CHAPTER 10

Responses of Breeding Bird Communities to Forest Fragmentation

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Field studies in eastern North America indicate that local densities of most forest-dwelling bird species are directly or indirectly influenced by forest insularization. Relevant site variables among those measured include patch area and isolation, tree stature and density, and development of herbaceous and shrub understorey. In general, highly migratory species that specialize on forest-interior habitat are adversely affected by forest fragmentation, whereas forest-edge species, particularly year-round inhabitants (here termed 'residents'), tend to achieve higher local densities in fragmented forests. In eastern North America, rates of nest parasitism and nest predation are correlated with patch insularity. Several life history characteristics appear to make highly migratory species especially sensitive to these direct agents of reproductive failure.

The regional integrity of eastern North America's avifauna is maintained by frequent exchange of propagules among forest patches, few of which are sufficiently large to maintain a stable avifauna *in vacuo*. This pattern of frequent re-invasion of small forested tracts may be less common at lower latitudes, where many bird species are sedentary habitat specialists.

In attempting to determine the optimal size and spatial arrangement of forest reserves for bird conservation, the absolute geometric scale of potential reserves, the functional 'grain' of the regional habitat mosaic, the degree of ecological specialization of the bird species to be conserved, and their dispersal all must be considered.

INTRODUCTION

OVER the past two decades, theoretical ecologists and conservationists have attempted to assess the effects of habitat insularity on bird populations and communities. MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography has provided a common theoretical framework for many of these studies (for a review, see Abbott 1980). The original focus on actual islands has expanded to include disjunct patches of terrestrial habitat. The latter are often (if somewhat euphemistically) depicted as 'islands' surrounded by a 'sea' of disturbed or otherwise unsuitable terrain. The extension of the insular metaphor from real to virtual islands was anticipated by MacArthur and Wilson (1967: 114), who also pointed out two important distinctions: (1) immigration rates are generally much lower on true islands because of their high degree of effective isolation, and (2) competition and other negative interactions with species intruding from neighboring habitats occur less frequently on true islands than in mainland habitat patches. Typically, the surroundings of mainland habitat 'islands' are not mere passive barriers to dispersal, but are staging areas for potential predators, parasites, and competitors.

Because the analogy between true islands and mainland habitat patches is imperfect, and because the validity of the equilibrium theory itself has increasingly been called into question (e.g., Simberloff 1976; Abbott 1980; Gilbert 1980; Higgs 1981; Margules *et al.* 1982; Simberloff and Abele 1982), attempts to apply the specific tenets of MacArthur and Wilson's equilibrium theory to habitat patches are controversial. Nevertheless, certain responses of birds to habitat fragmentation have been documented, whatever their underlying causal mechanisms ultimately prove to be.

The aim of this chapter is to summarize some of the major empirical findings concerning the effects of habitat insularization on forest-dwelling birds. I

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will emphasize my own research and that of other investigators who have worked in the Middle Atlantic region of the USA, an area that has been better studied in this regard than has any other section of North America. I will describe the patterns that have emerged, discuss possible causal mechanisms, note some conservation applications, and identify important questions which invite additional research. I will briefly compare the results of work done in North America with studies done elsewhere, particularly Britain and Australia. Throughout, I will emphasize small birds (mainly passerines) that inhabit forested tracts.

EFFECTS OF FRAGMENTATION ON THE AVIFAUNA OF EASTERN NORTH AMERICA

The Process and Pattern of Habitat Insularization

The arrival of European settlers in eastern North America in the early 17th century heralded two centuries of relentless forest-cutting. What must have been an essentially continuous expanse of forest was reduced to patches and strips of woodland in most of what is now the eastern United States. The farms cleared by settlers in the 17th and early 18th centuries were clustered along the Atlantic seaboard, but the most complete deforestation occurred in the midwestern states following the crossing of the Appalachian Mountain barrier in the late 18th and early 19th centuries. Thus, the Atlantic seaboard has remained a complex mosaic of farms, abandoned fields, woodlands, and riparian strips, and the percentage of forested land there has actually increased over the past century (Aldrich and Robbins 1970; Morse 1980). Although no sizeable tracts of virgin forest have survived at lower elevations anywhere in the eastern USA, second growth forest covers 30-50% of many of the states east of the Appalachian crest. In contrast, deforestation in much of the American midwest has been inexorable (e.g., Curtis 1956; Whitney and Somerlot 1985). Patterns of land use in the latter region resemble those in such well-studied regions as Britain and the wheatbelt of Western Australia. In all of these areas, forest survives mainly as small, disjunct patches.

Changes in the Avifauna and their Causes

What have been the net effects of post-settlement deforestation on the resident avifauna of the eastern USA? We can say with certainty that few species have become extinct. A continental avifauna that included perhaps 660 species at the time of the arrival of Europeans has suffered fewer than ten global extinctions. Within the eastern deciduous forest region, only the passenger pigeon, *Ectopistes migratorius* and Carolina parakeet, *Conuropsis carolinensis* are certainly extinct. Two additional species, the ivory-billed woodpecker, *Campephilis principalis* and Bachman's warbler, *Vermivora bachmanii,* have probably been extirpated, but only a few others are sufficiently rare to be in serious danger of global extinction.

At the local and regional levels, however, the future survival of the avifauna associated with the eastern deciduous forest is problematical (Whitcomb *et al.* 1981). Analysis of long-term census data for isolated parks and preserves in the eastern U.S. (Lynch and Whitcomb 1978) has revealed two major patterns. Firstly, the bird communities inhabiting individual forest patches are highly unstable. Mean annual species turnover rates are so high (often 10-25%) that only a minority of the local pool of bird species is present every year within any given forest tract. Secondly, a systematic decline in the abundance of a number of forest-dwelling species began in the 1950's and 1960's (Fig. 1). The explanation for these reductions, which have resulted in the total disappearance of many previously common species from wooded tracts, remains obscure. Among the causal mechanisms that have been suggested (Whitcomb *et al.* 1976, 1981; Lynch and Whitcomb 1978; Terborgh 1980; Morse 1980; Lynch and Whigham 1984) are: (1) increasing isolation of reserves and parks due to urbanization of their surroundings, (2) encroachment by predators, competitors, and nest-parasites from adjacent disturbed habitats, (3) mortality due to widespread use of pesticides in agriculture and forestry, and (4) global reduction in the abundance of many migratory species due to massive habitat destruction on their tropical wintering grounds. This last factor is potentially of overwhelming importance in eastern North America, where 50-75% of the individual breeding pairs of forest-dwelling birds are neotropical migrants. Moreover, these long-distance migrants are the very species that have shown the most severe declines in parks and woodlots of eastern North America (Lynch and Whitcomb 1978; Whitcomb *et al.* 1981). Most resident species, on the other hand, have either held their own, or actually have increased in abundance within isolated forest patches.

Effects on Breeding Birds of Forest Fragmentation in the Maryland Coastal Plain

With the foregoing historical perspective in mind, Dennis Whigham and I undertook a 2-year study of breeding birds associated with forested tracts in the Atlantic Coastal Plain province of Maryland, east of Washington, D.C. (Fig. 2). Although the 6-county study area lies within the heavily populated urban-suburban corridor of the eastern United States, considerable forest remains. Most water courses are bordered by strips of riparian woodlands, and upland forest covers from 35-65% of the land area in each of the six counties. Most of this forest has regenerated following the widespread abandonment of farming in the late 19th and early 20th centuries. The high proportion of forest extant in the study

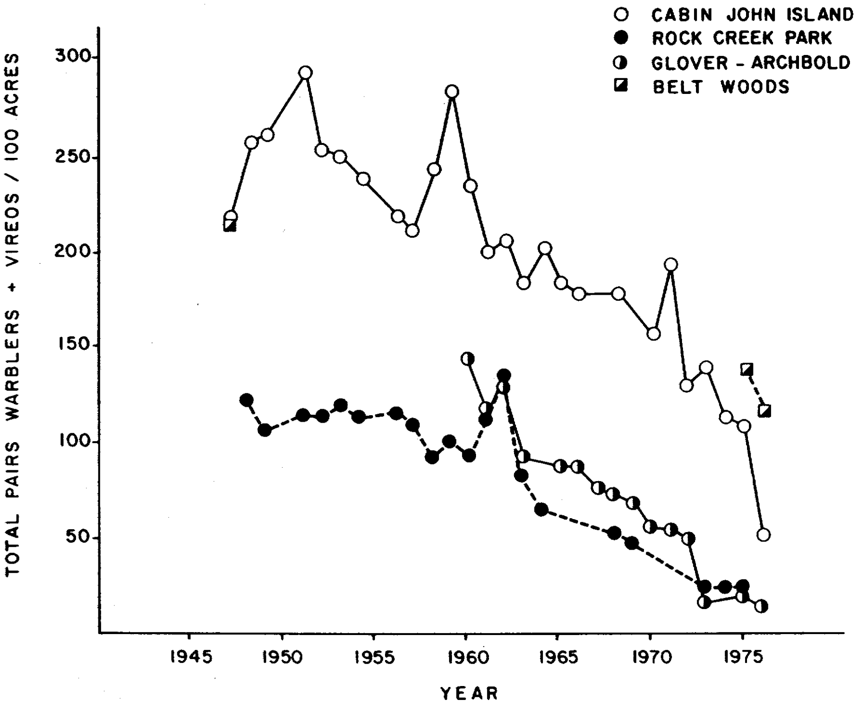

Fig. 1. Historical decline in the combined abundance of migratory wood warblers (Parulinae) and vireos (Vireonidae) in four isolated forest tracts in Maryland and the District of Columbia (USA). The patches themselves have undergone only minor disturbance over the past several decades, but the surrounding region has become increasingly urbanized. Figure redrawn from Lynch and Whitcomb (1978).

area, together with the high degree of connectivity imparted by riparian woodlands has resulted in a relatively low degree of functional insularization for the eastern Maryland landscape.

We surveyed breeding bird communities in 270 forest patches. We measured area, isolation, and various floristic and physiognomic features of the vegetation in 183 of these patches. Using stepwise linear multiple regression, we tested 13 habitat variables as predictors of (a) the local occurrence of each of the 31 most common forest-dwelling bird species, and (b) the magnitudes of several community variables (species richness, total number of pairs, number of species and pairs of migrants, number of species and pairs of residents). Our analysis (Lynch and Whigham 1984) revealed several major patterns (Tables 1 and 2).

1. Local abundance of all but one of the 31 bird species showed statistically significant associations with one or more of the habitat variables. The single exception was the pileated woodpecker *Dryocopus pileatus*; occurrence data for this species were too few for meaningful statistical analysis.
2. Vegetation descriptors and patch isolation indices were more efficient predictors of local abundance than was patch area *per se*. Although patch area (or its logarithm) made statistically significant contributions to the regressions for several species, it was the most important predictor of abundance for only one, the Kentucky warbler, *Oporornis formosus*.
3. As a group, long-distance migrants tended to respond negatively to what might loosely be termed 'habitat degradation' factors (e.g., reduction in patch area, increase in patch isolation, decrease in tree stature, reduction in plant diversity within patches). Residents tended to be less responsive to these factors, or to react in the opposite direction to long-distance migrants. Short-distance migrants were intermediate in their response to habitat insularization.

The density responses of highly migratory species (most of which require closed-canopy forest as breeding habitat) and residents (which, as a group, are more tolerant of 'edge' and other nonforest conditions) tend to be complementary. As a result, overall species diversity and total abundance of individuals remain fairly constant over a wide range of patch configurations and floristic types. If anything, bird abundance and species diversity tend to be *higher* in small forest patches in Maryland, due to an influx of common 'edge' species. This result highlights the pitfall of a simplistic numbers game in conservation planning. If one chooses to consider all species to be equal in conservation value, habitat fragmentation may not appear to be very harmful.

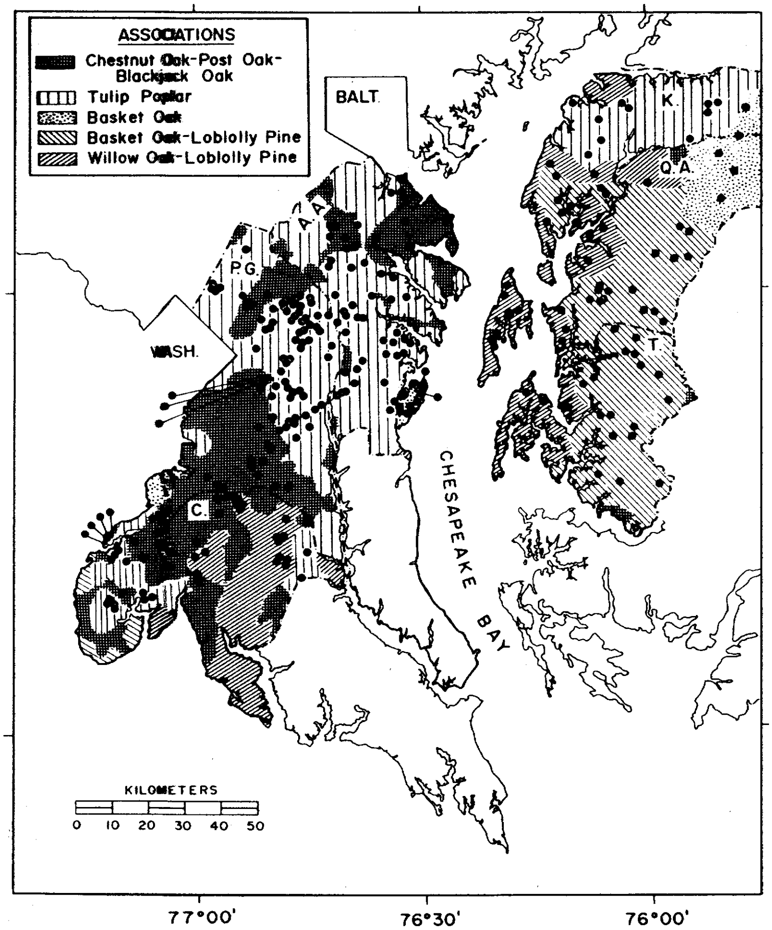

Fig. 2. Maryland study area of Lynch and Whigham (1984), showing the locations of the forest patches that were studied in relation to major vegetation types. Point surveys of breeding birds were conducted in 270 patches.

Table 1. Statistically significant predictors of breeding bird community properties in 270 forest patches located on the Atlantic coastal plain of Maryland (USA). Western Shore localities (n = 196) are west of Chesapeake Bay; Eastern Shore localities (n = 74) are east of the Bay. Table is based on results of stepwise linear multiple regression analysis (Lynch and Whigham 1984). Significance levels: * = P<.05; ** = P<.01; *** = P<.001. 'Neg' indicates that regression coefficient has negative sign.

	Significant Predictors	
Community Characteristic	Western Shore	Eastern Shore
Total bird species	Abundance of pines (neg)* Isolation (neg)*	Patch area (neg)*** Canopy height (neg)* Herbaceous cover (neg)*
Forest-interior species	Herb diversity** Isolation (neg)**	None
Edge-field species	Patch area (neg)*** Canopy height (neg)*	Patch area (neg)* Herbaceous cover* Canopy height*
Total pairs of birds	Isolation (neg)** Isolation (neg)*** Shrub density*	Patch area (neg)**
Forest-interior pairs	Herbaceous cover *** Isolation (neg)*** Total basal area of trees***	Isolation (neg)**
Edge-field pairs	Patch area (neg)*** Canopy closure (neg)* Total basal area of trees (neg)*	Patch area (neg)*** Number of plant species* Canopy height*

Table 2. Statistical significant predictors of the point density of individual breeding bird species in 270 forest patches on the Atlantic coastal plain of Maryland (data combined for eastern and western sides of Chesapeake Bay). Significance levels and source of data as in Table 1. Data from Lynch and Whigham (1984).

Species	Significant Predictors
NEOTROPICAL MIGRANTS	
Cuculidae	
Coccyzus americanus	Total plant species (neg)***, Isolation***
Trochilidae	
Archilochus colubris	Shrub diversity*
Tyrannidae	
Empidonax virescens	Total plant species***, Isolation (neg)***
Contopus virens	Canopy height***, Patch area*
Myiarchus crinatus	Isolation*, Herbaceous cover (neg)*, Abundance of pines**
Turdinae	
Hylocichla mustelina	Isolation (neg)***, Canopy height**, Total basal area of trees**
Parulinae	
Mniotilta varia	Total basal area of trees (neg)***, Isolation (neg)*, Patch Area*
Wilsonia citrina	Total plant species**, Herbaceous cover**, Shrub diversity (neg)*, Tree density (neg)*
Oporornis formosus	Patch area***, Herbaceous cover**, Shrub diversity (neg)*, Tree density (neg)*
Parula americana	Total plant species***, Patch area**
Seiurus auricapillus	Isolation (neg)***, Tree density***, Shrub diversity***, Herbaceous cover*
Helmitheros vermivorus	Abundance of pines***, Isolation (neg)**
Vireonidae	
Vireo olivaceus	Total plant species***, Abundance of pines (neg)**
Vireo griseus	Herbaceous cover**, total basal area of trees (neg)**
Vireo flavifrons	Shrub diversity**, Isolation (neg)**
Thraupinae	
Piranga olivacea	Shrub diversity**, Abundance of pines (neg)*
SHORT-DISTANCE MIGRANTS	
Picidae	
Colaptes auratus	Isolation***, Total plant species**
Mimidae	
Dumatella carolinensis	Patch area (neg)***, Shrub diversity (neg)**, Abundance of pines (neg)*
Corvidae	
Cyanocitta cristata	Total plant species (neg)***, Isolation**, Shrub density**, Canopy height*
Parulinae	
Dendroica pinus	Abundance of pines***, Canopy closure (neg)*, Shrub diversity*
Sylviidae	
Polioptila caerulea	Canopy closure (neg)**, Isolation (neg)**
Cardinalinae	
Pipilo erythropthtbalmus	Tree density**, Tree diversity (neg)**
RESIDENTS	
Picidae	
Picoides pubescens	Patch area (neg)**, Abundance of pines**, Isolation (neg)**, Canopy height*
Picoides villosus	Isolation**
Dryocopus pileatus	None
Melanerpes carolinus	Total basal area of trees***, Tree density (neg)***
Troglodytidae	
Thryothorus ludovicianus	Isolation**
Sittidae	
Sitta carolinensis	Canopy height***
Paridae	
Parus carolinensis	Shrub diversity (neg)**
Parus bicolor	Canopy closure (neg)*
Cardinalinae	
Cardinalis cardinalis	Herbaceous cover***, Shrub density (neg)**

Other Surveys in Maryland

General Background. A very extensive study of birds in forest patches has recently been completed by Robbins *et al.* (ms.), who studied 469 forested tracts in Maryland and adjacent portions of the states of Pennsylvania, Virginia, and West Virginia. Some of the results of this important study were discussed in earlier publications by Robbins and his co-workers (Anderson and Robbins 1981; Robbins 1980; Whitcomb *et al.* 1981). Robbins *et al.* used the same point census technique as did Lynch and Whigham (1984), and their study area encompassed most of Maryland, except for the six Coastal Plain counties surveyed by Lynch and Whigham. Robbins *et al.* quantified vegetation characteristics, as well as patch area and isolation, and used stepwise curvilinear regression to relate these habitat descriptors to bird occurrence in forest patches. Because of the broader geographic scope and greater sampling intensity of their study, Robbins *et al.* obtained sufficient data to analyse the distributions of 76 species (in comparison to the 31 considered by Lynch and Whigham).

Although the study of Robbins *et al.* is very similar in orientation to that of Lynch and Whigham, there are also some important differences between the two studies that must be kept in mind if they are to be compared. First, Robbins *et al.* included a wider range of major physiographic regions (coastal plain, piedmont, and montane formations were studied) than did Lynch and Whigham, whose study was restricted to the coastal plain. In addition, Robbins *et al.* surveyed both riparian and upland forests, whereas Lynch and Whigham considered only upland plots.

Robbins *et al.*'s study included a very broad range of patch sizes (0.1 to 3300 ha). Lynch and Whigham intentionally rejected patches smaller than 10 ha in order to minimize 'contamination' of their point surveys by species living outside the forest patches, and their largest tracts were only about 1000 ha. The greater range in size of the tracts surveyed by Robbins *et al.*, together with their use of curvilinear regression models (as opposed to the linear models employed by Lynch and Whigham), would be expected to increase the magnitude of any underlying correlations between forest area and bird occurrences, as indeed proved to be the case. On the other hand, Robbins *et al.* surveyed only mature stands of forest, whereas Lynch and Whigham also considered successional woodlands, so the latter authors placed more emphasis on local (as opposed to regional) habitat gradients. Finally, some of the specific habitat descriptors used by Robbins *et al.* differ from those employed by Lynch and Whigham, so the absolute values of correlation or regression coefficients cannot always be directly compared in the two studies.

Results of the Statewide Survey of Maryland. Robbins *et al.* (ms.) found patch isolation to be the single best predictor of bird occurrence. Isolation made a statistically significant contribution to the predictive multiple regression equation in 43 of 76 (57%) species. Patch area was a statistically significant predictor variable for 28 of 76 (37%) species. In at least nine of these 28 regressions the significance level (hence, partial correlation coefficient) for patch area was substantially lower than for one or more other predictor variables. Thus, patch area played a major role in predicting the occurrence of no more than 25% of the species studied. By comparison, isolation (estimated by Robbins *et al.* as the percentage of regional forest cover) played a substantial role in 45% of the species regressions, and various aspects of forest physiognomy were highly significant predictors for all but a handful of the 76 species. In discussing the results of their study Robbins *et al.* emphasize the utility of forest area as a predictor of bird occurrence, but their data suggest that within-patch habitat characteristics and regional forest cover together play a more important role than patch area *per se* in determining the suitability of individual forest tracts for particular bird species. This result is in agreement with the findings of Lynch and Whigham (1984). Both studies also agree in indicating that there is no absolute minimum critical area for the occurrence of the smaller bird species in the middle Atlantic region, although many species tend to be encountered more frequently in larger tracts. Given the existing mixture of large and small forest patches in Maryland, together with the relatively low degree of interpatch isolation that now characterizes much of the state, even small tracts are at least occasionally inhabited by almost any of the forest-associated bird species occurring in the state.

In summary, the Maryland studies indicate that complex of ecological variables, some of which are intercorrelated with patch area, act together to determine the suitability of a particular tract for any given bird species. The identities and the relative importance of these determining factors vary from species to species and from one habitat type to another. Nevertheless, if one restricts attention to bird species whose abundance is significantly correlated with patch area, and if patch area is viewed as a convenient index to a plethora of more immediate ecological factors, area-specific 'incidence functions' (*sensu* Diamond 1975) can be helpful in envisioning the impacts of insularization on different bird species (Figs 3 and 4). It is evident that some species, particularly highly migratory forms associated with the interior of forests, are considerably more likely to be encountered in a given sampling period within large tracts than in smaller ones (Fig. 3). The opposite is true for other species (Fig. 4), particularly 'edge' species, whose territories are organized along forest margins. Forest-interior species, on the other hand, either tend to avoid forest-edge, or to utilize the entire forest area for territories (Fig. 5). Finally, some species show no consistent positive or negative relationship with forest area or any of its ecological correlates (Fig. 4).

Limitations of the Point Survey Method

Although the Maryland studies just discussed constitute an extensive data base (more than 700 forest patches were sampled), they cannot be directly

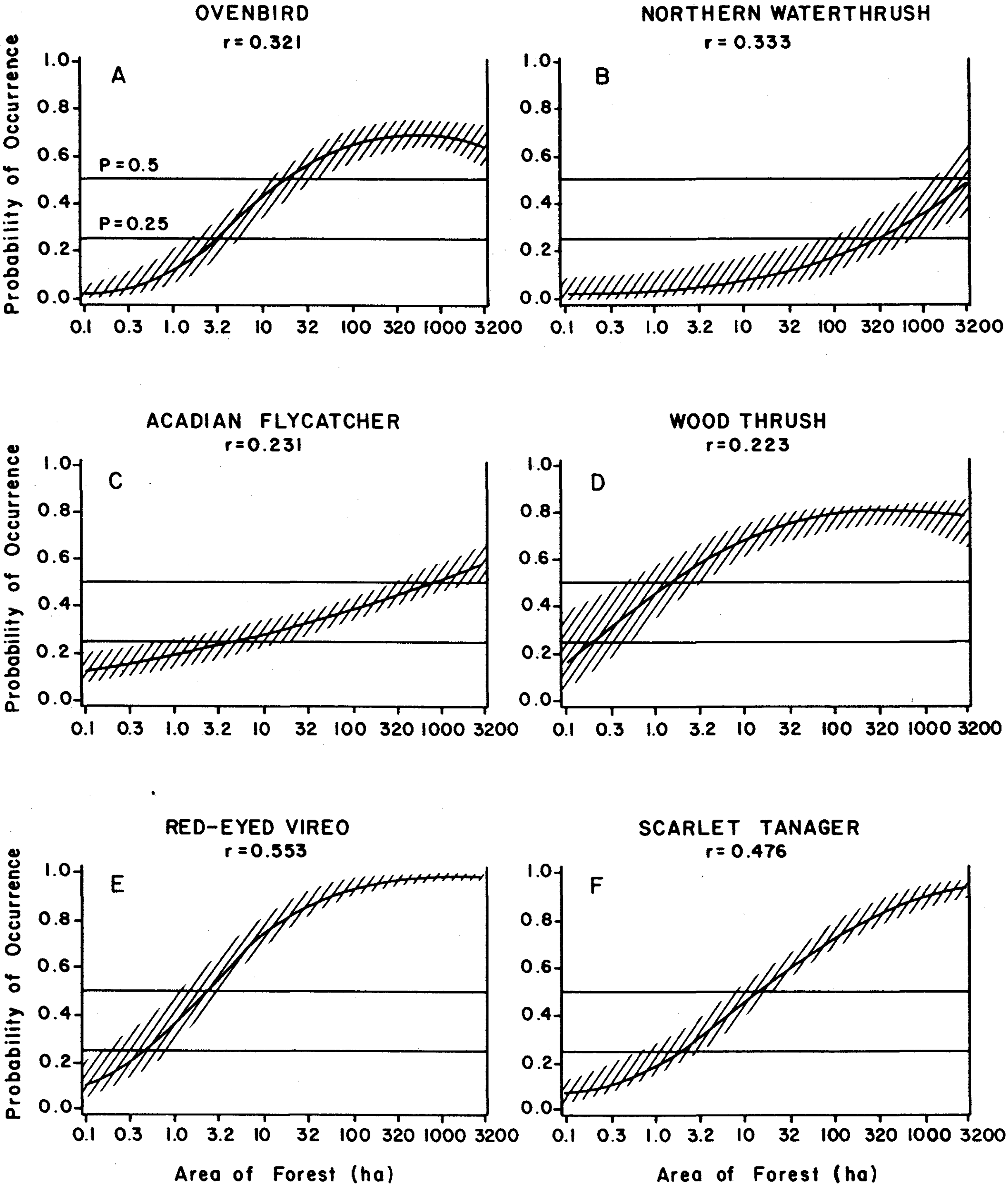

Fig. 3. Area-specific 'incidence functions' for six Maryland bird species that are more abundant in large tracts than in small ones. All six species are long-distance migrants: ovenbird *Seiurus auricapillus*, Northern waterthrush *S. noveboracensis*, acadian fly-catcher *Empidonax virescens*, wood thrush *Hylocichla mustelina*, red-eyed vireo *Vireo olivaceus*, and scarlet tanager *Piranga olivacea*. Figure modified from Robbins *et al.* (ms). Hatched areas represent 95% confidence limits of the regressions.

compared with studies that employed different methods. The point survey technique calls for equal sampling intensity (three visits of 20 min each) at a single station within each patch. This differs substantially from traditional spot-mapping methods, which attempt to enumerate all species and individuals within a large census plot.

Point surveys are quite efficient for detecting the presence of species within a small patch of forest. Because the detection distance for most Maryland bird species is in the range of 100-200 m (Whitcomb *et al.* 1981), the effective area censused in a point survey is in the order of 3-10 ha. This limitation unavoidably results in undersampling of larger tracts,

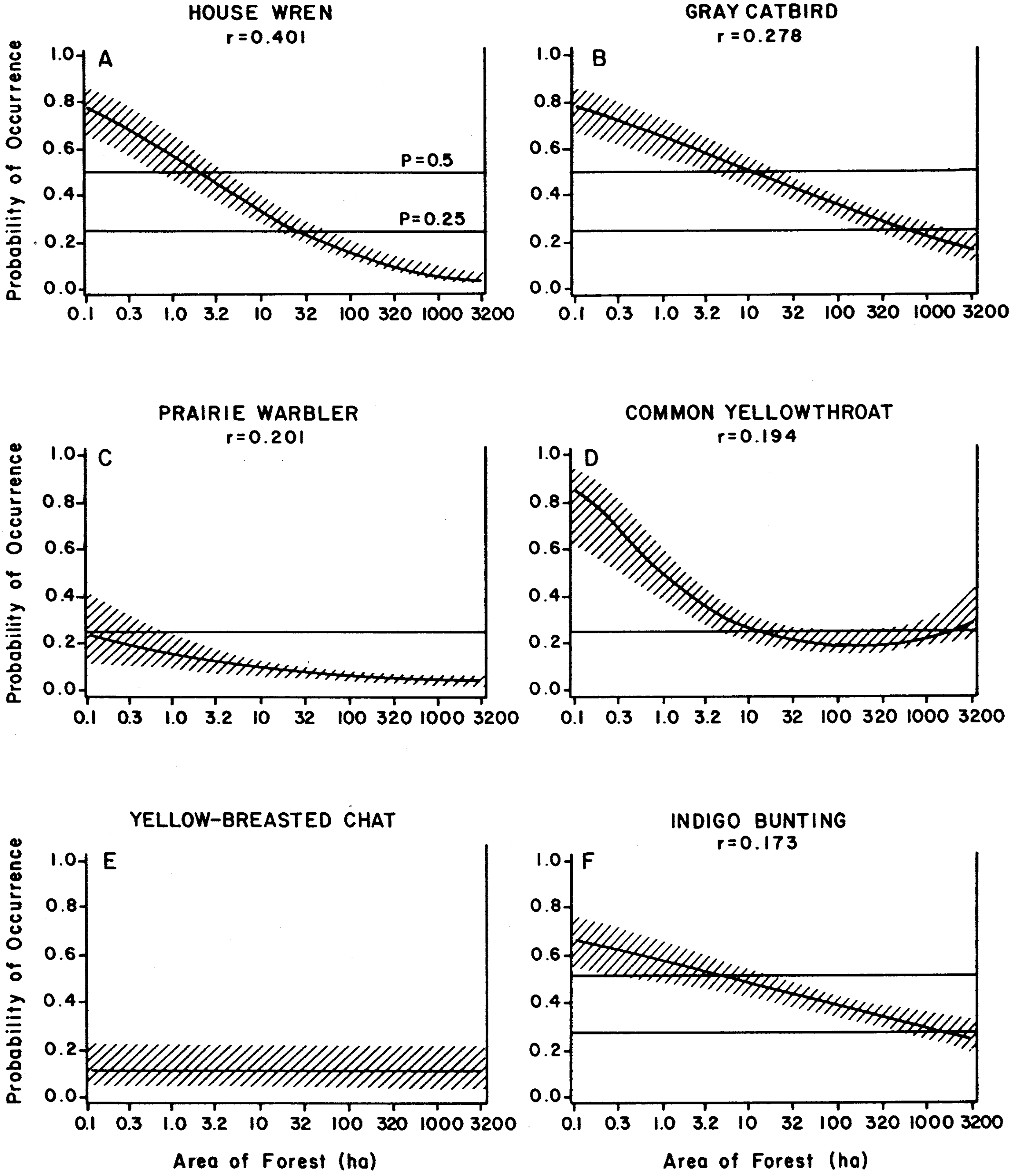

Fig. 4. Area-specific 'incidence functions' for five Maryland bird species that are more abundant in small forest tracts than in large ones, and a sixth species that shows no significant density response to patch area. All six species are more common in forest edge and scrub than in forest-interior. House wren *Troglodytes aedon*, gray catbird *Dumatella carolinensis,* and common yellowthroat *Geothlypis trichas* are short distance migrants, although some individuals of the latter two species migrate as far south as northern Central America. Prairie warbler *Dendroica discolor,* yellow-breasted chat *Icteria galbula,* and indigo bunting *Passerina cyanea* are neotropical migrants. Figure modified from Robbins *et al.* (ms).

and causes one to miss at least some of the uncommon species that may be scattered through an extensive area of forest. To give a concrete example, consider a species such as the Kentucky warbler which in Maryland has a 25% probability of being detected in a set of point surveys conducted within a 100 ha tract (Robbins *et al.* ms). If the area adequately covered by a point survey is 10 ha, then the probability of encountering at least one Kentucky warbler in an exhaustive census of a uniform 100 ha tract can be estimated as $(1\text{-}.75^{10}) = .96$. Thus, even if the point density (i.e., abundance per unit

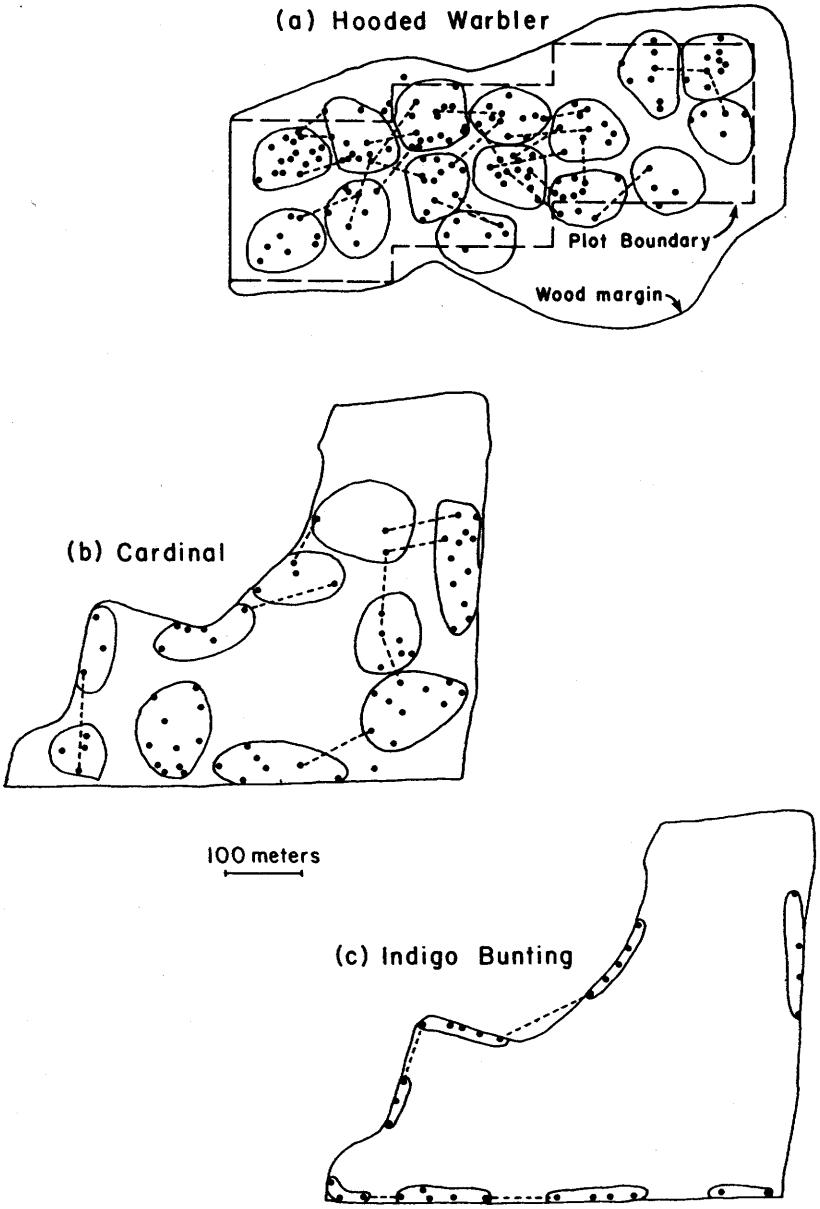

Fig. 5. Mapped territories of three Maryland bird species in forest fragments. Simultaneous registrations of territorial males are connected by dashed lines. (a) Hooded warbler *Wilsonia citrina*, a highly migratory forest-interior specialist that avoids forest edge. One additional unmapped territory was located outside the boundary of the study plot, in the lower right portion of the patch. (b) Cardinal *Cardinalis cardinalis*, an interior-edge species that is most common near the forest edge, but occurs throughout the forest. (c) Indigo bunting *Passerina cyanea*, a species that establishes its territories along the forest margins. Figure modified from Whitcomb *et al.* (1981).

area) of Kentucky warblers is similar in a 100 ha tract as in a 10 ha tract, there is a much higher probability that the species is present *somewhere* within the larger tract.

Thus, point survey data underestimate the frequency of species occurrence per tract, as opposed to the occurrence of individuals per unit area. As a general rule, however, adjusting point survey results to account for this bias will only *increase* the strength of any positive relationship between species incidence and forest area.

Differential Responses of Birds to Forest Fragmentation

In recent years a severely reductionist stance has emerged in zoogeography and conservation (e.g., Simberloff and Abele 1976a, 1976b; Higgs and Usher 1980; Simberloff and Gotelli 1984; Zimmerman and Bierregaard 1986). This position disparages previous attempts at community analysis, and invokes detailed autecological studies as the only valid basis for conservation action. A reductionist programme is indeed warranted if one is concerned with conserving individual species that are of sufficient concern to justify the expenditure of large amounts of time and money. Among North American birds, examples of such 'flagship' species would include the California condor, *Gymnogyps californianus*, with fewer than 20 surviving individuals in the wild (Snyder and Hamber 1985), and a few others. However, conservationists also must consider the long-term preservation of entire assemblages of species, most of which are relatively obscure, and which have no public constituency. Moreover, if the reductionist programme is taken literally, every local situation must be individually evaluated before recommending conservation action. Detailed studies are of course laudable, but given inevitable limitations of time and financial resources, there is not the slightest possibility of conducting in-depth autecological studies of every bird species in every local community, and one must therefore seek ways to generalize about groups of species. In addition to this purely practical consideration, there is the desire shared by many biologists to discern and to explain patterns in nature, as opposed to focusing exclusively on the idiosyncracies of individual species. To dismiss pattern-seeking on the grounds that every species is different is as misguided as to suppose that any two species are alike in every detail of their ecology. The trick, of course, is to define and analyze groups of species in ways that are simultaneously practical, realistic, and revealing. A judicious mix of in-depth autecological studies and broader, more inclusive community-level approaches would appear to offer the best basis for rational conservation action.

As was noted above, one useful way to categorize North American bird species is according to migratory strategy. Whitcomb *et al.* (1981) showed that, as a group, highly migratory species in eastern North America share a suite of ecological and behavioural traits (Table 3). For example, in comparison to sedentary species, long-distance migrants show a greater tendency to nest on or near the ground, to be insectivorous, and to produce smaller clutches. They also tend to react more strongly than do short-distance migrants or resident species to forest insularization. In a similar vein, Greenberg (1980) has drawn attention to a number of demographic correlates of long-distance migration in North American passerines.

Another useful grouping for North American forest birds differentiates 'forest-interior' species (which tend to avoid forest margins) from 'interior-edge' species (which occur throughout the forest) and 'edge-field' species (which occur only at the forest margin and adjacent open habitats). Examples of these three categories are shown in Figure 5. These three broad habitat categories can be combined with the three migratory categories to form nine habitat/migratory strategy classes (Table 3). The distribution of species among these categories has a strong phylogenetic element (Whitcomb *et al.* 1981). In the Maryland study area, for example, all Picidae, Sittidae, Paridae and Corvidae (12 species) are residents, showing, at most, local movements during the non-breeding season. Most of these 12 species are feeding generalists, eating both animal and plant material. On the other hand, 13 of the 15

Table 3. A 3X3 classification of 63 Maryland breeding bird species according to habitat and migratory pattern, showing mean values of key ecological variables. n = number of species in category; CS = mean number of eggs in first clutch; TF = tolerance to forest fragmentation, measured as the point density in small (6-14 ha) forest patches divided by the point density in large (>70 ha) patches; NH = mean nest height (m). Data from Whitcomb *et al.* (1981).

	Habitat Association			
Migratory Pattern	Forest Interior	Interior and Edge	Edge and Scrub	Totals
Resident	n = 3 spp	n = 7 spp	n = 4 spp	n = 14 spp
	CS = 4.1	CS = 6.2	CS = 9.9	CS = 6.8
	TF = 0.5	TF = 1.2	TF = 2.2	TF = 1.2
	NH = 8.4	NH = 4.8	NH = 4.0	NH = 5.3
Short-Distance Migrant	n = 1 spp	n = 6 spp	n = 11 spp	n = 18 spp
	CS = 3.8	CS = 7.7	CS = 8.2	CS = 7.8
	TF = 0.5	TF = 1.5	TF = 1.4	TF = 1.4
	NH = 10.4	NH = 2.0	NH = 2.5	NH = 2.8
Neotropical Migrant	n = 11 spp	n = 11 spp	n = 9 spp	n = 31 spp
	CS = 4.6	CS = 4.7	CS = 4.7	CS = 4.7
	TF = 0.2	TF = 0.7	TF (NA)	TF = 0.4
	NH = 2.5	NH = 4.2	NH = 3.1	NH = 3.3
Totals	n = 15 spp	n = 24 spp	n = 24 spp	n = 63 spp
	CS = 4.4	CS = 6.1	CS = 7.2	CS = 6.0
	TF = 0.3	TF = 1.0	TF = 1.6	TF = 0.9
	NH = 4.2	NH = 3.8	NH = 3.0	NH = 3.6

local species belonging to the subfamily Parulinae (New World warblers) are insectivorous neotropical migrants, the only two exceptions being short-distance migrants. Of the nine habitat/migration groups, the forest interior/neotropical migrant category shows the strongest negative reaction to forest fragmentation in Maryland (Table 3) and several species in this group have disappeared from entire regions in Maryland and nearby states as urbanization has increased (Robbins 1980; Whitcomb *et al.* 1981). It appears, then, that evolutionary constraints, migratory strategy and habitat use combine to determine the sensitivity of Maryland bird species to forest reduction. Interestingly, observations of North American migrants on their neotropical wintering grounds reveal that species which as breeders are restricted to forest-interior are often substantially more tolerant of disturbed vegetation and 'edge' conditions during the non-breeding season. Such observations indicate considerable latent flexibility in the behavioural-ecological repertoires of even the more highly specialized forest-interior species, and underscore the need for additional ecological data covering the non-breeding season of highly migratory species.

BIRDS IN WESTERN AUSTRALIAN WHEATBELT RESERVES

A classification of bird species based on their taxonomic affiliation, habitat specificity, and migratory pattern was used by Kitchener and his co-workers (Kitchener *et al.* 1982; Humphreys and Kitchener 1982) to define 10 categories of birds that occur in forest reserves within the wheatbelt of southwestern Western Australia. In comparison to the avifauna of eastern North America, Western Australia's avifauna includes a higher proportion of non-passerines and more species with irregular and rainfall-triggered temporal and spatial patterns of breeding and migration. This irregularity, which does not pertain to all parts of Australia (R. Loyn, *in litt.*), contrasts sharply with the highly predictable seasonality of breeding and latitudinal migration in temperate North America. Another notable difference in the two avifaunas is the much greater number of nectarivorous species (10) in the wheatbelt reserves than in Maryland forest patches, where only a single specialized nectarivore occurs. Such differences are potentially important in a conservation context, because nectarivores tend to be more specialized on particular plant species than are other birds. For example, flowers of *Dryandra* provide the key food resource for the entire honeyeater community in some of the areas studied by Kitchener *et al.* (1982). Such an extreme of food specialization, which is virtually non-existant in temperate North America bird communities, raises the possibility that Australian nectarivores might be especially sensitive to the absence of particular plant species from reserves, and hence to forest fragmentation.

Kitchener *et al.* (1982) showed that the total number of passerine species in the wheatbelt reserves was strongly influenced by the floristic composition of the vegetation, and by the number of major physiognomic types of vegetation present. Reserve area played a lesser role in predicting the total number of passerine species. However, the abundance of the species with the most specialized habitat requirements (so-called 'P_5' species) was highly correlated with reserve area. Kitchener *et al.* (1982) concluded that larger reserves are more likely to include the particular habitats required by P_5 species. This view was supported by the observation that the correlation exists between reserve area and habitat complexity only for reserves larger than about 600 ha. In the wheatbelt reserves, forest was found to be the vegetation type with the highest total number of resident and migratory bird species, the highest density of birds, and the highest degree of endemism.

One can envision a continuum of forest insularization ranging from the non-insularized forest of pre-settlement eastern North America to highly insularized patches of forest on offshore islands. The Maryland forest patches studied by Lynch and Whigham (1984) represent a relatively low degree of insularization, given the large total area of existing forest and the short average distance between patches. For even the most generalized forest-dwelling bird species of Western Australia, the wheatbelt reserves are functionally more insular than are Maryland's forests, although these generalists are capable of using a reasonably broad range of habitats both within and outside the reserve system; from the point of view of such species, the wheatbelt reserves are not completely isolated, either from one another or from other patches of woody vegetation outside the reserve system. By contrast, the P_5 species of Western Australia show greater habitat specialization, and tend to be restricted to particular sub-formations of native vegetation within the wheatbelt reserves (Kitchener *et al.* 1982). For such species, even the pristine landscape must have been patchy, hence insularized, and the existing archipelago of forest remnants is even more so. Indeed, Kitchener *et al.* (1982) showed that the community of P_5 species in the wheatbelt reserves resembles the avifauna of southern Australia's offshore islands in the slope (if not the absolute number of species) of its diversity response to habitat fragmentation.

The result of extreme insularization of a continental avifauna is exemplified by places such as Britain, where centuries of deforestation and other human disturbance may have winnowed out all bird species except those that are tolerant of extreme forest fragmentation. We lack reliable information on the pre-settlement avifauna of Britain, but none of the 56 bird species recorded by Moore and Hooper (1975) as breeding in British forest patches are restricted to forest, although some species attain their highest local density there. According to Arnold (1982), all of the British forest-dwelling species in question also breed in gardens, hedgerows, and other non-forest habitats. Thus, in the terminology of Kitchener *et al.* (1982), there are no P_5 species in these British woods. Compared with species found in Australia or North America, extant British birds are relatively tolerant of forest fragmentation, but this seems to reflect the fact that they are in fact rather generalized in their habitat requirements. Whether the depauperate nature of the British avifauna reflects the aftermath of glacial extinctions, human-related habitat disturbance, the insular character of Britain, or (as seems most likely) a combination of all of these factors, forest-interior specialist birds are markedly under-represented compared with what is seen in more pristine regions of the world. A similarly depauperate avifauna has come to be associated with small forest patches in extensively deforested regions of the eastern and midwestern regions of the USA (e.g., Galli *et al.* 1976; Whitcomb *et al.* 1976, 1981; Blake and Karr 1984), and is characteristic of much of present-day New Zealand (Diamond 1984).

MECHANISMS BY WHICH INSULARIZATION INFLUENCES BIRDS

The most obvious means by which forest fragmentation diminishes the diversity and abundance of forest-dwelling birds is through simple diminution of habitat. No bird species can persist if even one critical element of its habitat is completely eliminated. However, even if all critical elements are retained in a given patch of forest, the areal extent of habitat may be insufficient to maintain a viable population over the long term. Minimum population size is an especially serious constraint in the attempt to conserve larger species (e.g., birds of prey), whose feeding territories may encompass tens or hundreds of hectares.

As long as the total extent of forested land in a local landscape remains high, the area of individual forest patches above some critical minimum may not be a crucial factor in determining their use by birds, particularly if riparian strips, road verges, or other corridors of wooded habitat serve to interconnect the patches (e.g., Saunders 1980, 1982). However, many sedentary forest-dwelling birds, particularly tropical species, appear to have strong psychological aversions to crossing even narrow unforested barriers (Willis 1974; Diamond 1984). The failure of some 13 species of forest-adapted birds to persist in seemingly favourable habitat on Barro Colorado Island, which was isolated about 80 years ago by the rising waters of the Panama Canal, has been attributed to their moderate initial population size, followed by local population extinctions, and the lack of a 'rescue-effect' (*sensu* Brown and Kodric-Brown 1977) by immigrants from flourishing populations that exist less than a kilometre away on the mainland of Panama (Willis 1974).

As regional deforestation proceeds, inter-patch dispersal first lessens, then ceases altogether for habitat-specialized sedentary birds. In fully insularized reserves, bird populations will persist only if they are large enough to survive normal demographic fluctuations without periodic subsidization. Even very large populations may be driven to extinction by environmental changes (Leigh 1981), and an extensive and diverse mosaic or gradient of habitats is the best hedge against such extinctions. In practical terms, this means that truly isolated avifaunal reserves usually must be quite large, and that they may require active management interventions to prevent or recoup local extinctions. Again, it should be emphasized that the conservation problems posed by truly isolated reserves are fundamentally different from those encountered in a regional system of reserves that are capable of exchanging propagules. Species turnover events tend to dominate the avifaunal make-up of small forest patches in the eastern USA (Lynch and Whitcomb 1978); this reflects the fact that this avifauna is organized at the level of the regional landscape, not of the individual habit patch (Smith 1975). It is also important to recognize that species of birds with different habitat requirements and dispersal abilities may perceive a given configuration of reserves in totally different ways. Species-specific information is indeed needed on the ability of birds to cross barriers, utilize corridors, and occupy the available habitat gradient.

Non-sedentary birds, particularly long-distance migrants, present conceptual difficulties in the context of forest isolation. Thus, it seems unlikely that inter-patch isolation could directly control the distributions of birds whose annual migrations are several orders of magnitude greater than the normal inter-patch distances within the breeding range. Nevertheless, both major Maryland studies demonstrated that neotropical migrants have shown greater negative responses than other birds to forest fragmentation. How can this seeming anomaly be explained?

Several independent lines of evidence indicate that birds living in small forest patches are subject to a variety of ecological pressures that are correlated with the process and pattern of forest fragmentation. 'Edge' conditions, both physical and biotic, extend much further into a woodlot than is commonly realized (Levenson 1981; Ranney *et al.* 1981). Differences in plant species composition, canopy height and density, temperature, shading, and development of the understorey all can be detected far into the forest beyond the apparent edge boundary.

More importantly, many predators and nest-parasites concentrate their activities along forest margins, and range hundreds of metres into the forest proper (Gates and Gysel 1978; Kroodsma 1982; Brittingham and Temple 1983).

The activities of a single species of nest-parasite, the brown-headed cowbird *Molothrus ater*, has been implicated as a devastating cause of mortality for many North American forest passerines, including the globally endangered Kirtland's warbler (Mayfield 1977). Prior to the era of widespread forest-clearing, cowbirds were virtually confined to the prairie and prairie-forest ecotone of central North America, but over the past century and a half deforestation has allowed this species to spread throughout the entire eastern half of the continent, and has placed cowbirds into direct contact with an assemblage of forest-adapted birds that has not evolved the necessary behavioural mechanisms for dealing with nest parasitism. In contrast, species that have evolved in the same communities as cowbirds frequently thwart nest parasitism by ejecting cowbird eggs, or covering them with new nest material, or by renesting. Although cowbirds retain a strong association with open and 'edge' habitats, they are capable of deep penetration of forest patches from their margins. Cowbird nest parasitism declines with increasing distance from the forest margin, and is virtually non-existent in the interior of very large forested tracts, such as those in the southern Appalachian Mountains (D. Wilcove, pers. comm.).

That the brown-headed cowbird is not unique in its adverse impact on nesting birds is indicated by Wiley's (1985) report of a recent unaided range expansion of a tropical nest parasite, the shiny cowbird *M. bonariensis*, from South America into the West Indies. The effect of this species on the nesting success of evolutionary naive host passerines is every bit as dramatic as that of the brown-headed cowbird on North America species: 75-100% of the nests of some of the shiny cowbird's host species are parasitized in Puerto Rico. In the Old World, the common cuckoo, *Cuculus canorus* has been implicated as a causal agent in the extirpation of the sedge warbler *Acrocephalus schoenobaenus* in one local population (*fide* Wiley 1985), despite the long-term association of these two species elsewhere. The effects of the Cuculidae on reproductive success of host species in Old World forest reserves should be studied in relation to reserve area and isolation.

Other deleterious effects that emanate from edge habitat bordering on forest patches can be as pervasive as they are non-obvious. As an example, Kroodsma (1982) showed that many forest-dwelling birds are actually attracted to edge habitat for nesting. The original selective basis (if any) for this attraction is not known, but may involve better feeding conditions, denser concealing foliage, or other factors associated with treefall gaps and other small natural clearings. In any event, birds that nest in small forest patches, or along the margins of larger patches, suffer much higher rates of nest predation than do conspecifics that place their nests farther from the edge or in larger patches (Gates and Gysel 1978; Kroodsma 1982; Wilcove 1985).

OPTIMAL SIZES FOR RESERVES

Many recent studies have suggested that ecological attributes of reserves outweigh area *per se* as determinants of species occurrence (e.g., Lynch and Whigham 1984; Zimmerman and Bierregaard 1986). Nevertheless, reserve area is a useful 'shorthand' predictor of species diversity for many animal groups, including birds, and the question of optimal allocation of patch sizes for conservation purposes continues to generate heated controversy. Given the well-established and universally-accepted generalization that larger reserves will hold more species than smaller but otherwise similar ones, the conventional wisdom has been that 'bigger is better' when one plans reserves. Disagreement arises, however, when one seeks the optimum strategy for allocating a given total area of reserved land among individual parcels. Early attempts to apply the theoretical precepts of MacArthur and Wilson (1963, 1967) to the problem (e.g., Diamond 1975; May 1975; Terborgh 1975; Wilson and Willis 1975) were faulted by Simberloff and Abele (1976a, 1976b); the latter authors in turn were criticized by conservation-minded ecologists (Diamond 1976; Terborgh 1976; Whitcomb *et al.* 1976) who feared that Simberloff and Abele's largely theoretical critique would be seized upon by developers as a biologically defensible rationale for carving up large reserves into small pieces.

Since 1976, numerous theoretical and empirical studies have addressed the question of the optimal allocation of reserve areas (e.g., Gilpin and Diamond 1980; Higgs and Usher 1980; Simberloff and Abele 1982; Kindlman 1984; Simberloff and Gotelli 1984; Wilcox and Murphy 1985; McClellan *et al.* 1986). The results of theoretical simulations depend on the parameter values and functional forms chosen to represent species colonization probabilities, as summarized by Kindlman (1984). If one makes the simplifying (but patently false) assumption that all species have equal colonization probabilities, then the number of species preserved clearly increases with the degree of reserve subdivision (Fig. 6a). However, if species differ significantly in their area requirements and colonization potential, the advantages of subdivision are greatly reduced (6b), and may be eliminated or even reversed (Fig. 6c).

Empirical support for the conservation strategy of sequestering numerous small reserves has come from studies of plant diversity in small tracts (e.g.,

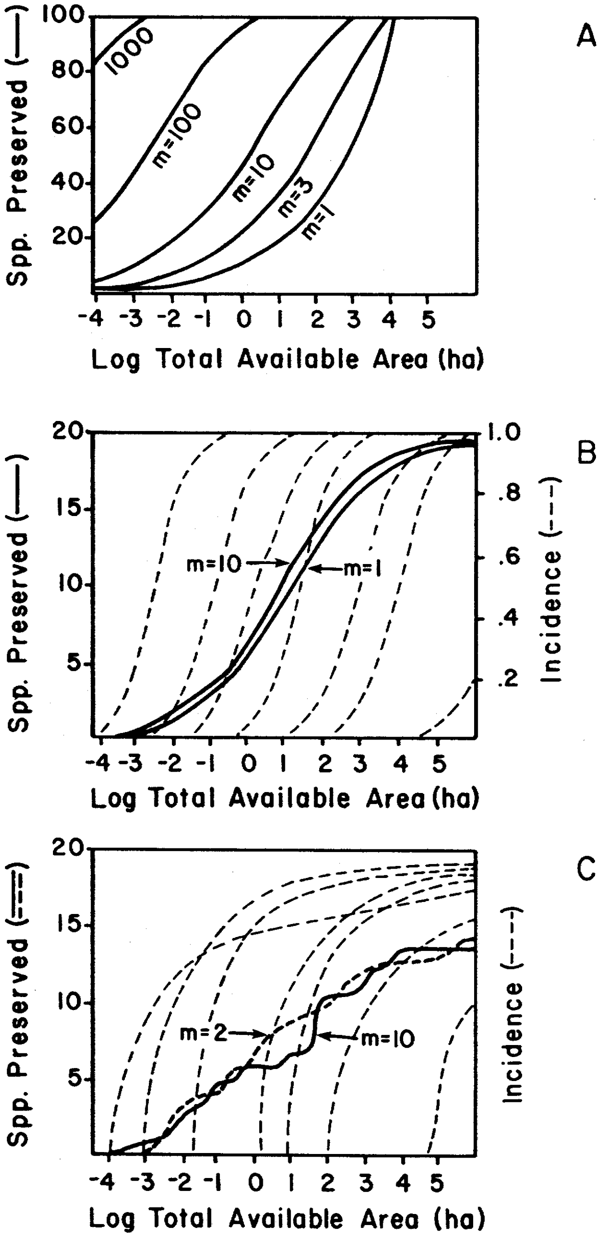

Fig. 6. Theoretical effects of reserve subdivision on the total number of species preserved, under varying assumptions of colonization potential. Details concerning construction of incidence functions and species richness curves are given in Kindlman (1984). Solid lines represent the number of species predicted to be preserved by subdividing a given total land area into m fragments. (a) All species have equal probabilities of colonizing reserve fragments of a given size. In this case, increasing reserve subdivision increases the total number of species contained in the reserve system as a whole. (b) Species differ in their area-specific colonization potentials and individual incidence functions (dashed lines) are sigmoidal. In this case, there is only a slight advantage gained by subdividing a single large reserve into 10 segments. (c) Species differ in their area-specific colonization potential, but incidence functions are hyperboloid. In this case, which Kindlman (1984) argues is more realistic than either (a) or (b), there is no consistent advantage to either reserve subdivision strategy.

Higgs and Usher 1980; Game and Peterken 1984; Simberloff and Gotelli 1984). This result reflects the fact that plants, as contrasted with vertebrate animals, are notably unresponsive to reserve area (e.g., Levenson 1981; Weaver and Kellman 1981). Given the empirical observation that few (if any) plant species are demonstrably 'area-sensitive,' the best strategy for preserving the maximum total species diversity of plants within a given total area of reserved land may be to place a number of relatively small reserves so as to include all important plant habitats and microhabitats. However, such an arrangement might fail to preserve important functional characteristics of large intact ecosystems (e.g., mineral cycling, population structure, co-evolved interactions, the normal mosaic of successional habitats).

As metabolically active and wide-ranging organisms, birds require much more habitat space than do individual plants of comparable (or even much greater) biomass. Accordingly, the concept of critical minimum habitat size is highly relevant for the survival of bird species populations, and even more so for the maintenance of intact avian communities. Nevertheless, over a considerable range of patch sizes, several fairly small reserves may be found to hold more species than does a single large reserve of the same total area. This can be illustrated by computing the number of species that would be encountered by combining survey data for various subsets of patch sizes for the Maryland data (McClellan *et al.* 1986; Fig. 7). However, this numerical exercise does not address the crucial problem of long-term survival probabilities of bird populations in truly isolated reserves (Wilcox and Murphy 1985). The list of birds found in a given tract of Maryland forest reflects not only the characteristics of that particular patch, but also the entire regional configuration of habitat.

Typically, theoretical studies of the optimal size allocation of reserves treat all species as having equal conservation significance, which of course is never the case. Area-sensitive species (e.g., birds with large body size, raptors, other feeding specialists) tend to be less common, and therefore, more in need of active preservation, than are small-sized generalist species, which tend to be relatively abundant. Aesthetic or economic consideration also may cause some species to have higher priority for preservation than others (Gilpin and Diamond 1980).

Humphreys and Kitchener (1982) demonstrated empirically that Western Australian bird species with specialized habitat requirements respond differently to reserve subdivision than do generalist species, which occupy a wider range of natural and disturbed vegetation types (Fig. 8). Within the latter group, scattered small reserves often will preserve more species than a single large reserve; for habitat specialists, on the other hand, a higher number of species will often be contained in a single large

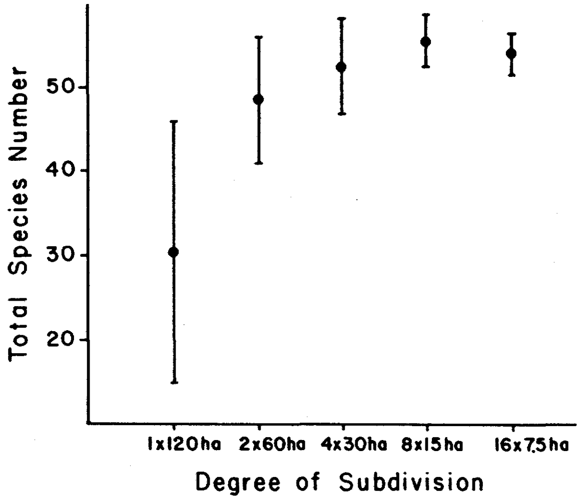

Fig. 7. Effect of patch subdivision on the number of bird species contained in Maryland forest tracts, based on point survey data in Lynch and Whigham (1984). The mean expected number of species (± one standard error) is plotted for varying numbers of small forest patches that add up to a total area of 120 ha. The figure does not take into account the undersampling of large tracts (< 60 ha) by the point survey method (see text), nor are forest-interior species distinguished from interior-edge and field-edge species. Nevertheless, the data suggest that forest subdivision does not increase total species richness for individual plots smaller than about 30 ha. Figure redrawn from McClellan *et al.* (1986).

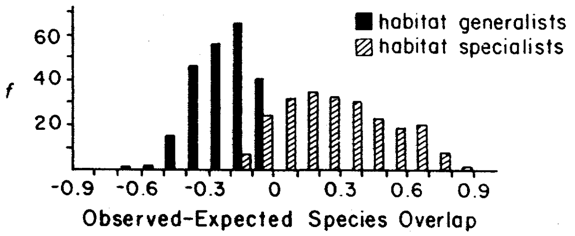

Fig. 8. Effect of reserve subdivision on bird species diversity in Western Austalian wheatbelt reserves. The abcissa plots the difference between the observed and expected overlap in species composition between a single large reserve and two small reserves of the same total area, based on a random sampling model. Positive overlap values indicate that a single large reserve contains more species than two smaller ones combined. Negative values indicate the opposite. Note the very different responses of habitat specialists (‘P_5’ species) and habitat generalists. Figure redrawn from Kitchener *et al.* (1982).

reserve than in two smaller ones of equivalent aggregate area. A preliminary analysis of birds in Victorian forest patches revealed more farmland bird species in groups of small forest patches than in single large patches, but numbers of forest-associated species were almost identical in the two patch-size configurations (Loyn, this volume). In a study of birds in Illinois (USA) forest patches, Blake and Karr (1984) concluded that aggregations of small reserves contained, on average, more sedentary, edge-associated species than did single, large reserves of the same total area, but the opposite was true for highly migratory forest-interior bird species.

It is important to recognize that the optimal strategy for reserve subdivision depends not only upon the taxa in question, but also on the absolute scale of the geographic region of interest. If one considers an entire continent, for example, several moderately large reserves that together encompass all major climatic-vegetational zones would be expected to contain more species than would any one reserve, no matter how large, that represents only a single ecological region. A very different situation arises, however, when one contemplates subdividing relatively small reserves within a single ecological association. In the extreme case, even a very large number of small preserves will be useless for the conservation of a species if each is smaller than its minimum territorial requirements, unless (as in the case of some raptors, parrots, and other vagile species) the species is capable of integrating a number of small patches into a single territory or home range. A continental strategy of establishing reserves could come close to maximizing all three of the main components of species diversity (Whittaker 1970) — purely local (‘alpha’), gradiential (‘beta’), and regional (‘gamma’) by judiciously placing moderately large reserves in all major biomes. A purely local strategy of reserve sub-division, on the other hand, would by definition forego the regional component of species diversity, and would not necessarily augment the two remaining components significantly.

If the bird species to be conserved are sufficiently sedentary that isolated reserves function as true islands, then extinction, not colonization, is the process that must dominate reserve planning and maintenance (Pickett and Thompson 1978). In the absence of a natural ‘rescue effect’ (Brown and Kodric-Brown 1977), by which the extinction of local populations is prevented by frequent recolonization by propagules from outside source areas, the number of individuals per population must be sufficiently large to reduce the risk of stochastic extinction to an acceptably low level. Maintenance of a diverse range of habitats, which almost by definition entails large areas, also provides buffering against potentially devastating environmental changes (Leigh 1981). A major challenge to conservationists is to determine the appropriate geographic scale for individual reserves and systems of reserves, based on the properties of real species or communities. Again, the obvious fact that area requirements and other ecological characteristics vary from species to species (and region to region), does not preclude useful generalizations based on body size, feeding category, migratory habits, or other salient characteristics.

THE NEED FOR A REGIONAL PERSPECTIVE

Fortunately, most continental bird species are not yet confined to a single park or reserve. Instead, we are normally dealing with *systems* of reserves, together with other, often much more extensive, areas of habitat that lie outside formal reserves. The most sensible way to approach avian conservation in such a context is on a regional basis, such that the entire assemblage of parks and unprotected lands is viewed as a system. From this broad perspective it may make more sense to devote scarce resources to assuring the survival of threatened species in the region as a whole, rather than becoming unduly distracted by the status of inherently non-viable subpopulations of birds in small, isolated forest patches.

The current resurgence of interest in landscape ecology (e.g., Noss 1983) reflects a growing awareness that ecosystems do not exist as isolated entities. For example, few, if any, of the forested tracts we studied in Maryland were large enough in themselves to support viable populations of any but the most abundant forest-interior passerines. The long-term survival of Maryland's avifauna at the regional level depends on the persistence of large numbers of forest patches, and on free movement of colonizing individuals among them. In Maryland, as in many parts of the world, most forest is not part of a formally designated reserve network, but protected and unprotected forests are functionally linked through their exchange of avian propagules. As has been pointed out by earlier investigators (e.g., Terborgh 1975; Wilson and Willis 1975), singular island preserves, for which recolonization is by definition precluded, must be large (often thousands or tens of thousands of hectares) if they are to maintain even short-term stability in the species composition of their vertebrate fauna. On the other hand, fairly small reserves (say 10-100 ha) can serve valuable conservation functions for birds, provided they are functionally connected, either to one another or to sources of colonists outside the reserve system. In extreme cases, as where formerly extensive species distributions have been reduced to a few scattered relicts, intensive human intervention may be required to maintain the viability of individual populations and to increase the functional connectivity of reserves.

In order to counter some of the negative side-effects of forest insularization, managers can work to increase effective reserve size. This can be done by increasing contiguous acreage of reserves, by promoting compatible land-use practices in adjacent non-reserved lands, or by allowing secondary succession to increase the proportion of forested land within a region. The isolation of individual forest patches can be reduced by planting (or by not removing) roadside forest strips, hedge rows, riparian corridors, etc. This technique has been advocated in Britain (Arnold 1982) and Australia (Suckling 1982). In Western Australia, Saunders (1980, 1982) has suggested that such corridors appear to be crucial as an incentive to inter-patch movement by Carnaby's black cockatoo *Calyptorhynchus funereus latirostris*. For some species corridors may provide important nesting or foraging habitat, as well as passageways between forest patches. However, the desirability, as well as the practicality, of increasing reserve connectivity must be judged on a case-by-case basis. In some situations, a high degree of reserve isolation actually serves a *positive* conservation function. In Australia and New Zealand, vermin-free offshore islands now harbour the sole (or main) populations of several previously widespread forest-dwelling species (Merton 1975; Williams 1977). Some of these island populations are natural remnants; others are the result of successful translocations by conservation officials, who have introduced endangered species onto islands in order to isolate them from adverse mainland conditions. Maintenance of several carefully monitored, highly isolated populations of such species may be better insurance against the ravages of disease, predation, or other catastrophic disturbance than would be the sequestering of a single poorly-isolated population of the same (or even larger) aggregate size.

SUMMARY AND CONCLUSIONS

The detailed effects of forest fragmentation on birds are complex and species-specific, yet some generalizations emerge. Firstly, reduction in habitat area is causally related to an entire syndrome of physical and biotic changes that may have a more direct influence than does area *per se* on populations. Edge effects, including changes in microclimate, floristic composition, vegetation structure, predation rates, and risk of nest parasitism, often extend far into a forest from its margins. Functionally, small forest patches up to a few hectares in an area may consist of nothing but 'edge' habitat (Levenson 1981). Breeding success of forest-dwelling birds is often depressed in the vicinity of forest margins, and it is this reproductive failure, rather than simply the amount of habitat available that may account for the scarcity or absence of many highly mobile forest-interior birds from small forest patches in eastern North America.

Where extensive mainland habitat exists nearby, and where predation/parasitism rates are not excessive, even tiny near-shore islands may support breeding populations (more accurately, sub-populations) of forest-interior neotropical migrants (Morse 1977; Whitcomb *et al.* 1981). However, such islands do not constitute self-contained ecosystems, relying as they do on continuous recruitment from mainland populations. Small, subsidized islets cannot be viewed as analogues of truly isolated preserves that are established for the long-term conservation of sedentary bird populations.

Our North American studies indicate that the responses of bird species to forest fragmentation are correlated with migratory habits, degree of habitat specialization, feeding ecology and other general biological characteristics. The North American data demonstrate that highly migratory bird species, particularly small insectivores, are more sensitive to the forest fragmentation syndrome than are year-round residents. The observed sensitivity to forest fragmentation appears to reflect facultative and numerical responses by migrants to immediate ecological factors, rather than being a direct result of the migration process *per se*. Different patterns may exist at low latitudes, where sedentary habitat specialists are more prevalent, and where regular large-scale latitudinal migration is uncommon.

In eastern North America, non-migratory species, particularly edge-loving forms, tend to profit from forest fragmentation, such that total species diversity and bird density may hold steady, or even increase, in fragmented forests. Such a pattern of compensation underscores the importance of differentiating between forest-interior specialists, many of which are regionally endangered by insularization of forest, and ecologically generalized edge-tolerant species, which are of little concern in a conservation context.

Finally, it is increasingly evident that long-term maintenance of some semblance of balanced natural bird communities in a fragmented landscape will require a regional perspective. In most (but not all) situations, efforts should be made to maintain or increase the functional connectivity of forest remnants. The optimal configuration of reserves needed to maintain regional diversity under real-world political and budgetary constraints will depend on the biologies of the particular species that are of concern, the aggregate area of available habitat, the functional connectivity of habitat patches, and the regional diversity and geographic scale of the habitat mosaic. When considering conservation of bird species, all of these factors must be assessed from a 'bird's eye' point of view.

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