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HISTORICAL ASPECTS OF HYBRIDIZATION BETWEEN BLUE-WINGED AND GOLDEN-WINGED WARBLERS

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ABSTRACT.—I summarize information on the historical patterns of changing abundance and hybridization in Blue-winged and Golden-winged warblers in southern Connecticut. Both were rare in the state before 1850. Golden-wings increased at some localities in the Connecticut River valley around 1880. Blue-wings increased dramatically on the southern coast from 1880–1900 and spread up the Connecticut River valley in 1900–1920. This expansion resulted in extensive hybridization and ultimately in replacement of the Golden-wings. The population increases of these warblers are attributable to the abandonment of small New England farms after the Erie Canal increased the competitive advantage of farms in the Great Lakes region.

Analysis of specimen phenotypes supports previous studies of the extent of introgressive hybridization but also shows how the phenotype composition changes with time. Comparison of samples from different localities requires that they each be taken over a limited time span and that the length of time Blue-wings were established at each locality be considered in the final interpretation.

A general pattern emerges of replacement of Golden-wings by Blue-wings within 50 yr of initial interaction. The decline of Golden-wings may be due to habitat changes *per se*, to competition from Blue-wings, and/or to destruction of the genotype through introgressive hybridization. If Blue-wings continue to expand during the next 50 yr, the continued survival of the Golden-winged Warbler may be threatened. *Received 6 April 1979, accepted 4 October 1979.*

THE interactions between Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers are probably the most intensively studied of any pair of hybridizing bird species in North America (Carter 1944; Parkes 1951; Short 1963; Gill and Lanyon 1964; Ficken and Ficken 1967, 1968a, b, c, d, 1969; Gill and Murray 1972a, b; Murray and Gill 1976; Adkisson and Campbell 1977). The appearance of conspicuous hybrid phenotypes has been correlated with the northeastward spread of Blue-wings during the last 150 yr into the range of Golden-wings (Berger 1958; Parkes 1951; Short 1963; Ficken and Ficken 1968a; Gill and Murray 1972a; Bull 1964, 1974). Hybrids may obtain mates less readily than parental phenotypes (Ficken and Ficken 1968b), but they do not otherwise appear to be at a major disadvantage. The frequency of hybridization and successful backcrossing, however, is not high enough in any known area to warrant a change in species status of these two warblers (Short 1969a). Blue-winged and Golden-winged warblers do not normally defend breeding territories against each other, despite their many ecological similarities (Ficken and Ficken 1968c, d; Murray and Gill 1976; Confer and Knapp 1977), some

reproductive harassment (Adkisson and Campbell 1977, Murray and Gill 1976), and, of course, occasional interspecific matings. As one aspect of speciation, such interactions will test their reproductive and ecological compatibility and thus will ultimately determine both their evolutionary independence and potential for stable coexistence (Lack 1944; Mayr 1963, 1970; Short 1969a, b; MacArthur 1972). Yet our understanding of the future consequences of sympatry in these warblers is still unsatisfactory—increasing cloudiness rather than clarity seems the result of the considerable effort that we have invested in the problem.

Southern Connecticut was especially well known at the turn of the century as a place where hybridization between these two warblers was relatively common (Bishop 1889, Sage 1893, Chapman 1906). Short (1963) analyzed many specimens from New Haven, as well as from other localities throughout the zone of secondary contact, and showed for the first time the extent of character recombination and introgression. Two additional samples of hybridizing Blue-winged and Golden-winged warblers from southcentral Connecticut have since become available, one from Portland-Middletown and the other from Thomaston. The Portland-Middletown specimens were collected just after Blue-wings colonized that locality in the late 1800's. The Thomaston specimens were collected in 1960. The rare opportunity to analyze the consequences of hybridization after 80–100 yr of secondary contact was the initial impetus for the present study.

My conclusion, however, is that local situations may be so unstable as to render such samples incomparable with respect to the evolutionary questions we usually have been asking. Moreover, it appears that Blue-wings predictably replace Golden-wings within 50 yr of local secondary contact and that perhaps attention to this aspect of the problem will help dissipate those clouds that lie between us and a satisfactory understanding of the Blue-winged and Golden-winged warbler complex.

METHODS

This study is based primarily on my examination of three major samples of specimens from south-central Connecticut (Fig. 1). The first sample comprises 135 specimens of males taken within 8 km of New Haven from 1899–1920 (Fig. 2). Localities within this radius include Hamden, Orange, Woodbridge, North Haven, East Haven, and West Haven. Of these specimens, 103 were obtained by L. B. Bishop, whose collection is now at the Chicago Field Museum of Natural History. Short (1963) examined these specimens. A second sample comprises 79 specimens of males taken from 1879–1920 (Fig. 2) at Portland (including Middletown), Connecticut, 39 km northeast of New Haven on the Connecticut River. Most of these specimens were obtained by J. H. Sage, the veteran collector and established ornithologist of Portland. His collection now resides at the University of Connecticut and only recently became available for study. The third sample comprises 54 specimens of males taken by D. H. Parsons in 1960–65 at Thomaston, 47 km north-northwest of New Haven. This locality is just north of the recently constructed (1960) Thomaston Dam on the Naugatuck River. These specimens are housed at the Peabody Museum of Yale University and include some mounted for public display. These series of specimens are so extensive that most individuals must have been collected when possible. I doubt that Bishop or Sage biased their collections toward particular phenotypes. Perhaps they took slightly more care to collect conspicuous hybrids defined by incongruent throat patch combinations, but in this paper I base my conclusions primarily on more subtle color and size differences. Parsons (pers. comm.) did try harder to collect intermediate phenotypes but, at the same time, wanted to obtain a large, representative sample of specimens.

I analyzed phenotypic characteristics of males collected between 1 May and 15 June at the above-mentioned localities. I assume these specimens represent local breeding populations, because these dates cover the presence of the warblers on their Connecticut breeding grounds (Cooke 1904, Chapman 1906, Sage and Bishop 1913, Bagg and Eliot 1937, Bull 1964). We used these dates for our analyses of Michigan specimens (Gill and Murray 1972a). Others might prefer a later date in May, but there is a difficult

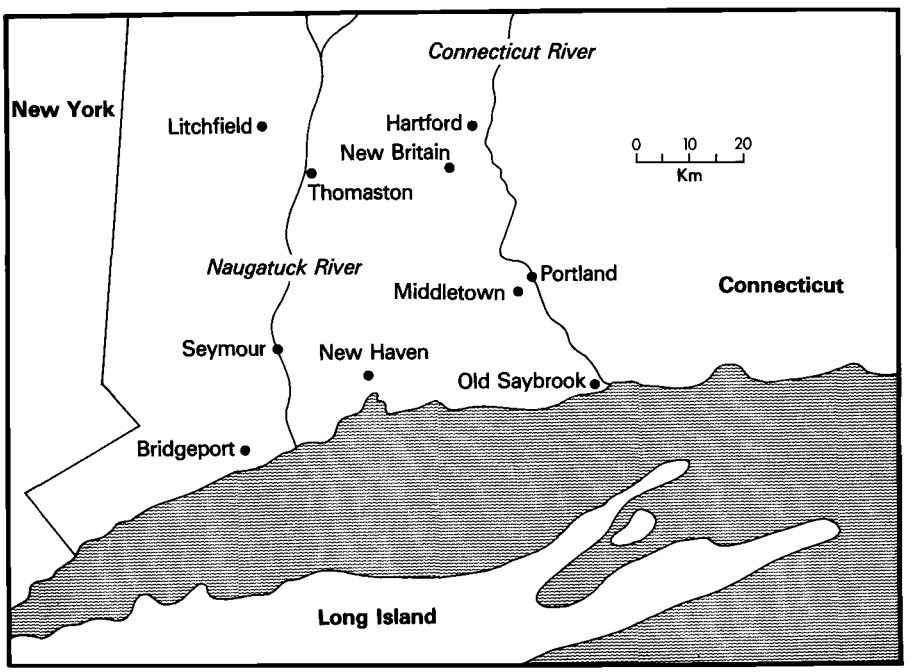

Fig. 1. Connecticut localities of particular importance to the history of hybridization between Blue-winged and Golden-winged warblers.

tradeoff between including the earliest breeding arrivals, and perhaps some migrants, versus biasing the sample toward Golden-wings, which may arrive later than Blue-wings (Ficken and Ficken 1968d), and also toward hybrid phenotypes, which may be more conspicuous later in the season because they are unmated (Ficken and Ficken 1968b, d).

I assessed plumage color in terms of seven characters, each of which was subdivided into character states ranging between those of extreme Blue-wings and extreme Golden-wings (Table 1). This character index system was the same as that used by Gill and Murray (1972a), except that I scored wing-bar color separately from wing-bar width and included scores for the chin and throat color in the analysis. My assistant, S. Peters, measured the bill length (from nostril), tarsus length, and wing length (arc) of each specimen to the nearest 0.5 mm. Principal components were then calculated from a correlation matrix of these characters using the program system NT-SYS (Rohlf et al. 1972). For this analysis I used all available male specimens from Connecticut. The accuracy of the relationships between specimens on the ordination plot relative to the actual Euclidean distances based on the original scale was excellent (mxcomp correlation = 0.996). Each specimen was designated by a single value on PC I, which accounted for most of the color variation. I compiled histograms of phenotype frequencies on this axis instead of the traditional character index system. It turns out that there is very little difference in the results of the two methods.

Results

Distribution and abundance.—The Golden-winged Warbler was originally a rare, locally distributed species in Connecticut (Merriam 1877). In 1843 it was known only as a rare migrant (Linsley 1843). There were no Connecticut breeding records of this species until 1875, when they were found breeding in small numbers at Suffield (Bagg and Eliot 1937). At Portland only five were seen between 1875 and 1882 (Sage 1882), but by 1888 Portland was known as a locality where they could be found regularly in small numbers (Bishop 1889). By 1893 they were common and regular at Portland but rare elsewhere in southern Connecticut and eastern Mas-

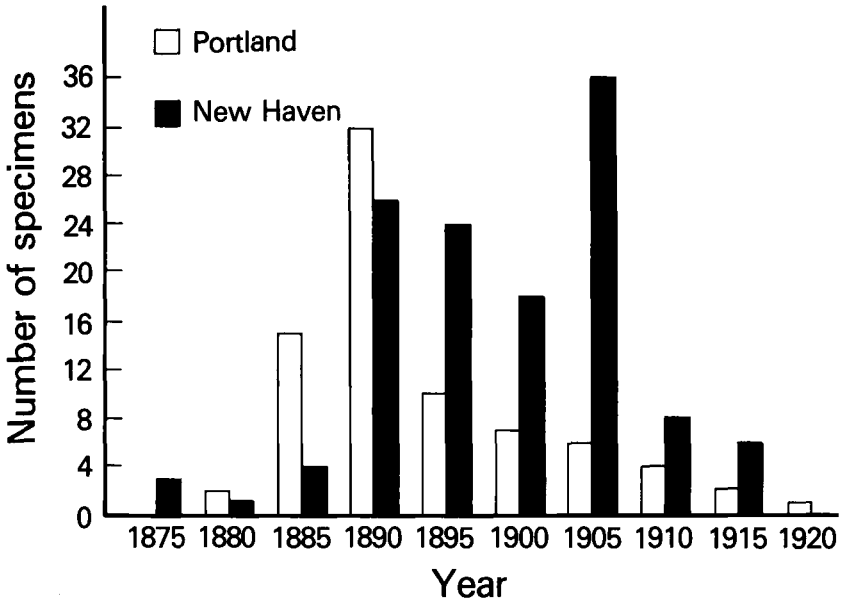

Fig. 2. Temporal composition of samples of Blue-winged and Golden-winged warblers (combined) collected at Portland and New Haven, Connecticut from 1875 to 1920.

sachusetts (Bagg and Eliot 1937). From 1898–1902 the Golden-winged Warbler was a common summer resident at New Britain, Connecticut, 13 km SSE of Hartford, but then it became less common and, in fact, rare after 1909 (Bagg and Eliot 1937). It is not clear from the old literature that Golden-wings ever bred commonly at New Haven, where they were considered "probably a rare summer resident" about 1900 (Burr 1908). Woodruff (1906) considered Golden-wings to be a very rare summer resident at Litchfield.

TABLE 1. Characters and character states employed in this study.

Character	Description of character states	Code
Wing-bar color	Pure white	0
	Slight yellow edging	1
	White with pronounced yellow	2
	Mixed yellow and white	3
	Yellow with pale bases	4
	Deep yellow	5
Wing-bar width	Narrow and well separated	0
	Broad and well separated	1
	Broad with slight separation	2
	Broad and confluent	3
General color (nape, back, rump, breast, and belly)	Yellow-green	0
	Yellow-green with slight gray	1
	Mixed gray and green	2
	Gray or white with slight yellow or yellow-green	3
	Gray or white	4
Chin/throat	No black in either	00
	No black in chin; throat black	02
	Chin black and white; throat black	12
	Chin and throat black	22

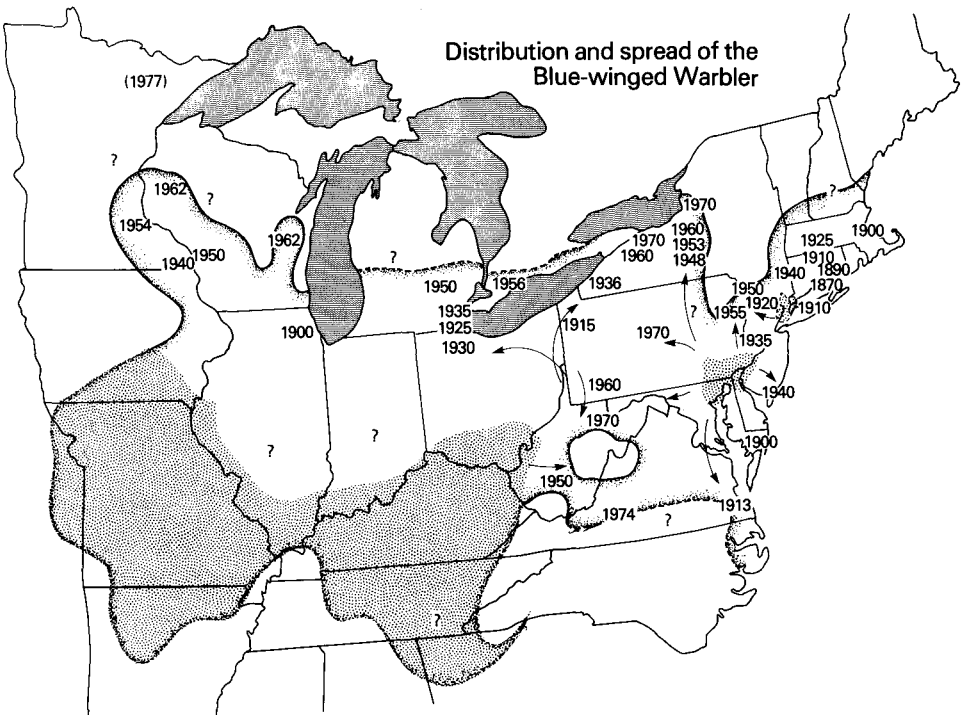

Fig. 3. Distribution and spread of the Blue-winged Warbler in the last century. Dates on the map indicate when Blue-wings first became established at a locality. Stippled area is approximate range in the mid-1800's. The populations in southeastern Pennsylvania and the New York City region were once isolated from each other and from the main population west of the Appalachians. Information on the early status in many areas is sketchy. Therefore, the range boundaries are approximations and the arrows indicating patterns of spread are hypotheses only. Similarly, the current northern boundaries require better definition. I would welcome input from all states.

Historically, Blue-wings occurred primarily west of the Appalachians (Cooke 1904, Short 1963, Fig. 3). Exactly when populations of this species became established in the Delaware Valley and in the Hudson Valley regions is not clear, but by the late 1800's they were well known and were isolated from the main western populations and also from each other.

Blue-wings probably became established on Connecticut's southern shore in 1850–1870. In one of the earliest lists of Connecticut birds, Linsley (1843) does not mention the species, which suggests it probably was uncommon or highly localized. Merriam (1877) prepared the first comprehensive work on Connecticut birds and considered Blue-wings to be rare to uncommon throughout the state except at Old Saybrook at the mouth of the Connecticut River, where they were quite common. Merriam considered Blue-wings to be uncommon at New Haven, where he, himself, was active. A few years later Brewer (1880) reported the first nest of this species from New Haven, though Merriam (1877) was quite sure Blue-wings were nesting. The earliest Connecticut records thus suggest establishment of Blue-wings at Saybrook followed by increases elsewhere on the coast.

Blue-wings increased dramatically on the south shore of Connecticut by 1890. Eames (1889) considered them common to abundant at Bridgeport "for years," and

TABLE 2. Matrix of character correlation coefficients.

Character	Throat	Wing-bar color	Wing-bar width	Nape	Back	Rump	Breast	Belly	Bill	Wing	Tarsus
Throat	1.00										
Wing-bar color	0.60	1.00									
Wing-bar width	0.63	0.81	1.00								
Nape	0.58	0.77	0.75	1.00							
Back	0.58	0.77	0.74	0.97	1.00						
Rump	0.59	0.79	0.76	0.97	0.98	1.00					
Breast	0.63	0.80	0.77	0.92	0.94	0.95	1.00				
Belly	0.59	0.78	0.75	0.97	0.96	0.96	0.95	1.00			
Bill	0.12	0.19	0.12	0.17	0.15	0.17	0.18	0.17	1.00		
Wing	0.26	0.37	0.38	0.36	0.35	0.38	0.35	0.34	0.08	1.00	
Tarsus	0.13	0.13	0.12	0.08	0.06	0.07	0.06	0.06	0.04	0.21	1.00

counted a remarkable 60 singing males there on 9 May 1889. Bishop (1889) noted that Blue-wings were generally common along the coast, including Seymour, 17 km northwest of New Haven on the Naugatuck River, but not at Bridgeport! By 1908 Blue-wings bred abundantly at New Haven (Burr 1908). By 1913 Blue-wings were abundant from Bridgeport to New Haven but were less common east of Branford except at Saybrook (Sage and Bishop 1913).

Blue-wings then spread up the Connecticut River valley. Blue-wings remained rare at Portland, 42 km up the river from Saybrook, until 1890 (Bishop 1889, Sage 1893), but then quickly increased to common by 1900 (Sage and Bishop 1913). The rapid spread of Blue-wings in coastal Connecticut and up the Connecticut River valley was accompanied by frequent sightings of hybrids (Purdie 1873, 1897; Sage 1884, 1885, 1889, 1893; Clark 1885; Eames 1888, 1889; Bishop 1889, 1893; Foster 1896). Blue-wings were rare at New Britain (17 km northwest of Portland) until 1908 and then began to increase in the general vicinity of Hartford (Bagg and Eliot 1937). This was about the same time (1910) that they spread into northern Long Island from the New York City region (Giraud 1844, Chapman 1906, Eaton 1914, Bull 1964). Blue-wings continued to spread up the Connecticut River valley into western Massachusetts, where they were rare until 1924 and were first found nesting in 1932 (Bagg and Eliot 1937).

Blue-wings bred sporadically inland in north-central Connecticut in the early 1900's (Meeker 1906, Bagg and Eliot 1937). Woodruff (1906) considered Blue-wings ("very rare—one fall record") at Litchfield. By the 1930's they bred uncommonly at Litchfield and Kent but were unknown north of these towns (Bagg and Eliot 1937). Blue-wings increased noticeably in adjacent Dutchess County, New York in the early 1930's (Griscom 1933). Loery (pers. comm.) recalls that Blue-wings became common around Litchfield about 1950.

In summary, Blue-wings apparently spread commonly along the south shore of Connecticut from Saybrook in 1879–1890, up the Connecticut River valley including Portland in 1900–1920, and into the hill country of north and west-central Connecticut, including Litchfield and probably Thomaston, in 1930–1950.

Phenotype distributions in Connecticut.—The plumage color characters are strongly correlated with each other. The correlation coefficient (r) for some pairs of characters was greater than 0.9 (Table 2). Wing-bar width and color were less strongly correlated with the other color characters ($r \approx 0.75$). Size characters were all poorly correlated with each other and with various color characters.

TABLE 3. Principal component analysis (factor loading values) of variation in characters of Blue-winged and Golden-winged warblers.

	Principal component		
Color characters	**1**	**2**	**3**
Wing-bar color	−0.347*	0.564*	0.742
Wing-bar width	−0.339*	0.661*	−0.667
Breast	−0.391*	−0.258	−0.058
Belly	−0.390*	−0.259	−0.029
Nape	−0.393*	−0.207	−0.002
Back	−0.389*	−0.118	−0.017
Rump	−0.392*	−0.231	−0.009
Cumulative variance explained	87.9%	94.7%	97.5%
All characters	**1**	**2**	**3**
Throat patch	0.710	−0.083	0.057
Wing-bar color	0.866*	−0.054	0.033
Wing-bar width	0.852*	−0.070	−0.029
Breast	0.957*	0.102	−0.064
Belly	0.956*	0.120	−0.052
Nape	0.966*	0.092	−0.039
Back	0.961*	0.103	−0.012
Rump	0.960*	0.120	−0.027
Bill	0.145	−0.049	0.985
Wing	0.430	−0.552*	−0.041
Tarsus	0.124	−0.863*	−0.056
Cumulative variance explained	61.9%	72.1%	81.1%

* Characters most strongly associated with each component.

When both size and color characters are included in the analysis, Principal Component I (PC I) explains 61.9% of the variance (Table 3). All the color characters load heavily on this component, body-plumage color more heavily than wing-bar or throat characters. PC II explains an additional 10.2% of the variance. The principal loadings on this component are the size characters, especially wing and tarsus lengths (Table 3). If size is excluded from the analysis and only color characters are considered, PC I accounts for 87.9% of the variance and PC II accounts for only 6.8% more, not enough to distinguish a second meaningful axis.

PC I (all characters) ranges in value from −0.2 to +1.6; I have divided this continuum into 25 divisions (Fig. 4). Low values of −0.2 to −0.9 indicate Blue-wing phenotypes; some introgression in wing-bar characters is evident in specimens scoring as low as −0.4. Intermediate values of 0 to +0.9 indicate conspicuous hybrids with mixtures of yellow and white coloration and intermediate wing-bar conditions. High values of 0.9 to 1.6 indicate Golden-wing phenotypes. Those with scores as low as 0.9 are actually quite yellow. The alternative throat colorations, apparently controlled by a single pair of alleles with complete dominance (Parkes 1951), occur in combination with most phenotype values on PC I.

Phenotype distributions differ among the three Connecticut samples (Table 4, Fig. 4). The Portland sample is significantly different from the Thomaston sample (2-sample Kolmogorov-Smirnov test, $D = 0.432$, $P < .001$) and the Thomaston sample is significantly different from the New Haven sample ($D = 0.226$, $P < .05$). Golden-wing phenotypes are more numerous than Blue-wing phenotypes in the Portland sample (53% vs. 25%); hybrids comprise 22%. Of the individuals with indices between 0.1 and 1.4, 14 (25%) have a plain throat. The Thomaston sample resembles the Portland sample in that "parental" phenotypes predominate (89% vs. 78%) but differs in that Blue-wings rather than Golden-wings comprise the majority of the specimens, and a rather high proportion of specimens

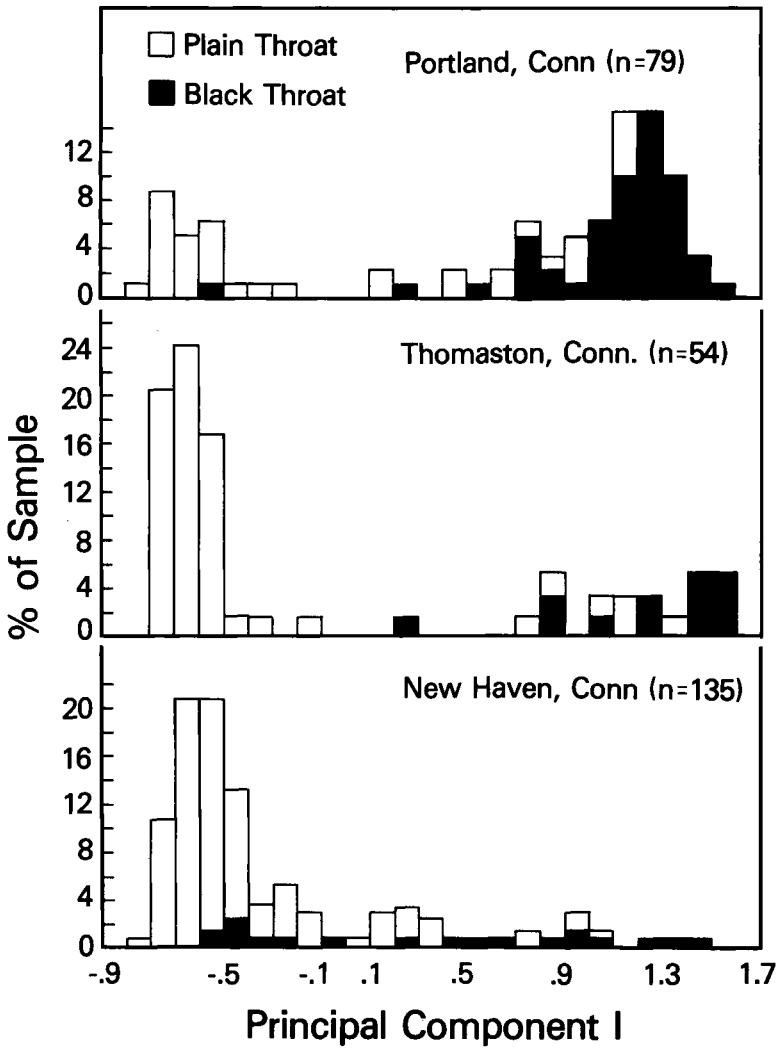

Fig. 4. Phenotype distributions in three Connecticut samples of Blue-winged and Golden-winged warblers. Black squares indicate face patterns typical of the Golden-winged Warbler. The abcissa is the first principal component, which accounted for 61.9% of the variance in both size and color characters.

with high (Golden-wing) indices have the plain throat. The difference in proportions of "parental" vs. "hybrid" phenotypes is not significant ($\chi^2 = 1.76$; $P > .05$). The New Haven sample contains mostly Blue-wing phenotypes but includes a few specimens in nearly every category on PC I. The Golden-wing throat character is distributed rather evenly among individuals with scores greater than -0.6.

I have analyzed selected subsamples of the full samples used in Fig. 4 to examine phenotype distributions at Portland and at New Haven during shorter time spans that can be related more precisely to the local establishment of Blue-wings (Fig. 5). For Portland, I used only specimens collected from 1885–1899, i.e. the core of that sample taken just as Blue-wings were starting to increase there. I divided the large New Haven sample into two subsamples, 1885–1899 and 1905–1920. I purposely

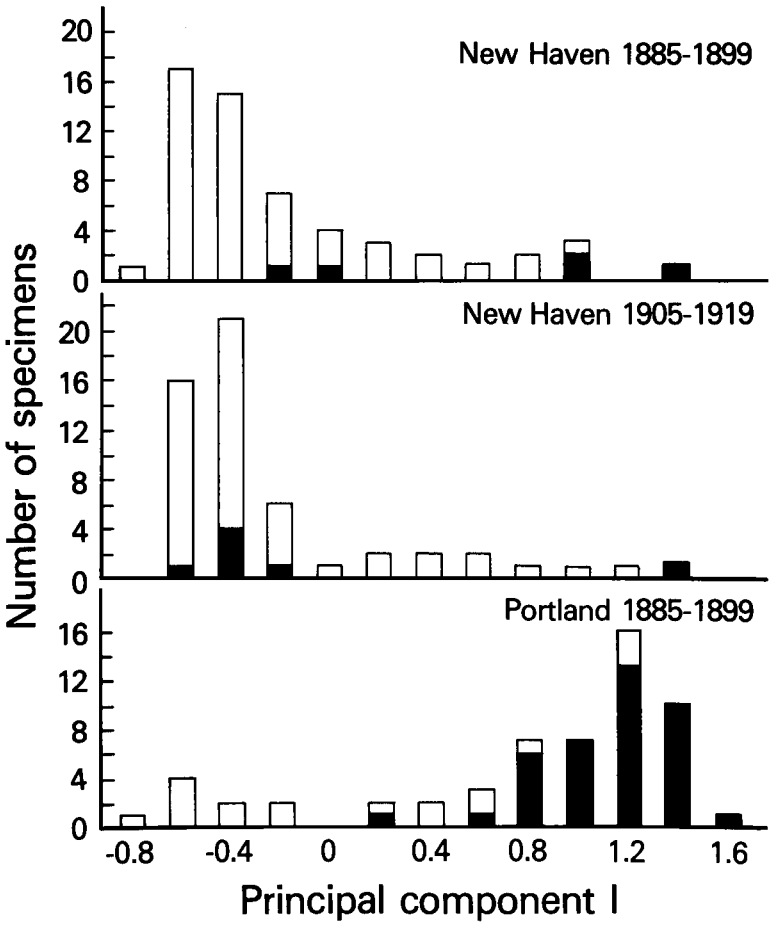

Fig. 5. Phenotype distributions during selected times spans from Portland and New Haven, Connecticut. Black boxes are as in Fig. 4. The differences between the two New Haven subsamples are not significant.

excluded specimens collected in 1900–1904 to increase the distinction of the two periods.

The restricted Portland sample has proportionately fewer Blue-wing phenotypes, which increased after 1900, and thus is skewed more strongly toward Golden-wing phenotypes. Of the specimens, 12% are strongly intermediate, hybrid phenotypes, a phenomenon that resembles more closely the Thomaston situation. The two New Haven subsamples are similar and are nearly the mirror image of the Portland phenotype distribution. The more recent subsample (1905–1920) shows a slight shift toward typical Blue-wing phenotypes with few conspicuous hybrids, but the difference is not significant at the 0.05 level ($\chi^2 = 2.49$, 1 df).

On 9 June 1976, I visited the Thomaston locality where Parsons had collected 10–15 yr previously. I carefully studied but could not collect 13 territorial male warblers. All were clearly Blue-wings and near Blue-wing phenotypes and would have had calculated phenotype scores of less than −0.1 on PC I. Two males had conspicuously introgressed wing bars that would have scored 2–3 on the Character Index scale for

TABLE 4. Proportions of Blue-wing, Golden-wing, and hybrid phenotypes in three Connecticut samples.

Phenotype score on PC I	Locality		
	Portland	Thomaston	New Haven
≥0.9 (GW)	42 (53)[a]	13 (24)	9 (7)
0.2–0.9 (hybrid)	17 (22)	6 (11)	24 (18)
≤−0.2 (BW)	20 (25)	35 (65)	102 (75)
Total	79 (100)	54 (100)	135 (100)

[a] Number of specimens followed (in parentheses) by percent of total sample.

wing-bar color. One of these appeared slightly grayish on the back and slightly pale on the breast and belly. It appears that the Golden-wing phenotypes of 10–15 yr ago have been replaced completely by (introgressed) Blue-wing phenotypes. This conclusion from my brief visit was supported by Parsons (pers. comm.), who has visited the locality periodically over the last 10 yr. All male Blue-wings but one at this locality sang typical Blue-wing songs (song type I; Gill and Murray 1972b). One male sang a typical Golden-wing song (Pattern C-C-C-C of Gill and Murray 1972b, including a drop in frequency after the first note).

DISCUSSION

The rough outlines of northward movement of Blue-wings into the range of the Golden-winged Warbler have been known for a long time. The details, however, are quite complex and have been affected by latitude, topography, deforestation patterns, and establishment of secondary or tertiary populations (Gill unpubl. data). Blue-wings have spread more quickly in river valleys and along lake plains, regardless of direction, than they have inland and uphill from these corridors. Thus, in Connecticut, Blue-wings spread more slowly up the Connecticut River valley than along the coast and very slowly into the adjacent hills toward Litchfield and Thomaston. In part, this may reflect deforestation patterns *per se,* but more information is needed to establish this. Nevertheless, the histories of interaction with Golden-wings at three Connecticut localities within 50 km of each other have been quite different. Future studies of these warblers must incorporate finer resolution of historical details at study sites than we have appreciated heretofore.

The population dynamics of these warblers in Connecticut relate in part to the abandonment of small farms in 1850–1900. Most of Connecticut was flourishing farmland by 1820 (Kingsley 1974). However, the Erie Canal, which opened in 1830, gave the large, mechanized farms of western New York, Ohio, and Indiana a competitive advantage over the small, stony farms of New England. Consequently, Connecticut farmers abandoned their farms and allowed the fields and pastures to revert to the successional habitats (Kingsley 1974, Fig. 6) required by Blue-winged and Golden-winged warblers (Berger 1958, Ficken and Ficken 1968c, Confer and Knapp 1979). This period of changing land use in the late 1800's coincides, I believe causally, with the increases in warbler populations. It seems probable that the details of changing distribution and density of these warblers elsewhere also are related to such patterns of deforestation and regrowth.

The relative abundances of Blue-wings and Golden-wings change following establishment of Blue-wings at a new (Golden-wing) locality—Blue-wings increase rapidly and Golden-wings tend to decrease. Observations from other states parallel

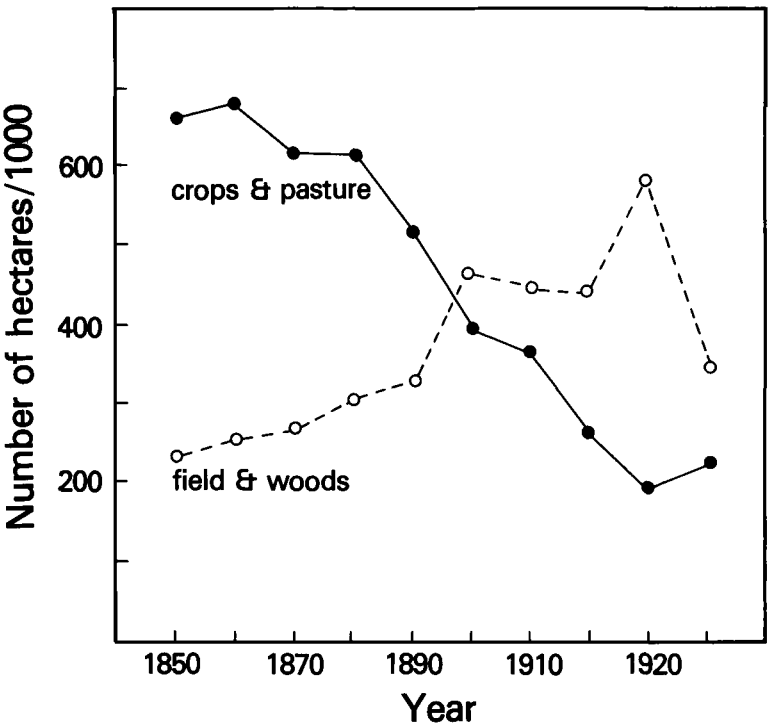

Fig. 6. Changes in the amount of privately owned farmland in Connecticut. The solid line indicates the decline in acreage of crops and pasture that resulted from farm abandonment, as farm products from the Great Lakes region dominated eastern markets after the Erie Canal opened in 1830. Acreage of fallow land with successional habitats used by Blue-winged and Golden-winged warblers (dotted line) increased in a corresponding fashion, most dramatically in 1890–1900. These data were compiled from decennial (Agriculture) census by the U.S. Bureau of the Census 1860–1950.

the information from southern Connecticut. For example, Blue-wings appeared near Detroit, Michigan in 1935 and increased to 30% of the warblers by 1946–52 (Berger 1958) and 70% by 1970 (Gill and Murray 1972a). Blue-wings also arrived in Toledo, Ohio about 1925–1930 and quickly increased in abundance (Campbell 1940, Mayfield pers. comm.). In the Oak Openings habitat near Toledo, Blue-wings increased from an average of 0.26 birds per location checked in 1928–32, through 1.07 in 1933–37, to 3.08 in 1944–48 (Campbell 1974). Golden-wings averaged 5.9, 6.0, and 2.0 per locality on these same censuses. Thus, Blue-wings increased from about 5% at the beginning, through 15% in 5 yr, to 50% of the population after 15 yr. Golden-wings decreased in absolute density such that the combined density of the two species remained about the same. Habitat disturbances, including destruction of bogs favored by Golden-wings, caused a decrease in the abundance of many bird species in Oak Openings after 1950. The last Golden-wing was seen in 1968, 40 yr after the first Blue-wing arrived. Blue-wings decreased to about 0.65 birds per location but are abundant elsewhere in the Toledo region. Golden-wings now rarely breed in this area.

Local ornithologists have documented the increases in Blue-wing abundance in western and central New York State especially well. Blue-wings reached south-

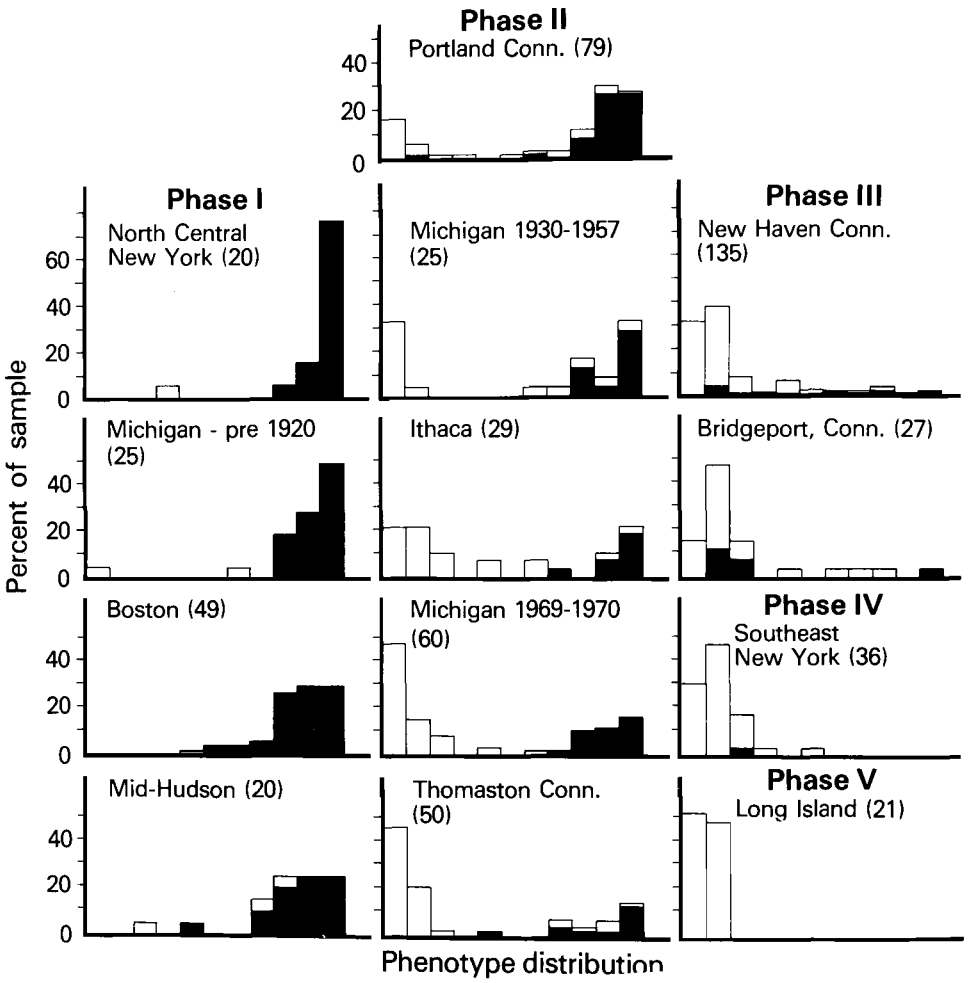

Fig. 7. Phenotype distributions in warbler samples analyzed by Short (1963), Gill and Murray (1972a), and here. The bars on the left side of each graph indicate Blue-wing phenotypes, bars on the right Golden-wing phenotypes, with hybrids in the middle. Black areas represent face patterns typical of Golden-winged Warblers. (See text for further explanation.)

western New York state in 1936–38 (Beardslee and Mitchell 1965, Taylor in litt.). There were three records prior to 1936, i.e. 1889, 1902 (nest), and 1928, but after 1938 they increased rapidly in abundance (Beardslee and Mitchell 1965). The first Brewster's phenotype was seen in 1939. Spring-count census data (Prothonotary 1939–1976) document an increase in Blue-wings per count from 1–2 in 1940 to over 100 per count in the last few years. The proportions have shifted from 5–10% to 95% Blue-wings in 40 yr, though details may vary considerably among localities in this area. The Erie lake plain is now occupied exclusively by Blue-wings (Sundell pers. comm.), but both Blue-wings and Golden-wings, and frequent hybrids, are found inland.

Blue-wings reached Ithaca (Tompkins County), New York in 1947–49 (Parkes 1949, 1951; Scheider 1959), and Brewster's phenotypes appeared shortly thereafter. By 1958 Blue-wings comprised about 60% of the warblers (Short 1962), and they

TABLE 5. Phenotype composition and relative timing of *Vermivora* samples.

Locality	Initial contact	Sample	Age of contact	Phenotype distribution
A. Boston, Massachusetts[a]	1900	1862–97	0	I
B. Mid-Hudson, New York[a]	1920	1878–1918 1920–30	0+	I
C. Onondaga County, New York[a]	1960	1915–30	0	I
D. Ithaca, New York[a]	1948	1960	10–15	II
E. Portland, Connecticut[c]	1890	1885–1910	0–10	I–II
F. Thomaston, Connecticut[c]	1940 F_1 F_2	1960–65 (1976)	20–25 40	II+ IV–V
G. New Haven, Connecticut[c]	1870	1890–1905	20–30	III
H. Southeast New York[a]	1850[d]	1878–1908	45	IV
I. Bridgeport, Connecticut[a]	1865	1888–1925	35	III
J. Western Long Island, New York[a]	1870	1876–1909	20–30?	V
K. Michigan, Washtenaw and Livingston counties[b]	1935	pre-1920	0	I
L. Michigan, Washtenaw and Livingston counties[b]	1935	1930–57	0–20	II
M. Michigan, Washtenaw and Livingston counties[b]	1935	1969–70	35	II+
N. Michigan, Clinton county[b]	1950	1969–70	20	I–II

[a] From Short 1963.
[b] From Gill and Murray 1972a.
[c] This study.
[d] Possibly later.

continue to increase in relative abundance (Temple and Temple 1976). Confer and Knapp's (1977, 1979) careful censuses indicate that Blue-wings have now increased to 84% in Tompkins County. Less quantitative information from other localities throughout the northeast supports this pattern of rapid increases in the relative numbers of Blue-wings vs. Golden-wings following Blue-wing establishment.

Golden-wing populations themselves have not been stable. Like the early situation at Portland, Connecticut, they increased from a rare to a common species in many different localities before the arrival of Blue-wings, dramatically so in central New York State, for example (Benton 1950, Scheider 1959, Taylor in litt.). Elsewhere, Todd (1940) noted that Golden-wings were increasing in the Pittsburgh region as a result of deforestation in some areas. Golden-wings were absent from Pine County, Minnesota in 1918–19 but now are common there (Greene and Jannsen 1975). They were virtually unknown at Itasca in northern Minnesota prior to 1940 (only three records); now they are abundant (Greene and Jannsen 1975, Parmalee 1977).

In most cases, increases in Golden-wing density have been followed by declines after Blue-wings arrived. In central New York around Rochester they were common through the 1950's and then began to decrease, so that they are no longer found in much of their former habitat (Taylor in litt.). They disappeared at Pymatuning, Pennsylvania after 1940 (Grimm 1952). Other declines in Golden-wing abundance have been noted in Dutchess County, New York (Griscom 1933), southern Michigan (Berger 1958), southwestern West Virginia (Hall MS, Shreve in litt.), and Ithaca, New York (Temple and Temple 1976).

Several factors may be causing the decline of Golden-wing populations. First, it is possible that Blue-wings actually outcompete and replace Golden-wings. They do overlap greatly in habitat usage. Their breeding territories normally overlap (Ficken and Ficken 1968d, Gill and Murray 1972a, Murray and Gill 1976), and there are no obvious differences in foraging ecology (Ficken and Ficken 1968c). Second, hybridization and introgression siphon off a fraction of each generation of "pure" Golden-wing genotypes. While the frequency of hybridization in this complex is not

great (5%–10%, Gill and Murray 1972a), it could contribute to the decline if Blue-wings increased more rapidly than Golden-wings for other reasons. Stabilizing selection within Blue-wing populations may then eliminate conspicuously introgressed genotypes and maintain the purity of Blue-wing populations after the period of hybridization and destruction of the Golden-wing genotype. This is suggested by our comparison of the two New Haven subsamples. Possibly introgression of some Golden-wing attributes broadens the ecological and physiological tolerances of Blue-wings, thereby fueling their expansion into latitudes and altitudes previously occupied only by Golden-wings, as described for insects (Lewontin and Birch 1966).

It is also possible, however, that Golden-wings decline because of advancing succession and their specialized habitat requirements. Some important work at Ithaca College at Ithaca, New York by J. Confer and K. Knapp (1977, 1979) suggests that Golden-wings are more highly specialized and require earlier stages of old field succession than do Blue-wings. This would explain why Golden-wings increased first at some localities, particularly in the late 1800's after the deforestation of the northeast. Subsequent declines in Golden-wing abundance then may be due to advancing succession and habitat change *per se,* rather than interactions with Blue-wings. Some local declines of Golden-wings, e.g. Detroit (Berger 1958) and Oak Openings, Toledo (Campbell 1974), are partly attributable to destruction of bogs and fields by advancing suburbia.

It appears that Blue-wings generally replace Golden-wings within 50 yr of the establishment of sympatry, as was the case at the Connecticut localities studied here. At present I know of no localities with breeding Golden-wings where Blue-wings have been established for 50 yr or more. Most dramatic is the situation at Charleston, West Virginia, where Blue-wings first became established in the late 1950's, having spread up the Kanawha River from the Ohio River. They then increased rapidly in relative abundance from 5% in 1960 through 50% in 1970, to 100% in 1978 (Shreve in litt.), i.e. Golden-wings disappeared in about 20 yr. If current trends continue, we can expect Golden-wings to disappear from Washtenaw and Livingston counties, Michigan, by the early 1980's and from Ithaca, New York, by the year 2000.

Phenotype distributions in samples from different localities vary greatly (Short 1963, Gill and Murray 1972a). The variations, however, are well correlated with the length of time the two warblers had been sympatric in an area prior to the time of sampling. I have established the approximate dates of Blue-wing establishment for a variety of localities where large numbers of warblers were collected (Table 5). I rendered the different samples as comparable as possible by arranging the data in terms of percent of sample on a standardized phenotype index scale. I arranged all samples in order, from high proportions of Golden-wings to high proportions of Blue-wings (Fig. 7), and I grouped them into five categories (phases) based on general phenotype distribution.

I. Predominately Golden-wing with a few Blue-wing and hybrid individuals.
II. Balanced proportions of Blue-wing and Golden-wing with some hybrid phenotypes; conspicuous combinations of Blue-wing throat color with Golden-wing plumage color (i.e. "Brewster's" phenotypes).
III. Predominately Blue-wing phenotypes with relatively few pure Golden-wings and a broad range of intermediate phenotypes spanning full range of character indices but with only a few individuals in any one category, i.e. high phenotype diversity. Appearance of Golden-wing throat patch in Blue-wing phenotypes (i.e. "Lawrence's" phenotypes).

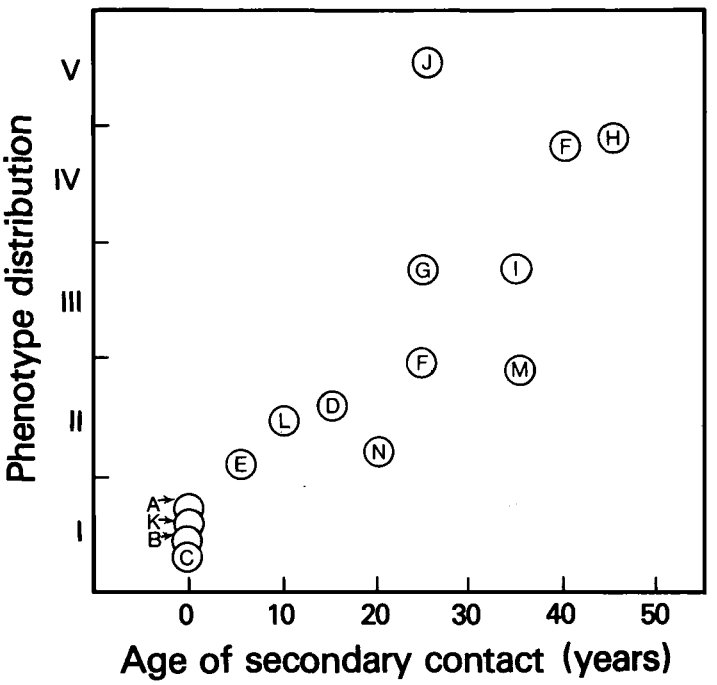

Fig. 8. Correlation between phenotype distribution in hybridizing warbler populations (see Fig. 7) and the number of years that elapsed between establishment of Blue-wings at a locality and the sampling of the population(s). The letters correspond to the localities listed in Table 5.

IV. Conspicuously introgressed Blue-wing population with few strongly intermediate phenotypes and no Golden-wings.

V. Blue-wing population with some variability in wing-bar color and occasional "Lawrence's" phenotypes.

The correlation between these phenotype distributions and the age of local sympatry is strong (Fig. 8). The only locality that is off the trend is Long Island (J), where Golden-wings were rare if they ever bred at all (Bull 1974) and where pure Blue-wings thus became established with little hybridization and introgression. Pooling these locations supports the hypothesis of a 50-yr process of Blue-wing establishment, hybridization, and introgression with Golden-wings and, finally, local extinction of Golden-wings. The phenotype distributions at many of these same localities have now shifted into phase IV or V. For example, New Haven is now virtually pure Blue-wing and probably reached phase V by 1930 (Arbib, pers. comm.). Thomaston (F) is now phase IV or V. Bridgeport is phase V and has been so for many years. Resampling of many of these localities in 1980 seems desirable and would permit testing of this hypothesis.

The future of the Golden-wing Warbler thus seems bleak, because there are fewer and fewer Golden-wing localities without Blue-wings. If the present trend continues for another 100 yr, it seems probable that the Golden-winged Warbler will be a very rare species, if not extinct. Two other, more optimistic possibilities exist. Pure Golden-wings may persist only in small, high altitude or high latitude refuges that Blue-wings cannot colonize. Alternatively, stable coexistence of the two warblers may be possible but is not yet apparent. Conceivably, Golden-wings can persist as a rare

fugitive species, specialized at colonizing and using ephemeral pockets of early succession stage habitats. Hybridization, however, must be minimized to achieve such ecological stability.

If Blue-wings predictably replace Golden-wings in less than 50 yr, then it is unlikely that there is adequate evolutionary time for the reinforcement of premating isolating mechanisms, especially in such dynamic, unstable hybrid zones. Selection against hybridization does not seem severe (Short 1969b), and its consequences are unlikely to be apparent from the study of actively hybridizing populations, because any evolutionary consequences of hybridization *per se* will be further obscured by nongenetic behavioral changes (Gill and Murray 1972a, Murray and Gill 1976) and probably by frequency dependent phenomena.

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