

REMOVAL AND REPOPULATION OF BREEDING BIRDS IN A SPRUCE-FIR FOREST COMMUNITY

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IN 1949, while engaged in population studies of birds in northern Maine, the authors accumulated considerable information concerning population dynamics of birds inhabiting the Spruce-Fir forest community. This information was obtained in connection with investigations of the effective control by breeding birds of an infestation of the spruce budworm, *Choristoneura fumiferana* Clem.

Field studies were conducted during June and July on two separate areas; a square 40-acre tract which was used as an experimental area, and a rectangular 30-acre tract that served as a control area. The two areas were 1.25 miles apart and were both within one-half mile of the shore of Cross Lake, located about 14 miles southeast of Fort Kent, Aroostook County, Maine. In the experimental area an attempt was made to eliminate or to reduce drastically the bird population by use of firearms, while in the control area the natural bird population was allowed to remain unmolested. Both skins and stomachs of the birds killed were preserved for the Fish and Wildlife Service collections. The spruce budworm populations were studied in both areas before, during, and after the removal of the birds in order to see if any differential developed between the two areas in their total populations. The entomological portion of the field study was conducted by Philip B. Dowden and V. M. Carolin of the Bureau of Entomology and Plant Quarantine of the U. S. Department of Agriculture. Stomach contents of the birds collected were analyzed by Robert T. Mitchell of the Fish and Wildlife Service. The results of the various phases of this work concerning the effective control by birds of spruce budworms will appear in a separate report. The present paper includes an analysis only of the data on removal and repopulation of birds in the experimental area.

The Spruce-Fir forest in the experimental area was somewhat varied. The canopy in certain sections of the forest had been partially opened by selective lumbering, resulting in a fairly dense understory growth of conifers. The other portions of the forest with a closed canopy contained little or no understory. Balsam fir, *Abies balsamea*, and black spruce, *Picea mariana*, were the primary dominant trees throughout the forest. The majority of the trees ranged between 40 and 60 feet in height. Small sections of mixed coniferous-deciduous

brushy undergrowth were present and the area was crossed by a state highway.

The population of territorial males in the area was determined prior to the removal of birds, by using the spot-mapping method (see Breeding-Bird Census, Audubon Field Notes, 4 (2): 185-187). Twenty-five census trips totaling 55 man-hours were conducted on the area from June 6 to June 14, inclusive. Most of the census trips were taken during early morning hours between 6:00 and 10:30 a.m. A few trips were also made in the evening for the determination of thrush populations.

Beginning on June 15 and extending through July 8, an attempt was made to remove all birds on the experimental area by shooting with 16-gauge shotguns. Shells used were loaded with very fine (No. 12) shot so that birds would not be too mutilated for specimens. By using this method the total population on the area was greatly reduced, although the actual degree of reduction could not be readily appraised. The chief difficulties were that the breeding territories were completely disrupted during the period when the original occupants were being removed and at the same time new adult males were constantly invading the area. Most of the adult females were so inconspicuous and secretive that it was not possible to census them accurately. In all, a total of about 130 man-hours were spent on the area collecting birds. The number of birds removed from this 40-acre tract during the entire collecting period was 455 (420 adults and 35 birds in juvenal or immature plumage).

Nearly all of the birds in the Spruce-Fir forests appeared to be at or near the peak of their breeding cycle during this study. With the exception of the American Crow, Golden-crowned Kinglet, and Red-breasted Nuthatch, it is doubtful if any species, at the onset of collecting, had produced nestlings. Nestlings, as well as three or four groups of fledglings, of the Golden-crowned Kinglet and Red-breasted Nuthatch were observed, but they were practically all removed from the area soon after they were first encountered during the first few days of collecting. The constant pressure of collecting and the resultant turn-over in adult birds completely prevented the development of other nestling populations in the study area during the collecting period.

Small, roving groups of adult non-breeding birds were found in the area from time to time. The most common of these were the American Robin and Cedar Waxwing, both species being occasionally represented by from one to nine individuals. These birds were noted with increasing frequency during the latter part of the collecting period,

from about July 2 to July 8. Other non-breeding birds occurring more rarely included the American Goldfinch, Pine Grosbeak, and Chipping Sparrow. A few wandering immature birds were also seen during the last few days of collecting. These had undoubtedly moved in from outside areas after having become independent of their parents. An attempt was made to collect all of these birds whenever they were encountered.

After the first nine days of collecting (June 15–June 23) the resident males of all species except the Myrtle Warbler and Olive-backed Thrush had been reduced to 15 per cent or less of the original numbers. Continued collecting coupled with a steady influx of new males maintained these species at about this level for the remainder of the collecting period. The number of male Magnolia Warblers was reduced to the 15 per cent level by June 23 even though only 16 males (67 per cent of original population) had been taken by that time. Possibly some of the males had deserted owing to the disturbance of walking and shooting in the area; the Magnolia Warbler, being an understory species, would probably be affected by such disturbance more than tree-top birds would be. The number of male Myrtle Warblers was reduced to about 25 per cent and maintained this approximate level thereafter. Apparently a proportionately larger number of non-territorial males of this species was present to fill evacuated territories. The Olive-backed Thrush was found to be a very difficult species to collect. It was much more wary and secretive than the other species and was seldom seen, although its songs and call-notes were evidence of its continual presence. Although a total of 18 adult Olive-backed Thrushes was taken during the collecting period, the rate of collection was so low and repopulation so fast that the resultant voids in the population were filled by new males almost as soon as the voids were produced. As a result, the population level for males of this species was reduced only slightly below (probably about 80 per cent of) the pre-collecting population.

The approximate reduction in total number of adult males of all species was from an average of 148 to 28 or, in other words, from a density of 370 males per 100 acres to 70 males per 100 acres (reduction of 81 per cent). This density of 70 males per 100 acres is the approximate level that was maintained from June 24 to July 8. With the exception of wandering non-breeding birds, including the Arctic Three-toed Woodpecker, Cedar Waxwing, Black-throated Green Warbler, Chestnut-sided Warbler, Pine Grosbeak, American Goldfinch, Chipping Sparrow, and most of the Robins, practically all of the adult males taken appeared to be on their breeding territories at the time they were collected.

Most of the new males which took possession of the evacuated territories probably arrived during the night or early morning, as practically all of them when first observed seemed to be actively establishing territory, and no evidence of any late arrivals during the day was noted. The males of many species appeared to be completely eradicated time after time, only to be replaced by other males on following days. The characteristic behavior pattern of most of the new arrivals was quite distinct from the behavior displayed by males with territories that had been maintained over a longer period. The songs of these newcomers were louder and uttered more frequently, while at the same time the birds were much more active in covering and inspecting the areas within their territories. It is probable that most of these new arrivals were unmated. Lack (1946) in his study of the English Robin found that "In the late spring nearly all the best robin song comes from cocks which are unmated." ". . . almost immediately after the cock has obtained a mate, its song declines to a rather moderate intensity and remains so, except during fights, unless the mate is lost, in which case the cock again comes into loud song."

Due to the variable nature and uneven growth of the Spruce-Fir forests in the area, the required habitat niches for the various resident species were not uniformly distributed. Because of this, the pre-collecting distributional pattern of breeding territories was quite different for each species. It was therefore of interest to note that subsequent to the collection of the original territorial males, the new males of each species almost invariably established territories in the same places that were occupied by their predecessors. Since an abundant food supply was available for birds throughout the area, these observations substantiate the importance of "the niche" in explaining local distribution of breeding birds.

Prior to the collecting period, the number of territorial males on the shooting area was 148, as determined by the spot-mapping method from June 6 to June 14. The number of adult males collected on the area during the period June 15 to July 8 was 302 + (Table 1). Thus, over twice as many males were removed from the area as were present before the collecting was started. The rapid influx and establishment of new territorial males, following the removal of the former occupants, account for the large number of males collected and are indicative of the amount of population pressure that was present in this community. It would appear that this pressure was due to severe competition, between individual males of the same species, for suitable areas to establish their territories. Apparently, the appropriate habitat

TABLE 1
PRE-COLLECTING POPULATION AND COLLECTION TOTALS OF ADULT MALES

Species	Pre-collecting population, territorial males June 6-14	Total males collected June 15-July 8	Collecting periods			
			June 15-23	June 24- July 1	July 2-8	
Tetraonidae						
Ruffed Grouse, <i>Bonasa umbellus</i>	+	1	1			
Picidae						
Yellow-shafted Flicker, <i>Colaptes auratus</i>	1	2	1		1	
Arctic Three-toed Woodpecker, <i>Picoides arcticus</i>	V	1		1		
Tyrannidae						
Yellow-bellied Flycatcher, <i>Empidonax flaviventris</i>	4	3 (4)	2		1	
Corvidae						
Blue Jay, <i>Cyanocitta cristata</i>	1.5	2	2			
American Crow, <i>Corvus brachyrhynchos</i>	+	1 (1)		1		
Paridae						
Black-capped Chickadee, <i>Parus atricapillus</i>	2	3 (4)	3			
Brown-capped Chickadee, <i>Parus hudsonicus</i>	2.5	3 (5)	3			
Sittidae						
Red-breasted Nuthatch, <i>Sitta canadensis</i>	3.5	4 (1)	4			
Troglodytidae						
Winter Wren, <i>Troglodytes troglodytes</i>	2	1	1			
Turdidae						
American Robin, <i>Turdus migratorius</i>	2	14 (4)	4	4	6	
Hermit Thrush, <i>Hylocichla guttata</i>	2	4	2	2		
Olive-backed Thrush, <i>Hylocichla ustulata</i>	7.5	11 (2)	4	2	5	
Regulidae						
Golden-crowned Kinglet, <i>Regulus satrapa</i>	4	4	3	1		
Ruby-crowned Kinglet, <i>Regulus calendula</i>	2	2	2			
Bombycillidae						
Cedar Waxwing, <i>Bombycilla cedrorum</i>	V	6 (2)			6	
Vireonidae						
Solitary Vireo, <i>Vireo solitarius</i>	3	4 (1)	3	1		
Red-eyed Vireo, <i>Vireo olivaceus</i>	1.5	7	2	3	2	
Parulidae						
Tennessee Warbler, <i>Vermivora peregrina</i>	3	1	1			
Nashville Warbler, <i>Vermivora ruficapilla</i>	4	6	5		1	
Parula Warbler, <i>Parula americana</i>	1	4	2		2	
Magnolia Warbler, <i>Dendroica magnolia</i>	24	36	16	10	10	
Cape May Warbler, <i>Dendroica tigrina</i>	12	23	13	10		
Myrtle Warbler, <i>Dendroica coronata</i>	8.5	29	11	9	9	
Black-throated Green Warbler, <i>Dendroica virens</i>	V	1		1		
Blackburnian Warbler, <i>Dendroica fusca</i>	9	15	7	2	6	
Chestnut-sided Warbler, <i>Dendroica pensylvanica</i>	V	1		1		
Bay-breasted Warbler, <i>Dendroica castanea</i>	35	81	34	21	26	
Oven-bird, <i>Seiurus aurocapillus</i>	1.5	1	1			
Canada Warbler, <i>Wilsonia canadensis</i>	.5	1	1			
Fringillidae						
Purple Finch, <i>Carpodacus purpureus</i>	2.5	6	3	1	2	
Pine Grosbeak, <i>Pinicola enucleator</i>	V	3			3	
American Goldfinch, <i>Spinus tristis</i>	V	2			2	
Slate-colored Junco, <i>Junco hyemalis</i>	5	13 (6)	6	2	5	
Chipping Sparrow, <i>Spizella passerina</i>	V	1 (1)			1	
White-throated Sparrow, <i>Zonotrichia albicollis</i>	3.5	5 (3)	5			
TOTAL		148	302 (34)	142	72	88

() undetermined sex

V visitor in area

+ indicates that less than .25 of one territory was present on area.

niches for most species were not numerous enough to satisfy the territorial requirements of all the males present.

The indications are that a large, surplus, "floating" population of unmated males must have been present in the Spruce-Fir forests of this region. Since there was no evidence that spring migration was still continuing at the time the collecting was initiated, it was assumed that the birds which invaded the area were largely unmated wandering males that had been in the general region for some time. Presumably these males were searching for suitable sites to establish territories, and whenever unoccupied habitat of the right type was found they lost little time in taking over and proclaiming their ownership by song. This is in line with the belief of Nice (1941) that "birds which fail to obtain territory, form a reserve supply from which replacements come in case of death of owners of territory." In a study of the territories of Marsh Tits, Southern (1950) stated that "the speed with which deaths among the breeding population were replaced suggests that there was definitely a non-breeding population throughout the spring."

It is probable that at least some of the new males that were collected were those that had established territories in areas adjacent to the collecting area. Upon the removal of the original territorial males in the collecting area, some of the males in outside areas could have taken advantage of the reduction in population pressure and expanded the boundaries of their territories into the collecting area. In a study of banded English Robins, Lack (1946) found that "when the owner of a territory disappears, the owners of the neighboring territories expand into the vacant site almost at once, and often the ground is fully occupied within twenty-four hours." In a comprehensive study of Ruffed Grouse, Bump, *et al.* (1947) discovered that the birds "tend quite rapidly to move into a covert whose population has been depleted out of proportion to those surrounding it." In the present study, however, the fact that more new males first appeared in the center of the collecting area than on the periphery would indicate that most of them were wandering, unmated birds rather than neighbors expanding their territories.

The ratio of males collected to the number of territorial males on the area prior to the collecting period was found to vary considerably with different species. In the case of birds belonging to Old World families such as the kinglets, chickadees, and nuthatches, there was very little difference between the two figures, indicating that their populations were comparatively stable. However, for most of the thrushes, vireos, warblers, and fringillids, the number of males collected was from one and one-half to three times as great as the number present in the area

before collecting. The Red-eyed Vireo showed the greatest difference of all with nearly five times as many males collected as were formerly present in the area (the relatively high numbers of American Robins and Cedar Waxwings that were collected were due to the presence of wandering non-territorial birds). These striking differences in ratios of individuals present before collection to those collected for the different species would seem to indicate that the surplus of males was much greater for some than for others. In the case of Brown-capped Chickadees, American Robins, Golden-crowned Kinglets, and Red-breasted Nuthatches, it is possible that because of their earlier period of nesting they might have passed that stage in their breeding cycle at which they were interested in establishing territories and, therefore, the number of individuals present before collecting was relatively similar to the number collected.

Differences in the ratio of males collected to number of males present in the area before collecting were quite pronounced even among species that were closely related and that had similar habits. The five most abundant species in the area were warblers, all belonging to the genus *Dendroica*. The number of males collected for every male that was present in the area before collecting is indicated for each of these species, as follows: Magnolia Warbler, 1.5; Blackburnian Warbler, 1.7; Cape May Warbler, 1.9; Bay-breasted Warbler, 2.3; and Myrtle Warbler, 3.4. Since these species are about equally conspicuous in the field, it is unlikely that such noticeable differences in the ratios can be attributed to variations in the ease with which they may be collected.

Those species that showed a definite surplus of males could be considered as having *supersaturated* populations (see Kendeigh, 1947). In other words for these species, the carrying capacity of the area, insofar as breeding territories were concerned, was insufficient to take care of the needs of all males present. Possibly, the presence of the infestation of spruce budworms could have accounted for this. The great abundance of food resulting from the budworm infestation might have attracted such a large number of males to the area that the territorial requirements of all of them could not be satisfied. The importance of territorial behavior in limiting bird population in a given habitat is stressed by Nice (1937) who stated, however, that "climate and other factors may keep the numbers of a species in a region so low that territorial behavior has no chance to limit populations." Thus, while various factors may affect the numbers of breeding birds occurring in an area, the true balancing agent between bird populations and environment is the competition for territories among

individual males of the same species. This is in accord with the findings of Nicholson (1933) who wrote "for balance, it is essential that the action of a controlling factor should be governed by the density of the population controlled, and competition seems to be the only factor that can be governed in this way."

It would seem probable that when certain elements, such as food supply, in the habitat vary, the saturation point for each species will vary also. For example, the saturation point for most insectivorous birds in a Spruce-Fir forest without a budworm infestation would probably be much lower than it was in the area studied. This belief is based on the assumption that the minimum territorial requirements are affected by the relative ease with which food can be obtained. Kendeigh (1947) has pointed out that in the case of the Tennessee, Cape May, and Bay-breasted warblers there appears to be a direct correlation between the abundance or occurrence of these species and the severity of spruce budworm infestations. The principle of balance between changing animal populations and environment was expounded by Nicholson (1933) who stated that "if a population is in a state of balance with the environment, its density must necessarily change in relation to any changes in the environment." This principle is further clarified by Elton (1936) who maintained that "the chief cause of fluctuations in animal populations is the instability of the environment."

The number of adult breeding females was also greatly reduced during the collecting period, although the actual degree of reduction could not be determined from the data available. The small number of females recorded at any time was somewhat puzzling. Although female birds are generally much more difficult to observe in the field than are males, the exceedingly small number actually seen and collected over a three-week period would, assuming that most males had been mated, indicate that a preponderance of the females deserted the area shortly after their mates had disappeared. The close attachment to the nests and general inconspicuousness of most females undoubtedly explains in part why such a small number was seen and collected during the first few days. The presence of large numbers of conspicuous territorial males at that time would naturally tend to overshadow the count of the females. However, the continued recording of low numbers of females following the initial period of collecting is thought to be due, in large part, to an extensive withdrawal of females from the area. After the majority of the males had been collected, any type of bird activity, slight though it might be, became much more noticeable; thus the presence of any appreciable number

of females would surely have been noted. At least 130 man-hours were spent in the area during the collecting period and practically all of the females seen were collected (Table 2). The females collected had well developed brood-patches on their breasts, indicating that they either were or had been sitting on eggs. If females had remained undetected in the area and continued to sit on eggs throughout the period, many of them would have been feeding young before the period was over and, therefore, would have become much more conspicuous at that time. The females of the later-breeding species did not become conspicuous at any time, and there was no evidence of young produced on the shooting area.

Certain species showed a much greater disparity in the proportions of the sexes seen and collected than others (Table 2). The greatest differences in the ratio of the sexes were found in the warblers (Parulidae) and vireos (Vireonidae). In the case of the warblers, the males of which comprised about 67 per cent of the total adult male population of all species, only 29 (13 per cent) of 228 adults collected proved to be females. For most birds, other than the warblers and vireos, the females were observed nearly as often as the males and were almost as readily collected from the start. It would seem to be significant that several species, of which almost equal numbers of males and females were collected, were earlier breeders which were caring for young at the time collecting began. This fact could be responsible for the females, being more conspicuous and more readily collected. It is well known also that females desert their nests and territories more readily before incubation becomes well advanced.

Variations in the sex ratios of the birds collected may be indicative of actual differences in sex ratios of certain of the species represented. The sex ratios, of birds collected, for the seven most abundant species are indicated as follows (ratio of males to females): Blackburnian Warbler, 15-1; Bay-breasted Warbler, 9-1; Magnolia Warbler, 6-1; Cape May Warbler, 6-1; Myrtle Warbler, 6-1; Slate-colored Junco, 2.5-1; Olive-backed Thrush, 2-1. It is unlikely that such marked differences as these could be due entirely to differences in comparative conspicuousness between males and females of the species listed.

SUMMARY

The number of territorial male birds in a 40-acre tract of Spruce-Fir forest in northern Maine was 148 during the period June 6 to June 14, 1949. Birds were removed from this area by shooting from June 15 to July 8, inclusive, with the intention of reducing the population to and keeping it at as low a level as possible. By this means the number

TABLE 2
NUMBERS OF ADULT MALES AND FEMALES COLLECTED

<i>Species</i>	<i>Males</i>	<i>Females</i>	<i>Undeter- mined sex</i> ¹
Tetraonidae			
Ruffed Grouse	1	1	
Picidae			
Yellow-shafted Flicker	2		
Arctic Three-toed Woodpecker	1		
Tyrannidae			
Yellow-bellied Flycatcher	3		4
Corvidae			
Blue Jay	2	1	
American Crow	1		1
Paridae			
Black-capped Chickadee	3	1	4
Brown-capped Chickadee	3	4	5
Sittidae			
Red-breasted Nuthatch	4	6	1
Troglodytidae			
Winter Wren	1	1	
Turdidae			
American Robin	14	11	4
Hermit Thrush	4		
Olive-backed Thrush	1	5	2
Regulidae			
Golden-crowned Kinglet	4	4	
Ruby-crowned Kinglet	2	1	
Bombycillidae			
Cedar Waxwing	6	2	2
Vireonidae			
Solitary Vireo	4	1	1
Red-eyed Vireo	7		
Parulidae			
Tennessee Warbler	1	1	
Nashville Warbler	6		
Parula Warbler	4		
Magnolia Warbler	36	6	
Cape May Warbler	23	4	
Myrtle Warbler	29	5	
Black-throated Green Warbler	1		
Blackburnian Warbler	15	1	
Chestnut-sided Warbler	1		
Bay-breasted Warbler	81	9	
Oven-bird	1	3	
Canada Warbler	1		
Fringillidae			
Purple Finch	6	3	
Pine Grosbeak	3	1	
American Goldfinch	2	3	
Slate-colored Junco	13	5	6
Chipping Sparrow	1		1
White-throated Sparrow	5	5	3
TOTAL	302	84	34

¹ Many birds lodged in tree-tops at time of collecting and were not examined closely.

of territorial males was reduced to approximately 19 per cent of the original by June 24. Continued collecting coupled with a steady influx of new birds maintained this low level until July 8. A total of 455 birds (420 adults and 35 young) were removed from the area during the entire collecting period.

Following the collection of the resident males, new males entered the area either during the night or early morning. The behavior of the new arrivals differed from the older residents in that they were much more active and vocal, singing more vigorously and more frequently. The importance of habitat niches in controlling the distribution of most species was indicated by the fact that most of the new arrivals established themselves in the same places that had been occupied by former residents of the same species.

For most species, over twice as many adult males were collected on the area as were present before the collecting started. This was due to the rapid influx and establishment of new territorial males following the removal of the original occupants. The carrying capacity of the forest from the standpoint of suitable sites to establish territories was not sufficient to accommodate all the males present, resulting in a surplus population. These surplus birds served as a reserve supply, replenishing areas that had been depleted. Some of the additional males collected were probably those that had territories adjacent to the shooting area, since the reduction in population pressure in the area due to collecting would permit an expansion of their territories into the shooting area. However, it is believed that the majority of evacuated territories were filled by entirely new birds. A few species were represented in the area only by wandering non-breeding birds.

The ratio of males collected to the number of territorial males on the area prior to collecting varied considerably with different species. The competition for territories among individual males of the same species appears to be the balancing agent between the size of bird populations and environment.

The number of adult females of later-breeding species collected was much less than the number of males. Although the general inconspicuousness of most breeding females undoubtedly explains in part why such small numbers were collected, there is evidence that a majority of the females in these species deserted the area after their mates had disappeared. The greatest differences in the ratios of the sexes collected occurred in the warblers (Parulidae) and vireos (Vireonidae).

In general, the later-breeding species, such as warblers, vireos, and thrushes, showed a greater disparity in the sexes of collected speci-

mens than did the earlier breeders, such as the chickadees, nuthatches and kinglets. This condition seemed to be correlated with the fact that these earlier breeders did not refill evacuated territories to nearly the extent that the later breeders did. This could indicate a smaller reservoir of non-territorial birds and thus a lower population pressure in these species; or it could be the result of a more advanced condition of the breeding cycle during which the instinct to establish territory is absent or diminished in intensity.

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