HYBRIDIZATION AND INTERACTION BETWEEN BLUE-WINGED AND GOLDEN-WINGED WARBLERS

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INTRODUCTION

Hybridizing populations have been intensively studied due to their evolutionary and ecological significance. The extent of hybridization will determine if the two populations can remain distinct (Mayr 1963), and if they remain genetically distinct, the degree of ecological overlap will determine if the two populations can coexist (Lack 1971). Blue-winged Warblers *(Vermivora pinus)* and Golden-winged Warblers *(V. chrysoptera)* are of particular interest partly due to the historically recorded increase in the frequency of hybridization between them, and partly because they are beautiful creatures with strikingly different phenotypes. The two species have somewhat different ranges: the Golden-wing ranges farther north and to higher altitudes, the Blue-wing extends farther to the southwest. Both species are extending their ranges northward, with the Blue-wing expanding its range more rapidly. Blue-winged Warblers now occupy areas which were first occupied by Golden-winged Warblers early in this century (Bull 1974). This large expansion of the range of the Blue-wing has produced a broad zone of sympatry. Despite the great differences in plumage, wherever these birds occur together there is extensive interbreeding (Short 1962). Our study was designed to help elucidate the consequence of this interbreeding and competition.

Ithaca, in Tompkins County, is located within the zone of sympatry and many studies have been done locally on the behavior, territory size, and introgression of the two species (*e.g.*, Ficken and Ficken 1967, Short 1962). In this paper we will compare the degree of hybridization in this area today to that observed by Short 18 years ago. In addition we will discuss several aspects of the birds' behavior.

STUDY AREA

Three colonies were observed near Ithaca with the main study area located adjacent to the Ithaca College campus. This field of secondary growth vegetation measures about 360 x 400 m. The vegetation consists mainly of *Viburnum,* hawthorn, Red-panicled and Red-osier Dogwood, with occasional Pin Cherry, White Ash, Red Maple, and White Pine. Small parts of the field are wet and swampy (about 5%).

Some of it is open with tall grasses and scattered hawthorn and dogwood (about 35%). Much of the area (about 45%) is covered with dense shrubby growth of 2 to 4 m height. The remaining area (about 15%) is covered with some taller trees of about 10 m height and an understory of shrubs.

METHODS

The study began 7 May 1977 and continued with almost daily field trips until 5 July 1977. Field trips were usually taken twice a day, when the birds were most active, around sunrise and before sunset. About 50 trips were made and about 140 hours were spent in the field by each of us.

The birds were watched until the center of their territory was roughly estimated. The birds were caught with mist nets to which some were attracted by a tape recording of their song provided by the Laboratory of Ornithology, Cornell University. Each bird was banded with a U.S. Fish and Wildlife aluminum band on one leg and a colored plastic band on the other. We code-named the birds, so that a Blue-wing with an aluminum band on his left leg and a white, plastic band on his right leg would be called B-AW.

The field was mapped by running seven east-west transects, placing a marker every 20 m. The transect rows were 40 m apart. Territory sizes were estimated by marking on a map where each bird was seen each day and connecting the peripheral dots. The territory shapes were traced onto paper, cut out, and weighed on a Mettler balance. The weights were then compared to the weight of 1 square hectare drawn to the same scale as the territories. Areas were estimated using the maximum territory used during the whole breeding season and do not reflect slight shifting or shrinking of the defended territory due to nesting, feeding, or arrival of an adjacent territorial bird. Occasionally a bird was seen far outside the estimated boundaries of his territory. Such rare instances were not included in the mapping of territories. We estimate that at least 8 hours were spent, and 15 trips were made by each of us to each territory before we were confident of its boundaries. Some territories were not mapped because of uncertainty about parts of the boundaries.

The degree of hybridization of each bird was measured according to the scale devised by Short (1962). Wing bars, nape, back, rump, and chest were each given a number from zero to four; zero for an idealized Blue-wing character and four for an idealized Golden-wing character. The value for each of the five characters was added and a

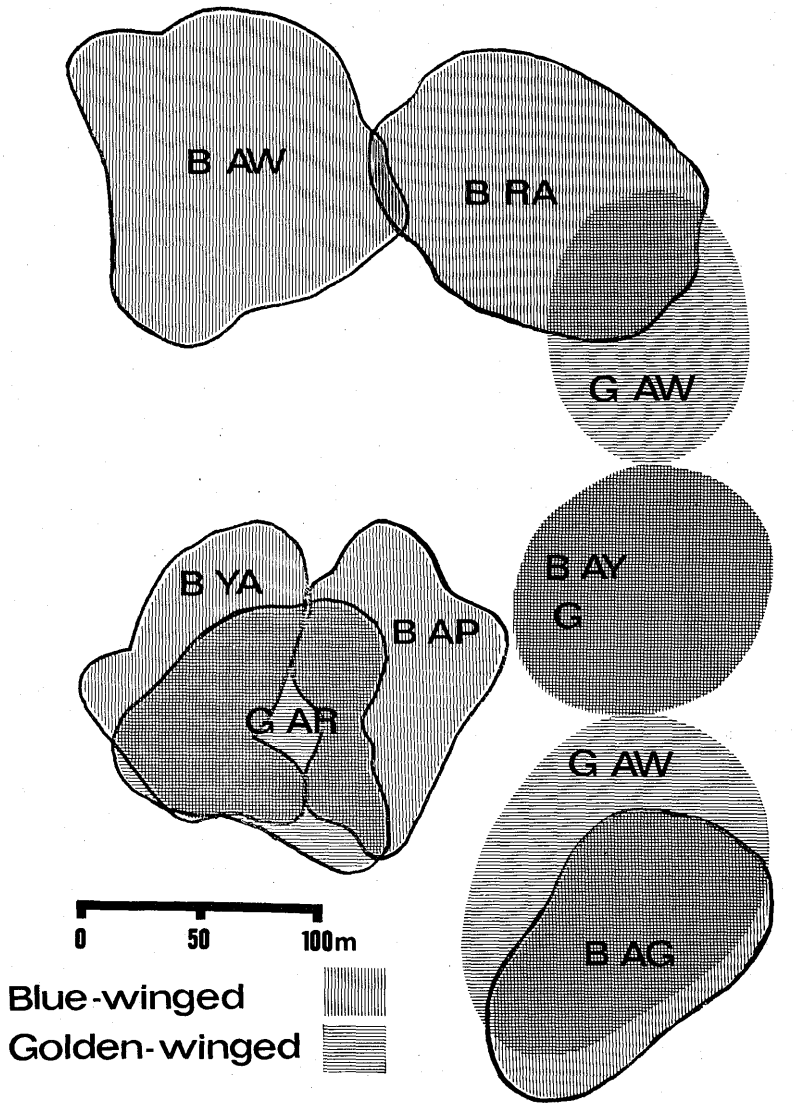
score from 0-20 was obtained. To familiarize ourselves with Short's scale we studied all the skins in the collection of Cornell University whose scale values had been reported by Short. We made slight modifications of Short's scale, scoring wing-bar width and wing-bar color separately, and counting the merest trace of Blue-wing and Golden-wing characters as .5 and 3.5, respectively, instead of 1 and 3 as had been done by Short. In order to adjust our data for comparison to Short's, we averaged the values obtained for wing-bar width and wing-bar color.

RESULTS

Out of ten territories in our study field we are confident of six boundary estimates (Fig. 1). Five of these are territories of Blue-winged Warblers ranging from 1.0 to 2.0 hectares and averaging 1.3 hectares (3.2 acres). The one Golden-wing territory that we measured was 1.1 hectares (2.7 acres). Color banding of the birds aided the certainty of our estimates.

Other estimates of the territory size of Blue-winged and Golden-winged Warblers have been published. Our territory sizes were larger than those of Ficken and Ficken (1968) who studied a colony at Varna, Tompkins Co., about 5 miles from our intensively studied colony. Our estimates are within the ranges found by Murray and Gill in Michigan (1976). Ficken and Ficken did not color band their birds and therefore had no way of visually distinguishing one bird from another. We visited the Fickens' colony in Varna and feel that the density of territorial males was obviously much greater than in our study area. It thus appeared to us that the territory sizes at the Varna colony were about the same as had been estimated by the Fickens 15 years before. The differences in territory size between these three areas suggests that the habitat of each colony influences the size of the area defended by each male.

Passerines that carry out courtship, feeding, nesting, and food-gathering all within one area usually do not tolerate another male of the same species within their territory. Male Blue-winged and female Golden-winged Warblers recognize each other as suitable mates and *vice versa,* as is evidenced by the frequency of hybrids. It is interesting to see if male Blue-wings recognize male Golden-wings as competitors and *vice versa.* If so, then one would expect all the territories to be mutually exclusive. In our colony we had four cases where Blue-wing and Golden-wing territories overlapped. Golden-wing AR shared territories with two different Blue-wings, YA and AP. An un-



banded Golden-wing overlapped territories with Blue-wing AY. Golden-wing AW began sharing territories with Blue-wing RA and then either shifted his territory or merely expanded it so as to include the territory of Blue-wing AG. There was no sharing of territories between one Blue-wing and another nor between any two Golden-wings. These observations support the previous reports of several

workers, including Ficken and Ficken (1968) and Murray and Gill (1976).

Territorial boundaries are usually fluid, influenced by competition, the ability of a bird to defend a given area, and seasonal in behavior. Blue-wing AW's eastern boundary was pushed slightly west due to the arrival of Blue-wing RA. Golden-wing AR's territory shrank considerably after apparent damage to its wing. After the bird's flight appeared to return to normal, the territory expanded to its original size.

INTROGRESSION

In our sample this summer, 1977, 37 different birds were caught with mist nets or studied with binoculars. Those that were only seen with binoculars were considered to be different birds when they were found in areas separated by several miles, or when a bird was repeatedly seen in a particular territory. By the criteria used in the standard field guides there were 23 Blue-wings, 2 Brewster's, 1 Lawrence's, 2 distinct hybrids that weren't like either Brewster's or Lawrence's, and 9 Golden-wings. That is, 62% of our sample were Blue-wings, 14% were hybrids, and 24% were Golden-wings.

To put this present condition in perspective, Blue-wings first appeared in Tompkins County in the early 1940's. By 1949 only four sightings had been reported (Parkes 1951), but by the mid 1950's Blue-wings were common. Short (1963) collected 29 birds during 1957 and 1958. By field guide criteria there were 15 Blue-wings, 8 hybrids, and 6 Golden-wings. That is, 52% of his sample would be recognized as Blue-wings, 28% as hybrids, and 21% as Golden-wings.

Our percentage of Blue-wings (62%) is higher than that reported by Short (52%). However, when we statistically tested our field guide criteria sample against Short's sample there was no statistically reliable difference (Chi-square 2 by 3 test comparing the distribution 23:5:9 to 15:8:6; Chi-square value equals 3.65). This means that the observed differences between these two samples could result solely from random variation, without any real change having occurred.

Use of Short's scale allows us to detect hybrids that would not be detected by applying the criteria of field guides. According to Short (1963) birds whose scale value range from 3 to 17 are "definite hybrids." However Short did not present any statistical analysis of his data to support his contention that allopatric populations would range only from 0 to 2 or 18 to 20. Fortunately, there are now 5 Golden-wing skins in the Cornell collection that were collected be-

tween 1918 and 1930 from Howland's Island near Syracuse. At that time and place this colony of Golden-wings was certainly allopatric (Bull 1972, Scheider 1959). Following Short's method, the scale values of these birds range from 15 to 20.. Since this sample is so very small it is quite possible, even probable that a larger sample would show even wider variation.

While pure Golden-wings can score from 20 down to as low as 15, Brewster's or other hybrids that have back-crossed with Golden-wings can score as high as 19, or very rarely 20 (Short 1963). Unfortunately, many skins studied by Short fall in the range of 15 to 20, where it is not possible to determine whether they are pure or hybrids. Tentatively, we suggest that only the following plumage types should be considered as definite hybrids: Brewster's and Lawrence's and other mixtures of Blue-wing and Golden-wing plumage characteristics that can be readily detected in the field with binoculars, and those birds which upon hand examination score between 3 and 14.5 on Short's scale.

Of the hand-examined birds, using our more restricted range for definite hybrids, eight (47%) were Blue-wings; five (29%) were hybrids; and four (24%) were indistinguishable from pure Golden-wings. Applying our more restricted range for definite hybrids to Short's sample he found 11 (38%) Blue-wings, 12 (41%) hybrids, and 6 (21%) birds indistinguishable from pure Golden-wings. Our hand-examined birds show a slightly higher proportion of Blue-wings now than did Short's sample in 1958-59. But once again there is no statistically reliable difference between Short's sample and ours. (Chi-square 2 x 3 test, Chi-square value equals 0.67).

Considering all the information for Tompkins County, there was clearly a major influx of Blue-wings between 1949 and 1959. From 1959 until 1977 the proportion of Blue-wings to Golden-wings has not changed to a statistically significant degree. Clearly the rapid rate of increase in the proportion of Blue-wings in the 1950's has either greatly slowed down in the last 18 years or has stopped completely. Perhaps with a larger sample size, which we hope to accumulate next year, we may be able to say with a greater degree of confidence whether the proportion of Blue-wings has stabilized, or is slowly continuing to increase.

BEHAVIORAL INTERACTIONS

The following brief discussion only supplements the extensive observations of Murray and Gill (1976), Ficken and Ficken (1968,

1969), Gill and Lanyon (1964) and Meyerricks and Baird (1968).

Despite the mutual tolerance of male Blue-wings and male Golden-wings, which allows some birds to establish overlapping territories, it is our experience that some aggression is shown between the males. This level of aggression is slightly more intense than that shown by males of either of these species to males of other warbler species. For instance, Blue-wings and Golden-wings pay almost no attention to Common Yellowthroats *(Geothlypis trichas),* and we frequently observed a male Golden-wing or male Blue-wing sitting in a treetop with a singing male Yellow Warbler *(Dendroica petechia)* without any display of aggression between the birds. However, we did observe a low level of aggression between male Blue-wings and male Golden-wings. One example of this degree of aggression is described below.

Within the territory of Blue-wing B-AW there is a row of dead elms frequently used by B-AW as singing perches. One of us observed a new Golden-wing singing from one of these perches on 17 May, two weeks after B-AW had established his territory. After the Golden-wing sang for about two minutes, B-AW was heard singing (Type 1 song as defined by Gill and Lanyon 1964) about 40 m from the Golden-wing. After singing four or five typical songs, in about half a minute, B-AW flew silently into the bottom of the tree with the Golden-wing. When B-AW hopped higher into the tree the Golden-wing flew out of the territory. No Golden-wing was heard in B-YA territory on the following day.

On 19 May a Golden-wing (the same one?) was observed singing for about one minute from one of the top perches in the same row of elms. Again Blue-wing B-AW began singing (Type 1 song) from about 40 m away, and then flew silently into the tree with the Golden-wing. After several seconds the Golden-wing flew further down the row of elms and again began to sing from a tree top. B-AW flew into the bottom of the tree with the Golden-wing after which the latter flew away. Both birds were then lost from sight and remained silent for about five minutes. At the end of this time the Golden-wing and the Blue-wing repeated this sequence in a virtually identical manner. Finally both birds became silent and they were last seen foraging, both within the boundary of B-AW territory.

On the following day a Golden-wing was singing repeatedly throughout the territory of Blue-wing B-AW using many of the same high perches used by B-AW without any pursuit by B-AW, who remained hidden. This was the last day that a Golden-wing was seen

within this territory, while B-AW was seen on many subsequent occasions.

This low level of aggression contrasts with the occasionally observed attacks between two Blue-wings which were non-stop, fast-flying, noisy with Type 2 song, and included direct pursuit. There is no doubt that Blue-wing to Blue-wing aggression was much more intense than the aggression shown between Blue-winged and Golden-winged Warblers.

DISCUSSION

None of our results provide statistical support for the belief that Blue-winged Warblers can replace Golden-winged Warblers. Yet we suspect that this may be occurring, and certainly believe that this is a possibility worth consideration. The following discussion of this possibility is highly speculative and should not be taken as documented, experimental evidence.

There are two lines of reasoning that lead us to suspect that Blue-wings are displacing Golden-wings, or at least that the two species cannot continue to coexist in the same area. The first is highly theoretical and is derived from the Competitive Exclusion Principle. This principle states that no two species that have the same ecological needs and that are limited by the same resource can coexist in a stable environment. Since so much about the ecology of the Blue-winged and Golden-winged Warblers seems identical, it would appear that the principle might apply to them. For instance, the territories of these birds seem to be located in identical habitat. We could not discern any consistent difference in the habitat chosen by the two species for their territories. Murray and Gill (1976) found that Golden-wings chose slightly wetter habitats, while Short (1963) found both Blue-wings and Golden-wings occurring in wet and dry habitats with about equal frequency. The only consistent ecological difference between these birds noted by us, and by Murray and Gill (1976), is that Blue-wings tend to arrive a week or two earlier than Golden-wings. Whether this difference or some other difference is sufficient to exempt these birds from the Competitive Exclusion Principle is unknown.

If this principle does apply to these birds, there must be some resource in such low supply that it limits the abundance of both species, but limits one species more than it does the other. This resource is not likely to be suitable nesting sites since the birds can set up overlapping territories. Food supply is believed to limit many

animal populations, but since the territories of these species are larger than the average for warblers, we have some doubt that food availability within the territory is the limiting factor for these birds. To stimulate further field observations and comments we suggest the possibility that the Competitive Exclusion Principle might apply in the following manner. We saw at least four transient male Golden-wings but no such Blue-wings. These birds were presumably looking for territories or mates. As described earlier, one of these transient male Golden-wings did succeed in establishing singing posts, but did not stay and apparently did not succeed in attracting a mate. With this bird and other transient male Golden-wings it seemed as if the "resource" in limiting supply was available females.

There is some weak empirical evidence that suggests that Blue-wings are replacing Golden-wings. On Long Island the arrival of Blue-wings was followed by the disappearance of Golden-wings. (Short (1962) makes this statement, although Bull (1974) states he could not find the original source of this information.) However, this sequence of events does not prove that Blue-wings caused the disappearance of Golden-wings, since the two events may be due to some other factor. In Tompkins County our sample this year showed a higher frequency of Blue-wings than in Short's sample in 1957-58. While this might mean that Blue-wings are continuing to increase, we must stress that with the small size of our sample we could not show that this increase in the proportion of Blue-wings was statistically real.

Obviously the above data are not convincing. We are unaware of other areas like Long Island where the arrival of Blue-wings has been followed by the virtual disappearance of Golden-wings. Nor are we aware of any long-term studies on the relative abundance of these two species at any particular locality. Unless this kind of circumstantial evidence can be consistently documented from a variety of locations, the ultimate balance between Blue-winged and Golden-winged Warblers can not be estimated. We would appreciate receiving correspondence about Blue-winged and Golden-winged Warblers. Hopefully, such correspondence would allow us to assess the historical changes and current status of these two species in New York.

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BIBLIOGRAPHY

Bull, John. 1974. *Birds of New York State.* Doubleday Natural History Press. Garden City, N.Y., 655 p.

Ficken, Millicent S. and Robert W. Ficken. 1967. Singing behavior of Blue-winged and Golden-winged Warblers and their hybrids. *Behavior* 28: 149-181.

——. 1968. Territorial relationships of Blue-winged Warblers, Golden-winged Warblers and their hybrids. *Wilson Bull.* 80: 442-451.

——. 1969. Responses of Blue-winged and Golden-winged Warblers to their own and the other species song. *Wilson Bull.* 81: 69-74.

Gill, Frank B. and Wesley F. Lanyon. 1964. Experiments on species discrimination in Blue-winged Warblers. *Auk.* 81: 53-64.

Lack, D. 1971. Ecological isolation in birds. Harvard Univ. Press. Cambridge, Mass.

Mayr, Ernst. 1963. Animal species and evolution. Harvard Univ. Press. Cambridge, Mass., 797 p.

Meyerricks, A. J. and J. Baird. 1968. Agonistic interactions between Blue-winged and "Brewster's" Warblers. *Wilson Bull.* 80: 150-160.

Murray, Bertram G. and Frank B. Gill. 1976. Behavioral interactions of Blue-winged and Golden-winged Warblers. *Wilson Bull.* 88: 231-254.

Parkes, Kenneth C. 1951. The genetics of the Golden-winged x Blue-winged Warbler complex. *Wilson Bull.* 63: 5-15.

Scheider, F. 1959. Warblers in southern New York. *Kingbird* 9: 13-19.

Short, Lester L., Jr. 1962. The Blue-winged Warbler and Golden-winged Warbler in central New York. *Kingbird* 12: 59-67.

——. 1963. Hybridization in the wood warblers *Vermivora pinus* and *v. chrysoptera.* Proc. 13th Intern. Ornith. Congress. 147-160.

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