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INFLUENCE OF BREEDING PHENOLOGY AND CLUTCH SIZE ON HYBRIDIZATION BETWEEN HERMIT AND TOWNSEND'S WARBLERS

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ABSTRACT.—In avian hybrid zones, differences in timing of breeding or clutch size may confer a selective advantage for one species over the other. We compared clutch sizes, arrival dates, pairing dates, and clutch initiation dates among Hermit Warblers (*Dendroica occidentalis*), Townsend's Warblers (*D. townsendi*), and their hybrids from areas within and adjacent to their hybrid zones in Oregon and Washington. Adult males of all phenotypes arrived first, with yearling males and females following by 10 and 18 days, respectively. Arrival was significantly later at higher elevations for adult males. The phenotypes did not differ in arrival dates when the effect of elevation was removed. Pairing dates were similar for the three male phenotypes, and clutch initiation dates were similar for the three female phenotypes. Thus, breeding phenology seems not to influence competition between these warblers and their hybrids. However, the clutches of Townsend's Warblers were 0.6 eggs larger than those of Hermit Warblers and 1.15 eggs larger than those of hybrids, suggesting a selective advantage for Townsend's Warblers. Hybrid females produced the smallest clutches we recorded (though not significantly smaller than Hermit Warbler clutches), suggesting that hybrids are inferior to both parental species. *Received 16 July 1997, accepted 5 February 1998.*

HERMIT (*DENDROICA OCCIDENTALIS*) and Townsend's (*D. TOWNSENDI*) warblers are sister species that apparently diverged in Rocky Mountain (Townsend's) and coastal (Hermit) refugia during the middle Pleistocene (Bermingham et al. 1992). Three geographically isolated hybrid zones connect the ranges of these species, one in the Olympic Mountains of Washington, another in the southern Cascade Mountains of Washington, and a third in the Cascade Mountains of Oregon south of Mt. Hood (Rohwer and Wood 1998). The two Washington hybrid zones have been described in detail. For both zones, 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 (Rohwer and Wood 1998). These rapid character transitions imply that strong selective forces prevent these zones from becoming wider (Barton and Hewitt 1985, 1989).

Rohwer and Wood (1998) evaluated a variety of models that might explain these narrow zones, and they concluded that both hybrid inferiority and parental fitness asymmetries are keeping these zones narrow and, further, that parental fitness asymmetries are causing them to move. Hybrid zones will remain narrow when selection against hybrids is balanced by immigration toward the center of the zone by parentals (Barton and Hewitt 1985, 1989, Barton and Gale 1993). Asymmetric character-transition curves also suggest that the Washington zones are moving southward, owing to the competitive superiority of Townsend's Warblers over both hybrids and Hermit Warblers (Rohwer and Wood 1998). Because this inference was based only on the shape of the character-transition curves, the competitive ranking of hybrids and Hermit Warblers could not be inferred.

Several alternative models that can explain abrupt character transitions are not applicable to these hybrid zones (Rohwer and Wood 1998, Pearson 1997a). These include recent contact (Endler 1977, Barrowclough 1980), hybrid superiority within an ecotone (Moore 1977, Moore and Price 1993) and habitat modification (Gill 1980, Wake et al. 1980, Hewitt 1989: table 4). These warbler hybrid zones are interesting because the inferred fitness asymmetry implies that Townsend's Warblers are replacing Hermit

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Warblers. Few moving hybrid zones have been described, no doubt in part because extinction through competition and hybridization must be ephemeral and therefore rarely available for study (Gill 1980, 1997, Harrison 1990).

In this paper, we assess fitness asymmetries between the parental species and their hybrids with respect to date of arrival on the breeding grounds, pairing date, clutch initiation date, and clutch size. In migratory passerines, early arrival, acquisition of good territories, early pairing and the production of early broods, and larger clutches often are correlated with fitness advantages (Lack 1968, Nolan 1978, Alatalo et al. 1984, Slagsvold 1986). Thus, we compare clutch sizes, pairing dates, and clutch initiation dates among phenotypes within and immediately adjacent to the three hybrid zones in Washington and Oregon. From the asymmetries in the character-transition curves (Rohwer and Wood 1998), we predicted that Townsend's Warblers might arrive earlier, pair earlier, initiate clutches earlier, and lay larger clutches than Hermit Warblers. If hybrid inferiority is also contributing to the narrowness of these hybrid zones, then hybrids should arrive later, pair later, initiate clutches later, and lay smaller clutches than both parentals. If hybrids are intermediate in fitness between the parentals, then their competitive superiority over the inferior parental would contribute to the movement of the zone. In this case, we would expect hybrids to rank below Townsend's Warblers, but above Hermit Warblers, in measures of fitness.

METHODS

Field work was conducted in the Gifford Pinchot National Forest along tributaries to the Cowlitz River (46°30'N, 121°45'W), which is near the phenotypic center of the hybrid zone of these two warbler species in the southern Cascades of western Washington. From 1994 to 1996, we banded 166 male warblers, of which 18.7% were Hermits, 59.6% were hybrids, and 21.7% were Townsend's (Pearson 1997a). Elevations ranged from 300 to 1,300 m. Forests were dominated by Douglas-fir (*Pseudotsuga menziesii*), the principal tree used for nesting and foraging by these species at low elevations. Other common trees in the study area included western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), grand fir (*Abies grandis*), Pacific silver fir (*Abies amabilis*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*).

We used U.S. Forest Service roads to survey appropriate habitat for new arrivals every two to three days from mid-April through early June. In almost every case, newly arrived males were actively singing. If we did not hear males singing, we encouraged singing with playbacks. Arrival dates were assigned as the date midway between the date a male was first observed on its territory and the date of our previous visit to that territory. Each newly occupied territory was counted as a new male arrival. We stopped counting male arrivals when females began arriving to avoid counting males that were shifting territories during arrival. We observed such shifts only after females had begun to settle.

As far as possible, we quantified the phenotype of individual male and female warblers using hybrid indices based on several plumage characters. We quantified the phenotypes of captured males following Rohwer and Wood (1998); photographs of voucher specimens were used to make this scoring as accurate as possible. For the female specimens used in our analyses of clutch size and clutch initiation dates, we used a hybrid index developed by C. M. Smith (unpubl. data). This index uses scores from the following characters: yellow on the crown, streaking on the mid and lower flanks, intensity of yellow on the breast, extent of yellow on the breast, and back color. When Smith applied this scoring system to large reference samples of females taken outside the hybrid zone, scores for pure Hermit females ranged from 0 to 0.2, pure Townsend's females from 0.8 to 1, and hybrid females from 0.2 and 0.8. Smith scored all of the female specimens whose ovarian conditions were used to determine clutch sizes and clutch initiation dates in the present study. Most of the females we worked with in the field could not be captured. When females were seen well in the field, we scored them visually; others were considered as "unknown" phenotype. Extent of yellow on the breast was omitted for females scored in the field because it was difficult to assess through binoculars. These field scores, which were used only to assess differences in arrival dates for females, also were scaled from 0 to 1 to make them comparable to scores for females evaluated in the hand.

We captured males for color banding using mist nets and playback of a locally recorded song. Captured birds were sexed by presence or absence of a cloacal protuberance, and males were aged as yearlings (first breeding season) or adults (second or later breeding season) following Jackson et al. (1992). Territories of banded males were rechecked the day following banding, and then every three to seven days thereafter, to determine how long males maintained their territories and whether they obtained a mate. When territories were rechecked, playbacks were used to confirm the identity of the male. For our analysis of arrival date, we included only males that remained on their territories for at least two days.

Occasionally, newly arrived females approached the playback speaker or gave distinct chips that, unlike those of males, were delivered in rapid succession. Female arrival dates were estimated as the date midway between the date a female was first observed and the date of our previous visit to that territory. Female warblers are difficult to detect, but we trust our data on female arrival because male song change occurred shortly after females arrived (see Results). Many parulid warblers change from a first-category song to a second-category song when pairing occurs (Morse 1967, Kroodsma 1981, Kroodsma et al. 1989, Spector 1992); thus, we used male song change to estimate pairing dates. The date of male song change was estimated as the date midway between the date when second-category song was first detected and the date of our previous visit to that territory.

The University of Washington Burke Museum has more than 90 female specimens of these warblers collected during the breeding season (late May through mid-June, 1986 to 1995) for research on hybridization. We estimated clutch initiation dates and clutch sizes from measurements of the pre- and postovulatory follicles of females that were collected during laying (Pearson and Rohwer 1998). To enlarge our samples of clutch sizes, we include in our analyses data from egg sets, published records (Bowles 1906, 1921, Decker and Bowles 1923, Burleigh 1930), and nests found during our field work. The clutches used in all of these analyses were known to be complete. Clutch sizes obtained by measurements of ovarian follicles did not differ from those obtained from egg sets and published records (Pearson and Rohwer 1998).

We restricted our analyses of phenotypic differences in clutch size and clutch initiation dates to records obtained within and immediately adjacent to the hybrid zones. For the Olympic zone, we used birds collected on the west side of the Olympics from the towns of Sequim to PeEll and Grays Harbor. For the Washington Cascades zone, we used birds from the towns of North Bend and Wenatchee south to the Mt. Adams and Mt. St. Helens regions. For the Oregon Cascades zone, we used birds from the towns of North Bonneville and Pine Grove south to Prineville, Bend, and Sisters (Rohwer and Wood 1998).

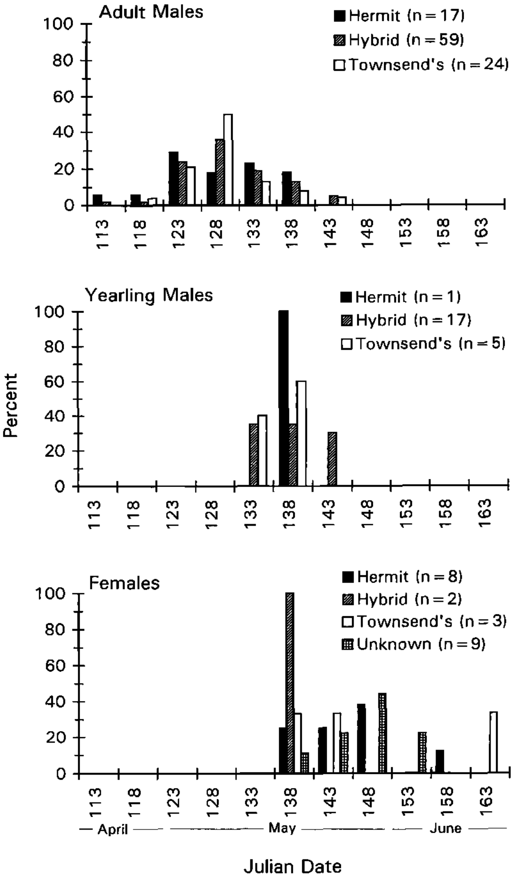

FIG. 1. Percent of birds arriving in the southern Washington Cascades by sex, age, and phenotype in five-day intervals between 21 April and 19 June, 1994 to 1996. Julian dates between tick marks are the midpoint for each five-day interval.

RESULTS

Combining all phenotypes, adult males arrived an average of 10 days earlier than yearlings (Fig. 1). Most adults arrived during the first and second weeks of May (mean = 8 May, SD = 6.31 days, n = 100), and most yearlings arrived during the third and fourth weeks of May (mean = 18 May, SD = 3.69 days, n = 23), after the peak of adult arrival. Females of all phenotypes arrived last (mean = 26 May, SD = 7.03 days, n = 22), peaking during the final two weeks of May.

We recorded few female and yearling male arrival dates at our study site, so arrival dates could be compared by phenotype only for adult males, all of which were scored in the hand. We removed the effects of elevation and year on arrival dates using analysis of covariance. Elevation had a strong effect on arrival dates, with males arriving later at higher sites (F = 58.4, df = 1 and 90, $P < 0.001$; Fig. 2); this relationship was the same for all phenotypes (F = 0.34, df = 2 and 90, P = 0.71). Arrival dates did not differ among the three years of the study (F = 1.78, df = 2 and 90, P = 0.18). With elevation effects controlled, arrival date did not differ by

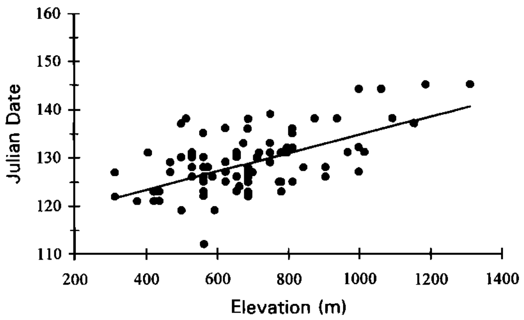

FIG. 2. Relationship between arrival date and elevation for adult male warblers in the southern Washington Cascades hybrid zone.

phenotype ($F = 0.85$, df = 2 and 90, $P = 0.43$). Box plots of the residuals from the regression of arrival date on elevation demonstrate the extensive overlap in arrival date by phenotype (Fig. 3).

Because we recorded few dates of song change for yearling males, date of song change (i.e. pairing) could be compared by phenotype only for adult males, all of which were scored in the hand. For adult males, the mean date of change from first- to second-category song was 29 May (SD = 6.9 days, $n = 26$). This change occurred three days after the mean date for female arrivals, suggesting that song change is a reliable index of male pairing. The use of song change to infer pairing is supported by two additional observations. First, of the 51 males that changed songs, 77% showed other evidence of pairing (i.e. female observed on two or more occasions, nest building, food carrying, etc.). Second, none of the 48 males that failed to change songs showed evidence of pairing. Controlling for elevation, the date of song change did not differ by phenotype (ANCOVA, $F = 0.66$, df = 2 and 22, $P = 0.52$); thus, pairing dates seemed to be similar across all phenotypes of adult males.

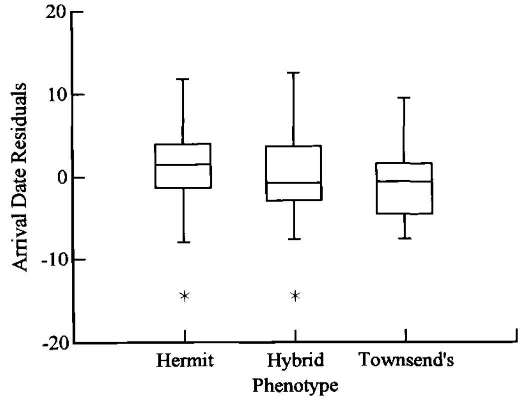

FIG. 3. Residual of arrival date by phenotype in Washington Cascades hybrid zone after controlling for elevation (see Fig. 2). Values are means (line), standard errors (boxes), 95% confidence intervals (bars), and outliers (asterisks).

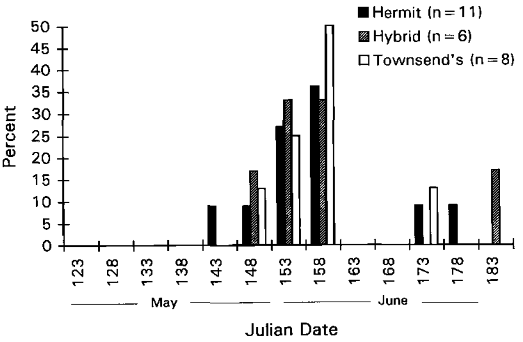

FIG. 4. Percent of clutches initiated in five-day intervals for female Hermit Warblers, Townsend's Warblers, and hybrids within and immediately adjacent to the Washington and Oregon hybrid zones.

The mean date of clutch initiation within and immediately adjacent to the hybrid zone was 7 June (SD = 9.6 days, $n = 25$). Clutch initiations appeared bimodal (Fig. 4). The group of late clutches apparently represents replacement (vs. second) clutches because the time separating this group of clutches from the earlier clutches is insufficient for a brood to have been fledged. With elevation controlled, clutch initiation date did not vary with the phenotype of these female specimens (ANCOVA, $F = 0.12$, df = 2 and 21, $P = 0.89$; Fig. 4).

Clutch size varied with phenotype within and immediately adjacent to the hybrid zones (ANOVA, $F = 13.8$, df = 2 and 23, $P < 0.001$; Table 1). Townsend's Warblers laid significantly larger clutches than Hermit Warblers and hy-

TABLE 1. Clutch size of Hermit Warblers, Townsend's Warblers, and hybrids within and adjacent to the hybrid zones of Washington and Oregon.

	Clutch size				
Phenotype	2	3	4	5	Mean
Townsend's Warbler	0	0	1	10	4.9
Hybrids	0	1	3	0	3.8
Hermit Warbler	0	0	8	3	4.3

brids (Scheffé test, *P*s < 0.004). Townsend's Warbler clutches averaged 0.6 eggs larger than those of Hermit Warblers and 1.2 eggs larger than those of hybrids (Table 1). Clutch sizes of Hermit Warblers and hybrids were not significantly different.

DISCUSSION

These observations represent the first direct measurements of fitness components that might help elucidate why the Hermit Warbler × Townsend's Warbler hybrid zones are both narrow and apparently moving. Differences in timing of breeding or clutch size would imply corresponding competitive asymmetries between parentals and between parentals and hybrids. We found no difference in arrival dates, pairing dates, or clutch initiation dates, suggesting that the timing of spring arrival and the initiation of breeding has little effect on competitive interactions either between parentals or between parentals and hybrids.

Larger clutches may give Townsend's Warblers a reproductive advantage over Hermit Warblers and hybrids. Within and immediately adjacent to the hybrid zones in Washington and Oregon, Townsend's Warblers laid 0.6 more eggs than did Hermits and 1.2 more eggs than did hybrids. The clutches of hybrids were not significantly smaller than those of Hermits, but hybrids produced some of the smallest clutches, suggesting that they may be less fit than either of the parental species (Table 1). Clutch sizes for Townsend's Warblers vary from less than five eggs near the southern edge of their range in Idaho and British Columbia to nearly six eggs at the northern edge of their range in Alaska (Pearson 1997a, Matsuoka 1997). However, our larger Townsend's clutches cannot be attributed to latitudinal variation because the latitudinal distributions for our Hermit and Townsend's clutches were similar. Clutch size for Hermit Warblers does not vary with latitude, averaging 4.3 eggs throughout the range of the species (Pearson 1997b).

We found data on reproductive success for six other avian hybrid zones. In the Pied Flycatcher (*Ficedula hypoleuca*) × Collared Flycatcher (*F. albicollis*) zone, hybrid clutches were not significantly different from either parental species, but hybrids hatched significantly fewer eggs and fledged fewer young than did parental species (Alatalo et al. 1982, 1990). For Black-capped (*Poecile atricapillus*) and Carolina (*P. carolinensis*) chickadees, the number of young fledged per egg was significantly lower for hybrids than for either parental species, again suggesting selection against hybrids (Brewer 1963). In four other hybrid zones, hybrids did as well as or better than parental species. For Glaucous-winged Gulls (*Larus glaucescens*) and Western Gulls (*L. occidentalis*), hybrids produced larger clutches and hatched more eggs than the parental species, suggesting hybrid vigor (Hoffman et al. 1978). For Carrion (*Corvus c. corone*) and Hooded (*C. c. cornix*) crows, and for Northern Flickers (*Colaptes auratus* complex), clutch sizes did not differ between hybrids and the parental species (Moore and Koenig 1986, Saino and Villa 1992). For Darwin's finches (*Geospiza* spp.), neither clutch size nor measures of nesting success differed between hybrids and parentals (Grant and Grant 1992).

The pattern of adult males arriving on the breeding grounds before yearling males and before females has been documented for many other temperate migrants (see Rohwer et al. 1980, Myers 1981). The earliest males to arrive should have an advantage in acquiring territories and site dominance. Consequently, they usually pair earlier, and their mates usually lay larger clutches and fledge more young (Nolan 1978, Alatalo et al. 1984, Slagsvold 1986). We found no difference in spring arrival date by phenotype within the Washington Cascades hybrid zone, suggesting that the timing of spring arrival has little effect on the competitive interactions between these species and their hybrids. We know of only two other comparisons of arrival dates within avian hybrid zones. Alatalo et al. (1990) found that male Pied Flycatchers arrived earlier than male Collared Flycatchers. Nonetheless, Pied Flycatchers mated later (Alatalo et al. 1990), suggesting that male arrival date had little influence on pairing date within that hybrid zone. For the Blue-winged Warbler (*Vermivora pinus*) × Golden-winged Warbler (*V. chrysoptera*) hybrid zone, Blue-winged Warblers are always the first to arrive, but arrival dates overlap broadly (Murray and Gill 1976). Because Blue-winged Warblers are replacing Golden-winged Warblers (Gill 1980), the slightly earlier arrival of the Blue-wings may contribute to the competitive asymmetries moving this zone.

Of the fitness components we were able to assess in this paper, only clutch size seems to contribute to the competitive asymmetries that may be keeping the hybrid zones between Hermit Warblers and Townsend's Warblers narrow and that may be causing Townsend's Warblers to replace Hermit Warblers. Because the nests of these warblers are so difficult to find in the tall conifers of Washington and Oregon, our information on clutch sizes are very limited for hybrids (Table 1). Nonetheless, the very small clutches we recorded for hybrids points to the value of further efforts to locate more nests within these hybrid zones and to determine the phenotypes of the attending parents. Comparisons of pairing success, aggression, and return rates for adult males all show Townsend's Warblers to be competitively superior to Hermit Warblers and hybrids, but the competitive ranking of hybrids and Hermit Warblers was mixed (Pearson 1997a).

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