Inception and Decline of an Allopatric Blue-winged Warbler Population in Central New Jersey

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ABSTRACT

We described 34 years, 1974-2008, of the inception and decline of a local Blue-winged Warbler (Vermivora cyanoptera*) population, its hybrids and variants (plumage intermediates of the hybrids) in central New Jersey. Using the Punnett Squares system, we tracked, in the absence of breeding Golden-winged Warblers* (V. chrysoptera)*, the contributions made by hybrids and subsequent variants to the observed plumage changes. High adult (up to 50%) and natal (8%) site fidelity and longevity (a record after nine years) implicated repeated contribution of introgressed and possibly cryptic genes to the local population. Through time these factors resulted in subtle but useful plumage indications of genetic introgression, namely yellow in the wing bars and the downward projecting spikes in the lores in front of the eyes, in an otherwise seemingly "pure" Blue-winged population. A pair of such individuals produced a hybrid, Lawrence's Warbler* "V. lawrencei".

INTRODUCTION

The Blue-winged Warbler *(Vermivora cyanoptera)* (Gill et al. 2001) and Golden-winged Warbler *(V. chrysoptera)* (Confer 1992) hybridize, producing hybrids resembling the parents, hybrids called the Brewster's Warbler (*"V. leucobronchialis"*) first described as a new species by Brewster (1874) in Massachusetts and the Lawrence's Warbler (*"V. lawrencei"*) first described as a new species by Herrick (1874) in New Jersey. Much debate followed as to the species status of these hybrids and their relationship with Blue-winged and Golden-winged warblers (Brewster 1881) until Nichols (1908) published a simple Mendelian model explaining their derivation. Parkes (1951), working with museum skins, expanded on that model. Later Parkes et al. (1991), and Shapiro (2005) explained the hybridization system to the birding world.

Intense studies in northern New Jersey (e.g., DeFalco and Dey 2003, 2005) and elsewhere (e.g., Gill et al. 2001, Confer et al. 2003, Shapiro et al. 2004, Dabrowski et al. 2005, Leichty and Grier 2006, Vallender et al. 2007, Buehler et al. 2007) on habitat loss, hybridization and severe decline of the Golden-winged Warbler have often overlooked the consequential decline of the pure Blue-winged Warbler. Researchers (Buehler et al. 2007) recognized the need to document Blue-winged Warbler populations across their entire range in northeastern and north-central North America and the long-term implications of bi-directional genetic introgression by hybridization.

Studies of Blue-winged Warblers and their hybrids with the Golden-winged Warbler are lacking in central New Jersey. The purpose of this paper is to document the rise and decline of a local, allopatric Blue-winged Warbler population in central New Jersey that appeared phenotypically pure Blue-winged at its inception in 1974 (Suthers 1987) and that appeared entirely but subtly phenotypically introgressed by its 34th year in 2008.

History of occurrence in New Jersey - Babson (1901) noted a rare Blue-winged Warbler breeding in Princeton Township, central New Jersey, and noted the Golden-winged Warbler only as a rare migrant. Short (1963) found the Blue-winged common in parts of New Jersey. Leck (1975) listed the Blue-winged Warbler as a common summer breeder. The New Jersey breeding bird atlas of 1991-1995 (Walsh et al.1999) indicated Blue-winged Warblers nesting in 98% of blocks in the Highlands, and 80% of blocks north of the Coastal Plain. Over 98% of the Golden-winged Warbler range in New Jersey was in the Highlands. Frech and Confer (1987), Confer and Larken (1998), and Confer and

Tupper (2000) worked in Sterling Forest State Park at the New York state and New Jersey border, where the two species have coexisted for a century (Eaton 1914). Scully (1999) surveyed both species in the Pequannock Watershed in north-central New Jersey.

The 1971 National Audubon Watch List of regionally declining birds listed the Blue-winged Warbler, mainly due to habitat loss by old field succession and human development. The 2004 New Jersey Audubon Important Bird and Birding Areas Program made an estimate of the New Jersey Blue-winged Warbler population at 8,163 individuals in the entire state, and the Golden-winged Warbler population at 170 individuals, calculated by the Cornell Laboratory of Ornithology and the U.S. Fish and Wildlife Service, based on Breeding Bird Survey data for New Jersey (Rosenberg 2004). In 2007, the National Audubon Watch List listed the Blue-winged as rare. The 1996-2010 North American Breeding Bird Survey by the U.S. Geological Survey, Patuxent Wildlife Research Center, found the Blue-winged Warbler to be declining 4.6% annually in the southern part of its total range (Sauer et al. 2011). Conservationists were concerned that if the warblers declined below a sustainable population they could go extinct.

METHODS

Study Area - This study was conducted at Featherbed Lane Bird Banding and Research Station in Sommer Park Preserve, a 43-ha former dairy farm in Hopewell, Mercer County, New Jersey (40° 24" 47' N, 0740° 46" 19' W) in the Sourland Mountains piedmont physiographic province of central New Jersey. At inception, the fields in this study were one 1.6-ha grassy meadow (GM) newly plowed, one 1.8-ha field 10 yr into succession (F10), four, 6.5-ha fields at 20 yr (F1-F4), and one 2.3-ha pasture at 40 yr (F40). Suthers made vegetation surveys according to James and Shugart (1970) from 1977 to 1988 (Suthers 1987), then according to Monitoring Avian Productivity and Survivorship (MAPS) protocol (Nott et al. 2003) from 1989 to present (Suthers et al. 2000). From 1998 forward, F2 and F10 field were managed by cutting or girdling saplings to remain at the shrubland stage with sparse saplings, and GM was managed by periodic mowing to remain as a meadow with a few fruiting shrubs and saplings.

Singing Male Spot-mapping.- Suthers mapped singing males on territory weekly during each breeding season since 1977 to supplement banding data. Grasser, who joined the project in 2007, called in singing males by playing songs on a hand-held birdsong player and looked for variation in plumage. He monitored a pair of introgressed (with Golden-winged genes) Blue-winged Warblers with a Lawrence's Warbler fledgling.

Mist Netting and Banding.- Suthers and crew started mist-netting birds in 1978 with 12 nets rotating through F10, F3, and F40 from daybreak for 5 hr, May through Jul, then staying in F2 in Aug, totaling ~ 1,080 net hr/yr (Suthers 1987). Since 1989, we added nets to follow the birds to more open microhabitats. We combined these nets together with the overgrown original nets into three sets of 20, 22, and 33 nets, operated each set in a three-week rotation five times from late-May (date according to MAPS protocol) through Aug, from daybreak for 5 hr, totaling 2,025 net hr/yr. Nets were checked every 20-30 min and captured birds were held in individual drawstring cloth bags until processed. Birds were banded with USGS serially numbered leg bands. Data were taken on age to document local productivity; wing and tail length for possible sex indication and possible hybrid (Short 1963) indication; sex by plumage, cloacal protuberance or brood patch, and breeding condition to determine local breeders; weight, fat and molt to help separate local birds from passage migrants. Crew members photographed hybrids and their variants with intermediate plumages for later analysis.

Pair and Family Determination - A male and female observed together and mist netted in breeding condition on the singing male's territory were assumed to be a pair. A male or female or both caught together on territory with dependent fledglings were assumed to be a family. Young fledglings caught together were considered siblings.

Plumage Scores - Using color photographs of bird-in-hand taken during banding, we scored the plumages of the hybrids and variants according to the Hybrid Indices of Short (1963) and Gill (1980).

Punnett Squares Analysis - Following Parkes' (1951) analysis, based on Nichols (1908), of Mendelian inheritance and Punnett Squares, we tracked theoretically the genetics of the phenotypes observed in the field. We used Parkes' symbol W for the dominant gene for white underparts, w for the recessive gene for yellow underparts; S for the dominant gene for a single yellow wing patch, s for the recessive gene for double white wing bars; P for the dominant plain throat, p for the recessive patterned throat. Thus, the Blue-winged Warbler is wwssPP, the Golden-winged Warbler is WWSSpp, the first generation Brewster's Warbler is WwSsPp, and the Lawrence's Warbler is wwsspp. Based on our observations of the variants of subsequent generations, we considered that perhaps the eyeline and throat patterns were not closely linked and that the variations in the eyeline were indeed valuable indicators of introgression. S. P. Graesser designated EE for the dominant narrow eyeline, and ee for the recessive expanded eyeline. Likewise, he designated CC for gold in the wing patch, and cc for white, respectively. Cc would be white with yellow tips. We used computer generated Punnett Squares by Chang Bioscience Inc. (2002-2004), and statistical analyses by Abacus Concepts (1991).

Museum Skins - To put our Blue-winged Warbler population and its hybrids in historical perspective with other Blue-winged Warblers collected from New Jersey and more southerly breeding ranges, Suthers examined specimens at Princeton University, NJ, and at the Smithsonian Museum in Washington, DC.

RESULTS

Spot-mapping Singing Males - Suthers listed birds on Featherbed Lane starting in 1969, spot-mapped the first territorial Blue-winged male in open shrubland in 1974 (Table 1), seven males by 1977 and 54 by 1992. They noticeably declined by 1996 (Table 1) as three of the four 6.5-ha fields allowed to succeed to second growth forest were shading out the shrubs. In 2008, eight territories remained on the remaining10 ha managed as shrubland with trees. Singing males in 1980 with atypical Blue-winged songs appeared to be introgressed Blue-winged Warblers, indicated by yellow-tipped or gold wing bars (Short 1963, Gill 1980). An adult male Golden-winged Warbler with yellow in the upper breast indicating introgression (Vallender et al. 2007) was singing on 25 May 2008 but was not seen again. There was no evidence of Golden-winged Warblers breeding at the site.

Banding Results - Table 1 shows the population size of banded birds, the same-year repeats, and the returns from previous years, from 1978-2008, and demonstrates the relative numbers of individuals by each age and sex group that contributed to the observed phenotypes. Adult males outnumbered adult females in every category. Captured together were 38 pairs; 13 families; 18 sets of fledgling(s) with male; 13 sets of fledgling(s) with female; and 11 sets of presumed sibling fledglings.

Table 1. Relative contribution of banded birds to the gene pool.

	New Banded	Same Year Repeats	Return Events	Total Encounters	Individuals Returning	Return Rate*
Adult Male	285	61	78	424	64	22%
HY Male	55	2	9	66	7	13%
Adult Female	97	14	26	137	18	18%
HY Female	47	0	1	48	1	2%
HY Sex Unknown	74	1	0	75	0	0%
Age and Sex Unkn	1	0	0	1	0	0%
Total	559	78	114	751	90	16%

* Return Rate is individuals returning divided by New Banded.

Table 2 shows the yearly proportions of phenotypes of the 559 birds banded in Hopewell, NJ, and the timing and pattern of their occurrences, including returns. A male heterozygous Golden-winged Warbler (Fig. 2) captured on 2 Sep 2001 and a hatch-year female Brewster's captured on 2 Sep 2002 were considered to be transients and therefore not included in the Table. However, it is not beyond possibility that they could have originated in our area.

Table 2. Yearly pattern of: 1) singing male census, banding and return encounters of the Blue-winged Warbler (BWWA) complex; 2) including banding and return encounters of BWWA Variants; and of 3) included banding (b) and return (r) encounters of the hybrids[Brewster's Warbler (BRWA), Lawrence's Warbler (LAWA) and Hybrid Variants] Fig. 1B, Fig. 1C.

Total	BWWA & Variants Encountered			BWWA Variants		Hybrids & Variants	
Year	Census	Band	Return	Male	Female	Male	Female
1974	1						
1977	7						
1978	12	0					
1979	24	19					
1980	32	29	0		1		
1981	43	34	4		1		
1982	24	52	3		1		
1983	43	33	5	1			
1984	46	25	4	2	3	b BRWA	b LAWA
1985	40	20	4			b LAWA	
1986	38	14	1				
1987	50	23	6	1	1		
1988	42	34	9	3	1		b BRWA(1B)
1989	49	43	14	8	1		r BRWA(1B)
1990	49	26	5	7	3	b LAWA(1C)	
1991	53	29	5	5	3		
1992	54	24	11	7	2		
1993	44	31	8	9	4		
1994	46	32	12	5	4	r LAWA(1C)	
1995	40	18	5	2	1		
1996	28	14	4	1			
1997	30	8	2	1			
1998	20	7	2	1			
1999	14	5	2	1	1		
2000	26	5	2				
2001	23	4	1				
2002	6	7	3				
2003	11	0	0				
2004	5	2	0				
2005	10	7	0	1	1		
2006	6	3	1	1	6		
2007	10	5	0	2	3		
2008	8	6	1	6	1	b LAWA	
TOTALS	934	559	114	64	38	5	3

(View pictures below in color at http://www.frontiernet.net/~bpbird/NABBpg141)

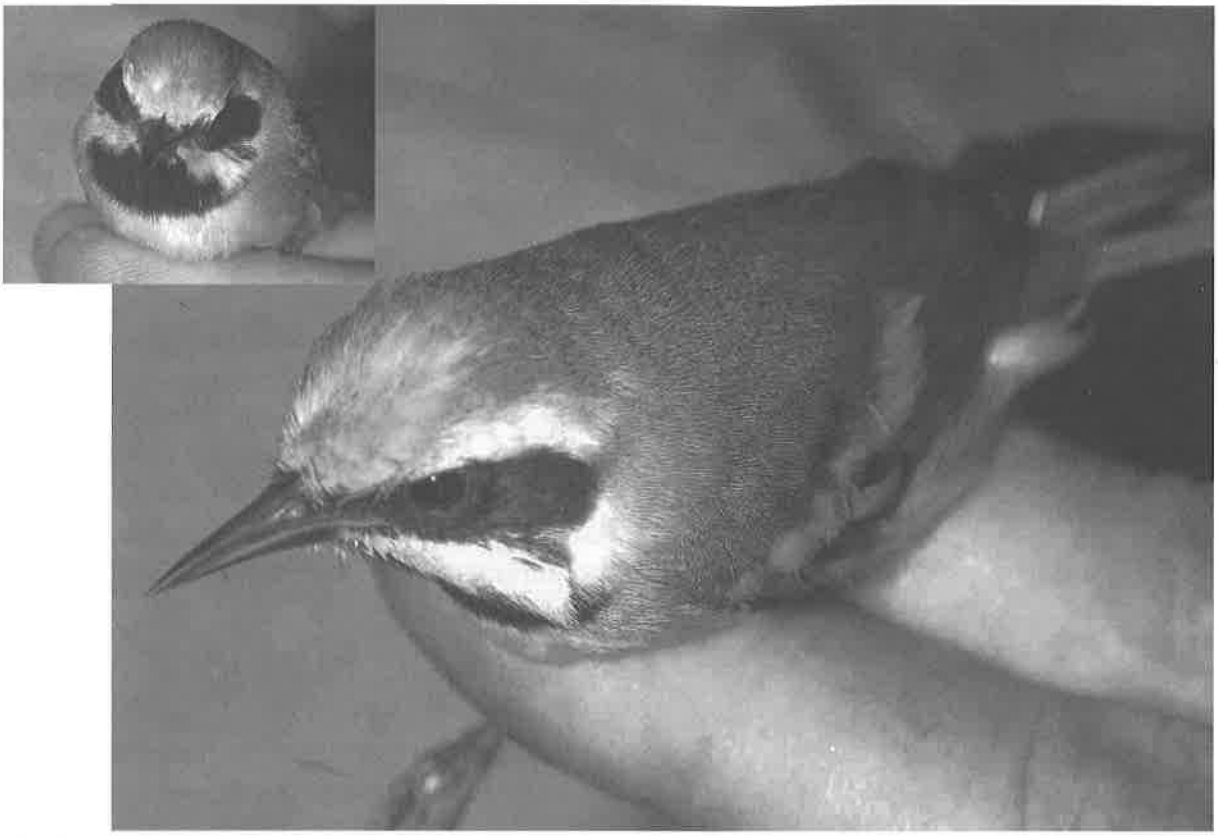

Fig. 2. Possible introgressed Golden-winged Warbler migrant of 2 Sep 2001. Indicators are the yellow wash in the breast and the fore-supercilium cut off by the gold crown meeting the lores.

Natal Philopatry - Eight known-sex fledglings, seven males out of 55 banded, 12.7%, and one female out of 47 banded, 2%, or eight of 176 fledglings including unknown sex, 4.5%, returned to the natal site to breed, in contrast to no known returns to natal sites for breeding reported by Gill et al. (2001) in his referenced sites. This natal philopatry occurred in the context of natal philopatry of 215 birds of 11other species of temperate and Neotropical migrants in our study area (Suthers 1987 and Suthers unpublished). Perhaps because of succession and rapid housing development in the surrounding townships, the birds had nowhere else to go (Suthers 1987, Suthers et al. 2000, Banisch Assoc. Inc. et al. 2010).

Adult Philopatry - Returns up to five breeding seasons by 64 of 285 individual adult males (22%), by 18 of 97 individual adult females (18%) gave an overall return rate of 21%. Yearly returns ranged from none in 1980 to a peak of 50% in 2002 (Table 2) compared to 24%-60% male return rates reported by Gill et al. (2001) from shorter studies in southern West Virginia, northcentral New York state, Ohio, and central Michigan. One male (after-nine-years) returned five times, seven returned three times, 14 returned twice, the others once. Most females returned once, two females returned twice, and four returned three times, suggesting site tenacity and contribution to the gene pool as long as they lived (after-seven-years) or got caught, though females are thought to be the dispersers (Gill 1997, 2004, Greenwood and Harvey 1982). Furthermore, we observed two cases of mate fidelity where pairs of Blue-winged Warblers banded together were caught together again the next year.

The multiple-returning individuals attained the ages of after-nine-years (one bird), after-seven-years (three), after-six-years (six), six years (two), after-five-years (nine), five years (one), after-four-years (nine), after-three-years (23), and after-second-year (58). The returning individuals had variations of wide wing bars and degrees of yellow tips, and

spiked lores. They contributed to this phenotype repeatedly together with 81 similar phenotypically introgressed new birds until only that phenotype was seen by the end of the study.

Hybrids and Variants - Two hybrids appeared on our site without the presence of breeding Golden-winged Warblers. We banded the first adult breeding male Brewster's Warbler on 26 May 1984. He varied from both first generation (F_1) cross and first backcrossed hybrids by having white wing bars with yellow tips. We also banded a breeding female Lawrence's Warbler on 3 Jun 1984 and a breeding male Lawrence's Warbler on 19 May 1985. These three hybrids, as new birds and returns, paired with Blue-winged Warblers. Rare variant plumages followed (Fig. 1). Plumages changed through the years to the return of the Blue-winged phenotype with subtle indications of introgression, described below. We banded three distinguishable plumage phenotypes (Parkes' Form 1-3) of introgressed Blue-winged Warblers (our h1-h3), and assigned best-fit genotype designations (Table 3), and the most likely parentage on site of these observed types. Table 2 shows how these variants clustered around each occurrence of banded Brewster's and Lawrence's hybrids. Twenty-six banded phenotypically 'pure' Blue-wings paired with banded 'pure' Blue-wings, eight 'pure' Blue-wings paired with introgressed Blue-wings, and four introgressed Blue-wings paired with introgressed Blue-wings. An introgressed female, banded on 1 Jul 2007 and recaptured 29 Jun 2008, paired with an introgressed male, banded on 29 Jun 2008, and produced a Lawrence's Warbler fledgling captured on 29 Jun 2008 with parents and recaptured on 13 Jul 2008.

Spiked Lores and Yellow Tips - Spiked lores, first described here by us, are downward pointed expansions of the dark lores in front of the eyes. Strongly spiked lores appeared in the 1984 introgressed female Blue-winged variant (Fig. 1A) and in a 1995 introgressed male Blue-winged variant. Small spikes, a subtle indication of introgression, occurred in all newly banded Blue-wings and fledglings of 2007 and 2008 (Fig.1D).

Yellow tips to white wing bars appeared sparsely at first in both males and females, starting with a female banded on 26 Jul 1980, then increased through the years until all new birds banded in 2007 and 2008 had this subtle indication of introgression (Fig. 1D). The parents of the above Lawrence's had both spikes and yellow tips.

Wing and Tail Measurements - We had hoped that wing and tail measurements would help indicate introgression, Golden-winged Warblers being larger (Short 1963, Confer 1992). But measurements of our phenotypically pure birds [Male wing 60 mm ±1.47 mm SD (45 birds), tail 45 ±2.12 mm (45), female wing 56 ±1.53 mm (26), tail 43 ±1.85 mm (26)] overlapped with our introgressed birds. Wing measurements concurred with Mulvihill et al. (2004) and Pyle (1997).

Plumage Scores - The scoring systems of Short (1963: table 1) and Gill (1980: modified Table 1) included wing bar color and width, color of underparts and upperparts, chin and throat. Both systems excluded the eye patch, transocular stripe, supercilium, lores and auricular area, because those characteristics were traditionally thought to be inherited together with the throat patch in the simple Mendelian manner (Nichols 1908, Parkes 1951) and, therefore, of little value in studying hybridization compared with studying characteristics controlled polygenically Short (1963). A pure Blue-winged Warbler phenotype scored 0 by Short (1963); it scored 0 color, 0 width by Gill(1980). A pure Golden-winged Warbler totaled 12 and 34, respectively.

Our hybrids scored as follows: Brewster's Warbler breeding male of 26 May 1984 scored Short 15+, and Gill 3, as a Golden-winged Warbler with strong Blue-winged Warbler influence. It had white wing bars with yellow tips and a touch of yellow in the white upper breast.

The three Lawrence's Warblers, breeding female of 3 Jun 1984, adult male of 19 May 1985, and hatch-year male of 29 Jun 2008 (recaptured 13 Jul 2008), scored Short 0 and Gill 22, as Blue-winged Warblers with the black throat and face patterns.

Fig. 1 A-D. Four hybrid variants resulting from crosses and backcrosses betwen introgressed Blue-winged Warblers and their hybrids.

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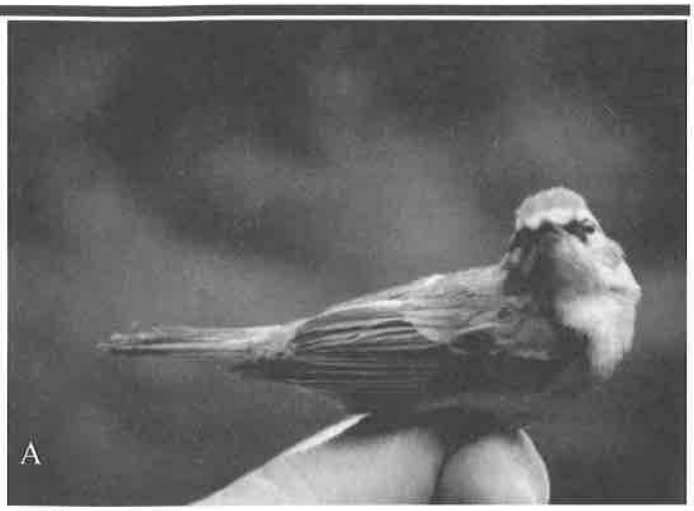
http://www.frontiernet.net/~bpbird/NABBpg143)



A. Rare introgressed Blue-winged Warbler breeding female of 17 Jun 1984 with large spiked lores and narrow white wing bars.

B. Rare Brewster's Warbler variant breeding female of 8 May (recaptured 4 Jun 1989 with nesting material) with trace of black in chin and throat, yellow wing bars, and yellow underparts with white mixed in sides.

C. Rare introgressed Blue-winged Warbler variant breeding male of 27 May 1990 (recaptured 12 Jun 1994) with black lower eye ring and partial ear patch and wide white wing bars with yellow tips.

D. Introgressed Blue-winged Warbler post-breeding male of 17 Aug 2008 with yellow tips to the white wing bars, eye arc (not always present), and widening of the lores into small downward pointing spikes in front of the eyes.

The male heterozygous Golden-winged Warbler of 2 Sep 2001 (Fig. 2) scored Short 11 and Gill 33, one point below the maximum because of the yellow in the upper breast.

Our variants scored between 0+ to 6 by Short, and 1 to 6 by Gill, as Blue-winged Warblers with slight to moderate Golden-winged Warbler influence. Our Blue-winged Warblers with yellow-tipped wing bars scored Short 0+ to 2, and Gill 1 to 3. See our Fig. 1A-C.

Punnett Squares Analysis - Our local population demonstrated what Parkes (1951) computed theoretically. At the time hybrids were thought not to interbreed (e.g., Moore 1916, Carter 1944) in Passaic Co., northern New Jersey. Then crossing and back-crossing of hybrids and of variants became well known (e.g., Parkes 1991, Parkes et al.1991, Allendorf et al. 2001, Vallender et al. 2007). We demonstrated with Punnett Squares how hybrids and variants in our population interbreeding with themselves, or crossing, or backcrossing with Blue-winged Warbler, could produce Brewster's Warbler, Lawrence's Warbler, and many variants, all in the absence of a breeding Golden-winged Warbler. Interbreeding variants also could recover Blue-winged Warbler and Golden-winged Warbler parental phenotypes (Table 3).

Four Blue-winged Warbler breeding males, three breeding females, and a fledgling, all with yellow wing bars, narrow eyeline, and plain throat are examples (wwSsPP) that derive from several of the above crossings or from backcrossing of a Brewster's with a Blue-winged (Table 3), without Parkes' (1951) postulated gene crossover. Our rare hybrid female (Fig. 1B) with narrow eyeline and trace of black in chin and throat was a variant that Parkes (1951:11-12) at the time was unaware of it.Subsequent workers observed broader and more continuous plumage variation (Shapiro et al. 2004 and unpublished data).

Our additional Punnet Square scheme for eyeline (EEee) concurred with (Parkes 1951) and our observations of our banded Blue-wings and the two hybrids, in showing an apparent correlation between a plain throat and narrow eyeline, and between a patterned throat and expanded eyeline. But the correlation breaks down in the variants in which the eyeline and throat seemed to behave independently, and the eyeline showed degrees of expansion. Another explanation would be that P, plain throat, is not completely dominant over p, and E, narrow eyeline, is not completely dominant over e, allowing for breakthrough of the plumage phenotype as seen in the trace of black in Fig. 1B, and the variation in the extent of the expanded eyeline in Fig.1A, C, D. Our scheme of wing patch gold or white colors (CCcc) explained the various combinations seen.

Museum Specimens (Princeton) - All adults, two females and a male from South Orange, NJ, of Jul 1896, showed yellow tips to white wing bars, and a male from South Orange of May 1897 had narrow white wing bars. Two females from Hopewell, NJ, Jun 1983 and May 1997, had olive tips on white median coverts, and a female near Princeton of May 1994 had narrow white wing bars.

Museum Specimens (Smithsonian) - Nine of 10 Blue-winged Warbler specimens at the Smithsonian dating from 1862 to 1969 had yellow tips on the white wing bars. The 1931 bird from Englewood, NJ, had not. The median and greater covert wing bars varied in width from 2 to 5 mm, and 2 to 7 mm, respectively. The 1907 Leona, NJ, and two 1915 Fort Lee, NJ, birds had wider wing bars and spiked lores, as did the 1878 Wabash County, IL, and the 1946 Port Tobaco, MD, birds. The 1878 Wabash County, IL, bird also showed black in the chin. The 1862 Verapaz, Coban, Guatemala, female showed an 8 mm long dusky wash on the chin.

An 1893 Brewster's from Morristown, NJ, and a 1920 Brewster's from Fort Lee, NJ, had white on olive or white on gray wing bars respectively, and yellow across the breast, much like our 1984 Brewster's. An 1885 Brewster's Warbler from Arlington, VA, and an 1895 Brewster's from Beltsville, MD, had wide wing bars with gold, like backcrossed birds. Lawrence's Warblers came from Fort Lee, NJ, in 1915, and from Plummer Island, MD, in 1907.

Table 3. Most likely origins of observed introgressed types (h1-h3) of Blue-winged Warblers (BWWA) and hybrids in the absence of breeding Golden-winged Warblers (GWWA). Brewster's Warbler (BRWA), Lawrence's Warbler (LAWA), HY (hatch-year), SY (second-year), F_1 (first generation). See text on plumage scores and Punnett Squares for complete descriptions.

Phenotype	Band Number	Date	Genotype	Plumage	Parental Types On Site	% Offspring
BWWA 'pure'	1550-140332	18 Jun 83 22 Jun 89	wwssPPEE	White wing bars, narrow eyeline	pure BWWA x pure BWWA h1 BWWA x BWWA F_1 BRWA x BWWA	100 50 1.25
h1 BWWA (h Type 1)	1550-14226	26 Jul 80	wwSsPPEE	White bars with yellow tips, narrow eyeline	h1 BWWA x BWWA F_1 BRWA x BWWA	50 12.5
Parkes' Crossover	2110-41780 Return	12 Jun 05 11 Jun 06	wwSsPPEE	Yellowish bars, narrow eyeline	Crossover BRWAxBWWA	rare
h2BWWA (h Type 2)	1960-14399 Return	18 Jun 95 25 May 97	wwSsPpEe	Wide white and gold bars wide spiked lores	F_1 BRWA x BWWA	12.5
(h Type 2) Fig. 1D	All banded birds	2007-2008	wwSsPpEe	White bars with yellow tips small spikes in lores	h2 BWWA x h2 BWWA h2 BWWA x BWWA F_1 BRWA x BWWA	25 25 12.5
h3BWWA (h Type 3, rare) Fig. 1A	1660-11301	17 Jun 84	wwssPpEe	White bars, large spiked lores	LAWA x BWWA h2 BWWA x BWWA F_1 BRWA x BWWA	100 25 12.5
F_1 BRWA	1660-11280	26 May 84	WwSsPpEe	Yellow in breast, white bars narrow eyeline	BWWA x F_1 BRWA	12.5
Rare BRWA variant, Fig. 1B	1720-70574 Return	8 May 88 4 Jun 89		Yellow, white in sides, gold bars, black line in throat, chin		
F_1 BRWA HY plumage	2110-41616	2 Sep 02	WwSsPpEe	Olive, yellow below, bars buff broken eyering, narrow eyeline	BWWA x F_1 BRWA	12.5
LAWA	1660-11289	3 Jun 84	wwssppee	White bars, black face and throat pattern	LAWA x h3 BWWA h3BWWA x h3 BWWA	50 25
LAWA	1660-11648	19 May 85	wwssppee	White bars, black face, throat, Yellow chin = SY	F_1 BRWA x h1 BWWA h2 BWWA x h2 BWWA	6.25 6.25
Rare LAWA variant, Fig. 1C	1780-16611	27 May 90	wwssppEe	White bars yellow tips, eye-line around eyes, auriculars		
LAWA	2230-36753	29 Jun 08	wwssppee	White wing bars, black face and throat pattern	h2BWWA 2390-16007 ♀ x h2 BWWA 2230-36752 ♂	6.25
Introgressed GWWA	2110-41536	2 Sep 01	WwSsppee	Yellow in breast, gold patch eyebrow ends front of eye	F_1 BRWA x h3 BWWA	6.25

Four Smithsonian specimens of Golden-winged Warblers show the yellow crown meeting the black lores in front of the eye, cutting off the white fore-supercilium. One 1890 bird was from Washington, DC, and the 1954, 1955 and 1964 birds were from Panama. Eleven Smithsonian Golden-winged Warbler specimens show the white supercilium continuing and narrowing over the lores to the maxilla. Three 1890-1901 birds were from West Point, NY, one 1893 bird from Bedford, MA. A 1955 bird came from Glenwood, IL, and a 1999 bird from Bath Co., VA. Five 1954-1970 birds came from Panama and Dominican Republic.

DISCUSSION

Punnett Square analysis of observed phenotypes is overly simplified in view of current molecular analysis. The Punnett Square schemes seemed to work, but in light of all that is known now about nuclear and mitochondrial DNA exchanges (Shapiro et al. 2004, Vallender et al. 2007) and of observed phenotypes, the inability of Punnett Squares to indicate quantitative inheritance remains. For example, a first generation (F1) Brewster's selfing, WwSsPp x WwSsPp, generates 27 possible Punnett Square combinations. Which combination would best fit the phenotype that we are seeing? Subtle plumage phenotypes, yellow tipped wing bars and spiked lores may be useful in the field as indicators that introgression may have occurred and are worthy of explicit testing in a molecular-genetics laboratory. As Vallender et al. (2009) suggested, studies including nuclear DNA, inherited from both parents, may make it possible to identify cryptic hybrids that screening by mitochondrial DNA, inherited from the female only, may miss; unless it is possible to see phenotypic differences without genetic differentiation at nuclear loci.

Our population may already have been introgressed from its inception and certain phenotypes may be increasing by inbreeding as the high return rate and multiple-return rate of individuals up to after-nine-years of age reduce the gene flow. An alternate hypothesis is that a southern plumage variation of Blue-winged Warblers with yellow tips and edges to the white wing bars Gill (1987) and Gill et al. (2001) has expanded northward. But Gill's (1980) five phases of replacement of Golden-wing phenotype by Blue-winged in eastern central Pennsylvania describes Stage V as Blue-winged with some variability in wing-bar color and an occasional Lawrence's phenotype. Evidence that these attributes may indicate introgression in our allopatric population was seen in the long-term increase of individuals with yellow tips, and spiked lores, and in the appearance of a Lawrence's offspring in 2008 from such a pairing of Blue-wings (Tables 2, 3). The spiked lores may indicate remnant Golden-winged ancestry in Blue-winged Warblers and may provide a useful plumage indicator of introgression that has been overlooked previously.

Likewise, the phenotypic plumage variation seen in the male Golden-winged Warbler banded on 2 Sep 2001 (Fig. 2) may deserve further exploration in a genetics laboratory. Phenotypically his yellow crown patch extended downward through the supraloral area, cutting off the white fore- supercilium, as seen across age and sex in four Smithsonian specimens (see Dunn and Garrett 1997, Sibley 2000 for topography). This head plumage is a variation of the typical phenotype (Dwight 1900, Roberts 1932, Bent 1953, Parkes 1991, Sibley 2000, Shapiro 2005) of the white supercilium extending broadly over the lores to the maxilla, as seen in 11 Smithsonian specimens. The variant may indicate heterozygosity or integration with Blue-winged (SPG pers. com. at Powdermill 2009, Powdermill Pictorial Highlights 2009). Depending upon the warbler's mates, other plumage phenotypes can emerge (Punnett Squares Analyses, Parkes 1951, 1991). The overlooked supercilium and lores in these two species may have a story to tell.

CONSERVATION IMPLICATIONS

Blue-winged Warblers are declining rapidly in some parts of their range partly because of loss of successional habitat (Hunter et al. 2001), as seen in New Jersey (Suthers 1987, Suthers et.al 2000, Banisch Assoc. Inc. et al. 2010). It seems that 'pure' Blue-winged Warblers also face genetic extinction

through hybridization, and that a new form of the two species is in the making, or is reverting back to their common ancestor, evolution happening before our eyes. The two species are similar genetically with cryptic hybrids in most populations throughout the breeding range so that plumage phenotypes of each can be recovered in cycles of interbreeding hybrids and variants. The best conservation of both species in parental plumage phenotypes may be by maintenance of the preferred habitat of each (e.g., Hunter et al. 2001, Buehler et al. 2007, Confer et al. 2010),where there may be pure or near pure genetic remnants, both on their breeding and wintering grounds. We can only hope that our second-chance attempts to reverse anthropocentric damage are well informed and valid.

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