

A PHENOTYPIC TEST OF HALDANE'S RULE IN AN AVIAN HYBRID ZONE

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ABSTRACT.—We introduce a phenotypic method to test for excess mortality in hybrids of the heterogametic sex, as expected from Haldane's rule, and apply this method to the unusually narrow hybrid zones between Hermit Warblers (*Dendroica occidentalis*) and Townsend's Warblers (*D. townsendi*) in the Pacific Northwest. Our test requires establishing comparable hybrid indices for male and female warblers. The hybrid index that we developed for females produced age-corrected distributions for phenotypically pure reference samples that closely matched those used by Rohwer and Wood (1998) for males. The similarity in these distributions enabled us to compare the relative frequency of males and females in hybrids and parentals. We detected no deficiency of hybrid females and thus no inviability in the heterogametic sex. Our failure to find evidence of the inviability component of Haldane's rule is not unexpected given the close relationship between these taxa; nonetheless, our methods should be generally useful for studies of hybrid zones. Received 7 December 1998, accepted 2 October 1999.

HERMIT (*DENDROICA OCCIDENTALIS*) and Townsend's (*D. townsendi*) warblers diverged during the middle Pleistocene, presumably in coastal (Hermit) and Rocky Mountain (Townsend's) refugia (Bermingham et al. 1992). Both species nest and forage in the canopies of tall conifers in the Pacific Northwest. Today, their ranges meet at three narrow hybrid zones: the Olympic Mountains of Washington, the southern Cascades of Washington, and the Cascades of Oregon south of Mount Hood (Rohwer and Wood 1998). Two well-described hybrid zones in Washington are slightly more than 100 km wide, making them only three to four times wider than estimates of the root mean square dispersal distance (31 km; Rohwer and Wood 1998). The narrowness of these zones suggests that some sort of balance between selection and dispersal is preventing them from becoming wider (Rohwer and Wood 1998, Barton and Gale 1993).

Considerable evidence suggests that these zones remain narrow because hybrids are competitively inferior to Townsend's Warblers, and, further, that these zones are moving southward because Townsend's Warblers and hybrids are competitively superior to Hermit Warblers (Rohwer and Wood, 1998, Pearson 2000, Pearson and Rohwer 2000). Most hybrid zones that

are narrow relative to root mean square dispersal are characterized by hybrid inferiority relative to parentals (Barton and Hewitt 1985, 1989). Here, we examine a component of this possibility by exploring the applicability of Haldane's rule to these warbler hybrid zones.

Reduced fertility and reduced viability in hybrids often are expressed in the heterogametic sex, a phenomenon first noted by J. B. S. Haldane in 1922 and now known as "Haldane's rule." Recent work has generated a strong consensus regarding the causal mechanism underlying Haldane's rule: alleles causing hybrid problems ("speciation genes") act as partial recessives, leading to preferential expression of deleterious recessives in hybrids of the heterogametic sex (Turelli and Orr 1995, Orr 1997). These partial recessives, or speciation genes, are expressed in hybrid offspring when the genomes of isolated lineages recombine through the initiation of hybridization during secondary contact. As long as "speciation genes" act, on average, as partial recessives in genomes of mixed ancestry, hybrids of the heterogametic sex will tend to fare worse than hybrids of the homogametic sex.

Haldane's rule appears to be a very important mechanism for speciation, with sterility or inviability of hybrids of the heterogametic sex characterizing speciation in a wide variety of animals (e.g. Grula and Taylor 1980, Coyne and

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Orr 1989, Virdee and Hewitt 1992). Using comparative data on hybridization in *Drosophila*, Coyne and Orr (1989) show that sterility or inviability in hybrid males (the heterogametic sex) may represent an early stage in speciation. Although research on Haldane's rule has been largely restricted to species that can be bred in captivity, field studies on hybridizing flycatchers (*Ficedula albicollis* and *F. hypoleuca*) revealed no exchange of mitochondrial genes through hybrid females (the heterogametic sex in birds) but dramatic evidence of interspecific flow of nuclear genes through hybrid males (Tegelström and Gelter 1990). In accordance with Haldane's rule, hybrid females were shown to be infertile, whereas hybrid males were not (Gelter et al. 1990).

Despite the relatively common occurrence of interspecific hybridization in birds (roughly 10% of species are known to hybridize; Grant and Grant 1992), avian field studies that address hybrid inferiority are rare, and hybridization is still studied largely through morphological analyses of collected specimens. Here, we develop a morphological approach to explore the applicability of Haldane's rule to studies of hybrid zones. Because female birds are heterogametic, hybrid females should be more prone to decreased fertility and survivorship than hybrid males (Haldane 1922, Coyne and Orr 1989). To compare males and females, we develop a hybrid index for female Hermit and Townsend's warblers and their hybrids that closely matches the index developed by Rohwer and Wood (1998) for males. If female hybrids are suffering excess mortality, there should be a shortage of female hybrids relative to male hybrids for phenotypes midway between the parentals. Should this prediction be upheld, "speciation genes" generating inferiority of hybrids to both parentals might help explain the narrowness of the hybrid zones between Hermit and Townsend's warblers.

METHODS

We examined 284 museum specimens of female Townsend's Warblers and Hermit Warblers and part of the male sample employed by Rohwer and Wood (1998). Females collected between 1 August and 31 December, with age information on their labels, were used to develop criteria for distinguishing birds in their first year of life (i.e. yearlings) and older females (i.e. adults). Females collected at least 250 km

from the hybrid zones between 20 May and 31 July were used as reference samples to assess the range of phenotypic variation in parentals. For Hermit Warblers, reference females were collected from the southwestern Cascades of Oregon and from California. For Townsend's Warblers, reference females were collected in regions to the north and west of the hybrid zones.

Age determination in females.—Townsend's Warblers of both sexes are more boldly marked than Hermit Warblers, and adult birds of both sexes are more boldly marked than yearlings. For this reason, yearling Hermits and hybrids on average have lower hybrid indices than adults. Consequently, reliably discriminating yearling and adult females is essential to combining their scores without introducing variance related to age differences rather than to hybrid parentage. Because our objective was to develop aging criteria applicable both to hybrids and parentals, known-age birds of both species were pooled for the development of aging criteria.

Reference specimens for aging included autumn females with data on skull ossification; females with remnants of juvenal plumage; and females labeled adult, immature, or juvenile by the collector. One late-summer female (AMNH89672) with sheathing on the base of P9 was included in the adult reference sample because young birds do not molt their primaries in the year they are born (Jackson et al. 1992, Pyle 1997). Heterogeneity in our initial reference sample forced us to reassess a number of specimens. We eliminated eight late-summer birds labeled as immatures but clearly in adult plumage (with the distinct markings that yearlings lack). We also eliminated four late-autumn birds with fully ossified skulls but in immature plumage, because yearlings may have completely ossified skulls by this time (Pyle 1997). With this modified reference sample of known-age birds, we identified traits that reliably predicted age and applied these criteria to spring and summer birds of unknown age.

Plumage characteristics that distinguish the age classes of males also may distinguish those of females. Adult males of both species have more white on their fourth rectrices than do yearlings (Jackson et al. 1992). In addition, yearling males tend to have thick, black, v-shaped streaks on the shafts of their medial secondary coverts, whereas adult males have more linear, narrow streaks (Jackson et al. 1992, Pyle 1997). We assessed these characters for all known-age females by measuring the white spot on the left and right fourth rectrices (greatest length \times greatest width, in mm²) and then averaging the two measurements, and by noting the type of streaking on the shafts of the medial secondary coverts.

Our sample of known-age females consisted of 10 adults and 85 yearlings. The distribution of tail-spot sizes was distinctly bimodal; the average size of the tail spots of all but one adult was greater than 25

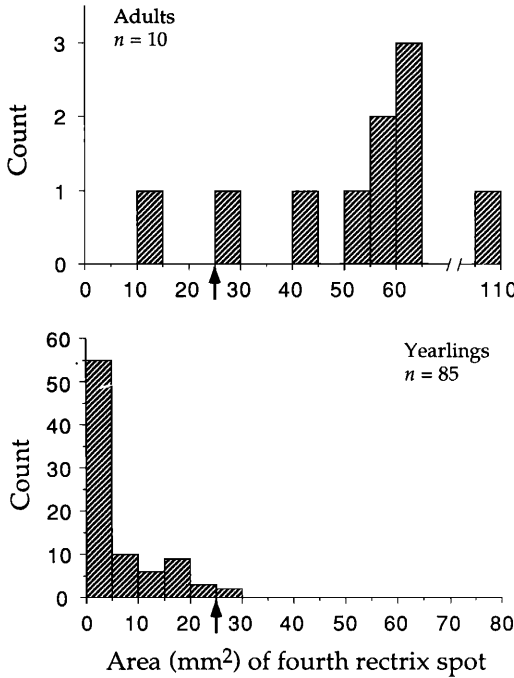


FIG. 1. Frequency distribution of tail-spot size for known-age warblers. Arrows at 25 mm² indicate the division used to separate females of unknown age.

mm², and the tail spots of all but two yearlings were less than 25 mm² (Fig. 1). Using 25 mm² as the division, the age of 92 of 95 birds (97%) was determined correctly based on the size of their tail spots. In addition, 78 of 94 birds (83%) were correctly aged by shaft streaking: 9 of 10 adults had narrow shaft streaking and 69 of 84 yearlings had thick shaft streaking. We used tail-spot size as our primary aging criterion, but we used shaft streaking to determine the age of 10 breeding birds that were missing both of their fourth rectrices.

Character scoring.—Following Rohwer and Wood (1998), we quantified color characters with numeric scores, using 0 for the most Hermit-like states and higher values for the most Townsend’s-like states (Table 1). Six of the seven characters used by Rohwer and Wood (1998) for males could be applied to females; “bib corner” could not be used because many yearling females do not have bibs. We assigned as many units as we could reliably distinguish to the remaining six characters (Table 1). Scores for each character were standardized to vary from 0 to 1 to equalize weighting. To facilitate future work, all of the reference specimens used to define character states (Table 1) are from the University of Washington Burke Museum (UWBM).

Character descriptions.—We scored flank streaking for the mid and the lower flanks, because these char-

TABLE 1. Characters, their definition, and voucher specimens used to measure character variation in Hermit Warblers, Townsend’s Warblers, and their hybrids.

Character	Definition	Reference series ^a
Intensity of yellow	0 = no yellow below bib shadow 7 = bright yellow below bib shadow	0 = 53548, 1 = 49114, 2 = 54714, 3 = 49064, 4 = 52488, 5 = 49872, 6 = 49087, 7 = 49090
Extent of yellow ^b	0 = 0 mm of yellow below bib shadow 26 = 26 mm of yellow below bib shadow	Measured directly, not scored with a reference series
Mid flank ^c	0 = no streaks 7 = heavily streaked	0 = 49114, 1 = 47905, 2 = 49064, 3 = 40646, 4 = 51340, 5 = 49096, 6 = 50854, 7 = 50776
Lower flank	0 = no streaks 6 = heavily streaked	0 = 49109, 1 = 46685, 2 = 49039, 3 = 52323, 4 = 49087, 5 = 51413, 6 = 50039
Back color ^d	0 = gray, minimal tinge of green 7 = bright yellowish olive green	0 = 53538, 1 = 53551, 2 = 49132, 3 = 49114, 4 = 49872, 5 = 49059, 6 = 49090, 7 = 51339
Crown ^e	0 = mostly yellow at base of crown feathers 7 = crown solid black	0 = 52488, 1 = 51359, 2 = 46686, 3 = 49039, 4 = 46690, 5 = 46685, 6 = 49064, 7 = 50776

^a Numbers from University of Washington Burke Museum (UWBM).

^b Values log-transformed prior to incorporation into hybrid index.

^c Scores for specimens listed below were standardized for the given character as specified in Methods. UWBM53994, UWBM50776, UWBM49090, UMMMZ192855, USNM165141.

^d AMNH89587, UCMVZ62154, UWBM49862.

^e AMNH89589.

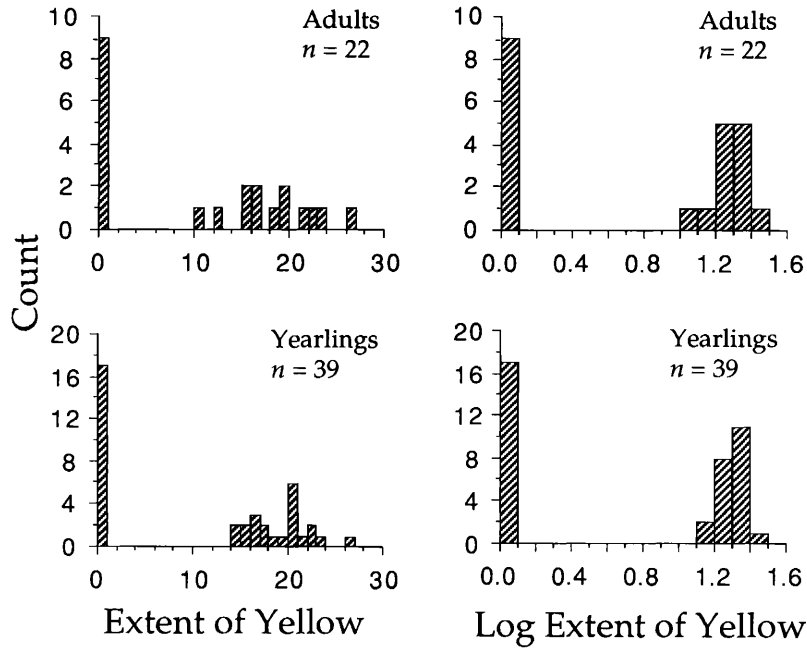


FIG. 2. Frequency distributions of the character "extent of yellow" (mm) for female reference adults (above) and yearlings (below) before (left) and after (right) log transformation.

acters appear to be under independent genetic control (Rohwer and Wood 1998). The flanks are often washed with a buffy tinge in yearling females; the streaks, if present, are gray, but often are indistinct in Hermits and hybrids. Buffiness was ignored in scoring flank streaking, and the gray streaking was scored. Extent of yellow on the breast was measured in mm from the posterior edge of the "shadow" corresponding to the bib typically found on adult males to the posterior edge of the yellow feathering. The shadow was apparent on virtually all specimens; for the few problematic yearlings, the posterior edge of the shadow was approximated. Intensity of yellow on the breast was scored from no yellow to very intense. Extent of yellow on the breast, measured in mm, is so highly variable in females that we transformed these scores to logs to make their distributions comparable to the other characters (Fig. 2). To make these transformed scores start at 0, we added 1 prior to converting scores to logs. Without this log transformation, the final hybrid index for the Townsend's reference females would be skewed to the left (left half of Fig. 2), making the female index incomparable to that for males. Extent of yellow on the crown is highly variable in hybrids but difficult to score because Hermits and hybrids often have green rather than yellow crowns. The head feathers of Townsend's Warblers are entirely gray or black from base to tip. We quantified crown color variation by gently lifting the head feathers and scoring the yel-

low coloration of their midshaft region. We scored back color (but not back streaking) emphasizing the rump, where streaking is reduced.

Standardizing scores and the hybrid index.—To eliminate age-related variation, we corrected for mean differences between age classes by standardizing the scores for adults and yearlings separately. For several characters, a few yearlings received fully adult scores. To better match the reference distributions for the two age classes, we assigned the next most frequent score to those few yearlings that were as boldly marked as adults. By dividing by the maximum value assigned to each age group, scores for each character were scaled to vary from 0 (Hermit extreme) to 1 (Townsend's extreme). The sum of these six standardized character scores was then divided by 6 to generate the final hybrid index for females, hereafter Sum6st, that was comparable to Sum7st for males (see Rohwer and Wood 1998).

Specimen localities.—Phenotypic tests of Haldane's rule apply only to birds of hybrid origin. For phenotypic comparison of the sexes, we used only hybrid localities, defined as localities with mean Sum7st for males between 0.2 and 0.8 (Rohwer and Wood 1998). We used mean locality scores for males to identify hybrid localities because females of these treetop warblers are rarely collected. Because no females were collected at many of the localities, we included males from a locality only if we also had females from that locality.

For our phenotypic test of Haldane's rule, the ideal hybrid sample would contain many males and females and would have been taken at the phenotypic center of the hybrid zone. In narrow hybrid zones, such localities may contain substantial numbers of F_1 hybrids, to which Haldane's rule is most applicable. The shortage of female specimens of these warblers precluded restricting our sampling to midpoint localities. Although this is less than ideal, the narrowness of their zones relative to root mean square dispersal distance suggests that most hybrid localities could contain F_1 hybrids. Furthermore, the "speciation genes" responsible for Haldane's rule can also be expressed in non- F_1 hybrids.

Analysis.—If Haldane's rule is operating, we would expect a deficiency of hybrids of the heterogametic sex (females in birds), which would be detected as a deficiency of hybrid females, especially of phenotypes midway between parentals. To test for a deficiency of mid-phenotype females, we compared the frequency of parentals and hybrids for females (using Sum6st) with those for males (using Sum7st). For this analysis, both distributions of standardized scores were divided into thirds. Birds scoring 0 to 0.333 were pure Hermits and Hermit-like backcrosses; those scoring 0.333 to 0.667 were mid-phenotype hybrids; and those scoring 0.667 to 1.000 were pure Townsend's and Townsend's-like backcrosses. Because Haldane's rule contrasts hybrids with parentals, birds with phenotypic scores from 0.333 to 0.667 were treated as hybrids, and the two extreme parental classes were pooled.

RESULTS

Can male and female hybrid indices be compared?—For the phenotypic comparison of males and females, the hybrid indices for samples of both sexes collected well outside the hybrid zones must have matching distributions. Moreover, the phenotypic space separating the reference samples of the two species (where hybrids should fall) must be of similar size for males and females. Evaluating this is a critical issue because our hybrid index for females (Sum6st) contained fewer characters and fewer character states than did that for males (Sum7st).

Phenotypic variation within males and females was remarkably similar (Fig. 3), leaving a similar gap for hybrid phenotypes. All Hermit reference females had scores of less than 0.2, and all but three Townsend's reference females had scores greater than 0.8 (Fig. 3). Thus, Sum6st for females was comparable to Sum7st for males, and these somewhat different hybrid

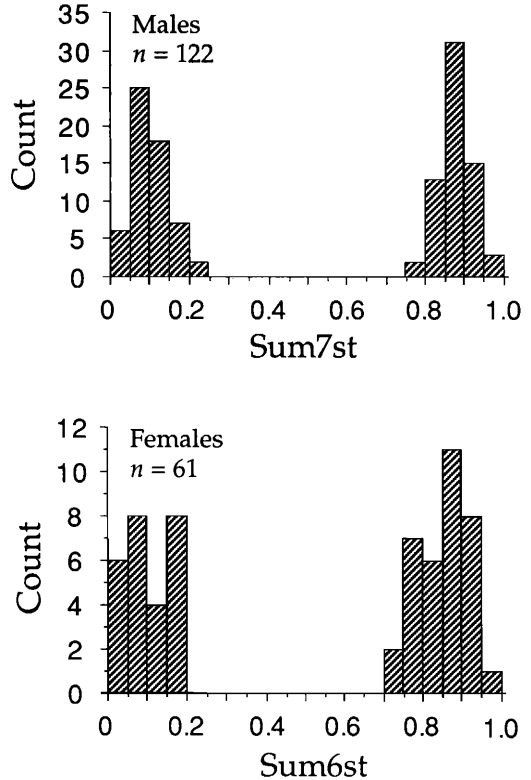


FIG. 3. Frequency distribution of hybrid index scores for reference males (above) and females (below). Note that the "phenotypic space" between Sum6st scores for reference females matches that of Sum7st scores for reference males and is similarly bimodal.

indices could be treated as equivalent in our phenotypic test of Haldane's rule.

Testing for Haldane's rule.—Across the three classes of phenotypes, the frequency of females nearly mirrored that of males, offering no suggestion of female inviability in these warbler hybrids (Fig. 4). Our samples contained more Hermit and Hermit-like hybrids of both sexes, but this merely reflected the greater geographic space covered by the Hermit side of these zones (Rohwer and Wood 1998).

Although Figure 4 divides phenotypic space into three regions, we pooled the two classes of parentals and parental-like backcrosses in our test for a deficiency of hybrid females (Table 2). Combining these classes to make this a 2×2 test for hybrid inviability in the heterogametic sex is important because the three-group analysis suggested by Figure 4 could be significant,

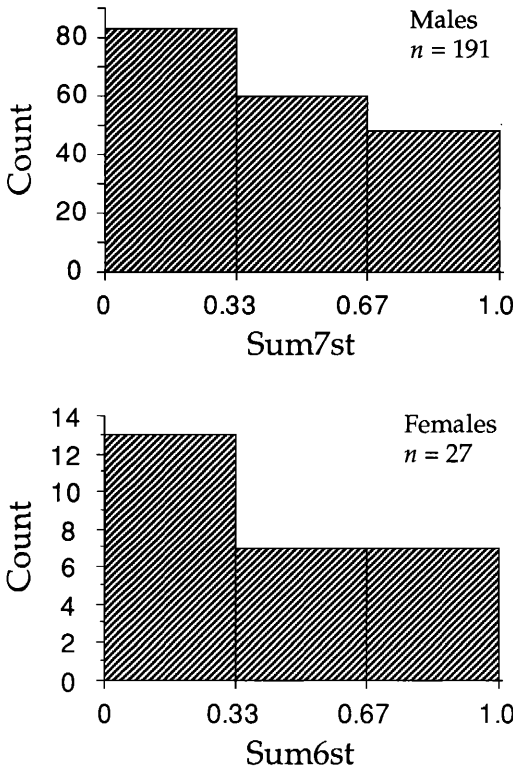


FIG. 4. Frequency distribution of hybrid male (above) and female (below) scores when phenotypic space is divided into thirds (0 to 0.333, 0.333 to 0.667, 0.667 to 1.0).

without supporting Haldane's rule. This would happen if females of one parental species were easier to collect, relative to males, than females of the other parental species. The 2 × 2 test showed no evidence of a deficiency of hybrid females in samples collected from hybrid localities (Fisher's exact test, *P* = 0.66; Table 2).

DISCUSSION

Our research makes two important contributions to the study of hybrid zones. First, we present data showing that the separate hybrid indices used for males and females in these sexually dichromatic warblers have similar distributions (Fig. 3). The similarity of these distributions makes it possible to pool males and females of sexually dimorphic species in studies of hybrid zones. Second, we show how comparisons of hybrid indices for males and females in samples of field-collected specimens

TABLE 2. Two-by-two table of male and female warblers from hybrid localities divided into "parental and parental-like backcrosses" (hybrid index 0 to 0.333 and 0.667 to 1.0) and "hybrids" (hybrid index 0.333 to 0.667) as described in Methods.

Phenotype	Males	Females
Parental	131 (69%)	20 (74%)
Hybrid	60 (31%)	7 (26%)

can be used to evaluate the inviability component of Haldane's rule.

The similarly large phenotypic gap separating parental phenotypes of males and females in these warblers suggests that hybrids should be equally detectable in both sexes (Fig. 3). We caution that the similar distributions of phenotypic scores for males and females could reflect the similar pattern of the coloration of the two sexes in these warblers. Because most of our characters could be scored for both sexes, they are likely controlled by largely overlapping sets of genes. Although this lends credence to our comparisons of male and female phenotypes in these warblers, such comparisons may not be possible for hybridizing taxa in which females do not resemble males.

Our phenotypic analyses failed to detect a shortage of female hybrids (Fig. 4, Table 2), indicating that viability of midpoint phenotypes is no less in females (the heterogametic sex) than in males. This suggests that male and female hybrids survive equally well. Haldane's rule may also be expressed by reduced fertility in hybrids, which cannot be addressed phenotypically. Pearson and Rohwer (1998) examined one component of reduced fertility in hybrids by comparing clutch sizes of hybrids with those of parentals from areas near the hybrid zones. Clutches of hybrids were smaller than those of both parentals and were significantly smaller than those of pure Townsend's, the parental species that lays the largest clutches (Pearson and Rohwer 1998).

Our failure to detect female inviability further supports the notion that competitive asymmetries account for the narrowness of the hybrid zones. If hybrids are inferior to one of the parentals, selection should keep the zones narrow. Character-transition analyses indicate that more Townsend's genes cross the zones into Hermit populations than vice versa, suggesting that the zones are moving (Rohwer and

Wood 1998). Within hybrid zones, male Townsend's are more successful at holding territories and attracting females than are male Hermits and hybrids (Pearson 2000). This is probably due to differences in aggressiveness; Townsend's males are more aggressive toward mounts of both parental phenotypes than are Hermit males (Pearson and Rohwer 2000). Unlike the case in many narrow zones where hybrids are less fit than parentals (Barton and Hewitt 1989), hybrid males are more aggressive than pure Hermits but less aggressive than pure Townsend's. Our failure to detect inviability in female hybrids adds to a growing body of information suggesting that behavioral asymmetries between parental species are largely responsible for the apparent southward movement of the zones and that the competitive inferiority of hybrids to parental Townsend's is responsible for the narrowness of the zones.

Discussions of Haldane's rule (see Orr 1997) reveal that viability of hybrids in these warblers may be expected. Using the correlation between genetic distance and divergence time in 119 species of *Drosophila*, Coyne and Orr (1989) show that as taxa diverge, disadvantage to the heterogametic sex is the first symptom of hybrid malfunction and, further, that sterility and viability disadvantages are less likely in hybrids between recently diverged taxa. Because of their conduciveness to laboratory study, breeding experiments with *Drosophila* form the only substantial body of work from which broader generalizations can be drawn. No such comparative work is available for birds.

Using mtDNA restriction-site data, Bermingham et al. (1992) found a nucleotide sequence divergence value (d_{xy}) of 0.0062 between Townsend's and Hermit warblers, by far the smallest divergence value for the five taxa examined in this clade. This is also one of the smallest estimates of divergence between congeneric species pairs in birds (Bermingham et al. 1992, Klicka and Zink 1997). Because mtDNA is maternally inherited, similarities between closely related species could reflect past hybridization as opposed to recent divergence. Bermingham et al. (1992) minimized this possibility by taking their Hermit Warbler samples from California and their Townsend's Warbler samples from the Rocky Mountains, areas that

are far removed from current hybrid zones (Rohwer and Wood 1998).

Although Coyne and Orr (1989) use Nei's (1987) genetic distance (D ; which cannot be directly compared with d_{xy}) to index divergence time, the pattern they detected should be applicable to other taxa. Because of the limited time since divergence, hybrids between closely related species are unlikely to be detrimentally affected by "speciation genes," which are deleterious recessives expressed only in individuals of hybrid ancestry. Thus, Hermit and Townsend's warblers may well be too closely related to show inviability in hybrids of the heterogametic sex. Our analyses provided no evidence of female inviability in these warbler hybrids, but we believe that the methods we developed for examining this question will be useful in studies of other hybrid zones.

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LITERATURE CITED

- BARTON, N. H., AND K. S. GALE. 1993. Genetic analysis of hybrid zones. Pages 13-45 in *Hybrid zones and the evolutionary process* (R. G. Harrison, Ed.). Oxford University Press, New York.
- BARTON, N. H., AND G. M. HEWITT. 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16:113-148.
- BARTON, N. H., AND G. M. HEWITT. 1989. Adaptation,

- speciation and hybrid zones. *Nature* 341:497–503.
- BERMINGHAM, E., S. ROHWER, S. FREEMAN, AND C. WOOD. 1992. Vicariance biogeography in the Pleistocene and speciation in North American wood warblers: A test of Mengel's model. *Proceedings of the National Academy of Sciences USA* 89:6624–6628.
- COYNE, J. A., AND H. A. ORR. 1989. Patterns of speciation in *Drosophila*. *Evolution* 43:362–381.
- GELTER, H. P., H. TEGELSTRÖM, AND L. GUSTAFSSON. 1990. Evidence from hatching success and DNA fingerprinting for the fertility of hybrid Pied × Collared flycatchers *Ficedula hypoleuca* × *F. albicollis*. *Ibis* 134:62–68.
- GRANT, P. R., AND B. R. GRANT. 1992. Hybridization of bird species. *Science* 256:93–197.
- GRULA, J. W., AND O. R. TAYLOR, JR. 1980. Some characteristics of hybrids derived from the sulfur butterflies, *Colias eurytheme* and *C. philodice*: Phenotypic effects of the x-chromosome. *Evolution* 34:673–687.
- HALDANE, J. B. S. 1922. Sex ratio and unisexual sterility in hybrid animals. *Journal of Genetics* 7: 101–109.
- JACKSON, W., 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.
- KLICKA, J., AND R. M. ZINK. 1997. The importance of recent ice ages in speciation: A failed paradigm. *Science* 277:1666–1669.
- NEI, M. 1987. *Molecular evolutionary genetics*. Columbia University Press, New York.
- ORR, H. A. 1997. Haldane's rule. *Annual Review of Ecology and Systematics* 28:195–218.
- PEARSON, S. F. 2000. Behavioral asymmetries in a moving hybrid zone. *Behavioral Ecology* 11:84–92.
- PEARSON, S. F., AND S. ROHWER. 1998. Influence of breeding phenology and clutch size on hybridization between Hermit and Townsend's warblers. *Auk* 115:739–745.
- PEARSON, S. F., AND S. ROHWER. 2000. Asymmetries in male aggression across an avian hybrid zone. *Behavioral Ecology* 11:93–101.
- PYLE, P. 1997. *Identification guide to North American birds. Part 1*. Slate Creek Press, Bolinas, California.
- ROHWER, S. A., AND C. S. WOOD. 1998. Three hybrid zones between Hermit and Townsend's warblers in Washington and Oregon. *Auk* 115:284–310.
- TEGELSTRÖM, H., AND H. P. GELTER. 1990. Haldane's rule and sex biased gene flow between two hybridizing flycatcher species (*Ficedula albicollis* and *F. hypoleuca*, Aves: Muscicapidae). *Evolution* 44:2012–2021.
- TURELLI, M., AND H. A. ORR. 1995. The dominance theory of Haldane's rule. *Genetics* 140:389–402.
- VIRDEE, S. R., AND G. M. HEWITT. 1992. Postzygotic isolation and Haldane's rule in a grasshopper. *Heredity* 69:527–538.

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