

PLUMAGE AND MITOCHONDRIAL DNA HAPLOTYPE VARIATION ACROSS A MOVING HYBRID ZONE

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Abstract.—We analyze variation in phenotypes and mitochondrial DNA (mtDNA) haplotypes over the breeding ranges of hermit and Townsend's warblers and across two of their three hybrid zones. Within these two hybrid zones, we demonstrate that the placement, shape, and width of transitions in seven plumage characters are remarkably similar, suggesting that a balance between dispersal and sexual selection keeps these hybrid zones narrow. A consistent asymmetry in these character transition curves suggests that Townsend's warblers have a selective advantage over hermit warblers, which is presumably due to the aggressive superiority of Townsend's over hermit males (Pearson and Rohwer 2000). An association between plumage and mtDNA haplotypes shows that pure Townsend's warblers, but not pure hermit warblers, immigrate into these hybrid zones, further supporting the competitive superiority of Townsend's warblers over hermit warblers. The mitochondrial haplotype transitions across these hybrid zones are much wider than the phenotypic transitions and provide no indication that the mtDNA haplotypes representing these two warblers are selectively maintained. More importantly, the phenotypically pure populations of Townsend's warblers throughout a 2000-km coastal strip north of the Washington hybrid zones contain a preponderance of hermit warbler mtDNA haplotypes. This result suggests massive movement of the hybrid zone between these warblers during the 5000 years since their most recent interglacial contact. We develop a model to explain the phenotypic and genetic divergence between these warblers and the evolution of their dramatic differences in aggressiveness; we also show how differences in male aggression, in combination with biased pairing patterns, can explain the haplotype footprint recording the historical movement of this hybrid zone.

Key words.—Character transition, cytonuclear linkage, *Dendroica occidentalis*, *Dendroica townsendi*, hybrid zone, mitochondrial DNA, phylogeography, sexual selection.

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The theoretical work of Barton and his collaborators has gone far toward linking morphological and genetic research on hybrid zones to fundamental principles of population biology (Barton 1979; Barton and Hewitt 1985, 1989; Barton and Gale 1993). For example, character variation across hybrid zones and covariances between independently assorting characters can be used to estimate dispersal distances, to infer the selective mechanisms maintaining narrow zones, and to calculate the number of genes controlling phenotypic differences in the hybridizing species. As we show in this paper, long histories of "aggressive" hybridization, which result in the competitive replacement of one species by another, can also be inferred with reasonable confidence by coupling detailed behavioral and morphological studies of hybrid zones with surveys of genetic variation over large geographic scales.

Hermit warblers (*Dendroica occidentalis*) and Townsend's warblers (*Dendroica townsendi*) hybridize in three geographically separate zones of the Pacific Northwest (Rohwer and Wood 1998). The two hybrid zones in the Olympic and Cascade Mountains of Washington are both about 125 km wide, making them narrow relative to root mean square dispersal. By Endler's (1977) diffusion model, these hybrid zones would reach this width in less than 10 generations, if Rohwer and Wood's (1998) dispersal estimate of 31 km (obtained by applying Barton and Gale's [1993] linkage analysis) is correct. The limited numbers of historical specimens available in collections show these zones have existed for considerably more than 10 generations (Rohwer and Wood 1998).

There are three general interpretations of hybrid zones that are narrow relative to dispersal. First, contact may be too

recent for gene flow to have resulted in a broad hybrid zone; this is not true for these warblers (Rohwer and Wood 1998). Second, by the bounded hybrid superiority model (Moore 1977; Moore and Price 1993), this hybrid zone could be located on a sharp ecotone where hybrids are more fit than parentals. This seems highly implausible for these warblers because no differences have been found between the parentals or between parentals and hybrids in habitat requirements (Rohwer and Wood 1998; Pearson and Manuwal 1999). Finally, narrow hybrid zones may be maintained by an equilibrium between dispersal, which increases zone width, and selection against hybrids, which reduces zone width (Barton and Hewitt 1985, 1989; Barton and Gale 1993). This model seems to fit these warbler hybrid zones partly because all three of the zones are similar in width even though contact was not simultaneous in the three zones (Rohwer and Wood 1998).

When hybrid zones are held narrow by the balance between dispersal and selection a key issue is the nature of the selection against hybrids. Following Moore and Price (1993) and Kruuk et al. (1999), we distinguish between endogenous and exogenous selection against hybrids. Endogenous selection against hybrids results from within-genome effects caused by the recombination in hybrids of coadapted genomes that are too divergent to be fully compatible. Exogenous selection against hybrids occurs when hybrids are less fit than parentals across geography, as will be the case when hybrids suffer because they are ecologically or socially less competitive than parentals.

The predominant mode of selection against hybrids is presumed to be endogenous (Barton and Hewitt 1985) and is

TABLE 1. New localities that were not described in the appendix of Rohwer and Wood (1998).

Number	Name	Locality	Elevation (ft)	Date
		Coastal		
101	Mapleton	OR, Lane Co., Mapleton, 8 km S, 7 km E	1400	28 June 1998
122	Cave Junction/ Happy Camp	OR, Josephine Co., Cave Junction, 18 km S, 6.5 km E; CA, Siskiyou Co., Happy Camp, 21.5 km N, 12.5 km W	3400 4900	24 June 1998 23 June 1998
		Cascade		
104	Roaring River	OR, Lane Co., Oakridge, 18 mi N, 32 mi E	4100	2 June 1998
115	Toketee Falls	OR, Douglas Co., Steamboat, 5 km S, 28 km E; 7 km S, 27 km E	3250	26 June 1998
120	Butte Falls	OR, Jackson Co., Butte Falls, 2.5 km S, 15.5 km E	3900	25 June 1998
123	Weaverville	CA, Trinity Co., Weaverville, 6 km E, 11 km N	3300	22–23 June 1998

usually first expressed as reduced fertility or viability in hybrids of the heterogametic sex (Haldane 1922). Smith and Rohwer (2000) could find no evidence that the viability of female hybrids was lower than that of males; females are the heterogametic sex in birds. The failure to find evidence of endogenous selection against Townsend's \times hermit hybrids is consistent with the parentals being very recently diverged sister taxa (Bermingham et al. 1992; Lovette and Bermingham 1999). Furthermore, a consequence of hybrid inferiority driven by the partial incompatibility of parental genomes is that the transitions for independently assorting characters should be coincident and concordant, as well as symmetrical (Barton and Gale 1993). However, for these warblers the transition in the composite hybrid index is asymmetrical in a way that suggests Townsend's warblers to be competitively superior to hermit warblers. The asymmetry suggests that exogenous selection is responsible for the inferiority of hybrids in this system.

This paper has three major goals. First, we compare the individual plumage transitions in two of the three hybrid zones between hermit and Townsend's warblers in Washington. This analysis is particularly interesting because behavioral studies show male Townsend's warblers to be competitively superior to male hermit warblers in measures of aggression and in success at holding territories (Pearson 2000; Pearson and Rohwer 2000). For this reason, all of the color differences between these warblers become signals of these aggressive differences; consequently, all of the plumage transitions may be held coincident and concordant by forces of sexual selection. Second, recognizing that parental competitive asymmetries could have driven considerable movement in these hybrid zones, we have sampled mitochondrial DNA (mtDNA) haplotypes from throughout much of the current range of phenotypically pure warblers of both parental species. The goal of this sampling was to evaluate the extent to which hermit warbler haplotypes may or may not be found in phenotypically pure Townsend's warblers north of the hybrid zones. Such haplotype polymorphisms could be expected if aggressive hybridization by Townsend's warblers had erased all phenotypic traces of past hybridization between these species north of the current zones. Finally, we conclude by presenting a model for the isolation, differentiation, and contact between these warblers and for the evolution of the extreme aggressive differences between the parentals; this model suggests additional predictions to test.

METHODS

Collecting and Character Scoring

Rohwer and Wood (1998) provide details on collecting procedures and list most of the collection localities. Table 1 gives locality descriptions for samples used in this study that were collected since Rohwer and Wood (1998). We excluded females from the phenotypic analyses because so few were collected. Genetic analyses are based on larger sample sizes, which include females, as well as additional samples from Oregon and California that are not part of the phenotypic analyses reported here.

Rohwer and Wood (1998) describe the scoring system for each of the eight plumage characters. Characters were weighted equally by standardizing them to vary from 0.0 to 1.0 before the summed hybrid index was computed; character scores were standardized separately for yearlings and adults because variation is more restricted among yearlings (Rohwer and Wood 1998). For seven of the eight plumage characters, variation among hybrids was continuous, suggesting additive inheritance and control by multiple loci (but see Bradshaw et al. 1998). Face coloration, however, appears to be principally controlled by a single locus with two alleles, with the dominant coding for the solid yellow face of hermit warblers and the recessive for the black face patch of Townsend's warblers (Rohwer and Wood 1998). To avoid confounding selection with Mendelian inheritance, we exclude face from most of our analyses. To reduce the number of pairwise comparisons of characters, we sometimes contrast one character against the combined hybrid index (also standardized to vary from 0.0 to 1.0) for the other characters. In the following analyses Sum7st is the hybrid index for the seven plumage characters (face excluded). Sum6st and Sum4st represent combinations of six and four standardized plumage characters, respectively.

Geography-Dependent Character Transition Curves

The shape of the transition curves describing phenotypic change across hybrid zones is of great importance in inferring the nature of selection acting on hybrids (Barton and Hewitt 1985; Harrison 1990; Barton and Gale 1993). Deviations from symmetry in these typically sigmoidal curves may indicate differential flow of genes resulting from competitive asymmetries or from population density differences in the parental species. Barring pleiotropy, curves for narrow hybrid

zones that are similar in both geographic width (concordant curves) and placement (coincident curves) indicate similar magnitudes of selection on all characters. Such matching curves may arise from shared endogenous or exogenous selective regimes or from the superiority of one parental form over the other. In contrast, character transition curves that are discordant in width or geographic position indicate that characters are reacting independently to drift or to selection.

To illustrate the dramatic similarity of our plumage transition curves in width, shape, and geographic placement, we superimpose the curves for each hybrid zone. Curves were fit with a Loess smoothing function with the tension set slightly differently in the two transects to accommodate differences in the density of sampling (SAS Institute 1998, p. 225). Because the means for different plumage characters varied considerably within zones, we subtracted the mean of the locality means for each character within transects. This approach gave the curves the same central placement on the y-axis, thus facilitating interpretations, which are based on contrasts and similarities in the width and position of these transitions on the x-axis.

Transect-Independent Tests of Similarity in Character Transitions

We analyzed the striking visual similarity in the placement and width of the different plumage transitions by plotting one character or a combination of characters against another (after Barton and Hewitt 1985; Kruuk 1997). This regression methodology allows all localities from a hybrid zone to be included in the analysis because no measure of geographic distance is needed. Thus, samples need not fall on a transect to be useful. When the transitions for two characters have identical widths and central placements, regressing one character on another will yield a straight line. If the transition for a character is displaced in space relative to another, then the quadratic term will be significant; if one character shows a more abrupt or a more drawn-out character transition relative to another, then the cubic term will be significant (Kruuk 1997).

Using these regression analyses to discover significant nonlinearities helps identify potential differences in the strength of selection operating on individual characters. Differential movement of specific characters may reveal complexities in the maintenance of hybrid zones that go beyond the generally presumed exogenous selection against hybrids (Barton and Hewitt 1985), thus helping target unusual characters for detailed analyses of function (e.g., Parsons et al. 1993). For the regression analyses of the Washington Cascades hybrid zone, we used all the hybrid localities defined in Rohwer and Wood (1998). We did not pool localities from the different hybrid zones because selective regimes could differ in the different zones.

Mitochondrial DNA Haplotype Scoring

MtDNA haplotypes were assessed for 1157 warblers by restriction fragment analyses of either the complete mitochondrial genome ($n = 663$) or of a polymerase-chain-reaction-amplified (PCR) region of the mitochondrial cytochrome oxidase I (COI) gene ($n = 591$). Ninety-seven in-

dividuals were analyzed using both methods, which accounts for the two assays summing to greater than 1157. Bermingham et al. (1992) and Lovette et al. (1999) have published mtDNA-based phylogenies of the *Dendroica virens* species group, including hermit and Townsend's warblers, and identified the species-specific mtDNA markers used in this study (referred to as Townsend's mtDNA and hermit mtDNA). To establish the expected haplotype fragment pattern for pure populations, we assessed the genotype of 66 Townsend's warblers from five interior localities that should never have been affected by hybridization (Fairbanks, Alaska and four widespread Rocky Mountain locations in British Columbia, Washington, and Oregon; localities 1, 6, 10, 33, and 96 in Rohwer and Wood 1998) and 51 hermit warblers from five southern locations also well removed from the hybrid zones (two in northern California and two in southern, coastal Oregon; locality numbers 97–99 and 101 in Rohwer and Wood [1998] and 122 of Table 1). We observed only Townsend's mtDNAs in birds from the Fairbanks and Rocky Mountain localities and only hermit mtDNAs in the southern Oregon and California warblers. Because we collected multiple and moderately large samples well outside the present-day hybrid zones, we are reasonably confident that our mtDNA markers diagnose historical species boundaries between Townsend's and hermit warblers.

In our restriction analysis of the complete mtDNA, we used cesium chloride gradient-purified mtDNA that had been radioactively labeled to hybridize Southern-blotted total genomic warbler DNA digested by either *HindIII* or *XbaI* to distinguish between Townsend's and hermit haplotypes. This approach characteristically yields a composite *HindIII/XbaI* mtDNA restriction-fragment-length-polymorphism (RFLP) haplotype designated BT for Townsend's warbler and ES for hermit warbler. The composite mtDNA haplotype of the hermit warbler represents the loss of a *HindIII* restriction site and a *XbaI* site relative to Townsend's warblers (Bermingham et al. 1992).

Samples collected more recently in our study were genotyped using PCR-RFLP. For this work we amplified a 681-bp portion of the mtDNA COI gene using the COIa-3' and COIf-5' primers of Kessing et al. (1989) and then separately digested the product with the restriction enzymes *AluI*, *MspI*, and *XmnI* (Lovette et al. 1999). The characteristic composite PCR-RFLP mtDNA COI haplotype for Townsend's warbler was designated AAA; hermit warblers were designated BBB or CBB. The Townsend's *AluI* A genotype represents the gain of a restriction site relative to hermit warblers, and the hermit *AluI* C genotype represents gain of a second *AluI* site relative to the hermit *AluI* B and Townsend's *AluI* A genotypes. The Townsend's *MspI* A and *XmnI* A genotypes each represent single restriction site losses relative to the hermit B genotypes for those two enzymes. Lovette et al. (1999) map the restriction site transitions used in this study to distinguish Townsend's and hermit warbler mtDNAs in their figure 1 representing a COI sequence-based phylogeny of 13 Townsend's and hermit mtDNA haplotypes.

In assigning haplotypes to individuals collected throughout the ranges of these species, those matching the complete mtDNA or mtDNA COI genotypes described above were assigned as carrying either hermit (ES, BBB, CBB) or Town-

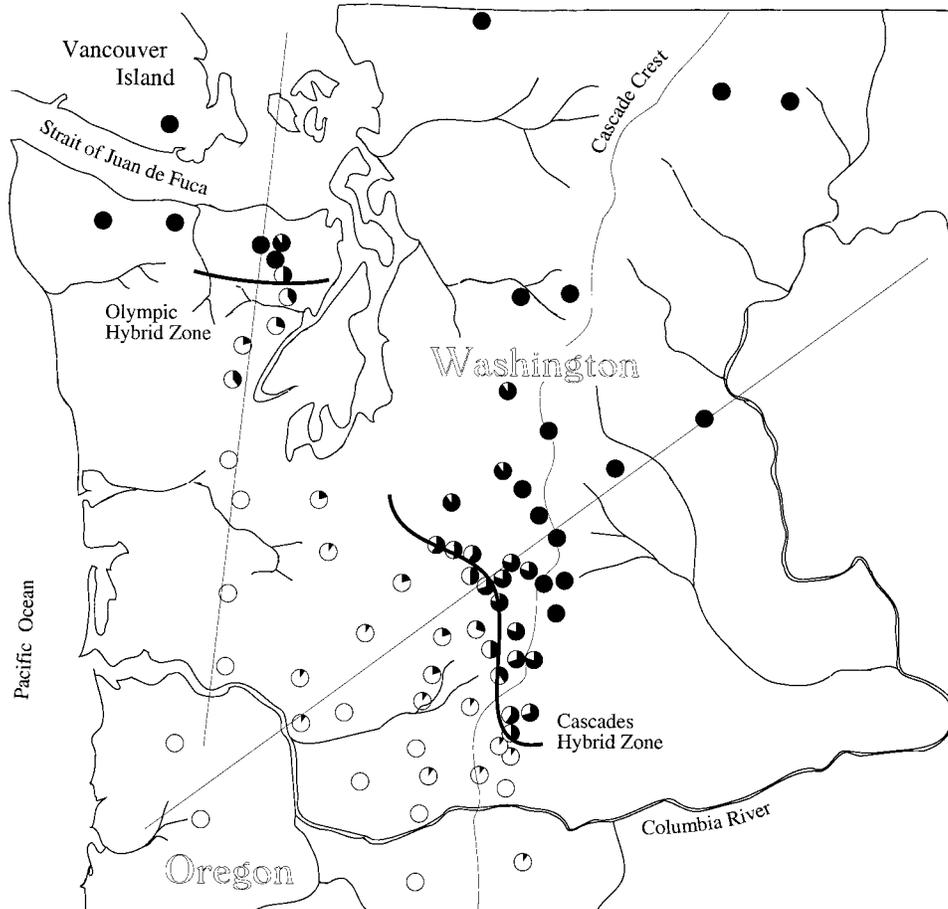


FIG. 1. Location of the Olympic and Cascade hybrid zones in Washington. Pies represent mean phenotypic scores (pure Townsend's warblers are filled, pure hermit warblers are open); heavy lines represent midpoint phenotypes in these zones; thin lines are transects used to plot character transitions shown in Figures 2 and 3.

send's (BT, AAA) haplotypes. Thirty warblers carried variants of these five mtDNA haplotypes. Classification of the four variant COI-RFLP haplotypes and the seven variant mtDNA full-genome-RFLP haplotypes was accomplished by sequencing one or two individuals representing each variant for the 614-bp fragment of mtDNA COI reported in Lovette et al. (1999). Subsequent phylogenetic analysis of the COI sequences permitted us to identify each of the 11 RFLP variants as a member of either the Townsend's or hermit mtDNA clade (unpublished Nexus file and phylogenetic hypothesis available from <http://nmg.si.edu/bermlab.htm>).

We used the computer package Arlequin (<http://anthropologie.unige.ch/arlequin>) and mtDNA haplotype frequency data to calculate F_{ST} -values among coastal populations of Townsend's warblers from British Columbia and Alaska.

RESULTS

Character Transitions

The general location of the Washington Cascade and the Olympic hybrid zones are shown in Figure 1, along with the transects we used for the character transition analyses. These transects were drawn to pass through the hybrid zones per-

pendicular to the line of midpoint-phenotypes. Samples in the regions on either side of the transect lines in Figure 1 were projected, perpendicularly, onto the transect for the character transition analyses (Rohwer and Wood 1998).

For the Washington Cascades transect (Fig. 1), where our sampling is strongest, we plot transitions for each character individually in Figure 2. In all of our character scoring, 0.0 represents the hermit warbler extreme and 1.0 represents the Townsend's warbler extreme. For some characters, parental samples taken well outside the hybrid zones show considerable variation. This causes the means for pure populations to fall above 0.0 and below 1.0, limiting the intermediate phenotypic space that defines hybrid populations. The horizontal grid lines in Figure 2 delimit the most intermediate character means for eight samples of hermit warblers and 15 samples of Townsend's warblers taken well outside any of the hybrid zones.

Except for one character, the composite plots for the individual character transitions are similar in central placement and width (Fig. 3). Only the curve for face coloration is displaced to the Townsend's side of the zone (Fig. 2). This happens because a single, dominant allele codes for the entirely yellow face of hermit warblers (Rohwer and Wood 1998); thus, we have omitted face from Figure 3. If these

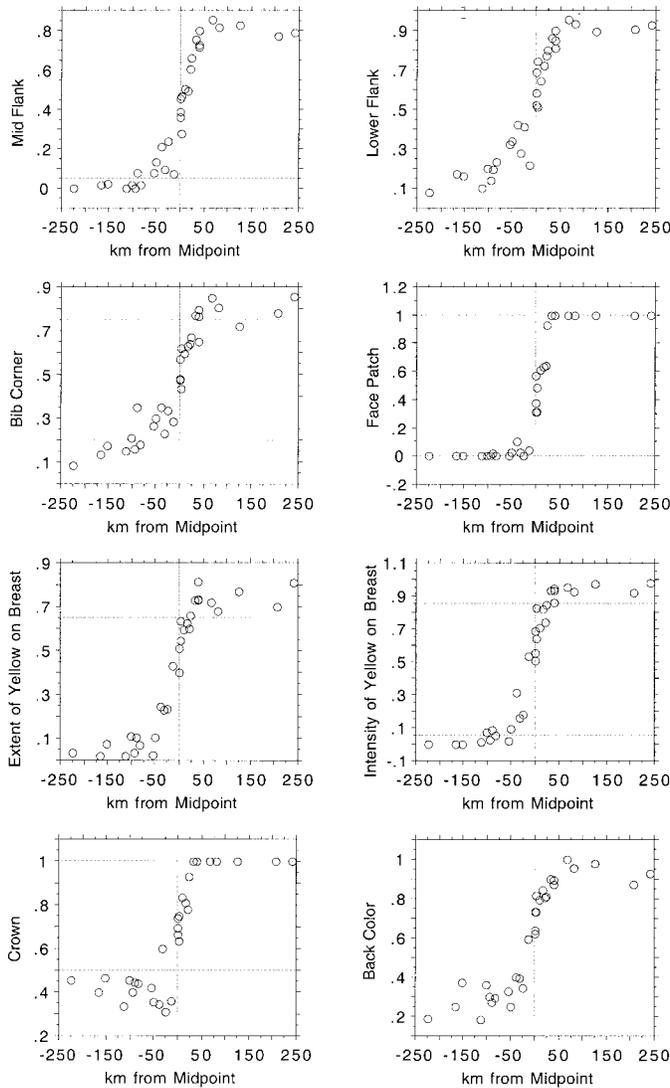


FIG. 2. Character transitions for the Washington Cascades transect for each of the eight plumage characters. Each point is a locality mean. The grid lines on the y-axis represent the limits of variation in locality means for the Townsend's warbler reference samples (higher values) and the hermit warbler reference samples (lower values).

hybrid zones have existed for many generations, then the close matches in the position and width of each of the character transitions implies that the zones are being maintained by general selective forces, such as hybrid inferiority (Barton and Hewitt 1985; Barton and Gale 1993) or sexual selection driven by the superiority of one parental over the other. In all the collecting associated with this study, no differences in the density of parental populations was observed on either side of these hybrid zones. Thus, we see no reason to infer that population density differences between hermit, Townsend's, or hybrid warblers are moving these zones (Barton and Hewitt 1985; Rohwer and Wood 1998).

What forces of selection maintain these zones? Symmetrical character transition curves suggest hybrid inferiority and imply that hybrids are equally inferior to both parental types. Asymmetrical character transitions suggest asymmetric gene

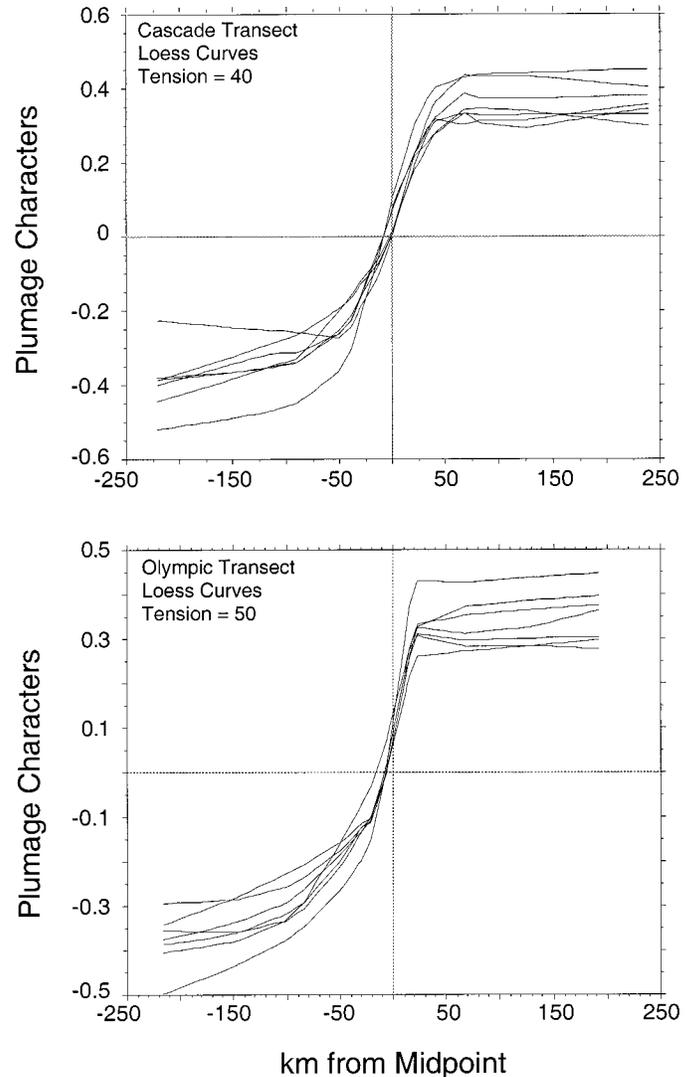


FIG. 3. Character transition curves for the Washington Cascades (A) and Olympic (B) transect for the seven plumage characters with additive inheritance. Each curve was fit with a Loess smoothing function with the tension set slightly differently in the two transects to accommodate the differences in the density of the sampling. Within each transect, the mean for each character was set to zero by subtracting the mean of the locality means.

flow. Most of the individual character transitions, as well as the composite index shown in Rohwer and Wood (1998), are asymmetrical in a way that suggests Townsend's warblers have a selective advantage over hermit warblers (Figs. 2, 3). At least five of the seven characters with additive inheritance have curves that are drawn out on the hermit side of the hybrid zones (crown and back color may be exceptions; Fig. 2). Two conclusions follow from this consistent asymmetry. First, Townsend's warblers should be replacing hermit warblers, causing the zones to move (Rohwer and Wood 1998). Second, the narrowness of these zones is most strongly maintained by the competitive inferiority of hybrids to parental Townsend's, a point that is confirmed by the extremely abrupt geographic transition from pure Townsend's phenotypes to hybrids of midpoint phenotype (Figs. 2, 3).

The 200-km separation between the Olympic and Cascade hybrid zones indicates that these zones represent at least partially independent evaluations of the width and shape of the character transitions. Plumage transitions across the two zones are strikingly similar in width and shape (Fig. 3), suggesting that hybrid inferiority to Townsend's warblers is constant in both selective environments.

Transect-Independent Measures of Similarity in Character Transitions

In this section, we test the similarity in geographic placement and width of the plumage transitions presented visually in Figure 3. We do so using Kruuk's (1997) transect-independent regression method, an analysis that employs all hybrid localities for a zone, regardless of whether they fall close to a linear transect crossing the zone (see Fig. 1).

Individual characters.—With Kruuk's (1997) procedure, we were able to use all 38 hybrid localities from the Washington Cascades zone to evaluate the similarity of the various plumage transitions. To reduce the number of pairwise analyses entrained by eight plumage characters, we regressed each individual character on the summed index for the other six plumage characters (see Methods). The focal character segregated on the y-axis was excluded from the x-axis. These regression analyses (Fig. 4) tell us if individual character transitions are displaced in space, have transitions, or differ in width from the transition for the other characters combined (see Parsons et al. 1993).

Quadratic regressions for each of the seven characters against Sum6st (the combined hybrid index less the character being analyzed) are shown for the Cascades transect (Fig. 4). We also analyzed the Olympic samples to assess the degree to which the results for the two hybrid zones are consistent (Table 2). Apart from face (see below), only one character in each hybrid zone had a significant quadratic term (Table 2). Because these quadratic terms were inconsistent in sign and magnitude between the two zones, we consider it likely that they are sampling artifacts and therefore do not interpret them. No character showed an unusually abrupt or wide transition; thus, no cubic model approached significance.

The plot of face against the sum of the standardized scores for the other seven characters illustrates the use of this regression method to uncover differences in the geographic placement of the transitions for different characters (Fig. 4). Because the black face of Townsend's warblers requires two recessive alleles to be expressed in hybrids (Rohwer and Wood 1998), the regression analysis should show face scores displaced to the Townsend's side of the hybrid zones. This follows because, individuals carrying an equal mix of hermit and Townsend's alleles should produce an excess of hermit like faces because the allele coding for a yellow face is dominant in hybrids. The highly significant quadratic regression for face on the composite score for the other seven characters supports this prediction (Fig. 4; Table 2). Although the quadratic coefficient for face has the same sign and is about the same magnitude for both hybrid zones (Table 2), it is not significant for the Olympic transect (Table 2; $P = 0.06$), presumably because we have so few Olympic localities. Although selection cannot be excluded as contributing to the

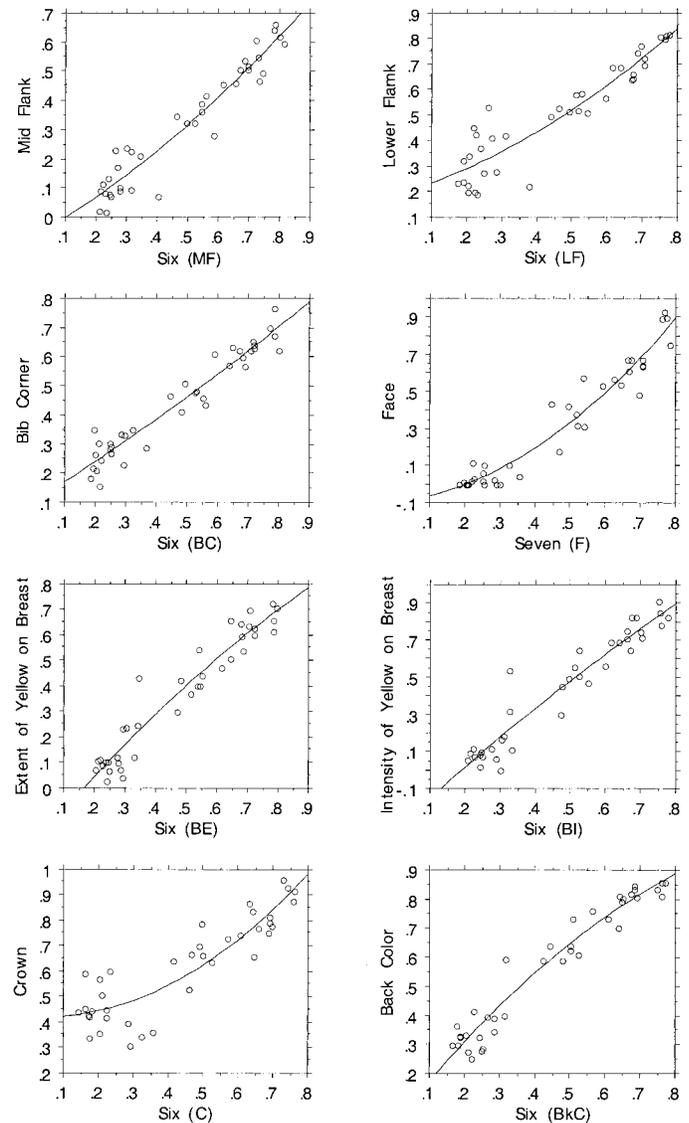


FIG. 4. Plumage character means regressed on the mean hybrid indices (less that character) for hybrid localities in the Washington Cascades (Rohwer and Wood 1998). Face and crown have significantly positive quadratic terms, indicating that their transition curves are displaced slightly to the Townsend's warbler side of the zone. The hermit warbler face pattern is produced by a single-locus dominant (Rohwer and Wood 1998), which causes this curve to be displaced to the Townsend's side of the zone. No cubic terms were significant, indicating that all of the transitions were of similar width (see Figs. 2 and 3). Regression coefficients and P values for these data and for the Olympic hybrid zone are presented in Table 2.

displacement of the transition for face, we see no reason to suggest a role for selection. The cubic regression of face on the other characters was not significant.

Yellow versus black characters.—Whereas the preceding analysis should identify unusual individual characters, it could fail to identify groups of associated characters. Imagine that our eight plumage characters constitute two groups of characters subject to somewhat different selective forces. If this were true, then characters from each of the different groups might show different character transitions. However,

TABLE 2. Regression statistics for the analyses associated with Figure 4. For the Washington Cascades we used all 38 hybrid localities (see Rohwer and Wood 1998); for the Olympics we used localities 17–27, all of which lie within or very close to the hybrid zone. A significantly b^2 term means that the transition for that character is geographically displaced to one side of the composite transition for the other characters. Face is displaced to the Townsend's side of these zones because the entirely yellow face of hermit warblers is controlled almost entirely by a single locus dominant (Rohwer and Wood 1998). With only 10 samples for the Olympics, b^2 is not significant for face; however, b^2 is positive and similar in magnitude to the b^2 found for the Cascade samples. The marginal significance of b^2 for intensity of yellow on the breast and for crown may be accidental, especially for intensity of yellow, because b^2 is not consistent between the two zones.

Focal character	WA Cascade zone		Olympic zone	
	b^2	P	b^2	P
Mid flank	0.31	0.36	-0.16	0.72
Lower flank	0.39	0.24	-0.76	0.14
Bib corner	0.11	0.68	0.39	0.23
Face	1.28	0.008	1.4	0.06
Extent yellow on breast	-0.33	0.40	-0.01	0.98
Intensity yellow on breast	-0.27	0.64	1.2	0.04
Crown	0.98	0.04	0.46	0.13
Back color	-0.55	0.07	-1.0	0.07

any one character, compared to a composite index of the others, might fail to stand out. Such a case might arise for our four characters that measure black and our three characters that measure yellow. For example, if selection or pleiotropy differentially affects black and yellow characters, segregating one measure of black on the y-axis as the focal character and including other measures of black in the composite index used for the x-axis causes the axes to become correlated.

We used factor analyses to assess the degree to which our seven plumage characters with additive inheritance (face excluded) might covary. The analysis was run on all individual males taken at hybrid localities in the Washington Cascade zone. Factors were extracted from a correlation matrix and rotated to search for a simple solution. Oblique rotations did not improve the results of the vari max rotation. Factor I explained 77% of the variation in the data and all seven characters had very high and positive loadings on factor I. The high variance explained by factor I means that most variation across individuals is correlated to the degree of backcrossing toward either parental. Factor II explained 13% of the variation in this dataset. Importantly, the four measures of black all received negative signs on factor II, whereas the three measures of yellow all received positive signs on factor II. We cannot exclude pleiotropy as the cause of the close covariation of black characters with other black characters and of yellow characters with other yellow characters. However, if regression analyses show the transitions between the set of black and the set of yellow characters to be significantly nonconcordant, then either selection or drift is affecting the two sets of characters independently.

To examine this possibility we created two new standardized hybrid indices, one for the three yellow characters and one for the four black characters, and regressed them against one another (Fig. 5). The cubic model was highly significant ($P = 0.006$), primarily because black characters penetrate the

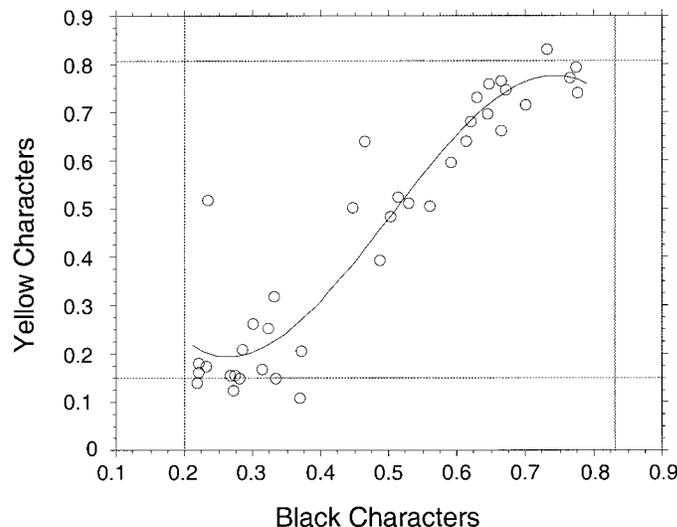


FIG. 5. Regression of the composite index for the three yellow characters (Sum3st) on the composite index for the four black characters (Sum4st) for the Washington Cascade hybrid localities. The significant cubic term indicates that the transitions for black characters are slightly wider than those for yellow characters, something that was apparent in every comparison of pairs of characters from these two color groups. Grid lines mark the uppermost mean for reference samples of hermit warblers and the lowermost means for reference samples of Townsend's warblers. When the outlier is removed (locality 62, $n = 4$), the cubic term remains significant ($P = 0.004$).

hermit side of the zone more effectively than the yellow characters (Fig. 5). The grid lines in Figure 5 mark extreme values for these new indices in 15 reference samples of pure Townsend's warblers and eight of pure hermit warblers, all collected outside the hybrid zones. These gridlines make it easy to see that several samples from hybrid localities collected on the hermit warbler side of the Washington Cascade zone are characterized as pure hermit warblers by their yellow characters but hybrids by their black characters. Thus, the transition for the four black characters is somewhat wider than the transition for the three yellow characters (Fig. 5). A quadratic regression model applied to these same data was not significant, thus the transitions for these two sets of color characters are not displaced geographically. To further evaluate these transitions, we analyzed all possible pairs of yellow and black characters. As in the summary plot (Fig. 5), these pairwise analyses showed black characters to be more drawn out on the hermit side of this hybrid zone.

Although the cubic term in the regression of the index for yellow characters on that for black characters (Fig. 5) is highly significant, the improvement of the cubic model over the linear model is minimal. A linear model fit to the data in Figure 5 has an adjusted r^2 of 0.855, whereas the cubic model has an adjusted r^2 of 0.878; thus, the cubic model explains just 2.3% more variance than the linear model. This amounts to very little difference in geographic space, which is apparent from an examination of Figure 3. Experimental work will probably be needed to determine why the black characters of Townsend's warblers penetrate hermit populations more effectively than do yellow characters.

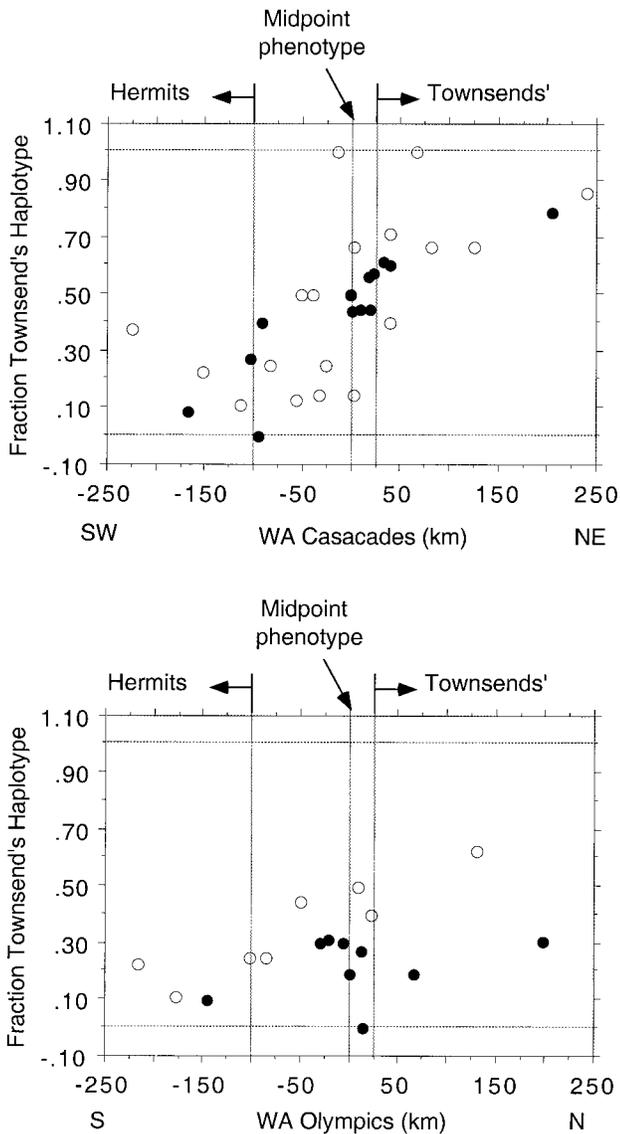


FIG. 6. Mitochondrial haplotype transitions along the Cascade and Olympic transects; open circles are samples of four to nine specimens; filled circles are samples of 10 or more specimens. The location of these transects is shown in Figure 1, and the unpooled sample localities are given in Rohwer and Wood (1998). The phenotypic center of the hybrid zone is marked by the vertical grid line at zero, the lines to either side of it delimit the distribution of hybrid localities. The association between mtDNA haplotype frequencies and phenotype in the Cascade zone is an artifact of this transect having a partially east-west orientation (see Fig. 1).

Haplotype Transitions

The pattern of geographic variation in haplotype frequencies differs dramatically from that for plumage transitions. We illustrate this point by plotting the change in haplotype frequencies across the same Washington transects used to analyze plumage transitions (Fig. 6). Vertical grid lines in Figure 6 contain the complete transition in plumage characters. For the Cascade transect, the frequency of Townsend's haplotypes declines significantly ($r^2 = 0.46$, $P < 0.001$) from

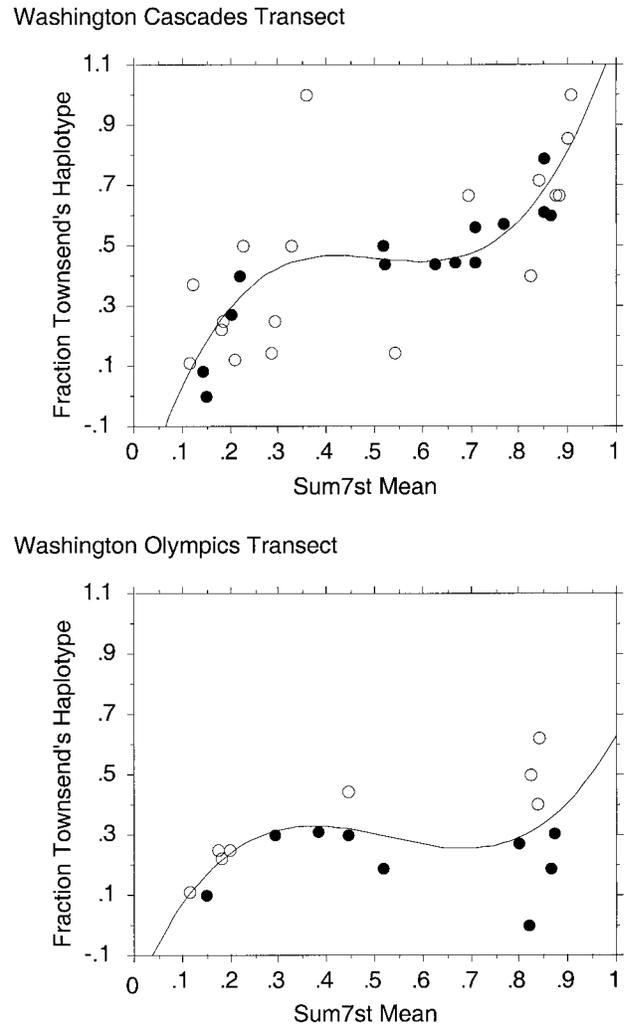


FIG. 7. Regressions of mtDNA haplotype frequencies on mean plumage scores for the Cascade and Olympic transects. Unlike individual plumage characters, both of these regressions had highly significant cubic terms because the haplotype transitions are greatly drawn out compared to the plumage transitions (see Fig. 6).

northeast to southwest, although haplotype frequencies are not fixed at either end of this 500-km transect.

To analyze similarities in width and placement of the haplotype transitions, we regressed locality frequencies on the combined hybrid index, Sum7st. For the Washington Cascade zone this regression has a significant cubic term (adjusted $r^2 = 0.59$, $P = 0.029$), showing the haplotype transition to be greatly drawn out relative to the plumage transition (Fig. 7). When just the localities with more than 10 birds are included, significance rises and r^2 increases to 0.85. For the coastal transect, which includes the Olympic hybrid zone (see Fig. 1), haplotype frequencies do not vary over distances of 250 km to the north and 250 km to the south of the center of the Olympic hybrid zone. The linear, cubic, and quadratic models were not significant (Fig. 7; cubic model: adjusted $r^2 = 0.04$, $P = 0.41$). As we show in the next section, this discordance between plumage and haplotype transitions results from the vastly larger spatial scale over which haplotype frequencies vary.

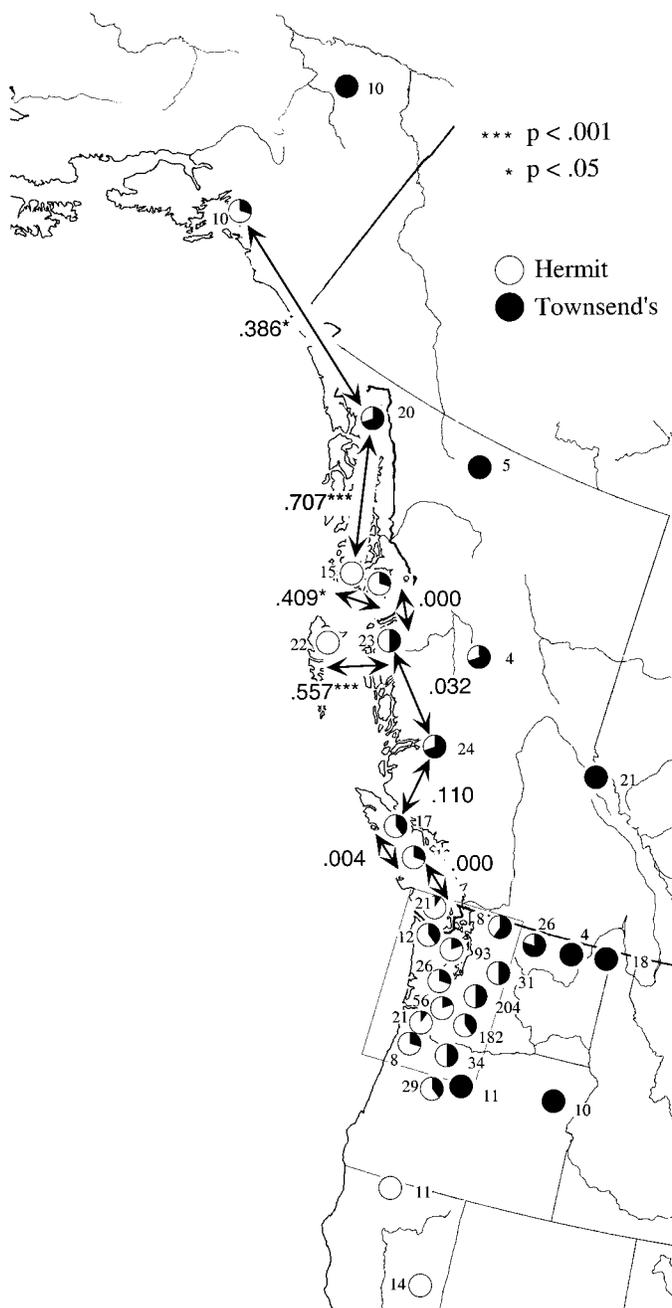


FIG. 8. Variation in mtDNA haplotype frequencies throughout the ranges of these warblers. Interior populations are fixed for the Townsend's haplotypes. Coastal populations north of the hybrid zones are phenotypically pure Townsend's warblers, but contain a predominance of hermit haplotypes. For the coastal samples to the north of the Washington hybrid zones, we compare the haplotype frequencies in adjacent samples using F_{ST} -values. Considerable geographic structure was evidenced by the significant F_{ST} differences among some populations. Washington and Oregon samples were extensively pooled to facilitate plotting; the locations of unpooled samples are shown in Rohwer and Wood (1998).

Large-Scale Variation in Haplotype Frequencies

To interpret geographic variation in haplotype frequencies, we collected samples of phenotypically pure warblers from well outside the hybrid zones and throughout most of the

range of the parental species. These samples provide valuable insights into the historic interactions between Townsend's and hermit warblers. Figure 8 presents haplotype frequencies for many samples taken far away from the three phenotypic hybrid zones in Washington and Oregon. We found only Townsend's mtDNA haplotypes ($n = 66$) in interior samples of Townsend's warblers from the Blue Mountains of eastern Oregon, from the Rocky Mountains of Washington and British Columbia, and from interior Alaska at Fairbanks. Similarly, we found only hermit mtDNA haplotypes ($n = 51$) in five samples of hermit warblers from the southern coastal region of Oregon and the northern half of California. Our sampling south and west of the hybrid zone in the Oregon Cascades is insufficient because we did not know this zone was geographically isolated from the zone in the Washington Cascades until most of the collecting for this study was completed.

The great surprise of this large-scale mtDNA survey is that all samples of phenotypically pure Townsend's warblers, taken anywhere along the coast up to 2000 km north of the Olympic hybrid zone, contain some to many hermit haplotypes (Fig. 8). Our northernmost coastal sample was taken at Valdez, Alaska, where the frequency of Townsend's haplotypes was just 0.22 in a sample of nine Townsend's warblers. How much further along the coast and into interior Alaska hermit haplotypes will be found in populations of phenotypically pure Townsend's warblers remains to be established. Coastal populations from Valdez, Alaska to central Oregon are polymorphic with a preponderance of hermit haplotypes. The phenotypically pure Townsend's warblers of the Queen Charlotte Islands ($n = 25$) and Prince of Wales Island ($n = 15$) carried only hermit haplotypes.

We present population genetic analyses of this haplotype variation only for coastal populations to the north of the Olympic hybrid zone, where coastal mountain ranges confine these warblers to a narrow east-west strip. This means that this analysis is little affected by the limited dispersal that may occur orthogonal to the axis of migration (unpubl. data). We recognize that water barriers may restrict dispersal between islands (Fig. 8). Variation in mtDNA haplotype frequency indicates that movement between some coastal populations is limited. The proportion of hermit mtDNA haplotypes in the 10 phenotypically pure Townsend's warbler populations sampled from this coastal region varied from 25% to 100%. Owing to the nonequilibrium population genetic dynamics that we assume for these populations, we use F_{ST} only as a simple index of mtDNA differentiation across populations and not to estimate coalescence or migration. The F_{ST} - and P -values between adjacent coastal populations of Townsend's warblers presented in Figure 8 suggest mtDNA gene flow among these populations is restricted. More generally, we obtain a qualitatively similar result regarding limits to mtDNA gene flow when we geographically map rare haplotypes. For example, one rare haplotype was found in eight Townsend's warblers distributed across four sample localities in northern British Columbia and Alaska.

Cytosynuclear Disequilibrium

Although we have not assessed nuclear genotypes, we can address cytosynuclear disequilibrium by comparing the associ-

ation of mtDNA haplotypes and plumage scores. Given random mating, associations between nuclear and mitochondrial genes decay by half with each generation (Arnold 1993). Thus, in any hybrid zone where most individuals are of mixed ancestry, cytonuclear disequilibria arise either because birds of correlated haplotype and phenotype are dispersing into the zone or because selection favors particular cytonuclear associations. The abundance of hybrids at the center of the zone implies many generations of hybrid \times hybrid matings, which should quickly disassociate nuclear and mitochondrial genes.

We have four large samples of individuals taken at localities lying on the phenotypic center of the Washington Cascade and Olympic hybrid zones (see Rohwer and Wood 1998, fig. 11). We used these samples to test the potential role of selection in maintaining associations between mitochondrial and nuclear genes. For this analysis Sum7st was divided into phenotypic hermits (0.0–0.20), four categories of hybrids (0.21–0.35, 0.36–0.50, 0.51–0.65, and 0.66–0.80), and phenotypic Townsend's (0.81–1.0). There is not even a hint of association between phenotype and haplotype in this combined sample of 80 birds (Table 3; $G = 2.72$, $df = 5$, $P = 0.74$) taken at the center of the zone. Thus, we conclude that mtDNA haplotypes are neutral with respect to phenotype.

To assess ongoing immigration of parental types into these hybrid zones, we examined cytonuclear associations at localities throughout the Washington Cascade and the Olympic hybrid zones. Within each zone we can address only one kind of dispersal, but the two zones together give us an assessment of dispersal by both parental types. For this analysis we assume that more long-distance dispersal occurs along the axis of migration than orthogonal to it (unpubl. data). The rectangles in Figure 9 delimit the samples used in these analyses. For the Washington Cascades, the samples included were 40–42, 44, 45, 47–59, 61–68, 70–76, 79–81, 83, and 84; for the Olympics, they were 17–26 and 43 (Rohwer and Wood 1998).

Linkage analyses can only reveal dispersal of Townsend's warblers into the Washington Cascade zone. This is because phenotypically pure Townsend's warblers from areas just north and east of this zone have a higher frequency of Townsend's haplotypes than are found within the zone, whereas pure hermit warblers from areas just south of the zone match the frequency of Townsend's haplotypes found within the zone (Fig. 9). In contrast, linkage analyses can only reveal dispersal of hermit warblers into the Olympic hybrid zone. This is because Townsend's warblers north of the Olympic zone have the same frequency of hermit haplotypes as Townsend's within the Olympic hybrid zone, whereas hermit warblers from areas just south of the zone have a higher frequency of hermit haplotypes than hermits warblers within the zone. Data from the two zones can tell the whole story. Thus, if pure hermit warblers are immigrating into the zones, then we expect an association between hermit phenotypes and haplotypes in the Olympic zone; if pure Townsend's warblers are immigrating into the zones, then we expect an association between Townsend's phenotypes and haplotypes in the Cascade zone.

There is no association between haplotype and phenotype for the 114 males from hybrid localities in the Olympics (Table 4; $G = 1.26$, $df = 5$, $P = 0.94$). In contrast, there is

a significant association between Townsend's haplotypes and phenotypes for the Cascade sample of 346 males (Table 5; $G = 18.01$, $df = 5$, $P = 0.003$). All of the cytonuclear association in the Cascades zone is due to higher than expected frequency of Townsend's mtDNA haplotypes in phenotypically pure Townsend's warblers (Table 5, $P < 0.001$). The association of Townsend's haplotypes with pure Townsend's phenotypes in males collected in and adjacent to the Washington Cascades zone also carries an interesting implication about mate choice. This disequilibrium in males could arise entirely from male dispersal. However, attributing this cytonuclear association exclusively to male dispersal seems unlikely because females disperse farther than males in most territorial passerine birds (Greenwood 1980). If some of this disequilibrium is due to the movement of pure Townsend's females into this region, then these pure females must preferentially be mating with Townsend's males; otherwise, we would also see excesses of Townsend's haplotypes in Townsend's-like backcrosses. This inference is consistent with results from a three-year field study of pairing patterns at a midpoint locality in the Cascades hybrid zone showing that Townsend's females preferentially mate with Townsend's males (Pearson 2000).

DISCUSSION

Evidence That Selection Keeps the Zones Narrow

Hybrid zones, like those between these warblers, that are narrow relative to σ , root mean square dispersal, but that are not situated on a sharp ecotone, have two interpretations. First, contact may be so recent that dispersal has not yet created a wide zone with shallow character transition curves. Alternatively, selection against hybrids may prevent dispersal from increasing the width of the zone, resulting in abrupt character transitions. Hybrid zones that are held narrow by a balance between selection and dispersal are referred to as "tension zones" and typically are less than 10σ in width (Barton and Hewitt 1985).

The character-by-character analyses of plumage transitions in this paper show all seven plumage transitions to be geographically coincident and concordant. For the seven characters for which inheritance seems additive, none differed significantly and consistently in both zones either in width or geographic placement from the composite curve for the other six characters (Table 2, Fig. 4). Thus, no individual plumage character seems to be being moved differentially by selection or drift. Without selection against hybrids affecting all seven plumage characters simultaneously, they should drift independently and fail to be similar in width and geographic location. This new evidence that these warbler hybrid zones are being held narrow by selection against hybrids presumes that the plumage characters are controlled by independently assorting genes, something we must assume without genetic linkage maps.

We did find that the character transitions for black characters were slightly wider than those for yellow characters. This difference seems to be driven by selection, rather than drift, because the greater width in the transect for black characters is caused by black characters penetrating the hermit warbler side of the zone more effectively than yellow char-

TABLE 3. Association of haplotypes (H, hermit; T, Townsend's) and phenotypes for 80 specimens from four samples collected at the phenotypic center of the Washington hybrid zones. Birds are divided into pure parentals and four phenotypic categories of hybrids, based on their Sum7st scores. Observed haplotype frequencies, column percents, and cell χ^2 -values are presented. The overall χ^2 is not significant ($\chi^2 = 2.76$, $P = 0.73$). These results suggest no cytonuclear linkage within localities at the phenotypic centers of the Washington hybrid zones.

Analysis/ haplotype	Hybrid Index (Sum7st score)						Totals
	Hermit 0.0–0.20	0.21–0.35	0.36–0.50	0.51–0.65	0.66–0.80	Townsend's 0.81–1.00	
Observed frequencies							
H	5	10	9	13	7	5	49
T	3	6	4	6	5	7	31
Column percents							
H	62.5	62.5	69.2	68.4	58.3	41.7	61.2
T	37.5	37.5	30.8	31.6	41.7	58.3	38.8
Cell χ^2							
H	0.002	0.004	0.135	0.160	0.017	0.751	—
T	0.003	0.006	0.214	0.252	0.026	1.188	—

acters (Fig. 5). The transitions for these two sets of color characters are not different on the Townsend's side of the zone.

With these analyses there are now three lines of evidence suggesting these zones are held narrow by selection against hybrids. First, this paper shows the individual character transitions are largely coincident and concordant (Fig. 2). Second, the zones are narrow, relative to an estimate of dispersal. Assuming Barton and Gale's (1993) linkage model can reliably be applied to plumage scores, Rohwer and Wood (1998) estimate that two of these hybrid zones are only about 4σ wide. This width would have been achieved in less than 10 generations if root mean square dispersal is 30 km (Endler 1977); yet, a few historical specimens show these zones have existed for more than 50 generations (Rohwer and Wood 1998). Finally, the three geographically isolated hybrid zones between these warblers are all similar in width, even though contact cannot have been simultaneous in all three zones (Rohwer and Wood 1998). This suggests that each of the zones is maintained by a similar balance between selection against hybrids that reduces zone width and dispersal that increases zone width.

Two kinds of general selective regimes are recognized as maintaining coincident and concordant clines for characters under independent genetic control (Moore and Price 1993; Kruuk et al. 1999). First there may be endogenous, genomic incompatibilities that result in hybrids being inferior to both parentals. In closely related species with sex chromosomes, such effects are usually first expressed as Haldane's rule, when the heterogametic sex suffers reduced fertility or viability (Haldane 1922; Orr 1997; Turelli 1998). Genetic divergence between hermit and Townsend's warblers is probably too recent for Haldane's rule to be a source of endogenous selection against hybrids (Smith and Rohwer 2000). Alternatively, the selective pressure may be exogenous when hybrids are unsuited to their physical or social environment. Given that detailed studies have failed to identify ecological differences between these warblers, we do not consider variables in the physical environment a plausible source of selection against hybrids. Furthermore, it would be surprising if our seven color characters were all related to habitat specialization given that all feature age and sex differences that suggest sexual selection (Rohwer and Wood 1998; Smith and

Rohwer 2000). Because Townsend's warblers are aggressively superior to hermit warblers (Pearson and Rohwer 2000), we believe that our seven color characters covary strongly across the hybrid zone because all act to signal aggressive difference between parentals, thus implicating warbler social environment as the source of exogenous selection against hybrids. Hybrid phenotypes signal the aggressive inferiority of hybrids to Townsend's warblers, but these same hybrid phenotypes signal the aggressive superiority of hybrids to hermit warblers, differences that are reflected in the asymmetry of the plumage transition curves.

Large-Scale Movement of These Warbler Hybrid Zones

The haplotype footprint as a ghost of past ranges.—The most stunning result of this paper is our discovery of a preponderance of hermit mtDNA haplotypes in pure Townsend's warblers taken throughout the 2000-km coastal strip north of the Washington hybrid zones (Fig. 8). Interior samples of Townsend's warblers contained no hermit haplotypes, and southern samples of hermit warblers contained no Townsend's haplotypes (Fig. 8). We see the haplotype polymorphism in coastal populations of Townsend's warblers to the north of the hybrid zones as a ghost of the range from which hermit warblers have been displaced by aggressive hybridization. Later in this discussion, we develop a model that accounts for the aggressive differences between these warblers and for the biased pairing patterns that produce the haplotype trail left by the movement of these zones.

Competitive asymmetries.—A variety of evidence from this and other studies support the competitive superiority of Townsend's warblers over hermit warblers. First, most of the individual character transition curves (Fig. 2), as well as the composite curves shown in Rohwer and Wood (1998), are asymmetrical in a way that suggests Townsend's characters are differentially penetrating hermit warbler populations. Second, contrasts in associations between phenotypes and mtDNA haplotypes suggest that Townsend's warblers are invading the Washington hybrid zones from the north, but that hermit warblers are not invading these zones from the south (Tables 3, 4). Third, Townsend's males are more aggressive than hermit males toward conspecific and heterospecific models (Pearson and Rohwer 2000). Fourth, Town-

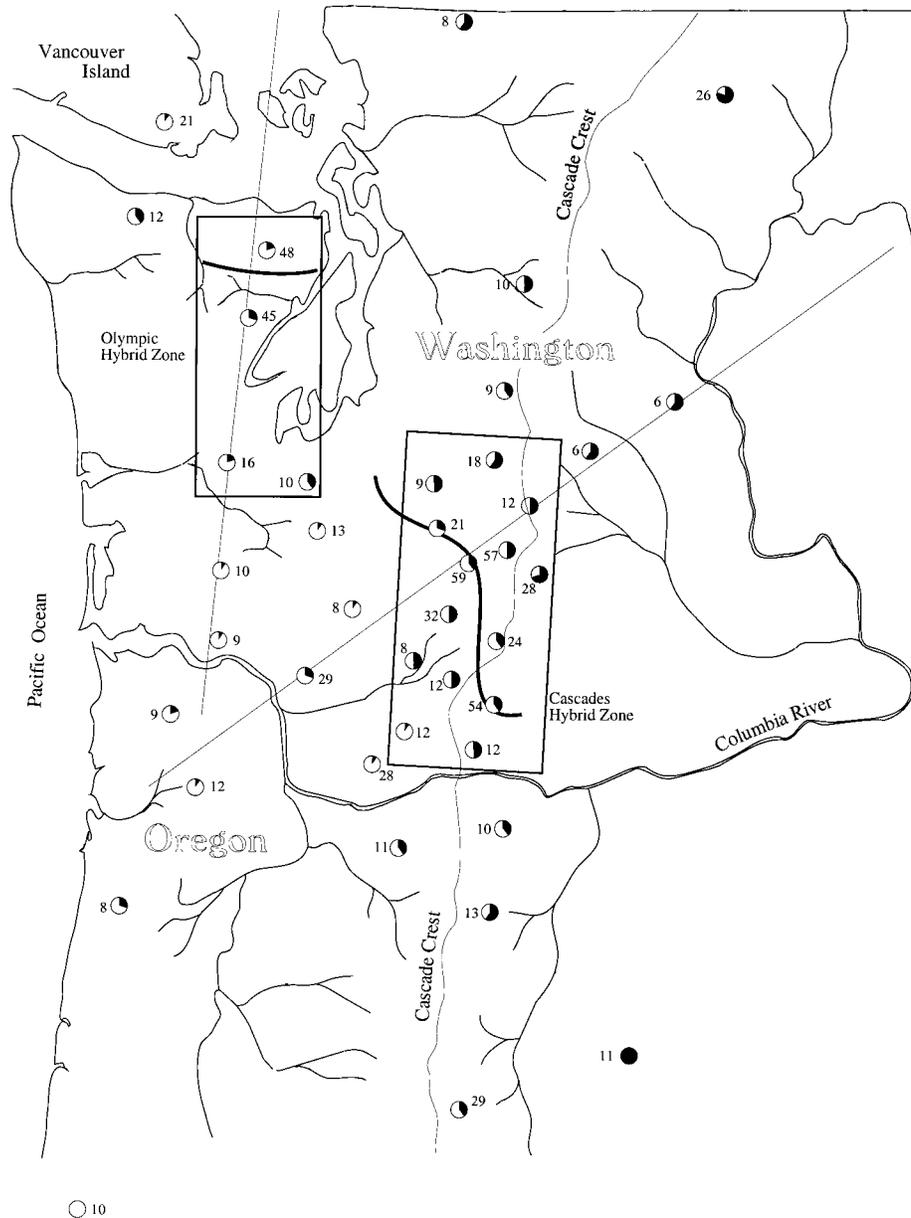


FIG. 9. Rectangles contain the samples used for the analysis of cytonuclear disequilibria in and near the Washington Cascade and the Olympic hybrid zones. Black and white in the pie diagrams represent the fraction of Townsend's and hermit warbler mtDNA haplotypes, respectively. Sample sizes are given beside each circle. Nearby samples were pooled to facilitate plotting haplotype frequencies; unpooled samples are plotted in Rohwer and Wood (1998).

send's males are more successful at holding territories and attracting females within the hybrid zone than are hermit males (Pearson 2000). Finally, in and near the Washington hybrid zones, Townsend's warblers lay larger clutches than hermit warblers (Pearson and Rohwer 1998).

The cytonuclear linkage analyses of this study are valuable for confirming these competitive asymmetries in an independent fashion. These analyses suggest movement of pure Townsend's, but not pure hermit warblers, into the hybrid zones. Townsend's warblers apparently disperse southward into the Cascade hybrid zone at a rate sufficient to maintain an excess of Townsend's haplotypes in phenotypically pure Townsend's warblers (Table 5). In contrast, hermit warblers

do not disperse northward into the Olympic hybrid zone in numbers sufficient to maintain an association between plumage and haplotypes in the Olympic zone (Table 4).

Asymmetries in character transition curves and asymmetries in parental dispersal cannot establish the ranking of hybrids relative to the two parentals. However, five measures of fitness rank hybrids relative to parentals. Male aggressiveness toward mounts (Pearson and Rohwer 2000), male persistence on territories, and male pairing success (Pearson 2000) rank Townsend's warblers superior to hermit warblers. For each of these measures, hybrids rank intermediate to parentals, a ranking that should accelerate movement of these zones. Clutch sizes of hermits warblers and hybrids are sim-

TABLE 4. Association of haplotypes (H, hermit; T, Townsend's) and phenotypes for 114 specimens collected near the Olympic hybrid zone. Birds are divided into pures and four phenotypic categories of hybrids. Observed haplotype frequencies, column percents, and cell χ^2 -values are presented. The overall χ^2 is not significant ($\chi^2 = 1.26$, $P = 0.94$). These results suggest no dispersal of pure hermit warblers northward into this zone.

Analysis/haplotype	Hybrid Index (Sum7st score)						Totals
	Hermit 0.0–0.20	0.21–0.35	0.36–0.50	0.51–0.65	0.66–0.80	Townsend's 0.81–1.00	
Observed frequencies							
H	11	19	17	11	9	16	83
T	6	7	6	5	3	4	31
Column percents							
H	64.7	73.1	73.9	68.8	75.0	80.0	72.8
T	35.3	26.9	26.1	31.2	25.0	20.0	27.2
Cell χ^2							
H	0.153	0.000	0.004	0.036	0.008	0.142	—
T	0.410	0.001	0.010	0.097	0.021	0.381	—

ilar and significantly lower than those for Townsend's warblers (Pearson and Rohwer 1998); in this case the ranking of hybrids should not accelerate zone movement. Overwinter return rates for males were similar for both parentals, but more parentals returned than hybrids (Pearson 2000); this is the only fitness measure where the inferiority of hybrids relative to, not one, but both parentals acts to keep the zone narrow.

Why are moving zones so rare?—In an extensive review of hybrid zones, Barton and Hewitt (1985) suggest that hybrid inferiority is the predominate selective force keeping most zones narrow. For animal zones, we know of no other case where parental fitness asymmetries have been inferred from asymmetric character transitions and where the genetic footprint of past positions of the zone has been examined across geographic scales spanning most of the ranges of the hybridizing taxa. For these reasons, the number of moving zones may be underestimated in Barton and Hewitt's (1985) review. Another serious problem is that most genetic data come from the conveniently analyzed mitochondrial genome. Yet, neutral mitochondrial genes are less well suited to documenting footprints of past hybridization than are neutral nuclear genes. This is true because the original pairing pattern may be biased in a way that causes no mtDNA haplotype trail to be left behind (e.g., Gill 1997) and because coalescent pro-

cesses cause allelic variation to be lost roughly four times faster in mitochondrial genes than in nuclear genes.

Although the search for moving zones has not been rigorous, we also recognize that they are improbable. Large asymmetries in parental fitness should quickly lead to the extinction of the inferior parental species, thus eliminating phenotypic evidence of past hybridization, as has been suggested for European voles (Tegelstrom 1987). Nonetheless, we find it remarkable that no discussion of the famous non-concordance between mitochondrial markers in the mouse hybrid zone of Scandinavia has suggested a zone movement (Ferris et al. 1983; Gyllensten and Wilson 1987; Harrison et al. 1987). Instead, "introgression" is argued to have taken *Mus domesticus* mtDNA haplotypes 600 km northward into populations of *M. musculus*. Yet, contact in northern Sweden, followed by a southward movement of the phenotypic zone, could equally as well explain the data.

A Model Explaining the Key Features of This Warbler Hybrid Zone

In this section we develop a single integrated picture of the dynamics of differentiation, secondary contact, and asymmetric hybridization between hermit and Townsend's warblers. Unlike many passerine sister taxa, hermit and Town-

TABLE 5. Association of haplotypes (H, hermit; T, Townsend's) and phenotypes for 346 specimens collected near the Washington Cascade hybrid zone. Birds are divided into pures and four phenotypic categories of hybrids. Observed haplotype frequencies, column percents, and cell χ^2 -values are presented. The overall χ^2 is significant ($\chi^2 = 17.8$, $P = 0.003$). These results suggest considerable dispersal of pure Townsend's southward into this zone.

Analysis/haplotype	Hybrid Index (Sum7st score)						Totals
	Hermit 0.0–0.20	0.21–0.35	0.36–0.50	0.51–0.65	0.66–0.80	Townsend's 0.81–1.00	
Observed frequencies							
H	23	31	22	24	30	43	173
T	18	21	13	19	22	80	173
Column percents							
H	56.1	59.6	62.9	55.8	57.7	35.0	50.0
T	43.9	40.4	37.1	44.2	42.3	65.0	50.0
Cell χ^2							
H	0.305	0.962	1.157	0.291	0.615	5.565	—
T	0.305	0.962	1.157	0.291	0.615	5.565	—

send's mtDNA haplotypes are distinguished by less than 1% sequence difference (Lovette et al. 1999), suggesting that they diverged as recently as the mid to late Pleistocene (Bermingham et al. 1992; Klicka and Zink 1997). Thus, we use the latest glacial cycle as a model for any sequence of cycles that may have driven the divergence of these species (Porter 1989; Webb and Barletta 1992). An important puzzle raised by this hybrid zone is the aggressive superiority of Townsend's warblers over hermit warblers, the principal factor that appears to be moving these warbler hybrid zones southward and the source of selection that appears to be keeping the plumage transition coincident and concordant. The large-scale temporal and geographic perspective we develop in this section suggests new and testable predictions.

Isolation and differentiation.—We assume these warblers diverged in phenotype and haplotype while isolated in two separate western refugia. Mitochondrial phylogenies for several species or population complexes are beginning to suggest the importance of at least two western forest isolations in the differentiation of North American birds (Johnson and Zink 1983; Johnson and Marten 1988; Bermingham et al. 1992; Johnson 1995; Cicero 1996; Barrowclough et al. 1999). Both hermit and Townsend's warblers prefer Douglas fir (*Pseudotsuga menziesii*) forests, though they also use true fir (*Abies*) and spruce (*Picea*) forests at higher elevations and latitudes. During a three-year field study at the phenotypic center of the Washington Cascades hybrid zone, Pearson and Manuwal (1999) found no difference in habitat preferences among pure Townsend's, pure hermits, or hybrids. The preference of these warblers for Douglas fir forests and their abundance in mature Douglas fir stands suggests an ancestral association with Douglas fir that predated their divergence. To the south of the southernmost extent of glacial ice, the largely interior distribution of Townsend's warblers and the largely coastal distribution of hermit warblers coincide with the northern interior and coastal races of Douglas fir, respectively (Whitlock 1992; Aagaard et al. 1995). This geographical concordance in the divergence of their preferred habitat tree is consistent with these warblers diverging in interior (Townsend's) and coastal (hermit) refugia.

Secondary contact.—As the ice sheets of North America melted, an ice-free corridor developed between the coastal Cordilleran sheet and the enormous Laurentide sheet to the east (Fulton 1989; Pielou 1991; Adams 1997). The last of these glacial retreats formed an ice-free corridor by 13,000 years ago, and open-country organisms, such as big-horned sheep, dispersed far northward in this corridor as early as 9300 years ago (Pielou 1991, p. 243). But reforestation of this corridor was slow. Boreal forests invaded it from the south only about 5000 years ago (Pielou 1991). We believe that present-day Townsend's warblers isolated in an interior Rocky Mountain refugium spread northward into British Columbia and Alaska through this reforested corridor.

In contrast, hermit warblers presumably spread northward along the Pacific Coast to Alaska as early as 10,000 years ago. Coastal conditions were mild close to the receding ice sheet, permitting coastal communities to persist very close to the Cordilleran glacier (Warner et al. 1982; Pielou 1991). Lodge-pole pine (*Pinus contorta*) forests, which are unsuitable for these warblers, immediately spread northward along

the Pacific Coast as the ice retreated. Then, abruptly, at about 10,000 years ago, warming caused Douglas fir to replace these pine forests. An abundance of bracken fern pollen and frequent fires evidenced by many charcoal deposits shows these early Douglas fir forests to have been much drier than present-day cedar (*Thuja plicata*) and hemlock (*Tsuga heterophylla*) forests along the Pacific Coast (Pielou 1991). It is hard to imagine a more perfect habitat description for hermit warblers than Pielou's (1991) characterization of the Douglas fir forests that developed along the Pacific Northwest coast about 10,000 years ago.

Contact between hermit and Townsend's warblers presumably occurred roughly 5000 years ago at the approximate latitude of the Queen Charlotte Islands in central British Columbia, when Townsend's warblers spilled through the Skeena River valley into coastal forests. Prehistoric environmental reconstructions based on palynological data suggest that earlier, more southerly contacts between these warblers did not occur. Earlier contact surely did not occur either through the Okanogon Highlands along the Washington–British Columbia border or through the Blue Mountains of Oregon, even though Townsend's warblers presently breed in low numbers in these corridors. The same dry conditions that lead to the development of Douglas fir forests along the coast about 10,000 years ago also produced sage (*Artemisia*) steppe habitats in these interior corridors connecting the Rockies with the Cascades that persisted until the late Holocene (Whitlock 1992; Thompson et al. 1993). This paleoecology has two implications for these warblers. First, hermit warblers presumably expanded their range to occupy the expansive and highly suitable coastal fir forests that developed in the mid Holocene; at this time Townsend's warblers presumably remained restricted to small patches of high elevation mountain forest owing to dry Holocene conditions in the interior (Fig. 10). Second, the most recent contact between these species occurred far north of the present hybrid zones.

Competitive dynamics on contact.—When Townsend's males first dispersed from the interior into coastal forests, they should have encountered hermit warblers that were already paired and breeding. The stage of the breeding cycle for coastal hermit warblers at the time of contact with Townsend's warblers is not critical. It suffices to know that males arrive on the breeding grounds earlier than females for both species (Pearson and Rohwer 1998) and that coastal populations of these warblers migrate and begin breeding much earlier than interior populations (Wright et al. 1998). These facts suggest that the first contact between these warblers would have been asymmetrical in a way that put female Townsend's warblers at a pairing disadvantage. By the time Townsend's females arrived from the interior, Townsend's males could already have paired with hermit females. We view this difference in the arrival times as the essential premise needed to explain the coastal predominance of hermit mtDNA haplotypes in what are now phenotypically pure populations of Townsend's warblers along the Pacific Coast far north of the present-day hybrid zones. The asymmetry in pairing patterns entrained by this difference in arrival times should have repeated itself for as long as Townsend's males continued invading coastal forests from the interior. Eventually, however, the descendants of Townsend's warblers that

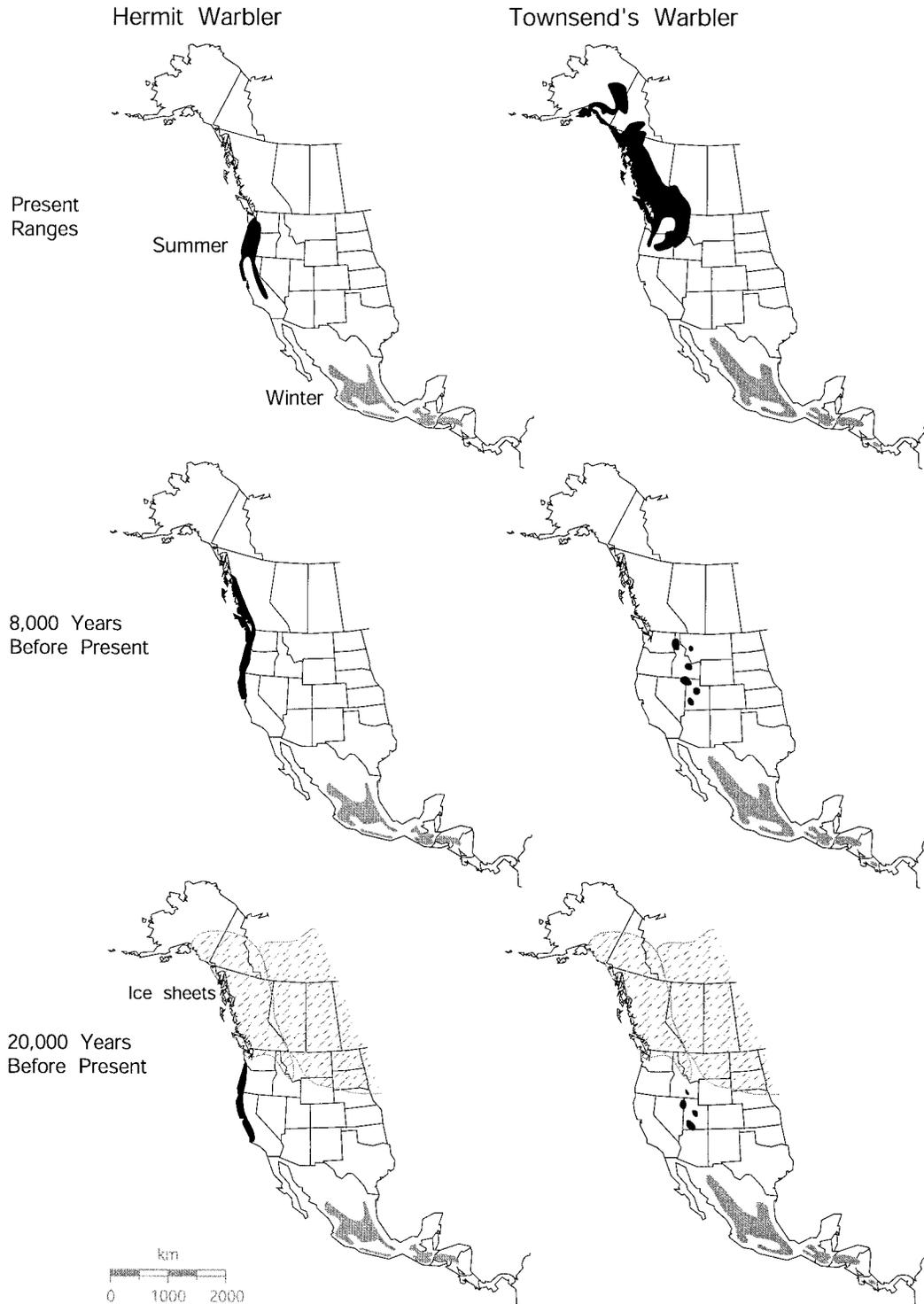


FIG. 10. (Top) Present ranges for hermit and Townsend's warblers, taken from Pearson (1997) and Wright et al. (1998); black is breeding range; gray is Central American winter range; birds wintering in the United States were dropped because their numbers are insignificant. (Middle) Postulated summer ranges 8000 years ago; present winter ranges are shown for reference. (Bottom) Postulated summer ranges at peak glaciation, 20,000 years ago; present winter ranges are shown for reference. Contrasts between the relative sizes of the winter and summer ranges suggest that summer competition for territories has been much more intense in the Townsend's lineage than the hermit warbler lineage. Even today, most of the vast interior and coastal range of Townsend's warblers is unoccupied because it lacks suitable warbler habitat. In the interior, Townsend's warblers are mostly restricted to wet, high-elevation forests, and much of their coastal range in British Columbia and Alaska is predominated by unsuitable forests of hemlock and western red cedar.

invaded coastal forests should have begun migrating along the coast because migratory orientation is highly heritable (Berthold and Querner 1981; Helbig 1991; Berthold and Pulido 1994).

But why should male Townsend's warblers have been able to outcompete male hermit warblers that were already holding territories, especially given the enormous advantage that prior residents accrue in the defense of resources as valuable as breeding territories and mates (Krebs 1982; Rohwer 1982; Beletsky and Orians 1989)? The proximate answer is easy. When responding to conspecific mounts, male Townsend's warblers from the Rockies are twice as aggressive as male hermit warblers from pure populations in southwestern Washington (Pearson and Rohwer 2000). Furthermore, pure Townsend's males are four times more aggressive toward mounts of hermit males than are pure hermit males toward mounts of Townsend's males (Pearson and Rohwer 2000). Male Townsend's warblers are simply much more aggressive than male hermit warblers.

Why should these sister species be so different in fighting ability? The respective sizes of their Pleistocene refugia suggest a possible explanation. At all phases of the most recent glacial cycle, and presumably of earlier glacial cycles, coastal habitats suitable to these warblers were more extensive than interior habitats (Fig. 10). Low- and moderate-elevation coastal forests have always been vast and contiguous, whereas interior forests have been patchy, with good habitats largely confined either to moist, north-facing slopes or to high elevations (Pielou 1991; Thompson et al. 1993). If, as is true now, the Central American winter ranges of these warblers were roughly similar in size throughout the Pleistocene, then hermit warblers would have been relatively more winter limited and Townsend's warblers relatively more summer limited when they were isolated (Fretwell 1972). Thus, during the long periods of glacial maxima and the early periods of glacial retreats, hermit warblers have had much more prime breeding habitat, compared to the size of their winter range, than have Townsend's warblers (Fig. 10). Although a simple measure of the sizes of current breeding ranges would suggest that this difference could be reversed during interglacials (Fig. 10), this is likely not true because little of the map-depicted range of Townsend's warblers contains suitable habitat.

Mitochondrial DNA haplotype polymorphism.—The footprint of mtDNA polymorphism left behind as the hybrid zone has moved south may be explained by selection driving the replacement of hermit nuclear genes controlling plumage by Townsend's nuclear genes, whereas no selection operates against the hermit mtDNA genome. As pointed out by Powell (1983) in a study of sibling *Drosophila* species, the only way to select against mtDNA introgression is to select against backcross females altogether. Selection on nuclear genes, in contrast, can act differentially across backcross offspring carrying varying degrees of the nuclear genes of parental species. Thus, in our view, the haplotype polymorphism in Townsend's warblers more than 2000 km to the north of the current hybrid zones represents a genetic footprint of the transformation of these populations from phenotypically pure hermit warblers to phenotypically pure Townsend's warblers through aggressive hybridization during the last 5000 years.

It is worth noting the contrast between our results and those for a study of *Vermivora* warblers in which no mtDNA footprint remains following hybridization (Gill 1997). The different outcomes are explained by the differential success of "invading" females in the two systems. As we noted above, Townsend's females would have been at a disadvantage relative to female hermit warblers at first contact, whereas no mating disadvantage has been noted for the golden-winged warbler (*Vermivora chrysoptera*), which is being replaced by the blue-winged warbler (*Vermivora pinus*). If F_1 s backcross at random with parentals, as may be the case for these *Vermivora*, then the frequency of the mtDNA haplotype of the invading species will quickly increase. What happens next will depend on the relative migration of the two parental species into the hybrid zone. In the case of *Vermivora*, only the mtDNA haplotype of the invading blue-winged warblers remains, suggesting that females of this more-southern species immigrate into this zone at higher rates than do females of the more-northern golden-winged warbler. In contrast, when the hermit \times townsend's warbler hybrid zone was established, F_1 males would mostly have backcrossed with earlier arriving hermit females. Assuming the mtDNA haplotypes are selectively neutral, polymorphisms established at contact can be maintained in the face of phenotypic replacement driven by the competitive superiority of Townsend's males. Thus, the mtDNA haplotype frequencies that persist in the wake of a moving hybrid zone will depend on sex-specific differences in demography. The preponderance of hermit mtDNAs in coastal populations of Townsend's warblers 2000 km to the north of their current hybrid zones shows that persistence of haplotype polymorphisms can be long term.

Further tests.—The preceding model for allopatric differentiation, secondary contact, and aggressive hybrid replacement can account for the polymorphic mtDNA haplotypes found far north of the current hybrid zones (Fig. 8). It also suggests genetic and behavioral predictions that await new data. If, as we argue, the breeding population of the hermit lineage isolated along the coast was substantially larger than the Townsend's lineage isolated in the interior, then the number of hermit mtDNA haplotypes (exclusive of any Townsend's haplotypes that may have arrived there through this current round of interbreeding) found near the southern edge of their range in the Coast Range and the Sierra Nevada of California should exceed the number of Townsend's mtDNA haplotypes found near the southern edge of their range in the Rocky Mountains. This follows because large populations lose lineages more slowly than small populations. Similarly, the divergence between these hermit haplotypes should be greater than the divergence between those found in Townsend's haplotypes from the Rockies.

Furthermore, data showing that mean aggressiveness varies concordantly with mean phenotypic score of hybrid males (Pearson and Rohwer 2000), strongly suggests that the extreme aggressive differences between interior Townsend's warblers and coastal hermit warblers is genetically controlled. If Townsend's warblers have replaced hermit warblers along the coasts far to the north of the current hybrid zones, nuclear genes from hermit warblers must have been incorporated into these coastal populations of Townsend's

warblers. Thus, we predict that Townsend's warblers from coastal populations will be less aggressive than Townsend's warblers from interior populations in the Rocky Mountains, which cannot have incorporated nuclear genes from hermit warblers through hybridization. If present-day selection still favors aggressive phenotypes in Townsend's warblers, this prediction should hold most strongly for coastal populations of Townsend's warblers close to the hybrid zones.

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