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OVERVIEW

BLUE-WINGED WARBLERS (*VERMIVORA PINUS*) VERSUS GOLDEN-WINGED WARBLERS (*V. CHRYSOPTERA*)

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HYBRID ZONES OFFER opportunities to study genetic and social architectures of speciation and biological diversification (Harrison 1993, Gill 1998). But hybrid zones vary greatly. Some may be bounded zones of hybrid superiority (Moore and Price 1993). Some shift location in response to asymmetries of selection or dispersal. Some are old and narrow continuing sinks of hybrid inferiority. Still others are new contacts in the early test phases of genetic and social confrontation that may be resolved through natural selection.

Mosaic hybrid zones are perhaps the most interesting and challenging of all speciation research opportunities. These are less “zones” than they are geographic arrays of local interactions between the same two species. The extent, pace, and pattern of introgressive hybridization can vary among localities that differ in details of the history of the contact, the ecology of the interface, the degree of isolation by distance or dispersal, and the roulette of genetic recombination. One of the best-studied cases of mosaic hybridization involves not birds but *Plethodon* salamanders of the Appalachian Mountains (Highton and Peabody 2000). Two species in particular, *P. jordani* and *P. glutinosus*, hybridize to varying extents at different locations, showing variable levels of reproductive isolation that reflect different histories and trajectories of their genetic contacts, and the inclusion of cryptic new species.

The classic case of mosaic hybridization in birds is that of Spotted Towhees (*Pipilo maculatus*) and Collared Towhees (*P. ocai*) in Mexico (Sibley 1954, Greenlaw 1996). The amount of introgressive hybridization and directions of gene flow differ among localities, including sympatric coexistence in Oaxaca without evidence of interbreeding. Most contacts are attributable to human alterations of habitat—some

old, others fairly recent, but none well documented. By contrast, in eastern North America, Blue-winged Warblers (*Vermivora pinus*) and Golden-winged Warblers (*V. chrysoptera*) exhibit a recent and well-documented time-based mosaic of secondary contact, hybridization, and replacement. A rich and deepening literature addresses their ecology, genetics, and species recognition behavior (Confer 1992, Gill et al. 2001).

Molecular studies confirm that *pinus* and *chrysoptera* are sister species that diverged ~1.5 mya, and that they are not specifically related to other *Vermivora* warblers (Lovette and Bermingham 2002, N. Klein and F. Gill unpubl. data). *Pinus* and *chrysoptera* differ by 3.0–3.2% in nucleotide composition of the mitochondrial (mt)DNA cytochrome-*b* gene (Gill 1997) and by 4.3–4.9% in the faster-evolving ND2 gene (Shapiro et al. 2004), but no nuclear gene markers have been identified to date.

Shapiro et al. (2004) add important new information. Their fresh genetic data challenge some previous hypotheses, including my own. More importantly, they deliver an expanded geographic and genetic perspective vital to the understanding and future prediction of real-time dynamics of transient hybridization and introgression in mosaic hybrid zones.

The published literature on these species goes back more than 240 years to their original descriptions by George Edwards (1760). Hybrids between the two were not reported until 1874, when the two principal hybrid phenotypes were described as new species—Brewster’s Warbler as *Helminthophaga leucobronchialis* (Brewster 1874) and Lawrence’s Warbler as *H. lawrencei* (Herrick 1874). There followed an extended debate as to their identity (e.g. Brewster 1881, Faxon 1911). Underlying that debate, we now know, was the dominant simple eye-line face pattern of *pinus* and Brewster’s Warbler versus the striking homozygous recessive black ear and throat patches of *chrysoptera* and Lawrence’s

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Warbler. Other plumage color differences, particularly amounts of yellow or green and white or gray, are controlled additively by multiple alleles (Parkes 1951).

The high historical profiles of *pinus* and *chrysoptera* and their hybrids, combined with growing ornithological interest, have produced strong documentation of local histories of contact and hybridization. The bottom line is that these warblers undergo a predictable pattern of introgression and replacement when they come into local secondary contact (Gill 1980, Confer 1992). Throughout the eastern United States in the last century, *pinus* repeatedly expanded its distribution northward, and locally upslope, into historically pure *chrysoptera* localities. The general pattern of developments following contact is predictable. Hybrid Brewster's (F1) phenotypes appear, followed by backcrossing and introgressed phenotypes, including the Lawrence's phenotype. *Pinus* phenotypes increase disproportionately. Within decades, *chrysoptera* phenotypes, even introgressed ones, are replaced by *pinus* phenotypes, both introgressed and seemingly pure. The pace of replacement, from initial contact through coexistence of diverse parental and hybrid phenotypes through conversion to *pinus* phenotypes, usually takes 20 to 50 years, but sometimes occurs in only 4 to 5 years.

In broad concert with the expansion of *pinus* populations, *chrysoptera* has declined rangewide from 1966 to 2003, with regional declines as high as 15–18% year⁻¹ (Sauer et al. 2004). General loss of suitable successional and old field habitats is a contributing factor, offset locally by positive responses to reclaimed strip-mine habitats in the Appalachians and by aspen regrowth in lumber clearcuts in the north. Conservation concerns about the future of *chrysoptera* have catalyzed a new wave of field studies (see Acknowledgments) with particular attention to management priorities and opportunities.

The fast pace of invasion of *chrysoptera* populations by *pinus* followed by introgressive hybridization and replacement should lead to a genetic footprint of *chrysoptera* genes in the *pinus* populations. The appearance of Lawrence's Warblers in seemingly pure *pinus* populations is probably attributable to that phenomenon, though local mutation and recombination could produce the same result. No footprint

of *chrysoptera* mtDNA, however, was evident in recently introgressed *pinus* populations in the Delaware River Valley of northeastern Pennsylvania (Gill 1997). Instead, and conversely, *pinus* mtDNA was well established in essentially pure *chrysoptera* phenotypes in an adjacent population uphill that was in the initial stages of contact. And most (eight of nine) of the (F1) Brewster phenotypes collected in the two populations had *pinus* mtDNA. To explain that asymmetry, I suggested that female *pinus* (the dispersing sex) drove the initial dynamics of hybridization as they dispersed (uphill) into *chrysoptera* populations, and that female F1 hybrids (Brewster's) preferentially backcrossed with male *chrysoptera*. My study, however, highlighted only one locality, raising the question of whether the phenomenon would prove to be more widespread or was a local phenomenon, real or artifactual.

Now, Shapiro et al. (2004) report the mtDNA compositions of a large sample of warblers from West Virginia, supplemented by data from Michigan. The West Virginia populations are in the initial stages of secondary contact and hybridization. In contrast to my findings in northern Pennsylvania, mtDNA introgresses symmetrically and reciprocally into both warbler species, with balanced proportions of *pinus* and *chrysoptera* mtDNA in F1 hybrids. Thus, my hypothesis of female-driven cytonuclear extinction of *chrysoptera* mtDNA is not broadly applicable to other locations. Different stages of contact history in Pennsylvania and West Virginia may be responsible for some of the differences. Alternatively, Shapiro et al. (2004) provide our first genetic indication of locality-specific dynamics, or a hybrid-zone mosaic. As in towhees and salamanders, *pinus* and *chrysoptera* coexist in at least one locality—Sterling Forest State Park in southern New York (Confer and Tupper 2000)—and perhaps others (Shapiro et al. 2004, R. Canterbury pers. comm.). Those warblers may be more similar from a speciation standpoint to the towhees of Mexico or the salamanders of the Appalachians than we have realized.

Some key features of the interactions between *pinus* and *chrysoptera* are established. First, *pinus* and *chrysoptera* typically maintain overlapping territories (Gill et al. 2001). That increases the potential for interspecific matings. Second, reproductive success of (upland) *chrysoptera*

drops in the presence of (unmated) *pinus* in West Virginia (R. Canterbury pers. comm.) and in upstate New York (Confer et al. 2003), but the specific reasons are not known. The literature is ambiguous as to whether one species is socially dominant to the other (see Gill et al. 2001). *Pinus* males, however, regularly harass *chrysoptera* pairs in the highlands of West Virginia (R. Canterbury pers. comm.).

With respect to hybridization, male Brewster's Warblers tend to be excluded from optimal territories and may be disadvantaged with respect to obtaining mates (Confer and Larkin 1998, Confer and Tupper 2000). Once paired, however, they appear fully fertile. Less is known about female hybrids, except that female Brewster's may backcross preferentially with male *chrysoptera* (Confer and Larkin 1998, see also Gill 1997). There is no evidence, pro or con, that female birds—the heterogametic sex—are more likely than males to exhibit negative effects of hybridization (i.e. Haldane's rule).

A recent study documented significant levels of extrapair fertilizations (EPFs) by *chrysoptera* and mixed parentage of young in their nests. Extrapair fertilizations affected the composition of 57% of nests (31 of 54) and accounted for 31% of the nestlings (76 of 240) in Ontario (Fraser et al. 2004 unpubl. data). Those revelations open up a critical new possibility, namely that EPFs may drive the observed levels and patterns of hybridization and directions of gene flow. Further, any biases in EPF dynamics that reflect social dominance or shifting proportions of *pinus* and *chrysoptera* as they progress through the local replacement dynamic should be expressed as asymmetries in the cytonuclear compositions of hybridizing populations. Local differences in that dynamic, especially during the initial stages of contact and hybridization, would define different genetic trajectories in a mosaic hybrid zone.

For the first time since the descriptions of Brewster's and Lawrence's warblers 130 years ago, we seem closer to deciphering the social and genetic architecture of hybridization between *pinus* and *chrysoptera*. Shapiro et al.'s (2004) new genetic data from West Virginia, combined with expanded studies of parentage and reproductive success in multiple populations, set the stage for identifying common essential elements of this time-dependent mosaic hybrid zone.

Our ability to explore alternative hybrid-zone dynamics is now empowered by genetic markers combined with theoretical models (see Barton and Gale 1993). Those models allow formal interpretation of phenotypic and genotypic interactions on the basis of transition curves from a transect of samples across a hybrid zone. Rohwer et al. (2001) have pioneered the application of such models to birds, specifically the hybrid zones of Hermit Warblers (*Dendroica occidentalis*) and Townsend's Warblers (*D. townsendi*) in the Pacific Northwest. Like *pinus* and *chrysoptera*, *occidentalis* and *townsendi* differ strikingly in their face color patterns that are controlled by one genetic locus with two alleles with simple dominance. Moreover, *townsendi*, the competitively superior, aggressive dominant, is steadily replacing *occidentalis* and has been doing so for thousands of years. The location of the hybrid zone moves steadily against the remaining *occidentalis* populations, producing a strong asymmetry in the phenotype transition curves. In contrast to the selective advantage of *townsendi* phenotypes and the behavioral disadvantage of hybrid phenotypes (which keeps the hybrid zone narrow), the broad mtDNA transition curves are symmetrical, as Shapiro et al. (2004) found for *pinus*–*chrysoptera* in West Virginia. The mtDNA haplotypes of the two Pacific northwestern species appear selectively neutral. In addition, there is a substantial genetic footprint of *occidentalis* mtDNA in the replacement *townsendi* populations, reflecting the “ghost” of the original Hermit Warbler range.

What then might be the future of *pinus* versus *chrysoptera*? My original suggestions (Gill 1980) still seem appropriate, namely that *chrysoptera* will be very rare toward the end of the century, perhaps persisting as a fugitive species in early-stage successional habitats, especially at higher elevations and latitudes, and perhaps in swamps. However, we can now better envision ways for *chrysoptera* to escape from Gaussian competitive exclusion. Considering, too, the teasing signs of coexistence in southern New York, Michigan, and West Virginia, it seems that *chrysoptera* will likely escape total replacement by advancing *pinus*.

As to the opportunities for future research, the best is yet to come. First, on the basis of Shapiro et al. (2004), we can hope to document the retention of cytonuclear hybrids as a genetic

footprint, and possibly the rate of their decay in replacement *pinus* populations. Second, we can really begin to study the reinforcement of species recognition behavior through genetic studies of parentage. Someday, an enterprising student will find critically needed, species-specific nuclear gene markers that will inform this behavioral research. And soon, the combination of intensive fieldwork with intensive molecular genetic lab work in multiple regions will allow deeper penetration of the social genetics of speciation. Expansion of simple cline models of hybrid zone dynamics to a new set of models appropriate to complex mosaic zones will then be possible.

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