

Hybrids of Golden-winged and Blue-winged Warblers

More Than Meets the

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Photography by Jim Zipp

My first Golden-winged Warbler was the last one I would see for a long time. As a teenage birder cutting my teeth in the magical birding wonderland of Central Park in New York City, I hurried across the Ramble one fine May morning to the enormous old oak where another birder had told me she'd just seen a Golden-wing.

There it was, buzzing its heart out, high in the sun-drenched upper reaches of the oak, mostly obscured by masses of golden oak catkins, but just barely visible. What a gem. Central Park would also introduce me to Brewster's Warbler, in the form of a male singing in a sapling at eye level in the Ramble. As my awareness of birds crystallized during my formative years in New York City and on eastern Long Island, the Blue-winged and Golden-winged Warblers established themselves as favorites. I was aware that Blue-wingeds and Golden-wingeds sometimes interbreed, producing the hybrid Brewster's and Lawrence's Warblers, but that was the extent of my knowledge of the matter. Years later, these birds would become a major focus of my attention as I tried to add my own small contribution to our understanding of the nature and significance of their interactions.

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Solving a Vexing Puzzle

Most readers of this article probably learned of the hybrid origin of Brewster's and Lawrence's Warblers early in their birding careers from a field guide or birding mentor, but at one time what is now received wisdom was grist for much colorful debate. The Blue-winged and Golden-winged Warblers (*Vermivora pinus* and *V. chrysoptera*) were formally described more than a century before the discovery of Brewster's and Lawrence's Warblers. The Blue-winged was initially confused with the Pine Warbler (hence the specific ep-



Litchfield County, Connecticut;
2 June 2004. © Jim Zipp.

Eye

ithet *pinus*), but its taxonomic status was later clarified by Alexander Wilson (see Gill et al. 2001). In 1874, William Brewster described a new warbler species, now known as Brewster's Warbler (and for some years known also as the White-throated Warbler), from a specimen collected in Newtonville, Massachusetts, in 1870. Also in 1874, Harold Herrick described another new warbler, Lawrence's Warbler, from a specimen collected on the Passaic River near Chatham, New Jersey. By 1881, Brewster suspected that both his and Herrick's species descriptions were in error and that the two forms were, in fact, hybrids between *pinus* and *chrysoptera*. He based this conclusion on a careful examination of specimens, observing that the characters defining Brewster's and Lawrence's Warblers were all "borrowed" from either *pinus* or *chrysoptera*, and that both new warblers were highly variable in plumage, with some intermediate specimens appearing to fall between *pinus* and either Brewster's or Lawrence's. Brewster also noted that nearly all known specimens of Brewster's and Lawrence's Warblers had been collected within an area in which both *pinus* and *chrysoptera* bred. In addition to arguing that they were not distinct species, Brewster further suggested that these hybrids could themselves backcross with parental types and possibly reproduce with each other.

Brewster's claim that these two rare warblers were being continuously generated through hybridization took some time to gain acceptance, particularly with respect to Brewster's Warbler, the status of which remained hotly debated into the twentieth century. The great ornithologist Robert Ridgway, for example, readily acknowledged that Lawrence's Warbler was the product of *pinus* × *chrysoptera* hybridization, based on its clear and supposedly consistent

Bethany, Connecticut;
30 May 2004. © Jim Zipp.



Despite striking differences in plumage between the **Blue-winged** (above) and **Golden-winged Warblers** (opposite), the two species are closely related and frequently hybridize. This article examines the complex nexus of genetics, environmental change, and population dynamics in the Blue-winged/Golden-winged complex, with particular emphasis on the consequences of hybridization and habitat change for Golden-winged Warbler population declines.



Picture yourself in the shoes of a nineteenth-century ornithologist. You come across this handsome adult male warbler, unknown to science. Clearly, it exhibits characters of the Golden-winged and Blue-winged Warblers. But it shows a white throat—a character exhibited by neither Golden-winged nor Blue-winged. What, exactly, is it? It took ornithologists decades to figure out for certain that most birds with this plumage, known today as **Brewster's Warblers**, are first-generation hybrids between Golden-winged and Blue-winged Warblers. Hamden, Connecticut; 29 May 2002. © Jim Zipp.

combination of plumage features from the putative parental species (Ridgway 1885). He forcefully argued, however, that Brewster's Warbler was a distinct species, basing this judgment on its pure white throat, which he found impossible to believe was the result of crossing between *pinus*, with its bright yellow throat, and *chrysoptera*, with its deep gray or black throat. Ridgway attributed the plumage variation seen among putative Brewster's Warblers to a failure to recognize these variant specimens as the hybrid progeny of Brewster's × *chrysoptera*, Brewster's × *pinus*, or Brewster's × Lawrence's matings. A short time later, Ridgway revised his opinion, now skeptical of both the hybrid origin of Lawrence's Warbler and the species status of Brewster's Warbler. Ridgway (1887) instead argued that these forms were simply color morphs of *chrysoptera* and *pinus*, respectively. With respect to Brewster's Warbler, at least, this new view was echoed by others (e.g., Bishop 1894, 1905; Thayer 1902).

A truly fantastical idea—from our twenty-first-century perspective, anyhow—was proposed in the journal *Science* by W. E. D. Scott (1905). In a misguided attempt to apply the theories of the plant geneticist Hugo DeVries, Scott argued that Brewster's and Lawrence's Warblers repeatedly appeared as spontaneous “mutants” of *pinus*, which would then back-cross with *pinus*, making *pinus* even more unstable

and increasing its tendency to spin off strange phenotypes. A scathing response to Scott's article immediately followed from J. A. Allen (1905), who made short shrift of Scott's arguments.

Although Brewster turned out to be right that both Brewster's and Lawrence's Warblers result from *pinus* × *chrysoptera* hybridization, his explanation of how hybridization could produce two such distinct forms was quite wrong when he asserted that the very different combinations of markings and colorings in the two hybrid forms were “unquestionably due to a reversal of the parents in each case” (Brewster 1881), i.e., that a hybrid cross would produce either Brewster's Warblers or Lawrence's Warblers depending on which parent was a Blue-winged and which was a Golden-winged. The true genetic explanation for the existence of two such different hybrid phenotypes would not be discovered for another quarter century.

It was not until 1908, just a few years after the re-discovery of Gregor Mendel's revolutionary work on inheritance in garden peas, that John T. Nichols, a young ichthyologist at the American Museum of Natural History, would publish a simple Mendelian model explaining the inheritance of plumage traits for parental *pinus* and *chrysoptera* and hybrid Brewster's Warblers (exhibiting genetically dominant characters) and Lawrence's Warblers (exhibiting recessive characters). This explanation later reached



Many hybrid pairings result in offspring that are sterile or otherwise debilitated. But that is not the case with the hybrid offspring between Golden-winged and Blue-winged Warblers, such as this adult male **Brewster's Warbler** in full song. The fact that Brewster's Warblers (and their progeny) are typically fertile raises numerous fascinating questions for bird biologists—or simply for those who want to try to put names on these complex and variable creatures. Litchfield County, Connecticut; 11 June 2004. © Jim Zipp.

a much broader audience when it was included, and graphically illustrated, in the classic *Audubon Bird Guide* by Richard Pough (1946). Nichols's analysis of the genetics underlying the genesis of Brewster's and Lawrence's Warblers represented a major advance; his model was further refined by Kenneth C. Parkes (1951), most importantly to better account for the coloration of Brewster's Warbler underparts actually seen in the field and in museum specimens.

Blue-winged and Golden-winged: One Species or Two?

Why have *pinus* and *chrysoptera* always been treated as distinct species? Some degree of hybridization is apparent everywhere they occur together. Hybrid males may have reduced pairing success (Canterbury et al. 1996, Confer and Tupper 2000); but when they mate, hybrids are fertile. So why not treat the two taxa as conspecific? This option has been consistently rejected, based mainly on the fact that despite widespread hybridization, *pinus* and *chrysoptera* seem for the most part to have maintained their distinct identities (Mayr 1942, 1963; Parkes 1951). This argument is sound, however, only if there is evidence of local, long-term coexistence (or ecological replacement with no indication of genetic fusion), which is surprisingly difficult to assess. The strongest justification for recognition of two species is probably genetic data showing that the mitochondrial DNA of *pinus* and *chrysoptera* differs by about 3–5% (Gill 1997; Shapiro et al. 2004), which is at the high end of the spectrum for uncontroversial avian sister species (Johnson and Cicero 2004) and implies a long period of genetic isolation. Just what constitutes a species, of course, has long been and still is a contentious question.

Early Investigations of *pinus* and *chrysoptera*

Although by 1908 Nichols had provided a convincing model to explain the occurrence of Brewster's and Lawrence's phenotypes, the status of Brewster's Warbler as the product of hybridization between *pinus* and *chrysoptera* was not confirmed by direct observation until nearly 40 years after its description. Walter Faxon (1911, 1913, 1917) monitored the breeding behavior of *pinus*, *chrysoptera*, and Brewster's Warblers in a swamp in Lexington, Massachusetts, and was the first to directly observe what others had inferred. Offspring phenotypes of Brewster's × *chrysoptera* and *pinus* × *chrysoptera* breeding pairs nicely matched the predictions of Nichols's model. (In genetics, a *phenotype* is the outward expression—in this case, the plumage—of the underlying *genotype*, which refers to the actual genes themselves.) The next half-century or so saw sporadic reports of matings among *pi-*



This bird clearly has Blue-winged and Golden-winged Warbler ancestry, but it is probably not a first-generation hybrid. The extensively white underparts suggest that it is a **backcross** between a first-generation Brewster's hybrid (which typically shows a yellow patch on its white underparts) and a Golden-winged Warbler. However, other crosses could also produce a bird with this appearance. Litchfield County, Connecticut; 4 June 2004. © Jim Zipp.

nus, *chrysoptera*, and their hybrids, but except for Parkes (1951) there were no focused studies of these intriguing birds.

In the 1960s, 1970s, and 1980s, several researchers carried out behavioral and ecological studies in areas with both *pinus* and *chrysoptera* (e.g., Gill and Lanyon 1964, Ficken and Ficken 1968a, Confer and Knapp 1977, Will 1986). It is difficult to glean broad conclusions from their work. For example, studies of *pinus-chrysoptera* behavior in different regions and ecological circumstances have reached different conclusions about the frequency, nature, and importance of aggressive interactions between the two species (e.g., Will 1986, Confer 1992, Confer and Larkin 1998, Gill et al. 2001). Similarly, descriptions of habitat use in different regions vary greatly (e.g., Parkes 1951, Short 1963, Will 1986, Confer 1992, Canterbury et al. 1996). The two species often maintain overlapping territories (e.g., Ficken and Ficken 1968b, Murray and Gill 1976, Confer and Knapp 1977, Frech and Confer 1987) and show a strong tendency to pair with their own kind (e.g., Confer and Larkin 1998); but when they mate with each other, their hybrid progeny are fertile. Despite intensive study, there is still no clear evidence of competition between the two.

Decline of the Golden-winged Warbler: Pattern and Explanation

The pattern of decline and replacement

The distribution of *pinus* and *chrysoptera* in the eastern Unit-



The stunning **Lawrence's Warbler**, another hybrid with Blue-winged and Golden-winged ancestry, exhibits key plumage characteristics that are recessive. It has been known for close to 100 years that plumage inheritance in the progeny of Golden-winged and Blue-winged Warblers follows basic Mendelian processes, but many details remain to be worked out. Bethany, Connecticut; 5 June 2000. © Jim Zipp.

ed States was aptly described by Brewster (1881) as “not strictly allopatric or sympatric”. More than a century later, Brewster’s statement still holds true. Although the distribution of *pinus* is, very roughly, more southern and western than that of *chrysoptera*, and *chrysoptera* often extends to higher elevations in the mountains, the actual distributions are very complex, with much overlap and local variation (see Dunn and Garrett 1997). They are also very dynamic. Both *pinus* and *chrysoptera* are shrubland specialists that experienced dramatic range expansions in the early twentieth century as desirable habitat was created by the early regrowth of cut-over forests and by the abandonment of tens of thousands of hectares of farmland (Gill 1980, Confer 1992, Gill et al. 2001). In recent decades, both *pinus* and *chrysoptera* have declined over much of the northeastern U.S. as their habitat has disappeared in the face of both urbanization and natural succession; *chrysoptera*, however, has experienced particularly precipitous declines in many areas (Sauer et al. 2004).

In 1980, Frank Gill published an analysis of changes in the frequencies of *pinus*, *chrysoptera*, and hybrid phenotypes through time, using all available published data and museum specimens for Connecticut, New York, Michigan, and Ohio. He documented an alarming and consistent pattern of *pinus*

expansion into areas where previously only *chrysoptera* had been present, followed by hybridization and subsequently by the disappearance of *chrysoptera* phenotypes within 50 years. In southern West Virginia, complete replacement has occurred within only five years of initial contact at some river valley sites (R.A. Canterbury, personal communication). Since the appearance of Gill’s paper, John Confer and others believe they have identified at least one area—Sterling Forest State Park in southern New York—where *pinus* and *chrysoptera* seem to have coexisted for at least a century (Frech and Confer 1987, Scully 1997, Confer et al. 1998, Confer and Tupper 2000). Long-term coexistence may prevail in some other areas as well, such as some upland sites in southern West Virginia (R.A. Canterbury, personal communication), but the basic pattern described by Gill appears to hold for most areas. Although the cause of the *chrysoptera* decline re-

mains uncertain, it has been associated in time and space with newly initiated contact with *pinus* resulting from an ongoing *pinus* expansion.

Possible causes of decline

Two phenomena are associated with the widespread decline of *chrysoptera*: a changing landscape and newly initiated contact with *pinus*. Whether either or both of these are actually causal associations remains uncertain. In western New York, Confer and Knapp (1981) found that *pinus* and *chrysoptera* used similar types of early successional breeding habitat, but that *pinus* used a broader temporal slice of early successional habitats. In addition to the very early successional habitats used by *chrysoptera*, *pinus* continued to use sites at far more advanced stages of succession as well. Confer and Knapp suggested that *chrysoptera* is a relative habitat specialist and *pinus* a relative generalist. Although this idea is appealing in its relative simplicity—and in that it implicitly suggests the testable hypothesis that local *pinus* declines should follow on the heels of local *chrysoptera* declines as habitat succession progresses—the generality of Confer and Knapp’s findings appears to be limited. Given the extensive overlap and apparent geographic variation in habitat preferences of *chrysoptera* and *pinus*, habitat succession can offer at best

only a partial explanation for the Golden-winged's troubles (e.g., Confer and Knapp 1981, Confer 1992). In fact, Confer and Knapp were very cautious in their original paper, emphasizing that their results applied to Tompkins County, New York, and that they believed that even in this region the apparent difference in habitat use by *pinus* and *chrysoptera* was only part of the story. However, because no other well-supported explanations for the relative changes in *pinus* and *chrysoptera* populations have been forthcoming, this one has received far more emphasis than is warranted by the data behind it.

The role of contact with *pinus* in the decline of *chrysoptera* remains unclear and has been difficult to study. It is likely that both *pinus* and *chrysoptera* were uncommon prior to European settlement, that they were “fugitive species” with small colonies blinking on and off across the landscape. In the pre-European era, however, *pinus* and *chrysoptera* may have been largely or entirely allopatric. The influential evolutionary biologist and ornithologist Ernst Mayr (1942, 1963) speculated that *pinus* and *chrysoptera* likely came into extensive contact only as a consequence of large-scale alteration of the landscape of eastern North America by Europeans, and that hybridization between them is thus a recent phenomenon. Other authors have also supported the idea that extensive hybridization between *pinus* and *chrysoptera* is recent. For example, Parkes (1951) pointed out that Brewster's and Lawrence's Warblers, which have frequently been observed since their discovery, were not recognized and described until 1874, despite intensive ornithological research in their core range in the 1700s and 1800s. And Gill et al. (2001) similarly note that ornithological pioneers Alexander Wilson and John James Audubon left no record of having ever encountered these hybrids. This general argument—that if these hybrids were as prevalent in the early nineteenth century as they are today, then we should expect to have seen them described far earlier than they were—was made at least as early as 1905 by W. E. D. Scott. However, Allen (1905) presented a detailed counter-argument questioning the significance of the fact that these forms were not recorded by early observers. He suggested that, given the low numbers and geographic habits of early collectors, they would likely not have encountered hybrids even if they were present in reasonable numbers. In any case, whether or not the true frequency of hybridization increased, subsequent to the discovery of

Brewster's and Lawrence's Warblers, additional records accumulated rapidly.

We still don't know what force or forces have driven the decline of *chrysoptera*. As discussed above, the evolving landscape itself, independent of the presence of *pinus*, may be an important factor in *chrysoptera*'s decline, as suitable breeding habitat has disappeared without replacement. However, recently initiated contact and hybridization with *pinus* could also be important in a variety of plausible scenarios (Shapiro et al. 2004). Most simply, if *pinus* becomes more locally abundant than *chrysoptera* for ecological reasons, *chrysoptera*'s woes could be secondarily exacerbated by genetic swamping. That is, a higher proportion of *chrysoptera* individuals might mate heterospecifically, leaving more progeny of mixed ancestry.

Molecular Genetic Markers: Dawn of a New Era?

In the mid-1980s, having successfully used plumage analysis to document the spatially and temporally replicated pattern of hybridization and eventual replacement of *chrysoptera* by *pinus*, Gill recognized that far greater insight into the genetic structure and dynamics of *pinus-chrysoptera* populations could be achieved with appropriate molecular genetic markers. These markers could be used to distinguish the genetic contributions of each species in individuals of mixed ancestry and in mixed populations. To look for species-specific markers for these two species, Gill first turned to enzyme



The genetic and ecological interactions between Golden-winged and Blue-winged Warblers are fascinating in their own right, but they take on special urgency in light of recent population declines in the former species. The “Golden-winged Warbler” pictured here shows conspicuous evidence of Blue-winged genes, but mixed ancestry is not always so obvious. The importance of “genetic swamping” of the Golden-winged by the Blue-winged is not yet clear. Litchfield, Connecticut; 13 June 2004. © Jim Zipp.



There is no box on the ABA Checklist for you to tick off this drop-dead gorgeous adult male **Lawrence's Warbler**. But that is no reason not to study, not to conserve, not to admire this beautiful bird and its close relatives. Bethany, Connecticut; 5 June 2000. © Jim Zipp.

electrophoresis, a technique for distinguishing variant forms of certain ubiquitous proteins (typically metabolic enzymes) that was widely used at the time for genetic analyses of animal and plant populations. To his disappointment, he found very little detectable genetic variation using this method, and what variation he found was not species-specific (Gill 1987). Undeterred, Gill waited for another useful molecular approach and eventually found it in the analysis of mitochondrial DNA (mtDNA), which has proven very useful in studies of the evolutionary relationships of animal populations and species. This time he was successful. He identified a battery of restriction enzymes (enzymes that cleave DNA at specific sequences, producing sets of fragments which may differ among populations or species) that could distinguish between *pinus* and *chrysoptera* mtDNA.

Gill then collected *pinus*, *chrysoptera*, and Brewster's phenotypes from two populations in Pennsylvania. Much to his surprise, he found *pinus* mtDNA not only in *pinus* and Brewster's phenotypes, but also in *chrysoptera* phenotypes; however, he found no *pinus* phenotypes—and just a single Brewster's phenotype—with *chrysoptera* mtDNA. In an actively hybridizing mixed population in the Delaware River valley

consisting of about two-thirds *pinus* phenotypes, 98% (40 of 41) of individuals sampled had *pinus* mtDNA, including all six *chrysoptera* phenotypes and 86% (6 of 7) of Brewster's phenotypes. In the second population, from upland regenerating clear-cuts in the nearby Pocono Mountains, no *pinus* phenotypes were seen, but 48% (10 of 21) of birds sampled (9 *chrysoptera* and the single Brewster's) nevertheless possessed *pinus* mtDNA.

Gill's results were unexpected and did not have an obvious explanation. Furthermore, it was not obvious what relevance his findings might have in explaining the replacement of *chrysoptera* by *pinus*. To investigate the generality of Gill's results and to establish a baseline for long-term genetic and ecological studies, I took on this problem as a post-doctoral project. I organized a collaboration to intensively sample a new study area in southern West Virginia. Southern West Virginia has breeding densities of *chrysoptera* that are among the highest known anywhere. It falls within the known historical distribution of *chrysoptera* and lies well east of the Ohio River drainage, a historical *pinus* stronghold. A recent arrival to southern West Virginia, *pinus* has moved across the Kanawha River Valley and through higher elevations in the Allegheny Plateau of West Virginia. My primary collaborator in this work, Ron Canterbury of Concord University in West Virginia, has been studying *chrysoptera* and *pinus* in this area for nearly 20 years and has pursued an active banding program here since 1993. Although *pinus* has been present in the Ohio and Kanawha River Valleys since at least the late 1950s, it was not observed in southern West Virginia until 1989 (Hall 1983, Canterbury 1990, Canterbury et al. 1993). Many West Virginia sites that now harbor *pinus* had none when monitoring first began in the late 1980s (Canterbury et al. 1993, Gill et al. 2001). Thus, this region offers an excellent opportunity for monitoring changes in warbler populations starting from an ecologically and genetically well documented first contact. In addition to our intensive sampling in West Virginia, we sampled smaller numbers of birds from several other areas (in Ohio and Michigan) that have experienced *pinus* invasions and *chrysoptera* declines, as well as several allopatric populations. Altogether, we collected data from 337 birds, including 222 from southern West Virginia.

Obtaining our samples was challenging. When we heard a singing bird, we would quickly set up a mist net and attempt to lure the singer into the net by playing a tape of a conspecific song. Occasionally, we were able to capture several individuals simultaneously, as others followed our target bird into the net, but more often each capture required hours of early morning scouting and luring. We banded and photographed each captured bird, recorded details of its plumage pattern, and took blood and feather samples. Back in the lab, we sequenced a selected small portion of the mitochondrial genome for each bird.

Results from our mtDNA analysis of mixed-species sites in southern West Virginia are clear (Shapiro et al. 2004). In sharp contrast to Gill's findings from Pennsylvania, we saw no indication of asymmetric introgression of mtDNA. In other words, we found *chrysoptera* mtDNA in birds with *pinus* phenotypes as often as we found *pinus* mtDNA in birds with *chrysoptera* phenotypes.

An interesting development was reported recently by Rachel Fraser, a graduate student at Queens University and a passionate *chrysoptera* enthusiast. Using microsatellite markers [see "California × Gambel's Quail Hybridization", pp. 246–247], Fraser analyzed the parentage of 240 nestlings in 54 *chrysoptera* nests. She found that 57% (31 of 54) of nests included nestlings that had not been sired by their putative father; overall, 32% (76 of 240) of nestlings were apparently the product of extra-pair fertilizations (R. Fraser, V.L. Friesen, and R.J. Robertson, unpublished data). Although this finding is perhaps unsurprising given the similarly high frequency of extra-pair fertilization in other warbler species (e.g., Stutchbury et al. 1997, Chuang et al. 1999, Byers et al. 2004), it opens up the exciting possibility of analyzing paternity patterns in mixed populations. Such a project would require labor-intensive nest finding and monitoring, as well as sampling of adult birds and their putative progeny, but the potential return on this investment is tremendous. Detailed information on extra-pair fertilization patterns could reveal how contact with *pinus* might play a direct role in the decline of *chrysoptera*, although less-variable nuclear DNA markers that are species-specific would still be essential to supplement species-specific mtDNA markers in analyzing the ancestry of birds in the population.

What Next?

The complexity of the *pinus-chrysoptera* system calls for a collaborative approach that integrates intensive behavioral and ecological field work with challenging lab work on a large geographic scale. One step in this direction is a project coordinated by the Cornell Lab of Ornithology's Citizen Science Program, the Golden-winged Warbler Atlas Project (GOWAP). The broad goal of GOWAP <www.birds.cornell.edu/gowap> is to determine the population status and habitat and area requirements of *pinus*, *chrysoptera*, and their hybrids over their entire range. GOWAP organizers hope to develop two detailed atlases: (1) a distribution map to identify areas with high concentrations of *chrysoptera* that could be targeted for preservation and management; and (2) a "hybrid index map" to indicate areas where *pinus* and *chrysoptera* may be coexisting with little hybridization.

On the laboratory front, success may hinge on finding the right molecular method for assessing genetic variation (not necessarily sequencing the DNA of specific genes) or checking

patterns of variation in the right genes (e.g., genes linked to the Z sex-chromosome, which for theoretical reasons are expected to change more quickly than many other nuclear genes).

Although captive-breeding experiments to tease apart details of plumage inheritance may not be practical, detailed documentation of the plumages, behavior, and reproductive success of naturally hybridizing *pinus*, *chrysoptera*, and hybrids and their offspring would be the next best thing, in conjunction with banding and feather and blood sampling for further analysis. It is likely that even with exquisite studies examining the relationship between plumage and genetic composition, many birds of mixed ancestry could not be recognized as such based only on plumage. And relying on songs may be equally problematic, since both *pinus* and *chrysoptera* songs may be delivered by *pinus*, *chrysoptera*, and hybrid singers. This raises the question—which I will not attempt to answer—of how birders might determine whether a particular bird is a Blue-winged, a Golden-winged, or a hybrid for purposes of listing.

The Blue-winged and Golden-winged Warblers—and, of course, their hybrids—have captured the imaginations of scientists and birders for centuries now. Their staggering beauty and lazy buzzing songs—the very essence of long, easy summer days—have endeared them to generations of birders. Ever since the first puzzling specimens of Brewster's and Lawrence's Warblers came to the attention of nineteenth-century ornithologists, these birds have presented a formidable challenge to scientists intent on understanding their ecology, behavior, and genetics. With the worrisome decline of the Golden-winged in recent decades, we can only hope that these research efforts yield answers quickly, before it is too late.

Acknowledgments

I thank Alexa Bely, Ron Canterbury, Ted Floyd, Rachel Fraser, Frank Gill, and Kevin Omland for their comments on earlier drafts of this article.

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