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A NEW HYBRID WARBLER (*DENDROICA NIGRESCENS* × *D. OCCIDENTALIS*) AND DIAGNOSIS OF SIMILAR *D. TOWNSENDI* × *D. OCCIDENTALIS* RECOMBINANTS[1]

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Abstract. We use 13 color characters to describe the first known *Dendroica nigrescens* × *D. occidentalis* hybrid. Because this specimen was collected in the southeastern Cascade Mountains of Washington during the breeding season, D. *townsendi, D. occidentalis,* and *D. nigrescens* are the only plausible parents for a hybrid male falling within the black-throated clade of *Dendroica* warblers. Multiple character states in the hybrid refute the alternative parental combinations, *townsendi* × *occidentalis* and *townsendi* × *nigrescens.* Two characteristics of this hybrid suggested further tests of the parentage of 38 problematic hybrids that were treated previously as *townsendi* × *occidentalis* recombinants by assumption only. These hybrids lack yellow on their breast, the only character that refutes a *nigrescens* × *occidentalis* parentage. The new hybrid is intermediate between *nigrescens* and *occidentalis* in the color of its posterior face and its anterior crown; thus, we scored these new characters in the 38 problematic hybrids. None of these 38 specimens was intermediate or white in either of these regions, and there was no correlation between having tinges of white in these regions and the extent of flank streaking. These results fail to support *nigrescens* in the parentage of these 38 specimens; furthermore, none of the problematic hybrids carried a *nigrescens* mitochondrial DNA haplotype. Thus, we conclude that all are unusual recombinants of *townsendi* × *occidentalis* hybridization, rather than *nigrescens* × *occidentalis* hybrids.

Key words: Dendroica nigrescens, Dendroica occidentalis, Dendroica townsendi, *hybrid, warbler.*

Rigorously determining the parentage of hybrids is challenging when the number of possible parental combinations is large, and when the number of useful characters is limited (Graves 1990). The first step in identifying hybrids is to limit the number of potential parental species. This is achieved by identifying the hybrid to the smallest taxonomic group possible (Graves 1990) and by excluding species whose breeding ranges clearly exclude the locality where the hybrid was collected, if it was collected on the breeding grounds. From this restricted pool, parentage is suggested by character states in hybrids that are intermediate to those of various parentals, and parentage tends to be refuted by character states in hybrids that fall outside the range of states defined by potential parentals (Graves 1990, 1996, Rohwer 1994).

A difficulty with intermediate character states is that they may be consistent with more than a single pair of parental species. When this is the case, contradictory states are of great help in excluding potential parental pairs (Rohwer 1994). Except for those apparently rare cases when hybrid genomes generate characteristics lying beyond the continuum of character states that might connect potential parentals (Harrison and Harrison 1963), contradictory character states reliably refute parental pairs. When these refutations leave just one potential pair of parental species as possibilities and when intermediate states also support that parentage, the parental combination of the hybrid is well established (Rohwer 1994).

Neither of these methods is perfect. Dominance may preclude the generation of intermediate character states (Rohwer and Wood 1998), and separate sets of alleles may code for different colors, precluding the generation of intermediate character states (Ford 1982). Furthermore, contradictory character states may not exist when character variation in the set of potential parentals is restricted to just a few characters with states that are shared by different potential parental pairs. When this is true, and when potential parentals are very dissimilar in appearance, there may be few or even no character states that can reject the most dissimilar potential pair of parentals. An absence of contradictory characters makes the parentage of individual hybrids impossible to determine with certainty.

Here we describe the first documented hybrid between *Dendroica nigrescens* (Black-throated Gray Warbler) and *D. occidentalis* (Hermit Warbler). This specimen is of interest to more extensive studies of hybridization between *D. occidentalis* and *D. townsendi* (Townsend's Warbler) because character variation among these three possible parentals (*occidentalis, nigrescens,* and *townsendi*) is such that only a single character can refute a *nigrescens* × *occidentalis* parentage. In contrast, five or more characters can refute both *townsendi* × *nigrescens* and *townsendi* × *occidentalis* as possible parental pairs. This situation arises because of the extreme ''pattern'' similarity between *nigrescens* and *townsendi.* Both have heavy flank streaks, both have all black crowns, and both have similar and prominent black face patches. They differ only by *nigrescens* being white on its face and breast, places

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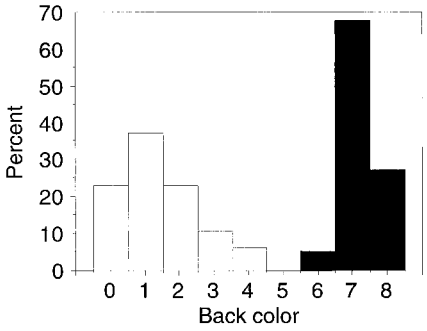

FIGURE 1. Percentage of specimens falling in each of nine scoring categories for 83 phenotypically pure *Dendroica occidentalis* (unshaded) and 210 phenotypically pure *D. townsendi* (dark). All of these specimens were collected well away from any of the three known hybrid zones between these species. The gray end of this scale (score 0 = grayest, 8 = greenest) is still much greener than the back color for pure *nigrescens* (see text).

where *townsendi* is yellow. The other potential parental, *occidentalis,* is yellow on its face and white on its breast.

Occidentalis and *townsendi* hybridize extensively in three narrow and geographically separated hybrid zones in the Pacific Northwest (Rohwer and Wood 1998). Because their hybrids are fertile, recombination can produce hybrids lacking the single character, yellow on the breast, that refutes a *nigrescens* × *occidentalis* parentage. In extensive collections from the *townsendi* × *occidentalis* hybrid zones in the Pacific Northwest, Rohwer and Wood (1998) have taken 38 of these problematic hybrids. Because *occidentalis* × *nigrescens* hybrids were unknown, we previously assumed, but could not prove, that these 38 hybrids were rare recombinants resulting from the long history of *townsendi* × *occidentalis* interbreeding. Here we use two additional characters, suggested by this new hybrid, to reevaluate our earlier assumption that these 38 problematic hybrids are recombinants of *townsendi* × *occidentalis* ancestry. None of these specimens was sufficiently intermediate in either of these new characters to suggest a *nigrescens* × *occidentalis* ancestry. Thus our assumption that these 38 specimens are rare recombinants resulting from *townsendi* × *occidentalis* interbreeding is supported, even though a *nigrescens* × *occidentalis* parentage cannot be refuted for any particular one of these individuals.

THE NEW HYBRID

On 16 June 1994, C. Wood collected a hybrid warbler (UWBM 49903) in the southeastern Cascade Mountains of Washington. The new hybrid was collected 1.6 km south and 3.2 km west of Trout Lake, Klickitat County, Washington at 700 m elevation. Its testes were fully enlarged (left 7 × 6 mm) and one of the paired knots of seminal glomeruli that create the cloacal protuberance measured 5 × 3 mm. It was presumably territorial as it was attracted to a playback of *townsendi* song that we were using to collect *townsendi, occidentalis,* and their hybrids (Rohwer and Wood 1998). Using the age characters for *townsendi* and *occidentalis* that distinguish older males from males in their first potential breeding season, this bird is an older male (Jackson et al. 1992). It was taken in a thinned stand of Douglas fir (*Pseudotsuga menziesii*), having trees up to 50-cm diameter at breast height. Canopy closure was 85%, with some oaks (*Quercus garrayna*) in grassy openings; the understory was a mix of conifers, as well as oaks and alders (*Alnus rubra*) up to 6 m tall.

Plumage. The specimen shows no character state that cannot be attributed to one of the three species of the black-throated warbler clade that breeds in the Pacific Northwest, *townsendi, occidentalis,* and *nigrescens* (Table 1). Because this bird was taken in the breeding season far from the ranges of either *D. virens* (Black-throated Green Warbler) or *D. chrysoparia* (Golden-cheeked Warbler), we have excluded these members of the clade in our analysis of its parentage. All but two of these characters are self-explanatory.

The first character requiring explanation is the absence of any trace of the bold black face patch that characterizes *nigrescens.* In *townsendi* × *occidentalis* hybrids, the *occidentalis* character state of ''no face patch'' (giving *occidentalis* its distinctive bright yellow head) is controlled almost exclusively by a single locus dominant (Rohwer and Wood 1998). In a sample of over 250 *townsendi* × *occidentalis* hybrids collected in Washington and Oregon, almost all birds had either yellow faces (like *occidentalis*) or large black face patches (like *townsendi*); very few were intermediate between the parental extremes. This new hybrid is intermediate in most of the other characters that distinguish *nigrescens* and *occidentalis* (Table 1). Thus, without knowledge of the special inheritance of the face patch in *occidentalis* × *townsendi* hybrids, a partial face patch would have been expected in this specimen.

The second character requiring special comment is back color. *Occidentalis* is often reported to have a gray back; however, comparison of pure *occidentalis* and pure *nigrescens* reveals that male *occidentalis* are always tinged with green on their backs. Figure 1 shows that pure *occidentalis* ($n = 83$) and pure *townsendi* ($n = 210$) do not overlap in back color. In this comparison, scores ranged from 0 (grayest) to 8 (greenest), but 0 on this scale is so tinged with green that pure *nigrescens* males would score as low as minus 3 to minus 5. Thus, *nigrescens* has a flat gray back without tinges of green and *occidentalis* is intermediate between *nigrescens* and *townsendi* in back color, without overlapping either. This new hybrid has a flat gray back, matching that of *nigrescens.*

We now consider contradictory character states that could refute alternate hypotheses of parentage by falling outside the range assumed by potential parental pairs (Rohwer 1994, Graves 1996). Five of the 13 characters can reject a *townsendi* × *nigrescens* parentage, and all 5 do so (Table 1). Seven of the 13 characters can reject a *townsendi* × *occidentalis* parentage, and 5 do so (Table 1). Because *nigrescens, townsendi,* and *occidentalis* exhaust the list of plausi-

TABLE 1. Character states for the new *townsendi* × *occidentalis* hybrid and contradictory character states for the possible parental combinations. Character states in the new hybrid that contradict parental combinations are in bold, whereas those that could, but do not, are not in bold. Potentially intermediate character states which cannot refute a parental combination are indicated with a dash (—).

Character	New hybrid (state relative to *nig.* and *occid.*)	Character states rejecting		
		nig. × *town.*	*town.* × *occid.*	*nig.* × *occid.*
Black face patch	absent (*occidentalis*)	**absent or reduced**	—	—
Color of ''face patch'' when black is absent	white and pale yellow (intermediate)	—	**white or pale yellow**	—
Color of lores	yellow (like both)	**any yellow (instead of black)**	—	—
Supercilium	complete (*occidentalis*)	—	broken with black	—
Color of superciliary stripe posterior to eye	white and pale yellow (intermediate)	—	**white or pale yellow**	—
Color of malar stripe	pale yellow (intermediate)	—	**white or pale yellow**	—
Color behind ''face patch''	mostly white, some pale yellow (intermediate)	—	**white or pale yellow**	—
Color of anterior crown	pale yellow (intermediate)	**some yellow (instead of black)**	—	—
Color of back	gray (*nigrescens*)	—	**gray**	—
Anterior flank streaking	moderate (intermediate)	**none or moderate**	—	—
Posterior flank streaking	moderate (intermediate)	**none or moderate**	—	—
Color below black bib	white (like both)	—	—	some yellow
Streaking on nape/upper back	moderate (intermediate)	—	none	—

ble parents, these two exclusions prove the specimen to be a *nigrescens* × *occidentalis* hybrid.

When all of the 13 characters are considered together, *nigrescens* and *occidentalis* are the most different of the three possible parental pairs. These two species share just one character state, both being entirely white (rather than yellow) on their breast posterior to the black bib. Thus the sole character state that could reject a *nigrescens* × *occidentalis* parentage—yellow on the breast below the black bib—fails to do so. The breast of this specimen is entirely white, without any tinge of yellow, suggesting a *nigrescens* × *occidentalis* parentage. Furthermore, its *occidentalis* parent was likely phenotypically pure, rather than being a *townsendi* × *occidentalis* hybrid because most *townsendi* × *occidentalis* hybrids have at least some yellow on their breasts (Rohwer and Wood 1998). The mix of white and pale yellow feathering of the anterior crown and posterior facial region of this specimen further supports a *nigrescens* × *occidentalis* parentage. In *occidentalis*, both of these areas are yellow. In *nigrescens*, the posterior face is white and, as we show below, the anterior crown is without underlying yellow.

Mitochondrial DNA. Because this specimen was collected at the southeastern edge of the Washington Cascade hybrid zone between *townsendi* and *occidentalis* (see map in Rohwer and Wood 1998), no mtDNA haplotype that it might carry could reject our conclusion that it was a *nigrescens* × *occidentalis* hybrid. Whereas *occidentalis* from California and *townsendi* from the Rocky Mountains have distinctive haplotypes (Bermingham et al. 1992, Lovette et al. 1999), both species carry both of these haplotypes in about equal frequencies near the Washington Cascade hybrid zone (Rohwer et al., unpubl. data). Thus, the *occidentalis* parent of this hybrid could have carried either an *occidentalis* or a *townsendi* haplotype. A *nigrescens* haplotype in this new hybrid would have confirmed our conclusion that one of its parents was *nigrescens.*

The mtDNA haplotype of this hybrid was *townsendi.* Because this new hybrid was collected on the edge of the *townsendi* × *occidentalis* hybrid zone, its *townsendi* haplotype is consistent with it being the product of a mating between an *occidentalis* female and a *nigrescens* male. In the southeastern-most area of the Washington Cascades where this warbler was collect-

ed, *nigrescens* occurs in pure stands of Douglas fir instead of its normal habitat of alders or oaks (Morrison 1982); elsewhere in Washington, *occidentalis* and *townsendi* exclude *nigrescens* from Douglas fir (Rohwer, unpubl. data). However, *townsendi* has just begun to penetrate as far to the south, and *occidentalis* has just begun to penetrate as far to the east, as the locality where this new hybrid was collected in the southeastern corner of the Cascades of Washington. Thus, a dispersing *occidentalis* female might have been forced to mate with a *nigrescens* male to breed at all in this area.

THE PROBLEM OF *TOWNSENDI* × *OCCIDENTALIS* RECOMBINANTS

In an analysis of three hybrid zones between *townsendi* and *occidentalis,* we have examined 256 males that were presumably hybrids because their phenotypes fell in the gap in the phenotypic space that separates parentals (Sum7st plumage scores between 0.250 and 0.750, from Rohwer and Wood 1998). However, 38 of these 256 hybrids resemble this new hybrid in having completely white breasts and well developed streaking on their flanks. Because all of these 38 hybrids lack yellow on their breasts, a *nigrescens* × *occidentalis* parentage cannot be refuted for them (Table 1, and discussion above). Discovery of this *nigrescens* × *occidentalis* hybrid begs further analysis of these 38 problematic hybrids because *nigrescens* × *occidentalis* hybrids always should have white breasts.

Intermediacy of face and crown color. A particular value of this new *nigrescens* × *occidentalis* hybrid is that it exhibits color characters on the face and crown that are intermediate between *occidentalis* and *nigrescens.* Intermediacy in the face and crown colors of this hybrid suggests that yellow pigments do not underlie the black face patch and the black crown of male *nigrescens,* in contrast to *townsendi.* To test this hypothesis, we bleached a male *nigrescens* and a male *townsendi* to remove melanins. Butcher (1984) showed that bleaching the black of the throat and back of adult male Bullock's Orioles (*Icterus bullockii*) unveils orange pigments in these regions that are just as bright as the orange on the breast of Bullock's Orioles. To control for the effects of bleach on yellow pigments, we also bleached these same regions in a male *townsendi.* For these bleachings we used two applications of Lady Clairol™ BW2 Powder Lightener mixed as per directions with Lady Clairol™ Pure White 20 Developer, the first applied for 10 min and the second applied for 20 min. Both specimens (*nigrescens,* UWBM 57809; *townsendi* UWBM 50314) were treated the same.

Our bleached *nigrescens* assumed a pale, dull reddish cast on its crown, face patch, and throat where it was black before being bleached. The gray feathers of the nape and in the posterior region of the face bleached to a still paler reddish cast. All bleached areas were changed to a dull reddish appearance, without the brightness that an exposure of yellow pigments would produce. The effect of bleaching the *townsendi* specimen was dramatically different. Bleaching did not affect the yellow of the posterior face or malar stripe. However, bleaching turned the black throat, crown, and face patch to a reddish cast, suffused with yellow and much brighter in quality than these same areas on the bleached *nigrescens.* The same was true of a small patch of the greenish feathers of the back that we also bleached in this *townsendi* specimen.

Bleaching these two specimens suggests that *nigrescens* is flat gray on its back because its back feathers lack carotenoids. Similarly, the black of the crown, throat, and face patch of *nigrescens* apparently does not mask yellow pigments. In contrast, the black face, throat, and crown, and the green back of *townsendi* males are heavily suffused with yellow pigments that are revealed by bleaching. Because *nigrescens* lacks yellow in its crown and face, a *nigrescens* × *occidentalis* hybrid should be pale yellow or white in these areas, character states that no *townsendi* × *occidentalis* F_1 hybrid, or backcross to either of these parents, should ever achieve. Assuming this new hybrid is an F_1, its *occidentalis* parent ''removed'' the black from these areas, and its *nigrescens* parent contributed no yellow to these areas, thus creating their ''washed-out'' appearance.

The pale yellow or white feathering in the posterior face and anterior crown of the new hybrid demonstrates that both of these characters can assume intermediate states in *nigrescens* × *occidentalis* hybrids. Thus an analysis of covariation between these two characters and the development of flank streaking in our 38 problematic hybrids can be informative. If some of these 38 specimens are the progeny of *nigrescens* × *occidentalis* hybrids that have backcrossed to *nigrescens,* then their posterior face and anterior crowns should be pale yellow or white. Furthermore, if any of these 38 unusual hybrids have black flank streaks because they were back-crossed with *nigrescens,* then they should tend to have correspondingly low scores (white or tinge of yellow) on their face and crown. To test these predictions, we scored both of these color characters for the 38 questionable hybrids. Both the posterior face and the anterior crown were scored as 0 = white (like *nigrescens*), 1 = white with a tinge of yellow, 2 = intermediate, 3 = yellow with a tinge of white, 4 = yellow (like *occidentalis*).

None of these 38 hybrids had enough white in their crown or face to receive scores of 0, 1, or 2 (Table 2). By this criterion all seem to be unusual recombinants of *townsendi* × *occidentalis* interbreeding. Specimens with face scores of 3 often were showing feather bases that are slightly whitish in this region. If scores of 3 in either of these regions were a consequence of *nigrescens* × *occidentalis* hybrids back-crossing to *nigrescens,* then specimens with bold flank streaks should be more likely to have traces of white in their crown and posterior face. Median tests of the frequencies in Table 2 fail to support this hypothesis (crown: $n = 32$, Fisher's exact $P = 0.34$; face: $n = 38$, Fisher's exact $P = 0.40$). Flank streaking had been scored earlier for these 38 hybrids, so we summed the scores assigned to anterior and posterior flank streaking by Rohwer and Wood (1998) for this analysis. The sample size for the crown is 32 because 6 of these problematic hybrids had fully black crowns, similar to *townsendi* or *nigrescens,* and could not be scored for white versus yellow in their anterior crown. Again, these 38 unusual

TABLE 2. Association between the amount of black streaking on the flanks and the amount of white in the face and crown for the group of putative *Dendroica townsendi* × *occidentalis* hybrids that could also be *nigrescens* × *occidentalis* hybrids backcrossed to *nigrescens*. Face and crown scores were scored as 0 = white (like *nigrescens*), 1 = white with a tinge of yellow, 2 = intermediate, 3 = yellow with a tinge of white, 4 = yellow (like *occidentalis*). Flank scores are the sum of anterior and posterior flank scores from Rohwer and Wood (1998).

	Flank scores			
	4–6	7–9	10–12	13–15
Face				
0, 1, or 2	0	0	0	0
3	6	5	2	2
4	11	7	2	1
Crown				
0, 1, or 2	0	0	0	0
3	2	1	1	0
4	14	10	2	0

hybrids seem to be recombinants of *townsendi* × *occidentalis* interbreeding.

mtDNA haplotypes. Every one of the 38 hybrid birds carried either an *occidentalis* or a *townsendi* haplotype. This lack of *nigrescens* haplotypes confirms our plumage analysis suggesting that these specimens are unusual recombinants of *townsendi* × *occidentalis* interbreeding. Of course if, for some reason, the parentage of all 38 of these hybrids had involved male *nigrescens* and female *occidentalis*, their haplotypes could not reveal *nigrescens* in their lineages. However, males, but not females, go unmated in these warblers (Pearson 2000), and *nigrescens* is the smallest of these three species, making the likelihood that every *nigrescens* × *occidentalis* hybrid would have had a *nigrescens* father extremely low. It would be more likely that *nigrescens* females would mate with *townsendi* or *occidentalis* males (or their hybrids), because males of these species are larger than male *nigrescens* and should be able to hold better territories. All three species overlap so much in their use of coniferous forests in Washington that they are frequently found in the same stands (Rohwer, unpubl. data).

Geography. The localities from which the 38 problematic hybrids were collected also suggest they are *townsendi* × *occidentalis* hybrids. Every one of the problematic hybrids was collected in areas where *townsendi* and *occidentalis* currently interbreed (Rohwer and Wood 1998). We also have collected 66 pure *occidentalis*, and 30 pure *nigrescens* to the south and east of the *townsendi* × *occidentalis* hybrid zones in Washington and Oregon. *Nigrescens* is sympatric with *occidentalis* at these out-of-zone localities just as it is with *townsendi*, *occidentalis*, and their hybrids within the hybrid zones. No bird of the problematic phenotype was collected at the localities where these pure *occidentalis* and *nigrescens* were taken. Finding these 38 problematic hybrids only within the *townsendi* × *occidentalis* hybrid zones further suggests that they are unusual recombinants of *townsendi* × *occidentalis* hybridization.

DISCUSSION

The primary value of this new *nigrescens* × *occidentalis* hybrid lies in the insights that its character states offer into other issues. Although the specimen is intermediate between *nigrescens* and *occidentalis* in most characters, it lacks any trace of the black face patch found in *nigrescens*, something that would not be expected if the face patch were controlled by multiple loci without dominance. However, Rohwer and Wood (1998) showed that the presence or absence of the black face patch in *townsendi* × *occidentalis* hybrids is controlled largely by a single locus dominant that ''removes'' the face patch. Thus, instead of being problematic, the *occidentalis*-like lack of a black face patch in this specimen provides an interesting insight into the evolutionary history of the black face patch in this clade of warblers. The split between *nigrescens* and the lineage containing *virens*, *townsendi*, and *occidentalis* is the deepest split in this warbler clade (Bermingham et al. 1992). Thus the face patch should be an ancestrally retained character in *nigrescens* and *townsendi*. In *virens*, the face patch has become green, but in *occidentalis* a single, dominant mutation has ''removed'' the face patch. Because this mutation ''removes'' the face patch both in *townsendi*, which is the sister to *occidentalis*, and in *nigrescens*, which is the most distant relative to *occidentalis* within this clade, we may infer that *townsendi* and *nigrescens* share the same mechanism for generating black face patches. Presumably that mechanism was inherited from their common ancestor.

The other useful insight offered by this specimen relates to the pale whitish appearance of its posterior face and anterior crown. That the color states of these areas are intermediate between the yellow and white states of its parentals suggests multilocus control and additive inheritance. Knowing that these areas could take on intermediate states suggested further analyses of an unusual group of 38 presumptive *townsendi* × *occidentalis* hybrids. These birds were problematic because they lack white on their breasts, the only character that refutes a *nigrescens* × *occidentalis* parentage. Recombination could produce white breasts in a lineage of *townsendi* × *occidentalis* hybrids, because *occidentalis* is completely white on its breast; thus, both *nigrescens* × *occidentalis* and *townsendi* × *occidentalis* ancestries are plausible for this group of unusual hybrids. That not one of these problematic hybrids is white or pale yellow on its posterior face or anterior crown suggests they are unusual recombinants of *townsendi* × *occidentalis* interbreeding. We also failed to find *nigrescens* haplotypes in any of these 38 problematic hybrids, and none have been collected outside of the three *townsendi* × *occidentalis* hybrid zones. Although none of this evidence can refute a *nigrescens* × *occidentalis* origin for particular specimens, such a parentage seems too unlikely to be worthy of further consideration.

The split between *nigrescens* and the lineage containing *occidentalis* and *townsendi* (sisters) is the deep-

est branch (3.7% mtDNA sequence divergence) in the clade to which these warblers belong (Bermingham et al. 1992). This divergence may be sufficient to make *nigrescens* × *occidentalis* and *nigrescens* × *townsendi* backcrosses sterile. Lanyon (1979) has shown that F_1 backcrosses are almost always sterile between *Sturnella magna* and *S. neglecta* (Eastern and Western Meadowlarks, respectively), which are separated by 5.3% mtDNA sequence divergence (Freeman and Zink 1995). Interestingly, only single *nigrescens* × *occidentalis* (this report) and *nigrescens* × *townsendi* (Rohwer 1994) hybrids are known, and both are probably F_1s. In contrast, *townsendi* and *occidentalis* interbreed extensively (Rohwer and Wood 1998), and are separated by just 0.7% sequence divergence (Bermingham et al. 1992).

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LITERATURE CITED

BERMINGHAM, E., S. ROHWER, S. FREEMAN, AND C. WOOD. 1992. Vicarance biogeography in the Pleistocene and speciation in North American wood warblers: a test of Mengel's model. Proc. Natl. Acad. Sci. 89:6624–6628.

BUTCHER, G. S. 1984. Sexual color dimorphism in orioles (the genus *Icterus*): tests of communication hypotheses. Ph.D. diss., Univ. Washington, Seattle.

FORD, J. 1982. Hybrid phenotypes in male Figbirds *Sphecotheres viridis* in Queensland. Emu 82:126–130.

FREEMAN, S., AND R. M. ZINK. 1995. A phylogenetic study of the blackbirds based on variation in mitochondrial DNA restriction sites. Syst. Biol. 44: 409–420.

GRAVES, G. R. 1990. Systematics of the ''Green-throated Sunangels'' (Aves: Trochilidae): valid taxa or hybrids? Proc. Biol. Soc. Wash. 103:6–25.

GRAVES, G. R. 1996. Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes. Proc. Biol. Soc. Wash. 109:373–390.

HARRISON, J. M., AND J. G. HARRISON. 1963. Comments on a hybrid Red Shoveler × Northern Shoveler. Bull. Brit. Ornithol. Club 83:21–25.

JACKSON, W. M., C. S. WOOD, AND S. ROHWER. 1992. Age-specific plumage characters and annual molt schedules of Hermit Warblers and Townsend's Warblers. Condor 94:490–501.

LANYON, W. E. 1979. Hybrid sterility in meadowlarks. Nature 279:557–558.

LOVETTE, I. J., E. BERMINGHAM, S. ROHWER AND C. WOOD. 1999. Mitochondrial RFLP and sequence variation among closely related avian species and the genetic characterization of hybrid *Dendroica* warblers. Mol. Ecol. 8:1431–1441.

MORRISON, M. L. 1982. The structure of western warbler assemblages: ecomorphological analysis of the Black-throated Gray and Hermit Warblers. Auk 99:503–513.

PEARSON, S. F. 2000. Behavioral asymmetries in a moving hybrid zone. Behavioral Ecology 11:84–92.

ROHWER, S. 1994. Two new hybrid *Dendroica* warblers and new methodology for inferring parental species. Auk 111:441–449.

ROHWER, S., AND C. WOOD. 1998. Three hybrid zones between Hermit and Townsend's Warblers in Washington and Oregon. Auk 115:284–310.