

THREE HYBRID ZONES BETWEEN HERMIT AND TOWNSEND'S WARBLERS IN WASHINGTON AND OREGON

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ABSTRACT.—We describe two hybrid zones between Hermit Warblers (*Dendroica occidentalis*) and Townsend's Warblers (*D. townsendi*) in Washington, and introduce a third zone in Oregon. To quantify phenotypes, we scored eight standardized characters in each age class and summed them to form a hybrid index score. Because no linear geographic feature delimits the hybrid zones between these warblers, we sampled the forests of Washington in a grid-like fashion to define the shape of the zones. For both Washington zones, the shape of the character-transition curves for the hybrid index suggests asymmetries in gene flow, with Townsend's-like phenotypes penetrating farther into the Hermit side of the zone than vice versa. Covariances between character states are high at the phenotypic center of the zone. Following Barton and Gale (1993), we use these covariances and the width of the zone to estimate σ , the root mean square dispersal distance. Both Washington zones are narrow relative to σ , indicating that selection is preventing these zones from increasing in width. Hybrid superiority within an ecotone, recency of contact, and habitat modification seem insufficient as explanations for the abrupt transition that takes place in these zones. Asymmetries in the character-transition curves suggest that the zones are moving. We find no evidence that this inferred movement can be attributed to habitat changes or to differences in dispersal between the parental species. Other studies suggest that the primary cause of this inferred movement is behavioral dominance of Townsend's males over Hermit males. The shape of the zone in the Washington Cascades also suggests that Townsend's on the east side of the Cascade Mountains are better adapted to dry forests, possibly due to gene flow from populations derived from the Rocky Mountains. The third, isolated zone in the Cascade Mountains of Oregon offers unique opportunities to test this hypothesis. Received 25 June 1997, accepted 30 September 1997.

THE PREDOMINANCE OF THE BIOLOGICAL SPECIES CONCEPT trivialized the study of hybrid zones during much of the last half-century. Because species were defined by the absence of interbreeding, most older studies of hybridization were justified primarily as tests of the species status of the taxa involved (Mayr 1963). The documentation of hybrid swarms justified lumping well-differentiated morphological forms into single species. An unfortunate consequence was that non-sister taxa often became conspecifics. This obscures the historical ordering of divergences within a clade and is now being rectified by the growing use of the phylogenetic species concept (Cracraft 1989, Zink and McKittrick 1995).

If studies of hybrid zones for insight into the species status of differentiated populations are passé, why should they be studied? Hybrid zones are interesting because they are natural

laboratories for some of most difficult and intractable questions in population biology. In a series of seminal papers, Barton and coworkers have developed mathematical models that tie the study of hybrid zones to many important components of population biology (Barton 1979, Barton and Hewitt 1985, 1989, Barton and Gale 1993). These models show hybrid zones to be ideally suited to studies of selection, dispersal, competition, mate choice, and the nature of genetic control of phenotypic characters (Endler 1977, Barton and Gale 1993, Gill 1997). Because the study of avian hybrid zones was waning before this theoretical literature developed (see reviews in Mayr and Short 1970, Rising 1983), these new models have scarcely been applied to the analysis of avian hybrid zones. This report, along with those of Moore and Price (1993) and Gill (1997), suggest that much can be gained by resurrecting this field of avian biology.

Hermit Warblers (*Dendroica occidentalis*) and Townsend's Warblers (*D. townsendi*) are two of

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the most abundant birds in the coniferous forests of the Pacific Northwest. Nonetheless, three major hybrid zones between these highly differentiated birds have gone largely undescribed for several quite different reasons. Their preferred habitat is the canopy of tall conifers, making breeding birds difficult to observe or collect without song playback. Furthermore, much of the area occupied by their hybrid zones was inaccessible before the recent proliferation of logging roads in northwest forests. Finally, field observers usually mistake hybrids for Hermit Warblers because most hybrids have entirely yellow faces. The yellow face of Hermit Warblers and hybrids is controlled almost exclusively by a single-locus dominant allele (see below); hybrids that have black face patches usually are sufficiently Townsend's-like in other characters that they are mistaken for pure Townsend's Warblers. Although hybrids between Hermit and Townsend's warblers have been illustrated in North American field guides, only two papers have been published on their hybridization. Jewett (1944) described four hybrids, noting that their most striking characteristic was "the full head markings of *occidentalis*, without any sign of the mask of *townsendi*. . . ." Morrison and Hardy (1983) also observed that most of the nine hybrid males they examined had yellow faces, suggesting to them an apparent absence of back crossing with pure Townsend's Warblers.

In this paper, we document the present position of the two Washington hybrid zones so that future collections can be used to assess movements of the zones. We also introduce a third hybrid zone in central Oregon, first noted by Morrison and Hardy (1983). This Oregon zone is poorly characterized, but a trip there in 1994 revealed it to be geographically isolated from the two zones in Washington. Apparently, this zone developed independently of the two Washington zones when Townsend's Warblers invaded the central and southern Cascades of Oregon from mountain ranges to the east.

Most hybrid zones are narrow, and many are probably ancient, suggesting that they have not been important arenas for the reinforcement of isolating mechanisms (Cracraft 1983, Barton and Hewett 1985; but see Howard 1993). Because our warbler zones are narrow, we examine four models that address the maintenance of narrow zones: (1) the tension model

balancing selection against hybrids with dispersal into the zone (Barton and Hewett 1985), (2) hybrid superiority within an ecotone (Moore 1977), (3) recent contact (Endler 1977), and (4) habitat modification (Gill 1980). Character-transition analyses (Barton and Gale 1993) suggest that the two Washington zones are moving such that Townsend's Warblers are displacing Hermit Warblers. Three models address the movement of hybrid zones: (1) habitat modification, (2) differences in dispersal between parentals, and (3) fitness asymmetries between parentals. Our results suggest the working hypothesis that these warbler hybrid zones are narrow because of selection against hybrids and moving because Townsend's Warblers are competitively superior to Hermit Warblers.

METHODS

Sample localities.—Although Townsend's Warblers occupy coastal forests from Washington to Alaska, they have a predominantly interior distribution, occurring from Fairbanks, Alaska, south through the Rocky Mountains to northwestern Wyoming (AOU 1983). In contrast, Hermit Warblers are restricted to the Cascades and coastal ranges of Washington and Oregon, the coastal ranges of California, and the Sierra Nevada of California and west-central Nevada (AOU 1983).

Prior to this work, published records of hybrids reliably taken on the breeding grounds consist of five June specimens; all were taken on the east slope of the Cascades in Oregon (Morrison and Hardy 1983). Our discovery of hybrids in the Cascades of Washington prompted us to sample Washington in a grid-like fashion to describe the location of the phenotypic center of the two zones (see below). When hybrid zones pass through large areas of continuous habitat, as is the case here, defining the line that follows the phenotypic center of a zone is essential for establishing perpendicular transects that minimize the distance between pure parental phenotypes (Fig. 5). Such transects are required for conducting the character-transition and linkage-disequilibrium analyses that make contemporary work on hybrid zones exciting (Barton and Hewitt 1985, 1989, Barton and Gale 1993). For our character-transition analyses we hoped to collect about 10 males per locality, but we could not always find enough suitable Douglas-fir (*Pseudotsuga menziesii*) or true fir (*Abies*) forests to do so (Appendix). In every case where these warblers occur in stands predominated by hemlock (*Tsuga*) or western red cedar (*Thuja plicata*), Douglas-fir and true firs always were mixed into the stand (see Morrison 1982).

At three localities in the Washington Cascades and at one in the Olympics, we collected large samples of birds from the phenotypic center of the zone. We used these "midpoint" samples to calculate character covariances for measuring linkage disequilibrium, and to estimate the variance in our hybrid index at the center of the zone.

Collecting.—Most of our collecting for this project took place from 1986 to 1988 and 1994 to 1995. Sample localities are listed in the Appendix and locality numbers are plotted on Figure 5. From 1986 to 1988, we drove forest logging roads listening for singing birds. Song playbacks were then used to bring the birds into range. Subsequently, we realized that we were vastly underestimating densities of these warblers by searching for singing birds. Thus, in 1994 to 1995 we often played tapes every 100 m along roads or trails, even when no bird was singing, and often were able to collect our samples from much smaller areas.

Because all of our collecting was done with playbacks, our samples are unbiased by any prior impression of the phenotype of the birds before they were shot. Townsend's Warblers often respond more vigorously to song playback than do Hermit Warblers, but they are so active once they have been brought down from the canopy that they are more difficult to collect. Hermit Warblers generally do not become as agitated by playbacks as do Townsend's, so they are more difficult to see when they respond but easier to collect. If appropriate songs are played, both species respond readily to playbacks and are easily collected, so we do not think our collecting was biased toward either phenotype.

In the coastal areas of southwestern Washington and western Oregon, Hermit Warblers are well isolated from Townsend's. In these areas, locally record songs were required to bring birds out of the canopy. In areas of contact we found no consistent difference between songs, although the songs were rather variable.

Dates of collection.—All specimens were taken from breeding territories. Hermits, Townsend's, and hybrids arrived over the same range of dates at a site near the center of the hybrid zone in the Cascades of western Washington. For several seasons, the average arrival date for males was 8 May for adults and 18 May for yearlings (Pearson and Rohwer unpubl. data).

Most of our samples were collected between 20 May and mid-July (Appendix). We sampled most high-elevation sites in June because there is considerable delay in the arrival of birds at high elevations in the Cascades. For birds taken early in the breeding season, we eliminated all individuals without well-developed seminal vesicles. Enlargement of the seminal vesicles is a better indicator of local breeding status than either testis size or song; most of these

specimens were acting territorial when collected, and all had enlarged testes.

Determining age classes.—Reliable aging was essential to combining yearlings and adults into the same analyses without biasing hybrid scores. We used the methods of Jackson et al. (1992) to divide breeding males into birds in their first potential breeding season (hereafter "yearlings") and older birds in their second or later breeding season (hereafter "adults"). By using the size of the white spot in rectrix four, the presence or absence of black shaft streaks on the middle secondary coverts, and rectrix shape, more than 99% of males can be aged correctly. Using tail spots and secondary coverts alone, 96% of males can be aged correctly.

Character scoring.—We measured variation in eight color characters that distinguish Hermit and Townsend's warblers (Table 1). Because we used these measurements to compute covariances and linkage disequilibria (Barton and Hewitt 1989), we assigned as many units as we could reliably distinguish to the eight scored variables. The Hermit extreme for each character was 0; the Townsend's extreme varied from 6 to 36; museum numbers assigned to these voucher specimens are listed in Table 1.

We used the following eight characters to generate our hybrid indices (Table 1). Mid-flank streaking was the anterior half of the flank streaking, exclusive of the bib corner. Lower-flank streaking was the posterior half of the flank streaking. We split the flank streaking into two characters because hybrids often are more heavily streaked in one of these regions than the other, suggesting independent genetic control (see front cover). Bib corner is an index of bib size; pure Hermits have a small bib that is completely separated both from the back and from the region of the flanks that are heavily streaked in Townsend's Warblers. We did not measure bib size quantitatively because it is strongly affected by the length of the neck in study skins. Face was a difficult character to score. Specimens that were intermediate in the coloration of their face were so rare that we could define only seven states, varying from the solid yellow of pure Hermits to the large black patch of pure Townsend's. The extent of yellow on the breast was measured in mm from the posterior edge of the bib to its posterior-most extent; differences in specimen preparation have little effect on the length of this region of the body. We also scored the intensity of yellow on the breast because hybrids showed considerable independence between the extent and intensity of yellow in this region. Hermit Warblers have a yellow forehead and crown, which, combined with their yellow face, produces their most distinguishing field mark, the yellow head. Unlike the face, however, the extent of yellow on the crown is highly variable in hybrids, suggesting polygenic control and no overdominance (see Results), so crown color became part of our final hybrid index. Last, we assessed the back-

TABLE 1. Characters, their definitions, and the voucher specimens used to measure character variation.

Character	Definition	Reference series (UWBM numbers)
Mid flank	0 = no streaks 7 = heavily streaked	0 = 46654; 1 = 46684; 2 = 52336; 3 = 52460; 4 = 50389; 5 = 52403; 6 = 50766; 7 = 50758
Lower flank	0 = no streaks 8 = heavily streaked	0 = 46692; 1 = 50786; 2 = 50799; 3 = 50839; 4 = 52407; 5 = 52331; 6 = 50894; 7 = 50341; 8 = 52380
Bib corner	0 = gap between bib and back 9 = broad black union	0 = 50803; 1 = 52455; 2 = 52492; 3 = 50815; 4 = 41743; 5 = 52317; 6 = 54587; 7 = 51419; 8 = 50274; 9 = 50777
Face	0 = no black in face 6 = large black face patch	0 = 50784; 1 = 52471; 2 = 52349; 3 = 49020; 4 = 49967; 5 = 52470; 6 = 50392
Extent of yellow	0 = 0 mm of yellow below bib 36 = 36 mm of yellow below bib	Measured directly, not scored with a reference series
Intensity of yellow	0 = no yellow at edge of bib 7 = intensely yellow at edge of bib	0 = 50783; 1 = 50796; 2 = 52412; 3 = 52477; 4 = 52462; 5 = 50845; 6 = 52456; 7 = 50896
Crown	0 = most yellow on crown 8 = crown solid black	0 = 46658; 1 = 46680; 2 = 52293; 3 = 52310; 4 = 52479; 5 = 51355; 6 = 52490; 7 = 52290; 8 = 52312
Back color	0 = gray, minimal tinge of green 8 = bright yellowish-olive green	0 = 46673; 1 = 46667; 2 = 50804; 3 = 50785; 4 = 50798; 5 = 51352; 6 = 52309; 7 = 50838; 8 = 51333

ground color of the back, emphasizing the rump and nape where the background color is less obliterated by streaking. Back color is highly variable between individuals but consistently different between parental populations, with Hermits tending to have gray backs and Townsend's green backs.

Two additional characters were discarded. In general, Townsend's are more heavily streaked on their backs than Hermits. However, the character is so variable that it failed to distinguish the reference samples, partly because Hermits from coastal locations are very heavily streaked. The undertail coverts tend to be immaculate in Hermits and streaked in Townsend's, but we did not score this character because it seemed too variable to be worth the effort.

Reference samples.—We used reference samples of pure Townsend's Warblers and pure Hermit Warblers to assess character variation within parental phenotypes (Appendix). Most of our 64 reference specimens of Townsend's Warblers were collected in interior regions to the north and west of the hybrid zones. Reference samples of Hermits were taken in the southwestern Cascades of Oregon and in California. About half of our 58 reference specimens for Hermit Warblers were older specimens taken in California. These are simply lumped in the Appendix as historical reference specimens, but localities and museum numbers are available upon request.

For analyses that required assessment of variation in sample means and standard deviations, we included as reference material additional localities of phenotypically pure warblers. For Hermit Warblers we used samples collected in coastal Oregon, the southwestern Cascades of Oregon (near Ashland), and California. For Townsend's Warblers we used samples from Alaska, British Columbia (except numbers 13 and 14 from central and southern Vancouver Island), the Rocky Mountains of northeastern Washington, and the Blue Mountains of Oregon. These samples do not represent all of our phenotypically pure populations, but all lie at least 250 km from the nearest known populations containing hybrids.

The hybrid index.—We originally planned to use a discriminant function analysis to generate a hybrid index. However, our discriminant analysis weighted characters having low variances in the reference samples so heavily that obvious hybrids were classified as parentals. Thus, we resorted to a more traditional additive hybrid index that weighted each character equally. To avoid weighting scores by scaling differences in their measurement, each character was standardized to vary from 0 to 1.

A hybrid index was created for each bird by summing the standardized score for the seven or eight variables being used in a particular analysis. This summed score was also standardized by dividing by its maximum potential value. Thus, regardless of the number of characters being used, the final hybrid index in all our analyses varied from 0 (Hermit ex-

TABLE 2. Extreme scores and associated sample sizes^a. Character scores assigned to yearlings and adults were standardized separately by dividing by the maximum score assigned to each age class. Because the lowest crown score assigned to yearlings was 1, yearling crown scores were adjusted to vary from 0 to 7 before being standardized.

	Minimum score (<i>n</i>)		Maximum score (<i>n</i>)	
	Yearlings	Adults	Yearlings	Adults
Mid flank	0 (80)	0 (226)	7 (18)	7 (42)
Lower flank	0 (34)	0 (81)	7 (64)	8 (149)
Bib corner	0 (6)	0 (20)	8 (13)	9 (32)
Face	0 (125)	0 (351)	6 (244)	6 (372)
Extent of yellow (mm)	0 (77)	0 (203)	33 (7)	36 (36)
Intensity of yellow	0 (87)	0 (237)	7 (46)	7 (300)
Crown	1 (17)	0 (13)	8 (244)	7 (372)
Back color	0 (9)	0 (26)	8 (25)	8 (156)

^a Specimens whose scores were changed to standardize data: UWBM 51333, adult, extent of yellow changed from 38 to 36 mm; UWBM 50920, yearling, black on crown changed from 0 to 1; MVZ 62155, yearling, black on crown changed from 0 to 1; PSM 3101, yearling, lower flank changed from 8 to 7; UWBM 50858, yearling, lower flank changed from 8 to 7; UWBM 50247, yearling, extent of yellow changed from 34 to 33; UWBM 50775, yearling, extent of yellow changed from 34 to 33; UWBM 52421, yearling, extent of yellow changed from 35 to 33.

treme), to 1 (Townsend's extreme). Standardized hybrid indices facilitate comparative studies and allow the age and sex classes to be combined within studies. In the following analyses, "Sum7st" refers to our standardized hybrid index, based on the sum of the seven characters that we used in the analyses. "Face" was eliminated from this index (see below).

Scores for yearlings and adults were standardized separately to eliminate age-class differences caused by mean differences in appearance (Table 2). Yearling males are variable in the extent of the spring molt of body feathers (Jackson et al. 1992) and in rare cases cannot be distinguished from females. Including yearlings in this study was problematic because female-like yearling male Townsend's Warblers are less boldly marked than adults (smaller bib, less yel-

low on the breast, reduced flank streaking) and, thus, more like male Hermit Warblers in appearance. When scores for adult and yearling males were standardized separately, their distributions became similar, justifying combining the age classes (illustrated for bib corner in Fig. 1). No yearling received a crown score of 0, so the crown scores for yearlings were adjusted to a minimum score of 0 by subtracting 1 from all of the crown scores of yearlings (Table 2).

Separately standardizing the character scoring for adults and yearlings corrects only for mean differences in their appearance, and not differences in variance. Yearling males are also more variable in appearance than adults because the extent of their spring molt is highly variable. Although we could not correct for differences in variance, we have included yearlings in our analyses because they constitute 32% of our total sample.

A practical problem with this method of standardization is that if very few birds score at the extreme states assigned to a character, then almost no birds will receive scores of 0 and 1. This was a problem because a small number of yearlings received extremely high scores for most characters. Had we used these few extremes to standardize character scores for yearlings, then the distribution of the standardized character scores for yearlings would not have matched that for adults. To avoid this problem, we simply reassigned the next-most frequent score to those few yearlings that were as boldly marked as adults. The birds so changed are listed in Table 2.

Defining hybrids.—In any situation in which a continuum of phenotypes is broken into categories, the placement of breaks needs to be appropriate to the question being explored. In our reference samples, all Hermits fell below 0.25 and all Townsend's fell above 0.75 on Sum7st (see Results). Thus, birds falling between 0.25 and 0.75 may be considered hybrids

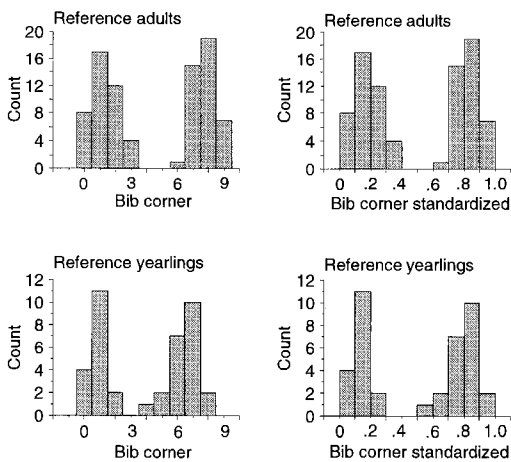


FIG. 1. Effects of standardizing character ranges for adults and yearlings separately, illustrated using bib corner which was scored on a scale of 0 to 9.

with great reliability. In our analysis of historical movement of the zone, such a conservative approach to the definition of hybrids was appropriate. However, when the entire sample of birds collected near the hybrid zones in Washington and Oregon is plotted together, many more birds fall in the tails of the parental distribution, as defined by 0.25 and 0.75, than would be expected from the distribution of scores in the reference samples. Presumably, these are highly backcrossed individuals, and a more reliable estimate of the number of hybrids in this sample is obtained by using 0.20 and 0.80 as the delimiters of phenotypically "pure" birds. These bounds cause about 3% of individuals in each reference sample to be called hybrids.

In most analyses, we avoided the need to identify individual birds as hybrid or pure by using means and standard deviations of scores to categorize localities as hybrid or pure. This approach eliminates the need to arbitrarily discriminate between backcrosses and parentals. Because the appropriate definition of hybrids depends upon the analysis, these definitions are given in each section.

RESULTS

Character variation in hybrids.—For characters to contribute usefully to a hybrid index they should distinguish the parental phenotypes, be under independent genetic control, and be controlled by multiple loci, thus following the rules of additive inheritance. When the precision of measurement varies between characters, the measurement for each character should be standardized to vary from 0 to 1 to avoid differentially weighting the characters.

To examine character variation in hybrids, we created a preliminary hybrid index using the standardized sum of our eight original variables (Sum8st); all individuals in the Hermit reference sample scored <0.25, and all individuals in the Townsend's sample scored >0.75. Thus, hybrids had phenotypes ranging from 0.25 to 0.75 on Sum8st. To analyze character variation, we then sorted the full data matrix for hybrids and plotted histograms for the raw plumage scores (without age corrections) for each of our plumage characters (Fig. 2).

Seven characters are distributed continuously between the parental extremes (Fig. 2). The continuity of the distributions and the lack of bimodality implies that these characters are controlled by multiple loci following rules of additive inheritance. This makes them ideally suited to summing into a single standardized

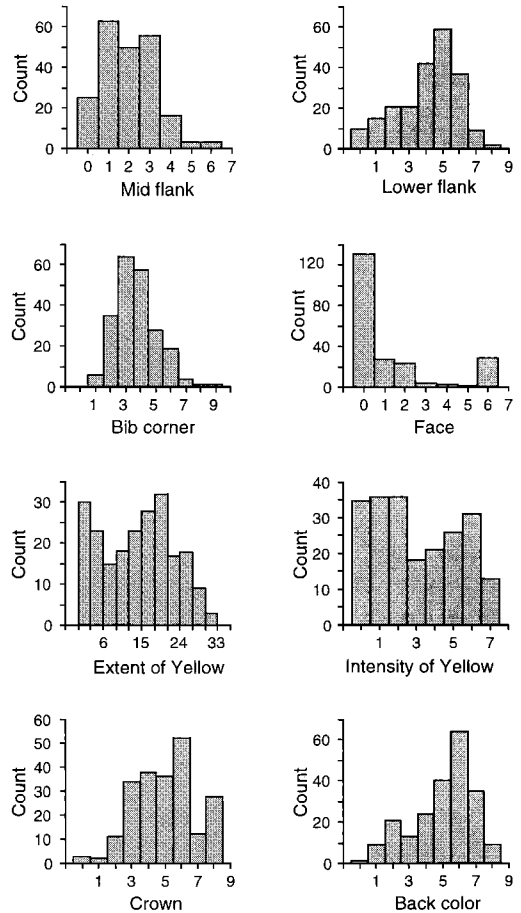


FIG. 2. Variation in raw plumage scores for all hybrids, defined as individuals of intermediate phenotypes (0.250 to 0.750) on Sum8st. Except for face, all characters look like they are characterized by additive inheritance and controlled by multiple loci. Because most hybrids score at one or the other of the parental extremes on face, face was eliminated from the hybrid index.

hybrid index. Face is the exception (Fig. 2); 74% of the 216 certain hybrids received face scores of one or the other parental extreme. Furthermore, many of the other intermediates received face scores of 1 and were yearling male Hermits, whose face and crown feathers were veiled with greenish tips. Although we attempted to score the green tips as yellow, we could not always distinguish green veiling from partially black feathers. The hybrid index that we use for the remainder of this paper is the standardized sum of the seven plumage

characters that appear to follow the rules of additive inheritance (Sum7st); face is excluded.

Inheritance of face.—The color of the face patch is mostly controlled by a single dominant allele. We illustrate this with histograms and with a comparison with Hardy-Weinberg expectations. Both analyses use all birds taken at hybrid localities in Washington and Oregon (mean Sum7st between 0.2 and 0.8, or standard deviation greater than 0.075). For this analysis of individuals, "pure" Hermits were defined as birds with Sum7st < 0.2; Hermit-like hybrids have Sum7st of 0.2 to 0.4; and so on to "pure" Townsend's, with Sum7st > 0.8.

"Pure" Hermits are plotted in the top panel of Figure 3, and "pure" Townsend's in the bottom panel. The relative shortage of intermediate phenotypes in the three groups of hybrids is strong evidence of nonadditivity in the inheritance of this character. The large excess of Hermit phenotypes in the three categories of hybrids suggests that a dominant allele codes for the solid yellow face characteristic of Hermit Warblers. Because the yellow face is the most remarkable field mark for Hermit Warblers, genetic dominance explains why most hybrids have yellow faces and are mistaken by field observers for pure Hermits.

Another way to examine the inheritance of face is to compare observed frequencies of the scores assigned to the face of birds from hybrid localities with expected Hardy-Weinberg frequencies. If the yellow face were controlled by a single dominant allele, then a double recessive would be required to produce a black face. Assuming that the frequency of this recessive gene is 0 for pure Hermits and 1 for pure Townsend's, then p , the frequency of the black-patch allele in any phenotypic category of hybrids, should correspond to a hybrid index of p , because our hybrid index has been standardized to vary from 0 to 1. Thus, equal frequencies of black and yellow faces should occur in birds with hybrid scores equal to $(0.5)^{0.5}$ ($=0.71$) if Sum7st reflects the relative frequency of parental alleles in hybrids (J. Felsenstein pers. comm.).

The top panel of Figure 4 shows the frequency of birds having either Hermit-like faces (scores of 0 and 1) or Townsend's-like faces (scores 5 and 6) against Sum7st (divided into 20 intervals). The two curves appear to cross only slightly to the Hermit side of the expected

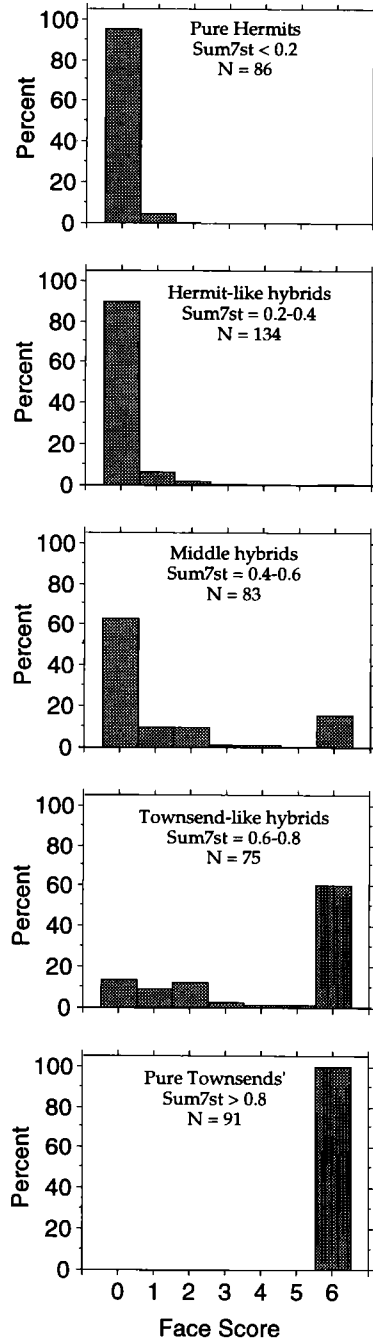


FIG. 3. Face scores for five phenotypic categories on the hybrid index, Sum7st.

value of 0.71. The lower panel of Figure 4 plots the percentage of individuals that received intermediate scores of 2 to 4. Because some middle-phenotype hybrids receive intermediate

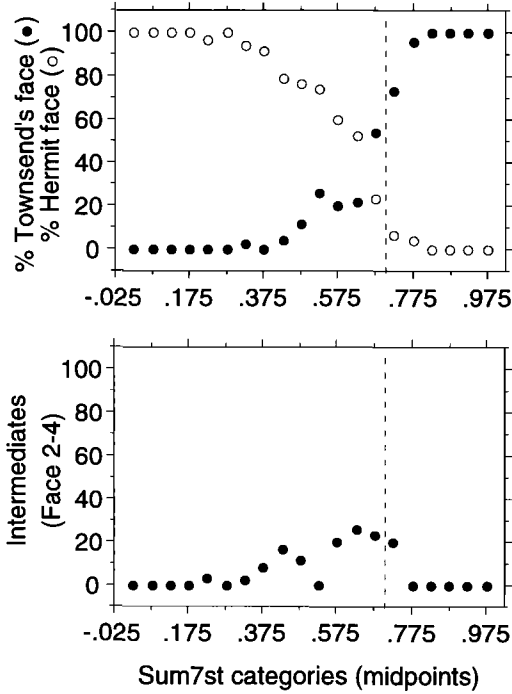


FIG. 4. Percentage of males from hybrid localities having pure Hermit and pure Townsend's faces (top) and intermediate faces (bottom), plotted against 0.05 intervals of Sum7st.

face scores, other minor loci must also affect this character. To eliminate errors in scoring, we pooled the character states 0 to 1 and 5 to 6. Combining 0 and 1 is justified because the proportion of yearlings was higher for birds receiving scores of 1 than for birds receiving scores of 0 (Fisher's exact test, $P = 0.042$), suggesting that we were not completely successful in distinguishing the green face veiling characteristic of young birds from the partially black faces occasionally found in hybrids. Combining categories 5 and 6 does the same for yearlings that receive scores of 5 because they did not complete the spring molt of their face, although in this case there are so few scores of 5 that no frequency test could be performed.

Plots of means and standard deviations.—Overviews of the hybrid zones are plotted as pie diagrams on maps. Figure 5 plots the mean for Sum7st for each of our collecting localities near the hybrid zones in Washington and Oregon, and Figure 6 plots standard deviation in Sum7st for each of these localities. These means

and standard deviations are listed by locality in the Appendix.

Localities with extreme means have low variation among individuals. The top panel of Figure 7 shows character variation in reference samples. For Hermit reference localities, all means fell below 0.2; for Townsend's localities all means fell above 0.8. For none did the standard deviation of Sum7st exceed 0.075. Localities with intermediate means have high variation among individuals, a classic observation for hybrid zones (Barton and Hewitt 1989). The middle panel of Figure 7 plots all hybrid localities, defined as having either a standard deviation >0.075 or a mean between 0.2 and 0.8 for Sum7st. Standard deviations for our four midpoint localities (20, 64, and 74, and 48 to 50 combined), each of which had a sample of 18 to 23 birds, varied from 0.168 to 0.295 ($\bar{x} = 0.232$). Because there is a strong correlation between means and variances, relatively few samples are characterized as pure by one criteria and hybrid by the other.

Turning locality means into pie diagrams was straightforward. Pure Hermits localities (0.0 to 0.2) were coded white, and pure Townsend's (0.8 to 1.0) were coded black. The range from 0.2 to 0.8 was divided into nine equally spaced intervals ranging from almost pure Hermit localities (10% fill) to almost pure Townsend's localities (90% fill).

Turning locality standard deviations into pie diagrams was more complex. Our goal was to have fully darkened circles represent localities with high variation among individuals (see Fig. 7) so that the geographic center of a gridded hybrid zone would appear on the map as a central spine of fully black circles. We used the standard deviations for our four midpoint localities to determine the minimum standard deviation for solidly filled circles. Standard deviations for these four samples varied from 0.168 to 0.295 ($\bar{x} = 0.232$), so we defined localities with standard deviations >0.225 as highly variable (100% filled pies). The region between 0.075 and 0.225 on the Y axis in Figure 7 was divided into nine intervals; pies with 10% fill represent hybrid localities of low variability.

The Olympic hybrid zone.—Our picture of this zone is incomplete because sampling on the Olympic Peninsula was highly constrained. Olympic National Park occupies much of the central part of the peninsula, and the adjacent

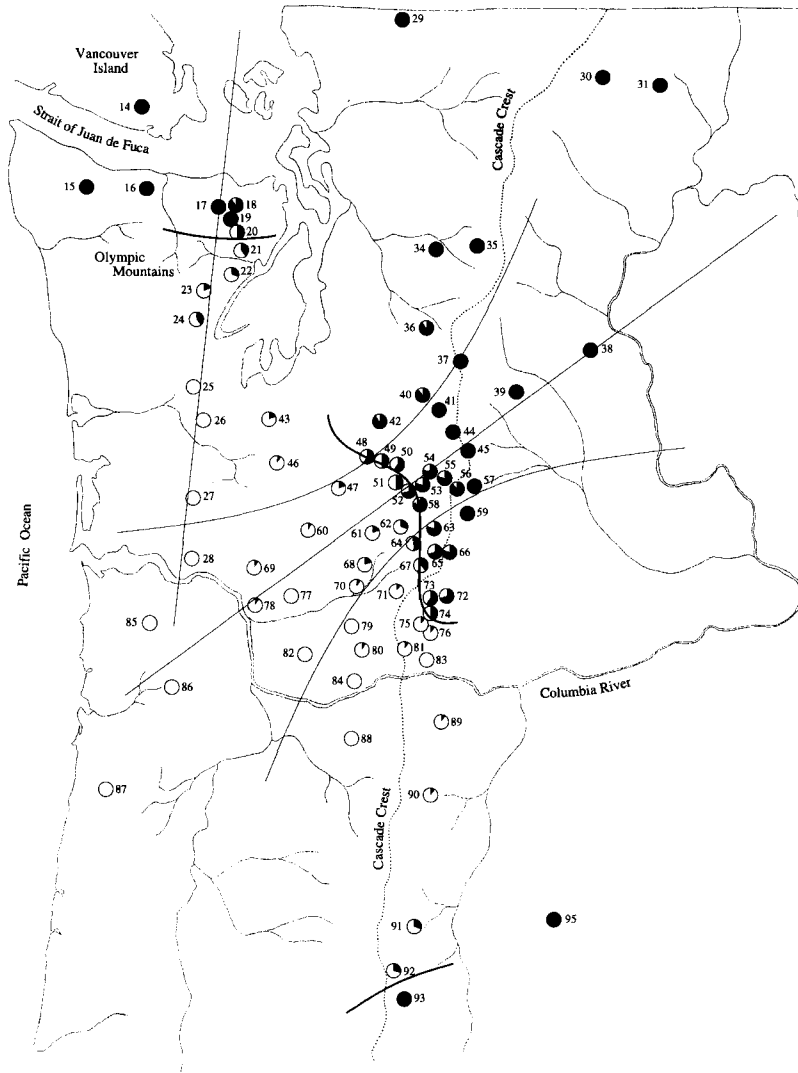


FIG. 5. Locality means for Sum7st for coast ranges and Cascade Mountains, Washington and Oregon. The figure also provides locality code numbers, our best estimate of the orientation of the Washington hybrid zones, and the transects and sampling regions used to measure linear distances over which the transition from one pure phenotype to the other occurs in the Washington hybrid zones.

lowlands have been clear cut so recently that accessible habitat suitable for warblers is rare. Consequently, most of our samples came from a relatively narrow border of national forest lands along the north and east sides of the park. Thus, the line of midpoint phenotypes is poorly defined by our sampling on the Olympic Peninsula. We presume that the contact in the Olympics is predominantly a north-south contact, because pure Townsend's Warblers are found to the north on Vancouver Island, and

across all of the north edge of the peninsula, and pure Hermit Warblers are found to the south of the peninsula in Washington. Collecting within the huge block of undisturbed habitat within the park would be essential to test this assumption. A major unresolved question is whether the large, lower-elevation valleys of the Elwha and Quinault rivers, which together roughly bisect the Olympic Mountains into eastern and western massifs, have provided another route of contact between these warblers.

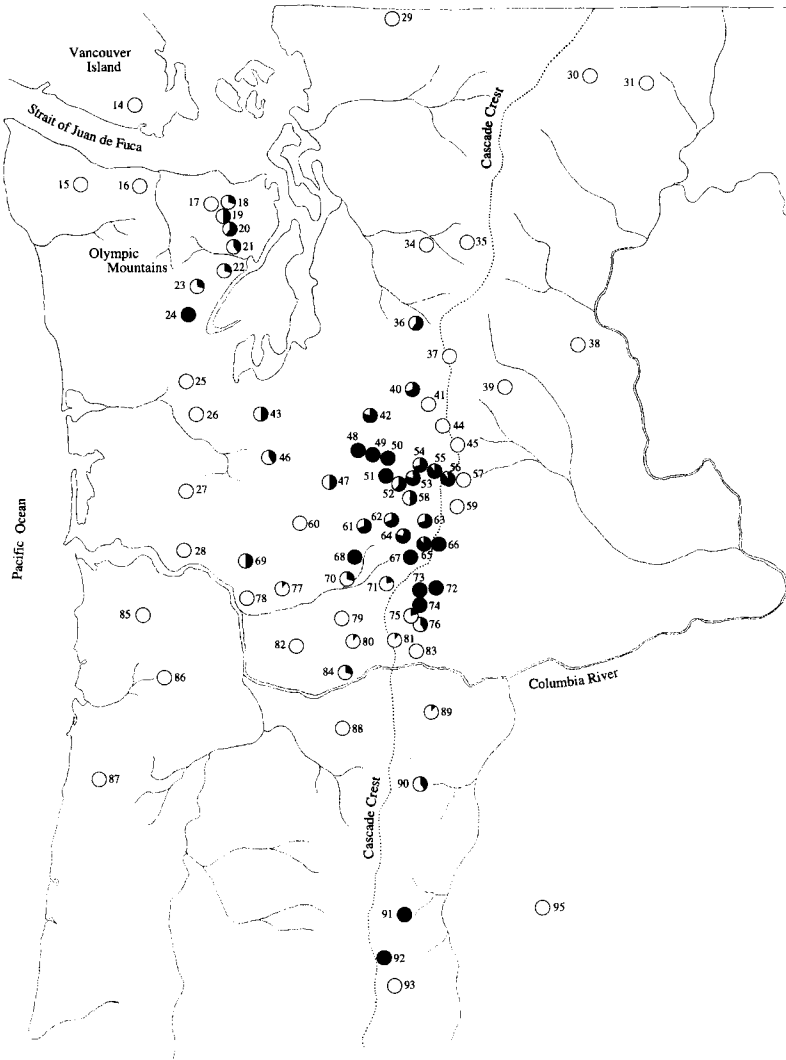


FIG. 6. Locality standard deviations for Sum7st for the coast ranges and the Cascade Mountains of Washington and Oregon.

As a result of these constraints, we oriented the transect for our character-transition analysis in a roughly north-south line, tilted slightly to reduce the distortions of distances between our hybrid samples along the east face of the Olympics (Fig. 5). The distances shown next to the histograms in Figure 8 are taken from locality projections onto this line, with the southernmost pure sample of Townsend's Warblers, Locality 17, defined as 0. All birds from the three localities (15 to 17) on the north side of the peninsula scored as pure Townsend's ($\text{Sum7st} > 0.80$). The hybrid zone starts imme-

diately to the east of these localities and, in a north-south distance of about 100 km, proceeds to phenotypically pure populations of Hermit Warblers by locality 25, which may be as much as 20 km south of the southern edge of the Olympic hybrid zone (Figs. 5, 6, and 8).

We show the relationship between the use of histograms and pie diagrams to describe hybrid localities in Figure 8. Pie diagrams for both the mean and standard deviation in Sum7st are shown next to the histograms for nine localities passing through the Olympic and Cascades transects.

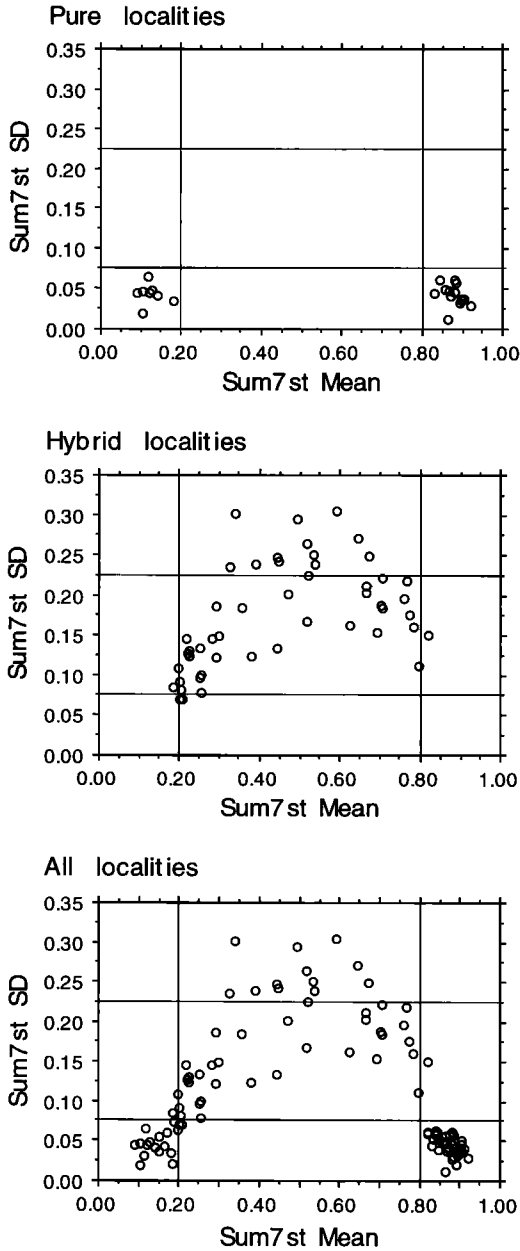


FIG. 7. Mean versus the standard deviation in Sum7st for pure localities (top), hybrid localities (center), and all localities (bottom). Within each plot, vertical grid lines delimit pure Hermit localities (left), hybrid localities (middle), and pure Townsend's (right). Horizontal grid lines delimit pure localities (bottom), moderately variable localities (middle region), and highly variable localities (top).

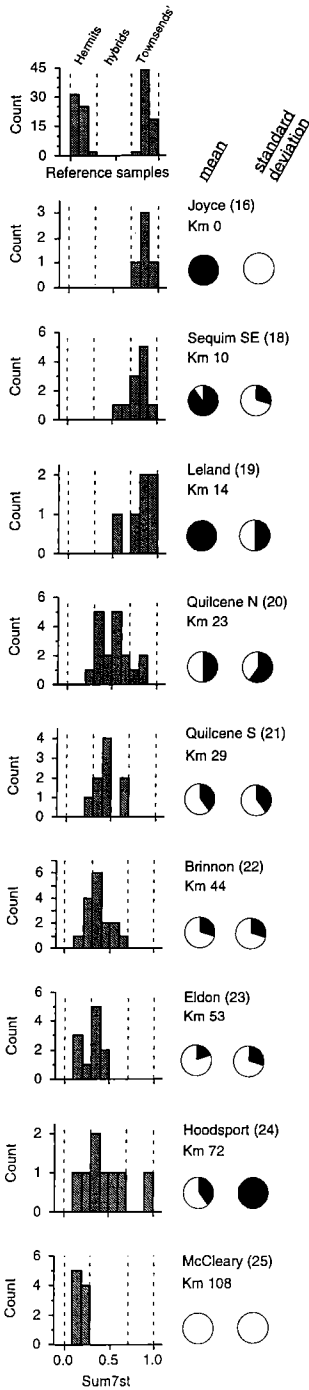
By either set of illustrations, Olympic locality 24 (Hoodsport) is an outlier. Birds at Hoodsport were more Townsend's-like in appearance than expected compared with neighboring samples. We can think of three possible explanations for this anomaly. First, our guess about the orientation of the zone may be wrong. If so, then sampling in the Elwha or Quinault river valleys in the Olympic National Park should show that the zone lies farther south in those river valleys than it does where we sampled, on the east face of the Olympics. Second, the area around Hoodsport recently has been extensively logged, making accessible warbler habitat difficult to find. If Townsend's Warblers were more inclined than Hermit Warblers to occupy small stands in heavily cutover areas, this area may have become a local sink for dispersing warblers with more Townsend's-like phenotypes.

Finally, the bias of the Hoodsport sample toward Townsend's phenotypes could be an artifact of the song we used in the playbacks to collect at this locality. On each of three visits there, we used tapes that had been successful in the Cascades and northern Olympics. However, these same tapes were completely ineffective at Pe Ell (Locality 27, 100 km south of Hoodsport) and at other localities in southwestern Washington. Only with locally recorded Hermit songs (and songs of Black-throated Gray Warblers [*D. nigrescens*], which in these localities were difficult to distinguish!) could birds be brought down from the canopy. In Hoodsport, it is conceivable that birds brought down with our original tapes were biased toward hybrids that had dispersed southward from the zone to the north, where they had learned that Townsend's songs were threatening. Resampling this locality with locally recorded songs would resolve this question.

The Washington Cascades hybrid zone.—With the exception of Mount Rainier National Park, most of the southern Cascade Mountains of Washington were accessible for collecting. As shown in Figures 5 and 6, we gridded this region fairly intensively to discover the placement of the hybrid zone and to plot the phenotypic center of the zone.

Pie diagrams plotting locality means for Sum7st show Townsend's inhabiting all of the Cascades north of Snoqualmie Pass (near Locality 37) and all of the Okanogan highlands

A. Olympic transect



B. Cascade transect

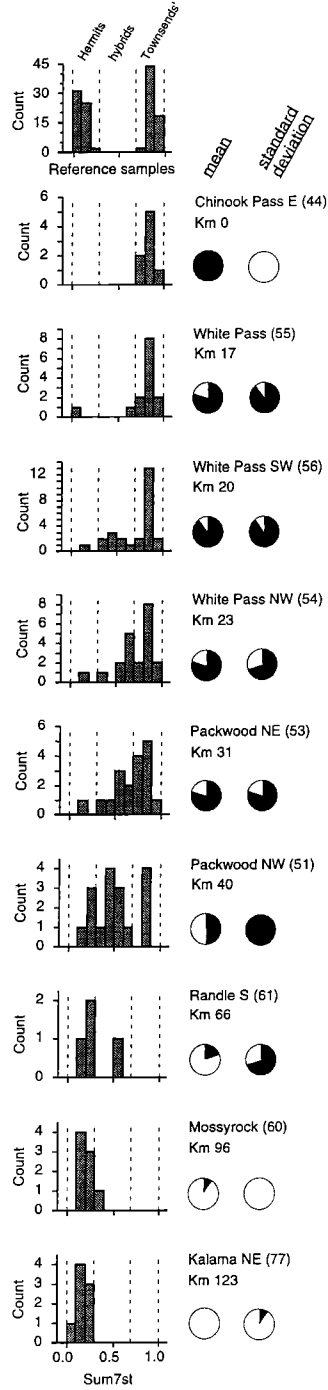


FIG. 8. The transition from Townsend's to Hermit phenotypes in the Olympic Mountains and in the Washington Cascades along the transects shown in Figure 5. Values are standardized hybrid indices (Sum7st) for the seven multilocus plumage characters without overdominance (face is omitted). Pie diagrams show the relationship between these more detailed histograms and our plots of means and standard deviations shown in Figures 3 and 4.

that join the Rockies in the northeastern corner of the Washington to the northern Cascades. Perhaps because of the influence of gene flow across the Okanogan highlands, or perhaps from having a competitive advantage in the drier east-side forests, pure Townsend's phenotypes are found farther south on the east than on the west side of the Cascades. As a consequence, the phenotypic center of the Washington Cascades zone is curved and runs almost due north-south for some 80 to 100 km along the eastern slope of the southern Cascades of Washington (Fig. 6). The Washington Cascade hybrid zone is about the same width as the Olympic zone when measured in transects running perpendicular to its phenotypic center.

Figure 5 shows our best interpretation of the shape of the Washington Cascades Zone. Because the zone is curved, meaningful transects must be drawn perpendicular to its curvature. Furthermore, samples projected onto this transect must be drawn from a narrow region in the vicinity of the zone to avoid contamination from genes flowing from other directions. Figure 5 also shows the transect we used to measure the width of the Washington Cascade zone. The hourglass shape of the region from which samples were projected onto this transect is dictated by the need for short projections close to the zone and by the competing need for more samples farther away from the zone.

To illustrate the phenotypic transition across this transect (Fig. 8), we chose nine localities on the basis of good sample sizes and equal spacing. Distances shown next to the histograms in Figure 8 are linear distances measured along the transect, with locality 44, the southwesternmost sample of pure Townsend's Warblers, defined as km 0 (Fig. 5). As was true for the Olympics, the histograms for the Washington Cascade zone depict an immediate geographic transition from pure Townsend's to a midpoint phenotype, followed by a more gradual transition to a pure Hermit phenotype (Fig. 8). The entire transition is completed in about 125 km, a figure that would hold for any transect struck through the spine of this zone (see Fig. 5).

Using projections to measure distances along a straight line may seem inappropriate when samples separated by 10 to 15 km in two-dimensional space may have projections with much shorter separations. However, our field

experience suggests that making projections as defined by the hourglass shape in Figure 5 does not generate an overly abrupt description of the phenotypic transition into this zone from pure Townsend's to the northeast. In our efforts to collect the large samples at the center of the zone needed for measuring covariances, we often completely missed the geographic placement of the phenotypic center of the zone, because we would move 30 km instead of the requisite 5 to 10 km. The zone is indeed so abrupt that huge changes in phenotype occur over very short straight-line distances between samples.

Character transitions.—Plots of locality means and standard deviations for morphological characters against distance along transects across hybrid zones clarify the forces that maintain the zones (Barton and Hewitt 1985, 1989, Barton and Gale 1993). We present such plots for our combined hybrid index (Sum7st) for the Olympic and Washington Cascade zones in Figures 9 and 10. Both character-transition curves for Sum7st means show an abrupt change from pure Townsend's phenotypes to the midpoint phenotype of 0.5, followed by a more gradual transition to pure Hermit phenotypes. In each graph (Figs. 9 and 10), distances in km have been measured from the locality nearest the center of the phenotypic transition. Thus, Townsend's and Townsend's-like localities are +km, and Hermit and Hermit-like localities are -km. The two hybrid zones are separated by about 200 km, yet both illustrate the same abrupt phenotypic cline between the parental phenotypes on either side of the zone, and the same asymmetries in shape.

We also plotted the standard deviation of Sum7st for these same transects (Figs. 9 and 10). For both the Washington Cascade and the Olympics transects, the asymmetries in character transitions are even more evident in the plots of standard deviations against distance along the transect. Variances increase in hybrid zones because of increased heterozygosity and, possibly, because of linkage disequilibrium. When some of the increase in variance is due to linkage disequilibrium, then the zone likely is maintained as a narrow cline (or suture zone) by a balance between selection against hybrids and dispersal of parentals into the zone (Barton and Hewitt 1985).

To evaluate linkage disequilibrium at the

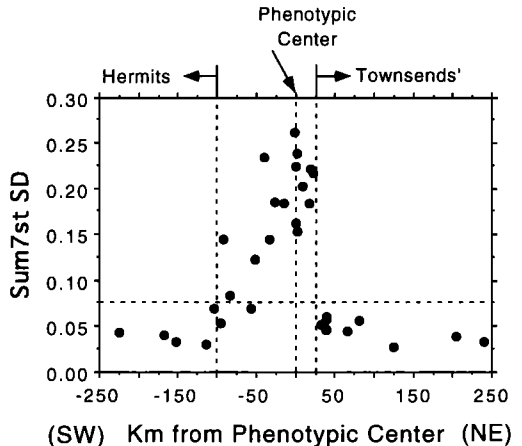
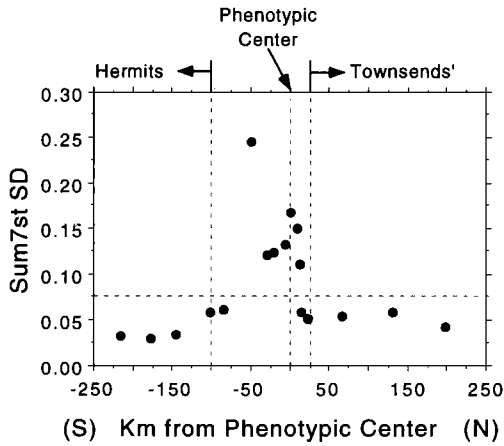
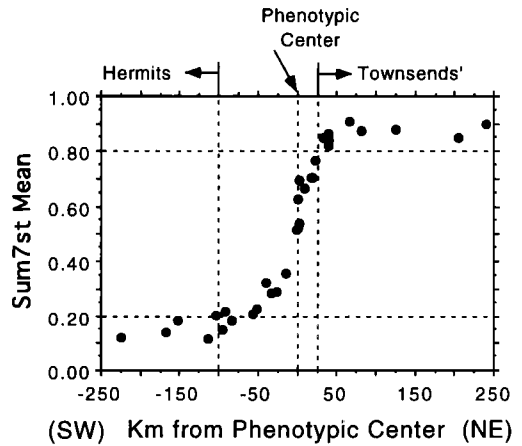
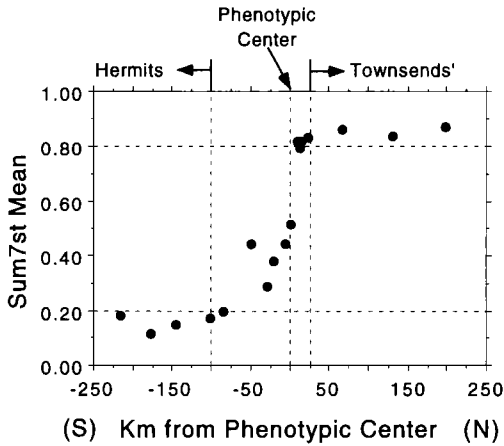


FIG. 9. Locality means (top) and standard deviations (bottom) in Sum7st plotted against distance along the transect running through the Olympics zone. The locality with its mean phenotype nearest to 0.5 was set at km = 0. In pure localities (defined by distance from the zones), the mean of Sum7st never falls below 0.80 for Townsend's or above 0.20 for Hermits. Note the asymmetry in the shape of the character-transition curve and in the distribution of localities with high standard deviations.

FIG. 10. Locality means (top) and standard deviations (bottom) in Sum7st plotted against distance along the transect running through the Washington Cascades zone. The locality with mean phenotype nearest to 0.5 was set at km = 0. In pure localities (defined by distance from the zones), the mean of Sum7st never falls below 0.80 for Townsend's or above 0.20 for Hermits. Note the asymmetry in the shape of the character-transition curve and in the distribution of localities with high standard deviations.

phenotypic center of the Washington hybrid zones, we computed a covariance matrix for all individuals collected at four midpoint localities. Stacked histograms for these localities (Fig. 11) show that differences in their means are not contributing to the estimates of covariances. Most covariances are high (Table 3), and all of the associated correlation coefficients are highly significant ($P < 0.001$). Thus, selection seems to play a strong role in maintaining these zones.

Character-transition curves across narrow hybrid zones maintained by a balance between hybrid inferiority and dispersal should be symmetrical (Barton and Hewitt 1989). Interestingly, the curves for both Washington hybrid zones are strongly asymmetrical. Asymmetries may reflect nonadditive inheritance, differences in population structure, or the competitive superiority of one parental form over the other (Barton and Hewitt 1985). Face was the only char-

acter with obvious nonadditive inheritance and has been eliminated from our hybrid index; thus, nonadditivity may be eliminated as the cause of the asymmetry of the character-transition curves for Sum7st. We treat population structure and competitive superiority in the Discussion.

Estimating dispersal distances.—The width of the hybrid zones is about 100 km in the Olympics and 125 km in the Washington Cascades. Whether zones of this width are wide or narrow depends on σ , the root mean square dispersal distance between birth and breeding site (Barton and Hewitt 1985, 1989). Because no direct estimates of dispersal have been made for these warblers (see Moore and Buchanan 1985, Moore and Dolbeer 1989, Payne 1990), we used Barton and Gale's (1993) indirect method to estimate dispersal distances, using only our seven characters with additive inheritance:

$$\sigma = \sqrt{\frac{2r(\text{cov } z, z^*)}{\frac{\Delta z \Delta z^*}{w w^*}}}, \quad (1)$$

where r is the recombination rate (assumed to be 0.5), w is the inverse of the maximum slope, and Δz is the change in the character. For each of the characters with additive inheritance, we plotted a character-transition curve similar to those in Figures 9 and 10. The greatest slope of these curves was conservatively estimated by lines drawn by eye through the cluster of points near the phenotypic center of the zone. In all cases, these lines were less than the maximum slope in the abrupt transition from Townsend's phenotypes to the midpoint phenotype. Δz was defined as the difference between the Townsend's and Hermit means in each of the standardized characters. We used the expanded reference samples to compute each of these pairs of means. Using equation 1 and covariances shown in Table 3, we obtained 21 dispersal estimates, varying from 20 to 43 km ($\bar{x} = 31$ km; Fig. 12). At a width of 125 km, the Washington Cascade zone is only about four times as wide as the average dispersal distance (σ) of 31 km. The zone for the Olympics is even narrower, being only three times as wide as σ .

By these estimates, the Washington hybrid zones are very narrow relative to dispersal. The implication is that both are being maintained

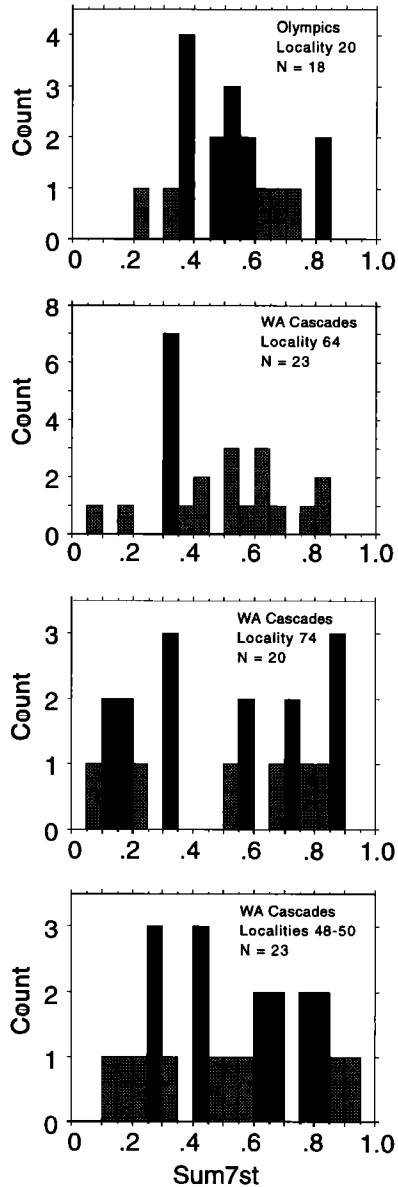


FIG. 11. Variation in the hybrid index at four samples located geographically at the phenotypic center of the zones. The similarity in these distributions of Sum7st justified pooling these samples to compute covariances used to estimate dispersal distances.

by selection. How much of this selection is due to hybrid inferiority and how much to the apparent superiority of Townsend's Warblers over Hermit Warblers and hybrids is unclear.

Historic specimens.—We examined possible recent changes in the position of these hybrid

TABLE 3. Variances (on diagonal), covariances (upper right), and correlations (lower left) among the eight standardized characters. To compute these values, the 84 specimens from the four midpoint localities were combined.

	Mid flank	Lower flank	Bib corner	Face	Extent of yellow	Intensity of yellow	Crown	Back color
Mid flank	0.065	0.074	0.046	0.091	0.032	0.035	0.063	0.031
Lower flank	0.937	0.095	0.053	0.100	0.037	0.041	0.077	0.038
Bib corner	0.849	0.819	0.045	0.074	0.027	0.035	0.049	0.025
Face	0.791	0.718	0.776	0.204	0.058	0.067	0.112	0.052
Extent of yellow	0.445	0.432	0.454	0.460	0.079	0.089	0.035	0.059
Intensity of yellow	0.392	0.375	0.473	0.419	0.899	0.125	0.040	0.073
Crown	0.807	0.825	0.770	0.814	0.414	0.374	0.092	0.035
Back color	0.452	0.451	0.437	0.425	0.780	0.768	0.426	0.073

zones using 13 historic specimens. Historic specimens were considered useful either if they had been collected in an area where our recent samples showed birds to be of intermediate phenotype, or if they were of an unexpected phenotype (hybrid or "wrong" parental) taken outside of the present hybrid zones (Fig. 13). None of the historic specimens met the second criterion. Because the second criterion depends on the identification of individual specimens that unambiguously are hybrids, the range of Sum7st scores used to define hybrids was 0.25 to 0.75. To avoid migrants, we included adults taken from 15 May to 10 July and yearlings taken from 25 May to 10 July.

The 13 historic specimens that could be used in this analysis were compared to 58 recent specimens taken at six localities (Fig. 13). We

standardized the Sum7st scores of both the historic and contemporary specimens from each locality by subtracting the median Sum7st score of the contemporary specimens for each locality. This produced a phenotype of 0 for each of the contemporary samples, regardless of their mean (Fig. 14). With this procedure, birds that are more Hermit-like relative to the locality mean fall to the left of 0 (negative scores), and birds that are more Townsend's-like fall to the right of 0 (positive scores). If the zones were moving southward, as we predicted from the character-transition analysis (see above), then the historic specimens should lie to the left of 0 relative to their matched contemporary samples (which will be centered on 0).

Stacked histograms comparing the historic and corresponding recent specimens are presented in Fig. 14. The distributions are very similar, with the mean for the 13 historic specimens being only 0.014 more negative (Hermit-like) than the recent samples (one-tailed *t*-test, *P* = 0.42). The average year of collection for the 13 historic specimens was 1933 (range 1898 to 1949) compared with 1992 (1987 to 1995) for the recent samples. Thus, in 59 years these hybrid zones have not moved enough to produce any measurable change in phenotype, using the 13 specimens that could be matched to modern samples. With additional collecting, at least five more old specimens from southern Oregon could be added to this analysis (Fig. 13).

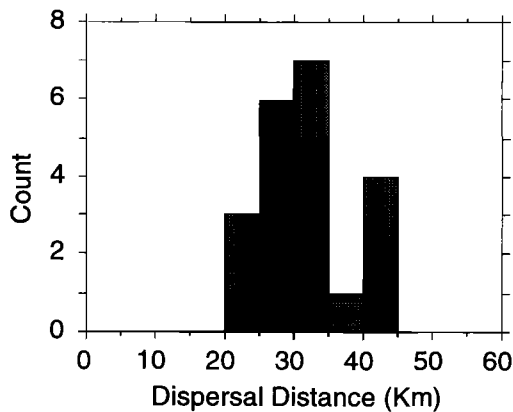


FIG. 12. With seven characters showing additive inheritance, there are 21 pairs of characters that can be used to estimate σ , the root mean square dispersal distance. Estimates ranged from 20 to 43 km, with a mean of 31 km.

DISCUSSION

SYNOPSIS OF NEW METHODS

This paper describes three hybrid zones between Hermit and Townsend's warblers in

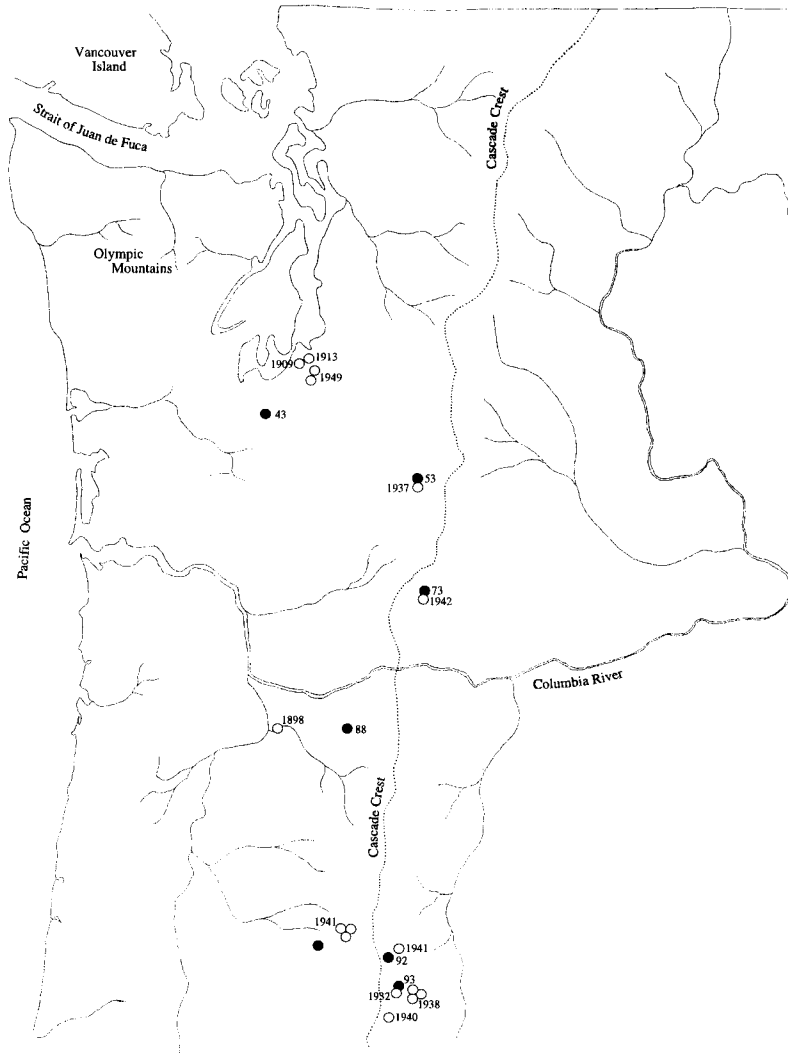


FIG. 13. Map of collecting localities for the historic specimens (open circles, with year of collection noted). Solid circles and locality numbers show location of recent samples to which historic specimens were compared (see Fig. 14).

Washington and Oregon. We have introduced several techniques new to the analysis of avian hybrid zones. (1) Scoring for each character was broken down into as many units as possible. This improves the estimation of covariances that are used to estimate dispersal distances (Barton and Gale 1993). (2) Before combining the scores for individual characters into a hybrid index, the scoring for each character was scaled from 0 to 1. This avoids weighting the characters by differences in their maximum values. (3) Age-related plumage differences

were removed by standardizing the scores of adults and yearlings separately. This improved the separation of yearlings in the reference samples and made the distribution of the hybrid index for yearlings superimpose nicely over that for adults. (4) Once a preliminary hybrid index was obtained, hybrid localities were identified as those with intermediate means or high variances (Fig. 7). All individuals from this set of localities were then pooled to examine the distribution of scores for each character individually.

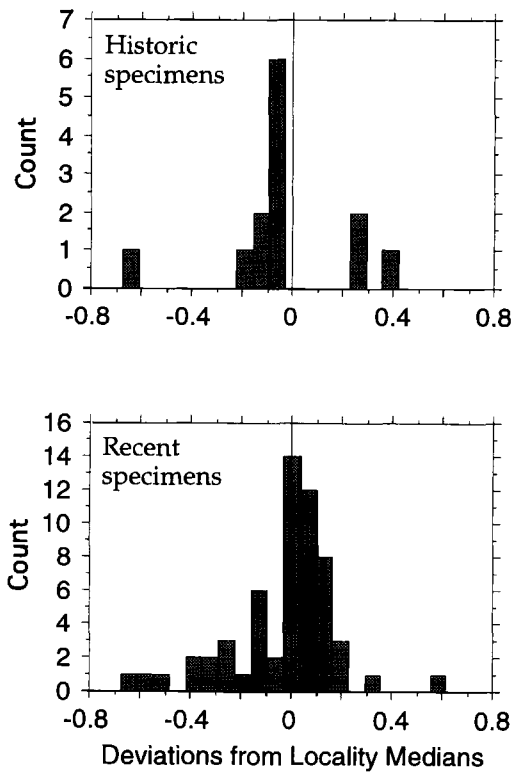


FIG. 14. Phenotypes of historic and recent specimens collected from the same places within the current hybrid zone. Sum7st scores for recent and historic specimens from each locality were standardized by subtracting the median score for the recent sample. This causes more Hermit-like phenotypes fall to the left of 0 and more Townsend's-like phenotypes to the right of 0.

Seven of our characters scored in a nearly continuous fashion, suggesting additive and multilocus inheritance. These characters were combined to generate our final hybrid index, Sum7st, which was standardized to vary from 0 to 1. The scores for face were strongly bimodal (Fig. 2). Our standardized hybrid index allowed us to apply Hardy-Weinberg logic to show that the yellow face of Hermit Warblers (and most hybrids) is controlled by a single-locus dominant allele (Figs. 3 and 4). Thus, we eliminated face from our analyses of the geography of the hybrid zone. Because of the non-additive inheritance of face color, field observers tend to dichotomize most hybrids into Hermit Warblers (birds with yellow faces) or Townsend's Warblers (the remainder with black faces). Without capture, individuals can rarely

be seen well enough to notice faint yellow washes on the breast or intermediate levels of streaking on the flanks.

DISPERSAL DISTANCES

Estimating σ , the root mean square dispersal distance, is essential to comparative work on hybrid zones involving the nature of selection maintaining these zones (Barton and Hewitt 1985). Barrowclough (1978, 1980a) has offered a model for correcting capture-recapture data from a single plot for long-distance dispersal. However, his method cannot correct for dispersal distances greater than the longest dimension of the study site (Barrowclough 1978). Moore and Buchanan (1985) review the difficulty of estimating σ and illustrate its dramatic effect on interpreting the widths of hybrid zones. From a limited number of band recoveries, they estimate σ at approximately 100 km per year for Northern Flickers (*Colaptes auratus*). Using the huge samples of band recoveries available for Red-winged Blackbirds (*Agelaius phoeniceus*) and Common Grackles (*Quiscalus quiscula*), Moore and Dolbeer (1989) estimate σ at 94.6 km for redwings and 111.4 km for grackles. A similar analysis by Payne (1990), using all of the recoveries from Kendeigh's (1941) study of House Wrens (*Troglodytes aedon*), increases the estimate of σ to 84 km, a 64-fold increase over Barrowclough's (1980a) estimate. Thus, direct estimates of σ from band recoveries are yielding values around 100 km, one to two orders of magnitude greater than estimates from single study plots. To illustrate the dramatic importance of long-distance movements on the estimate of σ , Moore and Dolbeer (1989) eliminated from their sample all Common Grackles that dispersed less than 100 km (96% of 1,252 records); the effect was to lower the estimate of σ for adults from 76.8 to 76.1 km!

The importance of σ to the interpretation of the forces responsible for generating clines is well illustrated by the hybrid zone between Myrtle and Audubon's warblers (*Dendroica coronata*). Using an estimate of σ of 1 km, Barrowclough (1980b) showed that the current width of that hybrid zone could be explained by the diffusion of neutral alleles over the past 7,500 years. However, if we substitute our indirect estimate of 30 km for σ into Barrowclough's (1980b) analysis, then the Myrtle-Audubon's

TABLE 4. Long-distance records of dispersal of Hermit (H) and Townsend's (T) warblers from the literature. None of the birds was identified by song alone.

Date ^a	Location	Species	Distance from nearest zone	Citation
2 June 1990	Whatcom Co., WA	H	120 km NNE	<i>American Birds</i> 44:1180
4 July 1981	Bellingham, WA	H	110 km NNE	<i>American Birds</i> 35:972
28 June 1979	North Bend, WA	H	85 km N	<i>American Birds</i> 33:892
9 June 1977	Olympic N.P., WA	T	40 km S	<i>American Birds</i> 31:1182
12 July 1967	Garibaldi, OR	T ^b	265 km S	<i>American Birds</i> 21:599
June 1979	Darrington, WA	H ^c	130 km N	Chapell and Ringer 1983
29 May 1971	Yakima Co., WA	H	98 km NE	<i>American Birds</i> 25:774
15 June 1978	Chelan Co., WA	H	140 km NE	Chapell and Ringer 1983
15 May 1946	Vancouver I., BC	H	170 km NNE	Hardy 1947
May/June 1994	Toad Lake, BC	Hybrid ^d	190 km NNW	Innes and Innes 1997
28–29 April 1992	Victoria, BC	H	95 km W	Taylor 1994
15 June 1996	Manning Park, BC	Hybrid	230 km N	Tilitsky 1996

^a Males included from 25 May (unless north of usual breeding range) through 10 July (unless feeding fledglings). Females included from 1 June (unless north of usual breeding range) through 10 July (unless feeding fledglings).

^b Pair of Townsend's feeding fledglings.

^c Two males.

^d Hybrid male and pure Townsend's female.

zone would have spread to its current width in less than 10 years after contact. This change of more than three orders of magnitude in the time since contact under a neutral model suggests strong selection against hybrids in the Myrtle-Audubon's zone. Estimates of σ strongly affect the interpretation of hybrid zones! For the remainder of this discussion, we assume that our estimate of σ (ca. 30 km per year) is reasonable (Fig. 12).

The relatively frequent observations by birders of Hermit or Townsend's warblers well to the "wrong" side of the hybrid zones is consistent with the magnitude of our indirect estimate of σ . Table 4 lists a set of these records that we accumulated from a systematic search of *American Birds* and the *Murrelet* (from their inception through 1995), as well as other records that we have found opportunistically. Despite the difficulty of observing these warblers in the field, numerous "parentals" or hybrids have been found holding territories at great distances from the midpoint of the nearest hybrid zone. These records suggest that dispersal distances of more than 100 km occur in these species (Table 4). There was no temporal pattern to these data supporting the alternative interpretation that they were artifacts of recent movement of these hybrid zones.

MODELS FOR THE MAINTENANCE OF NARROW ZONES

Following Moore (1977) and Barton and Hewitt (1985), we identify three alternate mod-

els capable of explaining narrow hybrid zones. Narrow zones have widths of the same order of magnitude as σ (Barton and Hewitt 1985). Using our indirect estimate of σ , the Olympic and Washington Cascade zones have widths of three to four times σ , values suggesting strong selection or very recent contact.

Recent contact.—As Barrowclough (1980b) has eloquently argued, hybrid zones may be narrow because of a combination of recency of contact and low dispersal; such an argument need not invoke hybrid inferiority. If σ is 30 km for our warblers, the approximately 125-km width of their hybrid zone suggests contact less than 10 years prior to our collections (Endler 1977, Barrowclough 1980b). This is clearly not the case, because at least six hybrids have been collected from 1913 to 1956 (Morrison and Hardy 1983), and the zone showed no sign of expanding during our nine years of collecting.

If contact were very recent, there is no reason to assume that it would have occurred simultaneously in both the Washington Olympics and the Washington Cascades. Yet these geographically separate zones differ little in width (Figs. 9 and 10), suggesting either that selection is independently maintaining them at similar widths, or that our estimate of σ is high by at least an order of magnitude. Because occasional individuals disperse much more than 100 km (Table 4), selection seems the more plausible explanation. Determining the width of the Oregon Cascades zone will provide a third test of these ideas.

Hybrid superiority within ecotones.—In a highly influential paper, Moore (1977) argued that narrow hybrid zones bridge ecotones and that their width is maintained by hybrid superiority (and parental inferiority) within the ecotone and the reverse outside the ecotone. In an elegant analysis of range boundaries of other North American birds and mammals, Moore and Price (1993) showed that the hybrid zone between Northern Flickers is narrow in areas where the range boundaries of other allopatric pairs of birds are concordant, and wide where the range boundaries of other allopatric pairs are less concordant.

No ecological or climatic transition seems to be associated with these three warbler hybrid zones. Both species are abundant in Douglas-fir and true fir forests, and both are absent from forests that consist only of pine or hemlock and cedar. In mixed forests their densities and the placement of individual territories seem largely determined by the abundance of Douglas-fir and true firs. To the east of the hybrid zone in the Olympics, pure Townsend's Warblers occur some 200 to 300 km farther south in the Washington Cascades before that zone is encountered. Furthermore, the Washington Cascades zone runs in a continuous fashion across the Cascades, spanning areas that vary up to tenfold in annual rainfall. Directly to the south of the Cascades zone, phenotypically pure Hermit Warblers breed near the Columbia River in Washington. Still farther south, a third zone is encountered in the southern Cascades of Oregon, an area that we suspect Townsend's Warblers invaded from the mountains to the east. In short, the existence of three zones in very different environments argues against the ecotonal model applying to these warblers.

Hybrid inferiority.—Barton and Hewitt (1985) define "tension zones" as those maintained by dispersal-selection balances. In such zones the inferiority of hybrids is balanced by dispersal of parental and backcrossed phenotypes into the zone. There can be no doubt that hybrids are reproducing, because the wide phenotypic space separating parental forms is filled continuously by hybrids (Figs. 2, 8, 11, front cover). Similar and narrow widths of the two Washington zones suggest that shared selective forces and shared patterns of dispersal are maintaining the similarity of these zones. Again, another replicate of this test will come from col-

lecting in the Oregon zone well enough to describe its width. Our limited north-south transect on the east slope of the Oregon Cascades suggests a similarly narrow zone.

Narrow zones, maintained by selection against hybrids and dispersal of pure and backcrossed phenotypes into the zone, generate coincidental clines for all characters and high levels of linkage disequilibrium near the phenotypic centers of such zones. The clines for the characters used to generate our Sum7st hybrid index are highly coincident (unpubl. data). Linkage disequilibrium among these characters was high, yielding an estimate for σ of approximately 30 km.

MODELS FOR THE MOVEMENT OF ZONES

The few historical specimens that exist failed to document any recent movement of these zones (Fig. 14). However, asymmetry in the character-transition curves of each zone indicate that the zones have been moving. Three models can account for moving zones.

Dispersal asymmetries.—Tension zones tend to become trapped geographically in areas of low population densities (Hewitt 1989). We see no reason to suspect that any of our zones has been trapped by areas of unsuitable or low-density habitat. These warblers seemed equally common within and to either side of the three zones within which we collected specimens.

Tension zones also may move in response to parental asymmetries in dispersal. We have no measures of possible differences in σ for Hermit and Townsend's warblers. However, the asymmetry in our character-transition curves suggests that more genes are flowing from the Townsend's to the Hermit side of the zones than vice versa. If this difference were due largely to differences in dispersal, rather than to the competitive superiority of Townsend's, then we might expect more of our out-of-range phenotypes to be Townsend's Warblers than Hermit Warblers. The data we assembled on long-distance dispersal suggest the opposite (Table 4).

Parental fitness asymmetries.—The asymmetries in the character-transition curves found in the two Washington hybrid zones are consistent with Townsend's Warblers being competitively superior to Hermit Warblers (Barton and Hewitt 1985). Two categories of competitive

asymmetries may be driving the presumed movement of our zones, one global and one provincial. The global asymmetry is that male Townsend's Warblers may be behaviorally dominant to male Hermit Warblers. Although this contradicts size differences (Hermit males are larger), it is consistent with the frenzied response of male Townsend's to song playbacks compared with the measured, passive response of male Hermits. Nothing in our morphological analysis provides independent support for this hypothesis, but work by Scott Pearson (pers. comm.) supports the view that Townsend's are dominant over Hermits. This hypothesis of behavioral dominance requires no differences in habitat preferences. Some general hypothesis, such as behavioral dominance, seems required to explain the similar asymmetries in the character-transition curves for the Olympic zone, which lies entirely on the wet side of the Cascades, and for the Cascade zone, which runs diagonally from the dry east side of the Cascades to the wet west side (Fig. 5).

We also suggest that a second, provincial asymmetry may have accelerated the movement of the zone on the dry east side of the Cascades. Here we suspect that Townsend's may be better adapted to slightly drier environments because of genes flowing into these east-side populations from the drier Rocky Mountains. The Okanogan Highlands of eastern Washington join the Cascade and Rocky mountains, and Townsend's Warblers occur in suitable habitat throughout these dry highlands. Exactly the same is true of the mountains of eastern Oregon. We suggest that gene flow from the Rockies into the Townsend's Warbler populations found on the east side of the Cascades both of Washington and of Oregon facilitated the adaptation of Townsend's Warblers to the drier east-side forests. This hypothesis is consistent with the strong southward turn of the zone on the east side of the Cascades of Washington (Figs. 5 and 6).

The best test of this model would be to contrast the east-west versus the north-south lengths of the range of Townsend's Warblers in the Oregon Cascades. Because this zone is isolated from the Washington zones, it must have developed when Townsend's Warblers from eastern Oregon invaded the Cascades near Bend. If adaptation to dry forests acquired in the Rockies has facilitated the colonization of

the dry east slope of the Cascades by Townsend's Warblers, then the north-south extent of Townsend's phenotypes should be more than twice their east-west extent. This is true because the westward dispersal of Townsend's should be impeded as they enter wet, west-side forests. If this prediction is refuted, some more-global model such as behavioral dominance will be sufficient to explain the apparent movement of these zones.

We know of no other hybrid analysis that suggests that a zone might be moving solely because of competitive superiority of one parental form over the other, without associated habitat differences. Although there is evidence of introduced species rapidly eliminating others through introgression (e.g. Woodruff and Gould 1987), there is little evidence for narrow zones being maintained through competitive superiority of one parental form over the other (Barton and Hewitt 1985, Hewitt 1989). A recent example in manakins does not involve the superiority of one parental form over another but, rather, involves a sexually selected color character that has moved some 45 km beyond the site of transition in other characters separating these forms (Parsons et al. 1993). Examples of the superior parental model may be lacking because such zones are ephemeral and rarely persist long enough in evolutionary time to be available for study.

If Townsend's Warblers are competitively superior to Hermit Warblers, then the relative ranking of hybrids is of interest. If hybrids are inferior to Townsend's but superior to Hermits, then the southward movement of the zone should be accelerated. However, hybrids may be less fit than either parental, in which case the southward movement of the zone would be slowed by the hybrid sink.

Habitat modification.—Some hybrid zones have been interpreted to be consequences of habitat alteration by humans. The best-studied case may be the replacement of Golden-winged Warblers (*Vermivora chrysoptera*) by Blue-winged Warblers (*V. pinus*) 30 to 50 years after initial contact (Gill 1980, 1997). Extensive reforestation of the eastern United States has provided an opportunity for Blue-winged Warblers to expand their range and replace Golden-winged Warblers. Male Blue-winged Warblers establish territories in a broad range of old-field succession types, whereas male Golden-

winged Warblers are restricted to initial succession stages (Confer and Knapp 1981). Where these species are sympatric, they hold overlapping territories, and interspecific aggression is rare (Ficken and Ficken 1968, Murray and Gill 1976). Thus, aggressive competition among males probably is not responsible for the movement of this zone. Rather, its movement seems to be due to differences in habitat preferences and to the birds tracking recent habitat changes (Gill 1980). Another avian zone in which one parental form seems to be replacing another is the Mallard (*Anas platyrhynchos*) \times American Black Duck (*A. rubripes*) hybrid zone in eastern North America. Again, the replacement of American Black Ducks by Mallards seems to be habitat related, with Mallards being superior in the urban and agricultural habitats of eastern North America (Brodsky and Weatherhead 1984, Heusmann 1991).

We began this study suspecting that hybridization between Hermit and Townsend's warblers was new and would somehow have been caused or exacerbated by logging. Our view is now very different. Explaining three separate zones on the basis of logging or other forest management practices is improbable. Indeed, we see no difference in the contacts between these warblers in western Washington (the Olympics and the Cascades), where logging has been intensive, and in the eastern slopes of the Cascades (Washington and Oregon), where habitat changes are less due to clearcuts and more due to a combination of logging pine and larch and the suppression of fire, which favors fir (Langston 1995). It is also unclear how logging should affect these zones. Both species live in Douglas-firs, the principal commercial tree planted in the Pacific Northwest. Thus, both logging and fire suppression have probably increased the total area of suitable habitat available to these warblers in both east-side and west-side forests.

Logging creates patches of unsuitable habitat and therefore may increase dispersal. Because most cuts are small relative to our estimate of σ , it is unlikely that logging would have greatly enhanced dispersal. Indeed, because Douglas-fir is a fire-successional species on the wet side of the Cascades, burns during prehistoric times would have created large islands of prime habitat that would have been ephemeral. As the quality of habitats in these burns deteriorates

through succession to hemlock and western red cedar, birds born in them might have had to disperse great distances to reach other fire-generated islands of Douglas-firs on the wet side of the Cascades. Thus, past dispersal may have been much higher than present-day dispersal. If Townsend's Warblers have been replacing Hermit Warblers in the Pacific Northwest, then modern forest management practices could be retarding this competitive replacement by reducing dispersal!

OVERVIEW

The hybrid zones between Hermit and Townsend's warblers are narrow relative to dispersal. Two models that explain narrow hybrid zones can be rejected. We find little evidence of habitat differences between these birds and no evidence that hybrids are confined to any sort of ecotone joining the ranges of the parentals. Neither can we find evidence for the combination of recent contact and limited dispersal that can explain narrow hybrid zones. On the other hand, the zone seems to be narrow because of selection against hybrids: character transitions are concordant (Rohwer unpubl. data), and dispersal into the zone generates high linkage disequilibrium near the center of the zone (Table 3).

Our character-transition analyses suggest that more Townsend's genes cross the zone to enter Hermit populations than vice versa. This implies moving zones, with Townsend's Warblers replacing Hermit Warblers. Three models can account for the movement of hybrid zones. Asymmetries in dispersal could cause the replacement of Hermit Warblers by Townsend's Warblers and hybrids; evaluating this idea will require separate measures of gene flow within the parental populations. Habitat modification seems unlikely to apply to these zones, because we find no differences in habitat preferences of parentals. Finally, Townsend's Warblers may be competitively superior to Hermit Warblers. Our morphological analyses were useful only in suggesting this hypothesis; other field projects support it (Pearson and Rohwer unpubl. data). At a study site near the center of the zone, Townsend's males are more aggressive toward taxidermic mounts, are more successful at maintaining their territories, and are better at attracting mates than are Hermit males (Pear-

son unpubl. data). In summary, we believe that this zone is narrow because of selection against hybrids and that it is moving because Townsend's Warblers are competitively superior to Hermit Warblers.

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APPENDIX. Locality numbers, sample sizes (n , no. of males), and other data associated with collecting localities for Hermit Warblers, Townsend's Warblers, and their hybrids.^a

Loc. no.	n	Sum 7st		Locality description	Collection dates	Elevation (feet)
		\bar{x}	SD			
Alaska						
1	9	0.833	0.044	Fairbanks	20–29 Jun 88	1,000
2	8	0.906	0.038	Valdez	28–30 May, 11 Jul 95	200–400
3	20	0.872	0.040	Haines	10–12 Jun 88	0–400
4	15	0.900	0.037	Prince of Wales Island	6–7 June 88	200
5	8	0.885	0.058	Ketchikan	5–8 Jun 88	200
British Columbia						
6	5	0.846	0.061	NW corner east of the Coast Range	13–14 Jun 88	1,530–2,970
7	22	0.921	0.028	Queen Charlotte Islands	May 87; 1–3 Jun 88	250–500
8	23	0.858	0.049	Prince Rupert	29 May to 3 Jun 88	100–200
9	4	0.899	0.035	Houston	15 Jun 88	2,500
10	23	0.897	0.032	McBride, Valemont	15–17 Jun 88	3,000–6,000
11	24	0.870	0.048	Bella Coola	18–19 Jun 88	1,500–4,500
12	17	0.891	0.042	Port McNeill, 27 mi S, 12 mi E	29–31 May 88	500
13	12	0.872	0.043	Gold River, Cumberland	1–2 Jun 88	330–800
14	20	0.864	0.055	Sooke, 5 mi N, 3 mi W	27–29 May 88	990–1,650
Washington: Olympics and Coast Range						
15	7	0.842	0.063	Clallam Co., Sappho, 6.5 mi E	29 May 86; 22 May 87	825–1,600
16	5	0.836	0.052	Clallam Co., Joyce, 4 mi S, 2 mi E	30 May 86	600–1,000
17	8	0.821	0.060	Clallam Co., Sequim, 7 mi S, 3 mi W	23 May 87	1,650–2,500
18	11	0.798	0.111	Clallam Co., Sequim, 8.5 mi S, 4 mi E	31 May 86; 23–24 May 87	1,250–2,550
19	6	0.822	0.151	Clallam Co., Leland, 1.5 mi N, 8.5 mi W	22 Jun 94	2,700
20	18	0.518	0.168	Jefferson and Clallam Cos., Quilcene, 2.5 mi N, 7 mi W (Townsend Ck.)	30 Mar 86; 24 May 87; 21–29 Jun 94	1,400–3,800
21	9	0.446	0.133	Jefferson Co., Quilcene, 2 mi S, 5 mi W (Tunnel Ck.)	28 May 86; 16 Jun 94	1,000–2,300
22	16	0.381	0.124	Jefferson Co., Brinnon, 2 mi S, 7 mi W (Duckabush R.)	25 May 87; 9–10 Jun 94	950–3,900
23	11	0.292	0.122	Mason Co., Eldon, 2 mi N, 8 mi W	20 May 86; 25–26 Jun 88	800–2,600
24	8	0.445	0.247	Mason Co., Hoodspout, 1 mi N, 7 mi W	19–20 May 86; 8, 23 Jun 94	500–1,500
25	8	0.198	0.062	Mason Co., McCleary, 3 mi N; Tumwater, 10 mi W	19 May 86; 16–19 May 94; 23 Jun 95	330–1,700
26	8	0.173	0.060	Grays Harbor Co., Oakville 7 mi N, 2.5 mi E	25 Jun 91	1,910
27	11	0.150	0.035	Lewis Co., Pe Ell, 1.5 mi S, 3 mi E	24, 30 Jun 94; 10 May 95	660–900
28	9	0.115	0.031	Wahkiakum Co., Cathlamet, 3 mi N, 8 mi E	25 May 91, 24–25 Jun 91; 8 May 94	660–1,980
Washington: Cascades and Rockies						
29	10	0.842	0.060	Whatcom Co., Glacier, 3 mi N, 3 mi E; Mt. Baker, 9 mi N, 7 mi E	3 Jun 87; 16–17 Jul 90	1,650–3,380
30	19	0.850	0.039	Okanogan Co., Mazama, 0.5 mi S, 2.25 mi W, and 5 mi N, 6.5 mi W	3–5 Jun 87	2,440–3,900
31	7	0.899	0.034	Okanogan Co., Conconully, 4 mi N, 11 mi W (2-mi stretch of Boulder Ck.)	6 Jun 87	4,650–5,200
32	4	0.867	0.012	Ferry Co., Republic, 5 mi S, 5 mi W, and 6 mi S, 10 mi E	20 Jun 89; 13–16 Jun 92	2,640–2,950
33	19	0.882	0.045	Pend Oreille Co., Blueside, 2 mi N, 6 mi E, and Metaline Falls, 1 mi N, 10 mi E	9–13 Jun 86	2,393–4,125
34	6	0.907	0.050	Snohomish Co., Index, 0.5 mi S, 3.5 mi W	24 May 94	825–1,320
35	4	0.892	0.021	Snohomish Co., Index, 2 mi S, 12.5 mi E	24 May 94	1,815
36	8	0.783	0.161	King Co., North Bend, 5 mi S, 8 mi E	7 May 94; 17 Jun 91	1,650
37	4	0.906	0.045	King Co., Stampede Pass	19 Jun 85; 3 Jun 88	1,000–2,640
38	6	0.881	0.027	Chelan Co., Wenatchee, 8 mi S, 6 mi W	14 Jun 95	4,950

APPENDIX. Continued.

Loc. no.	<i>n</i>	Sum 7st		Locality description	Collection dates	Elevation (feet)
		\bar{x}	SD			
39	6	0.875	0.057	Kittitas Co., Cle Elum, 6 mi S, 0.5 mi W	14 Jun 95	2,970
40	8	0.774	0.176	Pierce Co., Greenwater, 6 mi S, 0.5 mi W	1 Jul 86	1,980-3,135
41	9	0.863	0.047	Pierce Co., Greenwater, 10.5 mi S, 6 mi E (White R. and Silver Ck.)	30 Jun 86	2,475-5,280
42	9	0.761	0.196	Pierce Co., Carbonado, 5 mi S, 4 mi E	5-6 Jun 86	2,475-3,300
43	8	0.300	0.149	Thurston Co., Yelm, 6 mi W	1 Jun 95	400
44	8	0.841	0.058	Yakima Co., American R., 3-7 miles E of Chi- nook Pass	24 Jun 86	3,630-4,290
45	6	0.822	0.061	Yakima Co., Deep Creek 1-6 miles S of Bump- ing Lake	25 Jun 86	3,469-3,960
46	6	0.223	0.127	Lewis Co., Centralia, 15 mi E	1 Jun 95	1,550
47	7	0.284	0.145	Lewis Co., Morton, 3 mi N, 2 mi E	9, 14 Jun 95	1,400-2,200
48	7	0.537	0.250	Lewis Co., Ashford, 1.5 mi S, 2.5 mi E	3 Jun 86; 15, 28 Jun 87	1,840-2,720
49	8	0.519	0.263	Lewis Co., Ashford, 1.5 mi S, 6.5 mi E	3 Jun 86; 15 Jun 87	2,000-2,280
50	8	0.540	0.239	Lewis Co., Ashford, 2 mi S, 9.5 mi E	3 Jun 86; 25-27 May 87	2,400-2,950
51	17	0.522	0.225	Lewis Co., Packwood, 3 mi N, 6.5 mi W	27-28 May, 28 Jun 87; 25 May 89	2,500-3,800
52	15	0.626	0.163	Lewis Co., Packwood, 1.5 mi N, 2 mi W	28 May, 24 Jun 87	1,520-2,250
53	18	0.668	0.203	Lewis Co., Packwood, 3.5 mi N, 2.5 mi E	19 Jun 87	1,520-2,000
54	21	0.707	0.184	Lewis Co., White Pass, 3.5 mi N, 8 mi W	4, 27 Jun 86; 17-19 Jun 87; 25 May 89	1,840-3,120
55	28	0.707	0.222	Lewis Co., White Pass, 2.5 mi N, 5 mi W	4, 26-28 Jun 86; 16-17 Jun 87	2,720-4,240
56	14	0.769	0.218	Lewis Co., White Pass, 1 mi S, 1 mi W	26 Jun 86; 17 Jun 87	3,840-4,560
57	21	0.850	0.052	Yakima Co., White Pass, 4.5 mi	18 Jun 86; 14 Jun 95	3,000-4,400
58	9	0.695	0.154	Lewis Co., Packwood, 4.5 mi S, 2 mi E	28-29 May 87	1,280-2,300
59	10	0.912	0.040	Yakima Co., S. Fork Tieton River near Conrad Meadows	8-9 Jun 94	3,960-4,950
60	8	0.209	0.070	Lewis Co., Mossyrock, 9 mi S, 3 mi E	7 Jun 95	1,750
61	4	0.292	0.186	Lewis Co., Randle, 8.5 mi S	17 Jun 86; 14 Jun 87	1,100-2,200
62	4	0.357	0.184	Lewis Co., Mt. Adams, 16 mi N, 13 mi W	14 Jun 87	1,400-1,600
63	3	0.705	0.187	Lewis Co., Mt. Adams, 16 mi N, 2 mi W	29 May 87	3,200-3,900
64	23	0.471	0.202	Skamania Co., Mt. Adams, 10 mi N, 8 mi W (9-mi stretch of Cispus River)	10-13 Jun 87	2,300-3,150
65	6	0.665	0.211	Skamania Co., Mt. Adams, 8 mi N, 2.5 mi W	10-12 Jun 87	4,100-4,400
66	12	0.672	0.249	Yakima Co., Mt. Adams, 8.5 mi N to 7 mi N, 6 mi E	11 Jun 87; 17 Jun 94	4,125-4,800
67	14	0.447	0.241	Yakama Co., Council, Takhlakh, Ollalie Lakes	18 Jul 81; 30 Jun 84; 13, 30 Jun 85; 26-27 Jun 86; 21 Jun 94	3,700-4,700
68	5	0.326	0.235	Lewis Co., Randle, 20 mi S, 2 mi W	14 Jun 85; 17 Jun 86	2,400-3,625
69	10	0.219	0.145	Cowlitz Co., Kelso, 6 mi N, 7.5 mi E	23 Jun 91	1,320
70	6	0.225	0.123	Lewis Co., Randle, 28 mi S, 5 mi W	14 Jun 85; 18 Jun 86	2,840-3,100
71	10	0.252	0.096	Skamania Co., Trout Lake, 8 mi N, 12 mi W	3 Jun 95	4,125
72	5	0.646	0.270	Yakima Co., Mt. Adams, 8 mi S, 3 mi E	29 May 94; 15 Jun 94	4,000-4,125
73	11	0.593	0.304	Yakima Co., Mt. Adams, 10 mi S, 0.5 mi W	29-30 Jun 94	3,000
74	20	0.494	0.295	Klickitat Co., Trout Lake, 2 mi N, 0.5 mi E	15-16 Jun 94	2,100
75	10	0.257	0.099	Klickitat Co., Trout Lake, 1 mi S, 2 mi W	15-16 Jun 94; 3 Jun 95	2,300
76	9	0.252	0.133	Klickitat Co., BZ Corner, 5.5 mi N, 16 mi W	11 May 86; 14 Jun 94	2,160-2,500
77	8	0.184	0.084	Cowlitz Co., Kalama, 5.25 mi N, 16 mi E	9 Jun 95	1,650
78	10	0.203	0.070	Cowlitz Co., Kalama, 3 mi E	2 Jun 95	1,750
79	7	0.164	0.042	Skamania Co., Stabler, 9 mi N, 7 mi W	7-9 Jun 86	2,080-2,880
80	5	0.256	0.077	Skamania Co., Stabler, 1.5 mi N, 4.5 mi W	7-8 May 86	2,000-2,560
81	5	0.207	0.082	Skamania Co., Willard, 3 mi N, 5 mi W	9 May 86	2,700-2,800
82	10	0.151	0.054	Clark Co., Venersborg, 2 mi N, 1 mi E	2 Jun 95	1,800
83	7	0.184	0.020	Klickitat Co, Husum, 1 mi S, 4 mi W	16 Jun 94	1,100
84	13	0.197	0.108	Skamania Co., North Bonneville, 2 mi N, 4 mi W	27 May 94; 2 Jun 95	2,200

APPENDIX. Continued.

Loc. no.	<i>n</i>	Sum 7st		Locality description	Collection dates	Elevation (feet)
		\bar{x}	SD			
Oregon: Coast Range						
85	7	0.182	0.033	Clatsop Co., Seaside, 6 mi S, 21 mi E	16 May 94	1,200
86	10	0.142	0.041	Tillamook Co., Forest Grove, 7 mi N, 12 mi W	13-14 May 94	1,800-2,300
87	8	0.120	0.044	Yamhill Co., Willamina, 3 mi N, 13 mi W	15 May 94	1,200-1,700
Oregon: Cascades						
88	11	0.190	0.073	Clackamus Co., Brightwood, 2 mi N, 0.5 mi E	31 May, 1 Jun 94	1,800-2,400
89	9	0.203	0.091	Hood River Co., Parkdale, 3 mi S, 8 mi E	30-31 May 94	4,000
90	12	0.227	0.131	Wasco Co., Pine Grove, 2 mi N, 6.5 mi W	31 May to 1 Jun 94	3,600
91	12	0.392	0.239	Jefferson Co., Sisters, 15 mi N, 1 mi W	2-3 Jun 94	4,100
92	5	0.339	0.301	Deschutes Co., Sisters, 10 mi W	3 Jun 94	4,500
93	5	0.886	0.030	Deschutes Co., Sisters, 9.5 mi S, 4.5 mi W	2 Jun 94	5,100
94	3	0.103	0.018	Jackson Co., near Ashland	7-8 May 87	3,000-3,200
Oregon: Blue Mountains						
95	7	0.868	0.038	Crook Co., Prineville, 14.5 mi N, 11 mi E	4 Jun 94	4,500-4,900
96	9	0.882	0.061	Grant and Baker Cos., John Day, 26 mi N, 42 mi E and 31 mi N, 41 mi E	5 Jun 94	5,000-5,100
California: reference birds						
97	8	0.127	0.048	Siskiyou Co., Mt. Shasta City, 2.5 mi S, 2 mi W	9-10 May 87	3,300-4,300
98	13	0.103	0.046	Plumas Co., Quincy, 1 mi S, 3 mi W	10-11 May 87	3,960-4,950
99	6	0.117	0.064	Sierra Co., Sierraville, 2.5 mi S, 1 mi W	11-12 May 87	5,775
100		0.090	0.044	Historical reference		

* Additional details on collection localities available from the authors.