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OVERVIEW

SECONDARY CONTACT AND INTROGRESSION OF GOLDEN-WINGED WARBLERS (*VERMIVORA CHRYSOPTERA*): DOCUMENTING THE MECHANISM

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ANTHROPOGENIC INFLUENCES ON the ranges of species are among the dominant ecological events of our time. Many range changes, such as the global use of a few crop plants, are so ubiquitous that they often escape conscious assessment. Other pervasive changes caused by humans include introduction of invasive plants and predators. Indirect effects include habitat change and global warming, which facilitate secondary contact, the topic of this overview.

Ecological interactions that result from range changes raise environmental concerns, especially with regard to biodiversity. At the same time, secondary contact may enhance detection of ecological concepts by revitalizing the ghosts of competition and evolution. The impetus for this overview is an experimental study related to secondary contact and hybridization between Golden-winged Warblers (*Vermivora chrysoptera*) and Blue-winged Warblers (*V. pinus*) by Leichty and Grier (2006). This study is particularly interesting because it provides a mechanistic explanation for extirpation that may be relevant to many instances of secondary contact and because the results may improve management of this species complex.

Secondary contact between these shrubland species occurs in the footprint of the deciduous forest biome of eastern North America. Clearing of forests, followed by farmland abandonment and reforestation, started in New England and moved west and northwest across much of eastern North America (Litvaitis 2003a). Regionally synchronized patterns of land use initially

allowed grassland species to expand eastward. Subsequently, abandoned farmland supported an abundance of shrubland species. Among the shrubland beneficiaries, Golden-winged Warblers first expanded into the Northeast in the late 1800s (Gill 1980) and were widespread by the middle of the 20th century.

Reforestation, draining of beaver (*Castor canadensis*) wetlands, and urban expansion are major contributors to the decline of disturbance ecosystems, perhaps to below precolonial levels, which has produced dramatic decreases in almost all species of disturbance ecosystems (Sauer et al. 2005) and threatens their extirpation and even extinction (Litvaitis 2003b, Confer and Pascoe 2003). Even as Golden-winged Warblers continue to expand into the northern portions of the north-central states and adjacent Canada, they have declined at an estimated 8.6% yearly in the Northeast for the 40 years of the Breeding Bird Survey (Sauer et al. 2005). Extirpation has occurred in the Northeast even where utilities maintain shrublands dominated by herbs with patches of shrubs on their rights-of-ways (ROW). Both Golden-winged and Blue-winged warblers use very similar habitats in uplands, with territories that frequently overlap. In the Northeast, Blue-winged Warblers are common on ROW (Confer and Pascoe 2003). This suggests that much of the tens of thousands of hectares of shrublands on ROW provide a vegetative structure suitable for Golden-winged Warblers, even in areas where they are rapidly declining or have been extirpated. Habitat loss accounts for most of the decline in shrubland species in the Northeast, but extirpation of Golden-winged Warblers from large portions of their range is inexplicable on the basis of habitat availability alone.

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Blue-winged Warblers were probably once restricted to the prairie–forest ecotone, but anthropogenic shrublands have enabled them to cross former habitat barriers and expand into much of the Golden-winged Warbler range. As first noted by Gill (1980), blue-winged intrusion is almost always followed by golden-wing extirpation within 50 years and sometimes within 20 years (Canterbury and Stover 1999). The rapid and virtually complete elimination of the golden-wing phenotype from almost all regions with Blue-winged Warblers and apparently suitable habitat is compelling evidence that Blue-winged Warblers cause the disappearance of Golden-winged Warblers.

The challenge of determining the causal mechanism of the replacement of the Golden-winged Warbler has lured many research workers. Blue-winged Warblers may dominate Golden-winged Warblers at some sites (Will 1986), but a larger sample from other sites showed dominance by Golden-winged Warblers (Confer and Larkin 1998). All studies of sympatric populations of Golden-winged and Blue-winged warblers document overlapping breeding territories and infrequent occurrence of interspecific aggression. Given their general mutual tolerance, it seems unlikely that the level of interference competition that occurs (Confer et al. 2003) is severe enough to eliminate virtually all golden-wing phenotypes within a few decades.

Hybrids are fairly common at the leading edge of blue-winged intrusion, typically constituting ~7% of territorial males (Gill et al. 2001). Selection against hybrid males was first recognized in central New York (Ficken and Ficken 1968). Subsequently, a survey in north-central New York documented 121 social pairings, which included 13 hybrid females but only 5 hybrid males (Confer and Larkin 1998), though many more hybrid males were present. In southern New York, territorial male hybrids ($n = 13$) for two years did not obtain mates (Confer and Tupper 2000). Sexual selection against hybrid males also appears to occur in West Virginia (P. A. Canterbury pers. comm.). Sexual selection against hybrid males would help maintain genetic isolation but would not explain directional genetic replacement, unless some additional factor had a greater effect on Golden-winged Warblers.

The sample of 121 social pairs in north-central New York also showed that 12 phenotypically

pure male Golden-winged Warblers paired with hybrid females, which may occur because female hybrids of the “Brewster’s” type are largely gray and closely resemble pure female Golden-winged Warblers. By contrast, none of the phenotypically pure male Blue-winged Warblers formed a social pair with a female hybrid, perhaps because female Blue-winged Warblers are largely yellow. In this region, male Golden-winged Warblers, much more so than male Blue-winged Warblers, diluted their genes by mating with hybrids. Subsequently, their hybrid male progeny had reduced fitness because of negative sexual selection. The asymmetry in pairing frequencies observed in these backcrosses will favor introgression of the ancestral Blue-winged Warbler (ABW) mitochondrial DNA (mtDNA) into birds of golden-wing, but not blue-wing, phenotype. Furthermore, male Blue-winged Warblers commonly pursue female Golden-winged Warblers of golden-wing \times golden-wing pairs more often than male Golden-winged Warblers pursue female Blue-winged Warblers of blue-wing \times blue-wing pairs. This suggests asymmetry in the frequency of extraspecies extrapair fertility—a possible avenue for research. Thus, phenotype replacement, pairing patterns, and inferences from male sexual aggression lead to the primary prediction that hybridization will cause directional introgression of blue-wing genes into Golden-winged Warblers.

Predictions and inferences based on phenotype studies have been examined by insightful molecular-DNA studies. Two ancestral haplotypes that strongly correlate with the phenotypes of the two species have been detected. Between haplotypes, the nucleotide sequence differs by 3.0–3.2% (Gill 1997) or 4.3–4.9% (Shapiro et al. 2004) or 4.5% (Dabrowski et al. 2005). Other pairs of taxa that represent clearly accepted biological species have similar values.

Introgression was first analyzed in a population in the northern Delaware River valley (Gill 1997) where Blue-winged Warblers were replacing Golden-winged Warblers. Results fit the primary prediction showing nearly complete introgression of ABW mtDNA into Golden-winged Warblers. At a nearby site in northeastern Pennsylvania at 1,200 m, segregated altitudinally from Blue-winged Warblers, 50% of a phenotypically pure Golden-winged Warbler population had ABW mtDNA. This startling

introgression of mtDNA that preceded phenotypic invasion led Gill (1997) to suggest that introgressed females with ABW mtDNA led the range expansion by Blue-winged Warblers.

Additional mtDNA studies were conducted by Shapiro et al. (2004). In northern Ohio, where Blue-winged Warblers had replaced Golden-winged Warblers decades earlier, the ancestral golden-wing (AGW) mtDNA was very rare, in accord with the primary prediction. However, results from West Virginia showed balanced introgression, which is not compatible with predictions based on the mating patterns and behaviors described above. In Michigan, at a site with nearly all golden-wing phenotypes, all of two Golden-winged Warblers and three hybrid males had the AGW mtDNA. Blue-winged Warblers are expanding northward in Michigan, and the absence of ABW mtDNA even in hybrids contrasts with Gill's (2004) observations and does not support his prediction that intrusion is led by advancing females.

Introgression was sampled in two other populations, each in different stages of secondary contact (Dabrowski et al. 2005). In the Hudson Highlands of southern New York, Golden-winged and Blue-winged warblers have coexisted for more than a century (Confer and Tupper 2000). After prolonged coexistence, 13 of 15 of the blue-wing phenotypes retained ABW mtDNA, whereas a lower proportion of golden-wing phenotypes, 16 of 28, retained AGW mtDNA. We do not know whether introgression has stabilized in this region, but the trend supports the primary prediction and raises doubts about continuing coexistence. This study also sampled a population at the leading edge of blue-winged intrusion in northeastern Ontario. Thirty-eight of 42 phenotypically pure Golden-winged Warblers and 11 of 12 hybrids had AGW mtDNA. There and in Michigan, intrusion by Blue-winged Warblers was not dominated by females carrying ABW mtDNA.

Analyses of mtDNA in populations in the Delaware River Valley, the Pocono Mountains, northern Ohio, southern New York, and northeastern Ontario, but not in West Virginia, support the primary prediction of directional introgression of ABW mtDNA into golden-wing phenotypes. Leitchy and Grier (2006) link these descriptive studies of pair frequencies to genetic documentation of introgression by providing an experimental test of the enabling behavior. Their simple experimental structure provides a mecha-

nistic explanation for directional introgression and provides insight about new issues.

Bleaching the black throat patch of male Golden-winged Warblers created genetically pure males that looked like hybrids. This experiment conducted with an allopatric, golden-wing population provides a mechanism to inquire into the reciprocal response between pure Golden-winged Warblers and hybrid-like males. Because it seems unlikely that the bleached males unilaterally changed their behavior by responding directly to bleaching or their own reduced pigmentation, it seems likely that the experiment reveals the response of pure but bleached golden-wing males to being treated as if they were hybrids.

Overall, only 1 of 11 bleached males but 6 of 10 control males obtained mates. The experimental results confirm the descriptive studies that show sexual selection against hybrids. In combination with the high frequency of matings of phenotypically pure male Golden-winged Warblers with hybrid females, the results document why golden-wing genes will be eliminated following secondary contact by sexual selection against their progeny.

Considering that the bleached birds were genetically pure, the results suggest new studies to examine why the hybrid phenotype leads to sexual selection. Perhaps other males are more aggressive toward hybrids, which is compatible with the observation that 9 of 11 males lost their territories and 6 of them were never relocated, whereas only 3 of 10 control males lost their territories. Or, perhaps females do not respond to hybrid-like males that may reduce the mating behavior of males who get no reinforcement, which is compatible with the observation that only one of four hybrid-like males that held territories obtained a mate.

Leitchy and Grier's (2006) results provide additional support that premating isolating mechanisms provide a major barrier to gene flow in birds (Remsen 2005); but in this case, plumage—not song—appears to be the signal. As Gill (2004) predicted, an energetic student has provided further insight about the social genetics of speciation and suggests conditions that must be avoided in conservation of the severely declining Golden-winged Warbler.

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