EFFECT OF FOREST FRAGMENTATION ON BIRD POPULATIONS

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Abstract.--Many of the insectivorous songbird species that winter in the tropics are dependent on large unbroken tracts of forest during the breeding season. These species are disappearing from localities where forests are becoming fragmented. By long-range planning, managers can prevent local extinctions of these area-sensitive birds through use of such techniques as management in large units, retention of connecting corridors, and prevention of excessive isolation of forest fragments. Edge conditions can be provided, where appropriate to meet the needs of upland game species.

INTRODUCTION

Birds are sensitive indicators of habitat conditions, because each bird species has its own distinctive breeding range and habitat requirements. Habitats can be managed to increase or decrease abundance of bird species, with information derived from correlating bird populations with quantitative descriptions of the habitats in which they nest. Likewise, the presence or even abundance of certain species can be predicted on the basis of geographical location and habitat descriptions (Robbins 1978).

The purpose of this presentation is to discuss a relatively new concept in forest management: the dependence of many of the neotropical migrants on extensive tracts of forest. Just as many species of birds are restricted to certain types of habitats (woodland, prairie, desert, tundra), some species are adapted to living in the interior of an extensive forest while others utilize habitat boundaries such as wood margins and hedgerows. Each species has evolved over thousands of years and its populations have reached a state of equilibrium within its particular preferred environment. When habitat conditions change as a result of plant succession, climatic changes, or various influences brought about directly or indirectly by man, the survival potential of the species changes. When these changes favor a species, the population may spread into the favorable habitats and increase in size. When altered habitat conditions result in increased mortality or lowered reproductive rate, the population will decline unless it can be supported by immigration from nearby areas where a high reproductive rate produces a surplus of individuals. If a supply of invading individuals is not available or is insufficient to make up for the deficit, the population may decrease to a new lower equilibrium or even disappear entirely from the region of altered habitat.

I first present the results of some recent studies relating changes in breeding bird populations to changes taking place in the environment. Following that I suggest some guidelines for management of forests to benefit those nongame bird species that are disappearing as a result of failure to take their needs into consideration.

AREA SENSITIVITY

In the eastern and north central forest regions of the United States, there are many species of birds that are dependent on extensive forest systems. In recent decades these species have been retreating in the face of fragmentation of forest by such impacts as suburban sprawl, super highways, transmission lines, reservoirs, and surface mining. These sensitive birds have all but disappeared from suburban and highly agricultural areas.

Bird students have been aware of the sharp decline in breeding populations of flycatchers , vireos, warblers, and other long-distance migrants in woodland in and near the

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District of Columbia (Criswell et al. 1978). These decreases have been attributed by various investigators to a variety of causes, including sewer and highway construction, predation, greater human use, storm damage, pesticides, and loss of habitat in the vicinity of the study plots and on the wintering grounds.

Ornithologists in both Europe and America have shown that more bird species can be found nesting in large study plots than in small ones (Oelke 1966, Moore and Hooper 1975). This conclusion seems obvious, because birds are patchily distributed in most habitats, which in itself is because most habitats are structurally heterogeneous. A major reason for increased avian diversity in larger tracts, however, was overlooked by these authors.

Bond (1957), who studied bird populations in woodlots in southern Wisconsin, was the first to report that many species of small songbirds are dependent on relatively large forest tracts during the breeding season. MacArthur and Wilson (1963, 1967) demonstrated the relation between oceanic island avifaunas and the size and degree of isolation of the islands. They also suggested that the same equilibrium between colonizations and extinctions might exist on fragmented woodlots. In oceanic or mainland models, the number of breeding species increases with "island" size and decreases with distance from sources of repopulation. Whitcomb (1977) has summarized MacArthur and Wilson's widely accepted equilibrium theory of island biogeography, and discussed its implications for biotic diversity. He pointed out that: (1) as many as 92 percent of the breeding birds in some forests are migratory, (2) most of these are area-sensitive species that cannot persist in the face of forest fragmentation, and (3) they are not replaced by other species.

New Jersey Studies

In 1972 Galli et al. (1976) and Forman et al. (1976) studied bird populations on 30 forest fragments in central New Jersey. They used analysis of variance to detect those species dependent on the size of the forest fragment. Their forests varied in size from 0.01 to 24 ha. Unfortunately they did not present comparable data from a large area of continuous forest for comparison with their forest fragments. Furthermore, only one of their fragments was greater than 10 ha in size. Although they concluded that half of the forest species using their study plots were dependent on forest area, those species that are most critically dependent on area were lacking from all of their plots and consequently were not recognized as being area dependent.

Sources of Maryland Data

During the breeding seasons of 1974-76, R. F. Whitcomb and colleagues undertook a more extensive study of area sensitivity of eastern deciduous forest birds (Whitcomb et al., 1979). Realizing the urgency of obtaining a broad base of bird population data from forested plots of many sizes and degrees of isolation, they used four techniques. Breeding Bird Census (Williams 1936) and Point Survey data (Whitcomb et al., 1979) from 30 forest fragments ranging in size from 1 to 121 hectares were supplemented with data obtained from the results of Breeding Bird Survey Miniroutes (Bystrak 1978) and a Breeding Bird Atlas project (Klimkiewicz and Solem 1978). They used bird counts from 185 Miniroute stops scattered throughout Howard County, Maryland, and 700 stops throughout Prince Georges County; each of these Miniroute points was covered twice. The Atlas data, gathered by members of the Maryland Ornithological Society, showed which species were detected in each of the 25 square kilometer blocks throughout Montgomery County and 6.25 square kilometer blocks throughout Howard County.

Characteristics of Area-sensitive Species

Whitcomb et al. (1979) computed an index of area sensitivity for each forest bird species by dividing the average number of territories detected at sampling points within small (6-14 ha) forest islands by the number detected in large (80+ ha) forest tracts. They noted strong correlations between the area sensitivity of many bird species and their regional distribution and abundance in forest habitats. When they compared area sensitivity of each forest bird species with characteristics of its breeding biology, they found that most of the species sharply reduced by forest fragmentation have the following characteristics: (1) they are long-distance migrants that winter primarily in the New World tropics; (2) they are obligate inhabitants of forest interior; (3) they tend to nest on or near the ground; (4) they build nests in the open rather than in the protection of cavities; (5) they raise only a single brood of young per year; and (6) they have a comparatively small clutch size.

In contrast, many bird species that reproduce successfully under forest edge conditions are permanent residents or short-distance migrants that arrive early in the season and attempt two or more broods per season. The average nest height of these species is greater, more of them nest in cavities, and they raise many more young per year. Because of a higher reproductive potential, edge-inhabiting bird species have a much greater chance of reproductive success in areas where

predation from mammals, jays, and grackles is higher, nest parasitism from cowbirds is more frequent, and disturbance from humans is higher. On the other hand, some neotropical migrants that specialize in edge or scrub habitat (e.g., Prairie Warbler, Orchard Oriole, Blue Grosbeak) show some of the same tendencies for lower reproductive effort and higher sensitivity.

Area Sensitive Species

The area-sensitive forest interior species recognized by Whitcomb et al. (1979) include not only the Yellow-billed Cuckoo, Wood Thrush, Red-eyed Vireo, Black-and-white Warbler and Scarlet Tanager recognized by Galli et al. (1976), but also the Whip-poor-will, Pileated Woodpecker, Acadian Flycatcher, Veery, Yellow-throated Vireo, Worm-eating Warbler, Northern Parula Warbler, Ovenbird, Louisiana Waterthrush, Kentucky Warbler, Hooded Warbler, and American Redstart, as well as such wide-ranging species as hawks and owls.

Effects of Forest Fragmentation

A few specific examples will emphasize the dependence of area-sensitive species on large tracts of undisturbed forest interior, tracts greatly in excess of the 1-5 ha territory size actually defended by most small migratory nongame birds during the breeding season. The following examples are based on 3 long-term studies in which I have been involved, and 3 long-term Breeding Bird Censuses published in American Birds.

Laurel

In 1952, I moved into my present home beside the Patuxent River gorge on the outskirts of Laurel in central Maryland. At that time the forest along the river was interrupted 3/4 km below me by the City of Laurel, but continued essentially unbroken for 14 km upstream (fig. 1a). The contiguous forest totaled about 5260 ha at that time, but it became progressively more fragmented during the ensuing 25 years. First, Rocky Gorge Reservoir was created 3/4 km upstream from my home; next, Interstate 95 was constructed between my home and the reservoir; and then the hillside directly across the river was cleared of trees (fig. 1b).

Although my woods and the remaining contiguous area of forest totaling about 40 ha have not changed appreciably in character, half of the long-distance migrants that nested here 25 years ago have disappeared: Broad-winged Hawk, Whip-poor-will, Yellow-throated Vireo, Black-and-white Warbler, Worm-eating Warbler, Ovenbird, Louisiana Waterthrush, Kentucky Warbler, and Hooded Warbler (table 1). The Acadian Flycatcher, Eastern Wood Pewee, Wood Thrush, Red-eyed Vireo, Northern Parula Warbler, and Scarlet Tanager still nest here nearly every year, but in reduced numbers; and one pair of Red-shouldered Hawks still remains--perhaps

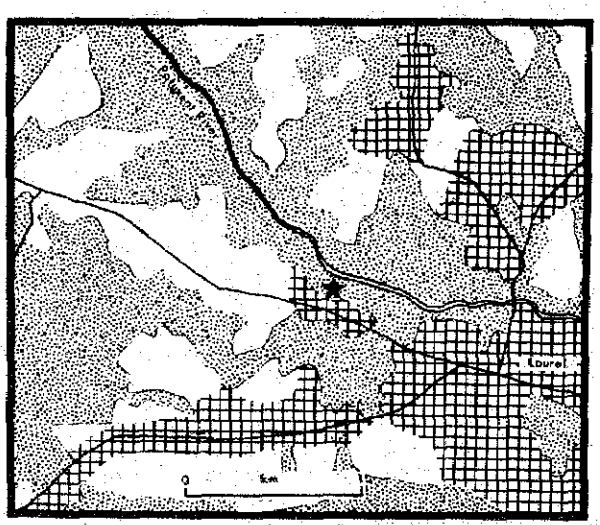

Figure 1a.--Vicinity of Laurel, Maryland, showing forest cover (dots), fields (white), urban areas (small squares), and main highways (black lines) as indicated in 1951. Woods referred to in the text are marked with a star. (USGS 7.5-min. Laurel, Md., quadrangle, 1951)

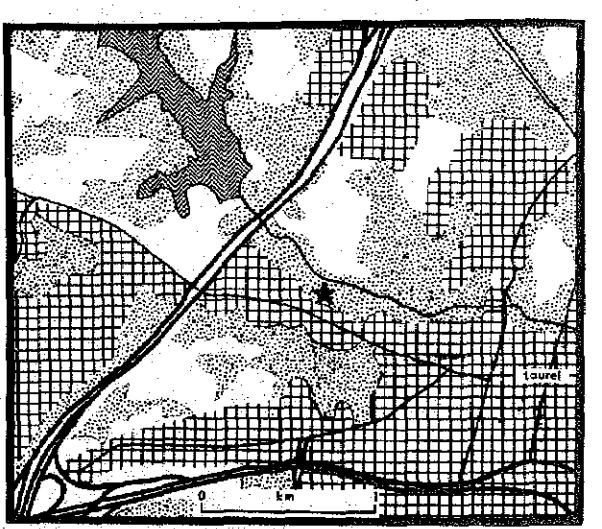

Figure 1b.--Same area in 1971, showing Rocky Gorge Reservoir, Interstate Route 95, Maryland Route 198 (bottom), and severe fragmentation of woodland. (USGS 7.5-min. topographic map, 1965, photorevised 1971)

Table 1. Population changes of long-distance migrants

Site	Laurel		Cabin John		Rock Creek		Glover-Archbold		Seton Belt		Patuxent WRC	
Plot size (acres)	--		18.75		80	65	35		36		90	135
Forest area (acres)	13,000	100	200	75	850		185		39		7400	
Years	1953 -54	1977 -78	1947 -48	1976 -77	1948 -49	1974 -77	1959 -60	1976 -77	1947	1975 -76	1959	1972
Broad-winged Hawk	X[1]	0										
Yellow-billed Cuckoo	X	X	5.0	0	1.0	0			3.0	1.5	0	3.0
Whip-poor-will	X	0										
Ruby-throated Hummingbird	X	X	5.0	0	3.0	0			4.0	+[2]	2.0	1.5
Great Crested Flycatcher	X	X	14.5	5.0	4.5	+	14.0	0	8.0	0	0	0.5
Acadian Flycatcher	X	X	34.5	34.5	27.0	1.0	25.5	3.0	33.0	18.1	25.0	14.5
Eastern Wood Pewee	X	X	26.5	8.0	7.0	2.0	8.5	1.0	19.0	20.1	4.0	0.5
Wood Thrush	X	X	21.5	0	20.0	8.5	32.0	4.5	40.0	81.9	20.5	14.0
Veery					0	5.5	40.0	57.5			0	+
Yellow-throated Vireo	X	0	9.5	0	8.0	0	3.5	0	19.0	2.1	2.0	3.5
Red-eyed Vireo	X	X	74.5	40.0	52.0	18.5	31.5	12.5	100.0	92.4	50.0	50.5
Black-and-white Warbler	X	0	V[3]	0	3.5	0			11.0	0	3.5	0
Worm-eating Warbler	X	0	V	0					3.0	0		
Northern Parula Warbler	X	X	70.5	8.0	0.5	0	11.5	0	4.0	+	3.5	2.0
Ovenbird	X	0			49.0	12.0	8.5	2.0	53.0	22.9	14.5	8.5
Louisiana Waterthrush	X	0	5.0	0	0	0.5	+	0			4.5	2.0
Kentucky Warbler	X	0	28.0	0	1.0	0	8.5	0	17.0	9.7	11.0	5.0
Hooded Warbler	X	0	11.0	0	5.0	0	15.0	0	8.0	1.4	19.0	0.5
American Redstart			68.0	13.5			34.0	+			9.0	7.0
Scarlet Tanager	X	X	13.5	0	9.0	6.5	8.5	0	26.0	12.5	15.5	7.5
Mean species per year	-	-	31.0	21.5	26.5	21.5	42.0	26.5	28.0	25.5	32.0	47.0
Percent change in species	-50%		-31%		-19%		-37%		- 9%		+47%	
Mean pairs/100 acres	-	-	658.5	364.0	223.1	126.9	718.6	453.6	437.0	390.3	289.4	260.5
Change in total population	-		-45%		-43%		-37%		-11%		-10%	
Pairs of long-distance migrants/100 acres	-	-	387.0	109.0	190.5	54.5	232.5	80.5	348.0	262.6	184.0	120.5
Change in long-distance migrants	-		-72%		-71%		-65%		-25%		-35%	

[1] X = Present, but density not determined
[2] + = Present in very small numbers, less than one-half territory
[3] V = Visitor, not nesting in study plot

receiving recruitment from the thriving population on the Patuxent Wildlife Research Center 8 km downstream.

Cabin John Island

A second example of a drastic change in bird population is evident on Cabin John Island in the Potomac River 4 km northwest of Washington, D. C., where breeding bird populations have been studied almost annually since 1947. This island is more than 500 m long and has an average width of 150 m (fig. 2a). Although vegetation of the island itself has not changed appreciably during the study period, there has been significant road construction, particularly the George Washington Memorial Parkway on both sides of the river, that has fragmented the formerly continuous forest that flanked both shores (fig. 2b). Many of the other nearby forests have yielded to housing developments.

During the 30-year study, five species that had originally been represented by two or more breeding pairs disappeared completely. These were the Wood Thrush, Yellow-throated Vireo, Kentucky Warbler, Hooded Warbler, and Scarlet Tanager. Three other less common species, the Yellow-billed Cuckoo, Ruby-throated Hummingbird, and Louisiana Waterthrush, also disappeared (table 1). Several other species declined 46% or more: Great Crested Flycatcher, Eastern Wood Pewee, White-breasted Nuthatch, Red-eyed Vireo, Northern Parula Warbler, and American Redstart (Thatcher 1948, Criswell and Gauthey 1977, and Criswell *et al.* 1948). The only neotropical

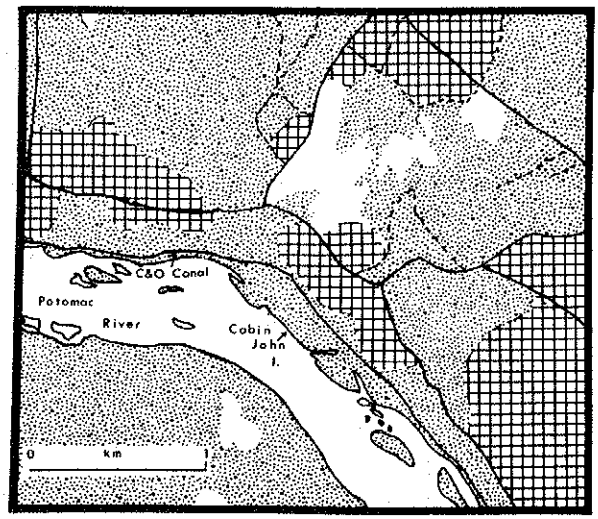

Figure 2a.--Vicinity of Cabin John Island as shown in 1951. (USGS 7.5-min. Falls Church, Va.-Md. quadrangle, 1951) Shading as in figure 1.

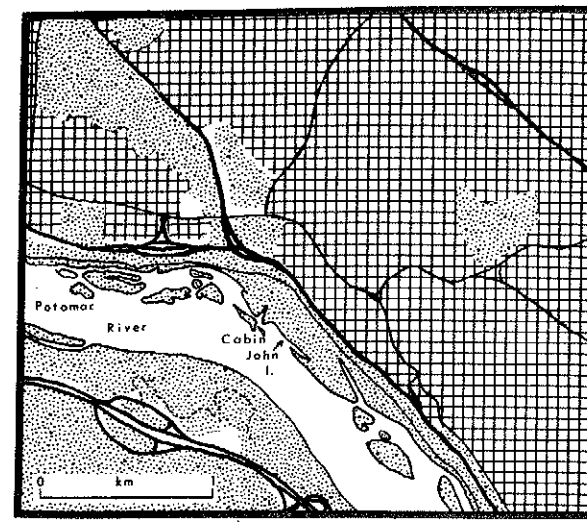

Figure 2b.--Same area in 1971, showing urban expansion and fragmentation of forest by major highways. (USGS 7.5-min. Falls Church, Va.-Md. quadrangle, 1965, photo-revised 1971)

migrant that did not decrease from 1947-48 to 1976-77 was the Acadian Flycatcher.

Rock Creek Park

Two similar long-term studies have been conducted in Rock Creek and Glover-Archbold parks, major wooded areas within the District of Columbia. Rock Creek Park is a long, narrow area of about 800 ha along Rock Creek. It is completely surrounded by city and for many years has not been connected to the narrow strip of forest along the Potomac River by even a wooded corridor. Near the center of Rock Creek Park is a 26 ha study plot in which breeding birds have been censused intermittently since 1947. The original study plot (32 ha) was part of a 345 ha tract bordered on the north by Military Road and on the south by Porter Street. Beach Drive, Glover Road, Tilden Street, and several minor roads traverse the 345 ha wooded tract, but the total amount of contiguous woodland present has changed very little during the 30-year period of the study. Automobile traffic and pedestrian use has increased in both the study plot and the Park in general. Comparing (table 1) the early studies of Thatcher (1949) with more recent studies by Craven et al. (1974) and Criswell et al. (1978) one notes that the Yellow-billed Cuckoo, Ruby-throated Hummingbird, Yellow-throated Vireo, Northern Parula Warbler, Kentucky Warbler, and Hooded Warbler no longer breed in the study plot. Other species that have decreased by more than 50% during this period are the Great Crested Flycatcher, Acadian Flycatcher, Eastern Wood Pewee, Wood Thrush, Red-eyed Vireo, and Ovenbird. Recent surveys indicate that changes in bird population recorded within the plot are characteristic of the entire Rock Creek Park forest system.

Glover-Archbold Park

Glover-Archbold Park and adjacent wooded areas make up about 75 ha of woodland that are connected by a narrow corridor to the fringe of woods along the Potomac River. Breeding birds in the park have been censused annually since 1959 (Briggs 1960, 1961, 1977, 1978). Except for the results of sewer construction in 1963, there has been no major change in the habitat of the study plot.

Neotropical migrants that were found nesting on the 14 ha study plot in 1959 or 1960 but were absent in 1976 and 1977 were Broad-winged Hawk, Great Crested Flycatcher, Yellow-throated Vireo, Northern Parula Warbler, Kentucky Warbler, Hooded Warbler, and Scarlet Tanager. The following additional species decreased more than 60% during the same period: Acadian Flycatcher, Eastern Wood Pewee, Wood Thrush, Red-eyed Vireo, Ovenbird, and American Redstart.

Seton Belt Mature Woodlot

In 1947, Stewart and Robbins (1947) censused the breeding bird population in a 15 ha plot within a fine stand of about 16 ha of mature tulip-tree--oak forest in southern Prince Georges County, Maryland. The results showed an exceptionally high density of breeding birds, 1,080 territorial males per

square km. It is believed to be the largest remnant of nearly virgin forest on the coastal plain of Maryland.

Whitcomb et al. (1977) censused this woodlot again in 1975 and 1976 using the same boundaries and techniques as in 1947. Their report includes a map showing the location of this South Tract plot with relation to highways and nearby woods. The changes in density of neotropical migrants are much less than in the other plots studied (table 1).

Patuxent Wildlife Research Center

In 1959, I censused the breeding bird population in an undisturbed 36 ha portion of the mature deciduous forest along the Patuxent River in Prince Georges County, Maryland. The census plot was a mosaic of well drained and poorly drained floodplain with small islands of the neighboring river terrace, into which one-third of the plot projected. This plot, by virtue of its size, lack of disturbance, habitat diversity, and location within a 3000 ha forest on the Patuxent Wildlife Research Center and adjacent Fort George G. Meade, contained the entire avian species pool of the eastern deciduous forest of coastal plain Maryland. Breeding populations of the neotropical migrants are listed in table 1; for populations of the other species see Stamm et al. (1960). The bird population was subsequently sampled annually by 12 days of mist netting each summer through 1972, and breeding bird censuses were repeated every few years.

Timber was not cut in or near the study plot; however, all of the following disturbances probably contributed to the change in avian populations shown in table 1: (1) One corner of the plot was permanently flooded by construction of a duck pond in a nearby field; in addition to loss of forest from the study plot itself, the flooding brought an array of edge species (plant and animal) into the plot. (2) Construction of Rocky Gorge Reservoir upstream just before the beginning of the study altered the flooding regime of the tract; instead of being inundated periodically for short intervals several times each year, the water table is lower and the floods are fewer but more catastrophic. (3) Effluent from the Laurel sewage treatment plant now provides a substantial part of the total flow of the Patuxent River during the summer months. (4) In 1962, as part of a simulated pesticide study, 174 breeding birds including 169 individuals of neotropical species were netted and removed from the plot to study the rate of repopulation. The intent was to return the removed birds to the plot; however, the cooperating agency that was caring for the birds could not keep them alive and thus none of the warblers and flycatchers survived.

The density of neotropical migrants decreased during this study (table 1), but only one breeding species disappeared entirely: the Black-and-white Warbler.

The Pattern

The pattern is quite clear. It is essentially the same group of species that are declining in each study plot, and these birds are the long-distance migrants. The permanent resident species, on the other hand, tend to maintain their populations despite suburban sprawl and forest fragmentation; the short-distance migrants that have adapted to survival in edge habitats, such as jays, House Wrens, catbirds, robins, starlings, blackbirds, and towhees, also are maintaining their populations.

Summarizing table 1 (in which the data are presented in the original English measurements of the investigators): there was an overwhelming decrease in every long-distance (neotropical) migrant except the Veery; there was a decrease in density of breeding birds in every plot, even those with minimum disturbance; and the percentage decrease in long-distance migrants was consistently much greater than the decrease in the total population. If the densities of long-distance migrants are subtracted from the total densities, the sum of the densities of permanent residents and short-distance migrants in five plots (no densities are available from Laurel) dropped from 984.5 in the early studies to 968.2, a decrease of only 1.7%.

The only species that showed increases in any of the study plots in table 1 (out of 96 pairs of observations) were the following: Great Crested Flycatcher and Yellow-throated Vireo, both present in very small numbers, increased at Patuxent; the vireo was present every year, while the flycatcher nested erratically. There were very small increases in the Eastern Wood Pewee on the Seton Belt tract and the Red-eyed Vireo at Patuxent. The Wood Thrush increased substantially on the Seton Belt tract. The Veery, a recent invader from more northern breeding grounds, established itself or increased on three plots. The Louisiana Waterthrush increased by a fraction of a territory in Rock Creek Park.

A Sample Species, the Worm-eating Warbler

Let us consider briefly the breeding distribution in Maryland of one of the species that no longer nests in any of the study plots in figure 1, the Worm-eating Warbler. The map in Birds of Maryland and the District of Columbia (Stewart and Robbins 1958) showed this species as nesting throughout the Ridge and Valley, Piedmont, and Western Shore

Coastal Plain Sections except for the highly agricultural Hagerstown, Middletown, and Frederick valleys and the flat bayshore necks of Baltimore, Harford, and Cecil counties. It also nested in forested areas along the Pocomoke River and its main tributaries and at seven isolated spots elsewhere in the State. A portion of the present-day distribution, based on the Breeding Bird Atlas of the Piedmont counties of Montgomery and Howard (Klimkiewicz and Solem 1978), is shown in figure 3. This species is strictly limited to the few remaining areas of extensive woodland.

Supporting Evidence from Breeding Bird Survey

To further test the area sensitivity of forest species and to gather information on the minimum forest area required to maintain populations of various species, comparisons were made between bird counts and habitat factors at 500 Breeding Bird Survey (Robbins and Van Velzen 1969) stops scattered through central and eastern Maryland. Each 3-minute Breeding Bird Survey stop was visited annually in the early morning in June, and data for 1974-78 were used in the analysis. Thirty habitat characteristics were recorded at each stop. One of these was a measure of the acreage of contiguous forest in and adjacent to the quarter-mile radius counting circle. I should stress that the measurement of amount of woodland included not just the wooded area within the quarter-mile circle, but it also included all contiguous forest connected to woodland within the counting circle. For purposes of the analysis the forest was categorized into units expressed as powers of three. For example, forest plots of less than 3 acres (1.2 ha) were coded 0, those between 3^1 and 3^2 (3 to 9 acres, 1.2 to 3.6 ha) were coded 1, those between 3^2 and 3^3 (9 to 27 acres, 3.6 to 10.9 ha) were coded 2, etc. The highest category encountered was coded 8 (between 6,561 and 19,683 acres, 2,655 and 7,966 ha).

Correlation coefficients were computed for 72 bird species; the recorded abundance of each bird at each stop (5-year sum) was matched against each of the following habitat factors: percentage of coniferous, deciduous, and mixed woods within a circle of 400 m (one-quarter mile) radius, and height of the canopy; percentage of brush, plowed, cultivated, pasture, hay, lawn and fallow land, and of tidal estuaries, salt, brackish, and fresh marsh, and disturbed or industrial areas; number of houses and of visible snags; presence of hedges, electric wires, fences, streams and

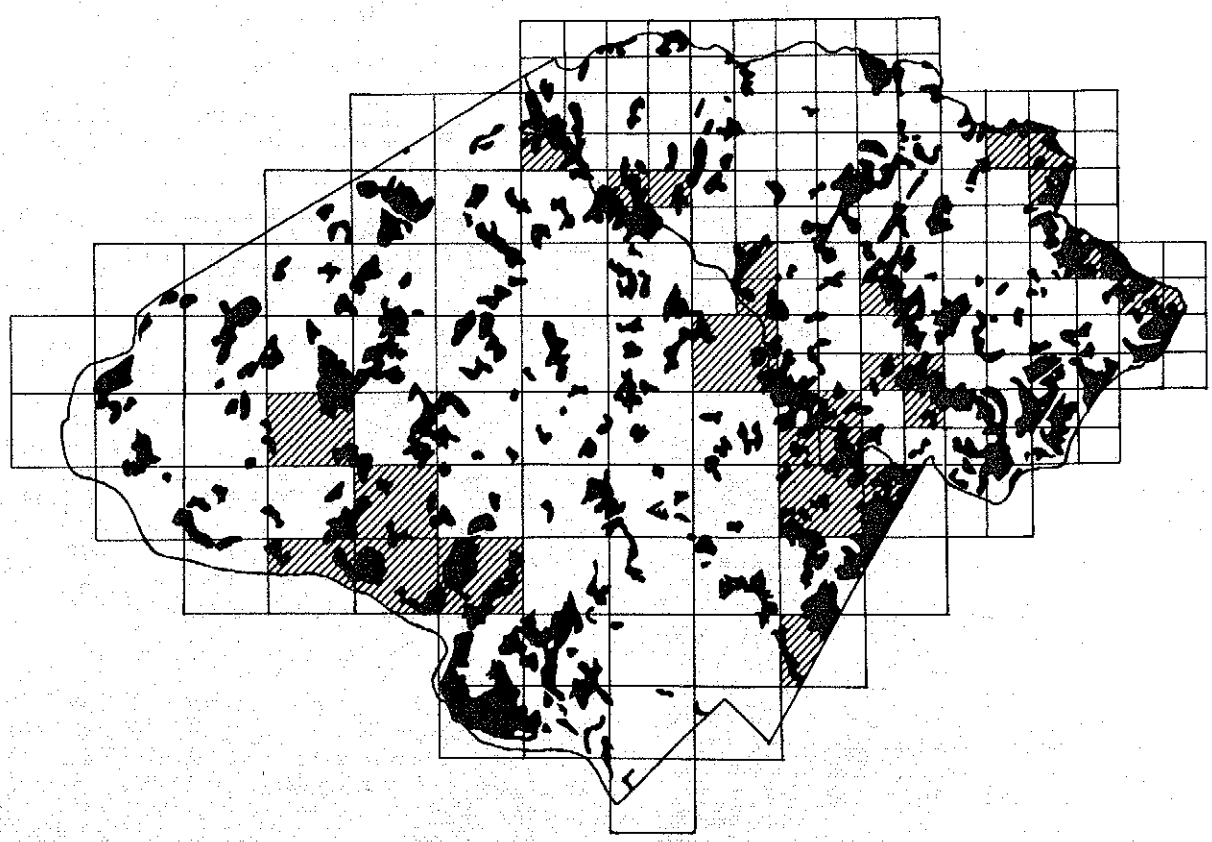

Figure 3.--Distribution of forest (solid black) and of breeding Worm-eating Warblers (shaded rectangles) in Montgomery and Howard Counties, Maryland. Data from Breeding Bird Atlas.

ponds; height of shrubs and width of roadside shoulder; also whether the road was paved, the time of morning when the bird counts were made, and the area of contiguous forest as described in the previous paragraph.

Considering only those correlations that were highly significant ($p < .01$) when each bird species was compared with each of 29 environmental factors, the only factor that was correlated with the abundance of more than half of the bird species was the area of contiguous forest (41 species). Other factors with a large number of highly significant correlations were: percentage of deciduous woods (36 species), percentage of coniferous woods, percentage of mixed woods and number of houses (24 species each), percentage of hayfield (23 species), and presence of fences (22 species).

Supporting Evidence from the Allegheny Mountains

In the Allegheny Mountains of Western Maryland and Western Pennsylvania, Deanna Dawson and colleagues from the Migratory Bird and Habitat Research Laboratory studied breeding bird populations with relation to numerical habitat descriptions in the summer of 1978. They included in their list of variables the same area measurement of contiguous forest that I had used in the above Breeding Bird Survey analyses. Their habitat variables were measurements of the tree size and density, shrub cover, canopy cover, ground cover, tree species, slope, and other criteria almost entirely different from those used in the Breeding Bird Survey analysis. It is important to note, however, that the one factor with the largest number of significant correlations with bird populations was the same one that was most significant in the Breeding Bird Survey analysis--the area of contiguous woodlands.

Determining Area Requirements for Sensitive Species

Problems in Making Estimates

Having established that a strong relationship exists between the extent of contiguous woodland and the populations of certain species of birds, the next question is one of defining the amount of contiguous forest needed for each of the area-sensitive species. Rough estimates can be obtained in several ways. One is to find the smallest forest fragment on which the species maintains at least one territory during the nesting season. The chief problem with this approach is that it does not take isolation into account. For example, MacClintock *et al.* (1977) found that a small fragment minimally isolated from a large continuous forest supported many of the neotropical migrant species characteristic of the larger woodland. Howe and Jones (1977) also pointed out that the least isolated of the small woodlots in southern Wisconsin supported the most species. Thus, any given small woodland is an integral part of a regional habitat mass that supports a regional population of the species in question. Subunits of this regional habitat mass are inadequate, by themselves, to support a population of sufficient size to retain genetic flexibility and to buffer against normal oscillations that characterize all populations. Also, it is difficult or impossible to know whether a given nesting attempt is successful, or even whether a singing male has a mate. Furthermore, it would be dangerous to draw conclusions from a single observation, which might be atypical. A pair of birds may succeed in rearing young in a year of super-abundant food. In years when food is in short supply, weather is abnormally wet, or predation is exceptionally high, nesting might be a complete failure. Thus, the critical area required for survival of an area-sensitive species is the area in which young can be produced in sufficient numbers to replace adult attrition under the poorest conditions of weather, food availability, competition from other wildlife, and other disturbances. All in all, the diversity of interacting factors presents a complex situation, and the investigator must exercize extreme caution in proposing "safe" definitions of forest area required.

Estimates from Breeding Bird Survey

To approach the problem in another way, I have computed for each area category the percentage of Breeding Bird Survey stops at which each area-sensitive species was recorded, using 5 years of data from 500 roadside stops in central and eastern Maryland. In this way I can determine not only the smallest forest fragment in which the species was recorded, but can determine at what point the frequency of occurrence begins to decrease as contiguous forest area decreases. Admittedly this method is biased to some degree by the proportion of the quarter-mile circle that is wooded, regardless of whether the woods are continuous or fragmented. In spite of this bias, there is for each of the area-sensitive species at least one point at which there is a noticeable decrease in frequency of occurrence. The percentage of stops at which Kentucky Warblers were found, for example, remained constant at about 13% at stops with 33 or more ha of contiguous forest, but dropped abruptly in smaller woodlots (fig. 4). The Ovenbird was found in the great majority of the very extensive forests, but was much less frequently recorded in the 885

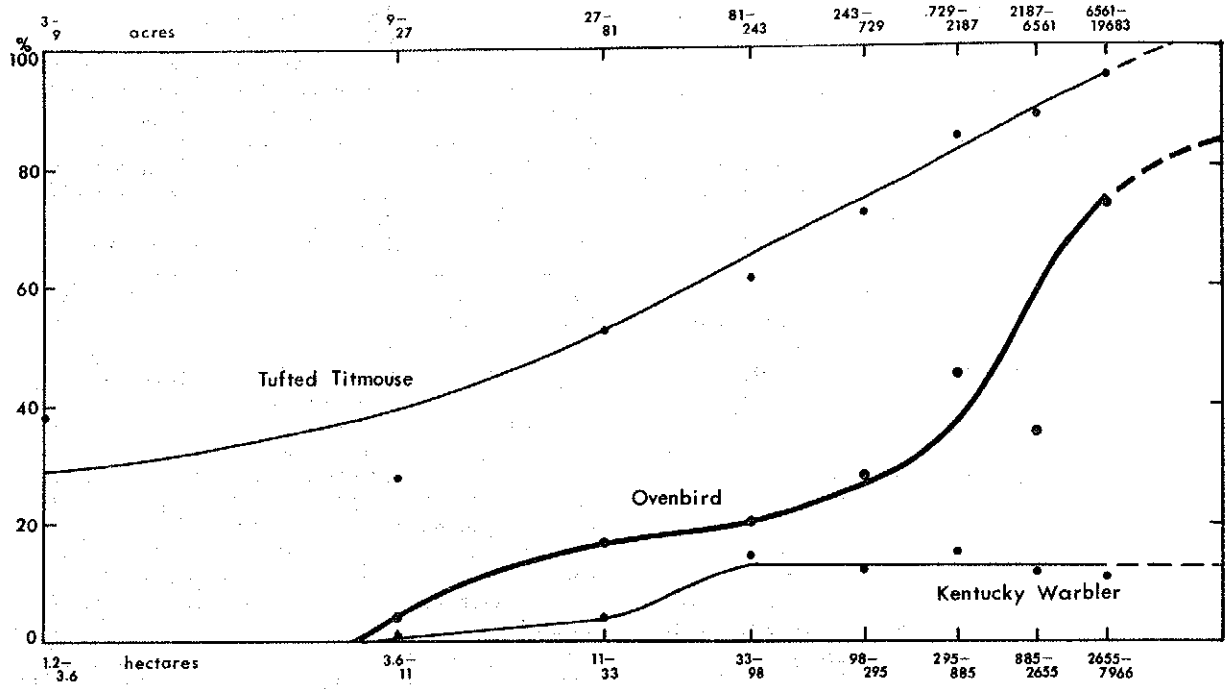

Figure 4.--Percentage of Breeding Bird Survey stops at which Tufted Titmouse, Ovenbird, and Kentucky Warbler were recorded. Stops are grouped according to the largest acreage of contiguous woodland present.

to 2,655 ha range; it was noted at nearly 20% of the stops with 11 to 98 ha of contiguous woodland, but at very few of the smaller woodlots (fig. 4). By comparison, the Tufted Titmouse, which is a permanent resident, did not show a sharp decline at any size class, and was present in woodlots of less than 3 ha. The size classes at which the frequency of occurrence of many of the area-sensitive species shows a sharp decline are presented in table 2, to give a preliminary estimate of the area sensitivity of each species.

From other breeding population data we know that figures in table 2 for the Worm-eating and Hooded Warblers are lower than the size these species require. This discrepancy results from an inadequate sample size for these species. Several of the other species registered an additional sharp decline at a lower size level: Ovenbird at 10 ha (fig. 4), and Wood Thrush and Red-eyed Vireo at 4 ha. The management concept shown by these studies is that large blocks of forest are necessary for the survival of entire nongame bird communities.

MANAGEMENT IMPLICATIONS

General Management Principles

From these early studies on forest fragmentation we can make some recommendations for management of forests to maintain or possibly increase the regional bird species pool. Some of these recommendations are counter to traditional game management approaches of opening up the forest to provide more shrub growth for deer or Ruffed Grouse. Openings do provide more food for certain species, most especially for support of seed-eating birds through the winter, but such openings as are desired for management of special interest species can be put in areas where they will not jeopardize a forest interior ecosystem.

First, a large undisturbed forest area needs to be maintained at all times. Where managed forests are contiguous with large natural areas (fig. 5a), such natural areas could serve as a nucleus for population maintenance. When the entire forest is subject to management, it is probably preferable to use a timber harvest rotation program under which a large contiguous tract remains undisturbed at any one time. Ideally,

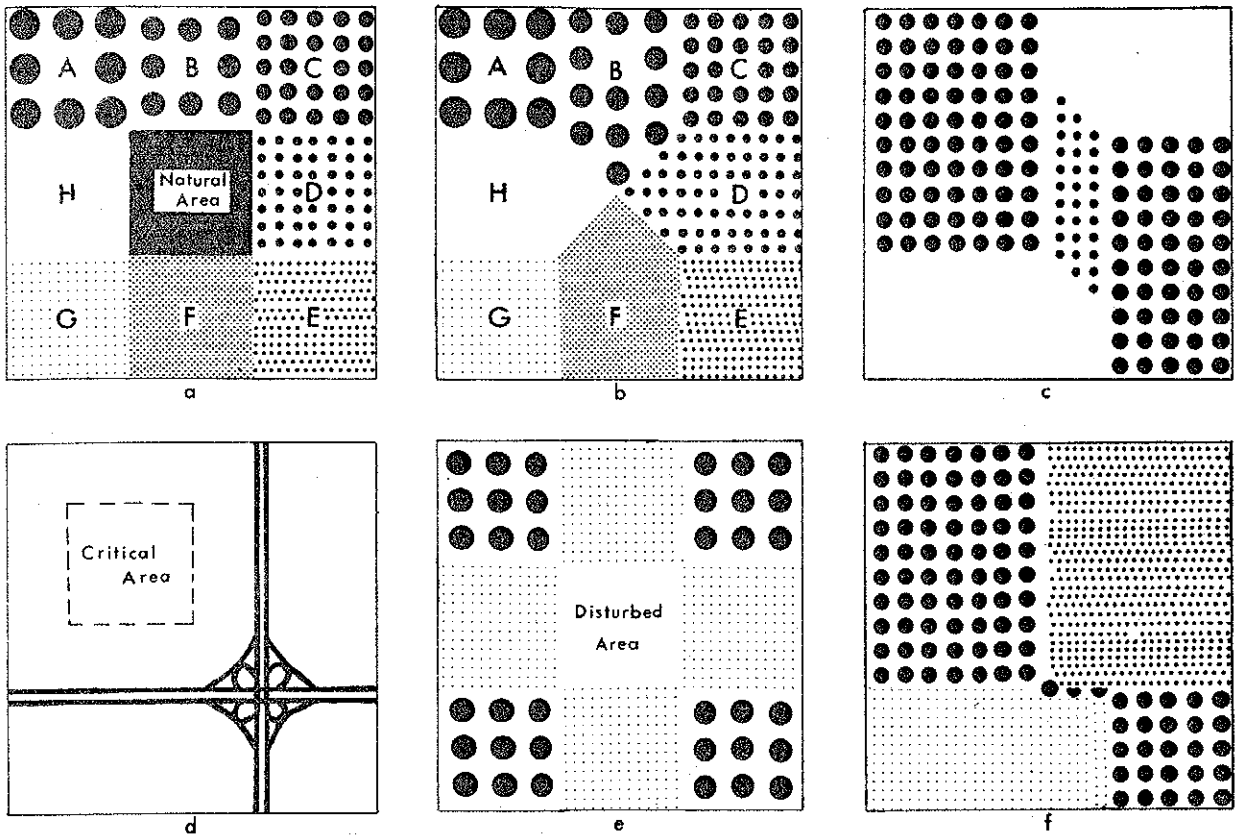

Figure 5.--Management implications for forests surrounded by other land use. Shading simulates age of forest.

a) Ideal management, with best opportunity to preserve all bird species present.
b) Good management, providing maximum adjacent habitat of each seral stage.
c) Avifauna can be preserved by planting to connect isolated woods with other forest.
d) Presence of highways or other disturbance requires change in management strategy.
e) Severe fragmentation leads to extinction of area-sensitive species.
f) Effects of fragmentation can be reduced by leaving connected wooded corridors.

harvest would occur in an orderly manner, such as a circular path (A, B, C, etc., in fig. 5b) with several hundred hectares cut in 1 or 2 years. The adjoining area would be cut several years later, and so on, in such a fashion that the bird population would move from one managed area to an adjacent one as the various seral stages moved across the landscape and as the area of mature forest gradually moved from one spot to another.

Robert Whitcomb (pers. comm.) has pointed out that when running Breeding Bird Survey routes in the West Virginia mountains he has been impressed with the great variety and abundance of warblers in areas heavily lumbered and disturbed by strip mining. Although most of the woods are in early and middle stages of growth, management has been in large units and the avian species pool has been preserved. Another advantage of managing forests in units of several hundred hectares is that disturbance in any given season is restricted to a small part of the entire management area. Conversely, if timber is harvested in many small isolated plots in the same season, the operations will impact not only the birds in the several plots, but also those along many access trails in other portions of the management area. Aesthetically, management of much smaller units might be more pleasing; but if we wish to maintain the integrity of the entire ecosystem, fragmentation into small blocks (fig. 5e) should be avoided where possible.

In states where forests are already greatly fragmented, one should view a forest management plan in the context of the adjoining forest areas and strive to coordinate management practices with nearby land owners to prevent inadvertent loss of area-sensitive species through simultaneous destruction of sources of avian repopulation.

These recommendations are derived from research on bird populations; however, they might apply to other forms of life as well. Special management techniques should be considered for locally sensitive species.

Table 2. Preliminary estimates of minimum forest areas required to sustain viable breeding populations of area-sensitive forest birds, based on 500 Breeding Bird Survey stops in central and eastern Maryland.

Species	Frequency[1]	Critical size[2] Acres	Hectares
Red-shouldered Hawk	14	250	100
Red-bellied Woodpecker	225	10	4
Hairy Woodpecker	22	10	4
Great Crested Flycatcher	146	25	10
Acadian Flycatcher	53	80	30
Eastern Wood Pewee	127	10	4
Blue Jay	262	10	4
Tufted Titmouse	294	10	4
Carolina Wren	300	25	10
Wood Thrush[3]	304	250	100
Yellow-throated Vireo	27	250	100
Red-eyed Vireo[3]	276	250	100
Black-and-white Warbler	24	750	300
Prothonotary Warbler	9	250	100
Worm-eating Warbler[3]	9	750	300
Northern Parula Warbler	19	250	100
Pine Warbler	71	80	30
Ovenbird[3]	84	6550	2650
Louisiana Waterthrush	6	250	100
Kentucky Warbler[3]	32	80	30
Hooded Warbler[3]	17	80	30
Scarlet Tanager	133	250	100
Summer Tanager	45	250	100

[1]Number of stops at which the species was found.
[2]Area at which the sharpest decrease occurred.
[3]See text for comment.

Snags

During the past 6 years several investigators have emphasized the value of snags to wildlife (e.g., see Conner 1978). There is no question that presence of snags will increase populations of hole-nesting species, especially in the early successional habitats containing few natural cavities. Snags also are used as perches for many species other than cavity nesters. Although snags increase the populations of some species, they may cause a decrease in others by introducing edge conditions into a forest interior. I doubt that anyone will challenge the benefits of leaving snags at or near the edge of a managed forest, but one must consider the consequences of permitting snags to be retained intentionally in forest interior situations. The principal problem is that snags are used by cowbirds for watching the activities of other species in whose nests they will lay their own eggs. Brown-headed Cowbirds have been increasing steadily since at least the mid-1960's (Bystrak and Robbins 1977), and are having a greater impact on nesting success of small insectivorous birds. Mayfield (1977) found the Brown-headed Cowbird to be one of the most serious threats to survival of the endangered Kirtland's Warbler. The introduction of cowbirds into forest interior situations where they do not normally occur (Lowther and Johnston 1977) will have a detrimental effect on many of the neotropical insect-eating migrants that are restricted to the forest interior. The forest interior specialists are not adapted to cope with nest parasitism from the cowbird. Nearly all build open nests that are easily found by the cowbird, and most also raise only a single brood per year; thus, cowbird parasitism may destroy their entire annual production.

I am not saying that snags are bad in all interior situations, but I stress that if use of snags is promoted in the forest interior such snags should be clustered in a few areas rather than permitted to exist throughout a managed forest. Furthermore, when feasible, I recommend that tall snags that break the canopy be removed and shorter snags within the canopy be retained because cowbirds tend to select exposed perches.

Bear in mind that snags at or near a forest edge will frequently attract nesting Starlings, and the Starlings in turn compete with native hole-nesting species, especially flickers, Red-headed Woodpeckers, and bluebirds.

Reservoirs

One of the greatest disasters that can befall a forest bird community is the creation of a reservoir. In large sections of north central and northeastern United States the most extensive wooded areas are those in stream valleys. When such valleys are impounded for water supply, flood control, or recreation purposes, the more moist and generally most productive forest areas are destroyed, and many of the adjacent upland forest areas are fragmented to the point that they can no longer support the area-sensitive species of migratory birds. As an example, I would like to refer again to Rocky Gorge Reservoir near my home (fig. 6). Within the flooded basin of the reservoir, all of the lowland forest was destroyed. In addition, the remaining upland has been fragmented so

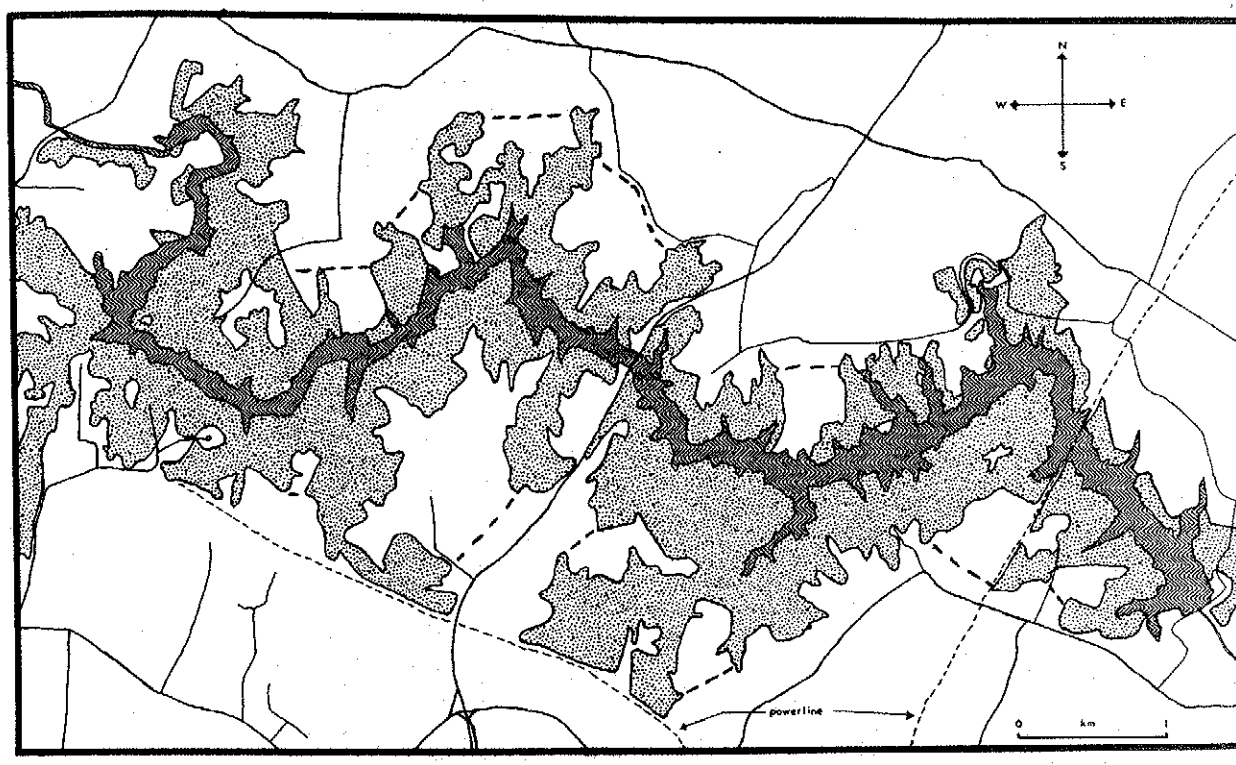

Figure 6.--Excessive fragmentation by Rocky Gorge Reservoir could have been prevented by planting forest within the dashed lines prior to destroying the original forest.

that now there is not a single point in the forest that is more than 300 meters from the forest edge. Although small numbers of many of the area-sensitive species still persist on these fragments, it is almost certain that these populations are doomed. The proximity of edge conditions throughout the area must inevitably lower reproductive rates of the present population, and there is no longer an adjacent mesic forest of higher productivity that can serve to offset losses in the peripheral population.

My reason for citing this example is that by means of proper long-range planning it would have been possible to protect or plant forest in strategically located areas adjacent to the impoundment before construction of the reservoir. If some of the areas marked with heavy dashed lines in figure 6 had been planted to forest before the area along the river was cut, several large areas of contiguous forest could have been retained, giving additional protection to the watershed and also providing refuge areas that could have served to perpetuate most of the avifauna typical of the original forest.

Corridors

One way to reduce the loss of area-sensitive species from forest fragments is by leaving (or planting) corridors that connect the fragment with a larger forested area (fig. 4f; see also MacClintock et al. 1977). The corridor concept has also been used successfully to bring woodland birds closer to residential areas during the non-breeding periods. Very few studies have documented effects of corridor width on bird populations, so no specific recommendations can be made now regarding the preferred width of such corridors or the extent that they are beneficial to certain species. Right now, I can only recommend retention of even a narrow corridor to prevent complete isolation of forest fragments. The corridor concept could also be carried too far. If a large number of small fragments were connected by corridors from the same source of repopulation, birds from a main forest might be enticed into fragmented woodlots where increased predation, competition from edge species, and other factors would prevent successful rearing of young (Whitcomb et al. 1979).

MANAGEMENT RECOMMENDATIONS

The following 16 recommendations stress steps that can be taken to retain the obligate forest-interior species in the breeding population. Nearly all of the edge species and those of the various seral stages will find suitable habitat regardless of the management techniques employed; these species are not so dependent upon large contiguous areas of similar habitat. Thus, most edge species of birds are not in danger of being eliminated from the species pool.

1. Avoid unnecessary fragmentation of forests (fig. 5e).

2. Manage in large blocks, or in such a way that small blocks are adjacent to more extensive forest.

3. In long-range plans designate tracts that will be mature or nearly mature at each stage in the management plan, and design normal management operations in such a way that repopulation of disturbed areas can proceed via wooded connections or over the smallest possible gaps in forest cover.

4. When possible, use a fairly uniform plan of rotation cutting (fig. 5a,b) so that the oldest sections at any time are adjacent to each other and the younger stages are adjacent to themselves, making the maximum usable area available to each bird species, no matter what its requirements.

5. Plan cooperatively with adjacent landowners so that maximum repopulation potential of those species that require extensive mature or near mature forest can be achieved.

6. In areas where mature forest is limited, consider preserving one or more strategically located mature tracts to serve as sources of avian repopulation.

7. In any management plan designate areas that are especially sensitive during any particular period of the year; and by posting or other means keep disturbance such as camping, hiking, picnicking, fishing, surveying, marking, or cutting to a minimum during the nesting season (May through early August).

8. When public use is part of a forest management plan, restrict activities to the edge of a sensitive area rather than permitting them to extend into its center.

9. Retain vegetational diversity to the extent feasible, because many studies have demonstrated a direct relation between vegetational diversity and avian diversity. It is not necessary to maintain high diversity in each separate management unit as long as there is diversity among different units. Grazing reduces diversity by removing or greatly reducing one or more of the important components of the forest vegetation.

10. Pending conclusion of more definitive studies on minimum habitat area requirements of various avian species, think in terms of 1,000 contiguous hectares (2,500 acres) of forest canopy as a desirable goal to preserve most or all of the avian species pool.

11. In smaller tracts (even down to 2 ha or less) it is beneficial to maintain the maximum contiguous woodland with the least amount of edge.

12. Management units that approach a square are much more effective in preserving forest-interior birds than are long, narrow ones--especially when managed tracts are small. The portions of a forest that are most beneficial to neotropical migrants are several hundred meters or more away from the forest edge.

13. Leave snags along forest edge or in patches in the forest interior, but not throughout the forest. In the forest interior select for preservation those snags that will not extend above the canopy of the nearly mature forest.

14. In any management plan consider the disruptive effects of other projects such as existing or proposed super highways, impoundments, transmission line corridors, or sewer lines (fig. 5d). Check with appropriate agencies on the timing of new construction, to avoid inadvertent loss of a critical area at the wrong time.

15. With reference to recommendation 14, provide mitigation planting as far in advance of the impending disturbance as possible (fig. 6).

16. If wooded fragments must be isolated from the forest proper, retain a connecting corridor, such as along a stream; or if a forest tract has already been separated, consider planting a corridor to reconnect it (fig. 5c,f).

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APPENDIX

Scientific Names of Birds

Area-sensitive Species

Nonpasserines	
Red-shouldered Hawk	Buteo lineatus
Broad-winged Hawk	Buteo platypterus
Yellow-billed Cuckoo	Coccyzus americanus
Whip-poor-will	Caprimulgus vociferus
Ruby-throated Hummingbird	Archilochus colubris
Pileated Woodpecker	Dryocopus pileatus
Flycatchers	
Great Crested Flycatcher	Myiarchus crinitus
Acadian Flycatcher	Empidonax virescens
Eastern Wood Pewee	Contopus virens
Thrushes	
Wood Thrush	Hylocichla mustelina
Veery	Catharus fuscescens
Vireos	
Yellow-throated Vireo	Vireo flavifrons
Red-eyed Vireo	Vireo olivaceus
Wood Warblers	
Black-and-white Warbler	Mniotilta varia
Prothonotary Warbler	Protonotaria citrea
Worm-eating Warbler	Helmitheros vermivorus
Northern Parula Warbler	Parula americana
Pine Warbler	Dendroica pinus
Ovenbird	Seiurus aurocapillus
Louisiana Waterthrush	Seiurus motacilla
Kentucky Warbler	Oporornis formosus
Hooded Warbler	Wilsonia citrina
American Redstart	Setophaga ruticilla
Tanagers	
Scarlet Tanager	Piranga olivacea
Summer Tanager	Piranga rubra

Other Species Mentioned

Ruffed Grouse	Bonasa umbellus
Red-bellied Woodpecker	Melanerpes carolinus
Red-headed Woodpecker	Melanerpes erythrocephalus
Hairy Woodpecker	Picoides villosus
Blue Jay	Cyanocitta cristata
Tufted Titmouse	Parus bicolor
White-breasted Nuthatch	Sitta carolinensis
House Wren	Troglodytes aedon
Carolina Wren	Thryothorus ludovicianus
Starling	Sturnus vulgaris
Kirtland's Warbler	Dendroica kirtlandii
Prairie Warbler	Dendroica discolor
Brown-headed Cowbird	Molothrus ater
Orchard Oriole	Icterus spurius
Blue Grosbeak	Guiraca caerulea

LITERATURE CITED

Bond, Richard R.
1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. Ecol. Monogr. 27:351-384.

Briggs, Shirley A.
1960. The first Glover-Archbold Park census. Atlantic Naturalist 15:42-43.

Briggs, Shirley A.
1961. 1960 Breeding bird population studies: Glover-Archbold Park. Atlantic Naturalist 16:45-46.

Briggs, Shirley A. (compiler)
1977. Breeding Bird Census: Mixed upland habitat. Amer. Birds 31:40.

Bystrak, Danny.
1978. Application of Miniroutes to bird population studies. Maryland Birdlife (in press).

Bystrak, Danny, and Chandler S. Robbins
1977. Bird population trends detected by the North American Breeding Bird Survey. Polish Ecological Studies 3:131-143.

Conner, Richard H.
1978. Snag management for cavity nesting birds. In U. S. Forest Serv. General Technical Rep. SE-14, pp. 120-128.

Craven, C. E. (compiler).
1974. Breeding Bird Census: Central hardwood forest with scattered pine. Amer. Birds 28:1015.

Criswell, Joan H., and J. R. Gauthey.
1977. Breeding Bird Census: Mature deciduous floodplain forest. Amer. Birds 31:39.

Criswell, Joan (compiler)
1978. Breeding Bird Census: Mature deciduous floodplain forest. Amer. Birds 32:60.

Forman, Richard T. T., Anne E. Galli, and Charles F. Leck.
1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. Oecologia 26:1-8.

Galli, Anne, Charles F. Leck, and Richard T. T. Forman.
1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356-364.

Klimkiewicz, M. Kathleen, and Joanne K. Solem.
1978. The breeding bird atlas of Montgomery and Howard Counties, Maryland. Maryland Birdlife 34:3-39.

Lowther, Peter E., and Richard F. Johnston.
1977. Influences of habitat on cowbird host selection. Kansas Ornithol. Soc. Bull. 28:36-40.

MacArthur, Robert H., and Edward O. Wilson.
1963. An equilibrium theory of insular zoogeography. Evolution 17:373-387.

MacArthur, Robert H., and Edward O. Wilson.
1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey. 203 p.

MacClintock, Lucy, Robert F. Whitcomb, and Bruce L. Whitcomb.
1977. Evidence for the value of corridors and minimization of isolation in preservation of biotic diversity. Amer. Birds 31:6-16.

Mayfield, Harold F.
1977. Brown-headed Cowbird: agent of extermination? Amer. Birds 31:107-113.

Moore, N. W., and M. D. Hooper.
1975. On the number of bird species in British Woods. Biol. Conserv. 8:239-250.

Oelke, Hans.
1966. 35 years of breeding bird census work in Europe. Audubon Field Notes 20:635-642.

Robbins, Chandler S.
1978. Determining habitat requirements of nongame species. Trans. North Amer. Wildlife and Natural Resources Conf. 43:57-68.

Robbins, Chandler S., and Willet T. Van Velzen.
1969. The Breeding Bird Survey, 1967-68. U. S. Fish and Wildlife Service, Special Scientific Report--Wildlife 124, 107 p.

Stamm, Donald D., David E. Davis, and Chandler S. Robbins.
1960. A method of studying wild bird populations by mist-netting and banding. Bird-Banding 31:15-130.

Stewart, Robert E., and Chandler S. Robbins.
1947. Breeding-bird Census: Virgin central hardwood deciduous forest. Audubon Field Notes 1:211-212.

Stewart, Robert E., and Chandler S. Robbins.
1958. Birds of Maryland and the District of Columbia. U. S. Fish and Wildlife Service, North Amer. Fauna 62. 401 p.

Thatcher, Donald M.
1948. Breeding-bird population studies. Wood Thrush 4:8-20.

Thatcher, Donald M.
1949. Breeding bird population studies. Wood Thrush 5:121-123.

Whitcomb, Bruce L., Robert F. Whitcomb, and Danny Bystrak.
1977. Long-term turnover and effects of selective logging on the avifauna of forest fragments. Amer. Birds 31:17-23.

Whitcomb, Robert F.
1977. Island biogeography and "habitat islands" of eastern forest. Amer. Birds 31:3-5.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak.
1979. Effect of forest fragmentation on avifauna of the eastern deciduous forest. In Forest island dynamics in man-dominated landscapes. Springer-Verlag, N.Y. (in press).

Williams, Arthur B.
1936. The composition and dynamics of a beech-maple climax community. Ecol. Monog. 6:318-408.