III. Long-term Turnover and Effects of Selective Logging on the Avifauna of Forest Fragments

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In 1947, Stewart and Robbins surveyed a possibly virgin Tulip-tree-oak tract in southern Prince George's County, Maryland. Although this tract was relatively small (less than 40 acres), their census revealed an unusually high species richness and density of forest interior birds. In the light of our recent studies of birds of deciduous woodlots, this census interested us, because we had noted that avifaunas of similarly sized, but isolated and younger deciduous tracts in most areas of Prince George's and Montgomery counties were relatively depauperate in forest interior species (Whitcomb *et al.*, in preparation). Because this tract (the South Tract) had remained essentially unchanged for 28 years, it seemed worthwhile to determine if any changes had occurred in its avifaunal composition during this interval.

When we surveyed the tract and its immediate vicinity for our census, we were surprised to discover the existence of a vegetationally similar woodland fragment nearby (the North Tract). However, in the winter of 1971, this 53-acre tract had been selectively logged for White Oak. As a result, there were numerous canopy breaks at the site of tree removals, and logging roads transected the shrub and ground zones. Because the position of the tract 0.5 miles north of the South Tract and adjacent to two other woodland tracts (Fig. 1) gave it a "stepping stone" status in the local forest ecosystem, it also seemed worthy of study. Therefore, we laid out a plot within the interior of this tract of approximately equal size with the plot in the South Tract.

At the outset, we recognized three significant features of the North and South Tracts which distinguished them from others we had studied. The first obvious feature is the maturity of the forests. The second feature is their location in the fertile Greensands soil district, where high soil fertility promotes development of mesic forest even under upland conditions. A third important feature is the local biogeographic context. For example, although both tracts are technically "islands" of forest, both are separated from larger second-growth forest only by narrow seldom-used farm roads or wide paths. On the east, the narrow width of Church Road separates the South Tract (Fig 1) from a wooded corridor that follows a small stream and is continuous with wooded tracts along a large stream (Collington Branch). The tract is located at the southeastern corner of a 624-acre farm (The Seton Belt Home Farm) willed to the present owners in 1959 and held since that time in its original use. Large sections of the farm are wooded and all such sections are interconnected to some extent by corridors of second-growth woodland or hedgerows. The sections are separated from each other by short, easily traversed distances. An important major woodland adjoins the property at its northeast corner and another major woodland, part of the Black Branch system, lies 0.5 miles to the south. The net effect of these interconnecting woodland systems is difficult to evaluate. Component pieces are neither true "islands" nor tracts of forest interior. Rather, they are fragments of a forest system that have long ecotonal interfaces with fields. Quantitative evaluation of the degree of isolation of habitat fragments is beyond the scope of this paper. But in any event, the isolation of component pieces of this system from each other and from surrounding forest is minimal.

RESULTS AND DISCUSSION

The North and South Tracts were censused by standard methods in 1975 and 1976; the results are presented as standard breeding bird censuses (Censuses nos. 169 and 170; pp. 91-93).

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Figure 1. Diagrammatic representation of local biogeographic context of 2 forest tracts. The two tracts, 'North Tract (N)", and "South Tract (S)" are composed of mature trees (1). There is no evidence of disturbance in the South Tract, but the North Tract was selectively logged for White Oak in the winter of 1971. Other important wooded areas are composed of open old-field Black Locust-Red Maple invaded by Bush Honeysuckle and Poison Ivy (2), extensive Sweet Gum-Pin Oak-Tulip-tree seepage forest (3), various mixed second growth forest (4), and young, predominantly Red Maple second growth forest (5). Areas not coded by textures are cultivated fields, pasture, or lawn; streams are represented by dashed lines.

Impact of tree removal. We had expected to encounter significant populations of "edge" species in the interior of the North Tract, as a result of the canopy openings and the proliferation of shrubs and saplings beneath them. This expectation was fully realized (Table 1). Edge species that utilized the disturbed sections of the forest were Rufous-sided Towhee, Indigo Bunting and White-eyed Vireo and, to a lesser extent, Mourning Dove, Com. Yellowthroat, Gray Catbird, Brown Thrasher and "Baltimore" Oriole. Although the invasion of edge species was the most conspicuous result of the 1971 logging, certain forest interior species also profited from these alterations. Hooded and Kentucky Warblers, in particular, were found in densities approaching reported maxima for those species (Stewart and Robbins, 1958). Ovenbirds, on the other hand, were rare. Territories of this species were located in the least impacted section of the forest. Similar changes have been observed by others. Robbins (1974) found a dramatic turnover in the avian community after extensive logging of an oak-maple ridge forest in western Maryland. The chief beneficiaries included shrub-dependent species such as Rufous-sided Towhee and several warbler species, including Hooded Warbler, but in that case the decrease in Ovenbirds was not very pronounced. Likewise, in the study of a gale-damaged oak forest in New Jersey, Eynon (1951-1954) noted that Rufous-sided Towhee and Hooded Warbler profited from the storm-induced stress.

In 1963, a tornado damaged a beech-maple forest in Indiana which had been censused during the previous 4 years (Webster, 1963, 1964) Canopy species such as Red-eyed Vireo, Cerulean Warbler and Blue-gray Gnatcatcher decreased in abundance, but the density of Kentucky Warbler was not affected or increased slightly.

From these studies and our censuses, one can draw some inferences concerning the expected impact on bird populations of tree removal from a mature forest. (1) The avian species richness increases as a result of increased habitat diversity; (2) the carrying capacity for canopy-dependent species is reduced; and (3) clearings beneath the opened canopy grow up with a rich assortment of saplings, shrubs and vines; additional nesting cover is created; and soil nutrients are presumably cycled at a more rapid rate into biomass of shrub-layer plants and their associated insects. These changes naturally result in a greater density of shrub-layer dependent species such as Hooded Warbler. However, if the forest floor becomes completely entangled with brushy growth, densities of ground foraging species such as Ovenbird will be severely reduced. The net change in carrying capacity of the forest may increase or decrease, depending on the extent of the change and the completeness of the available species pool of potential avian colonists.

The study of Adams (1974) provides some insight into changes that might be expected in future years in the North Tract. In her study, a virgin beech-maple forest, which had a rich avifauna (Beissinger and Adams, 1974) was compared with a similar disturbed forest. Three episodes of selective logging, the last occurring 18 years before the study, significantly altered the vegetational structure of the disturbed forest and certain features of the avifaunal community Therefore, it is probable that many years will have to elapse before the avifaunal communities in the North and South Tracts converge to a common composition.

Turnover. Several conspicuous changes in the composition of the avifauna of the undisturbed South Tract occurred during the 28-year interval between censuses (Table 2). These changes reflect regional trends for the disappearance of neotropical migrant species and a concomitant increase in densities of permanent resident species. For example, although we encountered a single territorial male Black-and-white Warbler in a disturbed tract of mature trees about 0.5 miles west of the North tract, this species and Worm-eating Warbler are now absent from both tracts that we cen-

Table 1. — Effect of selective logging on forest interior and edge species in the interiors of the North (Logged) and South Tracts.

Forest Interior Species	South Tract (36 acres)	North Tract (35 acres)
Red-eyed Vireo	36, 30.5[a]	22.5, 28
Ovenbird	9.5, 7	1.5, 1
Wood Thrush	38, 21	23, 24
Yellow-throated Vireo	0.5, 1	2.5, 2
Cardinal	9.5, 8	13, 11
Downy Woodpecker	5, 6	6, 8
Kentucky Warbler	4, 3	7, 5
Hooded Warbler	0, 1	11, 14.5
Edge Species		
Com Flicker	+, 1	2, 3
Gray Catbird	0, 0	1, +
Com Yellowthroat	0, 0	2, +
Indigo Bunting	0, 0	5.5, 3
Rufous-sided Towhee	2, 0	7, 6
White-eyed Vireo	0, 0	3.5, 1
Mourning Dove	0, 0	2, 2
Baltimore Oriole	0, 0	1, 0
Brown Thrasher	0, 0	+, +

[a] Number of territorial males in 1975, 1976.

Table 2. — Breeding birds in the South Tract plot in 1947, 1975 and 1976.

Species	1947	1975	1976
Raptors			
Turkey Vulture	+	0	0
Red-tailed Hawk	+	0	0
Barred Owl	0	+	0
Neotropical migrants			
Red-eyed Vireo	36[a]	36	30.5
Ovenbird	19	9.5	7
Wood Thrush	14.5	38	21
Acadian Flycatcher	12	6	7
Scarlet Tanager	9.3	5	4
E Wood Pewee	7	8.5	6
Yellow-throated Vireo	7	0.5	1
Kentucky Warbler	6	4	3
Black-and-white Warbler	4	0	0
Great Crested Flycatcher	3	0	0
Hooded Warbler	3	0	1
Ruby-throated Hummingbird	1.5	0	+
Northern Parula	1.5	+	0
Yellow-billed Cuckoo	1	1	+
Worm-eating Warbler	1	0	0
Blue-gray Gnatcatcher	0	+	0
Short-distance migrants			
Brown-headed Cowbird	1	2	3
Com. Flicker	0	+	1
Rufous-sided Towhee	0	2	0
Permanent residents			
Red-bellied Woodpecker	7	7	8
Cardinal	7	9.5	8
Downy Woodpecker	5	5	6
Tufted Titmouse	3.5	5.5	4.5
Carolina Wren	3	4.5	4.5
White-breasted Nuthatch	2	2.5	2.5
Hairy Woodpecker	1	1	1
Blue Jay	1	2	3
Carolina Chickadee	1	3.5	2
Com. Crow	+	+	+
Pileated Woodpecker	0	+	0
Starling	0	1	3
Total	157.3	154.0	127.0

[a] Number of territorial males.

sused and from most apparently suitable nearby habitat. The disappearance of these two species from fragmented woodland has become a common occurrence in the Maryland Coastal Plain and Piedmont, and one can speculate that these two turnovers represent local range retractions. Turnovers of this type might be compared with those which occur on oceanic islands, which, for one reason or another, carry more species than appropriate (Diamond, 1971). Other extinction turnovers, such as Hooded Warbler and Great Crested Flycatcher, may not be permanent. For example, Hooded Warbler, a common species in the North Tract and in suitable habitat elsewhere in the Seton Belt area, recolonized the South Tract in 1976 after being absent in 1975. In 1975, single unmated males sang during two of our visits but did not establish stable territories. The absence of Great Crested Flycatcher may also be reversed in subsequent years, since this species colonizes forest fragments readily (Bond, 1957; Whitcomb *et al.*, in preparation). Such observations also have parallels on oceanic islands, where in-and-out turnover may account for most of the total turnover on islands surveyed at 1-year intervals (J M Diamond, pers. comm.). Ruby-throated Hummingbird was not noted in either plot in 1975, but was recorded in both plots in 1976. However, it is difficult to be certain that this relatively inconspicuous species is actually absent from a plot; data on Blue-gray Gnatcatcher is similarly suspect. The absence of Red-tailed Hawk and Turkey Vulture from the South Tract also probably reflects our method of recording territories These species occurred on the Seton Belt Home Farm, but were not observed within the South Tract. Similarly, colonizations and extinctions by Barred Owl may represent observational artifacts, since the previous census probably was inadequate for detection of nocturnal species. On the other hand, colonizations by Com. Flicker, Starling and Pileated Woodpecker refer to conspicuous, easily detected species, and are in accord with regional trends (Whitcomb *et al.*, in prep.).

Computation of turnover for the South Tract as a whole requires consideration of the edge species as well as the forest interior species. Fortunately, the plot, as defined in 1947 and in our study, encompassed most of the field-woodland ecotone of the tract, and a large proportion of the edge territories were recorded in all censuses. A small fraction of the entire tract lay outside the plot boundaries in all 3 censuses. However, our observations indicated that no change in the species composition of the tract would have been noted in our 1975 or 1976 censuses if the excluded fraction had been included in the plot.

Five edge species occurred in the plot in all years. These included Gray Catbird (3 territorial males in 1947, 5 in 1975, 2 in 1976); Com. Yellowthroat (4, 5, 4); Indigo Bunting (4, 5, 7) and Am. Robin (3, +, +). Rufous-sided Towhee colonized both forest interior and edge in 1975, but only edge in 1974 and 1976 (3, 3, 3). Two species, White-eyed Vireo (3, 3, 0), and Am. Goldfinch (1, +, 0) were present in 1947 and 1975, but not 1976. Four species present in 1947 were absent in 1975. These included Field Sparrow (3, 0, 0), Yellow-breasted Chat (1, 0, 0), Blue Grosbeak (1, 0, 0), and Orchard Oriole (1, 0, 0). Although there may be a regional tendency for reductions in density of some of these species, it is also possible that changes in the structure of the edge may account for their absence in 1975 and 1976. There were no

colonizations by new edge species in 1975, but Mourning Dove, Mockingbird and Brown Thrasher colonized in 1976.

In summary, there were 11 apparent extinctions and 5 apparent colonizations in the South Tract between 1947 and 1975 (Table 3). Computed by the method of Diamond (1969), the 28-year apparent turnover rate (16/72) for this 36 acre plot was 22.2%. Corrected for possible observational artifacts, the minimum turnover rate, based on 8 extinctions and 3 colonizations, was 15.3%. The 29 year maximal and minimal turnover rates were 21 1% and 16.9%. The annual turnover rates from 1975 to 1976 were 16.9% or 10.8%. The extinctions and colonizations largely followed regional trends for the species involved. The resulting species diversity indices ($H' = -\Sigma p \log_e p$; p = proportion of each species in total population) were 2 725 in 1947, 2.474 in 1975 and 2.670 in 1976.

Thus, in a context of regional deforestation and in the presence of regionally intense human impacts, turnover is nonrandom, species richness and diversity (H') decrease, local extinction rates increase and the colonization rate, even in undisturbed tracts, decreases. Such events, of course, are not inconsistent with the equilibrium theory of island biogeography (MacArthur and Wilson, 1967); rather they enrich it and extend its applicability to conditions under which changes that would previously have occurred only on an evolutionary time scale are now occurring in contemporary time.

Alterations in densities. In addition to extinctions, there were also significant alterations in densities in the South Tract. The decrease in density of Yellow-throated Vireo parallels a regional decrease; this species may require mature trees (James, 1971; Adams, 1974) and was noted in the Seton Belt area only in the North and South tracts and in a third tract of disturbed mature trees in the northwest corner of the property. Other decreases, such as those for Ovenbird, Acadian Flycatcher, Scarlet Tanager, Kentucky Warbler, and Northern Parula are within the normal variation revealed by repeated censuses of undisturbed forest plots (e.g., Williams, 1947). On the other hand, it is exactly these migratory species that have responded negatively to urbanization and fragmentation of habitat, so it is likely that some if not all of these decreases are ominous warnings of changes yet to come. By contrast, permanent residents such as Cardinal, Carolina Wren, White-breasted Nuthatch, Blue Jay, Tufted Titmouse and Carolina Chickadee showed either no tendency to decrease or even a tendency to increase (Table 2). These observations parallel those of Briggs *et al.* (1970) and Criswell *et al.* (1972) in their long-term censuses in the District of Columbia and Maryland. Lack (1971) and Cody (1974) have accumulated impressive evidence for interspecific competition between bird species Applying such interpretations to the case of fragmented forest suggests that increases in the densities of some permanent resident species in local woodlands may have resulted from "competitive release" (Yeaton and Cody, 1974). For

Table 3. — Turnovers in the South Tract.

Species	Period of turnover 1947-1975	1947-1976	1975-1976
Raptors			
Turkey Vulture	e[a]	e	N
Red-tailed Hawk	e	e	N
Barred Owl	c	N	e
Neotropical migrants			
Black-and-white Warbler	E	E	N
Great Crested Flycatcher	E	E	N
Hooded Warbler	E	N	C
Ruby-throated Hummingbird	e	N	c
Northern Parula	N	E	E
Worm-eating Warbler	E	E	N
Blue-gray Gnatcatcher	c	N	e
Short-distance migrants			
Com. Flicker	C	C	N
Permanent residents			
Pileated Woodpecker	C	N	E
Starling	C	C	N
Edge species			
Field Sparrow	E	E	N
Yellow-breasted Chat	E	E	N
Blue Grosbeak	E	E	N
Orchard Oriole	E	E	N
Mourning Dove	N	C	C
Mockingbird	N	N	C
Brown Thrasher	N	N	C
White-eyed Vireo	N	e	e
Am. Goldfinch	N	E	E
Total apparent turnovers	16	15	11
Minimum turnovers	11	12	7
$S_1 + S_2$[b]	39 + 33 = 72	39 + 32 = 71	33 + 32 = 65

[a] Code: E = Certain extinctions; e = Apparent extinctions; C = Certain colonizations; c = Apparent colonizations; N = No change in status.

[b] S_1 and S_2 are numbers of breeding species in the earlier and later year.

example, the declines in the abundance of forest-interior specialists (especially warblers and vireos) unable to cope with the plowing and paving of the vast expanses that were once forest interior is followed by an increase in production of such birds as Carolina Chickadee and Tufted Titmouse.

High Carrying Capacity. In the context of our total studies, we were impressed not only with the local extinctions of bird species and reductions of densities in the South Tract, but also with the ability of this relatively small tract to retain the diversity and abundance of birds that it does. The most successful species was the Wood Thrush. The 1975 density of 105 territorial males per 100 acres (38 pairs) is one of the highest ever recorded for this species. We were careful to develop our territorial maps for this species almost entirely from simultaneous registrations. Along our census paths, spaced 330 ft. apart, we found 11 nests. This high density is reminiscent of an even higher density (121 males/100 acres) reported by Longcore *et al.* (1966) in an urban woodlot of similar size in Delaware. However, these authors found 76 nests! Most nests of this species found in the South Tract were about 15-25 ft. above ground in Flowering Dogwood trees and were readily visible. In 1976, the population of Wood Thrush fell dramatically to 21 pairs in the South Tract. Such fluctuations could be typical of small forest islands, which lack the buffering provided in habitat patches of similar size, but surrounded by extensive forest. Interestingly, the population of the Delaware woodlot also crashed (Jones and Stiner, 1968).

The general favorability of the South Tract for breeding birds must rest in part, as pointed out by Stewart and Robbins (1947), on the degree of maturity of the forest and the high fertility of the soil. Although mature homogeneous forests might be expected to have lower carrying capacities than younger forest, forest interior specialists such as Red-eyed Vireo and Ovenbird are supremely adapted to pack to high density in mature forest. There is, therefore, a perfect fit between the niches in a mature forest and the available species pool in a region where few bird species have become extinct.

Bond (1957) noted that richer (more mesic) forest tracts retained size-sensitive species more easily than similar-sized xeric tracts. Such tracts have higher carrying capacities, and probably lower turnover rates, than xeric tracts of comparable size.

Some wide-ranging species, such as Barred Owl, Red-tailed hawk and Pileated Woodpecker require large acreages of forest. Such birds are residents of small tracts only if the tracts are part of a large forest system that contains, overall, an area sufficient for their territorial requirements

Finally, there is a matter of the relative suitability of the South Tract in relation to surrounding forested environment. Summer residents select their nesting habitats within the forest interior during a short period in late spring. Ready response by such species as Hooded Warbler to changes in the shrub layer, as in the North Tract, suggests a high degree of selectivity in habitat selection. Such selectivity might keep a mature forest stocked, even in the face of regional declines; certainly species loss and declining densities of forest-interior species in such a tract should be viewed with special alarm. Such tracts may serve as "sinks" that accumulate high densities of some species as long as colonists remain to choose them.

SUMMARY

High breeding bird densities observed in two fragments of mature forest are ascribed to (1) high soil fertility with resultant high carrying capacity, (2) an available avian species pool that includes most of the original forest specialist species, and (3) a local biogeographic context of interrelated forest fragments sufficient to support the entire species pool, including wide ranging woodpeckers and raptors. Selective logging of one of the tracts increased species richness in the short run, but the long term prospects for such destabilized forests are uncertain. Two forest interior species, Worm-eating Warbler and Black-and-white Warbler, were present in the undisturbed tract in 1947 and absent in 1975. Their absence can be viewed as one type of "turnover" (local range retraction). Other species present in the South Tract in 1947, but absent in 1975 or 1976, may reasonably be expected to recolonize in future years. However, most turnovers and changes in densities of forest-interior specialists paralleled regional tendencies for loss of neotropical migrants and may portend future, more drastic changes in species composition.

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