Island Biogeography and "Habitat Islands" of Eastern Forest

Recent research sheds new light on the minimum size requirements and location of sanctuaries for birds of the eastern forest

I. Introduction

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Biologists have always been exceptionally interested in the study of island biota. One of the main observations to emerge from such studies is that fauna and flora of islands seem to be depleted when compared with appropriately similar mainland habitat. In 1967, MacArthur and Wilson published a detailed exposition of a theory (*the equilibrium theory of island biogeography*) which explained these observations. In its simplest form, the theory states that the number of species on an island represents a balance between immigration and extinction. On an island which has been newly created, for example, one would expect rapid colonization initially, as species most adept at dispersal begin to arrive. Eventually, most of these species would have colonized the island. Conversely, no species can become extinct at the very beginning, but later a substantial species pool would accumulate from which extinction would be possible Eventually, the curves for colonization and extinction rates must intersect at an equilibrium level that would determine the number of species on the island. According to the theory, one would also expect higher immigration rates and lower extinction rates on larger islands, or on islands relatively close to a mainland. There is much empirical data and some experimental data to support these ideas (reviewed by Simberloff, 1974), and the theory has now gained wide acceptance.

All islands, of course, are not oceanic. In the midst of today's disturbed landscapes one finds many islands of man's creation, fragments of once large and homogeneous ecosystems that are now surrounded by urban, suburban, or agricultural land. Many species cannot utilize these intervening "oceans" of unsuitable habitat. What suitable habitat remains is broken into pieces of various size, with different degrees of isolation Intuitively, one would imagine that at least some of the principles regulating species richness on oceanic islands would operate on these mainland "habitat islands" as well.

Since 1974, we have been examining oak-hickory woodlots in the Maryland Piedmont and Coastal Plain from the perspective of island biogeography (Whitcomb *et al.*, in preparation) In our studies, many "islands" in the form of isolated forest fragments were censused or surveyed for

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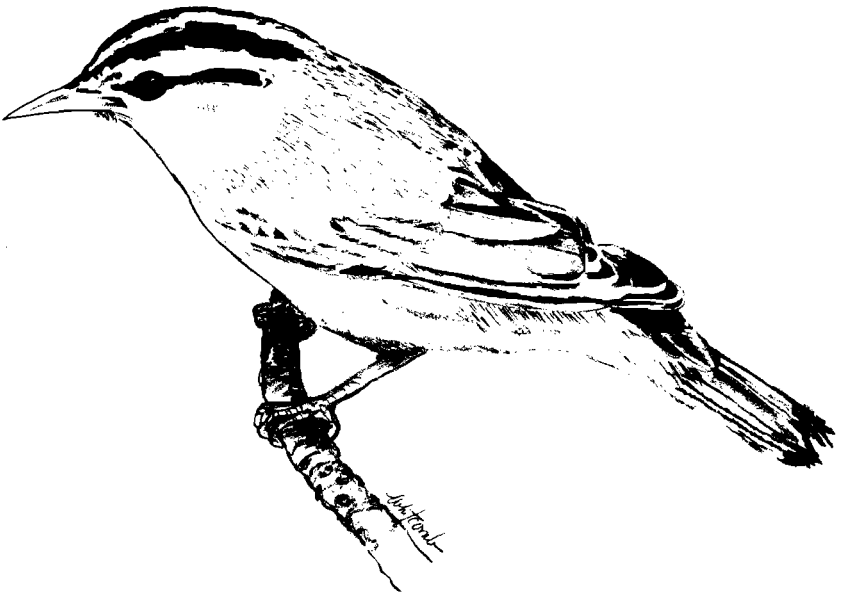
their avifaunal compositions. As a result, we can now make a general statement about the effect of fragmentation of the eastern forest on its bird inhabitants. We conclude that many of the neotropical migratory species that were once dominant in the forest interior tend to disappear from fragmented forests. They are not replaced by other species. Permanent resident, passerine species are less affected, or often profit from these changes. The degree of dominance of neotropical migrants in large eastern forests can be astonishing; as many as 92% of the territorial birds in some forests are migratory. But the special characteristics which account for the high degree of adaptation of these species to the large forest also make them sensitive to its fragmentation.

Several factors are probably working against the migratory species. These may include (1) *human impacts* such as trampling, which may have a more severe effect on the migrants, many of which nest on or near the ground; (2) *herbivore grazing* in woodlots, which severely affects the shrub and terrestrial layers and (3) *nest predation and parasitism* by small mammals, jays, grackles, crows and cowbirds which may increase quantitatively in fragmented environments. Other, more subtle effects may relate more directly to the fragmentation. For example, it is likely that certain patches of forest, particularly xeric (very dry) areas, were never fully productive for many species, in terms of their ability to support a stable population over long time periods (Diamond, 1975a). This concept of (4) *site-to-site variation in productivity* suggests that more mesic (relatively moist) forest patches may have "subsidized" such areas of low productivity. Removal of an adjacent forest or mesic forest patch might then remove the source of long-term stability. Another factor relating to forest fragmentation is the relative efficacy of (5) *competing feeding strategies.* Most permanent resident bird species, to insure survival throughout the year, must be feeding "generalists" — *i.e.,* they accept a wide variety of food items. Such a feeding strategy should work better in a patchy environment. Actually, feeding is only one aspect of species behavior. Each species has a set of biological attributes inextricably woven into a "life history strategy." In many respects, the life history strategies of disappearing migratory species are similar. For example, all are insectivorous specialists, a habit which requires neotropical migration. In turn, migration presents a number of complications. One of these is the consumption of enormous amounts of time and energy, which then results in an energy and time deficit for other important activities, such as reproduction. The (6) *lower reproductive rates* of migratory species may also affect their ability to adjust to forest fragmentation. A final important consideration is the matter of (7) *dispersal.* Permanent resident species have long periods of time to effect colonization. Perhaps the isolation of forest fragments is less devastating to species such as chickadees and titmice which can devote these long periods to territorial exploration. We believe that removal of nearby habitat reduces the colonization rate to a habitat island by reducing the number of available colonists and by making the remaining habitat less likely to be chosen by the potential colonists. Stated another way, habitat islands may leak progeny at a more rapid rate than they are colonized by first-year birds.

All of the factors we have suggested are probably operative in fragmented forest systems, the evaluation of their relative importance is a task for the future. For today, it is important to reemphasize that certain bird species, such as forest-interior warblers and vireos, disappear from fragmented forest systems. These species are in danger of regional extinction in areas such as Maryland's Coastal Plain and Piedmont, where forest fragmentation is especially severe. In very severely fragmented forest systems (for example, in Illinois), regional extinctions have probably already occurred. Today other species, even those associated with edge or secondary habitats, may in turn be threatened (Graber and Graber, 1963).

Thus, the comparative surveys and censuses we have undertaken have revealed disturbing patterns, which suggest that regional extinctions of neotropical migrant species will be forthcoming wherever measures are not taken to preserve forest systems of adequate size and continuity. In a larger sense, of course, avifaunal preservation is only one facet of the complex problems associated with preservation of biotic diversity. Recent attention (The Nature Conservancy, 1975) has focused on the imperative task of preservation of a diversity of natural communities, and the species which comprise them. Difficult practical questions arise when specific sites are to be designated and sizes determined for natural areas (Diamond, 1975b, Whitcomb *et al.,* 1976). Data from bird censuses have provided the answers to such questions in the past, and may do so for some time to come Because birds occupy a variety of trophic (nutritional) levels and are of moderate size, the minimal area requirements for bird species are neither unrepresentatively large or small. It is surely reasonable for conservationists to demand that forest preserves in eastern North America be large enough to support populations of the warblers and



Worm-eating Warbler, from a drawing by Miriam Whitcomb.

vireos which dominated the primeval forests. There are various approaches which might be used in estimating this critical area requirement, one of which involves the genetics of small populations. Since geneticists consider population sizes smaller than 1000 to be very vulnerable, *thousands of contiguous acres may be required to assure the long-term survival of the forest-interior bird species.* If sizes of this magnitude are involved, we can be reasonably confident that the preserves will also be adequate for the preservation of the vast majority of the many thousands of species of living organisms which comprise the forest community. Thus, imperatives for avifaunal preservation should be an important consideration whenever planners threaten to limit the size of regionally significant preserve areas. In this regard, it is of interest that both of the areas studied in the following two papers are under current scrutiny as candidates for regional natural areas in Maryland (CBPNA, 1976).

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