

## **Effects of Forest Fragmentation on Breeding Bird Communities in Maryland, USA**

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### *ABSTRACT*

*Point surveys were used to estimate the abundance and diversity of forest birds in relation to the size, degree of isolation, floristics, physiognomy, and successional maturity of 270 upland forest patches in the coastal plain province of Maryland. Physiognomic and floristic characteristics of the tree, shrub, and herb layers of the forest were measured at each site.*

*The local abundance of almost every bird species breeding in the interior of upland forests was found to be significantly influenced by forest area, isolation, structure, or floristics, or combinations of these factors. Highly migratory species tended to be most abundant in extensive stands of mature, floristically diverse forests that were only slightly isolated from sources of potential colonists. Densities of permanent residents and short-distance migrants tended to be less affected by these site characteristics, or showed responses opposite in sign to those of long-distance migrants.*

*The impacts of forest fragmentation on bird populations are complex and species-specific. Many bird species respond strongly to factors other than, or in addition to, forest patch area and isolation. Dissection of the landscape into small highly isolated patches of forest adversely affects some bird species, but structural and floristic characteristics of the forest are more important than patch size and isolation for many species, given the existing distribution of forest patches in the coastal plain of Maryland.*

## INTRODUCTION

Human activity has converted most of the formerly extensive upland forests of the central Atlantic coastal plain of the US into an archipelago of relatively small 'islands' and peninsulas of forest that are bordered by croplands, pastures, fallow fields, roads, and other non-forest habitat. The insularization process has accelerated in recent decades in the heavily populated coastal corridor of the eastern US, a fact that has potentially severe implications for the preservation of biotic diversity in this region (Forman *et al.*, 1976; Lynch & Whitcomb, 1978; Morse, 1980; Robbins, 1980; Whitcomb *et al.*, 1981). The objectives of the present research were to quantify some of the effects of habitat fragmentation on birds that inhabit tracts of upland forest in the coastal plain of Maryland. We wished to understand how forest-inhabiting bird species differ in their responses to habitat fragmentation, and to assess the overall suitability of different kinds of forest (e.g. mature hardwood stands, successional woods, pine-dominated forest) as habitat for forest-interior bird species.

## METHODS

### **Study area and selection of forest patches**

The study area comprised six counties (Anne Arundel, Prince Georges, Charles, Kent, Queen Annes and Talbot) in the coastal plain province of Maryland (Fig. 1). The first three counties are on the 'Western Shore' of Chesapeake Bay; the other three are 'Eastern Shore' counties. In general, the intensity of human disturbance decreases from north to south in the Western Shore counties, such that Anne Arundel and Prince Georges counties have less remaining forest than does Charles County (Brush *et al.*, 1980). This north-south gradient in disturbance is not evident on the Eastern Shore. The latter area is more intensively farmed, and remaining woodlots tend to be separated by extensive areas of cropland.

Patches were first selected by reference to USGS topographic maps. Final determination of patch area and isolation was made from measurements of recent aerial photographs provided by the US Department of Agriculture. We sought to include forest patches representing a broad size range. Tracts that were less than 5 ha were not included in the study, because the point surveys we used to estimate bird

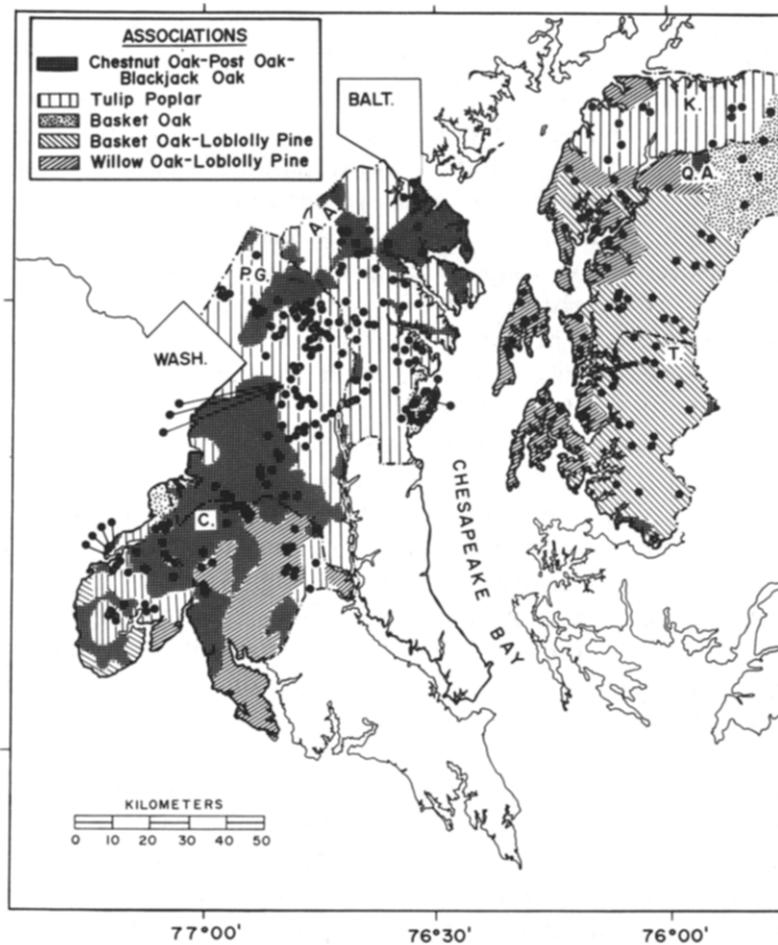


Fig. 1. Map of the six-county study area in Maryland, USA, showing vegetation types (after Brush *et al.*, 1980) and points where birds and vegetation were surveyed. A.A. = Anne Arundel, P.G. = Prince Georges, C = Charles, K = Kent, Q.A. = Queen Annes, T = Talbot.

densities may be 'contaminated' by species from surrounding open habitats in very small tracts. We set no upper limit to the area of the tracts surveyed, and some exceeded 1000 ha of essentially continuous forest. We also attempted to include a wide range of variation in the isolation of forest patches. Conceptual problems were evident with respect to both the definition and the measurement of isolation. We considered a tract to be isolated if it was separated from other forests on all sides by at least 10 m of open land. Thus, a large forested area that was bisected by a road was

considered to constitute two tracts, although the degree of isolation would be quite small in this example. Other workers might choose some other distance (say, 100 m) as the critical cutoff between isolated and non-isolated forest patches. However, any such criterion is arbitrary, and it seems unlikely that the cutoff we chose seriously biased the apparent responses of bird species to increasing isolation.

We computed three isolation indices, each of which measured a different aspect of patch separation. Isolation index ISA was defined as the shortest distance between the border of a given forest tract and the nearest forested area of at least 100 ha. We intended this metric to be appropriate for bird species that are unlikely to breed in patches of forests smaller than 100 ha. Isolation measure ISB was the shortest distance to the nearest forest of at least 50 ha. This measure might be relevant if tracts smaller than 100 ha are acceptable as breeding sites, population reservoirs, or 'stepping stones' that functionally connect larger forest patches. A third measure of isolation (ISC) was defined as the median of eight measurements of distance from the edge of a forest patch to the nearest tract of at least 50 ha, measured in each of the eight principal compass directions. ISC might be a relevant metric if the overall regional configuration of forest tracts, rather than any single interpatch distance, influences local species occurrences.

Because we initially decided to restrict our analysis to upland (i.e. non-riparian) forest tracts, we attempted to avoid tracts that contained sizeable streams. This was possible for most patches smaller than about 50 ha, but many larger patches unavoidably contained small, usually ephemeral, streams. In such instances we were careful to conduct our surveys as far as possible from the vicinity of the stream. Patches with extreme length:width ratios ( $l:w > 3.0$ ) were not included in order to minimize possible perimeter effects. Our only other conscious bias in the selection of patches for inclusion in the study was avoidance of tracts that recently had undergone severe human-related disturbance (e.g., logging, grazing, fire).

### **Point surveys of breeding birds**

The single point survey method (MacClintock *et al.*, 1977; Lynch & Whitcomb, 1978; Robbins, 1980; Whitcomb *et al.*, 1981) was used to obtain a quantitative index of the occurrence and relative abundance of breeding bird species. This technique is a modified version of the IPA

(Indice Ponctuel d'Abondance) developed by European workers (Blondel *et al.*, 1970; Ferry, 1974).

Results of the single point survey method have been compared with data obtained from the much more labour-intensive breeding bird spot-map technique by Whitcomb *et al.* (1981), who concluded that three 20-min point surveys are sufficient to discover about 90% of the species present in a local area. The two techniques yield comparable estimates of relative abundance of the commoner species.

On each of three visits the positions and identities of singing territorial males, calling individuals, and birds seen but not heard were recorded on a map. The seasonal total number of breeding pairs per point was estimated as the maximum number of territorial males perceived on any one visit. While the maximum distance of detectability, and hence the absolute estimate of density, varies from species to species, quantitative comparisons of the abundance of a given species can be made among plots (Whitcomb *et al.*, 1981). For tracts up to about 100 ha in extent, the centre of the tract was chosen as the survey point; in larger tracts the survey point was not always at the geometric centre, but was far enough from the margins to be representative of forest-interior conditions. In order to increase our coverage within large forest tracts, two survey points were chosen in patches of 50–100 ha, and three points were chosen for patches larger than 100 ha. A practised observer could perform as many as five 20-min point surveys during a morning period of observation, depending on logistical difficulties. All surveys were conducted during early to mid-morning (0530 h–1000 h) and each point was surveyed three times during the breeding season.

All birds encountered were noted, but we restricted our analysis to the smaller (body weight < 50 g) diurnal species that breed in upland forest habitat. Thus, 'edge' species (e.g., common crow, mourning dove) were excluded, as were hawks, owls and caprimulgids.

### **Vegetation surveys**

Vegetation was sampled in 196 forest patches on the Western Shore in 1979 and in 74 patches on the Eastern Shore in 1980. Sampling procedures were based on the methods of James & Shugart (1970). Five circular 0.04 ha plots were sampled in all patches that were less than 100 ha in size. Ten such plots were sampled in forests larger than 100 ha. The same central reference point was used for both the plant and bird

surveys. One 0.04 ha plant sampling plot was placed at this point, and the remaining four vegetation plots were located by random selection of bearing and distance from the central point. Stem diameters of all trees greater than 10 cm dbh were measured within each plot. Shrubs (i.e. all woody plants less than 10 cm dbh) were counted in two 2 m × 22 m transects that intersected at the centre of each plot. Four 1 m<sup>2</sup> herb plots were randomly positioned within each 0.04 ha plot.

Mean canopy height for each patch was determined at the central sampling plot by averaging 5 canopy height measurements made with a Haga altimeter. Percent canopy cover was visually estimated at the same location.

The following summary data were calculated for each species in each forest patch.

*Trees:* Density, relative density, frequency, relative frequency, basal area, relative basal area, relative dominance.

*Shrubs:* Density, relative density, frequency, relative frequency, relative dominance.

*Herbs:* Average cover class, relative cover class, average abundance class, relative abundance class, frequency, relative frequency, relative dominance.

### Data analysis

Our approach was statistically to screen a large set of potentially important predictor ('independent') variables in an effort to quantify their individual and combined effects on community-level and species-level response ('dependent') variables. The community-level response variables included the following measures of bird diversity and density:

1. *Total number of bird species (TBS)*—number of species encountered in a given tract during the three surveys.
2. *Total number of pairs of birds (TBP)*—minimum total number of different pairs encountered during the point surveys.
3. *Bird diversity (BDE)*—Calculated as the exponential form of the familiar Shannon-Weiner diversity statistic ( $BDE = \ln^{-1}(-\sum p_i \ln p_i)$ ), where  $p_i$  = proportion of total number of birds that is contributed by individuals of species  $i$ . BDE is the effective number of equally abundant species sampled.

4. *Number of forest interior bird species (FSP)*—number of surveyed species that normally breed within forest, as opposed to ‘edge’ or open habitats. Lynch & Whitcomb (1978) and Whitcomb *et al.* (1981) discuss criteria for assigning species to habitat categories. Our ‘forest interior’ group includes the interior and interior-edge groups of Whitcomb *et al.* (1981).
5. *Abundance of forest-interior species (FPR)*—number of pairs that belong to species which normally breed within forest.
6. *Number of ‘edge’ species (ESP)*—number of surveyed species that are primarily associated with ‘edge’ habitat, clearings, or other habitat besides forest-interior (Whitcomb *et al.*, 1981).
7. *Abundance of ‘edge’ species (EPR)*—number of pairs belonging to species that normally do not breed in undisturbed forest interior.

The species-level response variables we studied were the estimated point densities for each of the 31 most common forest-interior bird species.

We examined the statistical relationships between each of the above community-level and species-level response variables and the following predictor variables.

1. *Forest area (LAR)*—the natural logarithm of the area in hectares.
2. *Isolation from the nearest large forest tract (ISA)*—measured as the straight-line distance (in tenths of km) between the edge of a given tract and the nearest continuous forest of at least 100 ha.
3. *Isolation from nearest medium-sized forest tract (ISB)*—measured as the straight-line distance (in tenths of km) between the border of a given tract and the nearest continuous forest of at least 50 ha.
4. *Average isolation from medium-sized forest tracts (ISC)*—computed as the median distance (in tenths of km) from a given tract to the nearest continuous forest of at least 50 ha in each of the eight principal compass directions (N, NE, E, SE, S, SW, W, NW).
5. *Canopy height (CHT)*—average height (in metres) of canopy trees at centre of forest patch.
6. *Percent canopy cover (PCC)*—estimated canopy closure of forest at centre of forest patch.
7. *Pine dominance (PIN)*—sum of the relative densities of *Pinus virginiana* and *P. taeda* in each forest patch.
8. *Tree density (FDT)*—average number of woody stems (dbh 10 cm) per hectare.

9. *Shrub density (NSD)*—average number of woody stems (dbh 10 cm) per hectare.
10. *Herb density (HCT)*—average percent cover of herbs in each forest.
11. *Basal area of forest (BAF)*—average basal area ( $\text{m}^2 \text{ha}^{-1}$ ) of each forest patch sampled.

Stepwise linear regression (Draper & Smith, 1966) was used to generate equations relating community or species-level responses of birds to structural and floristic aspects of forest composition. The computed equations included all predictor variables that showed statistically significant partial correlations with the response variable in question. The stepwise method begins with the predictor variable that is most highly correlated with the response variable, then successively adds the remaining predictor variables in decreasing order of their ability to reduce 'unexplained' variation in the response variable. This stepwise procedure terminates when additional predictor variables fail to cause a statistically significant ( $p < 0.05$ ) reduction in unexplained variance.

## RESULTS

### Distribution and general characteristics of forest patches

Bird surveys were performed in 270 forest patches, but we obtained vegetation data for only 183 of those sites (Fig. 1). Although some of the vegetation associations mapped in Maryland by Brush *et al.* (1980) occur on both shores of Chesapeake Bay, there are geographic differences in their distribution. Thus, the tulip poplar and chestnut oak–post oak–blackjack oak associations are prevalent on the Western Shore, while the basket oak–loblolly pine and willow oak–loblolly pine associations are most common on the Eastern Shore (Fig. 1).

Most of the 196 study sites in the three Western Shore counties fell within the tulip poplar assemblage (115 patches) or the chestnut oak–basket oak–blackjack oak assemblage (46 patches); the 35 remaining patches were divided among four assemblages with restricted distribution in the study area (Table 1). Most of the 74 forest patches on the Eastern Shore were mapped by Brush *et al.* (1980) as basket oak–loblolly pine (39 patches) and willow oak–loblolly pine (19 patches) associations. A few of

TABLE 1

Classification of 270 Forest Patches Sampled in this Study according to Vegetation Types Defined and Mapped by Brush *et al.* (1980). Tabled Values are Numbers of Forest Patches that occur in the Associations Abbreviated as follows: TP = Tulip poplar, C-P-B = Chestnut oak-Post oak-Blackjack oak, BO = Basket oak, B-L = Basket oak-Loblolly pine, W-L = Willow oak-Loblolly pine, RB-S = River birch-Sycamore

County	Forest association					
	TP	C-P-B	BO	B-L	W-L	RB-S
Western Shore						
Anne Arundel	36	10	15	—	—	—
Prince Georges	63	20	—	—	—	—
Charles	16	16	—	2	16	2
Total	115	46	15	2	16	2
Eastern Shore						
Kent	11	—	2	7	2	—
Queen Annes	—	—	3	15	14	—
Talbot	—	—	—	17	3	—
Total	11	0	5	39	19	0

the northernmost patches on the Eastern Shore were in areas mapped as either tulip poplar or the basket oak assemblage.

Edaphic and topographic factors presumably are responsible for differences in the vegetation on the two sides of Chesapeake Bay, for the two areas are closely similar in climate. Typical agricultural and silvicultural practices also differ on the two sides of the Bay: farms are much larger, and woodlots are more intensively managed on the Eastern Shore than on the Western Shore. Comparison of USGS topographic maps and aerial photographs prepared over the past 20 years reveal little change in the configuration of forest tracts in Eastern Shore counties, whereas rapid suburbanization in the past 20–30 years has destroyed or fragmented many forest patches on the Western Shore.

As summarized in Table 2 and Fig. 2, average patch characteristics differed on the two shores of Chesapeake Bay, although large variances were associated with most variables. Compared with forest patches on the Eastern Shore, Western Shore woodlots tended to be larger (mean area = 31 vs 18 ha), less isolated (ISA = 0.7 vs 1.8 km), less dominated by pine

TABLE 2

Summary Statistics for Forest Patches. Variables are more fully described in the text. LAR = Logarithm of Patch Area; ISC = Median Distance to Nearest Patch of 50 ha; ISB = Shortest Distance to Patch of 50 ha; ISA = Shortest Distance to Patch of 100 ha; CHT = Canopy Height; PCC = Per cent Canopy Cover; BAF = Basal Area of Forest ( $\text{m}^2 \text{ha}^{-1}$ ); FDT = Tree Density; NSD = Shrub Density; HCT = Per cent Herb Cover; PIN = Relative Density of Pines; TPS = Total Plant Species; TDE = Tree Diversity; SDE = Shrub Diversity; HDE = Herb diversity

Variable	Western Shore (n = 169)		Eastern Shore (n = 74)	
	Mean	SD	Mean	SD
LAR	3.42	1.34	2.92	1.33
ISC	11.61	13.18	30.38	19.17
ISB	3.17	6.30	12.74	15.63
ISA	7.39	11.13	18.01	15.63
CHT	24.34	8.69	23.11	9.70
PCC	59.34	18.62	65.94	25.04
BAF	29.36	9.59	29.24	25.04
FDT	555.18	179.77	534.69	191.67
NSD	31 653	14 012	24 900	14 262
HCT	5.47	4.05	2.66	2.86
PIN	2.34	7.74	20.96	29.42
TPS	44.65	14.74	32.44	12.51
TDE	8.52	3.13	7.55	2.89
SDE	18.36	5.77	13.97	6.17
HDE	9.04	5.47	5.03	4.08

(PIN = 2.3 vs 21.0 trees  $\text{ha}^{-1}$ ), and richer in tree species (TDE = 8.5 vs 7.6 equally abundant species), shrub species (SDE = 18 vs 14 equally abundant species), and herb species (HCT = 9 vs 5 equally abundant species). On the other hand, forest tracts on both sides of Chesapeake Bay were closely similar in tree density (FDT = 555 vs 535 trees  $\text{ha}^{-1}$ ), basal area of trees (BAF = 29 vs 29  $\text{m}^2 \text{ha}^{-1}$ ) and mean canopy height (CHT = 24 vs 23 m).

#### Total bird species (TBS) and bird species diversity (BDE)

For the Western Shore sites the only significant correlations with the total number of bird species were negative associations with PIN and ISB (Table 3). Thus, non-isolated tracts with few pines tended to have more species. Although the relationship was statistically highly significant ( $p <$

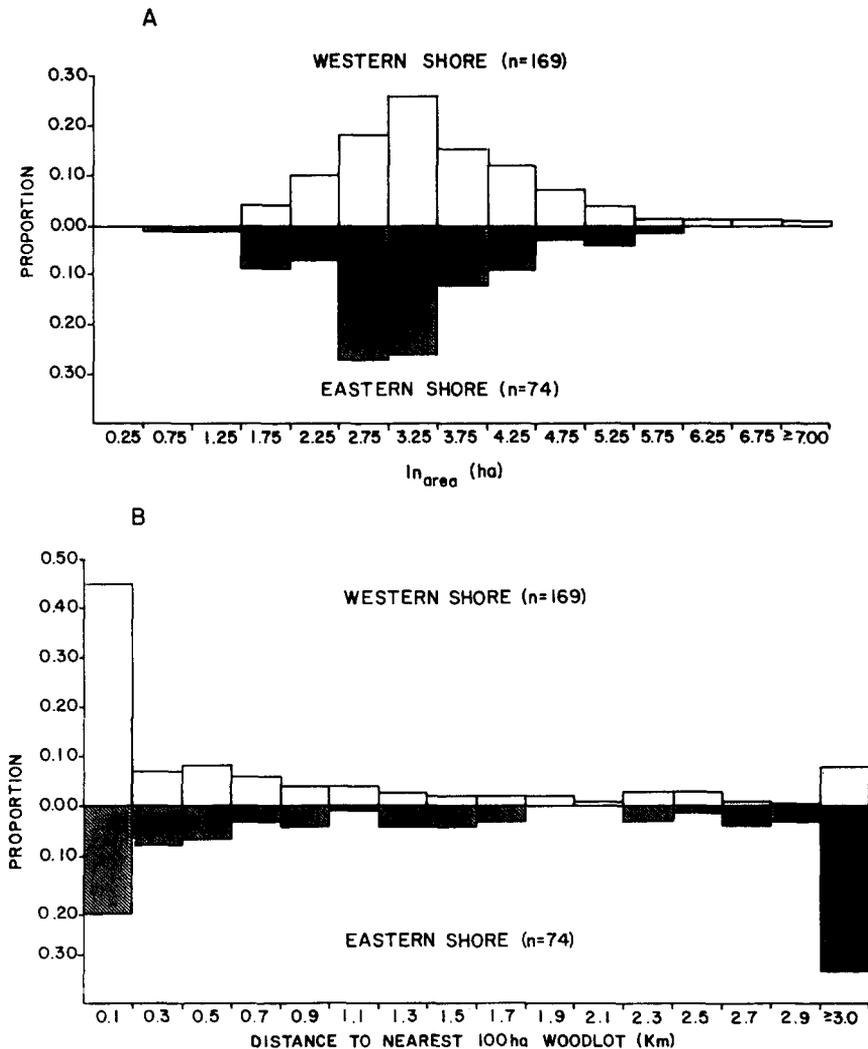


Fig. 2. Distributions of area (A) and isolation (B) of forest patches that were studied on the western and eastern shores of Chesapeake Bay.

0.001), only about 9% of the variation in TBS could be attributed to PIN and ISB (Table 3). The strongest determinant of total species number on the Eastern Shore was patch area (LAR) (Table 3). This relationship was negative, i.e. smaller tracts tended to have more bird species at a given point. Canopy height (CHT) and herb cover (HCT) also showed significant negative associations with TBS. The combined predictive

TABLE 3  
 Significant Responses of Bird Community Characteristics to Predictor Variables (\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ )

Community characteristic	Code	Western Shore	Eastern Shore	Combined
Total bird species	TBS	PIN* (neg), ISB* (neg)	LAR*** (neg), CHT* (neg), HCT* (neg)	LAR** (neg)
Total number of pairs of birds	TPB	ISA** (neg), HCT**, NSD*	LAR** (neg)	HCT***, ISA** (neg), LAR* (neg) FDT** (neg)
Exponential species diversity	BDE	FDT** (neg)	None	
Total forest-interior species	FSP	HDE**, ISA** (neg)	None	
Total forest-interior pairs	FPR	HCT***, ISA*** (neg), BAF***	ISB* (neg)	
Total edge-field species	ESP	LAR*** (neg), CHT (neg)*	LAR*** (neg), HCT**, CHT*	
Total edge-field pairs	EPR	LAR*** (neg), PCC* (neg), BAF* (neg)	LAR*** (neg), TPS*, CHT*	

power of the four independent variables was moderate ( $R = 0.53$ ;  $p < 0.001$ ), and 28% of the variance in species number could be accounted for by the combined effects of the predictor variables. When the results from both sides of Chesapeake Bay were combined, only patch area (LAR) remained a statistically significant predictor of TBS, and the relationship was a relatively weak negative one ( $r =$  simple correlation coefficient  $= -0.22$ ;  $p < 0.01$ ).

The exponential species diversity index was weakly related to tree density (FDT) on the Western Shore ( $r = 0.26$ ;  $p < 0.01$ ), and was not significantly correlated with any predictors on the Eastern Shore ( $p < 0.05$  for all predictor variables). For both shores combined, FDT was a weak but statistically significant predictor ( $r = 0.19$ ;  $p < 0.05$ ).

### **Total abundance of birds (TPB)**

For the Western Shore sites, the significant partial correlations with TPB were negative associations with isolation (ISA) and shrub density (NSD), and a positive association with herb density (HCT), ( $R = 0.42$ ;  $p < 0.001$ ). For the Eastern Shore counties, forest area (LAR) showed a significant negative correlation with TPB ( $r = -0.32$ ;  $p < 0.01$ ). For the two shores combined, HCT, ISB, BAF and LAR all contributed significantly to the prediction of TPB ( $R = 0.35$ ;  $p < 0.001$ ). Thus, total abundance of individual birds seems somewhat more predictable than bird species diversity, but the same habitat descriptors appear to be important for both community variables.

### **Number of forest-interior bird species (FSP) and individuals (FPR)**

Because a majority of the birds encountered in the point surveys were classed as forest-interior species, one would expect that the same predictor variables associated with total species number and total number of pairs of birds should also be correlated with the number of pairs and species of forest-interior birds (FPR and FSP). In fact, this proved to be true for only some of the important predictor variables.

On the Western Shore, HDE (positive) and ISA (negative) were the best predictors of FSP ( $R = 0.40$ ;  $p < 0.001$ ), whereas FPR was significantly influenced by HCT, ISA (negative) and BAF ( $R = 0.53$ ;  $p < 0.001$ ). For the Eastern Shore, there were no significant correlations between FSP and any of the predictor variables. FPR showed a statistically significant, but

weak, negative correlation with ISB ( $r = -0.22$ ;  $p < 0.05$ ). Pooled data for both shores revealed a weak but statistically significant relationship between FSP and HDE ( $r = 0.23$ ;  $p < 0.01$ ), and a stronger relationship between FPR and TBS, BAF, ISA and HCT ( $R = 0.56$ ;  $p < 0.001$ ).

### **Number of 'edge' species (ESP) and individuals (EPR)**

As expected, this group of birds responded differently from forest-interior species to disturbance. For both the Western and Eastern Shores, the best predictor of number of species and pairs of 'edge' birds was patch area (LAR). The sign of the correlation is negative, so small patches have more 'edge' species and individuals. For the Western Shore, LAR and CHT both showed significant negative correlations with ESP ( $R = 0.37$ ;  $p < 0.01$ ), while in the Eastern Shore these two variables plus HCT were significantly correlated with ESP ( $R = 0.66$ ;  $p < 0.001$ ). The number of pairs belonging to 'edge' species was negatively correlated with LAR, PCC and BAF on the Western Shore ( $R = 0.46$ ;  $p < 0.001$ ). On the Eastern Shore, EPR showed significant correlations with LAR, TPS and CHT ( $R = 0.69$ ;  $p < 0.001$ ).

### **Response of individual species**

In this discussion, only the combined occurrence of species on both shores are considered. Complete data for Eastern and Western Shore separately are given in Appendix B. The local abundances of 30 of the 31 most common forest interior species proved to be significantly correlated with at least one of the 15 predictor variables (Table 4). The sole exception was pileated woodpecker, a species that occurred in only 17 of the 183 forest patches for which we have complete data. The uncommonness of this species, combined with its very large territorial size, made it difficult to pinpoint the factors that control its occurrence.

It is convenient to summarize the association of local abundance levels of individual bird species with the 15 predictor variables by combining the latter into six functional groups: patch area (LAR), patch isolation (ISA, ISB, ISC), physiognomy of tree stratum (BAF, CHT, FDT, CHT), physiognomy of herbaceous and shrub understorey (HCT, NSD), abundance of conifers (PIN) and floristic diversity (TPS, TDE, SDE, HDE).

**TABLE 4**  
 Significant Responses of Individual Bird Species to Predictor Variables. Data Combined for Both Shores of Chesapeake Bay

<i>Species<sup>a</sup></i>	<i>Significant predictors</i>	<i>R<sup>b</sup></i>
<i>Neotropical migrants</i>		
Cuculidae		
Yellow-billed cuckoo	TPS (neg)***, ISC***, ISA (neg)***	0.42***
Trochilidae		
Ruby-throated hummingbird	SDE*	0.17*
Tyrannidae		
Acadian flycatcher	TPS***, ISC (neg)***	0.64***
Eastern wood pewee	CHT***, LAR (neg)*	0.26**
Great-crested flycatcher	ISC***, HCT (neg)***, PIN**	0.57***
Turdidae		
Wood thrush	ISB (neg)***, ISC**, CHT**, BAF**	0.44***
Parulidae		
Black-and-white warbler	BAF (neg)***, ISC (neg)*, LAR*	0.38***
Hooded warbler	TPS**, HCT**, SDE (neg), FDT (neg)*	0.45***
Kentucky warbler	LAR***, HCT**, SDE (neg)*, FDT (neg)*	0.39***
Parula warbler	TPS***, LAR**	0.43***
Ovenbird	ISC (neg)***, FDT***, SDE***, HCT*	0.53***
Worm-eating warbler	PIN***, ISB (neg)**	0.32***
Vireonidae		
Red-eyed vireo	TPS***, PIN (neg)***, ISC (neg)***, LAR**	0.65***
White-eyed vireo	HCT**, BAF (neg)**	0.27**
Yellow-throated vireo	SDE**, ISC (neg)**	0.29***
Thraupidae		
Scarlet tanager	SDE**, PIN (neg)*	0.33***
<i>Short-distance migrants</i>		
Picidae		
Common flicker	ISC***, TPS (neg)**	0.45***
Mimidae		
Catbird	LAR (neg)***, SDE (neg)***, PIN (neg)*	0.36***
Corvidae		
Blue jay	TPS (neg)***, ISC**, NSD**, CHT*	0.54***
Parulidae		
Pine warbler	PIN***, PCC (neg)*, SDE*	0.64***
Sylviidae		
Blue-gray gnatcatcher	PCC (neg)***, ISB (neg)**	0.30***
Fringillidae		
Rufous-sided towhee	FDT**, TDE (neg)*	0.26**

(continued)

TABLE 4—*contd.*

<i>Species</i> <sup>a</sup>	<i>Significant predictors</i>	<i>R</i> <sup>b</sup>
<i>Permanent residents</i>		
Picidae		
Downy woodpecker	LAR (neg)**, PIN**, ISC (neg)**, CHT*	0.25***
Hairy woodpecker	ISB**	0.26***
Pileated woodpecker	None	—
Red-bellied woodpecker	BAF***, FDT (neg)***	0.39***
Troglodytidae		
Carolina wren	ISA**	0.24**
Sittidae		
White-breasted nuthatch	CHT***	0.25***
Paridae		
Carolina chickadee	SDE (neg)**	0.20**
Tufted titmouse	PCC (neg)*	0.15*
Fringillidae		
Cardinal	HCT***, NSD (neg)**	0.47***

<sup>a</sup> Complete list of scientific names and common names given in Appendix A.

<sup>b</sup> Coefficient of multiple correlation; significant levels: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

### *Patch area*

Local density of eight bird species showed a statistically significant dependence on patch area (Tables 4–6). Five species, all neotropical migrants, had significantly higher point densities in larger tracts; three species (a neotropical migrant, a short-distance migrant, and a permanent resident) were more abundant in smaller tracts. These data tend to support our initial hypothesis that neotropical migrants as a group are more sensitive than resident species or short-distance migrants to reduction in forest size.

### *Patch isolation (ISA, ISB, TSC)*

The local density of about half (16 of 31) of the common bird species were significantly correlated with one or more of the three measures of patch isolation (Tables 4–6). Eleven species responded to ISC (median distance to a forest of at least 50 ha), four species responded to ISB (minimum distance to a forest of at least 50 ha) and three responded to ISA (minimum distance to a forest of at least 100). Thus, it would appear that the regional configuration of patches is more relevant to many bird

**TABLE 5**  
 Number of Bird Species (of 31 total) showing Significant ( $p < 0.05$ ) Positive (+) or Negative (-) Partial Correlations with 15 Habitat Variables. The Variable showing the Highest Partial Correlation for Each Species is given in Line b. ('Primary Vbl')

<i>Migratory group</i>	<i>Predictor variables</i>														
	LAR	ISC	ISB	ISA	BAF	CHT	FDT	PCC	HCT	NSD	PIN	HDE	SDE	TDE	TPS
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
Neotropical migrants															
a. total	5, 1	3, 5	0, 2	0, 2	2, 2	2, 0	1, 2		3, 1	0, 1	2, 2		4, 1		4, 1
b. primary Vbl	1, 0	1, 0	0, 1	0, 1	0, 1	1, 0		1, 0	1, 0		1, 0		3, 0		4, 1
Short distance migrants															
a. total	0, 1	2, 0	0, 1		1, 0		1, 0	0, 2		1, 0	1, 1		1, 1	0, 1	0, 2
b. primary Vbl	0, 1	1, 0			1, 0		1, 0	0, 1			1, 0				0, 1
Permanent residents															
a. total	0, 1	0, 1	1, 0	1, 0	1, 0	2, 0	0, 1	0, 1	1, 0	0, 1	0, 1		0, 1		
b. primary Vbl	0, 1		1, 0	1, 0	1, 0	1, 0		0, 1	1, 0						
All species															
a. total	5, 3	5, 6	1, 3	1, 2	3, 2	5, 0	2, 3	0, 3	4, 1	1, 2	4, 3	0, 0	5, 3	0, 1	4, 3
b. primary Vbl	1, 2	2, 0	1, 0	1, 1	1, 1	2, 0	1, 0	0, 1	2, 0	0, 0	1, 0	0, 0	3, 1	0, 0	4, 2

TABLE 6  
Summary of Patterns of Association between Bird Species Abundances and Functional Groups of Predictor Variables

Functional group	Individual variables	Number (and percentage) of species showing significant correlations			
		Neotropical migrants (n = 16)	S-D migrants (n = 6)	Residents (n = 8)	Total <sup>a</sup> (n = 30)
Patch area	LAR	6 (38)	1 (17)	1 (13)	8 (27)
Patch isolation	ISA, ISB, ISC	10 (63)	3 (50)	3 (38)	16 (53)
Tree physiognomy	BAF, CHT, FDT, PCC	8 (50)	4 (67)	4 (50)	16 (53)
Understorey physiognomy	HCT, NSD	3 (19)	0 (0)	1 (13)	4 (13)
Pine abundance	PIN	4 (25)	2 (33)	1 (13)	7 (23)
Plant diversity	HDE, SDE, TDE, TPS	10 (63)	5 (83)	1 (13)	16 (53)
<i>Summary</i>					
Median number significant predictors per species		2.9	2.7	1.6	
Median value of R (multiple correlation coefficient)		0.40	0.40	0.25	

<sup>a</sup> Does not include pileated woodpecker, which showed no significant correlations with any of the predictor variables.

species than is any single inter-patch distance. Neotropical migrants tended to be less abundant in isolated tracts (9 of 12 significant correlations negative), but no such pattern existed for residents and short-distance migrants (4 positive, 3 negative correlations). Again, this result tends to support our initial hypothesis that long-distance migratory species are more sensitive to forest fragmentation.

*Physiognomy of the tree stratum (BAF, CHT, FDT, PCC)*

Eighteen bird species showed significant relationships between their local density and one or more of the four descriptors of forest physiognomy (Tables 4–6). Basal area of the forest (BAF), canopy height (CHT) and density of trees (FDT) each influenced five species, and per cent canopy cover (PCC) influenced three species. Four of the five species whose abundance was correlated with BAF were neotropical migrants, but there is no indication of differences among the migratory groups in their responses to the other three variables. Tall forests with incomplete canopy closure were favourable to the greatest number of species.

*Physiognomy of understorey (HCT, NSD)*

Local densities of eight bird species were significantly correlated with herb cover (HCT) or shrub density (NSD), or both (Tables 4–6). There appeared to be a tendency for species to favour forests with a dense herbaceous ground cover (4 of 5 significant correlations with HCT positive).

*Abundance of pines (PIN)*

Point densities of seven bird species were significantly related to the abundance of pines (almost entirely *Pinus virginiana* and *P. taeda*) but there was no marked tendency for either positive or negative correlations to prevail (4 correlations positive, 3 negative).

*Floristic diversity (TDS, TDE, SDE, HDE)*

The abundances of more than half (16 of 31) of the commonest forest-interior bird species were significantly correlated with one or more plant diversity factors (Tables 4–6). Shrub diversity (SDE) accounted for eight significant correlations (5 of them positive), with total number of plant species (TPS) next in importance (7 significant correlations, 4 of them positive). The abundance of one species was negatively correlated with

tree diversity (TDE); no bird species abundance was significantly correlated with herb diversity (HDE).

Neotropical migrants as a group tended to favour diverse plant associations—8 of 10 significant correlations with plant diversity factors were positive. Residents and partial migrants showed an opposite trend—4 of 5 significant correlations that involved the latter two groups were negative.

### *Summary*

Measures of forest isolation, plant diversity and tree physiognomy were the best predictors of the local abundance of individual bird species, accounting for a total of 51 separate significant partial correlations among 29 of the 31 commonest breeding species. Only the abundances of pileated woodpecker and the northern cardinal were uncorrelated with one or more of these three functional groups of predictors. As noted earlier, pileated woodpecker was encountered too infrequently to allow a meaningful analysis of its habitat requirements using our methodology. In contrast, northern cardinal is an abundant species, but its abundance is influenced by the physiognomy of the understorey (NSD, HCT), rather than that of the tree stratum (Table 4 and Appendix A), as noted in an earlier study by Anderson & Shugart (1974).

Forest area (LAR) was significantly associated with the local density of only eight bird species, and area was the most important predictor of abundance for just three species. On the other hand, the three isolation measures accounted for 18 significant partial correlations.

## DISCUSSION

### **Importance of forest area vs other habitat factors**

Workers in Europe (Oelke, 1966), England (Moore & Hooper, 1975), Wisconsin (Bond, 1957), Delaware (Linehan *et al.*, 1967), New Jersey (Forman *et al.*, 1976; Galli *et al.*, 1976), and in the Piedmont and Appalachian sections of Maryland and adjacent states (Robbins, 1980; Anderson & Robbins, 1981; Whitcomb *et al.*, 1981) have studied the effects of habitat fragmentation on forest-associated birds. Evaluation of this previous research in the light of the present study is difficult, as most earlier workers considered only a limited number or size range of forest

patches, and few have assessed other potentially important patch characteristics such as isolation, floristics and forest physiognomy.

Some previous studies (e.g. Oelke, 1966; Linehan *et al.*, 1967) have documented a tendency for total bird numbers to increase in small forest patches; others (e.g. Moore & Hooper, 1975; Forman *et al.*, 1976; Galli *et al.*, 1976; Robbins, 1980; Anderson & Robbins, 1981; Whitcomb *et al.*, 1981) have focused on the effects of patch area on the species composition of bird communities. Only Robbins (1980) has statistically analysed the relative contributions of vegetation factors, isolation and area on bird community composition. Robbins used multiple regression analysis to quantify the effects of these predictor variables on the local abundance of bird species in 67 forest islands located in the Piedmont of Maryland, Pennsylvania, Virginia and West Virginia. He found that canopy height and forest isolation were the most consistently important predictors of the abundances of 51 analysed bird species, accounting for a total of 21 significant correlations. Patch area *per se* accounted for only six significant correlations, although a possibly correlated variable (distance from census point to edge of patch) contributed 10 additional significant correlations. Robbins (1980) also reported the results of a second regression analysis of data from 80 breeding bird census plots in the northeastern US. In the latter analysis, the area of contiguous habitat showed the highest number of statistically significant correlations with individual bird species abundances. However, because Robbins' second analysis did not include patch isolation as a predictor variable, the apparent inconsistency between the results of his two studies cannot be resolved. Similarly, Anderson & Robbins (1981) describe a multivariate analysis of the effect of patch area, isolation and vegetation on bird communities in the Appalachian province of western Maryland, but they present data only for patch area vs bird abundance. Thus, although several studies have concluded that patch area exerts a major constraint on the composition of breeding bird communities, the only previous study that presented data on a multivariate analysis of habitat factors in addition to area yielded ambiguous results. This may be due to statistical intercorrelations between patch area and other habitat variables, some of which may exert a more direct influence on bird numbers than does area *per se*. As a result of this pattern of intercorrelation, patch area often shows a large *simple* correlation with bird abundance or diversity, even though its *partial* correlation coefficient (which measures the contribution of area independent of other factors) is small or statistically insignificant.

The results of the present study help to clarify the relative importance of various habitat factors in controlling bird distribution. In general, our results are in agreement with those reported by Robbins (1980) for 67 woodlots in the Piedmont of Maryland, Virginia, West Virginia and Pennsylvania. In our study, patch isolation (ISA, ISB, ISC), forest physiognomy (BAF, CHT, FDT, PCC) and floristic diversity (HDE, SDE, TDE, TPS) together accounted for 44 of 66 statistically significant partial correlations with the abundances of 30 forest-interior bird species. Only eight species showed a statistically significant independent correlation with patch area (LAR), and three of these correlations were negative (i.e. three species were more abundant in smaller patches). Kentucky warbler was the only species for which patch area was the most important predictor of local abundance and ovenbird was the only species whose local abundance was most highly correlated with one of the three isolation indices (Table 4). In contrast, measures of forest physiognomy and plant richness were the most important predictors of the abundance of 19 species. Thus, within the range of patch area (generally 5–1 000 ha) and isolations (generally 0.1–1 km) we considered in our study, vegetation characteristics, rather than patch geometry, appear to play the dominant role in determining community composition and the local abundance of individual bird species.

The conclusion by earlier workers that area is the key characteristic that determines occurrence of many migrating bird species in forest tracts appears to be valid for certain species (e.g. Kentucky warbler) under a wide range of patch sizes and isolations. Other species evidently do not respond strongly to habitat fragmentation unless patches are smaller or more isolated (or both) than those considered in the present study. It seems likely that the previous tendency to emphasize area as the key habitat factor stems, at least in part, from insufficient appreciation of the complex inter-relationship between area, isolation, canopy height, tree density and other habitat characteristics. In the present study, forest area was significantly ( $p < 0.01$ ) intercorrelated with ISC, ISB and PCC; thus, small forest tracts also tended to be highly isolated and to possess a relatively dense canopy. Statistical analysis revealed that it was these latter features, rather than area itself, that influenced occurrences of many bird species. Simple correlation analysis of abundance vs patch area obscures these relationships. Small forest tracts do tend to support few or no individuals of certain bird species, but many of the species in question appear to respond directly to other habitat features that themselves are correlated with area.

The relatively low degree of isolation of forest patches on the Maryland coastal plain (Table 2), as opposed to the nearby Piedmont area studied by Robbins (1980) and Whitcomb *et al.* (1981) may have resulted in patch area having relatively low importance as an independent predictor of species occurrences in our study. Whitcomb *et al.* (1981) showed that fairly small forest patches can maintain a reasonably complete avifauna, provided their isolation from the nearest extensive 'mainland' source area is sufficiently low. In our study, the average distance to the nearest patch of at least 50 ha (ISB) was about 0.4 km, whereas in the Piedmont area studied by Robbins (1980), the equivalent figure (measured to the nearest 40 ha patch) was 4.7 km, or about ten times as great (C. S. Robbins, pers. comm.).

Finally, some bird species of high conservation interest may combine area-sensitivity with rarity, such that statistically significant patterns will be difficult to document, even if a large number of tracts are sampled. A case in point is the worm-eating warbler, a relatively uncommon species that has been characterized as area-sensitive in earlier studies in the middle Atlantic Piedmont region (Robbins, 1980; Whitcomb *et al.*, 1981). This species was encountered in only 15 of the 183 tracts where we conducted both point surveys and vegetation studies. As a result, our data for this species are dominated by a very large number of 'zero' entries. In such situations, non-parametric analysis of occurrence patterns, using presence-absence data, are more appropriate than our regression-correlation approach. Although non-parametric multiway contingency analysis was not attempted, a binomial test of the significance of differences in the percentage of all small tracts where the worm-eating warbler occurred ( $2/217 = 0.9\%$  of all tracts  $< 35 \text{ ha}^2$  where point surveys were conducted) vs the percentage occurrence in larger tracts ( $26/207 = 12.6\%$  of tracts  $> 35 \text{ ha}$  where point surveys were conducted) revealed a highly significant ( $p < 0.01$ ) association of the species with larger tracts. Whether area *per se* or some factor correlated with area plays the controlling role in the present distribution of the worm-eating warbler is yet to be determined. This relationship might have emerged from our correlation analysis if a sufficiently large number of very large forest tracts had been sampled (we surveyed only 14 tracts that exceeded 1000 ha). However, the few existing tracts of this size in our study area tend to be highly disturbed successional woods.

We would concur with the view put forth by Bond (1957), and seconded by Whitcomb *et al.* (1981), that habitat quality and area are to some extent compensatory in their influences on bird occurrences. Above some

critical minimum acceptable patch area, floristically and physiognomically 'rich' forest patches may support bird communities that are quantitatively and qualitatively similar to those found in larger, but 'poorer' forests. We suggest that patch isolation is another important compensatory factor, but we emphasize that these and other habitat characteristics are not completely interchangeable for any bird species. Thus, some species never utilize very small, highly isolated patches of forest, no matter how floristically 'rich' these forests may be.

Another potential problem is the possibly discontinuous nature of the response of birds to variation in some of our predictor variables. Our measurement of isolation is a case in point. It is possible that birds do not perceive a forest patch as functionally isolated unless the distance separating it from a neighbouring patch exceeds some minimum threshold value. Although most of our tracts were isolated by distances of hundreds of metres or more (Table 2), we considered forests as discrete patches if they were separated by distances as small as 10 m. Our admittedly conservative definition of isolation could have the effect of underestimating the functional area of forest tracts as perceived by birds. Thus, a 100 ha tract bisected by a roadway might be perceived as a single forest tract by at least some birds, whereas we would have treated it as two 50 ha fragments in our analysis. This reciprocity between isolation and area might blur the distinctions between the avifauna of smaller vs larger forest patches.

### **Habitat disruption and migratory strategies**

The results of the present study reinforce earlier suggestions (e.g. Lynch & Whitcomb, 1978; Greenberg, 1980; Robbins, 1980; Whitcomb *et al.*, 1981) that long-distance migration in forest-interior birds tends to be associated with a syndrome of biological characteristics. One such characteristic is sensitivity to habitat disruption (e.g. reduced forest area, increased isolation, decreased floristic and physiognomy richness). Fourteen of 18 significant correlations between the local density of individual neotropical migrant species and forest area or forest isolation were in the predicted direction (i.e. positive correlation with area, negative correlation with isolation). This is a statistically significant tendency ( $p < 0.05$ ; binomial test). Short-distance migrants and permanently resident species showed a very different pattern. Although the total number of species in these two migratory groups was nearly as great as the number of

neotropical migrants (14 vs 16), the former group showed only eight significant correlations with descriptors of forest area or isolation, and six of the eight coefficients had signs opposite those predicted for the neotropical migrants. Thus, most species that are not highly migratory either showed no significant response to patch area and isolation, or actually attained higher densities in tracts that were smaller or more isolated. We again emphasize that this result might not have been obtained if the available range of patch areas and isolation values had been very different.

Our results document a tendency for forest-associated neotropical migrants to respond positively to what many ecologists would consider to be habitat 'quality' factors. Thus 15 of the 16 common neotropical migrants showed a total of 21 statistically significant correlations between their local abundance and our measures of forest stature and floristic complexity (BAF, CHT, HCT, NSD, HDE, SDE, TDE, TPS). Importantly, the signs of these correlations were not arbitrary: neotropical migrants tended to be more abundant in forests where plant diversity is higher (8 of 10 significant correlations positive) and where the forest is tall with well-developed herb and shrub layers (7 of 11 significant correlations positive). The overall pattern (15 of 21 correlations in the predicted direction) is significantly different from random ( $p < 0.05$ ; binomial test).

In contrast, short-distance migrants and permanent residents tended either to be uncorrelated with indicators of forest stature and diversity (four species), or to exhibit correlations of opposite sign from that predicted for long-distance migrants (eight species). Early successional forests (characterised by high values for PIN and FDT, and low values for CHT and BAF) were utilized at least to some degree by all three migratory groups, but they were not generally the preferred habitat. Among the neotropical migrant species, 7 of 13 significant correlations of abundances with the named variables had signs that indicate higher abundance in more mature forest. Short-distance migrants and permanent residents showed a similar response to forest maturity: six of nine significant correlations had signs indicating preference of species for more mature forest.

The causal mechanisms by which migratory strategy interacts with habitat preference remains unclear, but Greenberg (1980) and Whitcomb *et al.* (1981) have suggested that demographic factors may explain at least some differential responses to habitat disruption. Some or all of the

following demographic characteristics that typify forest interior neotropical migrants may be related to their sensitivity to habitat degradation: low clutch size, low incidence of multiple clutches per breeding season, tendency to build open nests that are placed on or near the ground, tendency for young birds to disperse far from their home area following fledging. The significance of this last feature, which might increase the likelihood that first year birds will 'miss' their home forest patch when they return to breed following their first migration, has been discussed by Whitcomb *et al.* (1981), and the phenomenon has been mathematically modelled by May (1981).

### **Implications for conservation and management**

Some results of the present study may be relevant to the development of regional strategies for the conservation and management of bird population, but any broad generalizations must be tempered by sensitivity to the ecological uniqueness of each species. At the most general level, this study is a confirmation and quantification of what experienced field ornithologists would have predicted all along—each bird species responds to a unique combination of habitat features (e.g. James, 1971; Anderson & Shugart, 1974; Anderson, 1979). Because the 'niche Gestalt' (James, 1971) of each species is different, no single management intervention will benefit all species and almost any conceivable 'habitat enhancement' strategy will have negative impacts on many species. However, if it is agreed that particular species are of prime conservation interest because they are rare or threatened, management decisions may be somewhat less arbitrary.

For some local species (e.g. Kentucky warbler, ovenbird) the geographic configuration of habitat patches appears to be of paramount importance, and factors such as patch area and isolation importantly influence local breeding densities. But for a much larger group of species local density is not a simple continuous function of forest geometry, but instead is strongly dependent on habitat physiognomy and floristics. We recognize, of course, that all species are subject to the ultimate constraint of habitat areas too small to support minimal territorial requirements, and the minimal acceptable woodlot size may in fact be substantially larger than the minimum territorial size (cf. Whitcomb *et al.*, 1981). Nevertheless, many small passerines do not presently appear to be markedly restricted by the existing pattern of forest patch area and

isolation in eastern Maryland, at least for patches that exceed 5–10 ha. This is not to say that these species are presently as abundant regionally as they were prior to extensive deforestation of the Middle Atlantic region. Our point is rather that their density within remaining tracts of forested habitat does not appear to be markedly reduced. If we had considered woodlots of much smaller size, or if we had studied an area where average isolation of forest patches is greater (e.g. the Piedmont of Maryland or New Jersey) our results might have been very different (Forman *et al.*, 1976; Galli *et al.*, 1976; Robbins, 1980) and of course it is possible, even likely, that future changes in land-use in coastal Maryland will severely disrupt the present situation.

The ecological truism that each species is in some ways unique does not mean that meaningful patterns do not exist in the responses of birds to habitat degradation. The neotropical migrants, a group of birds that is of increasing concern to conservationists (Lynch & Whitcomb, 1978; Keast & Morton, 1980; Morse, 1980; Morton, 1980; Robbins, 1980; Whitcomb *et al.*, 1981), show a consistent syndrome of responses to habitat disturbance. For whatever reason, highly migratory species tend to respond negatively to habitat fragmentation (reduction of total habitat area, increased isolation of remaining habitat) and reduction of floristic and structural diversity of breeding habitat. This pattern is obscured if birds of all migratory categories and habitat associations are indiscriminately combined in an analysis, because the same factors that tend to depress local population densities of neotropical migrants often favour permanently resident and short-distance migrant species. Many species that belong to the latter two groups are ecological generalists. Some species are tolerant of a certain degree of habitat disturbance, and often utilize 'edge' habitat as well as forest-interior (Lynch & Whitcomb, 1978; Anderson, 1979; Anderson & Robbins, 1981; Whitcomb *et al.*, 1981). Examples of such habitat generalists include some of the commonest 'backyard' suburban birds within the study area (e.g. Carolina chickadee, gray catbird, blue jay, rufous-sided towhee), none of which is in danger of regional extinction or serious decline. Despite their considerable ecological importance and intrinsic interest, such species are not of urgent concern to conservationists (Anderson, 1979; Noon *et al.*, 1979; Whitcomb *et al.*, 1981).

The total diversity and density of birds may actually increase slightly in smaller forest tracts (see Table 4; also, Oelke, 1966; Linehan *et al.*, 1967), but this mainly reflects the influx of abundant, ecologically generalized

resident and short-distance migrant species. We must therefore avoid a simplistic numbers game when we assess the biological impact of habitat disruption. Because bird species differ in their ecological requirements, they also differ in their resiliency to disturbance, and hence in their conservation importance. The arrival in the US of the introduced European starling *Sturnus vulgaris* and house sparrow *Passer domesticus* did not in any meaningful sense compensate the loss of native forest-interior species such as passenger pigeon *Ectopistes migratorius* or ivory-billed woodpecker *Campephilus principalis*.

### Limitations of the point survey method

We emphasize that the point survey method we employed in the present study is a sampling technique, not an exhaustive censusing method. It yields a quantitative estimate of bird density and diversity in the vicinity of the survey point, but not a total count of individuals and species in an entire forest patch. The point survey method almost inevitably underestimates the true differences between the total avifauna of very small tracts (which may be adequately sampled by a single set of point surveys) and a large tract (which will be severely undersampled, even if two or three points are surveyed). This is simply a manifestation of the familiar species-area relationship (cf. James & Wamer, 1982). Species that have higher point densities in small wooded tracts than in larger forested areas may nevertheless be far less abundant regionally than they were prior to extensive deforestation.

Our data suggest that, above some minimum patch size, correlations between local point density and the area of individual forest patches will tend to be outweighed by the effects of habitat 'quality' and the total extent of suitable forest in a region. This implies that the best regional conservation strategy for some species may be to preserve the maximum total amount of breeding habitat, without unduly emphasizing the extent of each individual forest fragment. On theoretical grounds, Simberloff & Abele (1976, 1982) have suggested that a network of small reserves might contain more species than a single large reserve of the same total area. Although this suggestion has been roundly criticized by biologists who are wary of rationalizing the mindless destruction of remaining forested areas (Diamond, 1976; Terborgh, 1976; Whitcomb *et al.*, 1976), it may be that the crucial difference in these seemingly disparate conservation strategies may relate to just how small the fragmented reserves are in

relation to the size and dispersal abilities of the organisms to be protected. If each individual reserve in a network is large enough to support a breeding population of the target species, and if extinction rates of these species are sufficiently low in relation to recolonization rates, the network approach may be a reasonable one (cf. Higgs & Usher, 1980; Simberloff & Abele, 1982). As a group, small temperate-zone passerines appear better able than many animal groups to recolonize forest tracts following extinction of local populations (Whitcomb *et al.*, 1976; Lynch & Whitcomb, 1978), providing isolation is not excessive. A network of medium-sized forest patches might constitute a viable regional reserve for small migratory birds if each patch is large enough, in close enough proximity, and of high enough habitat 'quality' to be acceptable as breeding sites for the target species. Such a 'network reserve strategy' would not assume, as have previous recommendations by Lynch & Whitcomb (1978), Robbins (1980) and Whitcomb *et al.* (1981), that each individual patch in a system of reserves must be large enough independently to support stable, long-term populations of all target species. However, a very different conservation strategy would be required for more sedentary birds (e.g. many tropical forms), or for large mammals, especially predators, that require extensive home ranges for survival. Such groups may require enormous reserves (thousands or tens of thousands of hectares) if stable populations are to be maintained *in situ* (Terborgh, 1976). If, however, we restrict our attention to small migratory birds, it is unrealistic to consider the heavily fragmented archipelago of forest patches in the eastern US coastal corridor in other than a regional context. Reserves of thousands of hectares of contiguous old growth forest may indeed be optimal for some organisms, even in this region. Certainly, animals such as elk, timber wolf, black bear and mountain lion will never again roam the Atlantic Coastal plain of the US unless enormous reserves are set up for them. However, forested tracts of this size no longer exist in settled regions, and a conservation strategy in this region must have more reasonable goals. Even where relatively large continuous tracts of land can be acquired for conservation purposes, a closely spaced network of somewhat smaller tracts of greater aggregate area may better serve some conservation goals, including preservation of a regional pool of migratory forest bird species. A network of medium-sized avifaunal reserves might, for example, be better protected against catastrophic disruptions, less expensive to purchase, and easier to justify politically than would a single large tract of the same total area. Although

very small forest tracts (of the order of 1–4 ha) have little or no conservation value for most birds in which conservationists are interested, we believe that a system of somewhat larger tracts (10–100 ha) can play a useful role in conserving certain regionally endangered bird species, given the land-use pattern that presently exists in the middle Atlantic coastal plain. However, if average interpatch isolation increases substantially, with a concurrent reduction in the aggregate area of forest, an increasing proportion of the regional breeding population of uncommon migratory birds will be concentrated in the few remaining large tracts. Under such conditions, which would approach literal insularity, much larger avifaunal reserves would be required to maintain bird populations than present land-use conditions appear to dictate. Some species (e.g. worm-eating warbler) have already undergone substantial regional contraction of their former breeding range in the Maryland Piedmont, immediately to the west of the present study area (Robbins, 1980), and we cannot afford to be sanguine with respect to the long-term prospects for other migratory species that are sensitive to habitat degradation.

### **Importance of isolation**

Our results indicate that even a slight degree of habitat isolation importantly reduces the local abundance of some migratory bird species in forest patches. This result may seem surprising, given the long-distance flights undertaken annually by these species. The apparent avoidance by many birds of isolated forest tracts probably represents a 'psychological' avoidance of adjacent open habitats. Various studies have documented the unexpectedly deep penetration of forest-interior by edge-associated physical conditions, as well as edge-adapted predators, competitors, and nest-parasites (Gates & Gysel, 1978; Gates & Mosher, 1981; Ranney *et al.*, 1981; Whitcomb *et al.*, 1981). Whatever their ultimate causes, density responses to forest isolation were widespread among the birds we studied (Table 4). Familiar migratory species such as red-eyed vireo and wood thrush experience a mean decline of about 2% in their local density with each 100 m of isolation. For species such as these, interruption of continuous forest by non-forested corridors as wide as a powerline right of way or a multi-lane highway could have a small, but statistically significant, depressing effect on local population levels.

### **Management implications**

The strong responses of many bird species to what may be termed 'habitat quality factors' might suggest habitat modification as an effective management tool for increasing population levels of selected species. For example, creation of small canopy openings by selective tree removal might benefit blue-gray gnatcatcher, a species that prefers incomplete canopy closure. However, even relatively simple habitat manipulations will be prohibitively expensive if conducted on the geographic scale required for regional preservation. In addition, most of the habitat 'quality' factors that tend to favour neotropical migrants (e.g. increased plant species diversity, increased canopy height, increased dbh values for trees) are associated with old-growth forest. Such factors cannot be effectively enhanced by management interventions, except on a very long-term basis. Thus, the most practical management implications of our data will entail *avoidance* of practices (e.g. reduction of forest area, increase of isolation, removal of understorey vegetation) that have been shown to have negative impacts on target species of special conservation interest.

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## APPENDIX A

Common and scientific names for 31 most abundant birds that bred in upland forest-interior habitat within the eastern Maryland study area. Hawks, owls, and caprimulgids were not considered, due to difficulties in detection or very large home ranges, or both.

<i>Common name</i>	<i>Scientific name</i>
Acadian flycatcher	<i>Empidonax virescens</i>
Black-and-white warbler	<i>Mniotilta varia</i>
Blue-gray gnatcatcher	<i>Polioptila caerulea</i>
Blue jay	<i>Cyanocitta cristata</i>
Cardinal	<i>Cardinalis cardinalis</i>
Carolina chickadee	<i>Parus carolinensis</i>
Carolina wren	<i>Thryothorus ludovicianus</i>
Common flicker	<i>Colaptes auratus</i>
Downy woodpecker	<i>Picoides pubescens</i>
Eastern wood pewee	<i>Contopus virens</i>
Gray catbird	<i>Dumetella carolinensis</i>
Great crested flycatcher	<i>Myiarchus crinitus</i>
Hairy woodpecker	<i>Picoides villosus</i>
Hooded warbler	<i>Wilsonia citrina</i>
Kentucky warbler	<i>Oporornis formosus</i>
Northern parula warbler	<i>Parula americana</i>
Ovenbird	<i>Seiurus auropellus</i>
Pileated woodpecker	<i>Dryocopus pileatus</i>
Pine warbler	<i>Dendroica pinus</i>
Red-bellied woodpecker	<i>Melanerpes carolinus</i>
Red-eyed vireo	<i>Vireo olivaceus</i>
Ruby-throated hummingbird	<i>Archilochus colubris</i>
Rufous-sided towhee	<i>Pipilo erythrophthalmus</i>
Scarlet tanager	<i>Pirango olivacea</i>
Tufted titmouse	<i>Parus bicolor</i>

<i>Common name</i>	<i>Scientific name</i>
White-breasted nuthatch	<i>Sitta carolinensis</i>
White-eyed vireo	<i>Vireo griseus</i>
Wood thrush	<i>Hylocichla mustelina</i>
Worm-eating warbler	<i>Helmitheros vermivorus</i>
Yellow-billed cuckoo	<i>Coccyzus americanus</i>
Yellow-throated vireo	<i>Vireo flavifrons</i>

## APPENDIX B

Multiple regression equations for bird community properties and individual bird species abundances in 74 tracts on the Eastern Shore and 111 tracts on the Western Shore. Predictor variables with significant F-values ( $p > 0.05$ ) are listed in order of decreasing significance levels. Acronyms for predictor variables are defined in the text. Numbers in parentheses are the number of forest patches in which a given species occurred.

<i>Dependent variables</i>	<i>Best regression equation</i>	<i>P &gt; F</i>
<i>A. Community variables</i>		
1. Total number of bird species (NSB)		
a. Eastern Shore	NSB = 29.00 - 1.48 LAR - 0.10 CHT - 0.22 HCT	0.0001
b. Western Shore	NSB = 19.80 - 0.10 PIN - 0.12 ISB	0.0091
c. Both shores	NSB = 22.45 - 0.73 LAR	0.0027
2. Total number of pairs of birds (NPR)		
a. Eastern Shore	NPR = 18.82 - 0.83 LAR	0.0062
b. Western Shore	NPR = 19.07 - 0.10 ISA + 0.25 HCT - 0.0001 NSD	0.0002
c. Both shores	NPR = 16.31 + 23 HCT - 0.05 ISA + 0.07 BAF - 0.53 LAR	0.0001
3. Exponential diversity of bird species (BDE)		
a. Eastern Shore	No significant regression	ns
b. Western Shore	BDE = 12.41 - 0.003 FDT	0.0073
c. Both shores	BDE = 12.24 - 0.002 FDT	0.0131
4. Number of forest-interior bird species (FSP)		
a. Eastern Shore	No significant regression	ns
b. Western Shore	FSP = 13.92 + 0.17 HDE - 0.07 ISA	0.0041
c. Both shores	FSP = 14.38 + 0.09 HDE + 0.35 LAR - 0.002 FDT	0.0006
5. Number of pairs of forest-interior bird species (FPR)		
a. Eastern Shore	FPR = 11.02 - 0.42 ISA + 0.07 BAF	0.0295
b. Western Shore	FPR = 10.67 + 0.29 HCT - 0.10 ISA + 0.12 BAF	0.0001
c. Both shores	FPR = 7.89 + 0.10 BAF - 0.06 ISA + 0.07 TPS + 0.18 HCT	0.0001

<i>Dependent variables</i>	<i>Best regression equation</i>	<i>P &gt; F</i>
6. Number of 'edge' bird species (ESP)		
a. Eastern Shore	ESP = 14.59 - 1.68 LAR - 0.25 HCT - 0.08 CHT	0.0001
b. Western Shore	ESP = 7.99 - 0.63 LAR - 0.06 CHT	0.0005
c. Both shores	ESP = 12.48 - 1.02 LAR - 0.06 TPS - 0.06 CHT	0.0001
7. Number of pairs of 'edge' bird species (EPR)		
a. Eastern Shore	EPR = 9.74 - 1.30 LAR - 0.06 TPS	0.0001
b. Western Shore	EPR = 7.32 - 0.63 LAR - 0.03 PCC - 0.03 BAF	0.0001
c. Both shores	EPR = 7.43 - 0.82 LAR - 0.04 TPS	0.0001
<i>B. Species abundances</i>		
1. Acadian flycatcher (ACFL)		
a. Eastern Shore (n = 16)	ACFL = 0.02 HCT	0.0020
b. Western Shore (n = 85)	ACFL = 0.60 + 0.03 TPS - 0.02 ISC - 0.17 LAR	0.0001
c. Both shores (n = 101)	ACFL = -0.43 + 0.04 TPS - 0.02 ISC	0.0001
2. Black-and-white warbler (BAWW)		
a. Eastern Shore (n = 4)	No significant regression	ns
b. Western Shore (n = 12)	BAWW = 0.26 - 0.01 BAF	0.0006
c. Both shores (n = 16)	BAWW = 0.13 - 0.004 BAF - 0.001 ISC + 0.02 LAR	0.0001
3. Blue-gray gnatcatcher (BGGN)		
a. Eastern Shore (n = 11)	BGGN = 0.04 - 0.001 ISB	0.0315
b. Western Shore (n = 15)	BGGN = 0.29 - 0.003 PCC - 0.002 JSC	0.0032
c. Both shores (n = 26)	BGGN = 0.19 - 0.002 PCC - 0.002 ISB	0.0002
4. Blue jay (BLJA)		
a. Eastern Shore (n = 70)	BLJA = 0.88 - 0.05 HCT	0.0008
b. Western Shore (n = 86)	BLJA = 0.60 + 0.01 ISC - 0.01 TPS	0.0002
c. Both shores (n = 156)	BLJA = 0.52 - 0.01 TPS + 0.006 ISC + 0.0001 NSD + 0.01 CHT	0.0001
5. Cardinal (CARD)		
a. Eastern Shore (n = 72)	CARD = 0.70 + 0.08 HCT + 0.13 ISB	0.0001
b. Western Shore (n = 106)	CARD = 1.55 + 0.07 HCT - 0.0001 NSD	0.0001
c. Both shores (n = 178)	CARD = 1.31 + 0.07 HCT - 0.0001 NSD	0.0001
6. Carolina chickadee (CACH)		
a. Eastern Shore (n = 61)	CACH = 1.23 - 0.010 ISB - 0.01 TPS	0.0168
b. Western Shore (n = 98)	CACH = 0.40 + 0.01 ISC	0.0050
c. Both shores (n = 159)	CACH = 0.86 - 0.02 SDE	0.0009
7. Carolina wren (CAWR)		
a. Eastern Shore (n = 29)	CAWR = 0.11 + 0.01 ISA	0.0375
b. Western Shore (n = 46)	CAWR = 0.62 - 0.01 SDE - 0.05 LAR	0.0062
c. Both shores (n = 75)	CAWR = 0.12 + 0.006 ISA	0.0015
8. Common flicker (COFL)		
a. Eastern Shore (n = 65)	No significant regression	ns
b. Western Shore (n = 41)	COFL = 0.06 + 0.003 ISC	0.0077
c. Both shores (n = 106)	COFL = 0.42 + 0.005 ISC - 0.006 TPS	0.0001
9. Downy woodpecker (DOWO)		
a. Eastern Shore (n = 52)	DOWO = 0.58 + 0.0003 PIN - 0.01 ISC - 0.07 LAR	0.0001
b. Western Shore (n = 82)	DOWO = 0.03 + 0.005 ISA + 0.01 CHT	0.0008
c. Both shores (n = 134)	DOWO = 0.25 - 0.04 LAR + 0.01 CHT	0.0038

<i>Dependent variables</i>	<i>Best regression equation</i>	<i>P &gt; F</i>
10. Eastern wood pewee (EWPE)		
a. Eastern Shore (n = 57)	EWPE = 1.78 - 0.01 PIN - 0.09 TDE - 0.001 NSD	0.0007
b. Western Shore (n = 71)	EWPE = -0.16 + 0.03 CHT	0.0043
c. Both shores (n = 128)	EWPE = 0.42 + 0.02 CHT - 0.09 LAR	0.0026
11. Gray catbird (GRCA)		
a. Eastern Shore (n = 16)	GRCA = 0.60 - 0.14 LAR	0.0001
b. Western Shore (n = 24)	GRCA = 0.19 - 0.04 LAR	0.0324
c. Both shores (n = 40)	GRCA = 0.52 - 0.08 LAR - 0.02 TDE	0.0001
12. Great crested flycatcher (GCFL)		
a. Eastern Shore (n = 64)	GCFL = -0.24 + 0.01 BAF + 0.02 SDE	0.0033
b. Western Shore (n = 38)	GCFL = 0.13 - 0.01 HCT	0.0302
c. Both shores (n = 102)	GCFL = 0.15 + 0.006 ISC - 0.02 HCT + 0.002 PIN	0.0001
13. Hairy woodpecker (HAWO)		
a. Eastern Shore (n = 24)	HAWO = 0.05 + 0.002 ISB	0.0300
b. Western Shore (n = 20)	No significant regression	ns
c. Both shores (n = 44)	HAWO = 0.04 + 0.002 ISB	0.0006
14. Hooded warbler (HOWA)		
a. Eastern Shore (n = 2)	No significant regression	ns
b. Western Shore (n = 50)	HOWA = 0.31 + 0.12 LAR - 0.001 FDT	0.0039
c. Both shores (n = 52)	HOWA = -0.08 + 0.01 TPS + 0.08 LAR - 0.004 ISC + 0.0004 FDT	0.0001
15. Kentucky warbler (KEWA)		
a. Eastern Shore (n = 29)	KEWA = -0.26 + 0.18 LAR - 0.01 PIN	0.0001
b. Western Shore (n = 45)	KEWA = -0.27 + 0.04 HCT + 0.06 LAR	0.0001
c. Both shores (n = 74)	KEWA = -0.24 + 0.03 HCT + 0.09 LAR	0.0001
16. Northern parula warbler (NOPA)		
a. Eastern Shore (n = 3)	No significant regression	ns
b. Western Shore (n = 23)	NOPA = -0.81 + 0.01 TPS + 0.08 LAR	0.0001
c. Both shores (n = 26)	NOPA = -0.58 + 0.01 TPS + 0.06 LAR	0.0001
17. Ovenbird (OVEN)		
a. Eastern Shore (n = 29)	OVEN = -1.17 + 0.002 FDT + 0.18 LAR	0.0013
b. Western Shore (n = 79)	OVEN = -1.25 - 0.04 ISA + 0.002 FDT + 0.02 PCC + 0.06 SDE - 0.08 TDE	0.0001
c. Both shores (n = 108)	OVEN = -0.91 - 0.02 ISA + 0.002 FDT + 0.05 SDE + 0.04 HCT	0.0001
18. Pileated woodpecker (PIWO)		
a. Eastern Shore (n = 6)	PIWO = -0.06 + 0.02 LAR	0.0327
b. Western Shore (n = 11)	PIWO = 0.04 - 0.001 ISC	0.0480
c. Both shores (n = 17)	No significant regression	ns
19. Pine warbler (PIWA)		
a. Eastern Shore (n = 23)	PIWA = -0.33 + 0.01 PIN + 0.01 BAF	0.0001
b. Western Shore (n = 15)	PIWA = 0.38 + 0.02 PIN - 0.005 PCC	0.0001
c. Both shores (n = 38)	PIWA = 0.34 + 0.01 PIN - 0.004 PCC	0.0001
20. Red-bellied woodpecker (RBWO)		
a. Eastern Shore (n = 71)	RBWO = 0.77 - 0.03 HDE - 0.002 PIN	0.0023
b. Western Shore (n = 83)	RBWO = -0.17 + 0.02 CHT - 0.01 PIN	0.0001
c. Both shores (n = 154)	RBWO = 0.40 + 0.02 BAF - 0.0001 FDT	0.0001

<i>Dependent variables</i>	<i>Best regression equation</i>	<i>P &gt; F</i>
21. Red-eyed vireo (REVI)		
a. Eastern Shore (n = 63)	REVI = 0.79 + 0.09 HDE	0.0046
b. Western Shore (n = 109)	REVI = -0.17 + 0.02 CHT - 0.01 PIN	0.0001
c. Both shores (n = 172)	REVI = -0.005 + 0.04 TPS - 0.01 PIN - 0.02 ISC + 0.23 LAR - 0.0001 NSD + 0.02 BAF	0.0001
22. Ruby-throated hummingbird (RTHU)		
a. Eastern Shore (n = 0)	No occurrences	—
b. Western Shore (n = 10)	No significant regression	ns
c. Both shores (n = 10)	RTHU = -0.02 + 0.002 SDE	0.0247
23. Rufous-sided towhee (RSTO)		
a. Eastern Shore (n = 46)	RSTO = 1.06 - 0.08 TDE	0.0392
b. Western Shore (n = 70)	RSTO = -0.11 + 0.01 ISC + 0.001 FDT	0.0001
c. Both shores (n = 116)	RSTO = 0.47 + 0.001 FDT - 0.04 TDE	0.0021
24. Scarlet tanager (SCTA)		
a. Eastern Shore (n = 54)	SCTA = -0.22 + 0.04 SDE	0.0001
b. Western Shore (n = 101)	No significant regression	ns
c. Both shores (n = 155)	SCTA = 0.16 + 0.03 SDE - 0.004 PIN	0.0001
25. Tufted titmouse (TUTI)		
a. Eastern Shore (n = 73)	No significant regression	ns
b. Western Shore (n = 108)	No significant regression	ns
c. Both shores (n = 181)	TUTI = 1.50 - 0.005 PCC	0.0434
26. White-breasted nuthatch (WBNU)		
a. Eastern Shore (n = 4)	WBNU = 0.03 - 0.001 ISA	0.0435
b. Western Shore (n = 10)	WBNU = 0.04 + 0.01 CHT - 0.002 TPS	0.0004
c. Both shores (n = 14)	WBNU = -0.06 + 0.003 CHT	0.0009
27. White-eyed vireo (WEVI)		
a. Eastern Shore (n = 15)	WEVI = 0.14 - 0.002 PIN	0.0215
b. Western Shore (n = 19)	WEVI = -0.04 + 0.02 HCT + 0.06 LAR - 0.01 BAF	0.0012
c. Both shores (n = 34)	WEVI = 0.20 + 0.20 HCT - 0.005 BAF	0.0012
28. Worm-eating warbler (WEWA)		
a. Eastern Shore (n = 9)	WEWA = -0.19 + 0.01 BAF - 0.003 ISC	0.0041
b. Western Shore (n = 6)	WEWA = 0.10 - 0.002 TPS	0.0475
c. Both shores (n = 15)	WEWA = 0.03 + 0.003 PIN - 0.003 ISB	0.0001
29. Wood thrush (WOTH)		
a. Eastern Shore (n = 72)	WOTH = -0.05 + 0.04 TPS - 0.1802 ISB + 0.04 CHT	0.0001
b. Western Shore (n = 108)	WOTH = 0.22 - 0.023 ISB + 0.04 CHT + 0.01 ISC	0.0001
c. Both shores (n = 180)	WOTH = 0.22 - 0.02 ISB + 0.04 CHT + 0.01 ISC + 0.02 BAF	0.0001
30. Yellow-billed cuckoo (YBCU)		
a. Eastern Shore (n = 72)	YBCU = 0.70 - 0.01 ISA + 0.11 LAR	0.0059
b. Western Shore (n = 72)	YBCU = 0.06 + 0.07 LAR	0.0324
c. Both shores (n = 144)	YBCU = 1.04 - 0.01 TPS + 0.01 ISA - 0.01 ISC	0.0001
31. Yellow-throated vireo (YTVI)		
a. Eastern Shore (n = 1)	No significant regression	ns
b. Western Shore (n = 10)	YTVI = -0.16 + 0.01 SDE	0.0190
c. Both shores (n = 11)	YTVI = -0.05 + 0.01 SDE - 0.002 ISA	0.0005