Wilson Bull., 96(2), 1984, pp. 228–240

A LONG-TERM BIRD POPULATION STUDY IN AN APPALACHIAN SPRUCE FOREST

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Many studies have shown the relationships between changes in habitat due to plant succession and maturation and the corresponding changes in bird populations, but few of these investigations have been made in the same study area with repeated observations of both bird population and plant succession over a long period of years. Such studies have usually been completed in 1 or 2 years using several nearby areas in different stages of plant succession. These studies have been useful and instructive, but due to yearly population fluctuations such short-term studies may not be truly representative of existing conditions. The use of different areas for the different stages of succession is subject to error of interpretation.

Most of the few long-term studies which have been carried out were made in either nearly mature stands or in greatly disturbed habitats (e.g., city parks) and practically all of them have been done in some type of deciduous forest (see e.g., Kendeigh 1982 and Williams 1947). A long-term study of a hemlock-hardwoods forest using three areas representing three stages of succession in the southern Appalachians in which the areas were censused three times over a 25-year period has been reported (Holt 1974).

In this paper I present the results of population measurements made over a 36-year period, including 22 consecutive years, on a single area of second-growth red spruce forest in the southern Appalachians. The trees grew markedly during this time; bird species composition showed little change, although the populations of most species did change.

THE STUDY AREA

This study was carried out in a large tract of second-growth red spruce (*Picea rubens*) located on Gaudineer Knob, a high point on Shaver's Mountain on the boundary between Randolph and Pocahontas counties, West Virginia. The knob is relatively flat throughout the study area; the summit elevation is 1335 m. Prior to the present century this mountain top was covered with an almost pure stand of mature red spruce. Downslope from the summit the spruce forest changed to a northern hardwoods forest with a broad belt of mixed forest between the two. Sometime between 1905 and 1915 the study area was logged and may have been lightly burned (U.S.F.S. files). Soon after this cutting a second-growth stand of spruce was naturally seeded from the uncut forest nearby. The

FIG. 1. Gaudineer Knob study area and Fire Tower, June 1948.

result has been a dense, almost pure, stand of spruce which forms an effective island surrounded by a nearly pure hardwoods forest. A spruce tree which fell in 1973 had a ring count of just over 50, indicating germination of the seed sometime between 1915 and 1920.

In the 1930s the U.S. Forest Service built a fire-tower at the summit and opened the Knob to visitors by means of the access road. This narrow forest road terminates in a small parking lot at the tower. A few small picnic sites had been opened in the dense forest prior to the beginning of this study. After several years of disuse the tower was removed in 1982.

Ornithologists have been visiting the area since about 1937, at which time the spruce trees were about shoulder-high. There were then a few shrubs mixed with the spruce in a dense stand. Except on the road and a few trails, movement through the area was extremely difficult. At that time the Chestnut-sided and Mourning warblers and the Rufous-sided Towhee were the most common bird species present. (Scientific names of birds are given in the Appendix.)

In 1947 Stewart and Aldrich (1949:7) made a census of the bird population. They described the area as follows; "Vegetation: Dense young spruce averaging about 15 feet in height. Red spruce makes up more than 95% of the trees, the remainder being yellow birch (*Betula lutea*) and mountain ash (*Sorbus americana*). Dense understory of mountain laurel (*Kalmia latifolia*) and a few scattered patches of rhododendron (*Rhododendron maximum*)." At that time a few paths made it possible to move

FIG. 2. Gaudineer Knob study area and Fire Tower, June 1978.

somewhat freely through the Christmas-tree-sized spruces. Figure 1 shows the edge of the parking lot and the tower as they were in 1948.

By the early 1980s the trees were 10—15 m high and ranged from 10—30 cm in diameter. As the crowns of the spruce trees coalesced the understory was crowded out and except along the road and trails the stand has now become pure spruce. The ground is covered only with an accumulation of dead needles and in places, a carpet of mosses. The maximum density of spruce foliage at the level of the understory occurred in about 1958–1960. Since that time the lower branches of the trees have died and at ground level the forest has opened up, although passage through the area is still difficult. There is still no understory, but numerous dead spruce, laurel, and rhododendron stubs remain. During the severe winter of 1976–77 the tops and outer branches of many trees were winter-killed but by 1983 this was no longer evident. Phillips (1979) gives a detailed description of the tract as it was in 1978. Figure 2 shows the parking lot and tower as they appeared in 1978.

TABLE 1

WITHIN-YEAR VARIATION IN NUMBER OF SINGING MALES DETERMINED BY THE INDEX METHOD

Species[a]	1973		1978		1983	
Magnolia Warbler	4[b]	4[c]	5[d]	3[e]	2[f]	2[g]
Dark-eyed Junco	10	8	8	8	9	7
Swainson's Thrush	2	1	2	1	1	2
Golden-crowned Kinglet	3	2	4	2	5	4
American Robin	2	2	2	1	2	2
Winter Wren	1	2	—	—	2	2
Hermit Thrush	1	1	1	1	3	2
Black-capped Chickadee	—	1	—	1	—	—
Blue Jay	—	—	—	1	—	—
Yellow-rumped Warbler	—	—	2	3	1	2
Black-throated Green Warbler	—	1	—	—	—	—
Solitary Vireo	—	1	—	—	—	—
Black-throated Blue Warbler	—	—	—	1	—	—
Totals	23	22	24	22	25	23

[a] See Appendix for scientific names.
[b] = June 1.
[c] = June 11.
[d] = May 30.
[e] = June 6.
[f] = May 30.
[g] = June 11.

CENSUSING METHODS

The census area is a 6.08-ha rectangular plot (100.6 m × 803.6 m) centered on the road and one of the narrow trails. This area was censused by the spot map method (Hall 1964) in 1947 (Stewart and Aldrich 1949). In 1948 the members of the Brooks Bird Club began a series of censuses by the spot-mapping method made in early June, which have continued to the present at 5-year intervals (DeGarmo 1948, 1953; Hall 1958; Hurley 1964; Koch 1968; DeGarmo and Koch 1974; Phillips 1979, 1984).

In 1959 a program of annual censuses by a rather different "index method" was begun. The method adopted has the merit of giving a satisfactory index of the number of territorial males in a minimum amount of time—one overnight trip to the area.

The index method consists of traversing the length of the study area in a fairly rapid fashion, tallying all the birds seen and heard during the traverse. This traverse requires about 12 min to complete. After a wait of about 3 min the area is traversed in the reverse direction. This down-and-back procedure is then repeated giving four traverses of the same route. One set of four is made during the last hour before dark (approximately 19:45–20:45 EDT) and another set of four is made in the first hour of daylight the next morning (05:30–06:30). After the evening counts a tentative judgment is made as to the probable number of singing males of each species on the area, and at the end of the morning counts final judgment of the population is made. Counts of this nature have been made in the last 2

TABLE 2

SINGING MALE NUMBERS DETERMINED BY THE SPOT-MAPPING METHOD

Species[a]	1947	1948	1953	1958	1964	1968	1973	1978	1983
Magnolia Warbler	15	19	19	11	9	8	1.5	1	2.5
Dark-eyed Junco	8	10	8	4.5	6	10	6	8	5
Swainson's Thrush	6	2.5	6.5	5.5	3.5	1	0.5	1	—
Golden-crowned Kinglet	—	—	1	0.5	2	2	5	3	5
American Robin	2	4.5	4.5	3	1	3	2	1	1.5
Winter Wren	2	2	2	0.5	1.5	2	1	—	—
Hermit Thrush	0.5	—	1.5	—	—	0.5	—	—	—
Black-capped Chickadee	0.5	1	2	—	—	1.5	1	—	—
Blue Jay	—	—	—	—	—	2	1	—	—
Northern Waterthrush	—	—	3	1.5	1.5	—	—	—	—
Yellow-rumped Warbler	—	—	—	—	—	—	—	2	2.5
Rufous-sided Towhee	5	5.5	4	—	—	—	—	—	—
Black-throated Green Warbler	0.5	—	—	—	0.5	—	—	—	0.5
Blackburnian Warbler	—	0.5	—	—	—	0.5	—	—	—
Solitary Vireo	—	—	—	—	—	—	0.5	—	0.5
Veery	0.5	—	1.5	—	—	—	—	—	—
Black-throated Blue Warbler	—	3.5	0.5	—	—	—	—	—	—
Chestnut-sided Warbler	1	0.5	—	—	—	—	—	—	—
Purple Finch	1	1	1	0.5	—	0.5	—	—	—
Cedar Waxwing	—	1	—	—	—	—	—	—	—
Canada Warbler	—	0.5	1	—	—	—	—	—	—
Red-eyed Vireo	—	—	—	—	—	—	0.5	—	—
Species	12	13	14	8	8	12	10	6	7
Total (males)	42	51.5	55.5	27	25	31	19	16	17.5

[a] See Appendix for scientific names.

days of May or the first 2 days of June from 1959 through 1983. All counts through the years were made by the same observer. In the early years the index method counts were not too reliable while the method was being worked out, but with added experience the later counts have been good measures of the population. In 1973, 1978, and 1983 an additional index method count was made later in June to give some idea of the variation expected by this method. This comparison is given in Table 1. It is noted that most of the rarer species agree exactly but that some of the more numerous species differ by ±1 male, and the total population varies by ±2 males. In 1983 this variation in the Yellow-rumped Warbler and the Swainson's Thrush may have been due to the arrival of late migrants. In 1964, 1968, 1973, 1978, and 1983 it was possible to compare the index method results with those of the more conventional spot-mapping method (see Tables 2, 3, 4). For species with small populations the two methods agree quite well, but for the abundant species the index method appears to overestimate the population. This happens because this method makes no allowances for the fractions of certain territories being outside the boundaries of the study area. The difference is slight for individual species but the accumulated error in the total population is sometimes large. In 1983, when allowances were made for this effect, the

TABLE 3

SINGING MALE NUMBERS DETERMINED BY THE INDEX METHOD 1962–1972

Species*	1962	63	64	65	66	67	68	69	70	71	72
Magnolia Warbler	12	11	10	10	10	5	10	8	9	9	10
Dark-eyed Junco	3	4	5	7	7	7	7	7	10	10	9
Swainson's Thrush	3	4	4	4	3	2	2	2	2	2	3
Golden-crowned Kinglet	1	1	3	2	3	3	3	2	2	2	2
American Robin	—	3	1	3	3	3	3	2	3	3	3
Winter Wren	—	2	1	2	1	2	—	1	—	1	1
Hermit Thrush	1	2	—	—	1	—	—	1	—	2	2
Black-capped Chickadee	—	—	1	1	2	2	4	2	3	2	2
Blue Jay	—	2	—	1	1	2	2	—	1	1	1
Northern Waterthrush	3	4	3	2	2	3	3	—	2	—	1
Yellow-rumped Warbler	—	—	—	—	—	—	—	—	—	—	—
Rufous-sided Towhee	—	—	—	2	—	—	2	1	3	1	2
Black-throated Green Warbler	1	—	3	—	1	—	—	—	—	—	—
Blackburnian Warbler	—	—	—	1	1	—	—	—	—	—	—
Solitary Vireo	—	—	—	—	—	—	—	—	1	—	—
Wood Thrush	—	—	—	—	1	—	—	—	—	—	—
Veery	—	—	—	—	—	—	—	—	—	1	—
Black-throated Blue Warbler	1	—	—	—	1	—	—	—	—	—	—
Chestnut-sided Warbler	1	—	—	—	—	—	—	—	—	—	—
Purple Finch	—	—	—	—	—	—	—	—	—	—	—
Species	9	9	9	11	14	9	9	9	10	11	11
Total (males)	26	33	31	35	37	29	36	26	36	34	36

* See Appendix for scientific names.

population estimates agreed almost exactly. The accuracy of the index method is highly sensitive to the weather. Inclement weather on the one day selected for the count can cause large errors. This is the apparent cause of the low count for 1967, made in a cold drizzle on the only 2-day period available that season.

RESULTS

The results of the nine singing-male censuses are given in Table 2 and those for the 22 most recent index counts are given in Tables 3 and 4. These data are also plotted in Figs. 3 and 4.

Over the 35-year period the general species composition has remained the same, although the number of species decreased markedly during the period 1953–1958. This decrease resulted from the elimination of some marginal species such as the Chestnut-sided Warbler, Purple Finch, and Rufous-sided Towhee, rather than any change in the most numerous species. The population also declined during this period. This decline resulted largely from the decrease in Magnolia Warblers which had been

TABLE 4
SINGING MALE NUMBERS DETERMINED BY THE INDEX METHOD, 1973–1983

Species[a]	1973	74	75	76	77	78	79	80	81	82	83
Magnolia Warbler	4	8	9	5	4	3	3	2	3	3	2
Dark-eyed Junco	9	8	11	11	9	8	8	11	11	9	8
Swainson's Thrush	2	2	2	2	3	2	2	2	2	3	2
Golden-crowned Kinglet	3	5	4	6	3	4	4	5	5	5	5
American Robin	2	3	2	2	1	2	2	1	—	2	2
Winter Wren	1	—	2	2	1	—	2	1	1	3	2
Hermit Thrush	1	3	1	2	—	1	2	2	3	3	3
Black-capped Chickadee	1	—	3	—	2	—	1	1	—	—	—
Blue Jay	—	1	—	1	—	1	1	—	—	—	—
Northern Waterthrush	2	—	—	—	—	—	—	—	—	—	—
Yellow-rumped Warbler	—	—	1	1	1	2	1	1	3	3	3
Rufous-sided Towhee	—	—	—	—	—	—	1	—	—	1	—
Black-throated Green Warbler	—	1	—	—	—	—	1	—	—	—	—
Blackburnian Warbler	—	1	1	—	1	—	—	—	—	—	—
Solitary Vireo	1	—	1	—	—	—	1	—	—	—	—
Wood Thrush	—	—	—	—	—	—	—	—	—	—	—
Veery	—	—	—	—	—	—	—	—	—	—	—
Black-throated Blue Warbler	—	—	—	—	—	—	—	—	—	—	—
Chestnut-sided Warbler	—	—	—	—	—	—	—	—	—	—	—
Purple Finch	—	1	—	—	—	—	—	—	—	—	—
Species	10	10	11	9	9	8	13	9	7	9	8
Total (males)	26	33	37	32	25	23	29	26	28	32	27

[a] See Appendix for scientific names.

the most abundant species. The population of the other important species, the Dark-eyed Junco, remained essentially constant, although there were small year-to-year fluctuations. After this initial decline the total population has remained almost constant. Since 1963 there has been a slight, but statistically significant decrease ($r = 0.503$, $P = 0.02$), but since 1976 the total population has remained constant within the normal error of the counts. The Magnolia Warbler population has continued to decline, but this decrease has been made up by the increase in Yellow-rumped Warbler and Golden-crowned Kinglet populations.

DISCUSSION

The major change in population between 1953 and 1958, which resulted largely from the decline of Magnolia Warblers, coincided with the time at which the canopies of the young spruce trees coalesced, eliminating all other plant species. At this time the niche for ground-inhabiting birds was eliminated and these species, along with those requiring some plants

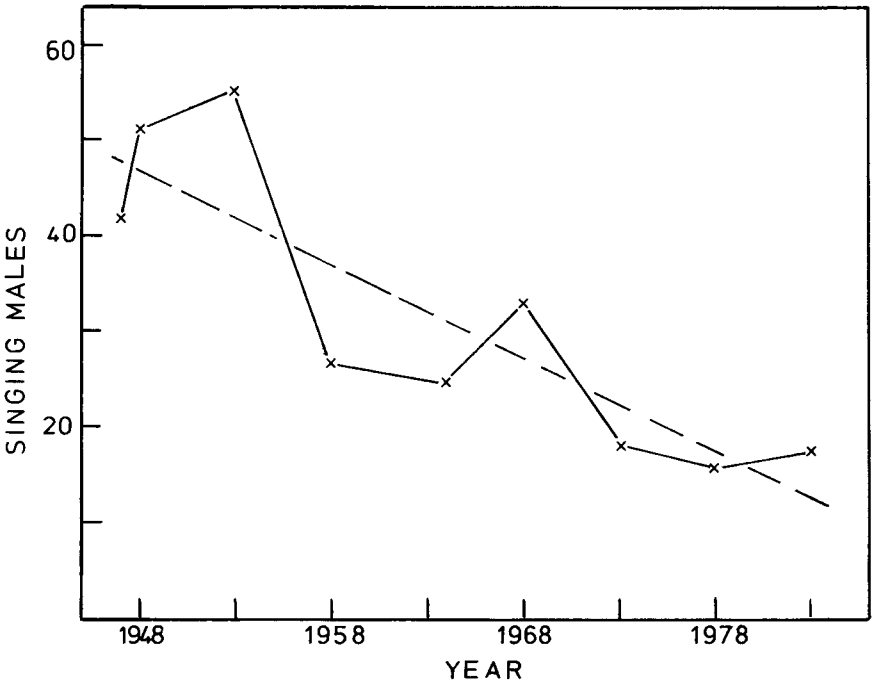

FIG. 3. Total number of singing males as determined by the spot-mapping method. (For the regression line $R = -0.862$, $df = 7$, $0.001 < P < 0.01$.)

besides spruce, disappeared. The lack of openings in the spruce was apparently unfavorable for the Magnolia Warbler whose numbers declined, although at this time it was still the most numerous species on the area. Morse (1968) has shown that this species forages mostly on the outer tips of conifer branches. The spire-like form of the young spruce trees assures that outer tips of branches will always be available in the open as the trees grow, although these will be at increasing heights.

Since 1958 the Magnolia Warbler population has continued to decline slowly. This may be related to the continued growth of the trees, but in mature habitats on this mountain, where plant growth is not as marked a factor, the populations of this species (which were never as large as the ones in the study area) have also declined (Hall 1984). The general decrease may be related to the possible continent-wide decline of Neotropical migrants (Criswell 1975, Terborgh 1980, Hall 1984).

The singing-male censuses taken at 5-year intervals also showed an abrupt drop in Magnolia Warbler populations between 1968 and 1973.

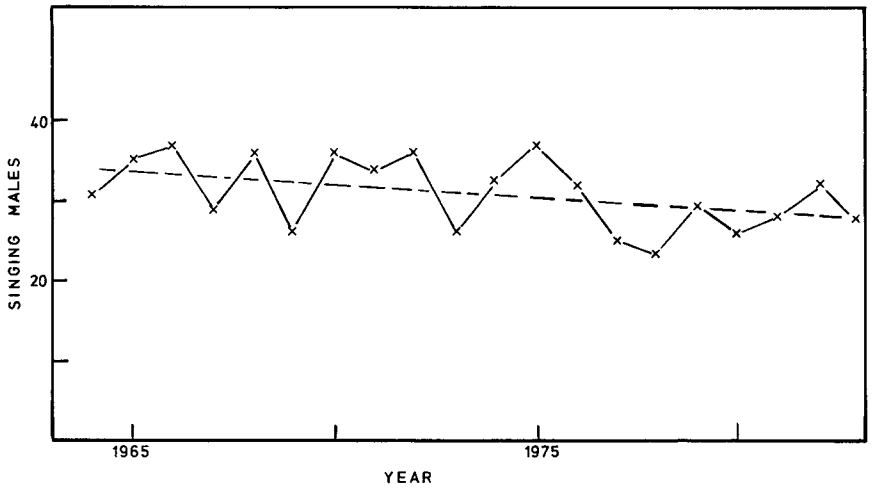

FIG. 4. Total number of singing males as determined by the index method. (For the regression line R = −0.503, df = 19, P = 0.02.)

If only these 5-year counts were available this drop might not seem unexpected but the yearly censuses show that this decrease took place all in 1 year, an event not to be expected. It seems likely that the low 1973 counts were produced by the conditions that prevailed when Hurricane Agnes moved through the eastern states in June 1972. As a result of this disturbance, which produced heavy flooding to the east and northeast of the study area, the mountain experienced fog with rain (and perhaps some snow) and abnormally low temperatures for perhaps 10 days. This occurred at a critical time in the nesting cycle and it is reasonable to assume that practically no Magnolia Warbler nestlings survived. All warbler species were in lower than normal numbers in these mountains in 1973. The population did return to a higher value in 1974, although the overall decline has continued.

The other common species, the Dark-eyed Junco, has shown an essentially stable population over the years, possibly with a small increase. This species is now nesting in the lower branches of the trees since most of the more usual ground-nesting sites have been eliminated. Juncos will nest several times during the summer, and so the breeding season of 1972 was not so disasterous for them as it was for the Magnolia Warbler. As the lower branches of the spruce disappear we might expect an eventual decline in junco populations also, but this is not evident as yet.

When the trees reached a sufficient height the Golden-crowned Kinglet

invaded the area. For about 10 years the kinglet population remained fairly constant and then the numbers increased markedly. This increase in population was not peculiar to this area but took place throughout the southern part of its range. The population of kinglets, both on this study area and in this general region, crashed suddenly in 1977. This was presumably due to a large winter-kill in late winter of 1977 when abnormally cold temperatures extended far into the winter range of this kinglet. Since 1977 the population has been building up again.

Swainson's Thrushes, which were one of the more common species in the early years, had a major decline in numbers at about the time the canopies coalesced, but have had an essentially constant population since about 1967. The Hermit Thrush has never been common on this tract, being more characteristic of the mixed hardwoods-spruce forest on the mountain side. In recent years Hermit Thrushes have appeared on the study area, and have shown a small increase in population. This increase may have resulted from the decline in Swainson's Thrushes which often displace Hermit Thrushes in this spruce forest (Hall 1983).

The Northern Waterthrush was first found on the area in 1953 and it remained, in essentially stable numbers, for 23 years and then disappeared. This appears to be a good example of a colonization of an area followed by ultimate extirpation. This mountaintop, far from any standing water, seems an unlikely place for this species, but it might be postulated that it is wet vegetation, or wet ground cover, and not water as such, that this species requires. During the breeding season this spruce forest is usually quite wet from the heavy rains which are characteristic of that season. The disappearance of the waterthrush coincided with the elimination of the lower branches of the spruce trees and the opening up of the forest floor.

Another example of a colonization is that of the Yellow-rumped Warbler. This species had not been known to nest south of northeastern Pennsylvania before 1975 when it appeared during the breeding season on this study area. Since that time the population has increased modestly, and the species has now been found in summer elsewhere in the West Virginia spruce forest. It will be of interest to follow this species to see if colonization will be successful or if, like the waterthrush, the Yellow-rumped Warbler will ultimately disappear.

The occasional appearance of Black-throated Green and Blackburnian warblers in this young spruce forest presents an interesting strategy by which a new species may arrive on an area. Both of these species should ultimately occupy this area when the trees reach adequate size, although the Black-throated Green Warbler may require more deciduous growth than is present here. Apparently from time to time pioneers enter the area

and attempt to breed in a habitat that is not quite suitable for them. The nesting is unsuccessful and the species is missing from the area until another pioneer makes the attempt. Eventually the habitat may become suitable and the species becomes established.

That this area has shown so little change in species composition over the years is apparently characteristic of the northern coniferous forest. A nearby area of deciduous growth at much the same elevation censused for the first time in 1947 (Stewart and Aldrich 1949) has shown a great change in species composition, and in population in this intervening time (see Phillips 1974).

Schreiber and Schreiber (in press) have recently pointed out that the effects of the Pacific Ocean phenomenon known as the Southern Oscillation (El Niño) may have far-reaching effects on bird populations even well away from the Pacific area. It is intriguing to note that the low populations in 1958, 1964, and 1973 were El Niño years, but so too was 1953, when the population was unusually high. No conclusions are to be drawn but the subject deserves thought.

The population of an area in a boreal forest at any particular time is highly dependent not only on climatic factors, but also on short-term weather factors. Thus, the 1973 values on this area are greatly influenced by the unfavorable weather events of the previous summer and are not representative of the long-term trends on the area. There is some evidence (Hall 1984) that there may be no "equilibrium" population in the mature boreal forest.

While the number of species on the area never exceeded 14 in any one year, 23 species have been listed over the years. Examination of the tables shows that many species fluctuate between being present and being absent. Such fluctuations lead to high rates of turnover in species presence. The average annual turnover rate on this plot is 22.8% (9.1–40.0%); the overall turnover rate is much higher. The present study area can be considered as being representative of an island of spruce forest in a sea of different habitat, and turnover rates of islands calculated on the basis of yearly counts are typically high (Diamond and May 1977). These turnover rates are somewhat higher than those reported from yearly counts on the California Channel Islands (Jones and Diamond 1976). The relatively small size of this study plot may serve to artifically exaggerate the turnover rate.

Much of ecological theory is derived from censuses made in only one year, but as the 1973 data given above show, the conclusions drawn from such "one-shot" counts may well be misleading. The index method used here is also a "one-shot" procedure for any given year and hence may be in error for that year, but over many years the effects of unusual conditions in any one count will be offset. Thus, as noted above, the 1967 count is probably highly unreliable.

In order to make valid ecological generalizations bird populations should be measured over a period of several years. Unfortunately, this is often not practical. Even more unfortunately, however, the limitations of a 1 or 2 year study are often not recognized.

SUMMARY

The breeding bird population in a stand of second growth red spruce forest in eastern West Virginia was determined at 5-year intervals by the spot-mapping method from 1947–1983. From 1962–1983 the population was also monitored annually by a somewhat cruder "index method." In these 36 years the overall species composition changed very little, although the number of species and the total number of males underwent a marked reduction at about the same time the crowns of the spruce trees coalesced and eliminated all other plant species from the area. Since that time the population has remained essentially constant, although a slow decline appears to be taking place.

In boreal habitats such as this one the population determined in any one year is very sensitive to weather factors. Possible fluctuations due to such factors must be considered in drawing ecological conclusions from data obtained in a single year.

ACKNOWLEDGMENTS

I would like to acknowledge the assistance of the several members of the Brooks Bird Club who participated in making the singing-male censuses, particularly G. Koch, G. F. Phillips, and the late W. R. DeGarmo. A. F. Schulz of the U.S. Forest Service and M. Brooks supplied useful information about the early history of the study area. D. James, D. Morse, C. Robbins, and R. Whitmore read and commented on an earlier draft of this paper. J. W. Aldrich and J. R. Faaborg made editorial comments which improved the presentation.

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APPENDIX

SCIENTIFIC NAMES OF BIRDS

Blue Jay (*Cyanocitta cristata*)
Black-capped Chickadee (*Parus atricapillus*)
Winter Wren (*Troglodytes troglodytes*)
Golden-crowned Kinglet (*Regulus satrapa*)
Veery (*Catharus fuscescens*)
Swainson's Thrush (*Catharus ustulatus*)
Hermit Thrush (*Catharus guttatus*)
Wood Thrush (*Hylocichla mustelina*)
American Robin (*Turdus migratorius*)
Cedar Waxwing (*Bombycilla cedrorum*)
Solitary Vireo (*Vireo solitarius*)
Red-eyed Vireo (*Vireo olivaceus*)
Chestnut-sided Warbler (*Dendroica pensylvanica*)
Magnolia Warbler (*Dendroica magnolia*)
Black-throated Blue Warbler (*Dendroica caerulescens*)
Yellow-rumped Warbler (*Dendroica coronata*)
Black-throated Green Warbler (*Dendroica virens*)
Blackburnian Warbler (*Dendroica fusca*)
Northern Waterthrush (*Seiurus noveboracensis*)
Mourning Warbler (*Oporornis philadelphia*)
Canada Warbler (*Wilsonia canadensis*)
Rufous-sided Towhee (*Pipilo erythrophthalmus*)
Dark-eyed Junco (*Junco hyemalis*)
Purple Finch (*Carpodacus purpureus*)