INFLUENCE OF NICHE OVERLAP AND TERRITORIALITY ON HYBRIDIZATION BETWEEN HERMIT WARBLERS AND TOWNSEND'S WARBLERS

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ABSTRACT.—Hybrid zones between Townsend's Warblers (*Dendroica townsendi*) and Hermit Warblers (*D. occidentalis*) in the Pacific Northwest are narrow relative to estimated dispersal distances and appear to be moving, with Townsend's replacing Hermits. We examined whether the habitat-transition and parental-fitness asymmetry models can explain why these zones are narrow and moving by comparing habitat variables associated with warbler territories in the Washington Cascades hybrid zone. Habitat variables did not differ among phenotypes, suggesting that the habitat-transition model cannot explain the narrow and dynamic nature of this hybrid zone. Habitat characteristics of Hermit Warbler territories did not differ inside versus outside the hybrid zone, also suggesting that this zone is not associated with a region of habitat transition. The lack of difference in habitat use could be the result of comparing variables that are not important to pairing success. However, warblers tended to select territories on west-southwest aspects. South aspects in the southern Washington Cascades are dominated by Douglas fir (*Pseudotsuga menziesii*) and true fir, which is a habitat selected by female warblers when choosing among territories and males. The parental-fitness asymmetry model does not necessarily make predictions about habitat use within the hybrid zone but predicts the superiority of one parental species over the other. However, if significant overlap occurs in habitat use or niche (as in these warblers), then competition between parental species is likely to occur. To determine whether these species compete, we mapped 12 warbler territories and monitored an additional 94 territories throughout the breeding season and found that all males with neighbors compete for and hold exclusive territories. Thus, the pattern of habitat use and territoriality is consistent with the parental-fitness asymmetry model. *Received 19 August 1998, accepted 16 June 1999.*

HYBRID ZONES that are narrow relative to dispersal distances raise an interesting evolutionary question: what selective forces prevent them from widening? Results from previous studies indicate that narrow hybrid zones are usually maintained either by strong selection against hybrids, or by environmental adaptation (Barton and Hewitt 1985). Four general models can account for narrow hybrid zones (Rohwer and Wood 1998): (1) hybrid inferiority or tension zone, (2) habitat transition, (3) parental-fitness asymmetry, and (4) recent contact. In the hybrid-inferiority or tension-zone model, hybrids are inferior to both parental species, and selection against hybrids is balanced by immigration into the hybrid zone by individuals from the adjacent parental populations (Barton and Gale 1993; Barton and

Hewitt 1985, 1989). The relative strengths of selection and dispersal determine zone width. In the habitat-transition model, hybrid zones exist between two different environments, each of which favors a different parental form (Moore 1977, Barton and Hewitt 1985, Grant and Grant 1992). If the area of ecological transition is narrow, then the associated hybrid zone will also be narrow. In the parental-fitness asymmetry model, one parental form is superior to the other, and hybrids are intermediate or lower in fitness, resulting in a moving zone (Hewitt 1989). The fitness of hybrids relative to the parental forms will affect zone width and movement. If hybrids are inferior to both parental species, then the zone will be narrow and the movement slow. If hybrids are intermediate in fitness, then the movement of the zone will be accelerated and the width will depend on the fitness differences between hybrids and parental species. Superior parental zones appear to be relatively rare because of their ephemeral nature (Gill

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1980, 1997; Hewitt 1989; Harrison 1990). Finally, hybrid zones may be narrow because of a combination of recent contact and low dispersal rate (Endler 1977, Barrowclough 1980).

Only two of these models, habitat transition and parental-fitness asymmetry, can explain a hybrid zone that is both narrow and moving. In the habitat-transition model, zones move if the area of ecological transition moves (e.g. Northern Flicker [*Colaptes auratus*], Moore and Price 1993; Carrion Crow [*Corvus corone corone*] and Hooded Crow [*C. corone cornix*], Cook 1975). Many of these zones are associated with human-caused habitat changes and may move as the environment changes (e.g. Blue-winged Warbler [*Vermivora pinus*] and Golden-winged Warbler [*V. chrysoptera*], Gill 1980; Common Grackle [*Quiscalus quiscula*], Yang and Selander 1968). In the parental-fitness asymmetry model, zones move as the competitively superior parental species replaces the other parental species (e.g. fire ants [*Solenopsis invicta* and *S. richteri*], Shoemaker et al. 1996; meadow katydids [*Orchelimum nigripes* and *O. pulchellum*], Shapiro 1998).

Recently, Rohwer and Wood (1998) described hybrid zones between Townsend's Warblers (*Dendroica townsendi*) and Hermit Warblers (*D. occidentalis*) in the Olympic Mountains of Washington, the southern Cascades of Washington, and the Cascades of Oregon south of Mount Hood. The two Washington hybrid zones have been described in detail, and both appear to be narrow and moving. Transitions from one parental phenotype to the other occur over 100 to 125 km, a distance only three to four times greater than estimates of root mean square dispersal distance (Rohwer and Wood 1998). These rapid changes in phenotype suggest that selective forces or environmental adaptations are preventing the zones from widening (Barton and Hewitt 1985, 1989). In addition, all plumage characters change abruptly from the Townsend's phenotype to the midpoint phenotype (a distance of 25 km), but change more gradually from the midpoint phenotype to the Hermit phenotype (a distance of 100 km). This pattern suggests that Townsend's Warbler alleles are flowing uniformly into Hermit Warbler populations. These hybrid zones may be moving because of changing environmental conditions or because Townsend's War-

blers have a selective advantage over Hermit Warblers.

Here, we examine whether the Washington Cascades hybrid zone fits the habitat-transition or parental-fitness asymmetry models by comparing habitat variables associated with warbler territories. The habitat-transition model predicts that habitat use differs among phenotypes. Thus, if these warblers and their hybrids use different habitats, and the region of ecological transition is moving, then the habitat-transition model may explain the narrow and dynamic nature of the hybrid zones. The parental-fitness asymmetry model does not necessarily make predictions about habitat use within the hybrid zone. However, if significant overlap occurs in habitat use or niche, and competition for habitat occurs, then the patterns of habitat use and competition are consistent with the superior parental model. In addition to comparing habitat use, we mapped warbler territories to assess whether these species and their hybrids compete for territories.

METHODS

Study area and species.—Field work was conducted in the Gifford Pinchot National Forest from 1994 to 1996 near the phenotypic center of the Washington Cascades hybrid zone along tributaries of the Cowlitz River between Randle and Packwood, Washington (46'30°N, 121'45°W). The study area is characterized by steep valleys and ridges. The forest is dominated by Douglas fir (*Pseudotsuga menziesii*); other major tree species include western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), grand fir (*Abies grandis*), Pacific silver fir (*Abies amabilis*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*). The shrub layer is dominated by vine maple (*Acer circinatum*), ocean spray (*Holodiscus discolor*), huckleberry (*Vaccinium parvifolium* and *V. membranaceum*), Oregon grape (*Berberis nervosa*), salal (*Gaultheria shallon*), and saplings of the overstory species.

Both warbler species nest and forage in conifer stands dominated by Douglas fir, true fir, spruce (*Picea*), and pine (*Pinus*) that exceed 30 cm in diameter and have high canopy volumes (Mannan and Meslow 1984, Verner and Larson 1989, Matsuoka et al. 1997, Pearson 1997b). These species appear to avoid stands dominated by deciduous trees, western hemlock, mountain hemlock (*Tsuga mertensiana*), and red cedar (Chappell and Ringer 1983, Pearson 1997a). Because of these habitat associations, we focused our search for territorial warblers in their preferred hab-

TABLE 1. Habitat variables ($\bar{x} \pm$ SE) for adult and yearling Townsend's Warblers, Hermit Warblers, and hybrids combined. *P*-values are from univariate comparisons between adult and yearling warblers.

Variable	Adult ($n = 74$)	Yearling ($n = 20$)	F^a	P
Elevation (m)	678 ± 23.1	760 ± 43.8	8.64	0.004
Aspect (degrees)	227 ± 6.9	226 ± 17.6	0.15	0.695
Canopy height (m)	38 ± 1.6	32 ± 3.6	5.17	0.025
Overstory cover (%)	92 ± 0.5	91 ± 1.3	1.39	0.241
Average tree diameter (cm)	51 ± 2.4	48 ± 5.9	2.27	0.156
Basal area of Douglas fir / true fir (m²)	2.29 ± 0.10	1.70 ± 0.27	6.70	0.011
Basal area of deciduous trees (m²)	0.08 ± 0.01	0.04 ± 0.02	6.18	0.015
Basal area of western hemlock / red cedar (m²)	0.16 ± 0.04	0.49 ± 0.12	5.33	0.023
Basal area of small deciduous trees (m²)	0.63 ± 0.07	0.73 ± 0.14	0.27	0.606
Basal area of small conifer trees (m²)	0.62 ± 0.12	0.88 ± 0.29	1.58	0.212
Tree-diversity index	0.57 ± 0.02	0.60 ± 0.05	0.04	0.845

^{a} ANOVA with df = 1 and 92.

itat, thus eliminating much of the natural variation in vegetation within the region.

Bird sampling.—We used logging roads to survey suitable habitat for new arrivals every two to three days from mid-April through early June, 1994 to 1996. Males were captured and color banded using the methods of Pearson and Rohwer (1998). We classified males as yearlings (in their first breeding season) or adults (in their second breeding season or older) based on plumage characters (Jackson et al. 1992). Phenotype was scored using the hybrid index developed by Rohwer and Wood (1998). This method uses seven standardized plumage characters to derive a single phenotypic score that ranges from 0 (Hermit extreme) to 1 (Townsend's extreme). To score phenotype in the field, captured males were compared with color photographs of voucher specimens for six plumage characters (extent of yellow on the crown, intensity of yellow on breast, back color, bib corner, mid-flank streaking, and lower-flank streaking). The seventh character, the extent of yellow on the breast, was measured using dial calipers as described by Rohwer and Wood (1998). Following Rohwer and Wood (1998) Hermit males ranged between 0 and 0.25, pure Townsend's males between 0.75 to 1.0, and hybrids between 0.25 and 0.75. The phenotypic scores of original territory holders were used in all comparisons.

From 1994 to 1996, we captured and banded 128 adult males and 38 yearling males. Of the adult birds, 19% were Hermits, 55% were hybrids, and 26% were Townsend's. Of the yearlings, 16% were Hermits, 65% were hybrids, and 18% were Townsend's. To avoid migrants, only birds that maintained their territories for at least one week were included in our analyses. A random subset of banded adult hybrids was used because we captured more than we could monitor. Different river drainages were sampled each year to avoid pseudoreplication. Territories were visited every three to seven days throughout

the breeding season, during which time we mapped singing locations on most visits.

Territories were mapped within an area of approximately 49 ha during 11 visits from 20 May to 29 June 1996. We delineated territories by plotting singing locations and locations of agonistic behaviors on a detailed contour map. Landmarks such as streams, clearcuts, logging roads and flagged singing locations were used as reference points. In addition, for each of the 94 warbler territories monitored, we also sketched territory boundaries and boundaries of neighboring warblers during most visits.

Habitat sampling.—To examine the relationship between habitat use and availability, we compared the slope aspect of warbler territories with available aspects. Available aspects were measured using a compass every 3.2 km along the same logging roads used to locate territorial warblers. These roads contoured steep slopes above streams, and the aspect measured was that of the prevailing slope. Because we focused our search for warblers in preferred habitats (see above), our estimate of aspect availability was conservative.

Habitat variables (see Table 1) were measured within 11.2-m radius plots centered on three non-overlapping, marked singing locations within each territory. Percent overstory cover was measured using a spherical densiometer (Lemmon 1957) in the center of the plot and at the perimeter of the plot in each of the four cardinal directions. We measured aspect at the center of each plot. Diameter of all trees (>4 m tall) was measured 1.4 m above the ground, and canopy height was estimated (we used a clinometer to check our estimates periodically). We estimated average tree diameter for canopy and subcanopy trees combined. The basal area of canopy, subcanopy, and short trees was calculated using diameter measurements. Short trees exceeded 4 m in height and were shorter than the lowest live branches of canopy trees. Dominant trees formed the can-

opy, and subdominant trees did not reach the canopy but were taller than the lowest live branches of canopy trees. Basal areas of dominant and subdominant trees were grouped together for the analysis of habitat use among phenotypes but were analyzed separately when used in the tree-diversity index described below. Basal areas of dominant and subdominant trees were grouped as either Douglas fir/true fir (*Abies*), western hemlock/western red cedar, or deciduous trees. These groupings were based on warbler habitat preferences (see above).

To evaluate the potential influence of tree age and structure on the width and movement of the Washington Cascades hybrid zone, we used the basal area of dominant, subdominant, and short trees in a Shannon-Weaver index instead of using the number of trees. Without using basal area, a short tree 10 cm in diameter would receive the same importance as a canopy tree 100 cm in diameter and 60 m tall. This method also recognizes the importance of foliage volume and stand structure to the life history of these canopy-dwelling warblers because basal area is a good predictor of foliage volume (Verner and Larson 1989). To evaluate the effectiveness of this method, stands associated with territories were assigned to one of two age/structure categories: (1) young, even-aged stands in which average canopy height was below 20 m, average canopy tree diameter was less than 30 cm, and the stand had been previously logged, planted, and thinned; or (2) old, uneven-aged stands in which canopy height exceeded 40 m, average canopy tree diameter was greater than 60 cm, and there was no evidence of logging. Using discriminant function analysis, the values produced by the tree-diversity index successfully separated these two age/structure categories 88% of the time ($F = 83.3$, df = 1 and 47, $P < 0.001$).

To determine whether habitat use within the hybrid zone was indicative of habitat use outside the zone, habitat on the territories of 16 adult Hermit Warblers within the Washington Cascades hybrid zone was compared with that on the territories of 9 adult Hermit Warblers south of the hybrid zone. Such an analysis is potentially influenced by regional differences in habitat variables that are unimportant to the fitness of these species. Therefore, only habitat variables determined to be important to pairing success (i.e. canopy closure, basal area of Douglas fir/true fir, aspect and basal area of small conifer trees) were compared (Pearson 2000). Birds south of the hybrid zone were captured and banded as described above and monitored every 10 to 14 days in 1995. These birds were located above tributaries to the Wind River in the Gifford Pinchot National Forest (45′55″N, 122′00″W).

Statistical analyses.—Individual territories were used for all statistical analyses, and all variables were averaged per territory. Habitat variables not meeting assumptions of normality (Kolmogorov-
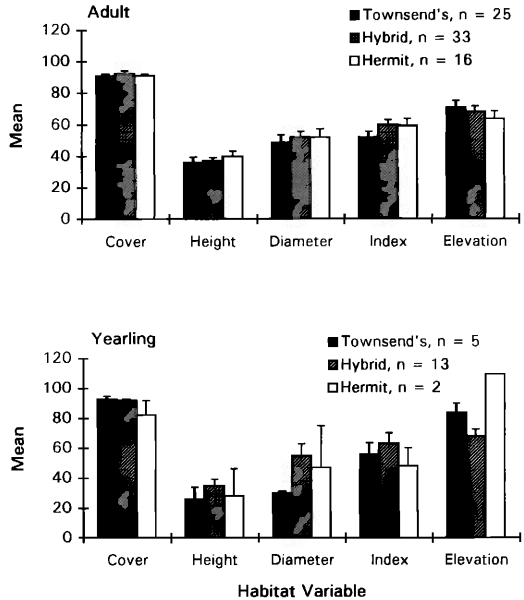

FIG. 1.   Stand structure and elevation on territories of adult and yearling Townsend's Warblers, Hermit Warblers, and hybrids. Values are $\bar{x}$ and SE. Cover = overstory cover (%); height = canopy height (m); diameter = tree diameter (cm); index = tree-diversity index; and elevation = elevation (m)/10.

Smirnov one-sample test) or homogeneity of group variances (Bartlett's *F*-test) were transformed using log or arcsine transformations (Zar 1984). Habitat variables associated with territories were compared among phenotypes and age classes of warblers using multivariate analysis of variance. We compared aspect on territories with available aspects in the study area using the Watson-Williams tests for two circular distributions (Zar 1984). Analyses were performed using SYSTAT (Wilkinson 1990).

RESULTS

Habitat comparisons within the hybrid zone.— The habitat characteristics that we measured did not differ among warbler phenotypes or age classes (phenotype, $F = 1.3$, df = 22 and 156, $P = 0.18$; age, $F = 1.4$, df = 11 and 78, $P = 0.19$; Figs. 1 and 2), but the interaction between age and phenotype was nearly significant ($F = 1.59$, df = 22 and 156, $P = 0.056$). Univariate tests indicated a significant difference among phenotypes only in overstory cover ($F = 3.3$, df = 2 and 88, $P = 0.04$). Looking at the effect of age, univariate tests indicated significant differences between yearling and adult males
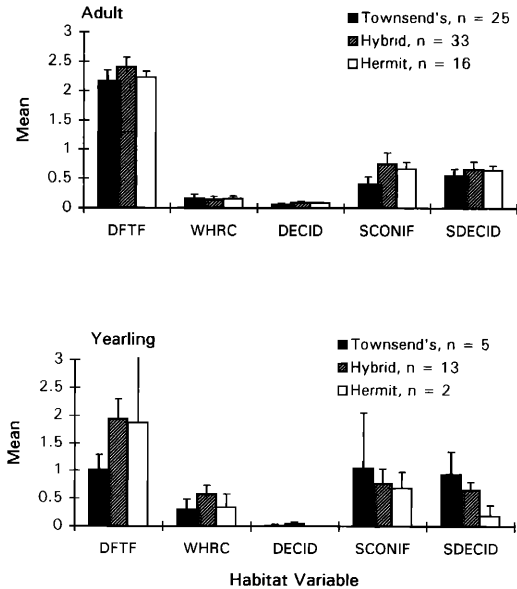
FIG. 2. Tree variables on territories of adult and yearling Townsend's Warblers, Hermit Warblers, and hybrids. Values are $\bar{x}$ and SE. DFTF = basal area of Douglas fir/true fir (m²); WHRC = basal area of western hemlock/red cedar (m²); DECID = basal area of canopy and subcanopy deciduous trees (m²); SCONIF = basal area of small conifer trees (m²); and SDECID = basal area of small deciduous trees (m²).

(species combined) in elevation; canopy height; and basal area of Douglas fir/true fir, western hemlock/red cedar, and deciduous trees (Table 1).

The nearly significant interaction between age and phenotype may have resulted from comparing habitat variables that were not important to pairing success. When comparing the four habitat variables that were important to pairing success (see Methods), we found no difference among phenotypes ($F = 1.29$, df = 8 and 170, $P = 0.21$) or between age classes ($F = 0.12$, df = 4 and 85, $P = 0.12$), and the interaction between age and phenotype was not significant ($F = 1.08$, df = 8 and 170, $P = 0.38$).

Overall, yearlings and adults occupied relatively dry mid-elevation sites dominated by larger Douglas firs and with southwest aspects, high canopy volumes, and moderate tree diversity (see Table 1). Relative to adults, yearlings occupied sites that were higher in elevation and contained more western hemlock/red cedar and less Douglas fir/true fir (Table 1).

Steep south-facing sites in the southern

Washington Cascades typically are dominated by Douglas fir, with little or no hemlock and cedar (Franklin and Dyrness 1988), which appears to be the habitat type selected by Townsend's Warblers, Hermit Warblers, and their hybrids (Table 1). Relative to availability, both yearling and adult warblers selected sites with more west-southwest aspects ($F = 4.2$, df = 1 and 172, $P < 0.05$; Fig. 3). The predominance of westerly aspects in the area sampled likely was a consequence of working on the west slope of the Cascades.

Habitat characteristics inside versus outside the hybrid zone.—Habitat characteristics of Hermit Warbler territories within the hybrid zone were remarkably similar to those of Hermit Warblers outside of the hybrid zone ($F = 0.21$, df = 4 and 20, $P = 0.93$; Fig. 4), suggesting that the Washington Cascades zone is not associated with a region of habitat transition.

Territoriality.—To determine whether these species and their hybrids hold exclusive territories, we mapped 12 territories (two Hermit, one Townsend's, and nine hybrids). All phenotypes maintained typical type A territories (Nice 1941), and most (if not all) of the foraging and breeding activity occurred within the defended areas. Territories did not overlap (Fig. 5), and six of the seven aggressive encounters that we observed occurred along territory boundaries. All eight of the territories of adult males shared common borders, whereas three of the four territories of yearling males did not share common borders and were separated by poor habitat. A Townsend's Warbler and a hybrid contested their common territory border on at least one occasion, and after the Townsend's Warbler abandoned its territory, the neighboring hybrid subsumed a portion of the territory (Fig. 5).

Sketches of an additional 30 Townsend's Warbler, 18 Hermit Warbler, and 46 hybrid territories indicated that all males that had immediate neighbors (78%) held and defended exclusive territories regardless of the phenotype of their neighbors. Actual examples of interspecific territoriality were rare ($n = 8$) because the zone is dominated by hybrid males. As above, the warblers without neighbors usually were males in their first breeding season and were located in poor habitats.
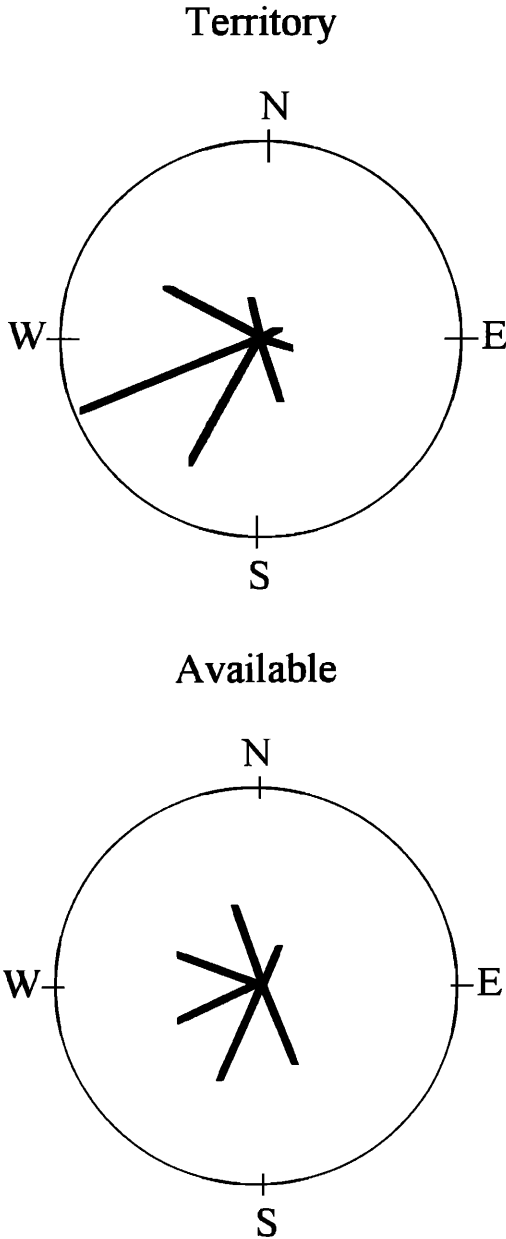
Territory

Available

FIG. 3. Slope aspect on territories of adult Hermit Warblers, Townsend's Warblers, and hybrids ($n = 74$) and aspect of available sites ($n = 83$). Length of bars reflects number of territories or number of available aspects that were found in each octant.
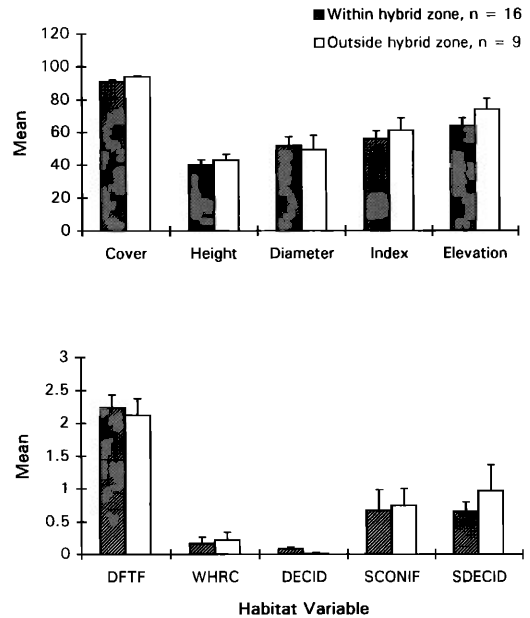

FIG. 4. Habitat variables associated with territories of adult Hermit Warblers inside and outside of the hybrid zone. Values are $\bar{x}$ and SE. See Figures 1 and 2 for identification of variables.

DISCUSSION

Overall, we found no difference among male Hermit Warblers, Townsend's Warblers, and hybrids in the habitat characteristics of their territories. Overlap in habitat on territories excludes the habitat-transition model as an explanation for the narrowness of the hybrid zone between these warblers. The lack of habitat differences between Hermit Warbler localities inside versus outside the hybrid zone also suggests that this zone is not associated with a region of ecological transition. Unfortunately, we have no information on Townsend's Warbler habitat characters north of the zone for a similar comparison. However, as with males within the hybrid zone, territorial male Townsend's Warblers to the north and east of the zone are associated with Douglas fir and true fir (Mannan and Meslow 1984) and with relatively dry sites (Manuwal 1991).

The lack of differences in habitat characters among warbler phenotypes may be the result of comparing habitat variables unimportant to their reproductive success. However, evidence suggests that the habitat features we evaluated are preferred by these warblers and are important to pairing success. These warblers settled selectively on relatively dry west-southwest sites. South aspects in the Cascades are dominated by Douglas fir / true fir and contain little western hemlock and red cedar in the canopy.
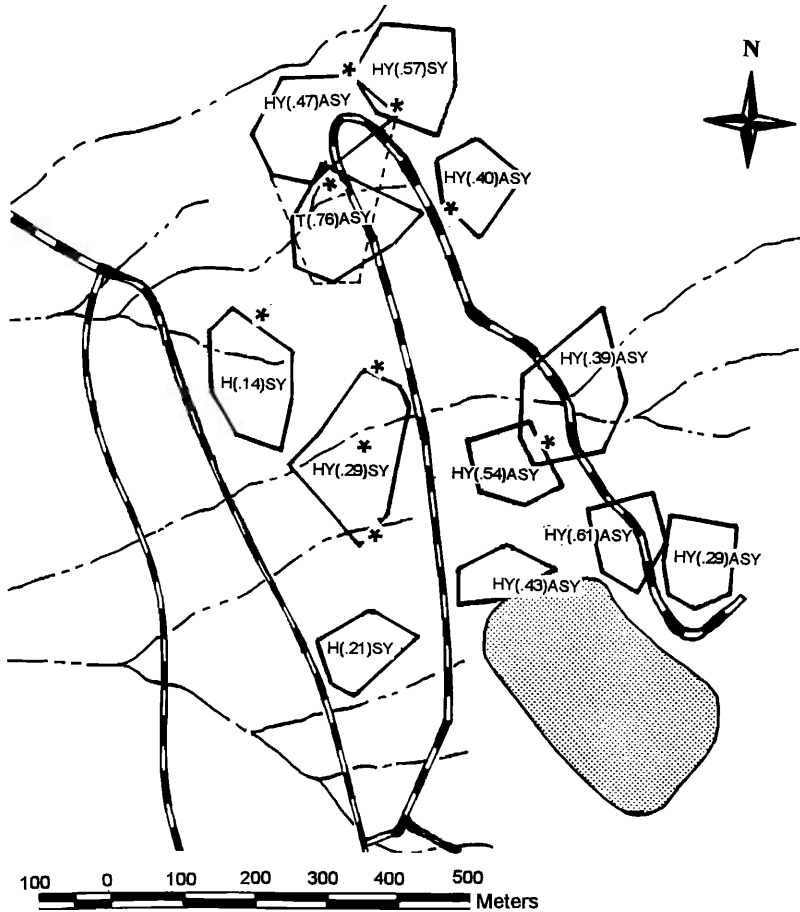
FIG. 5. Territories of Hermit Warblers (H), Townsend's Warblers (T), and hybrids (HY) on a 49-ha study site in the southern Washington Cascades. Phenotypic scores are in parentheses (Hermit = 0 to 0.25; hybrid = 0.25 to 0.75; Townsend's = 0.75 to 1). Dashed lines indicate a change in territory boundary after the neighboring territory was abandoned, asterisks denote locations of agonistic interactions, and stippled area denotes a clearcut.

These are the same habitat features selected by female warblers when choosing among territories and males (Pearson 2000). Moreover, we found no difference among phenotypes when comparing only the habitat variables that are important to pairing success. Other habitat attributes that are critical to reproductive success, such as nest sites and foraging locations, are not likely to differ among phenotypes because warbler territories contain all of the resources required for breeding.

All comparisons of habitat use suggest that Hermit Warblers, Townsend's Warblers, and hybrids overlap in the habitat characteristics on their territories. Overlap in habitat is a prerequisite for interspecific competition to occur be-

tween these species (MacArthur 1972, Wiens 1989). Territory mapping and evidence from monitoring 94 territories indicate that these species and their hybrids compete for and hold exclusive territories. Thus, if males of one species are superior competitors in territorial disputes, the parental-fitness asymmetry model may explain the narrow and dynamic nature of these hybrid zones.

There is some evidence for competitive asymmetry. Townsend's Warblers appear to be more aggressive than Hermit Warblers, both inside and outside the Washington Cascades hybrid zone (Pearson and Rohwer 2000). In addition, male Townsend's Warblers are more successful in maintaining territories and in at-

tracting mates than Hermit Warblers or hybrids within the Washington Cascades hybrid zone (Pearson 2000). Townsend's Warblers within and immediately adjacent to the hybrid zones also may have a reproductive advantage over Hermit Warblers because they lay larger clutches (Pearson and Rohwer 1998). All of these comparisons indicate a selective advantage for Townsend's Warblers and suggest that fitness asymmetries between the parental species could explain why these zones are narrow and moving.

If male Townsend's Warblers are indeed superior competitors in territorial contests, then they should occupy the best habitats. Surprisingly, we found no habitat differences between these species. Nor did we find evidence that male Townsend's Warblers "push" male Hermit Warblers into poor habitats in regions of sympatry, based on comparisons of Hermit Warbler habitat characteristic on territories outside versus inside the hybrid zone. Lack of habitat segregation may be explained by competitive sorting. Territorial contests between these species and their hybrids appear to be common (Pearson 2000). Territory owners that are inferior in their fighting ability to floaters and dispersing males could be displaced from their territories. The net result is that all males within a given locality will be of similar fighting ability regardless of phenotype, in which case each individual should occupy a territory of similar habitat quality.

The fitness of hybrids relative to the parental species influences the width and movement of hybrid zones. Comparisons of aggressiveness across the Washington Cascades zone and pairing success within the zone suggest that hybrids are intermediate in fitness between the parental species, which should accelerate the zone's movement. If, however, hybrids have reduced survivorship and fertility relative to the parental species, as suggested by clutch size (Pearson and Rohwer 1998) and reduced return rates (Pearson 2000), then the movement of the zone would be slowed and the width of the zone narrowed.

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