eastern Wood Pewee (*Contopus virens*)[1]
Blue Jay (*Cyanocitta cristata*)[1]
Common Crow (*Corvus brachyrhynchos*)[1]
Black-capped Chickadee (*Parus atricapillus*)[1]
Tufted Titmouse (*P. bicolor*)[1]
White-breasted Nuthatch (*Sitta carolinensis*)[1]
Gray Catbird (*Dumetella carolinensis*)[1]
Brown Thrasher (*Toxostoma rufum*)[1]
American Robin (*Turdus migratorius*)[1]
Wood Thrush (*Hylocichla mustelina*)[1]
Swainson's Thrush (*Catharus ustulatus*)
Eastern Bluebird (*Sialia sialis*)
Starling (*Sturnus vulgaris*)[1]
Vireo sp. (*Vireo* sp.)
Red-eyed Vireo (*V. olivaceus*)[1]
Black-and-white Warbler (*Mniotilta varia*)[1]
Blue-winged Warbler (*Vermivora pinus*)[1]
Yellow Warbler (*Dendroica petechia*)
Chestnut-sided Warbler (*D. pensylvanica*)
Ovenbird (*Seiurus aurocapillus*)[1]
House Sparrow (*Passer domesticus*)
Red-winged Blackbird (*Agelaius phoeniceus*)
Northern Oriole (*Icterus galbula*)[1]
Common Grackle (*Quiscalus quiscula*)
Scarlet Tanager (*Piranga olivacea*)[1]
Cardinal (*Cardinalis cardinalis*)[1]
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)[1]
Indigo Bunting (*Passerina cyanea*)
Rufous-sided Towhee (*Pipilo erythrophthalmus*)[1]
Field Sparrow (*Spizella pusilla*)
Song Sparrow (*Melospiza melodia*)

[1] Species known to breed in the oak forests on the New Jersey Piedmont (Swinebroad 1962, Bull 1964, Leck 1975).