



## TIME SINCE CONTACT AND GENE FLOW MAY EXPLAIN VARIATION IN HYBRID FREQUENCIES AMONG THREE *DENDROICA* *TOWNSENDI* × *D. OCCIDENTALIS* (PARULIDAE) HYBRID ZONES

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**ABSTRACT.**—Hermit Warblers (*Dendroica occidentalis*) and Townsend's Warblers (*D. townsendi*) meet and hybridize in three replicate zones in Washington and Oregon. Using male specimens, we show that the ratio of hybrid to parental phenotypes varies systematically across these three zones: there were 60.4% hybrids among 96 males from the Olympic zone, 43.3% hybrids among 411 males from the Washington Cascade zone, and 27.8% hybrids among 209 males from the Oregon Cascade zone. We found no evidence of habitat or climatic factors driving these systematic differences in hybrid frequencies, and we argue that they are related to differences among these zones in the immigration of pure parentals and time since contact. Building on earlier hypotheses about massive movement of the coastal zones (Rohwer and Wood 1998), we can infer that the Olympic and Washington Cascade zones are old and of similar age. The Washington Cascade zone, but not the Olympic zone, receives Townsend's immigrants from the Rocky Mountains through the Okanogan highlands, as shown by the linkage analyses in Rohwer et al. (2001). This immigration apparently accounts for the lower frequency of hybrids in the Washington Cascades. The Washington Cascade and Oregon Cascade zones are both situated adjacent to forest corridors that connect them to the Rocky Mountains to the east, so both of these zones should receive Townsend's immigrants from the east (linkage analyses have yet to be done for the Oregon Cascades because the mitochondrial DNA haplotypes for these specimens have not been determined). The Washington Cascade zone, however, is old, whereas the Oregon Cascade zone appears to have been established only recently in response to anthropogenic habitat changes, which accounts for its low frequency of hybrids. We are unaware of any other replicate set of hybrid zones where differences in time since contact and dispersal have been related to variation in hybrid frequencies. Received 24 February 2006, accepted 20 December 2006.

**Key words.**—*Dendroica occidentalis*, *D. townsendi*, dispersal, gene flow, Hermit Warbler, hybrid zone, time since contact, Townsend's Warbler.

### El Tiempo Transcurrido desde el Contacto y el Flujo Genético Podrían Explicar la Variación en la Frecuencia de los Híbridos entre Tres Zonas de Hibridación entre *Dendroica townsendi* y *D. occidentalis* (Parulidae)

**RESUMEN.**—*Dendroica occidentalis* y *D. townsendi* se encuentran y forman híbridos en tres zonas replicadas en Washington y Oregon. Utilizando especímenes machos, mostramos que el cociente entre fenotipos híbridos y parentales varía sistemáticamente entre las tres zonas. El 60.4% de 96 machos de la zona de las Montañas Olympic fueron híbridos, mientras que este porcentaje fue del 43.3% (de 411 machos) en la zona de las Montañas Cascade de Washington y del 27.8% (de 209 machos) en la zona de las

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Cascade de Oregon. No encontramos evidencia de que factores de hábitat o de clima podrían estar causando las diferencias en la frecuencia de los híbridos, y aducimos que éstas están relacionadas con diferencias entre las zonas en la inmigración de parentales puros y en el tiempo transcurrido desde el contacto entre las poblaciones. Construyendo sobre la base de hipótesis previas acerca del movimiento masivo de las zonas costeras (Rohwer and Wood 1998), podemos inferir que las zonas de las Olympic y las Cascade de Washington son antiguas y de la misma edad. La zona de las Cascade de Washington, pero no la de las Olympic, recibe inmigrantes de la especie *D. townsendi* desde las Montañas Rocallosas a través de las tierras altas de Okanogan, como lo han demostrado los análisis de ligamiento de Rohwer et al. (2001). Esta inmigración aparentemente explica la frecuencia de híbridos más baja en la zona de las Cascade de Washington. Las zonas de las Cascade de Washington y de Oregon están situadas junto a corredores de bosque que las conectan con las Rocallosas, por lo que estas dos zonas deben recibir inmigrantes de la especie *D. townsendi* desde el este (aún no se han hecho análisis de ligamiento para la zona de Oregon porque los haplotipos de ADN mitocondrial de esos especímenes no han sido determinados). Sin embargo, la zona de las Cascade de Washington es antigua, mientras que la de las Cascade de Oregon parece haberse establecido recientemente como respuesta a cambios antropogénicos en el hábitat, lo que permite explicar su baja frecuencia de híbridos. No conocemos otro conjunto de zonas de hibridación replicadas en el que las diferencias en el tiempo transcurrido desde el contacto y la dispersión hayan sido relacionadas con la variación en la frecuencia de los híbridos.

STUDIES OF NATURAL hybridization have provided a great deal of insight into evolutionary processes (Barton and Hewitt 1985, 1989; Harrison 1990, 1993). Comparisons among hybrid zones have highlighted important variation resulting from differences in selection, drift, time since contact, conditions of contact (secondary contact or clinal divergence), dispersal, and compatibility of parental genotypes (Barton and Hewitt 1985, 1989; Harrison 1990, 1993). Identifying the processes responsible for differences among the hybrid zones is often complicated by the many differences among diverse taxa (e.g., amphibians, insects, plants, birds, mammals). Close phylogenetic pairing of hybrid zones would alleviate many of these confounding factors, but studies of multiple hybrid zones involving the same species pairs are rarely reported in the literature.

In western North America, Townsend's Warblers (*Dendroica townsendi*) and Hermit Warblers (*D. occidentalis*) hybridize in three distinct zones of introgression in Washington and Oregon (Rohwer and Wood 1998). These distinct zones may differ in a variety of factors that can influence patterns of hybridization and the resulting frequency of phenotypes. We examined variation in the frequency of phenotypes (pure parental and hybrid plumages) in each of

these three hybrid zones, predicting that if factors influencing hybridization, such as natural or sexual selection, ecological preferences, dispersal, or time since contact, vary across zones of contact, then we should see concordant variation in phenotypic frequencies across the three hybrid zones.

Within each hybrid zone, we measured the frequency of hybrid and parental phenotypes for males using a previously defined hybrid-index score ranging from 0 to 1, with parental phenotypes indicated by individuals scoring 0.0–0.25 (Hermit Warblers) or 0.751–1.0 (Townsend's Warblers). Using this hybrid score to identify parental versus hybrid phenotypes, we examined variation in the prevalence of parental versus hybrid (0.251–0.75) birds within the three distinct zones.

#### TOWNSEND'S WARBLERS, HERMIT WARBLERS, AND THEIR HYBRIDS

Hermit and Townsend's warblers are sister taxa that diverged within the past 500,000 years (Bermingham et al. 1992, Lovette and Bermingham 1999, Lovette et al. 1999). Townsend's Warblers breed in western North America, from Alaska south to Oregon, both along the Pacific coast and along the Rocky

Mountain Cordillera (Wright et al. 1998). Hermit Warblers breed in coastal Washington, Oregon, and California (Pearson 1997), hybridizing with Townsend's Warblers in three distinct zones of introgression in the Olympic Mountains of Washington, the Cascade Mountains of Washington, and the Cascade Mountains of Oregon (Fig. 1). Townsend's Warblers winter along the west coast from extreme southern British Columbia to Baja California and in the mountains of Mexico through to Costa Rica (Wright et al. 1998). Hermit Warblers winter in small numbers along the coast of California and, more commonly, from Mexico to Nicaragua (Pearson 1997).

Within the hybrid zones, Townsend's and Hermit warblers and their hybrids compete for and maintain exclusive territories (Pearson and Manuwal 2000), sing the same songs (Pearson and Rohwer 2000), and hybridize and backcross frequently (Rohwer and Wood 1998, Rohwer et al. 2001). Breeding phenology is similar across both parental species and hybrids (Pearson and Rohwer 1998), and all birds prefer forests dominated by Douglas-fir (*Pseudotsuga menziesii*) at lower elevations and true fir (*Abies* spp.) and spruce (*Picea* spp.) at higher elevations (Rohwer and Wood 1998, Pearson and Manuwal 2000). Habitat use does not differ between Townsend's Warblers, Hermit Warblers, and hybrids, and hybrid zones are not associated with regions of ecological transition (Rohwer and Wood 1998, Pearson and Manuwal 2000). Townsend's Warblers are generally more aggressive and have higher levels of testosterone than Hermit Warblers (Pearson and Rohwer 2000, Owen-Ashley and Butler 2004), though within sites, all birds show similar levels of aggressive response to model presentations (fig. 5 in Pearson and Rohwer 2000). The two species differ in their life histories, with Townsend's Warblers laying more eggs per nesting attempt (Pearson and Rohwer 1998) but having reduced annual survival (Rohwer 2004) compared with Hermit Warblers.

Several lines of evidence suggest that the hybrid zones between Townsend's and Hermit warblers are moving and represent "tension zones" (Key 1968, Barton and Hewitt 1985) between dispersal and selection. An asymmetrical shape to phenotypic clines across the hybrid zones suggests a fitness advantage to Townsend's Warblers that may facilitate their distributional expansion southward (Rohwer

and Wood 1998). The expansion of Townsend's Warblers southward is supported by a discordance between mitochondrial DNA (mtDNA) haplotypes and phenotypes in Townsend's Warblers (Rohwer et al. 2001). In southeastern Alaska and coastal British Columbia, phenotypically pure Townsend's Warblers often contain Hermit Warbler mtDNA haplotypes, which suggests that Townsend's Warblers colonized this coastal region from the interior within the past 5,000 years and have since replaced Hermit Warblers from nearly two-thirds of their former distribution along the Pacific coast of western North America (fig. 8 in Rohwer et al. 2001, fig. 23.10 in Freeman 2002).

Estimates of fitness differences among Townsend's and Hermit warblers and their hybrids suggest that Townsend's Warblers may have higher fitness than either Hermit Warblers or hybrids (Pearson 2000). Male Townsend's Warblers had higher pairing success in marginal habitat and were more likely to maintain their territories, compared with hybrids and Hermit Warblers (Pearson 2000). Evidence for selection against hybrids is less clear. Small samples suggest that clutch sizes of hybrids may be smaller than those of either parental species (Pearson and Rohwer 1998). Male return rates were lower for hybrids than for either parental species (Pearson 2000), but age-ratio estimates of survival showed that hybrids survive as well as pure Townsend's Warblers (Rohwer 2004). Reduced viability of the heterogametic sex (females) has not been observed in these hybrids (Smith and Rohwer 2000), which is not surprising, because hybrid inviability is uncommon among closely related birds (Price and Bouvier 2002). By contrast, hybrids had higher pairing success and were better able to maintain their territories than pure Hermit Warblers (Pearson 2000), making fitness differences between Hermit Warblers and hybrids difficult to discern.

Overall, the narrow breadth of all three hybrid zones in relation to estimates of dispersal (Rohwer and Wood 1998), coupled with similar asymmetrical character transitions across the zones (Rohwer and Wood 1998, Rohwer et al. 2001), suggest that selection against hybrids and, to some degree, against pure Hermit Warblers, is similar in all three zones of introgression (Rohwer et al. 2001). Further, the behavioral dominance and higher fitness of Townsend's

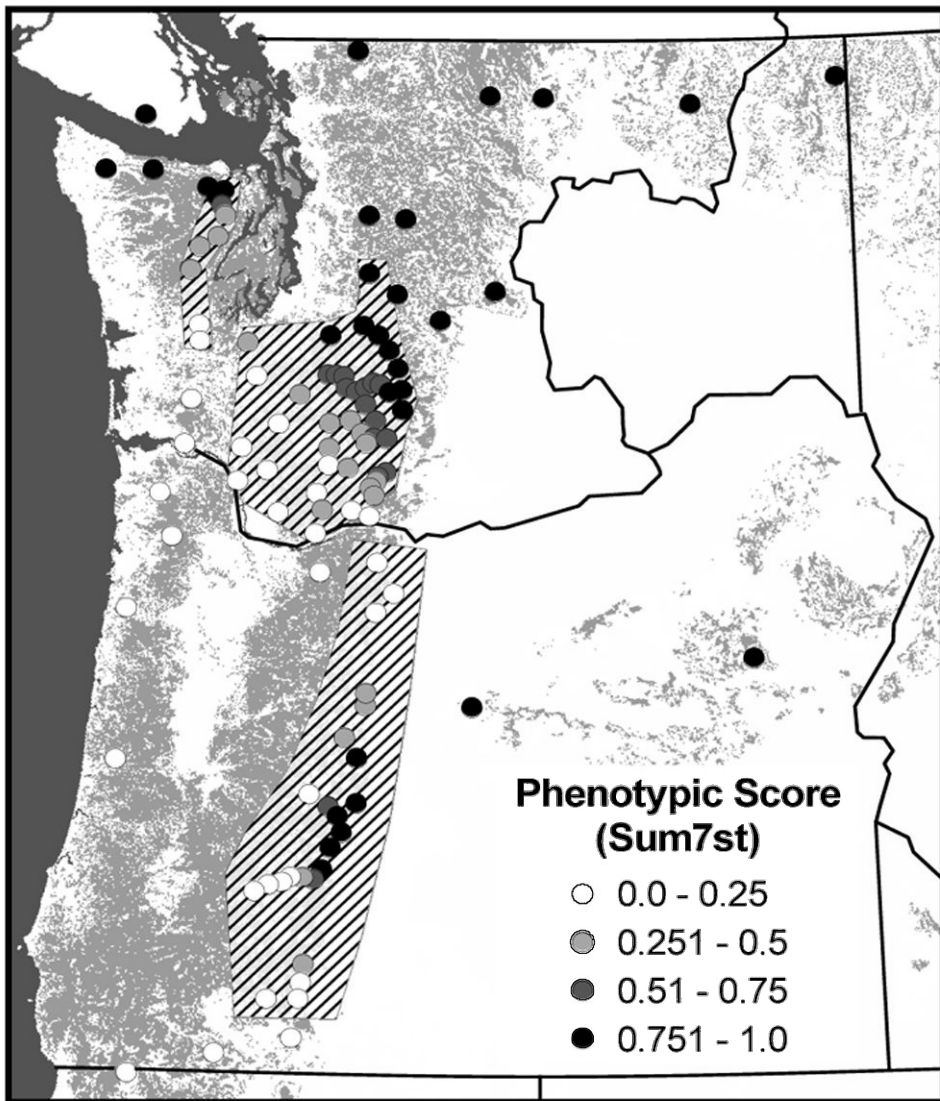


FIG. 1. From north to south, the three hybrid zones (crosshatching) between Townsend's and Hermit warblers: the Olympic zone, the Washington Cascade zone, and the Oregon Cascade zone. Gray background shading illustrates warbler breeding habitat. Note the broad highland corridor connecting the Cascades of Washington and the Rocky Mountains and the corridor of sparser habitat connecting the Oregon Cascades to the Rocky Mountains. (The Rockies lie mostly to the east of the region covered by this map.) Mean phenotypic scores of 0.0–0.25 reflect Hermit Warbler localities, 0.251–0.75 hybrid localities, and 0.751–1.0 Townsend's Warbler localities. Phenotypic scores reflect the combination of seven plumage color characters (SUM7st) and represent means for each population; except for the new localities for the Oregon Cascade zone (Table 1), the plotted scores are from Rohwer and Wood (1998).

Warblers compared with Hermit Warblers and hybrids supports other evidence that the hybrid zones are moving, with Townsend's Warblers replacing Hermit Warblers through hybridization (Rohwer et al. 2001).

#### THE THREE HYBRID ZONES

From north to south, the three hybrid zones lie in the Olympic Mountains of Washington, the Cascade Mountains of southern Washington, and



the Cascade Mountains of central Oregon (fig. 5 in Rohwer and Wood 1998). The two Washington zones probably represent a broad zone that moved south through British Columbia but became separated in Washington by the waters of Puget Sound and by the lowland forests of the Puget trough (Fig. 1), which, historically, were dominated by western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) (Whitlock 1992), neither of which is suitable for these warblers.

Two mountain corridors that create a connection between the Rocky Mountains and the Cascade Mountains have likely affected the Cascade zones of Washington and Oregon (Fig. 1). A forest corridor across the Okanogan Highlands connects the Cascade Mountains of central Washington with the Rocky Mountains of Montana, Idaho, and the northeastern corner of Washington. Townsend's Warblers are common in the Rocky Mountains and the Okanogan Highlands, and dispersal across the Okanogan corridor has likely influenced the shape and movement of the hybrid zone in the Cascades of Washington (Rohwer et al. 2001). In Oregon, the Blue Mountains form another forest corridor between the Rocky Mountains and the Oregon Cascades. Townsend's Warblers have apparently dispersed across this corridor to form a third, independently established hybrid zone on the east side of the Cascade Mountains of Oregon. Moving from north to south along the east slope of the Cascades of Washington and Oregon, one thus passes from pure Townsend's Warblers in central Washington, through the hybrid zone in the Washington Cascades, into pure or nearly pure Hermit Warblers near the Washington-Oregon border. Continuing farther south in Oregon, one then passes through another hybrid zone on the east side of the Oregon Cascades, into pure Townsend's Warblers, and then through another zone into pure Hermit Warblers in southern Oregon (Fig. 1).

Here, we show that the frequency of hybrid males varies dramatically among these zones. We further explore whether the frequency differences in hybrids can be accounted for by differences in time since contact, gene flow, and climatic factors.

#### METHODS

This work is based on 716 male specimens assembled from all the localities in these three

zones that contained at least a single individual that scored as a hybrid. We excluded females because so few were collected and because assigning plumage scores to generate a hybrid index is more difficult for females than for males (Smith and Rohwer 2000).

After correcting for age differences in appearance between yearling and older males, seven plumage color characters were combined to create a hybrid index (Sum7st) that was standardized to vary from 0.0 (Hermit extreme) to 1.0 (Townsend's extreme) (Rohwer and Wood 1998). Using reference samples collected well outside the hybrid zone, males with scores of 0.0–0.25 matched phenotypically pure Hermit Warblers and males with scores of 0.751–1.0 matched phenotypically pure Townsend's Warblers. Hybrids fell between 0.251 and 0.75 (Rohwer and Wood 1998).

Within each of the three hybrid zones, all birds from any locality were included in the analyses if at least one individual from that locality scored as a hybrid. Using all birds from a locality enabled us to compute unbiased estimates of the percentage of hybrids in the sample locality. Most sample localities contained 6 to 10 males, and eliminating small samples had no effect on the results reported below. New localities for the Oregon Cascades that are not listed in Rohwer and Wood (1998) or Rohwer et al. (2001) are listed in Table 1.

Two measures form the basis for comparing the three zones. (1) We compared the distribution of phenotypes for each of the three zones. This measure is potentially problematic, because bimodality could result from a biased representation of collecting localities if most samples in a zone came from areas near its edges (i.e., where parental phenotypes predominate). (2) To control for possible sampling biases, we plotted the fraction of hybrids versus the mean hybrid index for each locality within zones. These plots serve two functions. First, if sampling bias caused the differences in hybrid frequencies between zones, we should see an excess of samples along the edge of zones where one parental phenotype predominates. Such locations are revealed by skewed hybrid-index scores (Sum7st values) in favor of either Hermit Warblers (skewed toward 0) or Townsend's Warblers (skewed toward 1). If we did not adequately sample populations from the center of the hybrid zone, we should

TABLE 1. New localities in the Cascade Mountains of Oregon that are not described in Rohwer and Wood (1998) or Rohwer et al. (2001).

Location no.	n	$\bar{x}$	SD	Locality name	Locality description	Date collected	Elevation (feet)
102	7	0.247	0.135	Badger Creek	Wasco County, Maupin, 6.5 miles N, 12.5 miles W	1 July 1999	2,200
103	10	0.440	0.228	Green Ridge north	Jefferson County, Sisters, 21.5 miles N, 1 miles W	1 July 1999	4,800
105	10	0.785	0.158	Lolah Butte	Deschutes County, Sunriver, 16 km W, 3 km S	22 June 1999	4,900
106	10	0.711	0.299	Cultus Mountain	Deschutes County, Sunriver, 22 miles W, 3.5 miles S	22 June 1999	5,100–5,400
107	12	0.842	0.204	Browns Mountain	Deschutes County, Sunriver, 18 miles W, 8 miles S	22 June 1999	4,600
108	12	0.887	0.072	Davis Mountain	Deschutes County, La Pine, 1.5 miles S, 13 miles W	23 June 1999	4,700–5,200
109	9	0.901	0.098	Gilchrist	Klamath County, Gilchrist, 7.5 km N, 14 km W	27 June 1998	4,650
110	10	0.883	0.079	Beales Butte	Klamath County, Crescent, 4.5 miles S, 11.5 miles W	24 June 1999	5,100–5,700
111	11	0.745	0.268	Tolo Mountain	Klamath County, Crescent, 9 miles S, 15 miles W	28 June 1999	5,400
112	14	0.411	0.338	Bradley Creek	Douglas County, Steamboat, 32.5 miles E	28 June 1999	5,000
113	8	0.184	0.088	Kelsay Mountain	Douglas County, Steamboat, 27 miles E	29 June 1999	5,200
114	10	0.177	0.136	Loafer Creek	Douglas County, Steamboat, 2.5 miles S, 23.5 miles E	29 June 1999	4,200
116	10	0.118	0.089	Copeland Creek	Douglas County, Steamboat, 7 miles S, 11.5 miles E	30 June 1999	2,700
117	11	0.325	0.325	South Crater Lake	Klamath County, Chiloquin, 12.5 miles N, 10 miles W	25–26 June 1999	4,900
118	11	0.203	0.083	Threemile Creek	Klamath County, Chiloquin, 4 miles N, 11 miles W	26 June 1999	5,400
119	11	0.129	0.060	Pelican Butte	Klamath County, Chiloquin, 3.5 miles S, 12 miles W	26 June 1999	5,200
121	10	0.097	0.034	Klamath Falls W	Klamath County, Klamath Falls, 19 miles W, 2.5 miles N	25 June 1999	5,100

see a deficiency in the number of populations occurring in the center region of the hybrid-index scores (Sum7st). Second, the peak in these curves estimates the maximum hybrid frequency across all populations within each hybrid zone. This maximum hybrid frequency obviates concerns that skewed sampling may have biased means and provides a comparable relative index of hybridization found near the phenotypic center of the hybrid zones (i.e., where contributions of parental species are equivalent). We fit these curves using a Loess smoothing function with a tension of 80.

To examine the effects of abiotic factors on the proportion of hybrids, we plotted the percentage of hybrids at localities against total annual precipitation (sum across all months, in millimeters) and mean temperature during the breeding season (May, June, July; °C), separated by zone. Temperature and precipitation data came from a 10-min-resolution grid of mean monthly values averaged across a 30-year period (1961–1990) (New et al. 2002).

### RESULTS

The three zones are dramatically different with respect to the distribution of phenotypes. Hybrids predominate in the Olympic hybrid zone (60.4% hybrids); by contrast, the Washington Cascade zone shows an intermediate proportion of hybrid phenotypes (43.3% hybrids), and the Oregon Cascade zone shows the fewest hybrid phenotypes (27.8% hybrids; Table 2 and Fig. 2). These differences are highly significant, as revealed by a comparison of frequencies of pure parental versus hybrid birds ( $\chi^2 = 31.0$ ,  $df = 2$ ,  $P < 0.001$ ).

Because parts of the Oregon Cascade zone lie in the Pine Ridge Indian Reservation and in Crater Lake National Park, we could not collect continuous transects through this zone.

Further, habitats are patchily distributed in the high-elevation parts of this zone near the Cascade crest, because stands of lodgepole pine (*P. contorta*) break up more mesic patches of true fir and Douglas-fir in the porous volcanic soils of this region (S. Rohwer and C. Wood pers. obs.). These sampling issues made it important to compare the fraction of hybrids versus the mean hybrid index for each of the zones to demonstrate that the differences in phenotypic distributions (Fig. 2) are not the result of biased sampling across the three zones. These distributions are plotted in Figure 3, which makes two distinct points. First, the mean hybrid index peaks near the phenotypic center of each zone, which is what one would expect if sampling were thorough and hybrid frequencies were not affected by complex ecological patterning. Thus, sampling artifacts cannot account for the striking differences in the distributions of phenotypes shown in Figure 2. Second, the peaks of these curves correspond well with the frequency data presented in Table 2: the highest peak is for the Olympic zone at ~85% hybrids, the intermediate peak is for the Washington Cascades at ~55% hybrids, and the lowest peak is for the Oregon Cascades at ~45% hybrids (Fig. 2).

We were unable to sample localities with mean phenotypes between 0.5 and 0.65 in the Oregon Cascades (Fig. 3). Nonetheless, the more-or-less continuous sampling from the pure Hermit Warbler side of the zone to localities with mean scores of 0.45 and the more-or-less continuous sampling from the pure Townsend's Warbler side of the zone to localities with scores of 0.7 make it clear that the fraction of hybrids is really lower for this zone than for either of the Washington zones. Remarkably, collecting bias was far more extreme in the Olympic hybrid zone than it was in the Oregon Cascades; in the Olympic hybrid zone, no samples with hybrids had mean hybrid indices between 0.55 and 0.80.

TABLE 2. Frequency of hybrids and pure parentals for the three hybrid zones based on phenotypic scores for male specimens; pure Hermit Warblers scored 0.0–0.25, hybrids 0.251–0.75, and pure Townsend's Warblers 0.751–1.0.

Hybrid zone	Number of hybrids	Number of parentals		Percentage hybrids
		Townsend's	Hermits	
Washington Olympics	58	21	17	60.4
Washington Cascades	178	101	132	43.3
Oregon Cascades	58	93	58	27.8

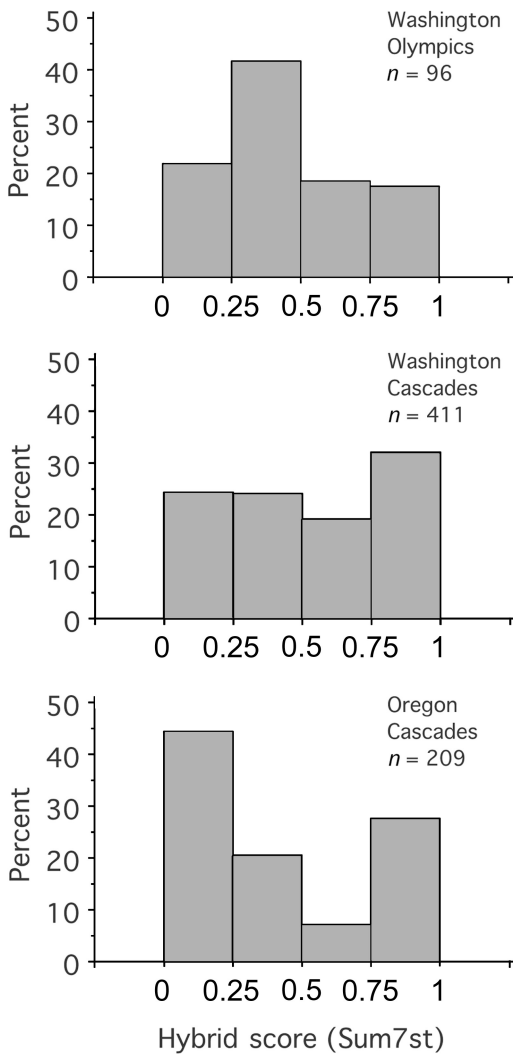


FIG. 2. Percentage of pure Hermit Warblers (hybrid index of 0.0–0.25), hybrids (0.251–0.750), and pure Townsend's Warblers (0.751–1.0), in the three hybrid zones. Note the decreasing proportion of hybrids as one moves from north to south. Because the Olympic and Washington Cascade zones are likely of similar age, the contrast between them supports the hypothesized importance of immigration from the Rocky Mountains. Because the Washington Cascade zone and the Oregon Cascade zone likely both receive immigrant Townsend's Warblers from forest corridors connecting them to the Rocky Mountains, the contrast between these two zones is likely attributable to the Oregon zone being newly established.

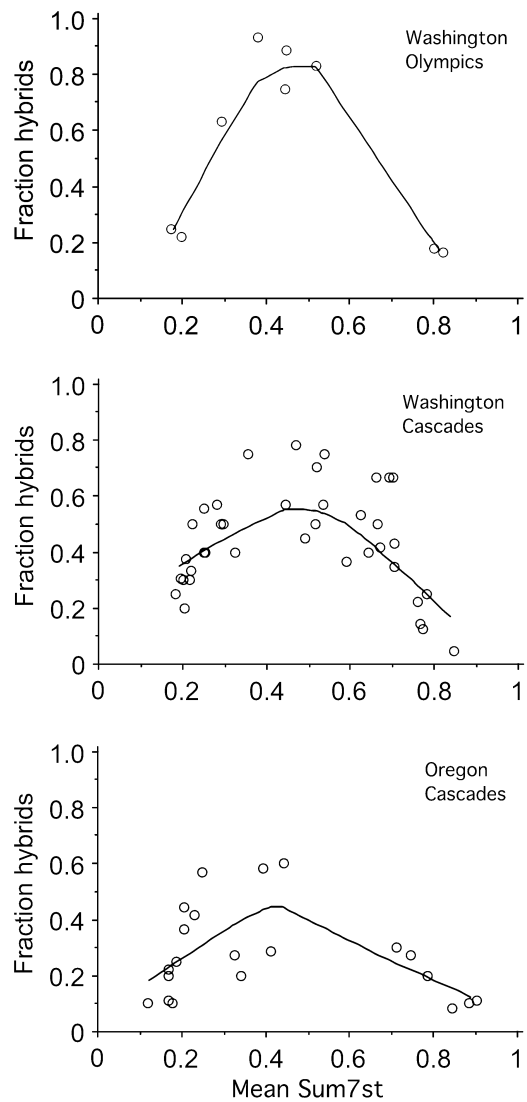


FIG. 3. Fraction of hybrids at each locality having at least one hybrid male, plotted against the mean hybrid index for that locality (Sum7st), split by hybrid zone. The curves were fit to the points using Loess smoothing. Because all three zones show a rise in hybrid frequency at their centers, we can reject the hypothesis that the pattern of Figure 2 results from sampling bias. Note also that the differences in maximum hybrid frequency corroborate the north-to-south decline in hybrid frequency shown in Figure 2.



Despite this bias in sampling, all of our Olympic samples with phenotypic means of 0.35 to 0.55 have >80% of individuals scoring as hybrids. Clearly, sampling is not the cause of the distribution difference shown in Figure 2.

Climatic factors did not explain the variation in percentage of hybrid warblers among the three zones (Fig. 4). Neither annual precipitation ( $r^2 = 0.006$ ,  $F = 0.4$ ,  $df = 1$ ,  $P = 0.5$ ) nor mean

temperature during the breeding season ( $r^2 = 0.007$ ,  $F = 0.4$ ,  $df = 1$ ,  $P = 0.5$ ) varied with the percentage of hybrids across populations, and there were no climatic trends across the three zones (Fig. 4).

## DISCUSSION

The three hybrid zones between Townsend's and Hermit warblers differ in their frequencies of hybrid and parental phenotypes. The northernmost Washington Olympic hybrid zone had the greatest proportion of hybrid phenotypes (60.4%), followed by the Washington Cascade zone (43.3%) and, finally, the southernmost Oregon Cascade zone (27.8%). This pattern of hybrid frequency is also reflected in maximum frequencies of hybrids found per sample across the three zones, with the northernmost Olympic hybrid zone having the highest (93.8% hybrids), followed by the Washington Cascade zone (78.3% hybrids) and, finally, the Oregon Cascade zone (60.0% hybrids). Such variation in hybrid frequency across hybrid zones is unlikely to result from biased sampling, because populations near the center of the hybrid zones were sampled in all populations (Fig. 3).

Variation in the frequency of hybrid phenotypes across the three distinct hybrid zones could be caused by one or more factors differing between the three zones: (1) natural or sexual selection, (2) dispersal of parental or hybrid birds, or (3) time since secondary contact. Other factors, such as differences in genetic compatibility of parental genotypes (Price and Bouvier 2002), are unlikely to explain differences between the zones, given that the same species are involved in a relatively small area of repeated contact (Fig. 1). Data on potential abiotic selection pressures (annual precipitation and temperatures during the breeding season) do not covary with the proportion of hybrids within a population (Fig. 4). Similarly, no habitat differences between territories of Townsend's Warblers, Hermit Warblers, and hybrids within the hybrid zones have been found (Pearson and Manuwal 2000), and none of the three hybrid zones is associated with ecological transitions (Rohwer and Wood 1998, Pearson and Manuwal 2000), as is often true of other zones (Moore and Price 1993). Similarities in the shapes of character transitions across the hybrid zones (and across almost all phenotypic traits) suggest that

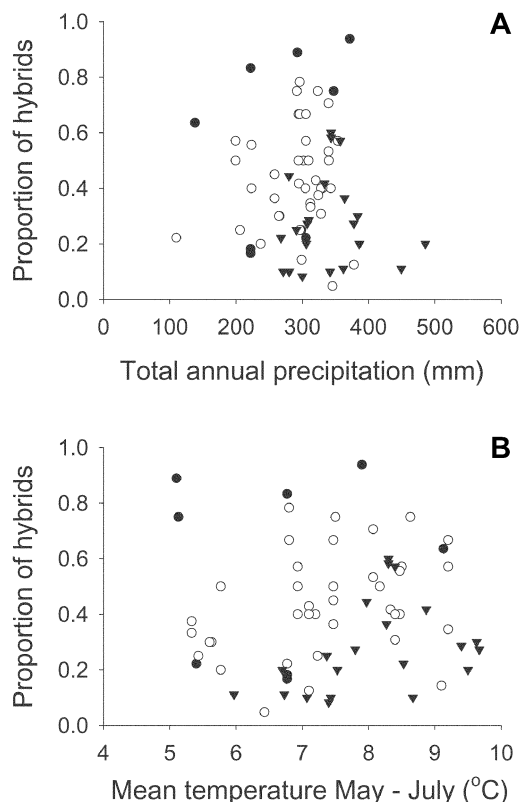


FIG. 4. The proportion of hybrids within a population did not covary with either (A) total annual precipitation (mm) or (B) mean temperature during the breeding season. Given that habitats and other features were similar among the zones, we find no support for differences in selective pressure accounting for the varying relative frequencies of hybrids, in contrast to the strong support for explanations based on time since contact and difference in immigration from the Rocky Mountains. Climate data are from New et al. (2002). Black circles = Washington Olympics hybrid zone, white circles = Washington Cascade hybrid zone, and black triangles = Oregon Cascade hybrid zone.

selection acts in similar ways across the hybrid zones (Barton and Hewitt 1985, 1989; Rohwer et al. 2001). Together, this evidence suggests that selection is unlikely to explain the variation in hybrid frequency across the three zones of introgression.

The three zones form two interesting contrasts that, combined with the recent history of northwestern forests, suggest that differences in dispersal and time since contact explain the differences in their distributions of phenotypes (Fig. 2). The Olympic and Washington Cascade zones lie fairly close together (Fig. 1) and likely became isolated only recently, as the southward movement of the hybrid zone pushed them to either side of the Puget trough (Rohwer et al. 2001). The preponderance of Hermit Warbler mtDNA north and south of these zones and within them (fig. 9 in Rohwer et al. 2001) suggests that they have moved to their current position from the north and have existed for several thousand years (Rohwer et al. 2001). Because these two zones are likely similar in age, the contrast in the shape of their phenotypic distributions (Fig. 2) is likely attributable to higher dispersal of parental Townsend's Warblers into the Washington Cascade zone from the Rocky Mountains to the east, compared with a lack of such immigration in the Olympic zone.

Our suggestion that the difference in hybrid frequency between the Olympics and the Washington Cascades is caused by higher dispersal of Townsend's Warblers from the Rocky Mountains is supported by several observations. First, Rohwer et al. (2001) showed a cytonuclear disequilibrium for the Washington Cascade zone, but not the Olympic zone, that was caused entirely by an excessive association of pure Townsend's Warbler phenotypes and haplotypes at hybrid localities in the Washington Cascades. Because the Washington Cascade zone is situated near the Okanogan highlands, which hosts a forest corridor joining the Rocky Mountains with the Cascade Mountains of Washington (Fig. 1), pure Townsend's Warblers that were unaffected by a long history of hybridization can readily disperse into this zone from the east. Second, the Olympic zone lies 100 km west of the Washington Cascade zone and is relatively isolated from Rocky Mountain Townsend's Warbler by distance, water, and unsuitable forests of the Puget trough. Finally, excess dispersal of Townsend's Warblers into

the Washington Cascade zone is reflected in pure Townsend's phenotypes ( $\text{Sum7st} > 0.75$ ) being the highest-frequency class for this zone (Fig. 2). This excess of Townsend's phenotypes is not a consequence of more sampling on the Townsend's side of this zone, because sampling for the Washington Cascade zone was equally dense on its two parental sides (Fig. 3).

The Washington and Oregon Cascade zones are both situated close to forest corridors that connect the Cascade and Rocky mountains. These forest corridors facilitate dispersal of Townsend's Warblers from the east (Fig. 1). Massive historical efforts to transform the old-growth pine parklands of these regions into productive young forests, together with fire suppression, have created extensive tracts of Douglas-fir across the Ochoco and Blue mountains of Oregon and on the east side of the Cascades (Langston 1995). These changes in forest cover have created some of the highest-density warbler habitats that S.R. and C. Wood have seen in their work on this project and likely facilitated the expansion of Townsend's Warblers westward into the Cascades of Washington and Oregon.

In a rough sense, dispersal of Townsend's Warblers through the modified forest corridors into the Washington Cascades should have been similar to that in the Oregon Cascades, and higher than dispersal of Townsend's Warblers into the Olympic Mountains. Zone age, however, likely differs dramatically between the Washington and Oregon Cascades. As we argued above, the Washington Cascade zone is part of a larger southward-moving zone of contact between Hermit and Townsend's warblers that has existed for several thousand years. By contrast, the Oregon Cascade zone is likely newly established in response to fire control and the development of fir forests across the Blue and Ochocho mountains. If the Oregon Cascade zone were as old as the Olympic and Washington Cascade zones, then it should have fused with the Washington Cascade zone long ago, given the history of movement of the two Washington zones. Presumably, the Oregon zone exists today as a separate "island" contact because it has only recently been established, accounting for its great excess of parental phenotypes. Greater dispersal of Townsend's Warblers into this zone is unlikely to explain the high frequency of parental phenotypes,

because the forest corridor in Oregon is much less substantial than the forest corridor across the Okanogan highlands of Washington (Fig. 1), and pure Townsend's Warblers are still outnumbered by pure Hermit Warblers (Fig. 2).

## CONCLUSIONS

The frequency of hybrid phenotypes varies significantly across the three hybrid zones, being highest in the northernmost Olympics, intermediate in the Washington Cascades, and lowest in the southernmost Oregon Cascades. This pattern could result from differences in selection, dispersal, or time since contact between the three zones. Evidence suggests that variation in dispersal and time since contact are the most likely explanations for variation in hybrid frequency. The Olympic and Washington Cascade zones appear to be old and to have shifted to their current locations from the north over the course of thousands of years (Rohwer et al. 2001). Because of its location near the Pacific coast, the Olympic zone has remained relatively free of dispersal from eastern Rocky Mountain populations of Townsend's Warblers, whereas the Washington Cascade zone likely experiences more dispersal of Townsend's Warblers entering from the east. The southernmost Oregon Cascade zone shows the lowest frequency of hybrids, presumably because it was recently established by Rocky Mountain populations of Townsend's Warblers dispersing into the Oregon Cascades. Both the increased dispersal of pure Townsend's Warblers into the Washington Cascades and the recent contact of Townsend's Warblers with Hermit Warblers in the Oregon Cascades may have been facilitated by anthropogenic changes in forest cover.

## ACKNOWLEDGMENTS

G. Eddy supported most of the field work for this project; additional support has come from the Burke Museum Endowment for Ornithology. C. Wood helped collect and score the specimens, and D. McDonald and B. Curry provided helpful comments on the manuscript. We appreciate authorization to collect for this project in Alaska, British Columbia, Washington, Oregon, Idaho, and California. For specimen loans, we thank the American Museum of Natural History, California Academy of Natural

Sciences, Carnegie Museum of Natural History, Field Museum of Natural history, Louisiana State University Museum of Natural Science, Oregon State University Department of Fish and Wildlife, U.S. National Museum, University of California Museum of Vertebrate Zoology, San Diego Museum of Natural History, University of California at Los Angeles, University of Puget Sound, and Washington State University. Most of the specimens used in this project are housed at the University of Washington Burke Museum.

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Associate Editor: D. B. McDonald