

# Bird/Habitat Relationships along a Successional Gradient in the Maryland Coastal Plain

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**ABSTRACT:** Bird occurrences were studied over four breeding seasons in a series of habitats representing a transition from recently abandoned pasture to mature hardwood forest. Principal component analysis (PCA) of vegetation data gathered at 59 mist-net sites yielded a habitat ordination reflecting the successional gradient. The capture rates of most breeding bird species in mist nets were monotonic functions of the vegetation scores of mist-net sites on the dominant PCA axis. Species with the highest maximum abundance activity in early successional habitats (*e.g.*, yellow-breasted chat, white-eyed vireo) tended to make less use of the entire successional gradient than did species primarily associated with mature forest. Total mist-net capture rates increased from early successional habitat to mature forest. After adjustment by rarefaction to compensate for differences in sample size, bird species richness was highest in forest of intermediate age. Several measures of dominance increased with succession due to the very high abundance of a few species, combined with the occurrences of many rare species in more mature habitats. Areas of high capture rates for particular species did not correspond with the locations of singing males of those species, suggesting that habitat suitable for singing perches may differ substantially from habitat used for feeding and other activities.

## INTRODUCTION

Given the common scenario of shrinking total forest area, combined with increasing physical and biotic disturbance of remaining forest, the question of how different bird species and communities respond to particular modes and intensities of forest disturbance assumes importance both to conservationists and theoretical ecologists. A convenient conceptual framework for connecting a series of man-modified ecological communities into a logical and temporal continuum is the paradigm of secondary succession, whereby natural vegetation gradually (and somewhat predictably) regenerates following the cessation of agriculture, grazing or other intense disruption. Successional trajectories continue to be generated on a very large scale, even in eastern North America, where a century-old pattern of farm abandonment continues at a somewhat reduced rate. This "re-starting" of successional sequences is even more widespread in the tropics, where farms and cattle ranches are often abandoned a few years after establishment. Clearly, the future abundance and distribution of many forest-associated bird species at both temperate and tropical latitudes will be determined largely by their resistance to habitat disturbance and their ability to recolonize regenerating woodlands.

In the present day, we attempt to characterize species-level and community-level aspects of local bird distribution as functions of the physiognomy of a typical temperate-zone successional continuum.

## STUDY AREA

The study was conducted between 1970 and 1974 at the Smithsonian Environmental Research Center, a 1000-ha tract that borders the Chesapeake Bay approximately 10 km SSW of Annapolis, Anne Arundel Co., Maryland (38° 53' N, 76° 33' W). We quantified bird occurrences and vegetational physiognomy in three contiguous patches of woodland that represented distinct stages of secondary succession. The three sites were located within an area of uniform soil type and topography, and undisturbed up-

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land portions of all three would support the Tulip Poplar forest association (Brush *et al.*, 1980). The earliest successional site was a 4-ha patch that had grown up after a pasture was released from grazing 7-10 years before the study. We recognize that a tract of this size is unlikely to support the full complement of old-field bird species. However, habitat patchiness on this scale is typical of the Middle Atlantic Coastal Plain region, and it is important to document avian responses to this level of habitat fragmentation. The ground and shrub levels of this early successional site supported a dense growth of Japanese honeysuckle (*Lonicera japonica* Thunb.) and a relatively sparse population of sapling trees, principally black cherry (*Prunus serotina* (Ehrhart) ), sassafras (*Sassafras albidum* (Nutt.) Nees) and sweet gum (*Liquidambar styraciflua* L.).

The second study site was part of a 20-ha patch of forest growing on a former pasture that had been abandoned approximately 25 years before the study began. Except for a few scattered mature canopy trees that had been spared when the area was originally cleared for grazing, this forest was an even-aged, closed canopy stand composed of hardwood species that had grown up since abandonment. Dominant trees were sassafras, sweet gum and red maple (*Acer rubrum* L.).

The third and most mature successional site was located within an extensive (ca. 100 ha) tract of late successional tulip poplar woodland (approximate age, 100-120 years). This stand encompassed a well-drained upland section and a floodplain adjacent to a small intermittent stream. Dominant trees were tulip poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* L.), several oak species (*Quercus alba* L., *Q. rubra* L., *Q. velutina* Lam., *Q. falcata* Michaux), mockernut hickory (*Carya tomentosa* (Poiret)), pignut hickory (*C. glabra* (Millet)) and flowering dogwood (*Cornus florida* L.). The shrub layer was well-developed, particularly in the floodplain section, and a rich herbaceous understory was present. Virginia pine (*Pinus virginiana* Mill.) was the only common conifer, and occurred mainly in small patches within the upland section.

#### METHODS

*Mist nesting.*—Girds of 12-m X 2-m nylon mist nets were operated in the three study sites during the 1970-1974 breeding seasons. Within a representative section of habitat at each site, nets were placed in a regular grid at 50-m intervals in rows 100 m apart. Forty-three nets were divided between the upland and floodplain sections of the mature forest site, and eight each were placed in the young and intermediate successional sites. Between 18 May and 7 July, 15-28 nets at a time were operated on dry days between first light and late morning. Total netting effort each year varied from 4-6 days per net, but for the sake of uniform comparison we standardized annual netting effort at 4 days per net by deleting data from extreme dates in late May and early July (when all species may not have been on territory), and by randomly eliminating any remaining "extra" net-days as needed. Thus, our analysis is based on capture records for a total of 20 net-days for each of the 59 net stations, or 1180 total net-days.

Captured birds were individually marked with numbered U.S. Fish and Wildlife Service bands. Species, net location and band number were recorded; sex and age (adult vs. juvenile) were noted where possible. Records of known juveniles, as determined by plumage characteristics or skull ossification, were deleted from the final analysis. Our primary datum was, therefore, the number of captures of putative adults per species per net. We chose this index over possible alternatives (*e.g.*, number of known different individuals per species per net) for two major reasons. First, we wished to quantify the *intensity* of activity (not merely the number of territories present) in the specific sites sampled by our nets. Secondly, given the land-use mosaic and the human resources available to us, expansion of the study to encompass a sufficiently large number of territories for statistical analysis would have been impractical.

*Singing male censuses.*—Standard spot-mapping censuses of singing males (Robbins, 1978) were conducted on the net grids in June during 3 years of the study (1972-1974). We assumed that the presence of a singing male during the height of the breeding sea-

son indicated that a breeding pair occupied the site. Each year, 2-4 censuses were conducted by walking the mist-net rows in the early morning. This sampling intensity was inadequate for an accurate determination of territory size or breeding density in a given year (International Bird Census Committee, 1970), but cumulative records of singing male locations over 3 years should provide an overview of the use of the study area by territorial males of the commoner species, assuming that no major directional changes in community composition occurred over the 3-year period. This assumption might appear less justifiable for the earliest successional site than for the other two, but in the former site the heavy understory of Japanese honeysuckle served to slow the normal rate of succession. To compare distribution of singing males with the mist-net data, we tabulated the number of singing male observations within 25 m of each of the 59 net stations. These occurrence values were then correlated with capture rates species by species. For the mature forest site, where successional change was not evident over the period 1970-1984, we also compared total net capture rates with the results of a standard spot-mapping breeding bird census (8 visits) conducted in 1983.

*Vegetation analysis.* — Prior to statistical analysis of the vegetation data, one of us (PM) subjectively assigned the vegetation at each of the 59 net sites to one of the following five general habitat categories: mature upland hardwood forest (24 sites), mature upland mixed hardwood-conifer forest (7), mature hardwood floodplain forest (12), mid-successional hardwood forest (8), and brushy old field with open or partially open canopy (8).

Measurements and counts of structural characteristics of the vegetation were made at each net station during the summer of 1973, using the method of James and Shugart (1970). The midpoint of each net lane was the center of a 0.04-ha vegetation sampling plot, but the lane itself was avoided when we assessed ground cover and shrub density. As noted above, the nets were placed in a regular rectilinear grid pattern, so that net locations were not biased to sample what we considered subjectively to be favorable microsites for capturing birds. In all, 13 habitat physiognomy variables were measured (Table 1).

TABLE 1. — Loadings of vegetation variables on the first two principal component axes. Values are correlations between the variable and the principal component. Relative ranks of the most important vegetation variables are in parentheses

Mnemonic	Variable	PCA axis	
		1	2
SAPLING	No. trees 7.5 - 15 cm DBH	-0.247	0.792 (2)
SMTREE	No. trees 15 - 37.5 cm DBH	-0.257	0.798 (1)
MEDTREE	No. trees 37.5 - 76 cm DBH	0.255	0.461 (4)
LGTREE	No. trees 76 - 227 cm DBH	0.557	0.166
VLGTREE	No. trees >227 cm DBH	0.681	-0.339
CONIFER	No. conifers	-0.181	0.600 (3)
CANHT	Mean canopy height	0.891 (1)	-0.049
CANRNG	Canopy range (difference between max. and min. canopy ht.)	0.805 (2)	-0.076
CANCOV	% canopy cover*	0.751 (4)	0.211
GNDCOV	% ground cover*	-0.760 (3)	-0.246
LOSHRUB	% horizontal cover 25 cm above ground	-0.662	-0.119
HISHRUB	% horizontal cover 150 cm above ground	-0.587	-0.141
TWIGDEN	Twig density at breast height (ca. 150 cm)	-0.716 (5)	-0.179
Eigenvalue		4.9	2.2
Percent variation explained		38%	17%

\*Transformed to  $[\log_{10}(x+1)/(101-x)]$

Vegetation data were subjected to Principal Components Analysis (PCA) ordination. In order to achieve a projection of multidimensional data into one or a few dimensions, the PCA algorithm creates a series of statistically independent axes, each of which linearly combines the effects of several variables. PCA may not achieve complete statistical independence of axes, particularly where nonlinear correlations exist among the original variables. Such quadratic relationships often produce an arch-shaped distribution (the so-called "arch distortion") when PCA scores for two axes are shown on a biplot. The effects of higher order correlations sometimes can be removed by nonlinear rescaling of the axes, using Detrended Correspondence Analysis (DCA) or related multivariate methods. However, DCA also tends to force the original multivariate pattern of variation into a single dimension (Hill, 1979; Hill and Gauch, 1980), a property that is biologically realistic only if the underlying pattern variation also reflects a single major gradient. When the data describe two or more independent gradients, important information may be lost by DCA ordination. An additional drawback of DCA is that the method is inappropriate for analysis of mixed counts and measurements of continuous characteristics of the vegetation, such as canopy height, percent cover, and number of trees (M.O. Hill, pers. comm.). In view of these problems, we decided against the use of DCA and restricted our gradient analysis to the better-established PCA method. We include these somewhat lengthy comments as a caution to other ecologists who may consider DCA and related nonlinear multivariate methods as panaceas to the problem of vegetation ordination.

Abundances of the most prevalent bird species (based on numbers of captures) were compared with the PCA scores of the 59 net sites to determine whether the intensity of use of the habitat by breeding birds corresponded to distinct regions of multivariate habitat space. Interpretation was simplified by delineating five habitat intervals along the major PCA axis. Interval boundaries were defined so as to include roughly equivalent numbers of net sites in each interval. The score for a species at a particular net site was defined as the site's PCA score multiplied by the number of captures of the species in question. A mean species score for each interval was then computed by averaging the scores for the individual net sites within that interval. The following community characteristics were computed: species richness, diversity of birds active in the understory, evenness and dominance. The number of captures per species per net was our measure of abundance, which in the present context refers to total activity in the understory stratum, not to territorial density *per se*. We used the number of captures per species to compute  $N_2$ , the reciprocal of Simpson's index (Hill, 1973):

$$N_2 = 1/(p_1^2 + p_2^2 + \dots + p_i^2)$$

where  $p_i$  is the number of captures of the  $i$ -th species.  $N_2$  is sensitive to the relative abundance of the commoner species in an assemblage, so it necessarily reflects equitability as well as species richness. In contrast, species richness ( $N_0$ ), the total number of species present, is insensitive to differences in the relative abundance of species, but is highly dependent on sample size, more species being expected in larger samples.

Evenness (E) was computed using the exponential transformation of the Shannon-Weiner diversity index ( $H^1$ ), as recommended by Hill (1973):

$$E = N_1/N_0$$

where  $N_0$  = the total number of species in the sample, and  $N_1 = \exp(-\sum p_i \ln p_i)$ . Thus,  $N_1$  is a number of equally abundant species (as judged by their rate of capture) that would have the same Shannon-Weiner diversity as the observed assemblage.

Some workers (*e.g.*, Engen, 1979; Routledge, 1983) have argued that all evenness indices are inherently biased, and have recommended the use of simple dominance indices as alternatives. To accommodate this viewpoint, we computed three measures of

dominance from the capture data:  $D_1$  = the proportion of total captures contributed by the single most abundant species,  $D_3$  = the proportion of total captures contributed by the three most abundant species, and  $S_{50}$  = the number of species needed to account for 50% of the total captures. As "evenness" decreases,  $D_1$  and  $D_3$  tend to increase, whereas  $S_{50}$  should decrease.

Straightforward comparison of diversity patterns in different communities is complicated by the fact that all diversity indices tend to vary as a function of sample size, independent of underlying patterns of community structure. To compensate for sample size differences among our major habitats, we employed rarefaction. This is a statistical method that estimates the number of species (or other entities) that would be expected in a random subsample of a specified size (*e.g.*, a particular number of captures) taken from a larger, completely enumerated collection of individuals (Simberloff, 1978). The rarefaction procedure entails drawing repeated random subsamples of  $n_s$  "individuals" (in this case, captures) from the larger ( $n_1$  of two samples,  $n_1$  and  $n_2$ ) whose species richnesses are to be compared. The standard deviation of the expected number of species in the subsamples can be calculated (Heck *et al.*, 1975), so the statistical significance of between-sample differences in species richness can be determined. Applications of rarefaction to bird community data are contained in James and Wamer (1982) and James and Rathbun (1981).

### RESULTS

A total of 38 bird species were captured during the 4 breeding seasons of the study (Appendix). Correlations between the number of individuals of a given species that were netted at a given station vs. the relative abundance of singing males within 25 m of the station generally were statistically significant, but their magnitude was very low (Table 2). This result suggests that the requirements for a suitable singing perch or nest site may be somewhat independent of other uses of the habitat (*e.g.*, foraging). However, at least for the upland mature forest section of the study area, the Spearman Rank Correlation between the number of net captures per species vs. the number of breeding pairs per species (based on the 1983 singing male census) was relatively high (Table 3,  $r_s = 0.78$ ;  $p < .01$ ;  $n = 15$  species). A species-by-species comparison of the two survey methods shows they yielded similar relative abundance rankings for most species. However, some canopy specialists (*e.g.*, red-bellied woodpecker, Carolina chickadee) were underrepresented in the net captures, while a few understory specialists (*e.g.*, Kentucky warbler, hooded warbler) were overrepresented.

*Habitat ordination.*—The major PCA-defined habitat gradient appeared to correspond approximately to the successional continuum (Fig. 1, Table 1). PCA axis 1 explained 38% of the total variation in the vegetation data, and defined a transition from sites with dense ground cover and abundant shrubs (strongly negative loadings on GNDCOV, CANCOV, HISHRUB, TWIGDEN), to those with a tall, deep, fully

TABLE 2.—Correlations between captures/net and number of occurrences of singing males within 25 m of the net for all species and for the six most frequently captured.  $n = 59$  for each test

Species	Number of captures	r	Probability
All species	1583	0.244	< 0.05
Wood thrush	450	0.243	< 0.05
Northern cardinal	222	0.041	NS
Red-eyed vireo	187	0.340	< 0.01
Acadian flycatcher	94	0.235	< 0.05
Carolina wren	89	0.214	< 0.05
Ovenbird	74	0.332	< 0.01

closed canopy (strongly positive loadings on CANHT, CANRNG, CANCOV). PCA axis 2 (17% of the variation) seemed to represent a transition from sites with very large trees and abundant ground cover (negative VLGTREE, GNDCOV), to sites dominated by small deciduous trees and Virginia pine (positive loadings on SAPLING, SMTREE, CONIFER). Since the only conifer regularly encountered in the study area (*Pinus virginiana*) tends to be a successional species in the local region, this second PCA axis may represent a secondary successional dimension or a transition from richer to poorer edaphic conditions, or both.

To simplify interpretation of the relationship among the multivariate axes and their underlying variables, we used the stepwise elimination method of James and Wamer (1982) to remove redundant habitat variables from the original list. Variables were dropped one at a time from the PCA until a substantial reduction in the percent variation explained by each axis occurred. This procedure enabled us to reduce the 13 original variables to six residual variables (canopy cover, ground cover, density of the high shrub layer, and the numbers of small, large, and very large trees) without an appreciable loss in the percentage of overall variance explained by the first two PCA axes (Fig. 1). In the reduced PCA, axis 1 distinguished open sites with dense shrub and ground-layer vegetation from those with closed canopy and a high density of large trees, whereas axis 2 emphasized differences in tree diameter.

Our a priori classification of the study area into four major successional "patch" types (early, middle, late/upland, late/floodplain) was not reflected in a sharply delineated mosaic of habitat types in PCA space, although net sites corresponding to our subjective major patch types tended to form diffuse overlapping clouds in different subregions of PCA space. Floodplain and upland mature forest sites overlapped considerably in their physiognomic characteristics. Sites with conifers formed an overlapping transitional zone between immature and mature hardwood forest, a reasonable pattern given

TABLE 3.—Comparison of the relative abundance of bird species in mature upland forest habitat, based on mist-net captures (1970-1974) and a standard singing male census based on eight visits during the 1983 breeding season. The singing male census plot (10 ha) included the mist net grid (6 ha). Data for the Carolina wren are omitted from the computation of the Spearman Rank Correlation ( $r_s$ ) between the two data sets, because this species experienced a catastrophic regional decline in abundance following the severe winter of 1975-1976

Species	Mist-net captures (1971-1974)		Singing male census (1983)		Difference in ranks
	Captures	Rank	Pairs	Rank	
Wood thrush	403	1	14	3	+2
Red-eyed vireo	166	2	21	1	-1
Northern cardinal	165	3	6	5	+2
Acadian flycatcher	81	4	11.5	4	0
Ovenbird	73	5	16	2	-3
Kentucky warbler	64	6	2	11	+5
(Carolina wren*)	55	7	0	15.5	+8.5
Scarlet tanager	40	8	4.5	8	0
Tufted titmouse	36	9	4	9	0
Hooded warbler	27	10	1	13	+3
Carolina chickadee	16	11.5	5	6.5	-5
Eastern wood-pewee	16	11.5	4	10	-1.5
Red-bellied woodpecker	15	13	5	6.5	-6.5
Louisiana waterthrush	13	14	0	15.5	1.5
Great crested flycatcher	12	15	1	13.5	-1.5
Northern parula	0	16	1	13.5	-2.5

$r_s = 0.78$

( $p < .01$ )

\*Omitted from calculation of  $r_s$ .

the above-mentioned association of Virginia pine with midsuccessional forest in the local region.

*Bird occurrences.*—Capture frequencies of most bird species were correlated with the position of the mist nets along the successional gradient defined by the PCA ordination (Fig. 2). With few exceptions, even species that occurred over the entire habitat gradient tended to increase or decrease monotonically as a function of the PCA score of the net site. The only marked exception to this pattern was Louisiana water thrush, a species whose local occurrence is controlled more by proximity to water than by the successional gradient expressed by PCA axis 1.

Ovenbird, Kentucky warbler, wood thrush, red-eyed vireo, and tufted titmouse were notably more abundant in mature forest than in other habitats, but all of these species also occurred regularly in the earliest successional stands (Fig. 2). According to Whitcomb *et al.*'s (1981) classification scheme, ovenbird and Kentucky warbler are long-distance migrants that occupy forest interior habitat and tend to avoid forest edge,

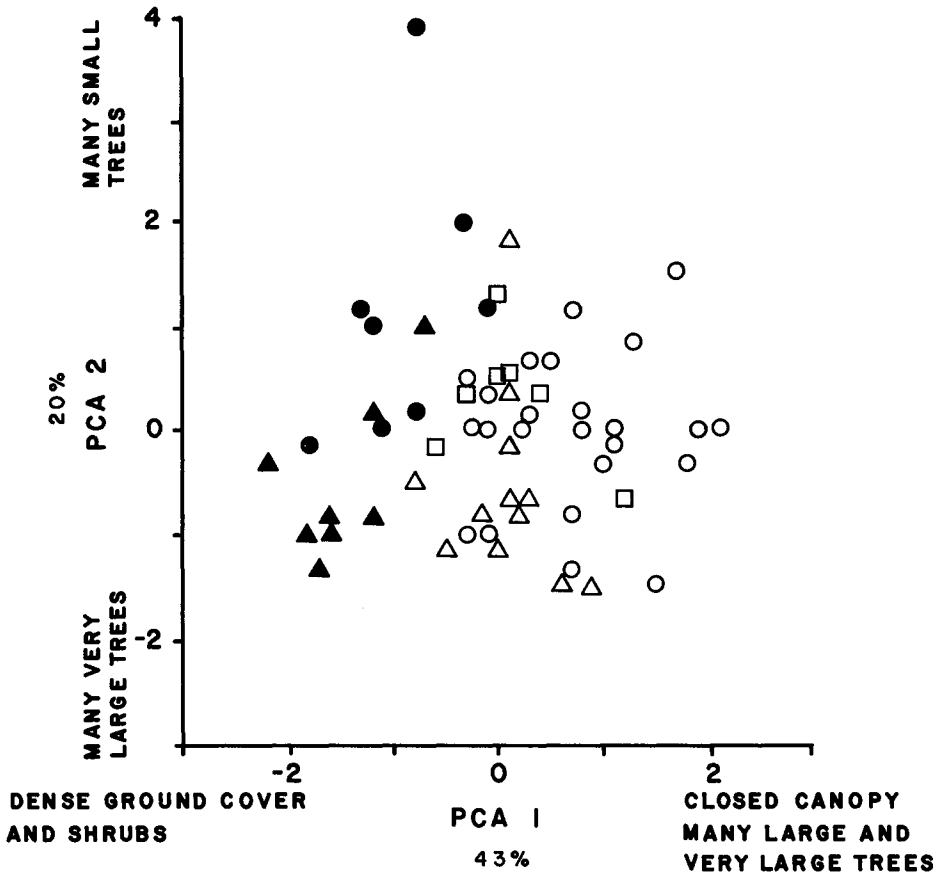


Fig. 1. — Breeding bird capture sites arrayed along first two axes defined by PCA of six variables measuring vegetation structure. The percent variation in the data that is explained by the ordination is given for each axis. Open circles—mature upland hardwood forest; open triangles—mature floodplain hardwood forest; open squares—upland mixed hardwood/conifer forest; closed circles—young upland hardwood forest; closed triangles—brushy old-field with partially open canopy

whereas wood thrush and red-eyed vireo (long-distance migrants) and tufted titmouse (a permanent resident) use both forest interior and forest edge. Scarlet tanager occurred somewhat more frequently in mature forest than in younger vegetation, but its capture rates did not vary markedly with successional maturity. This species was categorized by Whitcomb *et al.* (1981) and Ambuel and Temple (1983) as a long-distance migrant that occupies both forest interior and forest edge habitat, and Lynch and Whigham (1984) found that it was relatively insensitive to forest fragmentation or forest stature.

Acadian flycatcher, an insect-hawking migratory species of forest interiors (Whitcomb *et al.*, 1981; Ambuel and Temple, 1983), showed an anomalous bimodal distribution along the major PCA axis. These small flycatchers tend to use edges and forest clearings for their sallying flights. Regularly spaced net lanes such as were employed in the present study may fall within closed or open portions of an Acadian flycatcher's territory, and some of our net lanes included both microhabitats. The secondary peak in capture rates for Acadian flycatcher in the more "open" portions of the PCA gradient reflected the fact that one net station happened to be located within a small clearing surrounded by rich floodplain forest. Data from this single site, which accounted for the highest number of captures of Acadian flycatcher ( $n = 8$ ) observed at any single net location, produced a secondary modality in abundance. This result illustrates the problems of interpretation that may occur when species organize their activities around specific

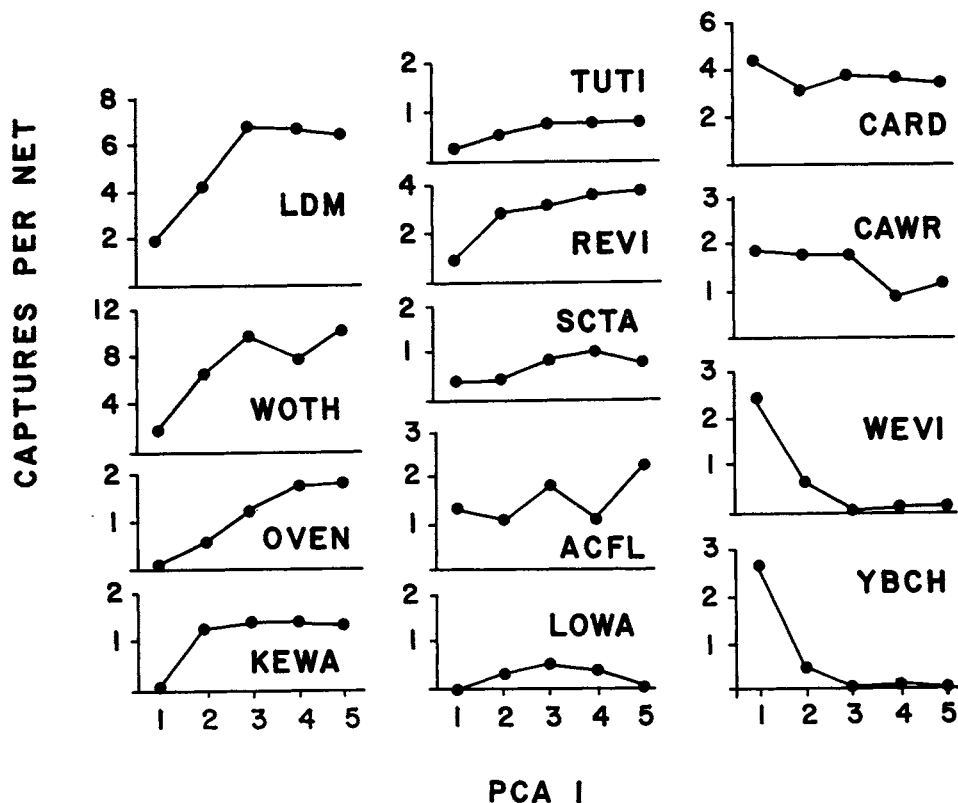


Fig. 2. — Avian use of forested habitat along gradient defined by PCA axis 1 (divided into five intervals), from young to mature forest. LDM = all long-distance forest migrants combined. See Appendix for other abbreviations



microhabitat features, rather than responding to more general features of the vegetation gradient.

Louisiana water thrush is another species whose specialized habitat requirements were not well-expressed by the major PCA gradient. This species nests and forages in riparian forests, and was virtually restricted to mature floodplain forest in our study area. However, because the major PCA gradient did not differentiate upland and floodplain forests, Louisiana water thrush occurrences did not show a monotonic increase or decrease along the dominant axis.

Six of the most frequently netted species (wood thrush, red-eyed vireo, Acadian flycatcher, ovenbird, scarlet tanager and Kentucky warbler) are characterized by Whitcomb *et al.* (1981) as long-distance migrants associated with forest-interior habitat. All six species were captured with substantially higher frequency in late successional forest than in earlier stages (Fig. 2), an indication that they prefer more mature woodlands, as well as interior locations.

Northern cardinal and Carolina wren are nonmigratory species that inhabit forest interiors and edges, as well as brushy habitats (Whitcomb *et al.*, 1981). These two species occurred in essentially all of the habitats we studied, but both were more abundant in dense young forest than in more open mature stands. Northern cardinal was the only one of the six commonest species that did not show a statistically significant correlation between its rate of capture in mist nets and the location of nearby singing males (Table 2). This reflects the fact that male cardinals often sing from the tops of tall trees, whereas foraging individuals are observed in a wide variety of brushy and forested habitats.

The two common species that were most closely associated with the immature end of the successional gradient were white-eyed vireo and yellow-breasted chat, both migratory species what are characterized by Whitcomb *et al.* (1981) as preferring shrub and forest edge. Whereas most species that preferred mature forest also occurred regularly in early successional woods (habitat intervals 2 and 3), the vireo and chat exhibited an abrupt drop in abundance between habitat intervals 1 (partially open, brushy old-field) and 2 (closed canopy sapling woods), an indication that these two species sharply perceive the forest-nonforest transition.

*Community properties.*—Bird species diversity based on numbers of captures ( $N_2$ ) showed a weak but statistically significant negative correlation with successional maturity, as indicated by habitat scores on PCA axis 1 ( $r = -0.254$ ;  $p < 0.05$ ;  $n = 59$ ), but simple species richness ( $N_0$ ) showed no such relationship ( $r = 0.042$ ,  $p > 0.50$ ;  $n = 59$ ). This suggests that observed changes in the diversity index across the successional gradient are mainly a function of changing evenness of the distribution of individuals among species, and do not reflect changes in species richness per se. However, because the evenness index ( $E$ ) may be somewhat sensitive to sample size (Peet, 1974; Routledge, 1983), and because the number of captures per net increased with forest maturity as measured by the value of PCA axis 1 ( $r = 0.413$ ,  $P < 0.01$ ;  $n = 59$ ), the rarefaction technique was a useful adjunct to our analysis. Rarefaction indicated that a part of the between-habitat difference in species richness is indeed attributable to different sample sizes (Table 4). However, equalizing sampling intensity did not result in a monotonic change in species richness as a function of successional maturity. When captures for all five intervals along PCA axis 1 were rarefied to the smallest common denominator ( $N = 242$  captures for interval 1), the lowest projected species richness per sample of captures occurred in the earliest and next to latest successional intervals, with 22-24 species per 242 captures. Intervals 2 and 3, which correspond to closed-canopy forest, showed the highest projected species richness per standard sampling effort (27-28 species per 242 captures). The most mature habitat (interval 5) yielded a rarefied species richness of 24 species, but the relatively high proportion of very rare species in this habitat produced such a large standard deviation that its species richness could not be statistically distinguished from that of any of the other habitats (Table 4).

TABLE 4.—Results of rarefaction analysis of species richness. Mist net samples are assigned to one of five habitat classes based on vegetation scores for PCA axis 1 (*see text*). Values are mean predicted species totals ( $\pm 2$  SD) for different numbers of net captures

Habitat interval	Forest age	Actual captures	Observed species number	Rarified sample size (n)				
				1 (n = 242)	2 (n = 284)	3 (n = 343)	4 (n = 358)	5 (n = 399)
1	Youngest	242	24	24	—	—	—	—
2		284	29	28.2 (26.2-29.8)	29	—	—	—
3		343	28	26.8 (24.9-28.8)	27.5 (26.2-28.8)	28	—	—
4		358	24	22.0 (19.7-24.4)	22.6 (20.9-24.8)	23.8 (22.9-24.7)	24	—
5	Oldest	399	28	24.2 (21.1-27.3)	25.4 (22.7-28.1)	26.8 (24.8-28.8)	27.1 (25.4-28.9)	28

All three dominance indices ( $D_1$ ,  $D_3$ ,  $S_{50}$ ) showed a consistent pattern; a higher proportion of captures was concentrated in the most abundant species in the mature forest community than in earlier seral stages (Table 5, Fig. 3). Thus, northern cardinal, the single most abundant species in the brushy old-field stage, accounted for 20% of the captures in this habitat, whereas the most abundant species in the old-growth forest (wood thrush) made up 37% of the total captures. Similarly, the three commonest species together constituted 44% of the total captures in the brushy oldfield habitat vs. 63% in the mature forest. The higher dominance values observed in the later seral community can in part be attributed to an absolute increase in the abundance (or at least the capture frequency) of a few very common species (wood thrush, red-eyed vireo, northern cardinal), but an additional factor is the capture of a disproportionate number of "rare" species in the mature forest sites: eight of 28 species captured at the 13 net sites with the highest scores on PCA axis 1 were encountered only once.

Thus, three patterns emerged clearly from our mist-netting: (1) capture rates tended to increase with forest maturity; (2) species richness per standardized sample was highest in young forest, and (3) dominance increased with successional age of the vegetation.

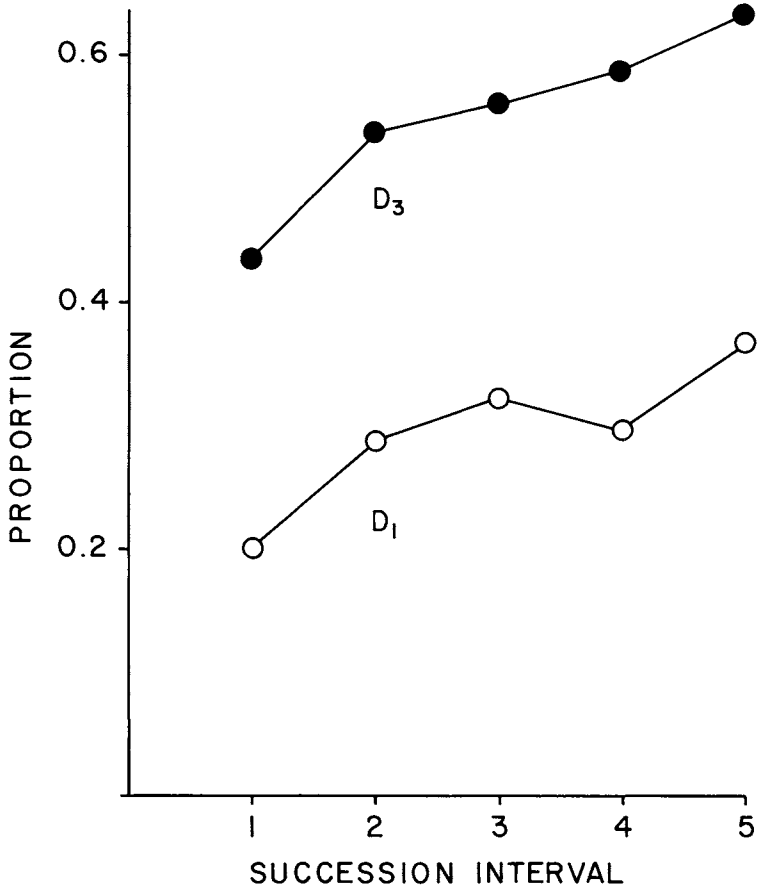


Fig. 3.—Proportional dominance of the most abundant ( $D_1$ ) and the three most abundant ( $D_3$ ) species of breeding birds at sites arrayed along a successional gradient defined by PCA axis 1 (grouped into intervals 1-5), from young to mature forest

## DISCUSSION

In a review of successional trends in eastern North American bird communities, May (1982) defined four major stages within a regenerating forest: herbaceous (his Type A), herb-shrub-sapling (Type B), young forest (Type C) and older forest (Type D). The present study included sites representing May's Types B-D, with most of our net locations corresponding to May's Types C and D. May documented substantial variation in community properties within a given seral stage, but both density and species richness of bird communities tended to decline between the herb-shrub-sapling stage and the young forest stage. However, density and species richness reached their maximum values in mature forest. This "J"-shaped pattern of mid-to-late successional development was especially marked for bird density, which showed nearly a threefold increase between May's Type C and Type D habitats (143 vs. 413 pairs per 40 ha). The corresponding increase in species richness ( $N_0$ ) was somewhat less dramatic (13 vs. 24 species per census plot).

Some of the successional patterns revealed by the present study appear to differ substantially from May's (1982). Our capture rates increased by only about a third between the brushy sapling stage and mature forest stage, and in our study species richness peaked in the young forest and changed little in later successional stages (Table 5). James and Wamer (1982) actually found a slightly *higher* average number of bird species in young deciduous forests than in more mature ones. These authors concluded that this somewhat surprising pattern was a function of successional changes in both the number of individuals/species and the number of individuals/unit area. The density of individual birds was shown by James and Wamer (1982) to be considerably lower in young forests than in mature stands. At least some of the apparent discrepancies among our results and those of James and Wamer (1982) and May's (1982) may be artifacts that reflect different sampling methods. May's generalizations were based on his analysis of 40 data sets gleaned from the Audubon Society's annual breeding bird censuses. These censuses are designed to determine the number of territories of breeding pairs on defined plots, and do not reflect the intensity of use of specified subareas or microhabitats by species within individual territories, nor is the activity of nonterritorial or non-breeding individuals taken into account. As forcefully pointed out by Kricher (1973), extensive use of early successional vegetation is often made by foraging birds that nest in adjacent mature woodlands. Our methodology monitored the activity of all birds active within the understory stratum within specific plots, and thereby produced a profile of habitat use weighted according to the amount of time birds spent in the vicinity of each net site. This approach should yield a more detailed picture of habitat use than can be obtained from the relatively coarse "presence-absence" data obtained by mapping territories within a large census tract. On the other hand, our data are insufficient to

TABLE 5.—Dominance of the single most abundant species ( $D_1$ ), the three most abundant species ( $D_3$ ), and the number of species required to account for 50% of all captures ( $S_{50}$ ), arrayed according to increasing scores on PCA axis 1. See text for definitions of indices

Habitat interval	Forest age	No. nets	Individuals per net	Number of species	$D_1$	$D_3$	$S_{50}$
1	Youngest	11	22.0	24	0.20	0.44	4
2		11	24.6	29	0.29	0.54	3
3		11	31.2	28	0.32	0.56	3
4		13	27.5	24	0.29	0.58	3
5	Oldest	13	28.4	28	0.37	0.63	2

give an accurate estimate of population densities across the successional gradient. Thus neither of the two survey methods is ideal for all purposes, but we would argue that documenting the intensity of feeding activity or other habitat use is highly relevant if one wishes to correlate energy flow, secondary productivity, trophic organization or other ecological variables with the position of vegetation within a gradient or mosaic. We recognize that mist-net surveys have inherent disadvantages. Mist-netting does not yield reliable density estimates without a very great sampling effort, and the method is inherently ineffectual for species or individuals that forage primarily above the 2 m height of the nets. This sampling bias is particularly troublesome when, as in the present study, habitats of very different stature are compared (*cf.*, Karr, 1981). However, even if we assume that our mist-net surveys provided us with accurate information only for birds that are active close to the ground, some of our data results appear to contradict generally accepted successional trends (*e.g.*, Odum, 1969; May, 1982). The observed tendency for a few very common species to strongly dominate the understory of the mature forest was especially surprising to us, in view of the predicted pattern of reduced dominance in succession (May, 1982). Perhaps the high species diversity and low dominance that is thought to characterize the avifauna of mature forest (May, 1982) mainly reflect species abundance patterns in the higher strata of the forest. On average, there was a better than 1 in 3 chance that a bird netted in the forest understory of our study area would belong to a single species—wood thrush. The latter species nests and feeds in the understory, but many of the commonest canopy-feeders (*e.g.*, red-eyed vireo, scarlet tanager) were also captured regularly in our nets. One might assume a priori that the actual abundance of such species would be severely underrepresented by their rate of capture in mist nets, but comparisons of capture rates with the singing male census in the mature forest habitat (Table 3) showed that red-eyed vireo ranked almost as high in both studies (second vs. first), whereas scarlet tanager was the eighth most frequently encountered species by both methods.

We suggest that a more complete sampling of forest birds would have certainly increased total bird density in the taller (*i.e.*, more mature) forest. In addition, an exhaustive census probably would have increased the equability of the mature forest bird community, by increasing the incidence of some relatively common canopy-foraging species (*e.g.*, Carolina chickadee, red-bellied woodpecker) that were rarely caught in our mist nets. These trends, if confirmed, would tend to bring our results more into line with the general successional patterns documented by May (1982).

The sharpest delineation in habitat use by the birds we studied occurred between the early shrub stage with partial canopy closure (interval 1 on PCA axis 1), and young forest with a closed canopy of saplings (intervals 2 and 3 on PCA axis 1). Forest-dwelling species made some use of the earliest available stages of shrubby growth, but species typically associated with old fields and forest edges rarely or never occurred in young or mature forest with closed canopy and low shrub density. Willson (1974) and May (1982) also found that the sharpest changes in birds species diversity along the successional gradient occurred in the early seral stages, and Collins (1983) defined two basic assemblages of breeding northern wood warblers—those associated with forest and those found in shrub-forest edges. Willson (1974) showed that bird species diversity reaches a plateau once a stand is sufficiently mature to contain large trees; further successional increases in foliage volume or height diversity are not associated with higher bird species diversity. Our results are in general accord with these cited studies, although we would not wish to overemphasize the importance of tree presence and stature (*cf.*, James and Wamer, 1982), as the density of ground cover and shrubs also appear to influence the occurrence of species along the generalized successional gradient. The responses of individual birds (as opposed to populations and communities) to habitat heterogeneity were not specifically addressed in this study. Collins (1983) and May (1982) have shown that between-individual variation contributes strongly to overall heterogeneity in habitat use. Existence of several levels of complexity in habitat selection and

use decreases the likelihood that one or a few simple vegetation variables can adequately describe or predict habitat use by a given species, much less an entire assemblage.

Lynch and Whigham (1984) showed that species-specific responses to forest floristics and physiognomy must be considered in conjunction with island biogeography if avian responses to forest fragmentation are to be realistically assessed. We have shown in the present study that once a plot of successional forest within a larger matrix of mature forest is sufficiently mature to achieve nearly complete canopy closure, it will be used at least to some degree by many forest-dwelling bird species, but will cease to be occupied by species characteristic of old fields and forest edges. We emphasize that we have not purported to define essential breeding habitat for bird species. Instead, we have attempted to identify sections of a successional gradient where substantial bird activity does or does not occur. Defining the quality and quantity of habitat essential for long-term success in foraging and breeding of bird species remains a pressing challenge for ecologists and conservationists alike.

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#### APPENDIX

Bird species captured in mist nets, with acronyms used in the text, and tables in parenthesis

*Archilochus colubris*, Ruby-throated hummingbird; *Colaptes auratus*, Northern flicker; *Dryocopus pileatus*, Pileated woodpecker; *Melanerpes carolinus*, Red-bellied woodpecker; *Picoides villosus*, Hairy woodpecker; *P. pubescens*, Downy woodpecker; *Myiarchus crinitus*\*, Great crested flycatcher; *Empidonax virescens*, Acadian flycatcher (ACFL); *Contopus virens*, Eastern wood-pewee; *Cyanocitta cristata*, Blue jay; *Parus carolinensis*, Carolina chickadee; *P. bicolor*, Tufted titmouse; *Sitta carolinensis*, White-breasted nuthatch; *Thryothorus ludovicianus*, Carolina wren (CAWR); *Mimus polyglottos*, Northern mockingbird; *Dumetella carolinensis*, Gray catbird; *Toxostoma rufum*, Brown thrasher; *Turdus migratorius*, American robin; *Hylocichla mustelina*, Wood thrush (WOTH); *Poliophtila caerulea*, Blue-gray gnatcatcher; *Vireo griseus*, White-eyed vireo (WEVI); *V. olivaceus*, Red-eyed vireo (REVI), *Parula americana*, Northern parula; *Dendroica discolor*, Prairie warbler; *Seiurus aurocapillus*, Ovenbird (OVEN); *S. motacilla*, Louisiana waterthrush (LOWA); *Geothlypis trichas*, Common yellowthroat; *Icteria virens*, Yellow-breasted chat (YBCA); *Oporornis formosus*, Kentucky warbler (KEWA); *Wilsonia citrina*, Hooded warbler (HOWA); *Quiscalus quiscula*, Common grackle, *Molothrus ater*, Brown-headed cowbird; *Prianga olivacea*, Scarlet tanager (SCTA); *Cardinalis cardinalis*, Northern cardinal (NOCA); *Passerina cyanea*, Indigo bunting; *Carduelis tristis*, American goldfinch; *Pipilo erythrophthalmus*, Rufous-sided towhee; *Spizella pusilla*, Field sparrow; *Zonotrichia albicollis*, White-throated sparrow

\*Only encountered in singing male census