

THE CONTEXTS OF SONGS IN BLACK-THROATED GREEN AND BLACKBURNIAN WARBLERS

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SOME recent studies of the family Parulidae demonstrate that in several species there is more than one type of male song; these song types evidently result from different motivations (Ficken and Ficken, 1962, 1965; Morse, 1966).

The purposes of this investigation were to observe a situation where two or more closely related species are found within a homogenous, floristically simple habitat in order to determine the motivations of their songs, the relationship of the songs to the environment, and the degree of effect that the congeners have upon each others' songs. In the northeastern United States Black-throated Green Warblers (*Dendroica virens*) and Blackburnian Warblers (*D. fusca*) are characteristically birds of the conifers, and while they may be found in mixed forests, it is in the coniferous forests that they reach their highest densities. Here they sometimes form the most prominent element of the local avifauna. Several other *Dendroica* warblers also occur in these forests. The pure spruce forests probably represent one of the simplest of arboreal habitats to support such an impressive array of closely related species of breeding birds.

It appears probable that the existing ecological and behavioral relationships between Black-throated Green and Blackburnian warblers are the result of a past history of intense interactions between themselves and the other closely related sympatric species. As song appears to be an important part of warbler communication during the breeding season, an examination of vocalizations of these birds appeared to be a fruitful subject for study.

These studies were made in the spring and summer from 1962 to 1965. Most of the work was done on Hog Island (Todd Wildlife Sanctuary), Bremen, Lincoln County, Maine, with additional work being done in several other areas in Maine, including the adjacent mainland and other coastal islands in Lincoln County. Further brief observations were made at Tremont, Hancock County, and Webster, Androscoggin County.

Most of the area studied on Hog Island is a mature red and white spruce (*Picea rubens* and *P. glauca*) forest, with the larger trees reaching a maximum height of 18 to 25 meters. The hurricanes of 1954 and winds of following years have severely damaged the forest on many parts of the island, but most of the work in this paper was conducted in relatively undisturbed areas. The growth of such a spruce forest is quite dense and results in considerable difficulties in studying and following birds. The warblers of similar stands

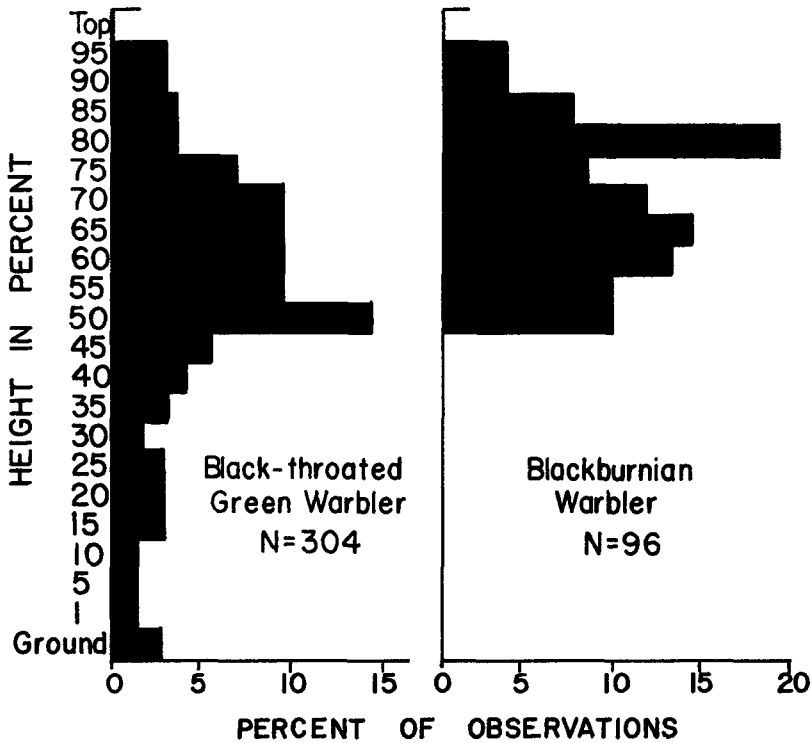


FIG. 1. Foraging height.

of trees were studied briefly in other areas, and they were studied also in mixed white pine (*Pinus strobus*)—deciduous forests on the mainland.

SPACE OCCUPIED IN THE HABITAT

The foraging area of both species (and other spruce-woods warblers) was figured and discussed by MacArthur (1958), who found that Blackburnian Warblers usually foraged at greater heights in the spruce forest than did Black-throated Green Warblers. In my study area, Blackburnian Warblers foraged higher than did any other species present, and Black-throated Green Warblers worked directly below them (Figure 1), with the other two congeners, Magnolia (*D. magnolia*) and Myrtle (*D. coronata*) warblers, usually foraging noticeably lower. While the centers of foraging of all species studied differed, there was considerable overlap in each instance. Cape May (*D. tigrina*) and Bay-breasted (*D. castanea*) warblers, two other spruce-woods species treated by MacArthur, were absent in the principal study area.

In addition to some songs that were given when the birds were foraging,

both species did a large percentage of their singing in a stationary or nearly stationary position from the top, or the tip of a high exposed limb, of a spruce tree. Both species sang for considerable periods in this sort of situation, remaining motionless except for "fidgeting" in the immediate vicinity of their song perch. Fidgeting here refers to an action in which an individual frequently flicks its wings and tail, hops about very deliberately within a limited area, and regularly pecks at the foliage, though apparently not feeding. These movements are frequently accompanied by songs and chipping notes. The term will be used in this sense throughout this paper.

RELATIVE DENSITY OF THE TWO SPECIES

The relative density of from two to three and one-half Black-throated Green Warblers to one Blackburnian Warbler found by Cadbury and Cruickshank (1937) in their long series of breeding-bird censuses on one part of this island probably is an accurate estimate of the present population. Frequent counts of the number of Black-throated Green and Blackburnian warbler songs heard along a transect through the middle of this forest suggested a similar or even greater ratio. Since their principal foraging areas are above the Black-throated Green Warblers, Blackburnian Warblers did not have as great an area in these spire-shaped trees in which to forage as did Black-throated Green Warblers, and this factor may account for part of the difference in density. Let us take an 18 meter spruce for an example, and assume that the Black-throated Green Warblers did the majority of their foraging at a height of between 5.4 and 12.6 meters (30-70 per cent of the height of the tree), and Blackburnian Warblers foraged from 9.0 to 16.2 meters (50-90 per cent of the height of the tree). Black-throated Green Warblers would then have approximately two and one-half times as great a volume of both bark surface and foliage in which to forage if this tree with its foliage had a normal radius of 3.4 meters at the minimum height here considered, 5.4 meters.

SONG PATTERNS

Both the Black-throated Green and Blackburnian warblers in this population possess two distinct song patterns, a male of either species typically rendering either one or the other, depending upon the motivation involved. To remain consistent with the literature, Black-throated Green Warbler songs are referred to as Type A Songs and Type B Songs (see Nice and Nice, 1932; Stein, 1962). Peterson (1947) described the Type A Songs as *zoo zee zoo zoo zee* and the Type B Song as *zee zee zee zee zoo zee*. Since the two Blackburnian Warbler songs are given in contexts essentially similar to those of the Black-throated Green Warbler, they will also be referred to as Type A

Songs and Type B Songs, but this designation is not intended to imply that these songs are necessarily homologous to those of Black-throated Green Warblers. Peterson (1947) described the Blackburnian Warbler Type A Song as *zip zip zip zip titi tseeeee* and the Type B Song as *tizip tizip tizip tizip zizizizizizizi*.

Songs classified as intermediate between Type A and Type B, comparable to "Intermediate Song" of the Yellow Warbler (*Dendroica petechia*) (Morse, 1966), were not recorded from either species. While the Yellow Warblers sometimes sang Intermediate Songs while switching from one major song pattern to the other, Black-throated Green and Blackburnian warblers were not observed to do this. Occasionally a bird of either species would sing only part of a song pattern and then become silent. At the end of the breeding season many aberrant songs were heard, including some songs that were approximately intermediate to the two major patterns. However, these songs were not heard during the breeding season. Blackburnian Warblers occasionally rapidly alternated their two basic song patterns, but Black-throated Green Warblers were not observed to do so.

STRATIFICATION OF SONGS

A noticeable stratification of individuals singing either of the two song patterns into distinct parts of the habitat occurred in the Black-throated Green Warbler (Fig. 2). The Type A Song was strongly associated with the treetops and almost all Type A Songs were given from a high elevation. This song was usually given while the bird was nearly stationary in the treetops, but sometimes it was given while the singer alternately foraged. Type B Songs were strongly associated with a lower position (moderate height) during most of the season, and in contrast to Type A Songs were usually given while the bird was actively foraging. Early in the season during the period in which males were setting up territories and acquiring mates, stationary birds in high exposed positions frequently gave Type B Songs, probably acting as an advertising song.

The two basic song patterns of Blackburnian Warblers (Fig. 3) occurred in situations rather similar to those of Black-throated Green Warblers. Type A Songs were also most frequently given while stationary in the top of spruces, and Type B Songs were most frequently sung while foraging. However, the tendency for this species to forage higher than any other species in the study area led to a superficial difference from Black-throated Green Warblers in that there was a strong tendency for the Type B Song (the foraging song) to be given from a considerable height. The two songs sometimes were even alternated by a single bird at a high elevation. There also was a strong tendency for this species to sing Type B Songs while in a

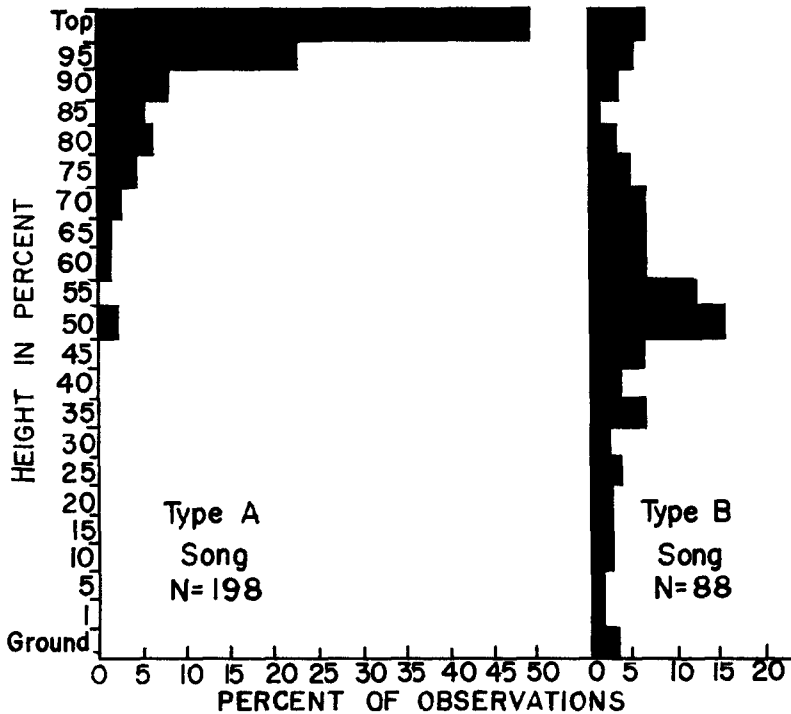


FIG. 2. Singing height of Black-throated Green Warbler.

stationary position early in the season in conjunction with its apparent role as an advertising song at that time. The heavy incidence of Type B Song recorded in or near the top of the trees is attributable to this effect in both Black-throated Green and Blackburnian warblers.

BEHAVIOR ACCOMPANYING THE SONGS

Black-throated Green Warbler Type A Songs were most frequently heard from stationary birds in exposed positions that appeared to sing this pattern as a territorial proclamation. These songs were also associated with activities related to direct territorial defense. Whenever a male Black-throated Green Warbler became conspicuous to other Black-throated Green Warblers at close range (except in the case of apparently unmated birds), they responded with Type A Songs from a prominent position, even if they had previously been singing Type B Songs. This song (sometimes muted) followed fights and chases between male Black-throated Green Warblers and also the less frequent interspecific fights or chases with Parula (*Parula americana*), Myrtle, or Blackburnian warblers (Table 1). "Muted Songs" almost always followed

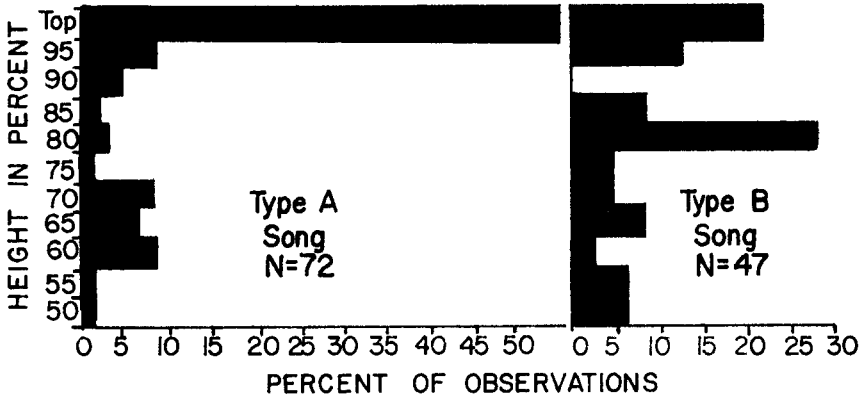


FIG. 3. Singing height of Blackburnian Warbler.

the same contexts as normal volume songs did, though usually being given in particularly strong or long encounters. In the course of a single fight between two male Black-throated Green Warblers, both Muted Type A Songs and Muted Type B Songs were heard. During such encounters, frequent "Metallic Double Chips" were given between Type A Songs, and at times of most intense aggression and excitement the song was sometimes even temporarily suspended. These chips, which are of a distinctly metallic character, are usually given rapidly in groups of two.

Type B Songs frequently appeared directed toward females in one way or another. On the few occasions that the male was seen singing in the direct company of a female of the same species, Type B Songs were always given (Table 1). These meetings probably occurred upon the frequent other occasions when males dropped out of sight to lower positions from treetop singing perches and changed from Type A to Type B patterns. Type B Songs are the typical foraging songs, and most foraging is performed at the height where females are most frequently encountered and where nesting occurs (see Cruickshank, 1956). Metallic Double Chips never accompanied this song, a characteristic noted also by Nice and Nice (1932). Occasional individuals that sang Type B Songs while stationary in the treetops for several minutes at a time into mid-June appeared to be unpaired birds. A noticeable decrease of this behavior occurred during early June.

Blackburnian Warbler Type A Songs usually were correlated with activities quite similar to those of Black-throated Green Warblers while singing Type A Songs (Table 2), occurring in both interspecific and intraspecific situations. A larger fraction (40.0 per cent) of the strong or long encounters were interspecific in this species than in Black-throated Green Warblers (22.4 per cent). Blackburnian Warblers tended to remain in one position while singing

TABLE 1
APPARENT CONTEXT FOR SOME SONGS OF MALE BLACK-THROATED GREEN WARBLERS*

| Activity | Number of responses |
|---|---------------------|
| <i>Type A Song</i> | |
| Fight with male Black-throated Green Warbler | 32 (8 muted) |
| Extremely close contact with male Black-throated Green Warbler | 4 |
| Close contact with male Black-throated Green Warbler | many |
| Song suspended and only metallic double chips given accompanying fight with male Black-throated Green Warbler | 2 |
| Fight with male Blackburnian Warbler | 4 |
| Extremely close contact with male Blackburnian Warbler | 2 |
| Fight with male Myrtle Warbler | 1 (muted) |
| Extremely close contact with male Myrtle Warbler | 2 (1 muted) |
| Fight with male Magnolia Warbler | 1 |
| Fight with male Parula Warbler | 1 |
| Interference of observer | 2 |
| <i>Type B Song</i> | |
| Following copulation with female Black-throated Green Warbler | 1 |
| Following courtship of female Black-throated Green Warbler | 2 (1 muted) |
| Extremely near female Black-throated Green Warbler | 3 (1 muted) |
| Continual singing early in the season from an exposed perch | many |
| N = 57 | |

* Upon one occasion, after two male Black-throated Green Warblers fought they alternated Muted Type A and Muted Type B Songs.

Type A Songs somewhat longer than did Black-throated Green Warblers, averaging 4.8 minutes per singing station, while Black-throated Green Warblers averaged 3.9 minutes per singing station. Blackburnian Warbler encounters with Parula Warblers, as well as with Black-throated Green Warblers, were observed. Under circumstances resulting in high aggression, frequent chipping, occasionally of a double nature, was given. The birds sometimes foraged at this time.

In this species also, Type B Songs were the ones given in the immediate presence of females (Table 2). Individuals consistently singing this song for long periods of time in the treetops were probably birds that had not obtained a mate. Two birds sang in such a manner through most of June, though most ceased this pattern by early June. Only on very rare occasions (two observations) were the chips heard accompanying Type B Songs.

DISCUSSION

The contexts in which both species sing Type A Songs and Type B Songs suggest that the Type A Songs are given in situations where there is a high attack tendency or a conflict of attack and escape tendencies. Type B Songs

TABLE 2
APPARENT CONTEXT FOR SOME SONGS OF MALE BLACKBURNIAN WARBLERS

| Activity | Number of responses |
|--|---------------------|
| <i>Type A Song</i> | |
| Fight with male Blackburnian Warbler | 4 |
| Extremely close contact with male Blackburnian Warbler | 8 |
| Close contact with male Blackburnian Warbler | many |
| Fight with male Black-throated Green Warbler | 4 (2 muted) |
| Extremely close contact with male Black-throated Green Warbler | 2 |
| Extremely close contact with male Parula Warbler | 2 |
| <i>Type B Song</i> | |
| Following copulation with female Blackburnian Warbler | 1 |
| Following female Blackburnian Warbler | 1 |
| Extremely close contact with female Blackburnian Warbler | 1 (muted) |
| Continual singing early in the season from an exposed perch | many |
| $N = 23$ | |

appear to be given under circumstances in which these tendencies are less strongly activated, and in which *sexual* tendencies may be high. Type A Songs appeared to be the territorial songs and were usually delivered from exposed perches while nearly stationary. Type B Songs were typically foraging songs and were also given in the presence of females. They were also given as apparent advertising songs early in the season from exposed positions.

The contexts of the Type A Songs of the Black-throated Green and Blackburnian warblers most closely resemble those that accompanied the Yellow and Chestnut-sided (*Dendroica pensylvanica*) warbler Unaccented Ending Songs (see Morse, 1966), all of these songs usually being given in the close presence of other males of the same species. Type B Songs occurred in contexts suggesting those in which Yellow and Chestnut-sided warblers sang Accented Ending Songs; however, there appeared to be no distinction made by Black-throated Green and Blackburnian warblers in response to other closely related species nesting in the same areas. The difference between a response of a Black-throated Green Warbler male to another male of its species and to one of some other species was not marked, both intraspecific and interspecific hostile activities usually being accompanied by the same song pattern (Type A Song). In several populations in Maine, Yellow Warblers responded to their most closely related sympatric species, the Chestnut-sided Warbler, with the same song pattern that they directed toward the female.

The factors governing the singing of a particular song pattern differ somewhat in the two cases. The level of hostile behavior among spruce-woods

Dendroica warblers probably is considerably more intense than it is between Yellow and Chestnut-sided warblers, and the problem of frequent interspecific interaction may be more important than is that of simple recognition. The habitat separation between Yellow and Chestnut-sided warblers is more clearly delimited than it is between the spruce-woods *Dendroica* species, only limited habitat overlap occurring in the populations studied. Black-throated Green and Blackburnian warblers both utilize very similar habitats, having their principal foraging and nesting areas at slightly different heights (Cruickshank, 1956) and parts of the trees, and foraging somewhat differently (see MacArthur, 1958), but nevertheless overlapping considerably in all these characteristics. Many more closely related species are found in the spruce forests than in the favored wet bushy habitat of the Yellow Warbler. Thus, a high level of interspecific interaction among the birds of the spruce forest may result in stronger attack or escape tendencies than occur in Yellow or Chestnut-sided warblers.

The slight difference in context accompanying a particular song pattern or foraging in these two species may be partly attributable to the difference in the part of the habitat foraged by them. The stratification of birds singing the two song types was less marked in Blackburnian Warblers than in Black-throated Green Warblers, and the former spent most of their time within an area in which it was customary to give either song or to forage. They were thus exposed to a slightly different set of stimuli at this height than were Black-throated Green Warblers both in the treetops and at lower heights. This difference in foraging height is in turn probably enforced by interactions between the two species.

The context of muted songs in both of these species, based upon a limited number of observations (see Tables 1 and 2), was slightly more predictable than in Yellow Warblers (see Morse, 1966). The difference is perhaps a result of the heavy incidence of interspecific interactions in the spruce forest.

The higher ratio of interspecific fights and chases to intraspecific ones in the Blackburnian Warbler in comparison to the Black-throated Green Warbler was probably largely the result of the lower density of the Blackburnian Warbler in the study area. The somewhat longer periods of stationary singing in Blackburnian Warblers may also be the result of this low density. No noticeable difference in the intensity and duration of hostile activities was noted between the two species.

Because of their particular foraging station, Black-throated Green Warblers would experience more potential conflicts with Magnolia and Myrtle warblers than would Blackburnian Warblers. However, the foraging of Magnolia Warblers (pers. obs.) and Myrtle Warblers (MacArthur, 1958) is not as similar to Black-throated Green Warbler foraging as is Blackburnian Warbler

foraging, and much of the Black-throated Green Warbler foraging is performed above the major foraging areas of Magnolia and Myrtle warblers. Fewer Black-throated Green Warbler encounters with Magnolia and Myrtle warblers were noted than between Black-throated Green and Blackburnian warblers. Magnolia and Myrtle warblers also were not as abundant as were Black-throated Green and even Blackburnian Warblers in the study area. Thus Blackburnian Warblers expend more energy in interspecific encounters (at least their fights and chases) in this forest than do Black-throated Green Warblers.

It is not definite whether the warblers of this forest are utilizing limited food sources at this season, but they definitely interfere with each other in the procurement of quite similar food sources. Thus they fulfill requirements for competition laid out by Birch (1957). The most important competitor of the Blackburnian Warbler in this forest probably is the Black-throated Green Warbler, the only species of warbler it frequently comes into contact with, and which forages in a manner suggestive of, though not identical to, its own species. Conversely, Blackburnian Warblers probably are the most important competitors of Black-throated Green Warblers in this forest, but because of their lower density their effect is quantitatively less important than the effect that Black-throated Green Warblers have upon Blackburnian Warblers. This pattern will necessarily be modified depending upon the local species compositions, but it appears likely that these two species have more foraging similarities than do any other *Dendroica* warblers in the spruce forests of the northeast.

SUMMARY

Songs and accompanying behavior of Black-throated Green and Blackburnian warblers were studied in Maine from 1962 to 1965. Work was concentrated in a climax spruce forest containing two additional species of *Dendroica*, Magnolia and Myrtle warblers. Blackburnian Warblers foraged higher than did other species, with Black-throated Green Warblers directly below them. Both possess Type A and Type B Songs, usually singing Type A Songs in the presence of other singing warblers of either their own or other species. These vocalizations appeared to be the territorial songs and were usually delivered from exposed perches while nearly stationary. Metallic Double Chips often accompanied Type A Songs. Type B Songs were typically foraging songs and were also given in the presence of females. They were also given as apparent advertising songs early in the season from exposed positions. Type A Songs were apparently sung when a high attack tendency or a conflict of attack and escape tendencies existed; Type B Songs occurred when these tendencies were less strongly activated, and when sexual tendencies were high. The slight difference in context accompanying certain responses in the two species may be partly attributable to their differences in foraging height. Black-throated Green Warblers were more abundant than Blackburnian Warblers in the study area, and a greater portion of their hostile activities were intra-specific. Both species probably were the other's most important competitor.

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