BLUE- AND GOLDEN-WINGED WARBLERS AND THEIR HYBRIDS

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The Golden-winged Warbler (Vermivora chrysoptera) and the Blue-winged Warbler (Vermivora pinus) were known to Linnaeus, the father of modern taxonomy, and both were described in the 12th edition (1766) of his Systema Naturae. These two closely-related species most probably diverged from each other during the glaciations of the Pleistocene period, when the Mississippi River was an enormous bay some 100-200 miles in width. The Blue-winged Warbler evolved to the west of the river; the Golden-winged, along the Atlantic Coast.

Both species extended their ranges northward with the retreat of the glaciers but probably remained allopatric, separated by a "prairie peninsula" (extending from Iowa eastward into Ohio) and by the dense forests of the Appalachian range. Continuing improvement of the climate eventually allowed the two species to re-establish contact in the Great Lakes area. Secondary contact in the Northeastern states may be more recent and is perhaps the result of man's deforestation and agricultural activities. Mayr[1] suggests that this contact is only about 200 years old.

Today, the Blue-winged Warbler remains the more southerly and westerly form, and the Golden-winged Warbler is restricted to the more northern areas; but the ranges of both species are undergoing change. Particularly well-documented is the northern expansion of the Blue-winged Warbler, and the following dates should interest the local birder:

According to Bagg and Eliot,[2] the first recorded Blue-winged Warbler in Massachusetts was found in Dedham in 1857, and the species was not recorded here again until 1878 (West Roxbury), and then again in 1896. A pair successfully nested in Sudbury in 1909, and by 1913 Blue-winged Warblers were already hybridizing with Golden-winged Warblers in Lexington. The first Essex County record dates from May 31, 1931, but the record is in doubt inasmuch as the bird was only heard and could not be seen.

Blue-winged Warblers became common in the Connecticut Valley during the early 1930s, and for many years this was their only center of abundance in the state. As recently as 1955, Bailey wrote of this species: "...a rare visitor from the South...It is found primarily in the Connecticut Valley, is regularly reported in Berkshire County, and is an irregular visitor in Eastern Massachusetts...The observer is fortunate to see more than 1 or 2 birds per year."[3]

Today, along the Atlantic coast, I find them much more regular than Golden-winged Warblers. Each year brings an increased number of records from Mt. Auburn, where Golden-winged Warblers are now decidedly rare. The situation in the West Newbury area seems entirely parallel.

These two warblers hybridize throughout all areas of sympatry, and most field guides and reference works suggest that there are two "types" of hybrids:

1. Brewster's Warbler ("V. leucobronchialis"), which is described as being "like Golden-wings without the black throat...[with a] thin black eye-mark, as in the Blue-wing, and the white or largely white, instead of solid yellow, underparts."[4] The type was first described in the scientific literature by William Brewster in 1874.
2. Lawrence's Warbler ("V. lawrencei"), which is yellowish "with white wing-bars... but with black face-pattern of Golden-wing."[5] This hybrid was likewise first recognized in the literature in 1874.

As early as 1881, Brewster[6] recognized that the two forms were in fact hybrids, but for many years it was thought that each hybrid "conformed to type," i.e., presented a standardized appearance with little or no variation. Certain of the genetic principles were recognized quite early, among which were the following:

1. The gene transmitting the black throat-patch is recessive and thus cannot evidence itself unless it is inherited from each parent. The parents themselves must obviously have descended (at least in part) from Golden-winged Warblers.
2. The gene transmitting the yellow underparts is likewise recessive. Again, both parents must have carried it, and we may therefore infer that each parent must have descended (at least in part) from Blue-winged Warblers.

(Note: It is now clear that this character, yellow underparts, is controlled by many

genes, not by one. Hence, the genetic analysis presented here and found also in much of the literature is unduly simplified.)

3. Points 1 and 2 above together imply that a Lawrence's Warbler must be the offspring of two parents, each of which is itself a hybrid of the Brewster-type. This fact alone suffices to account for the relative scarcity of the Lawrence-type hybrid. In fact, one would expect fewer than 1 out of 16 hybrids to be of this "type."

The absurdity of this particular two-way categorization is well-recognized by modern ornithologists, especially as it pertains to the face-mask-eye-stripe variation. Blue- and Golden-winged Warblers are two distinct species, differing genetically from each other in hundreds of genes. Hybrid offspring are fully fertile and mate both with each other and with individuals of either parental species (a phenomenon known as backcrossing). As a result, the hybrids exhibit a continuous spectrum of variation, with the two parental types as extremes. The presence or absence of a face mask is indeed controlled by a single gene or gene complex, and hence this character is inappropriately used as a classificatory criterion for hybrids.

(An analogy might help here. Eye color in humans is controlled by a small number of genes. Certainly, we should resist the argument that a blue-eyed child is more closely related to all other blue-eyed humans than he is to his own brown-eyed brothers and sisters!)

A proper classification of hybrids should be based on a survey of the full range of variation, representing the totality of the genetic differences between the two parental species. Lester L. Short attempted such an analysis in a 1962 article published in the Proceedings XIII International Ornithological Congress, Vol. I (available from the A.O.U.). The remainder of this article is largely abstracted from that work; page references without footnote citation are to this paper.

Both parental species are hard to know well. The birds are unobtrusive; their songs are weak and buzzy and do not carry well; and breeding birds depart for their winter homes almost immediately after nesting, i.e., the birds are only with us for approximately two months. As a consequence, much of the information available in current field guides is at best misleading. I shall attempt to correct some of these statements in two final paragraphs, but first, the analysis of the nature and extent of the hybridization process.

Short examined 1,028 adult warbler specimens, 500 of which were taken in the breeding season and another 288 of which were spring birds. He utilized five color characteristics in his analysis, and he found these to be essentially independent of each other. Blue-wings have 1) a greenish-yellow hindneck, 2) yellowish rump, 3) greenish-yellow back, 4) yellow underparts, and 5) two narrow, pure white wing bars. Golden-wings have 1-3) a blue-gray hindneck, rump and back, 4) white underparts, and 5) a single, broad (i.e., fused) yellow wing bar (p. 149). These characteristics vary continuously in the specimens from one extreme to the other. In technical language, the characters intergrade. Each individual specimen was therefore given a score of 0 to 4 for each character, depending upon the degree of similarity to one or the other parental phenotype. The over-all sum (hybrid index) may thus range from 0 (for "pure" Blue-wings) to 20.

Using the old-fashioned "Brewster-Lawrence" classification, only 117 hybrids (11 percent) were detected (p. 151). However, subjecting these same specimens to the more sophisticated hybrid index analysis showed that only 10.8 percent (113 individuals) were in fact "pure-bred" specimens. 89.2 percent were hybrids! (p. 151) Even after broadening the definitions of what constituted a phenotypically pure specimen, Short still found that 41.9 percent were hybrids.[7] Of these, he says, "I feel that, of the 431 specimens I regard as definite hybrids, up to 312 would not be identified as hybrids by most field observers." (p. 152)

Interestingly, there were two specimens, both from New Haven, Connecticut, which represented extremes of the "Brewster-Lawrence" phenomenon. One of these specimens was in every respect a "pure" Golden-winged Warbler, except that it possessed a transocular stripe rather than the expected face mask; the other specimen represented the opposite extreme--a "pure" Blue-winged Warbler with a black face mask. Brewster-type and Lawrence-type hybrids (i.e., hybrids without and with face masks) were found for all values of the hybrid index, from 0 to 20. Short says, "This tremendous variation again stresses that the terms 'Lawrence's' and 'Brewster's' cannot be applied precisely, and should be avoided wherever possible in favor of careful observation and notation of all features of color pattern." (p. 156)

Song

According to the field guides, Blue-winged and Golden-winged Warblers differ in song. In part, this is true, but the actual situation is rather complex.

The early territorial song of the Blue-winged Warbler is usually rendered "bee-bzzz," with a descending pitch pattern. The two notes are quite dissimilar in timbre, the second note giving the effect of a loose and disconnected rattle. The early territorial song of the Golden-winged Warbler is usually rendered "bee-bzz-bzz-bzz." (There may be fewer or more "bzz"-notes.) This song is rather more uniform in quality, although the first note is quite definitely unlike the remainder of the series. I hear this song as being on one pitch except for the first note, which is lower by a whole tone---in musical notation, C-D-D-D. However, other individuals listening to the same bird will hear a different tonal sequence, and some will even insist that the bird sings a "melody" with a descending pitch sequence.

A quick glance at the Sonagram in Robbins, et al[8] will explain this disparity. The Golden-wing's notes are "blurs" of sound. In fact, the non-initial notes cover almost an entire octave. Out of this complex of tones, each individual human will single out certain frequencies to be the pitch "heard," but since this is a largely subjective process, different birders will "hear" different notes.

Both species have an alternate song. It is similar in the two species and may occasionally be heard during migration. Both species also have similar nesting songs, which can be heard later in the season.

Note that of the three songs, only the early territorial songs are well-differentiated in the two species; AND EVEN THEY ARE NOT DIAGNOSTIC! Phenotypically pure individuals of either parental species may sing the early territorial song of the other species exclusively. Moreover, there are at least 3 reports in the literature of individuals that sang both early territorial songs alternately (p. 156). In a subsample which Short studied more intensively, approximately one-third of the birds were heard singing the "wrong" song, at least part of the time!

Habitat

Blue-winged Warblers are supposed to prefer low, swampy, semi-open areas; Golden-wings, drier, upland, woodland edges. In the Midwest, however, the reverse is true.[9] Short reports that over 60 percent of his specimens from central New York (for which habitat information was available) were in the "wrong" habitat. In fact, all of the phenotypically pure Golden-winged Warblers were so mislocated (pp. 156-157).

An alternate hypothesis may, in fact, be valid, viz., that both species tend to occur together in the same habitat in mixed colonies, but the preferred habitat varies in nature geographically. Certainly, this thesis is correct for the West Newbury, Bramanville and Longmeadow colonies in Massachusetts.

Summary and Conclusions

Blue- and Golden-winged Warblers may well be two separate species which have not evolved sufficiently to allow for the development of effective isolating mechanisms. The course of future evolution is thus difficult to predict. The two forms may continue to diverge, developing more effective isolating mechanisms under the pressure of natural selection; or these two forms may begin to merge, resulting in one composite polymorphic species. At present, extensive hybridization is taking place with the result that differences in song and habitat preference are no longer species-characteristic (if, indeed, they ever were).

The genetic constitution of an individual hybrid can be analyzed in terms of five color characters. The presence or absence of a black face mask is a character of little or no utility for the determination of the genetic affinities of a given specimen. Consequently, the terms "Brewster's" and "Lawrence's" Warblers should be dropped.

Footnotes

[1] Mayr, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge. p.117

[2] Bagg, A.C., and Eliot, S.A., Jr. 1937. Birds of the Connecticut Valley in Massachusetts. The Hampshire Bookshop, Northhampton. p. 543.

[3] Bailey, W. 1955. Birds in Massachusetts, When and Where to Find Them. The College Press, South Lancaster. p. 176.

[4] Peterson, R.T. 1947. A Field Guide to the Birds, 2nd ed. Houghton Mifflin, Boston. p. 138.

[5] Ibid., p. 139.

[6] Brewster, W. 1881. On the relationship of Helminthophaga leucobronchialis, Brewster, and Helminthophaga lawrencei, Herrick; with some conjectures respecting certain other North American birds. Bull. Nuttall Ornithol. Club 6:218-225.

[7] To be precise, only 10.8% of the specimens had a score of 0 or 20, and 41.9% had a hybrid index ranging from 3 to 17.

[8] Robbins, C.S., Bruun, B., and Zim, H.S. 1966. Birds of North America. Golden Press, New York. p. 254.

[9] Berger, A.J. 1958. The Golden-winged--Blue-winged Warbler complex in Michigan and the Great Lakes area. Jack-Pine Warbler 36:37-73.

Page references without citation refer to Lester L. Short, Jr., 1962. Hybridization in the Wood Warblers Vermivora pinus and V. chrysoptera in Proceedings XIII International Ornithological Congress, Vol. I, pp. 147-160.

MONK PARAKEET UPDATE, No. 2

The United States Department of the Interior has officially classified the Monk Parakeet (Myiopsittus monachus) as a potential agricultural pest in this country (Bureau of Sport Fisheries and Wildlife Leaflet, 496, 1971). In its native Argentina, it is particularly common in the vicinity of human habitation, destroying up to 45 percent of certain crops, notably cultivated fruits and grains (esp. maize and sorghum) and sunflower crops. The official status of the species as a potential pest was predicated on its destructiveness to these agricultural crops, but now it appears that there is more to the story.

William T. Shields, et al., report in the June 1974 issue of THE WILSON BULLETIN (Vol. 86, No. 2) on the feeding habits of a pair nesting in a park in Middlesex County, New Jersey. During March and April of 1973, 33 percent of their food consisted of buds, flowers and fruits of the American elm (Ulmus americanus), supplemented by seeds, acorns and buds of other native trees. All of the elms within the feeding range of this pair had the top three feet of their crowns completely stripped of foliage. Damage to willows in the area was also severe. The authors comment that, had a normal-sized flock of 15-50 individuals been present, the depredations on these trees would have been indeed serious.

Please report any sightings of this species to the Massachusetts Audubon Society or to the Massachusetts Division of Fisheries and Game. The species breeds in the metropolitan New York area. Let's try to keep it out of New England.

(For a brief description of the species, cf. BIRD OBSERVER, Vol. 1, No. 6, p. 131.)

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