

THE BLUE-WINGED WARBLER AND GOLDEN-WINGED WARBLER IN CENTRAL NEW YORK

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INTRODUCTION

The northward extension of the range of the Blue-winged Warbler (*Vermivora pinus*) toward the northern limit of the range of the Golden-winged Warbler (*V. chrysoptera*) has been noted in New York (Parkes, 1949 and 1951; Scheider, 1959) and in certain mid-western states, especially Michigan (Berger, 1958). The phenomenon appears to be occurring generally in the northern part of the ranges of these forms. Prior to the late 1940's, Golden-winged Warblers were uncommon and local in occurrence in New York (their presence in Central New York dates back at least to the latter part of the last century, according to Benton, 1960), while Blue-wings were virtually unknown outside the New York City and Buffalo regions. Blue-winged Warblers began moving into the Ithaca area between 1946 and 1949 according to Parkes (1949), who mentioned but one record of the form before 1946 and three more up to 1949. By 1953 Blue-wings had reached the Syracuse region (Scheider, 1959). Scheider mentions the occurrence of a Blue-winged Warbler near Watertown in late May, 1956. These observations indicate the movement into the area of the Blue-winged Warbler, and the extension of its range northward to closely approach the northern limit of the Golden-wing's range.

Since Parkes (1949) discussed the situation in the Ithaca region further changes have taken place. During the 1958 and 1959 breeding seasons Blue-wings were observed as commonly as Golden-wings near Ithaca. In these periods 25 males of the two forms (and hybrids) were secured from two colonies near Ithaca and one in the vicinity of Camillus (each year at least several males and all females were left at the colonies to perpetuate them). Since both forms are equally common around Ithaca at the present time, it is obvious that there exists considerable opportunity for interbreeding. The purpose of this paper is to discuss evidence for hybridization and introgression in these forms in Central New York, as provided by analysis of specimens and field observations.

HABITATS OF THE WARBLERS IN CENTRAL NEW YORK

Both colonies studied near Ithaca occur on hilly slopes close to swampy, riparian areas and woodlands. The Varna colony occupied several fields containing heavy ground cover and scattered trees and bushes of various heights. The fields are surrounded by deciduous woodland on the west and south, a pine plantation along the east side, and swampy deciduous woodland bordering Fall Creek on the North side. The ground slopes gently down to the creek on the north, and several swampy areas are located in the fields above the creek wherever drainage is poor. A specimen of *pinus* was taken in this area in 1949 by Stephen Eaton (Cornell University collection no. 21981), indicating that the colony may be ten or more years old.

The Danby colony occupies a steep hillside in Michigan Hollow (south-west of Danby), and extends down the hill to second growth along a stream at its base. The entire area surrounding the colony is old agricultural land belonging to the State. A *pinus*-like male (C.U. no. 24129) was taken in this vicinity by W. J. Hamilton III, in 1953.

No difference in habitat was noted in the Varna colony between areas occupied by *pinus*-like individuals and those occupied by *chrysoptera*-like birds. However, the wettest area was occupied by a male Blue-wing (no. 781, table 2). In the Danby colony two *pinus*-like and one *chrysoptera*-like individuals were obtained on territories in swampy cover along the stream. On the hillside several *chrysoptera*-like individuals were observed (singing), one of which was taken, and only one *pinus*-like bird was seen (no. 773, table 2). A "Brewster's" warbler was seen in this area on May 18, 1958 by William C. Dilger (pers. comm.). These observations agree with those of Parkes (1951) that *chrysoptera* tends to occupy upland areas, while *pinus* is more likely to inhabit wetter areas. Overlap is indicated, however, since a *pinus*-like bird was taken in an upland area, a *chrysoptera*-like male was secured in swampy cover, and both forms were found in the same field in Varna. The common breeding birds in the vicinity of the warbler colonies were Yellowthroats (*Geothlypis trichas*), Chestnut-sided Warblers (*Dendroica pensylvanica*), Rufous-sided Towhees (*Pipilo erythrophthalmus*), Field Sparrows (*Spizella pusilla*) and Indigo Buntings (*Passerina cyanea*). Other colonies (one near Ithaca, one near Camillus) were not studied in detail.

ANALYSIS OF COLOR CHARACTERS AND DISCUSSION

Parkes (1951) has presented a report on the possible genetics of the *pinus-chrysoptera* complex. A fine plate (p. 5) illustrates the hybrids of various supposed genotypes (it might be noted that the suggested genotype of the third bird from the bottom should read "Ww Ss pp" rather than "Ww Ss PP"). The dominance of the plain ("P") throat of *pinus* over the black ("p") throat of *chrysoptera* is discussed. The suggestion that this character is controlled by a single gene is perhaps valid, although the throat patch is sufficiently variable in Golden-wing and "Lawrence's" Warblers examined from other areas to further suggest the action of modifier genes. The other characters discussed by Parkes (wings bars, color of underparts) are apparently controlled by polygenes. The suggested incomplete dominance of white over yellow underparts is again possible, but a number of genes may be involved in a more complex fashion. The suggestion that color of wing bars and color of underparts are correlated due to genetic linkage is not upheld by my examination of specimens. These two characters, and a complex of dorsal color characters (back color, color of hind-neck and rump color) seem to vary more or less independently (see tables 1 and 2 and discussion below). Linkage of auricular patch color and throat color determining genes appears valid. Other characters of value in the study of variation in these forms, if not in the study of their interbreeding, include: green coloration of secondaries, pattern of whitemarking in the tail, and extent of the yellow forehead patch. The tail markings are very interesting, showing great variability in both forms, often with some asymmetry of pattern.

Male specimens of both forms in the Cornell Collection were examined, in addition to those collected. Specimens of both forms and hybrids in the American Museum of Natural History and other museums were also examined. The results of analysis of the Central New York specimens are contained in tables 2 and 3. Studies of specimens from other areas are incomplete and will be reported separately. Throat color is indicated in table 2 by a "P" for a plain throat and "p" for a black throat (after Parkes, 1951). Five other characters (color of underparts, wing bars, back color, color of hind-neck and rump color) have been analyzed using the "hybrid index" technique (see Sibley, 1950, 1954). A score of "4" is given the expression of a character as exhibited by *chrysoptera*. A "0" is assigned a character expressed as in *pinus*. Intermediates are scored "1", "2" and "3", depending on whether the character is exactly intermediate or nearly so ("2"), more like *pinus*, but with indications of *chrysoptera* ("1"), or more like *chrysoptera*, but with traces of *pinus* ("3"). A synopsis of the characters, their graduation, and their scores is contained in table 1. A synopsis of the characters, songs and habitats of the Central New York males appears in table 2. Songs indicated are those noted for each individual heard singing just prior to being collected. The numbers for the specimens are the original collectors numbers; with the exception of one specimen in the American Museum of Natural History, all specimens are in the Cornell collection. The habitat in which each specimen was taken, and the year collected are indicated in table 2. Under the column "Assignment", the individuals are designated as one form or the other, or notation is made concerning over-all characteristics of the specimen as indicated by its index scores for various color characters.

TABLE 1
SYNOPSIS OF WARBLER CHARACTER INDEX

Color of Underparts

- 0—Yellow, as in Blue-wing.
- 1—Yellow with white traces.
- 2—Yellow and White; usually breast and malar more or less yellow, throat and belly more or less white.
- 3—White below, with yellow traces, usually as a yellow wash on breast and perhaps faint yellow in the malar area.
- 4—White, as in Golden-wing.

Back Color

- 0—Olive-yellow, as in Blue-wing.
- 1—Olive-yellow with blue-gray traces.
- 2—Mixture of considerable blue-gray and yellow-green.
- 3—Blue-gray with yellow-green traces.
- 4—Blue-gray, as in Golden-wing.

Gradations for Rump Color and Color of Hind-neck same as for Back Color, except that the Blue-winged Warbler Rump Color is more yellow, tending to be yellow-olive rather than olive-yellow, as in Back Color.

Wing Bars

- 0—Two narrow white bars, as in Blue-wing.
- 1—Two white bars with yellow traces.
- 2—Two broadened, pale yellowish bars.
- 3—Merging yellow bars, whitish traces.
- 4—Single broad yellow bar, as in Golden-wing.

The information presented in table 2 affords many points for discussion. Simple dominance of plain throat color over the black throat color is generally upheld by the lack of intermediacy of this character in the specimens (it should be noted, however, that several Golden-winged Warblers showed some variation in the degree of completeness of the throat patch, although none exhibited a patch that could in any way be called intermediate). As suggested by Grant (1957), the simple dominance type of inheritance of a character renders that character unimportant in critical analysis of hybrid or possible hybrid individuals. This should be taken into account in studies of warbler hybrids. Unfortunately, such a striking character is difficult to ignore, but investigators interested in the effects of gene exchange find that characters controlled by a number of genes provide a great deal more information than those under control of but one gene.

The so-called Brewster's warbler has unfortunately been generally thought of as the F 1 product of the crossing of *chrysoptera* and *pinus*. Observers list as "Brewster's" warblers all *apparent* hybrids *lacking a black throat and possessing either partially or completely white underparts*. It has been recognized that such hybrids vary in the expression of yellow color of the underparts. Parkes (1951, pp. 10-11) has indicated that several possible crosses (as F 1, F 2, F 3, and various backcrosses) may produce "Brewster's" warblers. However, in distinguishing white-breasted backcross "Brewster's" warblers from partially yellow-breasted ones Parkes infers that all the latter are F 1's. The information in table 2 shows the considerable variation in color of underparts and other characters as well in hybrids. It is suggested that various backcross "Brewster's" warblers have a wide range of variation in the amount of yellow in the underparts (from none at all to nearly complete yellow coloring below), depending on the nature of the cross producing them, and that such patterns may provide an index to the amount of gene flow between the forms. As shown in table 2, some hybrids may be very close to *chrysoptera*, some more nearly intermediate, and others more like *pinus* in color characters. Thus, the first "Brewster's" warbler in the table (no. 783) is like *chrysoptera* except for the lack of the black throat patch, the *pinus* traces in its wing bars and similar traces in color of underparts. The specimen listed just above the first "Brewster's" warbler has a black throat, but shows *pinus* influence in three of the other five characters studied. Disregarding throat color, the latter specimen is actually more nearly intermediate than is the first "Brewster's" warbler — *yet it would be noted in the field by the observer as simply a Golden-winged Warbler*. The second "Brewster's" warbler (no. 777) is more intermediate than the first, having the color of the underparts, back and hind neck scoring "2". The wing bars and rump color of this specimen are closer to *chrysoptera*. The third

TABLE 2 SYNOPSIS OF CHARACTERS, SONGS, AND HABITATS OF SOME CENTRAL NEW YORK VERMIVORA.

Locality	Year	Sex	Collector's Number	Characters					Song**	Assignment	Habitat
				T	Be	W	B	N			
Ithaca	1953	M	—	p	4	4	4	4	4	?	?
Danby	1958	M	S772	p	4	4	4	4	4	G	Swamp along stream
Camillus	1959	M	W811	p	4	4	4	4	4	?	chrysoptera —Cedar swamp
Camillus	1959	M	W812	p	4	4	4	4	4	?	Cedar swamp
Camillus	1959	M	W809	p	4	4	4	4	4	?	Cedar swamp
Varna	1958	M	S782	p	4	4	3	4	4	G	Hillside scrubby field
Danby	1958	M	S775	p	4	4	3	4	4	G	?
Varna	1958	M	S771	p	4	4	3	4	4	G	chrysoptera —Hillside slope in trees
Howland Is.	1929	M	—	p	4	4	4	3	4	?	?
Camillus	1959	M	W808	p	4	3	4	4	4	?	pinus Cedar swamp
Camillus	1959	F	S791	p	3	4	3	3	4	?	Cedar swamp
Camillus	1959	M	W810	p	4	2	4	4	4	G and B	Cedar swamp
Varna	1958	M	S778	p	4	4	3	3	3	?	Hillside scrubby field
Howland Is.	1915	M	—	p	3	4	3	3	4	?	?
Varna	1958	M	S783	P	3	3	4	4	4	B	Hillside scrubby field
Varna	1958	M	S777	P	2	3	2	2	3	G+	Hillside scrubby field
Danby	1959	M	S792	P	2	3	2	2	3	G+	"Brewster's" Hillside second growth
Dryden	1955	M	CS3628	P	1	2	2	1	1	G	?
Camillus	1958	M	S786	P	2	2	1	0	0	G+	Cedar swamp
Varna	1958	M	S779	P	0-	2	1	0	1	?	Wet wooded field
Danby	1958	M	S774	P	0-	1	2	0	0	G	Second growth along stream
Danby	1958	M	S776	P	0	1	1	0	0	G	pinus Hillside second growth
Danby	1958	M	S773	P	0	1	0	0	0	B	Hillside second growth
Danby	1953	M	—	P	0	1	0	0	0	?	?
Danby	1959	M	S788	P	0	1	0	0	0	B	chrysoptera —Swampy thicket along stream
Danby	1959	M	S789	P	0	1	0	0	0	?	Hillside scrubby field
Danby	1959	M	S790	P	0	1	0	0	0	B	Hillside second growth
Danby	1959	M	S787	P	0	0	0	0	0	G and B	Swampy thicket along stream
Varna	1949	M	—	P	0	0	0	0	0	?	?
Varna	1958	M	S780	P	0	0	0	0	0	B	pinus Wet wooded field
Varna	1958	M	S781	P	0	0	0	0	0	?	Wet wooded field
Varna	1958	M	S784	P	0	0	0	0	0	B	Hillside scrubby field

* Letters stand for: throat color (T), color below (Be), wing bars (W), back color (B), color of hind neck (N) and rump color (R)

** G "bee-bzz-bzz" (golden-wing), B "bee-bzzzzzz" (blue-wing). G+ "bee-zee-zee-zee"

"Brewster's" warbler is similar to the second. The fourth is intermediate in two characters, but more like *pinus* in three. The fifth (no. 786) is intermediate in color of underparts and wing bars, but very like *pinus* in the other three characters. Such variation suggests complex genetic control of the characters involved, although data are lacking on the degree of phenotypic variation due to environment influence (information on color pattern variation in true F 1 progeny would be most welcome in this regard). Needless to say, field studies of this problem should be undertaken with care, since backcross "Brewster's" warblers are impossible to distinguish (as far as is known) from F 1 individuals. The advantages of capturing and color banding of individuals to be studied, along with notation of their color characteristics, are obvious.

The number of "impure" specimens secured in the course of the investigation is of considerable interest. Four of the specimens taken in 1958 and 1959 were phenotypically pure Blue-winged Warblers, four were phenotypically pure Golden-winged Warblers, and eighteen were variously intermediate. A number of otherwise "pure" *chrysoptera* and *pinus* individuals show traces of characters found in the other form. These results are similar to those obtained from examination of specimens from other areas (Short, in prep.). The abundance of intermediate types indicates considerable independence in action of genes controlling the various color characters. It also suggests that widespread interbreeding and backcrossing are permitting a great deal of gene flow (introgression) between the forms. It is most unlikely that chance mutation or crossover of genes would affect such a large proportion of the population.

Linkage of genes controlling the color characters is a possibility, but this study provides no evidence for its occurrence. The information obtained does indicate, however, that close linkage does not occur. Even in color of underparts, only one of 14 specimens showing indications of hybridization in one or more of the three characters (back, rump and hind neck color) exhibits approximately equal expression of traces in all three of them.

No "Lawrence's" warblers were obtained in 1958 or 1959. On the basis of the extensive interbreeding noted in the Ithaca region, it is expected that individuals of this type will shortly be found in Central New York. It has been shown (Parkes, 1951; and others dating back to Nichols, 1908) that "Lawrence's" warblers are not produced by an initial (F 1) cross of Golden-wing X Blue-wing, but can only result from backcrossing or an F 2 cross. In view of the apparent degree of gene flow between the two forms, and the infrequency of occurrence (one in 16 progeny) of "Lawrence's" warblers in the F 2 cross, it is likely that most of these individuals are backcross products.

MEASUREMENTS

A summary of the range of variation in mensural characters of Central New York specimens is contained in table 3. Although the sample sizes were insufficient for detailed statistical treatment, a number of points are apparent from perusal of the table. The Golden-winged Warbler is slightly larger than the Blue-wing, with definitely longer wings and tail, a generally

longer bill, and about the same tarsal length. The hybrids are more or less intermediate between the parental forms in their measurements. An important point is that individuals of *pinus* or *chrysoptera* which exhibit traces of the other form in color pattern also tend toward that form in measurements. This strengthens the view that the color pattern traces are the result of introgression.

TABLE 3
SUMMARY OF MENSURAL CHARACTERS OF CENTRAL NEW YORK
VERMIVORA

FORM	N	Weight	Wing Length	RANGES IN VARIATION IN:		
				Tail Length	Bill Length	Tarsal Length
chrysoptera *	12	8.5-9.5gms.	61.1-65.7mm.	46.4-51.5mm.	7.8-9.6mm.	15.4-17.6mm.
chrysoptera with pinus traces	9	8.3-9.9gms.	61.5-65.1mm.	46.8-51.5mm.	8.2-9.0mm.	16.5-18.0mm.
"Brewster's" warblers	5	7.9-9.5gms.	59.3-64.6mm.	47.6-51.2mm.	8.5-9.2mm.	17.0-17.6mm.
pinus with chrysoptera traces	8	8.2-9.3gms.	58.5-60.7mm.	46.4-48.8mm.	8.2-8.8mm.	16.7-18.4mm.
pinus	5	7.1-9.1gms.	57.5-58.5mm.	45.1-47.0mm.	7.9-8.3mm.	15.9-17.1mm.

* *chrysoptera* in table 2 plus several others from Cayuga County.

SONG

Songs noted for individuals of various phenotypes are also of interest (see table 2). Eisenmann (1946) has pointed out that individuals of one form may sing the song of the other. No detailed study of song was attempted, but most singing males listed in the table were heard, and notes taken on their songs, for some period of time before they were collected. Three Blue-wing males were heard singing, one giving the typical Blue-wing song ("bee-bzzzzzzz"), a second the typical Golden-wing song ("bee-bzz-bzz"), while the third sang both types interchangeably. Three of the five *pinus*-like individuals with *chrysoptera* traces heard singing gave Blue-wing songs, while two sang like Golden-wings. The "Brewster's" warbler most like *chrysoptera* in color characters (no. 783) sang like a Blue-wing. The other four sang like *chrysoptera* (except that an extra "bzz" note was added in three cases). Three of the four males of the "*chrysoptera*" with traces of *pinus*" group which were heard singing uttered Golden-wing songs. One, however, sang both song types interchangeably. The one Golden-wing for which the song was noted gave the Golden-wing song. The songs of these warblers are unlike those of other members of the genus *Vermivora*, and similar to those of certain warblers of the genus *Dendroica*. Songs of the Black-throated Green Warbler (*Dendroica virens*) and the Cerulean Warbler (*D. caerulea*) in particular can be mistaken for those of the Blue-wing or Golden-wing at a distance. When singing ceases in July the birds become extremely difficult to find, as noted by Berger (1958, p. 50), and others. The interchangeability of the songs, as indicated above by Eisenmann (1946) and myself is of importance, since it suggests that learning may play a role in determination of songs used by males, as occurs in meadowlarks (*Sturnella*,

see Lanyon, 1957, p. 50). At any rate the forms *cannot be identified with certainty* by song. It is unlikely that the song is involved as an isolating mechanism acting to reduce interbreeding between the two forms.

THE VARNA COLONY

The situation at the Varna colony where nine males were taken in 1958 is worthy of more detailed discussion. The colony contained about a dozen pairs of warblers, though females were observed so infrequently that it is not certain whether all males were paired. In one field of about six acres five males were secured from territories, four on June 7 and one on June 24, 1958. Two of the five were "Brewster's" warblers (table 2, nos. 777 and 783), one was a "pure" Blue-winged Warbler (no. 780), another was a *pinus* showing *chrysoptera* influence (no. 779), and the fifth was a *chrysoptera* with slight *pinus* back color traces (no. 782). The Blue-wing sang a Golden-wing song. One "Brewster's" (no. 783) sang like a Blue-wing; the other more nearly intermediate in color pattern, sang a Golden-wing song (typical except for an additional syllable). Songs of the other two birds were of the Goldenwing (one bird) and Blue-wing (the second bird) types, but since neither was heard singing just prior to being taken, song-types could not be definitely ascribed to the birds. One "Brewster's" male was observed (no. 777) to fly to a perch in a young elm tree, sing once, be attacked by an apparent Bluewing, and drive the intruder off before flying back to its perch to resume singing. The "Blue-wing" was collected (no. 779), and was found to exhibit *chrysoptera* traces in several characters. The other "Brewster's" warbler was collected as it sang on June 24 in a small elm from which the *pinus* (no. 780) was taken three weeks before.

Two fields were adjacent to the main field where the five warblers were taken. One field was quite wet, with standing water and swampy conditions in several places. In this field of about four acres two Blue-wings (nos. 781 and 784) were taken. Number 781 was secured while feeding about a foot from the ground on June 12. The other was collected on June 24 about 150 feet from where the first was obtained. The other field was on a hillside between the fields previously mentioned and the creek. In this sloping, well-drained field were many small trees and several of larger size. In this area one *chrysoptera*-like warbler (no. 771) was secured while singing a typical Golden-wing song. Another specimen (no. 778) was taken in this vicinity by W. J. Bock on May 27. This bird showed *pinus* influence in back, hind neck and rump color, but was otherwise like *chrysoptera*.

No evidence was found in this colony, or in others visited, for the action of isolating mechanisms restricted interbreeding between the forms.

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SUMMARY

An analysis of Central New York specimens of Blue-winged Warblers and Golden-winged Warblers and their hybrids was undertaken using the "hybrid index" technique. Most specimens were hybrids. The Blue-winged Warbler is now as common as the Golden-winged Warbler near the northern limit of the range of the latter form in the state. Songs, measurements and habitats of warblers with various phenotypes are discussed. The data indicate that gene flow between populations of the two forms is considerable. The tendency of field observers to simply "type" warblers observed as Blue-winged Warblers, Golden-winged Warblers, "Brewster's" Warblers or "Lawrence's" Warblers should be discouraged in favor of the careful noting of color characters. Hybrids vary greatly in color pattern, and birds appearing at first glance to be either Blue-wings or Golden-wings may actually show indications of introgression when studied carefully. Song is so variable that it cannot be used alone to identify warblers as Blue-wings or Golden-wings. There is so far *no* evidence to indicate the existence of isolating mechanisms acting to prevent or limit gene flow between the two forms.

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