Predictable outcomes of warbler hybridization: Synthesis and an exceptional Yellow × Black-throated Blue Warbler (Setophaga petechia × S. caerulescens) pairing

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Predictable outcomes of warbler hybridization: Synthesis and an exceptional Yellow × Black-throated Blue Warbler (*Setophaga petechia* × *S. caerulescens*) pairing

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ABSTRACT—Hybridization can have profound effects on biological diversity. However, predictable inheritance of plumage traits remains poorly understood, especially for rare hybrids. We reviewed the literature and compiled a comprehensive list of hybrids from the New World warbler family Parulidae, a diverse radiation of songbirds with divergent plumage traits. We used our compilation to analyze modes of inheritance in wing bar patterns and carotenoid coloration. Finally, we describe an unusual hybrid from the University of New Mexico in Albuquerque, New Mexico, southwestern USA. We identified evidence of hybridization in 44 of 47 (93%) North American parulid species, with the highest number of hybrids found in the genus *Setophaga*. Plumage patterns between hybrid offspring and parental forms in our 2 focal traits were predictable, supporting the identification of our hybrid as a Yellow × Black-throated Blue Warbler (*S. petechia* × *S. caerulescens*). We based our identification on the extent and pattern of white in the tail, a prominent white wing flag, and our ability to confidently rule out all other alternative parentals. Our results suggest that phenotypes of rare hybrid warblers likely have some degree of predictability. *Received 5 March 2021. Accepted 12 June 2021.*

Key words: hybrid identification, hybridization, New World warbler, Parulidae, plumage, *Setophaga*.

Resultados predecibles de la hibridación de reinitas: síntesis y una pareja excepcional de *Setophaga petechia* × *S. caerulescens*

RESUMEN (Spanish)—La hibridación puede tener efectos profundos en la diversidad biológica. Sin embargo, la herencia predecible de los rasgos del plumaje es poco conocida, especialmente en el caso de los híbridos raros. Revisamos la literatura y recopilamos una lista completa de reinitas híbridos de la familia Parulidae, una radiación diversa de aves cantoras con rasgos de plumaje divergentes. Utilizamos nuestra compilación para analizar los modos de herencia en los patrones de las barras alares y la coloración carotenoide. Por último, describimos un híbrido inusual de la Universidad de Nuevo México en Albuquerque, Nuevo México, al suroeste de los Estados Unidos. Identificamos evidencia de hibridación en 44 de las 47 (93%) especies de parúlidos norteamericanos, siendo el mayor número de híbridos encontrados en el género *Setophaga*. Encontramos una herencia predecible de los patrones de plumaje entre la descendencia híbrida y las formas parentales en nuestros dos rasgos focales, lo que apoya la identificación de nuestro híbrido como una reinita amarilla × reinita azul y negra (*Setophaga petechia* × *S. caerulescens*). Basamos nuestra identificación en la extensión y el patrón de blanco en la cola, una prominente bandera de ala blanca y nuestra capacidad para descartar con seguridad todos los demás orígenes parentales alternativos. Nuestros resultados sugieren que los fenotipos de los parúlidos híbridos raros probablemente tienen un cierto grado de predictibilidad.

Palabras clave: hibridación, identificación de híbridos, Parulidae, plumaje, reinita, *Setophaga*.

Hybridization is a phenomenon that has long captivated birders and evolutionary biologists alike (Mayr 1942, Mallet and Barton 1989, Mallet 2005, Toews et al. 2016, Baiz et al. 2020). Until recently, the role of hybridization in evolution was contentious (Dowling and Secor 1997); however, we now understand the consequences of hybridization on adaptive introgression and speciation, and how these forces can have profound effects on biological diversity (Seehausen 2004, Mallet 2005, Meier et al. 2017). Notably, hybrid zones often encompass recently diverged species pairs that inform our understanding of the drivers and patterns of speciation and diversification (i.e., Pearson 2000, Vallender et al. 2007, Irwin et al. 2009). Research on hybridization has also been extended to deepen our understanding of diverse topics ranging from migratory behavior (Toews et al. 2014, Lundberg et al. 2017) to the genomic basis for pigmentation (Toews et al. 2016, Brelsford et al. 2017).

Although hybridization and hybrid zones have been studied across the tree of life (McEntee et al. 2020), rare hybrids are difficult to study because they occur and/or are detected infrequently. Low abundance of rare hybrids can limit understanding of the dominance patterns of plumage and structural traits and it can prevent robust tests of genomic differentiation, as is possible in hybrid zones (e.g., Toews et al. 2016, Brelsford et al. 2017). Despite their overall scarcity, rare hybrids can be used to study evolutionary questions related to reproductive isolation and ecological divergence

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(Willis et al. 2014), and documenting rare hybrids is one method by which we can continue to expand our knowledge of evolutionary patterns.

One family with notably high instances of hybridization, and several well-studied hybrids, is the New World warbler family, Parulidae. The Parulidae radiation began in the late Miocene, ~7 million years ago, and was quite rapid despite a relative lack of ecological differentiation typical of other rapid radiations (Lovette et al. 2010, Oliveros et al. 2019). Despite ecological niche overlap, many warbler species finely partition resources and are able to coexist in sympatry with congenerics (MacArthur 1957), and even closely related and ecologically similar species display exceptional variation in plumage color (Baiz et al. 2020). It has been estimated that hybridization occurs in ~72% of parulid warbler species that breed in North America (Willis et al. 2014). Hybridization within Parulidae is diverse and includes many instances of intrageneric and intergeneric crosses, as well as one exceptional intergeneric three-way hybrid (Toews et al. 2018). The family boasts a number of rare hybrids (Willis et al. 2014) and thoroughly researched hybrid zones (Krosby and Rohwer 2010, Toews et al. 2016, Brelsford et al. 2017).

The rate of hybridization within Parulidae is notably higher than in most other avian families (Ottenburghs 2019). Although propensity for hybridization has not been formally quantified within Parulidae, it is thought that the overall high incidence of hybridization, combined with striking plumage divergence, have resulted in parulid hybrids being generally easier to identify than more cryptic hybrids (e.g., Cronemberger et al. 2020). These same characteristics make warbler hybrid zones some of the most productive for identifying genomic regions responsible for pigmentation differences between species (Funk and Taylor 2019). In particular, previous work has revealed that 2 key genes have a pronounced effect on pigmentation in hybridizing warblers: the agouti signaling protein (ASIP) is associated with black patterning, including face mask, throat patch, and streaking patterns (Toews et al. 2016, Wang et al. 2020); and beta-carotene oxygenase 2 (BCO2) is responsible for a variety of carotenoid-based phenotypes, including dramatic full-body yellow coloration (Toews et al. 2016, Baiz et al. 2020).

The high frequency and diversity of hybrid pairings, the long-term importance of gene flow, and a small number of known pigmentation genes of large effect make Parulidae an ideal group in which to study the predictability of hybrid phenotypes.

Here, we synthesize documented New World warbler hybrids from past to present to understand patterns of inheritance in variable traits, thereby building upon previously proposed trait-based approaches to hybrid identification (Graves 1990, Rohwer 1994). We focused our analysis on 2 key traits: carotenoid pigmentation and wing bar patterns. These traits were chosen due to their high variability within Parulidae and relevance to our focal individual. Specifically, we sought to understand patterns of inheritance in presence vs. absence and extent of wing bars, and in degree of pigmentation and extent of whole-body carotenoids, of hybrid offspring relative to parental forms. We then applied our results to present and identify a striking Yellow × Black-throated Blue Warbler (*Setophaga petechia* × *S. caerulescens*) hybrid from New Mexico, southwestern USA.

Methods

Data collection

We compiled a list of parulid hybrids and their attributes from published literature, websites, books, guides, photos, and natural history observations (Table 1). In our search, we considered well-substantiated parulid hybrids whose parentage is/was largely undisputed, hybrids with disputed parentage, and several instances of partial uncertain parentage where the identity of at least one parent was known. We classified a hybrid as having undisputed parentage based on cumulative strength of evidence, including certainty of the original identification, certainty of later publications to elaborate on or correct the initial identification, and/or consensus among experts. We acknowledge that future genetic analysis may result in identification revisions for hybrids presently considered to have undisputed parentage. We included records from any time in the past to roughly February 2021 from a variety of sources, including written documentation and descriptions, photos, audio recordings, genetic evidence, and vouchered museum specimens (Table 1). Additionally, we limited our search to those hybrids

whose parents spend at least part of the year in North America, including Canada, the United States, and Mexico. Although several hybrids in our compilation were identified outside of North America, they are included because the parentals occur in North America for at least a portion of their annual cycle. We focused on North American hybrids due to their extensive history of study and the higher likelihood that they will be photographed and posted to online sites such as eBird and Facebook Advanced Bird ID.

We reviewed all possible hybrids from published peer-reviewed sources, including Dunn and Garrett (1997), McCarthy (2006), and Willis et al. (2014), as well as web sources, including the Avian Hybrids website (https://avianhybrids.wordpress.com/parulidae/), eBird (https://ebird.org/home), the Facebook Advanced Bird ID group (https://www.facebook.com/groups/357272384368972), the Facebook Bird Hybrids of North America group (https://www.facebook.com/groups/2408162756138343), and others (Table 1). In eBird, we searched for all possible parulid hybrids by typing "warbler hybrid" (as well as comparable searches for species without "warbler" in the common name, e.g., "yellowthroat hybrid") into the species search box and accessing all records for each hybrid combination. We additionally conducted a nonsystematic, ad hoc eBird search for obvious hybrids using the keyword "warbler sp."; however, most birds with this designation are not hybrids, but rather species that observers were unable to identify for a variety of reasons (i.e., poor lighting, poor photos, observer inexperience) and this search yielded unusable and/or non-novel results only. Data and hybrid combinations suggested from Facebook bird groups allowed us to incorporate crowdsourced information from biologists and community scientists around the world; in most cases, crowdsourced suggestions were supported by published documentation and/or written descriptions, photos, and audio recordings available in eBird and/or on xeno-canto (https://www.xeno-canto.org/).

We coupled database and open platform search efforts with targeted searches in Google and Google Scholar for specific hybrid pairs of interest. For example, we searched "Connecticut Warbler and Mourning Warbler hybrid" and/or "Connecticut × Mourning Warbler" to attempt to retrieve more information about specific hybrids. Searches in Google Scholar focused our efforts on academic texts, whereas Google searches focused on bird observation websites and personal accounts (e.g., http://amazilia.net/images/Birds/NewWarblers/Hybrid_Warbler.htm). When possible, we obtained information about the presence of vouchered museum specimens and their identifiers by searching published sources and museum search engines (e.g., Arctos, www.arctosdb.org), or specific museum collections websites. We present our full compilation of parulid hybrids in Table 1, the evidence used to substantiate the hybrid identification, identifiers for vouchered museum specimens, and references. We acknowledge that other hybrid combinations likely exist that we failed to detect and that more parulid hybrid combinations await discovery.

Trait analysis

We used hybrid pairings from Table 1 to summarize and analyze patterns of carotenoid and wing bar variation. Carotenoid coloration and wing bars are 2 variable traits relevant to our hybrid case study (Fig. 1a–d), and multiple studies have linked a causal gene (BCO2) to carotenoid pigmentation (Toews et al. 2016, Baiz et al. 2020).

For carotenoid analysis, we chose hybrids with notable body-wide or patch-specific carotenoid differences, as estimated by presence of yellow and orange colors, and we qualitatively catalogued and compared the extent of the carotenoid pigmentation among parentals and hybrid offspring (Table 2). EFG scored whether the extent of carotenoid distribution was more or less than "intermediate" in the hybrid compared to parental forms (Fig. 2a). The classification of "intermediate" was made with respect to both the spatial extent and saturation of yellow coloration, based on the assumption that "intermediate" coloration should have approximately midpoint color saturation and midpoint spatial extent of yellow, as described in Thompson et al. (2021). An individual was described as "more" or "less" than intermediate if either the saturation *or* the spatial extent was more or less than the midpoint between parents, respectively (Fig. 2a). Many cases were clear-cut, but in instances where scoring was unclear, we defaulted conservatively to the "intermediate" designation. We used the same evalua-

Table 1. Hybrid crosses of North American parulid warblers from the 1900s to roughly February 2021. Hybrid pairs were taken from review of published peer-reviewed articles, books, and online sources. For each combination, we provide the nature of identification, information for vouchered museum specimens (whether or not specimens exist, number of specimens ["U" if unknown], and specimen identifiers, if available), and references from peer-reviewed literature, open-source databases, and online discussion forums. Names for known hybrid pairs (i.e., "Sutton's Warbler") are given next to the hybrid cross. When >1 eBird checklist was found for a particular hybrid, one or more (but not necessarily all) representative checklists are cited. "Unknown" indicates unknown information; "NA" indicates that a field was not applicable. Links to online sources are provided below the table.

Hybrid cross	Nature of identification	Specimen (#)	Specimen identifiers	References
***Geothlypis formosa* (Kentucky Warbler)**				
× *Vermivora cyanoptera* (Blue-winged Warbler); "Cincinnati Warbler"	plumage, morphology, morphological analyses	yes (2)	unknown	Graves 1988, McCarthy 2006
***Geothlypis philadelphia* (Mourning Warbler)**				
× *Cardellina canadensis* (Canada Warbler)	plumage, morphology	yes (1)	USNM 403437	Bledsoe 1988, McCarthy 2006, Dunn and Garrett 1997
× *Geothlypis formosa* (Kentucky Warbler); "Junkin's Warbler"	plumage, morphology, genetics	no	NA	Bonter and Lovette 2007
× *Geothlypis trichas* (Common Yellowthroat)	plumage, morphology	yes (U)	unknown	Bledsoe 1988, Dunn and Garrett 1997, eBird [1]
× *Geothlypis tolmiei* (MacGillivray's Warbler)	plumage, morphology, hybrid zone study, genetics, song differentiation	yes (4)	unknown	Cox 1973, Hall 1979, Patti and Myers 1976, Irwin et al. 2009, Kenyon et al. 2011, eBird [2], Facebook Advanced Bird ID [1]
× *Oporornis agilis* (Connecticut Warbler)	plumage, morphology	yes (2)	SNOMNH 3565	Sutton 1967, McCarthy 2006
***Geothlypis trichas* (Common Yellowthroat)**				
× *Basileuterus rufifrons* (Rufous-capped Warbler)	plumage, song	no	NA	eBird [3]
× *Geothlypis poliocephala* (Gray-crowned Yellowthroat)	plumage, morphology, video, audio	no	NA	Dunn and Garrett 1997, Sibley 2000, McCarthy 2006, Texas Rare Birds records
× *Geothlypis tolmiei* (MacGillivray's Warbler)	plumage	no	NA	eBird [4] [5]
× *Setophaga petechia* (Yellow Warbler)	plumage, genetics	no	NA	Griffiths et al. 2008, Ventana Wildlife Society Big Sur Ornithology Lab, eBird [6]
***Leiothlypis virginiae* (Virginia's Warbler)**				
× *Leiothlypis crissalis* (Colima Warbler)	plumage, morphology, song	unknown	unknown	Bryan and Lockwood 2018
***Leiothlypis ruficapilla* (Nashville Warbler)**				
× *Leiothlypis peregrina* (Tennessee Warbler)	plumage, morphology	yes (U)	unknown	Bledsoe 1988, Parkes 1996, Dunn and Garrett 1997
× *Leiothlypis celata* (Orange-crowned Warbler)	plumage, morphology, genetics	yes (U)	unknown	Ralston et al. 2015
× *Setophaga caerulescens* (Black-throated Blue Warbler)	plumage	yes (1)	unknown	Dunn and Garrett 1997
× *Setophaga magnolia* (Magnolia Warbler)	plumage	no	NA	eBird [7]
***Mniotilta varia* (Black-and-white Warbler)**				
× *Setophaga cerulea* (Cerulean Warbler)	plumage, morphology	yes (U)	unknown	Parkes 1978, Dunn and Garrett 1997

Table 1. Continued.

Hybrid cross	Nature of identification	Specimen (#)	Specimen identifiers	References
× *Setophaga coronata* (Yellow-rumped Warbler)	plumage, morphology, molt, song, genetics	no	NA	Vallender et al. 2009
× *Setophaga virens* (Black-throated Green Warbler)	plumage	no	NA	Bledsoe 1988, Curson et al. 1994, McCarthy 2006
× *Setophaga pensylvanica* (Chestnut-sided Warbler)	plumage	no	NA	eBird [8]
× *Vermivora chrysoptera* (Golden-winged Warbler) / *Setophaga pensylvanica* (Chestnut-sided Warbler)*	plumage, morphology, song	no	NA	McCarthy 2006, Amazilia.net [1]
***Oreothlypis superciliosa* (Crescent-chested Warbler)**				
× *Setophaga pitiayumi* (Tropical Parula)	plumage	no	NA	Rappole and Blacklock 1994, Thornton and Thornton 1999, McCarthy 2006
***Parkesia noveboracencis* (Northern Waterthrush)**				
× *Setophaga striata* (Blackpoll Warbler) / *Setophaga tigrina* (Cape May Warbler)*	plumage, morphology	yes (1)	USNM 481595	Short and Robbins 1967, Parkes 1995, Dunn and Garrett 1997
***Protonotaria citrea* (Prothonotary Warbler)**				
× *Setophaga petechia* (Yellow Warbler)	plumage	no	NA	Beardslee and Mitchell 1965, Gunn 1958, McCarthy 2006
***Setophaga americana* (Northern Parula)**				
× *Setophaga cerulea* (Cerulean Warbler)	plumage, observation, song, genetics	no	NA	Trimbath et al. 2019, MacDonald 2018, Rowe and Rowe 2019, Nirschl 2004, Lindsay and Vezo 1995, eBird [9] [10]
× *Setophaga coronata coronata* ("Myrtle" Yellow-rumped Warbler)	plumage	no	NA	Dunn and Garrett 1997, Graves 1993
× *Setophaga dominica* (Yellow-throated Warbler); "Sutton's Warbler"	plumage	no	NA	Anich et al. 2012, Ulrich and Ulrich 1981, Stevenson and Anderson 1994
× *Setophaga magnolia* (Magnolia Warbler)	plumage, song	no	NA	Sudol 2004, McCarthy 2006
× *Setophaga pitiayumi* (Tropical Parula)	plumage, mixed nesting pairs, hybrid zone	no	NA	Lockwood and Freeman 2004, Rappole and Blacklock 1994, Thornton and Thornton 1999, McCarthy 2006
× *Setophaga ruticilla* (American Redstart)	plumage, morphology	yes (1)	USNM 396083	Burleigh 1944, McCarthy 2006
***Setophaga caerulescens* (Black-throated Blue Warbler)**				
× *Setophaga cerulea* (Cerulean Warbler)	plumage, behavioral observation at nest, song	no	NA	Delancey et al. 2019, MacDonald 2018, eBird [9] [10], xeno-canto [1]
× *Setophaga magnolia* (Magnolia Warbler)	plumage, song	no	NA	eBird [11]
× *Setophaga petechia* (Yellow Warbler)	plumage	unknown	unknown	Ducharme and Lamontagne 1992, *present study* (Facebook Advanced Bird ID [2])

Table 1. Continued.

Hybrid cross	Nature of identification	Specimen (#)	Specimen identifiers	References
***Setophaga castanea* (Bay-breasted Warbler)**				
× *Setophaga coronata coronata* ("Myrtle" Yellow-rumped Warbler)	plumage	yes (1)	USNM 567882	Banks and Baird 1978, Dunn and Garrett 1997, Facebook Advanced Bird ID [3]
× *Setophaga striata* (Blackpoll Warbler)	plumage, morphology, song, breeding bird survey	yes (3)	UMMZ 53692, UMMZ 216628, SBCM	Powdermill Nature Reserve, Graves 1996, Dunn and Garrett 1997, Brodkorb 1934, eBird [12]
× *Setophaga fusca* (Blackburnian Warbler)	nest provisioning observation	no	NA	Hurley and Jones 1983, Dunn and Garrett 1997
***Setophaga cerulea* (Cerulean Warbler)**				
× *Vermivora cyanoptera* (Blue-winged Warbler)	plumage, genetics	no	NA	Toews et al. 2020
***Setophaga citrina* (Hooded Warbler)**				
× *Setophaga petechia* (Yellow Warbler)	plumage	no	NA	eBird [13]
***Setophaga coronata auduboni* ("Audubon's" Yellow-rumped Warbler)**				
× *Setophaga graciae* (Grace's Warbler)	plumage	yes (1)	DMNH 36657	Bledsoe 1988, Dunn and Garrett 1997, McCarthy 2006
× *Setophaga nigrescens* (Black-throated Gray Warbler)	plumage	no	NA	eBird [14]
***Setophaga coronata coronata* ("Myrtle" Yellow-rumped Warbler)**				
× *Setophaga dominica* (Yellow-throated Warbler)	plumage	no	NA	eBird [15] [16]
× *Setophaga magnolia* (Magnolia Warbler)	specimen, morphology, plumage, photos, calls	yes (1)	UMMZ DR002 (prep no.)	Latta et al. 1998
× *Setophaga palmarum* (Palm Warbler)	plumage, song	yes (1)	unknown	Dunn and Garrett 1997, eBird [17]
× *Setophaga pinus* (Pine Warbler)	plumage	yes (1)	USNM 567885	Dunn and Garrett 1997, Hubbard 1977, McCarthy 2006
× *Setophaga tigrina* (Cape May Warbler)	plumage	yes (1)	unknown	Marks and Willard 1996, Dunn and Garrett 1997, eBird [18]
× *Setophaga townsendi* (Townsend's Warbler)	plumage	yes (1)	SBCM	Dunn and Garret 1997, McCaskie 1984
***Setophaga discolor* (Prairie Warbler)**				
× *Setophaga petechia* (Yellow Warbler)	plumage, song	no	NA	eBird [19]
× *Vermivora cyanoptera* (Blue-winged Warbler)	plumage	no	NA	eBird [20] [21]
***Setophaga fusca* (Blackburnian Warbler)**				
× *Setophaga kirtlandii* (Kirtland's Warbler)	photos, plumage, morphology	no	NA	Latta and Parkes 2001
× *Mniotilta varia* (Black-and-white Warbler) / *Setophaga pensylvanica* (Chestnut-sided Warbler)*	plumage	unknown	unknown	Parkes 1983, Bain 1996, Dunn and Garrett 1997
***Setophaga graciae* (Grace's Warbler)**				
× *Setophaga nigrescens* (Black-throated Gray Warbler)	plumage	no	NA	eBird [22]

Table 1. Continued.

Hybrid cross	Nature of identification	Specimen (#)	Specimen identifiers	References
***Setophaga magnolia* (Magnolia Warbler)**				
× *Setophaga ruticilla* (American Redstart)	plumage, genetics, morphology	no	NA	Brennan et al. 2021
***Setophaga nigrescens* (Black-throated Gray Warbler)**				
× *Setophaga townsendi* (Townsend's Warbler)	plumage, genetics	yes (1)	unknown	Rohwer 1994, Dunn and Garrett 1997, eBird [23]
× *Setophaga occidentalis* (Hermit Warbler)	specimen, morphology, plumage character states, nesting observations	yes (1)	UWBM 49903	Rohwer et al. 2000, Dunn and Garrett 1997
***Setophaga occidentalis* (Hermit Warbler)**				
× *Setophaga palmarum* (Palm Warbler)	plumage	no	NA	Dunn and Garrett 1997, Griscom and Sprunt 1957, McCarthy 2006
× *Setophaga townsendi* (Townsend's Warbler)	plumage, morphology, observation, hybrid zone study	yes (U)	unknown	Rohwer and Wood 1998, Pearson 2000
***Setophaga palmarum* (Palm Warbler)**				
× *Setophaga magnolia* (Magnolia Warbler)	plumage	no	NA	eBird [24]
***Setophaga pensylvanica* (Chestnut-sided Warbler)**				
× *Setophaga magnolia* (Magnolia Warbler)	plumage, morphology, genetics	no	NA	Burrell et al. 2016, eBird [25]
× Brewster's Warbler (hybrid *V. chrysoptera* × *V. cyanoptera*)†	plumage, pairing, genetics	no	NA	Toews et al. 2018
***Setophaga ruticilla* (American Redstart)**				
× ?**	plumage	no	NA	Arizona Field Ornithologists [1]
***Setophaga tigrina* (Cape May Warbler)**				
× ?** (Probable *Setophaga virens* (Black-throated Green Warbler))	plumage	no	NA	eBird [26], Facebook Advanced Bird ID [4]
***Vermivora chrysoptera* (Golden-winged Warbler)**				
× *Vermivora cyanoptera* (Blue-winged Warbler); "Brewster's Warbler" and "Lawrence's Warbler"	plumage, song, breeding bird surveys, genetics, nesting biology and behavior	no	NA	Confer and Tupper 2000, Confer 2006, Vallender et al. 2007 (many others)

* Indicates disputed parentage; ** indicates uncertain parentage; † indicates 3-way hybrid between 2 genera. Links to web sources:

Amazilia.net: [1] http://amazilia.net/images/Birds/NewWarblers/Hybrid_Warbler.htm;

Arizona Field Ornithologists: [1] http://www.azfo.net/gallery/2017/html01/American_Redstart_hybrid__DB_Strand_13_August_2015_636140629473272410.html;

eBird: [1] https://ebird.org/qc/checklist/S30370092; [2] https://ebird.org/checklist/S74107054; [3] https://ebird.org/checklist/S14052566; [4] https://ebird.org/checklist/S25114901; [5] https://ebird.org/checklist/S6610768; [6] https://ebird.org/checklist/S6221734; [7] https://ebird.org/checklist/S15576209; [8] https://ebird.org/checklist/S73633494; [9] https://ebird.org/checklist/S38299087; [10] https://ebird.org/checklist/S38045374; [11] https://ebird.org/checklist/S14608513; [12] https://ebird.org/checklist/S37090859; [13] https://ebird.org/checklist/S18431003; [14] https://ebird.org/checklist/S36877384; [15] https://ebird.org/checklist/S44837997; [16] https://ebird.org/checklist/S44828969; [17] https://ebird.org/checklist/S5304578; [18] https://ebird.org/checklist/S59015589; [19] https://ebird.org/checklist/S24026450; [20] https://ebird.org/checklist?subID=S8360155; [21] https://ebird.org/checklist/S18629563; [22] https://ebird.org/checklist/S6893705; [23] https://ebird.org/checklist/S33211134; [24] https://ebird.org/checklist/S18270828; [25] https://ebird.org/canada/checklist/S18555314; [26] https://ebird.org/checklist/S74462221;

Facebook Advanced Bird ID: [1] https://www.facebook.com/groups/357272384368972/permalink/3258469697582545/; [2] https://www.facebook.com/groups/357272384368972/permalink/3229363953826453; [3] https://www.facebook.com/groups/357272384368972/permalink/3335643726531808/; [4] https://www.facebook.com/groups/357272384368972/permalink/3289608571135324/;

xeno-canto: [1] https://www.xeno-canto.org/378982

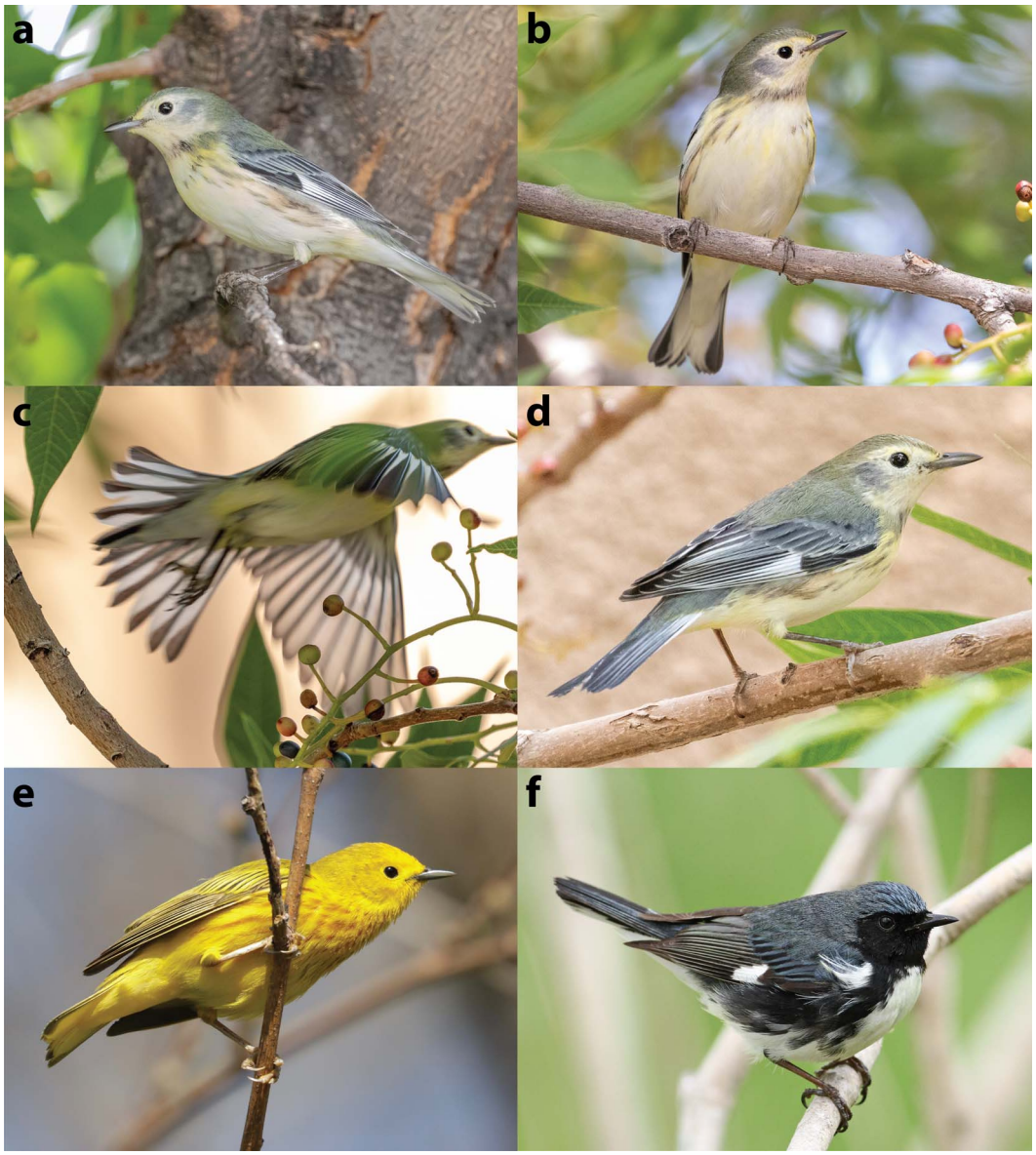

Figure 1. Putative Yellow × Black-throated Blue Warbler (*S. petechia* × *S. caerulescens*) hybrid discovered on the University of New Mexico Main Campus in Albuquerque, New Mexico, on 16–17 September 2020 (a–d) and putative parental species Yellow Warbler (e) and Black-throated Blue Warbler (f). Photos illustrate key plumage traits that were central to identification of the hybrid. Note that in photo (c) the bright green in the middle of the wing (see online color version of this figure) is due to leaves in the foreground. Photos: (a–d) Michael J. Andersen; (e) © Aaron Marshall / Macaulay Library (ML148831801); (f) © Luke Seitz / Macaulay Library (ML61061191).

tion criteria regardless of age and sex and attempted to infer what would constitute "intermediate" based only on hypothesized intermediate hybrid plumage relative to the 2 parentals. It is worth noting that, due to the potential importance of male pigmentation in speciation, bias may exist for divergent selection resulting in stronger mismatch in male-specific pigmentation mechanisms (Sibley 1957). This could result in hybrid males, as opposed to females and duller-plumaged

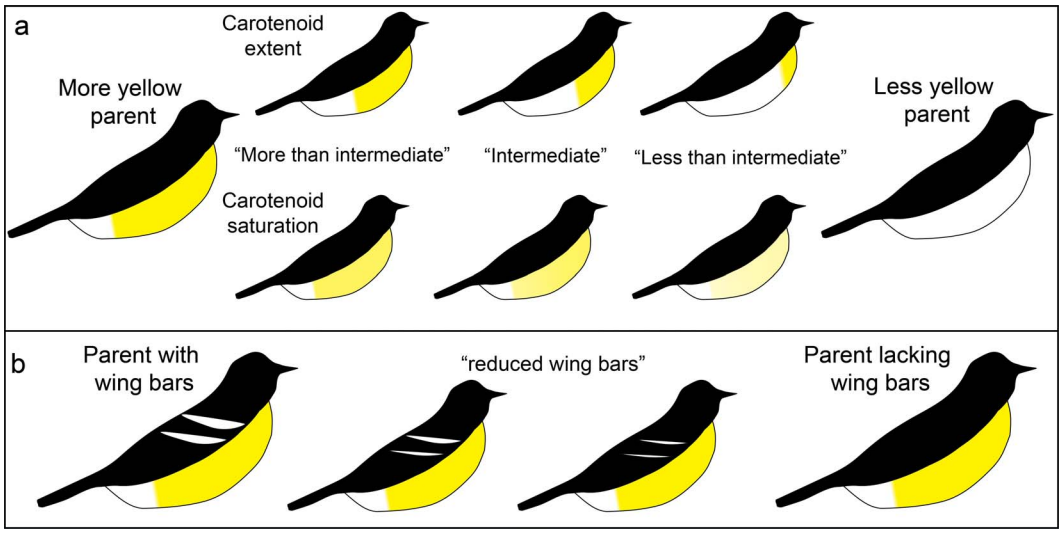

Figure 2. Conceptual illustration of scoring criteria for carotenoid coloration and extent and wing bar extent of hybrid offspring relative to parental forms. (a) Carotenoid extent (top) and carotenoid saturation (bottom) relative to the "more yellow" parent and "less yellow" parent (see online color version of this figure). Carotenoid extent saturation are illustrated in a gradient from greatest to least (left to right) saturation and extent, respectively. (b) Wing bar presence/absence and width relative to one parent with wing bars and one parent without wing bars. Illustrations of "offspring" (middle) depict 2 different examples of "reduced" wing bars relative to parents.

immatures, with stronger parental bias. When available, we preferred photos for scoring, but well-described plumage traits were used when needed.

We chose wing bar pairings based on 3 criteria: (1) presence of wing bars on one parent and absence of wing bars on the other; (2) notable differences in wing bar extent between parental forms; and (3) notable differences in wing bar color between parental forms (e.g., yellow in one parent, white in the other). We defined wing bars as a line or lines of contrasting color (including white, yellow, or tan) across the middle of a bird's wings caused by markings on the coverts. Specifically, we considered wing bars to be any contrasting light edges of wing covert tips, notably differentiated from the color at the center of the coverts and edges along the lengthwise axis of the feather. EFG scored relevant pairings based on presence/absence of wing bars and whether wing bars had reduced width in hybrid offspring relative to the parent with more pronounced wing bars (Table 3; Fig. 2b). Width of wing bars was qualitatively defined based on the extent of pale tips in the relevant wing covert feathers, as demonstrated in Figure 2b. These evaluation criteria were chosen because in most cases it was difficult to score whether wing bars on hybrid offspring were "more than" or "less than" intermediate.

Hybrid field encounter

On 16 September 2020, MJA briefly observed an unusual warbler on the University of New Mexico (UNM) Main Campus at approximately 35.0831N, −106.6208W. Based on plumage patterns, particularly the presence of a pronounced collar and the bird's overall muted color, MJA tentatively identified the bird as an odd Cerulean Warbler (*Setophaga cerulea*), a species for which only 3 New Mexico records existed at the time. On 17 September 2020, MJA returned to the same location and found the bird foraging actively in a mixed flock of Wilson's (*Cardellina pusilla*) and Townsend's (*Setophaga townsendi*) warblers. The bird was observed and photographed for ~1.5 h by all coauthors. The authors analyzed plumage features, coloration, and behavior extensively, debating many hybrid parent combinations, as well as the possibility that the bird was a hypoxanthic (color-depleted) Yellow Warbler or

Table 2. Summary of parulid hybrid pairings with parental differences in carotenoid pigmentation. All pairings were taken from hybrids listed in Table 1. Pairings with a slash ("/") indicate disputed parentage. For each, we provide the extent of carotenoid-colored plumage (simplified as "yellow," although some have orange plumage) in the more yellow parent, less yellow parent, and the hybrid offspring. We describe the extent and strength of yellow coloration in offspring relative to strict intermediacy (i.e., halfway between parentals). "Magnitude of difference" describes the magnitude of carotenoid difference relative to parentals, with "complete" referring to the case where one parent lacks carotenoids entirely. Hybrid pairs are sorted first by magnitude of difference, then hybrid extent, then alphabetically. The first species listed is the parent with yellower plumage, followed by the parent with less yellow plumage.

Hybrid pairing	Extent on more yellow parental	Extent on less yellow parental	Extent of yellow on offspring	Hybrid extent summarized	Magnitude of difference
Chestnut-sided Warbler × Black-and-white Warbler	Crown; back (fall only); trace in wing bars	None	Trace in wing bars; trace in crown	Less than intermediate	Complete
Golden-winged/Chestnut-sided Warbler × Black-and-white Warbler	Wing bars; crown	None	Faintly yellowish wing bars	Less than intermediate	Complete
"Myrtle" Yellow-rumped Warbler × Black-and-white Warbler	Few patches (especially rump)	None	Very limited patch on rump	Less than intermediate	Complete
Magnolia Warbler × Black-throated Blue Warbler	Extensive on underparts	None	Very reduced; few faint patches	Less than intermediate	Complete
Blue-winged Warbler × Cerulean Warbler	Nearly whole body	None	Small light-yellow patches on underparts	Less than intermediate	Complete
Northern Parula × Cerulean Warbler	Throat; yellow green back	None	Very reduced; few faint patches	Less than intermediate	Complete
Blue-winged Warbler × Golden-winged Warbler	Nearly whole body	Only wing bars and crown	Strongly reduced in F1; otherwise varies	Less than intermediate	Strong
Magnolia Warbler × American Redstart	Extensive on underparts	Below bend of wing and in base of tail	Flanks (more than Redstart); patchy breast	Less than intermediate	Strong
Magnolia Warbler × Chestnut-sided Warbler	Yellow underparts; white wing bars	Crown; trace in wing bars	Limited and patchy; traces in wing bars	Less than intermediate	Strong
Magnolia Warbler × "Myrtle" Yellow-rumped Warbler	Extensive on underparts	Few patches (especially rump)	Like "Myrtle" below, but with yellowish wash to breast	Less than intermediate	Strong
Townsend's Warbler × Black-throated Gray Warbler	Face down to breast	Lores only	Patchy on underparts; reduced toward back of face	Less than intermediate	Strong
Grace's Warbler × Black-throated Gray Warbler	Throat and loral stripe	Lores only	Some on throat; lores	Intermediate	Strong
Hermit Warbler × Black-throated Gray Warbler	Face only	Lores only	Limited pale yellow to face	Intermediate	Strong
Pine Warbler × "Myrtle" Yellow-rumped Warbler	Breast and head	Few patches (especially rump)	Yellow on throat, breast, back, and rump	Likely intermediate	Strong
Nashville Warbler × Tennessee Warbler	Nearly whole body	Varies (yellowish wash; chartreuse back)	Extensive in male; limited in female	More or less (varies)	Strong

Table 2. Continued.

Hybrid pairing	Extent on more yellow parental	Extent on less yellow parental	Extent of yellow on offspring	Hybrid extent summarized	Magnitude of difference
Magnolia Warbler × Palm Warbler	Extensive on underparts	Throat and undertail (western subspecies)	Extensive; like Magnolia	More than intermediate	Strong
Cape May Warbler × "Myrtle" Yellow-rumped Warbler	Face and breast; sometimes below	Few patches (especially rump)	Extensive below; some on face	More than intermediate	Strong
Northern Parula × American Redstart	Throat and breast	Below bend of wing and in base of tail	Light yellow on tail; flanks; and breast	Intermediate	Variable
Cape May Warbler × Black-throated Green Warbler (Probable)	Face and breast; sometimes below	Face down to breast (variable by parent)	Reduced from Cape May, but extensive on breast and belly	Intermediate	Moderate
Northern Parula × "Myrtle" Yellow-rumped Warbler	Throat and breast	Few patches (especially rump)	Breast pale yellow; throat pale yellow	Intermediate	Moderate
Townsend's Warbler × "Audubon's" Yellow-rumped Warbler	Face down to breast	Few patches (rump and throat)	Intermediate between parents	Intermediate	Moderate
Townsend's Warbler × Hermit Warbler	Face down to breast	Face only	Variable	Intermediate	Minor
Yellow-throated Warbler × Yellow-rumped Warbler	Throat	Few patches (especially rump)	Pale on throat; corner of wings; and rump	Intermediate	Minor

Table 3. Summary of parulid hybrid pairings with major differences in prominence of parental wing bars. All pairings were taken from hybrids listed in Table 1. The first species listed for each hybrid pairing is the parent with wing bars, while the second parent listed is the parent without wing bars. The extent of wing bars on each parent (with and without wing bars) was evaluated qualitatively based on relative width (i.e., "none," "weak," "moderate," "strong"). The extent in hybrid offspring describes the magnitude of wing bar difference relative to the parental with wing bars. Pairings are sorted in ascending order by relative width of extent on the parent without wing bars.

Hybrid pairing	Extent parental with wing bars	Extent on parent without wing bars	Extent in hybrid offspring
Magnolia Warbler × Nashville Warbler	Moderate to strong	None	Weak (reduced)
Blackpoll Warbler × Northern Waterthrush	Moderate to strong	None	Weak (reduced)
Blue-winged Warbler × Kentucky Warbler	Strong	None	Weak (reduced)
Magnolia Warbler × Black-throated Blue Warbler	Moderate to strong	None	Moderate wing panel (reduced)
Magnolia Warbler × Palm Warbler	Moderate to strong	None	Weak (reduced)
"Myrtle" Yellow-rumped Warbler × Palm Warbler	Weak-moderate	None	Weak (reduced)
Prairie Warbler × Yellow Warbler	Weak to moderate yellow	None	Weak (slightly reduced from Prairie)
Magnolia Warbler × American Redstart	Moderate to strong	None	Weak (reduced)
Northern Parula × American Redstart	Moderate	None	Seemingly reduced
Blackburnian Warbler × Kirtland's Warbler	Moderate-strong	Weak in female-types	Moderate (close to female Blackburnian)
Blue-winged Warbler × Prairie Warbler	Strong	Weak to moderate yellow	Weak (reduced); closer to Prairie

hypoxanthic member of the Black-throated Green (*Setophaga virens*) complex.

We noted a fairly large warbler with a thick and relatively long bill that was overall blue gray/green dorsally and white with darker streaking ventrally (Fig. 1a–d). We observed pronounced green/gray tones on the bird's head, nape, and back; pale and hardly noticeable white edging to the wing coverts; a bold white wing flag on each wing that extended down the primaries; a gray necklace of dense streaks separating the throat from the breast with a faint chestnut wash to parts of the base coloration of the necklace; gray flank streaks with a chestnut wash to the base coloration of the upper flanks; and faint yellow patches on an overall white breast, belly, and vent. The bird had white undertail coverts, and importantly, we noted that at least 50% of the 5 outermost rectrices were white (Fig. 1b–c). The bird seemed to respond to several species' calls and songs (including Black-throated Blue, Yellow, and Townsend's warblers) that we played back to it by approaching the sound source, but we felt like any conclusions drawn from these unsystematic playback attempts were equivocal. The original description of our encounter and photos taken by MJA can be found in the respective eBird checklists: https://ebird.org/checklist/S73710816 and https://ebird.org/checklist/S73717047. The full set of high-resolution images taken by MJA and KDO to document the hybrid is accessible on Dryad at https://doi.org/10.5061/dryad.4b8gthtbw.

The authors are affiliated with the Museum of Southwestern Biology (MSB) at the University of New Mexico and discussed the ethics of collecting the hybrid to obtain genetic samples. For permitting and logistical reasons, we did not collect the individual, nor was it possible to obtain feather samples for genetic analysis. We attempted to collect noninvasive fecal samples; however, we could not identify and distinguish fecal samples of our putative hybrid from other species in the flock. As such, we rely on detailed observations, photos, and analysis of plumage traits to substantiate our identification. A comparison of wing and tail colors and patterns between the hybrid and its putative parents is presented (Fig. 3) with comparable photographs of both the hybrid and specimens from the MSB (Table S1).

Results

Hybridization in Parulidae

We documented 61 hybrid crosses among 44 North American parulid warbler species from the 1900s to present (Table 1). Of these, 56 hybrids

Figure 3. Diagnostic trait comparison of the putative Yellow × Black-throated Blue Warbler (*Setophaga petechia* × *S. caerulescens*) hybrid with parental forms. The tail of the hybrid (a) is a near-perfect match for the tail pattern of Yellow Warbler (b), but with yellow and olive replaced by white and black, respectively. The white "wing flag" at the base of the primaries (c) is very similar to that of Black-throated Blue Warbler (d), but the extent of white is intermediate between the bold white wing flag of Black-throated Blue Warbler and the limited edging on the inner vane of Yellow Warbler (e). The broad white edge on the underside of the secondaries (f) is a strong match for Black-throated Blue Warbler (g) and is much more extensive and curved toward the base of the feathers than in Yellow Warbler (h). All photographed specimens are from the Museum of Southwestern Biology (Supplemental Table S1). Photos: Ethan F. Gyllenhaal.

had undisputed parentage, an additional 3 hybrids had disputed parentage or parentage that was called into question after the initial hybrid description (e.g., Parkes 1995), and 2 had uncertain parentage (Table 1). Consistent with intrageneric species richness within Parulidae, the genus *Setophaga* had the highest number of hybrid crosses ($n = 40$), followed by *Geothlypis* ($n = 6$), and then *Vermivora* ($n = 5$). We found 40 intrageneric hybrids and 16 intergeneric hybrids. Of hybrids with undisputed parentage, the species with the highest number of crosses was Yellow-rumped Warbler (*S. coronata*; $n = 11$), including 10 intrageneric crosses and one intergeneric cross. Magnolia Warbler (*S. magnolia*) had the second-highest number of hybrid crosses with $n = 7$ each. Most parulid species displayed higher rates of intrageneric than intergeneric crossing, but hybrid crosses involving the monotypic Black-and-white Warbler (*Mniotilta varia*) were necessarily intergeneric (all with *Setophaga* species) and 3 of 4 crosses involving Blue-winged Warbler (*V. cyanoptera*) were intergeneric (2 with *Setophaga* species and one with *G. formosa*; Table 1). One unusual hybrid was identified as a "triple hybrid" cross between a Brewster's Warbler (*V. chrysoptera* × *V. cyanoptera*) and a Chestnut-sided Warbler (*S. pensylvanica*), providing an example of both intrageneric and intergeneric hybridization (Table 1; Toews et al. 2018).

The most common method of diagnosing hybrids from past to present has been analysis and comparison of plumage types through field observations, photos, and handling of mist-netted birds; >96% ($n = 59$) of hybrid identifications have been made, at least in part, through plumage analysis (Table 1). More than 36% ($n = 22$) of hybrid crosses have been identified in part by morphological comparisons or formal analysis of morphology (i.e., principal component analysis and other statistical analyses), and ~20% ($n = 12$) have used vocalizations to determine parental identity. Only ~33% ($n = 20$) of the hybrids in our compilation have had identification confirmed by molecular analysis and/or observations of nesting behavior by known parents (Table 1). In a few instances, certain hybrids have been subjects of extensive and formal hybrid zone study, including crosses such as Mourning × MacGillivray's Warbler (*Geothlypis philadelphia* × *G. tolmiei*; Irwin et al. 2009), Hermit × Townsend's Warbler (*Setophaga occidentalis* × *S. townsendi*; Pearson 2000), and Golden-winged × Blue-winged Warbler (*Vermivora chrysoptera* × *V. cyanoptera*; e.g., Vallender et al. 2007; Table 1). A total of ~36% ($n = 22$) of the hybrid crosses listed in Table 1 have representative specimens in museum collections; these vouchered specimens represent one method by which past hybrid descriptions might be extended in future research.

Carotenoid plumage pattern inheritance

Hybrid carotenoid inheritance was highly variable (Table 2). Of 23 pairings studied, 48% were scored as "less than intermediate" (however, the majority included examples where one parent lacked carotenoids), 39% were scored as "intermediate," 9% were classified as "more than intermediate" but less than parentals, and one hybrid combination was variable (2 different individuals of Nashville × Tennessee Warbler [*Leiothlypis ruficapilla* × *L. peregrina*] had different levels of carotenoids present in different individuals; Parkes 1995). One prominent trend was that when one parent had carotenoid pigmentation and one parent lacked carotenoid pigmentation, hybrid offspring showed a significant reduction in carotenoids (all $n = 6$ pairings with "complete" magnitude of difference; Table 2). Notable examples of carotenoid reduction in hybrid offspring compared to parentals included genetically confirmed combinations such as Cerulean × Blue-winged Warbler (Toews et al. 2020) and Black-and-white × "Myrtle" Yellow-rumped Warbler (Vallender et al. 2009).

A unique pattern seen in hybrids whose parents had a strong difference in carotenoid pigmentation on the underparts was presence of asymmetrical and patchy pale-yellow coloration on a whitish background. Examples of this pattern include Black-throated Blue × Magnolia Warbler, Cerulean × Blue-winged Warbler (Tables 1–2), and our case study (Fig. 1a–d). Generally, offspring phenotypes were not predictable for pairings where one parent had far more carotenoid pigmentation than the other (i.e., $n = 11$ scored as "strong" magnitude of difference; Table 2). For these pairings, 45% were less than intermediate, 27% were intermediate, 18% were more than intermediate, and one hybrid combination was

variable (2 individuals of Nashville × Tennessee Warbler, see above).

Wing bar inheritance

Based on 11 pairings examined, we found that hybrids strongly and consistently inherited wing bar patterns from parents (Table 3). Wing bars were present but reduced in hybrid offspring for all pairings where one parent had wing bars and the other did not ($n = 9$). The relative width of the wing bars on hybrids was always intermediate between the width of the 2 parents (as shown in Fig. 2b), but without specimens of hybrids and parents it was not possible to quantify the intensity of hybrid offspring relative to the parental with wing bars. In the 2 cases where both parents possessed wing bars differing only in extent, Blackburnian Warbler × Kirtland's Warbler (*S. fusca* × *S. kirtlandii*) and Blue-winged × Prairie Warbler (*V. cyanoptera* × *S. discolor*), hybrid wing bars were clearly more similar to those of one parent than the other (Table 3).

Identification of the UNM hybrid

Based on extensive analysis of size, shape, plumage features, color pattern, and general "gestalt," we put forth the identification of Yellow Warbler × Black-throated Blue Warbler for the UNM hybrid individual (Fig. 1a–d). Our observation is the first photo-documented record of a hybrid between these 2 species, with one previous written description from Quebec, Canada (Ducharme and Lamontagne 1992).

Discussion

Our synthesis revealed evidence of hybridization in >93% of New World warbler species (44 of 47), an increase from the previously estimated 72% (34 of 47 species; Willis et al. 2014). We found predictable inheritance of plumage patterns between hybrid offspring and parental forms in 2 focal traits, carotenoid coloration and wing bar patterns, and these results support our identification of an unusual Yellow × Black-throated Blue Warbler hybrid observed in Albuquerque, New Mexico, USA (Fig. 1a–d). Our analysis suggests that the phenotypes of rare hybrid warblers likely have some degree of predictability.

Inheritance of plumage characteristics

Warbler hybrids have long been central to studies of patterns and modes of inheritance (e.g., work with *Vermivora* species; Toews et al. 2016), and recent work has highlighted the influence of a few genes that have large effects on phenotype. For example, the high prevalence of BCO2 introgression (Baiz et al. 2020) and the apparent near dominance of "no-carotenoid" phenotypes (Table 2) suggests that whole-body carotenoid deposition may be governed by few nearly recessive genes. One warbler species with elevated levels of BCO2 evolution and gene tree discordance is the Yellow Warbler (Baiz et al. 2020), one of the parentals of our putative Yellow × Black-throated Blue Warbler hybrid, and these evolutionary patterns could partly explain plumage coloration patterns in this hybrid cross.

Although BCO2 may be an important gene underlying plumage patterns, its effects are by no means universal. In our analysis we found many cases where pairings with strong differences in parental carotenoids produced intermediate hybrids. This is exemplified by Black-throated Gray × Grace's Warbler (*Setophaga nigrescens* × *S. graciae*), where both parentals have similar BCO2 genes but major differences in levels of carotenoid pigmentation (Baiz et al. 2020). Similarly, despite American Redstart (*Setophaga ruticilla*) having "Yellow Warbler–like" BCO2, the hybrid with Magnolia Warbler shows very little yellow on the breast and belly (Brennan et al. 2021). Additionally, admixture mapping and inferred polygenic inheritance of phenotypes in "Audubon's" × "Myrtle" Yellow-rumped Warblers (*Setophaga coronata* complex) has revealed a dozen other genetic regions associated with throat coloration, including a candidate gene for carotenoid transport (SCARF2), but not BCO2 or ASIP (Brelsford et al. 2017). Polygenic modes of inheritance for carotenoid genes have also been found in the Northern Flicker (*Colaptes auratus*; Hudon et al. 2015, Aguillon et al. 2021).

Our carotenoid coloration analysis revealed that pairings where only one parent possessed carotenoids resulted in hybrids with substantially less yellow than the bright parent (Fig. 2; Table 2). This pattern is consistent with predictions of parental bias, where a hybrid's bivariate phenotype tends to resemble one parent about 50% more than

the other, or mismatch due to different traits having dominance in conflicting directions (Thompson et al. 2021). Even in the most extreme examples (e.g., Blue-winged × Cerulean Warbler; Toews et al. 2020), we never observed complete dominance of non-carotenoid pigments. In pairings where both parents had carotenoid pigmentation, even when one parent had limited carotenoid pigmentation and the other had extensive yellow, coloration of hybrid offspring varied substantially (e.g., Magnolia × Palm Warbler and Magnolia × Chestnut-sided Warbler; Table 2). In such cases, it was therefore difficult to consistently predict carotenoid extent in hybrid phenotype. Hybrids did not show carotenoid pigmentation beyond what was apparent in parentals, consistent with the contradictory character approach (Rohwer 1994).

Wing bar inheritance followed a more consistent pattern; in most cases, the wing bars of hybrid offspring appeared close to strictly intermediate between parental forms (Fig. 2; Table 3). We found 2 apparent exceptions where wing bar width in hybrid offspring was closer to one parent than the other: one was Blue-winged × Prairie Warbler, which appeared more phenotypically similar to the Prairie Warbler parent (Tables 1 and 3); the other was Blackburnian × Kirtland's Warbler, which was much more similar to the Blackburnian Warbler parent (Table 3). Notably, we did not find any examples where 2 wing-barred parentals produced hybrid offspring *without* wing bars; even in cases where one parent had wing bars and the other lacked wing bars, offspring always possessed some degree of wing bars. This suggests that while wing bars may be reduced in hybrid offspring relative to parents, the presence or absence of wing bars in hybrids is governed by the presence or absence in one of the parental forms. The observed patterns of wing bar inheritance may be important for ornithologists and bird watchers to use when identifying hybrids in the field, especially in cases where the use of molecular markers is not possible.

In our analysis, we used a relatively coarse and subjective method to estimate degree of carotenoid saturation and wing bar extent. Many technical methods exist for precisely quantifying plumage coloration (e.g., Mason and Bowie 2020); however, we did not pursue such methods, as most of the hybrids we studied are not associated with vouchered museum specimens. We note that future studies could build upon our work by using computational methods to determine the relative extent of color and level of carotenoids in hybrid plumage, as well as modes of inheritance of both carotenoids and wing bars.

Identification of a striking Yellow × Black-throated Blue Warbler hybrid

The identification of the UNM hybrid was made by extensive study and consideration of many structural and plumage features, including overall size and shape of body and bill, coloration, and distinctive tail and wing patterns. Despite considerations of several structural and plumage features, 2 traits were critical in shaping our identification of this hybrid. The first trait was the extent of white in the tail. Our observed hybrid showed at least 50% white in the 5 outermost rectrices (Fig. 1b–c). Although no warbler species has extensive white on 5 rectrices, the tail pattern is identical to that of a Yellow Warbler lacking carotenoid pigmentation (Fig. 1b–c, e; Fig. 3a–b). The angle and shape of the coloration in the rectrices is also consistent with the angle and shape of rectrix coloration in the Yellow Warbler (Fig. 3a–b). Additionally, our bird's overall size, large bill, and "blank" face are consistent with the general appearance of Yellow Warbler. We therefore consider the combination of traits observed, particularly tail plumage patterns, to be diagnostic of a Yellow Warbler parent.

The second trait instrumental in cementing our identification of this hybrid was the white "wing flag" concentrated at the base of the primaries and faintly extending onto the secondaries, as seen on the folded wing (Fig. 1a, d). Among the Parulidae, this distinctive plumage feature is unique to Black-throated Blue Warbler (Fig. 1f). Although American Redstart has a similar wing flag colored with carotenoids that is evenly distributed across the bases of both the primaries and the secondaries, these patterns were not present in our hybrid. We note that the feather-specific pattern of the wing flag on our hybrid is not perfectly consistent with the wing flag pattern of Black-throated Blue Warbler, and we attribute this to mixed parentage with Yellow Warbler (Fig. 3c-e). This observed reduction of wing flag extent is additionally consistent with both documented examples of American Redstart × Magnolia Warbler (Brennan et al. 2021). The extent of smudgy yellow on our

hybrid suggests one parent had extensive carotenoid pigmentation while the other had little to none, and the results of our analysis of wing bar inheritance strongly support that both parents of the UNM hybrid lacked wing bars (Tables 2–3). Additionally, the white instead of yellow coloration in the outer rectrices of the UNM hybrid relative to Yellow Warbler is consistent with the hybrid pairing of American Redstart × Northern Parula (Burleigh 1944), and the general pattern of carotenoid suppression in hybrid offspring when one parent lacks carotenoids. Taken together, several lines of evidence support Black-throated Blue Warbler as the second parent to our bird.

It is important to consider all possible parental combinations and alternatives. We initially debated whether the UNM hybrid was a hypoxanthic Yellow Warbler; however, a hypoxanthic individual would not display a pronounced white wing flag or the Black-throated Blue–like pattern of white on the underwing (Fig. 3f–h). A few other subtle plumage features appear to superficially complicate parental identification. First, the faint chestnut wash on the throat and flanks appears consistent with Bay-breasted Warbler (*Setophaga castanea*) or Chestnut-sided Warbler (Fig. 1). However, pigmentation that appears to be purely eumelanin-based (i.e., black feathers) can conceal pheomelanin (i.e., rufous). This pheomelanin-derived coloration may then be visible in hybrid offspring, as has been shown in titmouse hybrids (Paridae: *Baeolophus*; Curry and Patten 2014). The chestnut in the flanks on our hybrid may also be explained by the presence of pheomelanin chestnut streaks on the breast and flanks of the Yellow Warbler parent, the distribution of which may have been altered by unknown pigmentation mechanisms of the other parent. Additionally, lack of wing bars and presence of a wing flag, as well as gray to black coloration of the underpart streaking of the UNM hybrid, further rule out Bay-breasted Warbler as a parental candidate. A number of these same features also rule out Chestnut-sided Warbler. Finally, although the overall appearance and "necklace" of streaks on the throat of the UNM bird are strongly reminiscent of Cerulean Warbler, the position of throat streaking on the UNM bird is higher on the throat than that of Cerulean Warbler, and the lack of wing bars and presence of a wing flag rule out Cerulean Warbler as a possible parent. Thoughtful discussion about the UNM hybrid, including rationale for and against many parental candidates, can be accessed in our permanently archived Facebook Advanced Birding ID post (Table 1).

Likelihood of Yellow × Black-throated Blue Warbler hybridization

Hybridization of Yellow × Black-throated Blue Warbler has been reported once before from Havre-Saint-Pierre, Quebec, Canada, in 1992, where the 2 species' breeding ranges overlap (Ducharme and Lamontagne 1992). However, this pair seems especially unlikely in New Mexico, southwestern USA. Although the Yellow Warbler is a common migrant and regular riparian-breeding species in parts of New Mexico, the Black-throated Blue Warbler does not migrate through or breed in the state; it is considered casual in spring and very rare in fall, with most reports from the Rio Grande Valley eastward (Parmeter et al. 2002). It is therefore remarkable that a Yellow × Black-throated Blue Warbler hybrid was found so far outside of the core range of one of its putative parents, although this pattern is consistent with other rare hybrids, which often result from breeding events between one parent within its core range and one parent on the edge or outside of its breeding range (Short 1969). Accordingly, the only other report of Yellow × Black-throated Blue Warbler is from Havre-Saint-Pierre, Quebec, Canada, a locality northeast of the expected core range of the Black-throated Blue Warbler (Ducharme and Lamontagne 1992).

Based on known distributions, breeding ranges, and migratory routes of both Yellow and Black-throated Blue Warblers, we posit that a vagrant Black-throated Blue Warbler occurring far west of its expected range may have bred with a Yellow Warbler in the northern United States or southern Canada (i.e., Montana, Alberta, or Saskatchewan, all three of which have late June records of singing Black-throated Blue Warbler; Cornell Lab of Ornithology 2021), and that the hybrid offspring followed a Yellow Warbler–like fall migration route through New Mexico en route to its nonbreeding grounds. While it is possible that the hybridization event occurred locally within New Mexico, the Black-throated Blue Warbler's higher-latitude, northerly breeding range suggests that a northern origin is more likely. Other possible

breeding localities for this pair certainly exist, but without genetic or feather samples we could not confirm the site of origin for the UNM hybrid.

We note that Yellow Warbler and Black-throated Blue Warbler are 2 species with a relatively high number of documented hybrid pairings, especially compared to other species in the genus *Setophaga* (Table 1). In total, we found 5 instances of Yellow Warbler hybrids (3 intrageneric, 2 intergeneric) and 4 instances of Black-throated Blue Warbler hybrids (3 intrageneric, 1 intergeneric). Although this does not speak to the probability of hybridization between these 2 species, it may suggest that they have a higher propensity for hybridization than related warbler species. Propensity for hybridization and predictability of intrageneric and intergeneric hybridization within Parulidae are promising subjects for future work.

Boundaries of reproductive isolation among warblers

Species boundaries between and among warblers appear porous, with increasingly documented rates of hybridization between distantly related taxa (McCarthy 2006, Willis et al. 2014). This is detectable in genomic data, particularly with excess introgression of the carotenoid-related gene BCO2 (Baiz et al. 2020). The fact that many hybrid zones occur between sister pairs (Krosby and Rohwer 2010, Toews et al. 2016, Brelsford et al. 2017), together with the likely introgression of the gene BCO2 between distantly related species, suggests that some hybrids—even rare combinations—may provide fodder for adaptive introgression. Simulations have confirmed that a few migrants are sufficient to provide novel adaptive alleles to populations (Galloway et al. 2020), and these events of unexpected gene flow between non-sister taxa may have helped fuel this colorful radiation. The importance of gene flow in rapid radiations has received increasing attention in recent years (Meier et al. 2017, Marques et al. 2019, Gillespie et al. 2020). Future modeling and bioinformatic developments may elucidate whether adaptive introgression events are more likely to be fueled by hybrid zones or rare hybrids. The imperfect reproductive isolation between species with dramatic plumage and vocal differences, as in the example of Yellow Warbler × Black-throated Blue Warbler, remains a curious pattern whose importance (or lack thereof) we have just begun to unveil.

In conclusion, we uncovered instances of hybridization in >93% of North American parulid warbler species and we found consistent patterns in carotenoid and wing bar inheritance between parental species pairs, consistent with past genomic studies of warbler pigmentation. We identified a striking cross of a Yellow × Black-throated Blue Warbler, whose identification was supported by evidence of plumage pattern inheritance without genetic markers. Our results may provide a framework for hybrid identification based on phenotype and they suggest several promising lines of future research on rare hybrids: (1) models and bioinformatic assessment of the prediction that rare hybrids may have helped fuel dramatic color patterns seen in Parulidae (as in Galloway et al. 2020); (2) spectrographic and biochemical analysis of pigmentation concealing patterns (i.e., black eumelanins concealing rufous pheomelanin, as we hypothesized could be the case for the Black-throated Blue Warbler); and (3) quantification of hybridization propensity within Parulidae and heterogeneity of plumage pattern inheritance. These topics have the potential to deepen our understanding of evolutionary patterns, rapid radiations, and polygenic inheritance.

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