

A New Intrageneric *Dendroica* Hybrid from Hispaniola

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On 7 November 1993, while Latta (SCL) and Wunderle (JMW) were mist-netting in a shade coffee plantation 2 km northwest of Jumunucu, La Vega Province, Dominican Republic (elevation 600 m), an unusual-appearing warbler was captured when it responded to the playback of American Redstart (*Setophaga ruticilla*) chip-notes. Because they were unable to identify the individual (which appeared to be a *Dendroica*), SCL and JMW made extensive notes on plumage characteristics and measurements, and photographed and color-banded the bird. It was seen repeatedly in the following eight days in the same coffee plantation, after which time SCL and JMW left the area. Comparisons of their descriptions with specimens at the University of Michigan Museum of Zoology (UMMZ) failed to provide an identification of the bird. It was still present at the same location when SCL and JMW returned on 22 January 1994, at which time it was collected.

Materials and methods.—The bird was prepared as an alcohol specimen (field no. DR002, UMMZ 233,474) and sent to Parkes (KCP) for a detailed analysis. It was identified as a male by the presence of a left testis. The plumage was dried with a hand-held hair drier. It was identified as a second-year (SY) bird by the worn condition of its primary wing coverts (Pyle et al. 1987:135). All measurements were made with birds of the same sex/age class, including the flattened wing, tail, and chord of hind claw. The need for segregating specimens by age class was demonstrated by comparisons of Magnolia Warblers (*Dendroica magnolia*); for the flattened wing measurement, 11 hatching-year (HY) and SY males had a range of 59 to 62 mm ($\bar{x} = 60.3 \pm \text{SD of } 0.093 \text{ mm}$), whereas 12 after-second-year (ASY) males had a range of 59.5 to 65 mm ($\bar{x} = 62.25 \pm 0.062 \text{ mm}$).

The general color pattern, body size, and the shapes of the bill, wing, and tail identified the bird as a *Dendroica* warbler. Accepting that it was a hybrid and not merely an aberrantly plumaged individual, a search was made among male *Dendroica* for the most likely parents. Factors to be considered included the breeding ranges of the potential parent species and whether one or both winters in the West Indies. These factors, plus the face pattern (including a

blackish mask, white supercilium, and white crescent below the eye), eliminated all male *Dendroica* except *coronata*, *dominica*, and *magnolia*. Resemblance to *D. dominica* was slight; the pattern of the white patches of the rectrices, various details of body plumage, and bill length served to eliminate that species from consideration. On the other hand, resemblance to *D. coronata* and *D. magnolia* was immediately obvious. All comparisons were made with SY male specimens of *D. magnolia* and *D. c. coronata* in the collection of Carnegie Museum of Natural History, where long series of both are available. The two species are broadly sympatric in their breeding ranges. The *D. coronata* sample used for comparisons represented the nominate race; the larger *D. c. hooveri* breeds well north of the range of *D. magnolia* (AOU 1957). Both species winter in Hispaniola. *Dendroica coronata* is generally uncommon, but locally common at some sites; *D. magnolia* is a rare but regular winter resident (Wunderle and Waide 1993, S. C. Latta pers. obs.). Detailed comparisons are presented later in this paper.

Discussion.—Hybridization among North American passerines is best known in the wood warblers (Parulidae), with more than 20 species having been reported as parents of hybrids. Parkes (1961, 1978) stated that the majority of parulid hybrids were intergeneric rather than intrageneric, with the latter almost completely confined to closely related species pairs such as *Vermivora pinus* \times *V. chrysoptera* and *Dendroica townsendi* \times *D. occidentalis*. He proposed a hypothesis, independently suggested by Banks and Johnson (1961) for North American hummingbirds, to explain the prevalence of intergeneric hybrids among manakins (Pipridae) and among North American parulids. Briefly, selection has produced reproductive isolating mechanisms among sympatric North American wood warblers. These mechanisms rarely break down, but when they do, it is either among the closely related pairs or between species so distantly related and so improbable as mates that no selection against such a crossing has evolved. This hypothesis was criticized by Short and Phillips (1966; with respect to hummingbirds only), Short and Robbins (1967), and Short (1969). The argument of Short and Phillips was that the hummingbirds are oversplit generically, so that “intergeneric hybrids” are artifacts of genus-level taxonomy. As demonstrated by Parkes (1978), this argument is not applicable to most of the intergeneric manakin and wood warbler hybrids.

Since the appearance of the publications cited

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FIG. 1. Lateral and dorsal views of second-year male *Dendroica magnolia* × *D. c. coronata* mist-netted in a shade coffee plantation in the Cordillera Central of the Dominican Republic, 22 January 1994.

above, more and more hybrid parulids have been reported as specimens, photographs and field sketches. Both intergeneric (*Dendroica fusca* × *Mniotilta varia*; Bain 1996) and intrageneric (*Vermivora ruficapilla* × *V. peregrina*; Parkes 1996) hybrids are represented. All in all, intergeneric hybrids still outnumber intrageneric hybrids.

If there is any substance to Parkes's hypothesis,

what needs to be explained is why there are any intrageneric hybrids at all, if the postulated isolating mechanisms are so strong. A common explanation for hybridization in wild birds is that one of the parental species is rare, at the very edge of the area of sympatry (or syntopy) with the other parent. This hypothesis is difficult to apply to most hybrid wood warblers, because the great majority have been col-

lected or seen during migration, so that their natal locality is unknown. The present hybrid conceivably could have originated either at the northern edge of the breeding range of *D. magnolia*, or within the general area of sympatry, where the distribution of either of the species is by no means uniform, as Douglass Morse has pointed out to us (pers. comm.), "the habitat choices of these two species differ enough so that there are large areas where one is likely to be very rare and the other common." This is the first hybrid reported that involves *Dendroica magnolia*. Among the few intrageneric hybrids within the genus *Dendroica*, it is interesting to note that with the exception of species pairs, the widely distributed *D. coronata* (including both "Myrtle" and "Audubon's") has been identified as one of the parents in all of the combinations (*D. coronata* × *castanea*, *graciae*, *pinus*, *townsendi*, and now *magnolia*).

Two reviewers of an earlier draft of this note suggested that we mention that we don't know whether the putative hybrid arose from birds that were pair-bonded or from an extrapair fertilization. Whether the parents had undergone normal pair-formation behavior is irrelevant; the important thing is the product of the fertilization, namely the hybrid, from which the species identity of the parents is deduced.

Detailed comparisons.—The plumage of the presumed hybrid in some respects more closely recalls the first alternate rather than the first basic, which both species would still normally be wearing in January.

The face pattern, with a distinct blackish mask, is the character most closely resembling the alternate rather than the basic plumage. There is no indication of a mask in basic-plumaged *magnolia*, in which the ear coverts are brown, more or less washed with yellow. Although a full mask is lacking in males of *coronata* in first basic plumage, often a few scattered black feathers occur in the area of the face where the mask appears in the alternate plumage. The hybrid has a well-developed mask of black mixed with yellow. Both species have a white superciliary line in alternate plumage; in basic-plumaged *coronata*, it is buffy white or occasionally white and seldom extends forward of the eye. There may be a buffy white or white crescent below the eye, in extreme specimens combining with the superciliary to give the appearance of a broken eye ring. This is much more conspicuous in the definitive basic plumage (see photograph in Farrand 1983:137). In *magnolia*, the superciliary line is often absent in the first basic plumage. However, there is a rather distinct yellowish-white eye ring, sometimes complete, sometimes broken at the front end, back end, or both. The faint superciliary, when present, extends back or more often forward from the top of the eye ring. In alternate-plumaged *magnolia*, the superciliary is white and conspicuous, but it extends back, not forward, from the eye ring. Furthermore, the eye ring is distinctly

interrupted both front and back. In the hybrid, the eye ring and associated superciliary resembles the maximum development of this pattern in basic-plumaged *magnolia*.

The crown of basic-plumaged *coronata* is brown, finely if at all streaked with black, with a more-or-less concealed central patch of yellow. In basic-plumaged *magnolia*, the crown is gray, washed (often strongly) with greenish, and with streaks, rarely present, finer than those of *coronata*. In alternate plumage the crown of *coronata* is slate gray and so heavily streaked with black as to obscure the ground color, with a much larger and brighter yellow central patch than in basic plumage. The crown in alternate-plumaged *magnolia* is unmarked gray, somewhat paler than in *coronata*, and sometimes is very faintly washed with greenish toward the nape. There is no yellow patch on the crown of *magnolia* or that of the hybrid. The ground color of the crown of the hybrid is gray, somewhat darker than in alternate-plumaged *magnolia* and nearer that of *coronata*. Several feathers of the hybrid's crown have mostly concealed black centers, less extensive than those of *coronata* but lacking in *magnolia*. Some of the black-centered feathers of the forehead and anteriormost crown are white at the base.

In first basic plumage, most of the back of *coronata* is brown, concolorous with the crown, and heavily streaked with black (partly concealed). In some individuals, a few of the anteriormost mantle feathers are blue-gray, similarly streaked with black. In this plumage, the back of *magnolia* is greenish, with varying amounts of partly concealed black streaks, which tend to be less linear and more arrowhead-shaped than in most *coronata*. In alternate plumage, the back feathers of *coronata* are best described as black with broad blue-gray (sometimes brownish) edgings, giving an impression of strong black streaking. The back of alternate-plumaged *magnolia* is black, sometimes very narrowly edged with yellow-green anteriorly, with the black extending posteriorly from about 1/3 to all of the distance to the yellow rump; between the black back and yellow rump, the color is yellowish green as in basic plumage. In the hybrid, the back posterior to the gray nape is greenish with concealed black feather centers as in basic-plumaged *magnolia*, but duller green.

In both species, the rump is bright yellow (slightly greener in *magnolia*) in both seasonal plumages. The adjacent uppertail coverts in *magnolia* are black with broad gray margins in basic plumage. These feathers are longer in *coronata*, and the black centers are blunter, less pointed. In alternate plumage, the edgings are narrower, and in *magnolia* are washed with yellow. Unfortunately, the feathers of the rump and uppertail coverts are missing in the prepared specimen. When the bird was captured, the rump feathers were noted as being greenish, similar to those of the back, but with yellowish margins. The uppertail co-

TABLE 1. Flattened wing length, tail length, culmen length from base, and chord of hind claw for *Dendroica magnolia*, *D. c. coronata*, and presumed hybrid (UMMZ 233,474). Measurements are in mm; values are $\bar{x} \pm$ SD (range, *n* in parentheses).

Variable	<i>D. magnolia</i>	Hybrid	<i>D. c. coronata</i>
Wing	60.3 \pm 0.93 (59.0–62.0, 11)	63.5	73.9 \pm 1.50 (71.0–77.0, 12)
Tail	47.9 \pm 1.00 (46.5–49.5, 11)	52.5	56.4 \pm 1.33 (54.5–58.0, 11)
Culmen	12.3 \pm 0.39 (11.8–13.0, 10)	13.5	12.6 \pm 0.59 (11.4–13.3, 10)
Hind claw	4.6 \pm 0.47 (4.1–5.3, 10)	6.5	5.7 \pm 0.44 (5.2–6.6, 10)

verts were black with narrow gray or greenish margins.

The tail of *magnolia* is black with narrow gray edges to the feathers, and pronounced white patches on rectrices 2 to 6. The edges of the white patches on rectrices 3 to 6 are perpendicular to the feather axis. In *coronata*, the white patches extend only from rectrix 4 or 5 to 6, and the edges are more diagonally oriented. The spots of the hybrid, on rectrices 3 to 6, are midway in shape and size between those of the two presumed parent species.

The underparts of *magnolia* are bright yellow; in basic plumage there is usually an area of grayish white of variable extent across the lower throat. The sides and flanks bear variable black streaks. In alternate plumage the breast is crossed with heavy black streaks, sometimes virtually coalesced. In *coronata*, the underparts are white, variably washed with buff on the throat, sides, and flanks in basic plumage; the sides and flanks are streaked with black, and small streaks or spots of black may cross the upper breast. In alternate plumage the ground color of the underparts is pure white, and the breast is heavily marked with black spots that tend to coalesce anteriorly. There is a spot of bright yellow on the sides, just posterior to the bend of the folded wing; in first basic plumage this spot is smaller, more poorly defined, and often mixed with buff. In the hybrid, the throat and abdomen are pure white as in *coronata*. The breast is stained pale yellow. The area of the side where *coronata* has a yellow patch is slightly deeper in color than the breast. It appears that white is incompletely dominant over yellow in this cross, just as in first generation hybrids of *Vermivora pinus* and *V. chrysoptera* (Parkes 1951). There are asymmetrical black markings at the sides of the breast (mostly on the left side). These are pointed posteriorly as in *coronata*, not rounded as in *magnolia*.

The wings of the two species in first basic plumage are closely similar in pattern and in wing formula. In both species the wings are black with narrow gray outer margins, somewhat greenish in *magnolia* and brownish in *coronata*. White tips to the greater and median wing coverts form two relatively narrow wingbars (in *magnolia* these coverts are replaced at the prealternate molt by feathers with broader white edgings, giving the impression of a white patch). In *coronata*, the white wingbars are variably washed

with buff (the tips of the median coverts completely buff in some individuals). In the hybrid, the wingbars are white, showing only a faint trace of the buff typical of *coronata*.

Measurements.—The two species show no overlap in flat wing or tail measurements, with *coronata* the larger of the two (Table 1). The wing of the hybrid is slightly longer than the largest *magnolia* measured, whereas its tail length is almost exactly midway between the mean tail lengths of the two species. The bill measurements of *magnolia* and *coronata* are almost identical; that of the hybrid is 0.5 mm longer than the longest *magnolia* measured, and 0.2 mm longer than the longest *coronata*. In the chord of the hind claw, there is virtually no overlap; that of the hybrid is only 0.1 mm shorter than the largest *coronata*.

With all factors considered, we are satisfied that *Magnolia* \times "Myrtle" warbler represents the best hypothesis for the parentage of UMMZ 233,474.

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Allozymic and Morphometric Comparisons among Indigo and Lazuli buntings and their Hybrids

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Analyses of genetic variation, as inferred from morphological and biochemical traits, have contributed to our understanding of avian hybridization (Braun and Robbins 1986, Avise and Zink 1988, Gelter et al. 1989). Such analyses, together with behavioral studies in the field and laboratory (Emlen et al. 1975, Robbins et al. 1986, Baker and Baker 1990), provide an important component in understanding causes and consequences of interspecific hybridization. Conclusions about the degree of genetic isolation between two species and the geographic extent of introgression may depend upon the trait examined. Thus, by necessity, it is important to use all of the possible information available in attempting to reach a general conclusion about hybridization in any case study of a species pair. We examined allozymes, morphometric traits, and plumage patterns in Indigo Buntings (*Passerina cyanea*), Lazuli Buntings (*P. amoena*), and their hybrids to gain further understanding of events in a zone of overlap and hybridization.

Methods.—Morphological measurements and allozyme frequencies were obtained from adult males in allopatric populations of Indigo and Lazuli buntings and from a population exhibiting Lazuli, Indigo, and hybrid plumage characteristics in an area of sympatry in northeastern Wyoming (1 to 5 km south of

Beulah, along Sand Creek). Samples for allozyme analysis and for morphological measurements were taken from different individuals; specimens were obtained or individuals measured during the course of a number of field behavioral studies and laboratory experiments spanning a period of four years. Enzyme electrophoresis was conducted initially with the objective of finding one or more electrophoretic markers that could be used to identify hybrid offspring in the nest or soon after they fledged. We analyzed five morphological traits to see how well they corresponded with plumage traits that have been used traditionally to describe Lazuli, Indigo, and hybrid phenotypes (Sibley and Short 1959, Emlen et al. 1975, Kroodsma 1975).

For electrophoretic analyses, buntings were obtained from allopatric and sympatric populations. Assignment of individuals from the hybridizing population to the three morphs (Indigo, Lazuli, hybrid) was based on plumage characteristics (Emlen et al. 1975). Allopatric Indigos ($n = 12$) were sampled near Vinton, Iowa, and allopatric Lazulis near Gateway, Colorado ($n = 6$); Pocatello, Idaho ($n = 9$); and Logan, Utah ($n = 12$). In none of the allopatric populations were birds of the alternative species observed during several years of field studies. Sympatric Indigos ($n = 4$), sympatric Lazulis ($n = 12$), and hybrids ($n = 6$) were from northeastern Wyoming where the morphological data were collected. In this mixed population, all three forms could be found in

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