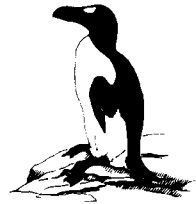


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OVERVIEWS

HYBRIDIZATION IN BIRDS

FRANK B. GILL¹

National Audubon Society, 700 Broadway, New York, New York 10003, USA

HYBRID. The word itself immediately evokes the powerful concepts of novelty, strength, and sterility. Hybrids symbolize both inferiority and superiority. Hybrids violate racial purity and clan identity. Hybrids challenge breeders, defy taxonomists, and fascinate ornithologists. Three papers in this issue of *The Auk* feature hybrid birds—testimony to their continued central role in modern ornithology. Novel phenotypes, for example, instantly capture our attention. Recall Audubon's Cincinnati Warbler (*Helminthophaga cincinnatiensis*), only recently diagnosed to be a hybrid between Kentucky Warbler (*Oporornis formosus*) and Blue-winged Warbler (*Vermivora pinus*; Graves 1988). Recall also Sutton's Warbler (*Dendroica potomac*), a tantalizing hybrid between Northern Parulas (*Parula americana*) and advancing Yellow-throated Warblers (*Dendroica dominica*; Dunn and Garrett 1997). Now, *The Auk* reports a new "wonder warbler," which Steve Latta and Joseph Wunderle found wintering on Puerto Rico. Ken Parkes diagnosed it to be the first known Magnolia Warbler (*Dendroica magnolia*) × "Myrtle" Warbler (*D. c. coronata*) hybrid (Latta et al. 1998).

This latest discovery adds to the list of odd wood-warbler hybrids, the source of Parkes' Paradox: "Why are wood warblers in different genera more prone to occasional hybridization than are wood warblers classified in the same genus?" (Parkes 1978). The Magnolia × Myrtle

hybrid increases the score for intrageneric hybrids, but it adds to the pile of evidence of odd hybrid viability. Parkes' Paradox points to issues beyond wood warblers, specifically the widespread genomic compatibility and potential for hybridization among strikingly different birds (Grant and Grant 1992). Retained genomic compatibility permits successful hybridization between unlikely parents. The ideology that hybridizing species must be closely related is dead.

Why, then, don't birds hybridize more often than they apparently do? Why don't we find "wonder warblers" more often, if intergeneric hybrids are viable? The answer lies in the powers of avian social recognition. Early imprinting starts a process of social preferences that rigorously segregates coexisting individuals into distinct cultural clusters. Assortative pairing follows, with few mistakes. Projected to its full conclusion, this line of thinking suggests that speciation in birds is as much a cultural phenomenon as it is a genetic phenomenon.

Beyond novelties lies continued interest in hybrid zones. The biological species concept focused attention appropriately on hybrid zones to evaluate whether certain taxa interbred freely or assortatively. Now, hybrid zones invite probes of increasing sophistication into the dynamics of secondary contact between divergent taxa.

Field study of hybridization between Lazuli Buntings (*Passerina amoena*) and invading Indigo Buntings (*P. cyanea*) has lagged behind interest in flickers and other well-known Great

¹ E-mail: fgill@audubon.org

Plains hybrid zones. In this issue of *The Auk*, Myron Baker and Michael Johnson (1998) start to catch up. They report that hybridizing male Lazuli Buntings and Indigo Buntings show greater distinction in plumage color than in size characteristics, suggesting differential introgression of characters. Data on genetic introgression in buntings remain limited; Baker and Johnson's survey of allozymes proved essentially noninformative. Yet, their results lend modest support to previous studies of Northern Flickers (*Colaptes auratus*), which also show steeper clines in plumage characters than in other characters. Bill Moore hypothesized that social preferences for parental phenotypes steepened the character clines and limited the width of the hybrid zone (Moore 1995).

The lead contribution in this issue of *The Auk* is an analysis of newly discovered zones of hybridization between Hermit Warblers (*Dendroica occidentalis*) and Townsend's Warblers (*D. townsendi*) in the Pacific Northwest. This article by Sievert Rohwer and Christopher Wood (1998) offers lessons of ornithological history. Two factors contributed to the belated discovery. First was new accessibility to key sites opened by logging roads that violate remnant old-growth forests. Second was the disguising of hybrids by the genetic dominance of the face pattern of the Hermit Warbler. Detailed and creative analyses of plumage differences and age changes were required to separate the effects of hybridization from intraspecific variations. The dramatic differences in facial color pattern controlled by simple Mendelian genetic traits reinforce the view that the distinctions of plumage by which ornithologists tend to define species may reflect only minor genetic changes. Parkes' Paradox echoes again backstage.

More than discovery of new hybrid zones, the confrontation between Hermit and Townsend's warblers strongly heightens our growing awareness of dynamic, transient hybrid zones that may drive the extinction of one species and replacement by a competitive superior (Rhymer and Simberloff 1996). These Pacific Northwest hybrid zones are narrow, apparently because of (social?) selection against hybrids. These hybrid zones also are moving southward, apparently because territorial Townsend's Warblers are dominant and competitively superior to Hermit Warblers. In contrast, the predictable local extinction of Golden-

winged Warblers (*Vermivora chrysoptera*) after invasion and hybridization with Blue-winged Warblers (*V. pinus*) seems to be driven by female Blue-wings with their marker mtDNA (Gill 1997), rather than by social dominance of territorial males (Confer and Larkin 1998).

The papers on hybrids in this issue of *The Auk* provide testimony to the progress of ornithology. Contrary to Rohwer et al.'s provocative first line, viz. "The predominance of the biological species concept trivialized the study of hybrid zones during much of the last half-century," we bear witness here to maturing ornithological studies of hybrids that mirror maturing theory and technology. This progress is timely. Ongoing transformations of natural landscapes guarantee more cases of population expansion, confrontation, and transient hybridization, all of which provide opportunities for new insights.

The history of Blue-winged Warblers, Golden-winged Warblers, and their hybrids offers a concluding metaphor of the constructively changing ornithological landscape. The description in 1874 of the first Brewster's Warbler (*Helminthophaga leucobronchialis*), and also of the first Lawrence's Warbler (*Helminthophaga lawrencei*), provoked a 40-year debate whether these "wonder warblers" were distinct species, color morphs, hybrids, or age variants. Then followed an era of inquiry prompted by interest in the biological species concept, inquiries that revealed limited interbreeding with local extinction and replacement. The process of replacement dominates current research. Now we probe the dynamics of ecological competition, genetic invasion, and cytonuclear disequilibria to gain insights into genetic and social architectures. Only the study of hybrid zones affords these research opportunities (Harrison 1993).

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