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AGE-SPECIFIC PLUMAGE CHARACTERS AND ANNUAL MOLT SCHEDULES OF HERMIT WARBLERS AND TOWNSEND'S WARBLERS[1]

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Abstract. We investigated age-specific plumage characters and the annual molt schedules of Hermit Warblers (*Dendroica occidentalis*) and Townsend's Warblers (*D. townsendi*), two closely related wood warblers that hybridize extensively where their breeding ranges overlap. First, we developed a method for aging spring males based on plumage characters. Previous authors have shown that adults of both species have black throats and immatures have yellow throats before their first prealternate molt. However, because the throats of most immatures become largely black in this molt, distinguishing between the two classes becomes problematic in spring and summer. We established aging criteria based on the appearance of the rectrices and wing coverts that allowed us to age correctly 99% of birds whose age could be determined independently by throat color. Furthermore, we could assign 96% of birds to age cohorts based on either throat color or these criteria.

Second, we documented the annual molt schedules for males of both age cohorts of both species. Birds complete the prealternate molt on the wintering grounds, and the prebasic molt is essentially completed before birds arrive on the wintering grounds, although we found several birds in light molt south of the breeding range. Finally, we discovered several immature males of both species growing yellow, female-like feathers in the spring, supporting summer explanations for delayed maturation of the breeding plumage in these two species. Immature males differed from adults during the breeding season in several other plumage characters in addition to throat color.

Key words: Aging characters; molt; molt schedules; delayed plumage maturation; Hermit Warbler; Townsend's Warbler; Dendroica occidentalis; Dendroica townsendi.

INTRODUCTION

Hermit Warblers (*Dendroica occidentalis*) and Townsend's Warblers (*D. townsendi*), two closely related species of wood warblers, hybridize extensively where their ranges meet in the Pacific Northwest (Morrison and Hardy 1983; S. Rohwer, C. S. Wood, and G. Eddy, unpubl. data). We investigated the molt cycles of these species to validate plumage characters that would enable us to distinguish spring and summer males in their second calender year from older adults. We sought to do so for two reasons. First, while most wood warblers are not recognized as having subadult breeding plumages (Rohwer et al. 1980, Lyon and Montgomerie 1986), many show substantial plumage variability in summer. When this variation is age related (i.e., younger males differ in appearance from older males) and biases hybrid indices, it constitutes a source of noise in the phenotypic analysis of interbreeding. Second, our ability to look for selection against hybrids in the form of decreased survivorship over the first winter (i.e., prior to the first breeding season) requires that we be able to assign birds to age classes. Thus, this study is a necessary prerequisite to our ultimate goal of studying hybridization of these two species.

Throughout the paper we use the molt terminology of Humphrey and Parkes (1959), and we draw upon the aging system used by Pyle et al. (1987). Hatching year males (males in their first calender year, or HY males) and males in their second calender year (SY males), prior to their first prealternate molt, have yellow throats in both species, while males in at least their third calender year (ASY males) have black throats in both species (Pyle et al. 1987, pers. observ.). Thus, these two groups of birds can be distinguished readily. However, because most SY males develop extensive black feathering in their throats in the spring (pers. observ.), once SY males are well along in their first prealternate molt, throat color cannot be used as an aging criterion. One of our goals here is to establish reliable aging criteria for spring males.

The aging criteria we developed are based on the appearance of the rectrices and secondary wing coverts. To demonstrate the reliability of

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these characters for aging spring males, we must show that these feathers are not molted during the prealternate molt. If they are molted, then some spring birds with the appearance of an ASY male may, in fact, be SY males. Categorizing such birds as ASY males would lead us to underestimate the survivorship of males over their first winter. Our second goal, then, is to document that neither species replaces in its prealternate molt the juvenile feathers used as age characters.

In addition to checking birds for molt of the specific feathers mentioned above, we describe the general molt of both species throughout the year. Few quantitative studies of molt in passerines have been performed, yet much useful information can be obtained from such studies (Rohwer and Butcher 1988, Rohwer and Manning 1990, Thompson 1991, Young 1991). We collected molt data with the following specific questions in mind: When do these two species molt, when do they migrate, and where do they molt relative to migration? That is, do they molt before they begin migration, do they interrupt their migration to molt, or do they wait until they've completed migration to molt? Are adults and immatures on the same molt schedule? Answers to these questions will prove useful when researchers consider how birds partition energy into the costly activities of migration and molt. In addition, if the two species are characterized by different molt patterns, then hybrids could suffer from deleterious recombinations of different molt-migration schedules or different numbers of molts (Rohwer and Manning 1990, Young 1991).

Finally, examining SY males in the spring allowed us to look for delayed plumage maturation in males. As noted above, spring SY males of both species have yellow, female-like throats prior to the prealternate molt, and most of these males grow at least some (and usually many) black throat feathers in the prealternate molt. However, some SY males maintain their yellow throats, at least in part (pers. observ.). Hypotheses to explain why young males sport female-like plumage in their first potential breeding season fall into two categories (Rohwer and Butcher 1988). Winter Hypotheses propose that this female-like plumage is really an adaptation to conditions faced in the winter, and that energetic constraints prevent males from molting all of these female-like feathers and growing adult male-like feathers in the prealternate molt. Summer Hypotheses propose that the female-like plumage is an adaptation to conditions faced in the breeding season. Summer Hypotheses predict that we should find SY males growing at least some female-like plumage during the prealternate molt. We examined which of these sets of hypotheses is likely to apply to Hermit and Townsend's Warblers by noting the color of the incoming throat feathers of spring SY males. We also examined whether SY males that have completed their first prealternate molt are female-like in other plumage characters in addition to throat color.

METHODS

DISTINGUISHING IMMATURES AND ADULTS

We examined 211 male Hermit Warbler specimens and 262 male Townsend's Warbler specimens from the collections of the museums listed in the Acknowledgments. Because we wished to compare the first prebasic molt with definitive prebasic molt, and the first prealternate molt with definitive prealternate molt, and because we ultimately want to look for selection against hybrids over their first winter, we divided birds into two age cohorts: immatures and adults. Immatures are birds in their first calender year that have begun their first prebasic molt, birds in their first and second calender years in first basic plumage, birds in their second calender year undergoing first prealternate molt, and birds in their second calender year that have recently come into first alternate plumage (all prior to the end of the first potential breeding season [from 1 May–15 June]). Adults are birds in their second calender year in alternate plumage but about to undergo prebasic molt (all after the breeding season), birds in their second calender year undergoing prebasic molt, birds in their second calender year in basic plumage, and birds in their third calender year and beyond.

We assigned birds to these two age cohorts in one of three ways. As noted earlier, males have yellow throats prior to or in the early stages of their first prealternate molt—all 35 birds that we discovered with skulls that were not completely ossified (i.e., were known to be in their hatching year) had yellow throats—while older males had black throats. Thus, the following types of birds were considered adults: males collected from 16 June–31 January with black throats (prealternate molt begins in February), and males collected from 16 June–31 July with partly yellow throats and worn plumage. The following types of birds were considered immatures: males collected from 16 June–31 July with yellow throats and fresh plumage, and all males with yellow throats that were collected from 1 August–30 April.

Males collected from 1 February–30 April with black throats were problematic because some may be immatures that had molted their yellow throat feathers and grown black ones. We aged these birds by the following means. Birds of both species known to be in definitive plumage (i.e., adults) tend to have larger white spots on their fourth rectrices than do birds in first basic or first alternate plumage (i.e., immatures; Pyle et al. 1987). In addition, immature birds tend to have black streaks along the length of the shafts of the secondary wing coverts, while adults do not (Pyle et al. 1987).

To see how reliably we could age males using these two traits, we measured the white spot size as the greatest width multiplied by the greatest length (in mm^2), and noted the presence or absence of shaft streaks of 325 known-age birds (i.e., birds that were aged on the basis of throat color—this sample includes males that were not examined for molt). We calculated how well each trait could predict a bird's age, and then how accurately the combination of these two traits could distinguish immatures from adults. We then applied these aging criteria to spring, black-throated males.

Finally, a few birds with black throats could not be aged on the basis of the tail spot/shaft streak criteria because the two traits were contradictory. We aged these birds with a third criterion, the shape of the rectrices. Adult Hermit and Townsend's Warblers have truncated and less-worn rectrices, while immatures taken at the same time have rectrices that are more rounded and show more wear because they are feathers of the juvenile plumage (Pyle et al. 1987). We noted the shape of the rectrices for 15 known-age birds (12 adults and three immatures) to examine how accurately we could distinguish the two age cohorts on the basis of this criterion. We then applied this aging criterion to the birds that could not be aged with the first two criteria.

MOLT AND MIGRATION

We examined each specimen for molt in six body areas: face, crown, throat, back, breast and flanks. Using forceps, we lifted feathers at 4–6 random points in each body area, looking for pin feathers and feathers sheathed at their bases. When we found pin or sheathed feathers, we noted whether they accounted for $<10\%$ of the feathers in the area (corresponding to 1–6 feathers), 10–20% of the feathers in the area, or $>20\%$ of the feathers in the area. For flight feathers (i.e., remiges and rectrices) we noted which feathers had been molted, and we estimated the length of any incoming feathers relative to their eventual full length (from 0–100%, in increments of 10%). We considered missing or partially grown flight feathers to have been molted if the corresponding feathers on the opposite side of the body were in a similar stage of molt. Otherwise we considered the feather to have been lost accidentally.

We divided each month in half between the 15th and 16th. We aimed to acquire 10 adults of each species for each time period from the first half of February through the second half of April, and from the second half of June through the first half of August, and five from each remaining time period (excluding the breeding season from 1 May–15 June). For immatures, we hoped to acquire 10 of each species for each time period from the first half of February through the second half of April, and five from each remaining time period (excluding the breeding season). We were unable to obtain these numbers for several time periods (especially in January, June and July), although most time periods are represented by at least four specimens (see Figs. 2–5).

We noted where each specimen was collected, and divided localities into two groups: those in the breeding range and those south of the breeding range. The breeding range of Townsend's Warblers encompasses Alaska, British Columbia, Idaho, Montana, and parts of montane Washington and montane Oregon (American Ornithologists' Union 1983). The breeding range of Hermit Warblers includes parts of western Washington, Oregon, northern and central California (American Ornithologists' Union 1983).

DELAYED PLUMAGE MATURATION

To determine whether Winter or Summer Hypotheses for delayed plumage maturation are likely to apply to Hermit Warblers and Townsend's Warblers, we examined birds from 1 February–30 April that were in molt and that had yellow in their throats to determine the color of if their incoming or new throat feathers.

We also examined the extent to which im-

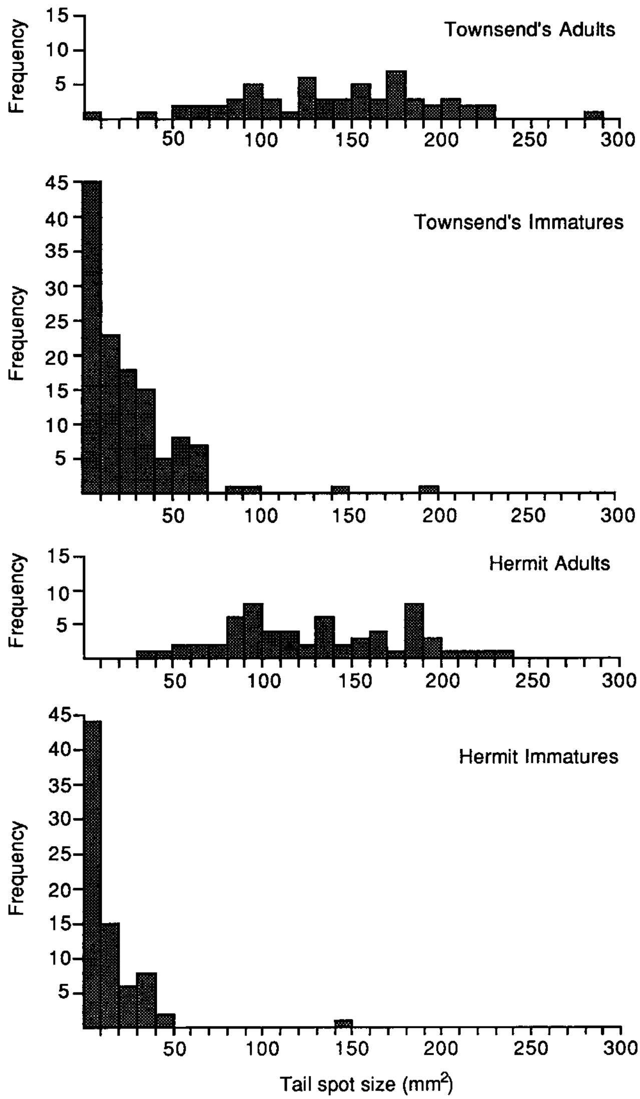

FIGURE 1. Frequency distributions of tail spot size (in mm^2) for adult and immature Townsend's Warblers (top graphs), and for adult and immature Hermit Warblers (bottom graphs).

mature males differ from adult males in other plumage characters during the breeding season. We examined 84 Townsend's Warblers and 72 Hermit Warblers, all of which were collected in the last week of May or in June after they had completed their prealternate molt. We scored each specimen for characters that were chosen in a different study for purposes of creating a hybrid index (S. Rohwer, C. S. Wood, and G. Eddy, unpubl. data). Coincidentally, the ranges of these characters seen among hybrids (ranging from pure Townsend's Warbler to pure Hermit Warbler) incorporate the ranges seen in the two age classes. We scored Townsend's Warblers for 8 characters as follows: streaking on the mid-flanks (0 = none–7 = extensive), streaking on the lower-flanks (0 = none–8 = extensive), extent of yellow down the breast (in mm, 0–35), intensity of yellow on the breast (0 = no yellow–7 = intense), size of the bib corner (the patch of feathers between the bib and the back; 0 = none–10 = largest), amount of yellow in the crown (0 = all yellow–8 = none), streaking on the back (0 = extensive–10 = none) and the color of the back (0 = gray–8 = green).

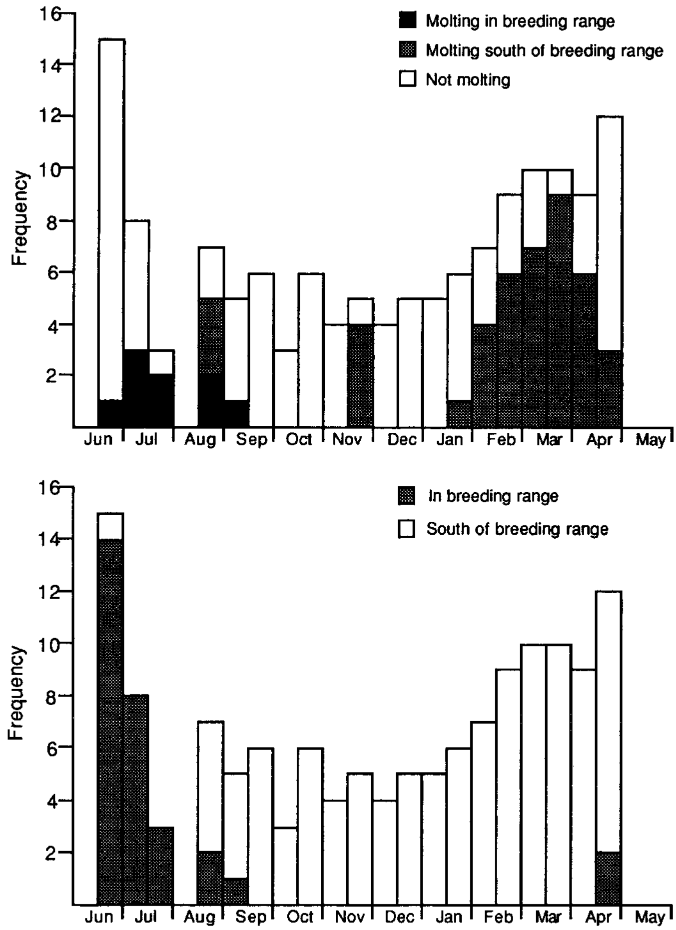

FIGURE 2. Top graph: Frequency distribution of adult Townsend's Warblers molting in the breeding range, molting south of the breeding range, or not molting per time period. Bottom graph: Frequency distribution of adult Townsend's Warblers collected in the breeding range or south of the breeding range per time period.

For Hermit Warblers, we scored each specimen for the latter four characters (the first four do not apply to this species).

We aged all of these birds by the three criteria we developed for the molt study. For each species, we compared the two age cohorts using the normal approximation of the Mann-Whitney *U*-Test.

Finally, we scored 16 female Townsend's Warblers and five female Hermit Warblers for these same characters to show that, when immature males differ from adult males in appearance, immatures always look more like females.

RESULTS

DISTINGUISHING IMMATURES AND ADULTS

First, in Townsend's Warblers that could be aged on the basis of throat color, we noted that 121 of 125 (97%) immatures had shaft streaks, while only 10 of 60 (17%) adults did ($G = 133.95$, $df = 1$, $P < 0.001$). Furthermore, of the 10 adults with shaft streaks, seven had streaks that were either faint or confined to just one feather, typically the proximal covert. Likewise, 73 of 76 (96%) immature Hermit Warblers had shaft streaks while none of the 64 adults did ($G = 168.55$, $df = 1$, $P < 0.001$).

Adult Townsend's Warblers had significantly larger tail spots than did immature Townsend's Warblers (Mann-Whitney *U*-Test, $Z = 10.15$, $P < 0.001$) (Fig. 1). Likewise, in Hermit Warblers, adults had significantly larger tail spots than did immatures (Mann-Whitney *U*-Test, $Z = 9.99$, $P < 0.001$) (Fig. 1). There was no significant difference in tail spot size between adult Hermit and Townsend's Warblers (134.9 mm^2 vs. 139.9

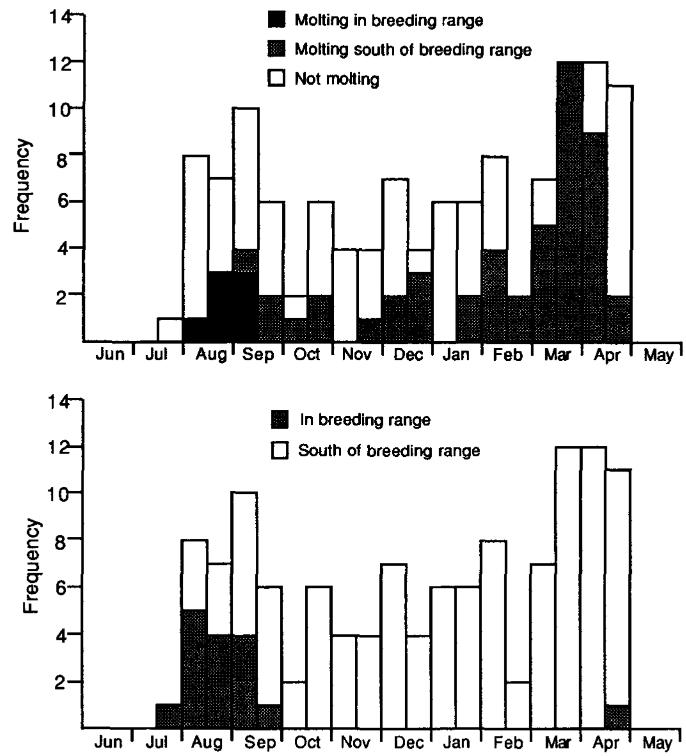

FIGURE 3. Top graph: Frequency distribution of immature Townsend's Warblers molting in the breeding range, molting south of the breeding range, or not molting per time period. Bottom graph: Frequency distribution of immature Townsend's Warblers collected in the breeding range or south of the breeding range per time period.

mm^2; Mann-Whitney U-Test, $Z = 0.92$, $P > 0.05$). Immature Hermit Warblers had significantly smaller tail spots than did immature Townsend's Warblers (13.2 mm^2 vs. 24.8 mm^2; Mann-Whitney U-Test, $Z = 3.77$, $P < 0.001$). Despite the difference in tail spot size between immatures of the two species, most adults (117 of 124, or 94%) had tail spots larger than 55 mm^2, while most immatures (184 of 201, or 92%) had tail spots less than or equal to 55 mm^2. Therefore, in the subsequent analyses we combined the data for Hermit and Townsend's Warblers so that we could establish aging criteria that will prove useful for aging hybrids that cannot be assigned to one species or the other.

We examined how accurately we could age fall and early winter birds by combining these two traits. This is the category of birds that can be aged by throat color. We labeled birds with shaft streaks and with tail spots ≤ 55.0 mm^2 to be immatures and found that of the 180 birds in this category, 179 of them were known to be immatures based on throat color or skull pneumatization. The remaining bird with shaft streaks and a relatively small tail spot was known to be an adult because of its throat color. We labeled birds lacking shaft streaks and with tail spots >55.0 mm^2 to be adults and found that of the 110 birds in this category, 108 of them were known to be adults by the possession of black throats. The remaining two birds were known to be immatures because they had partly yellow throats. Thus, we correctly aged 287 of 290 (or 99%) of the birds with this method.

However, 35 of the 325 known-age birds could not be aged with this method. They either had large tail spots as well as shaft streaks, or they had small tail spots but lacked shaft streaks. We used our third method for aging these birds, based on the shape of the rectrices. To see how reliable this method is, we aged 15 known-age birds, and all were aged correctly.

We then applied these three aging criteria to the 473 birds examined for molt (Table 1). We were unable to age four Townsend's and two Hermit Warblers with any method.

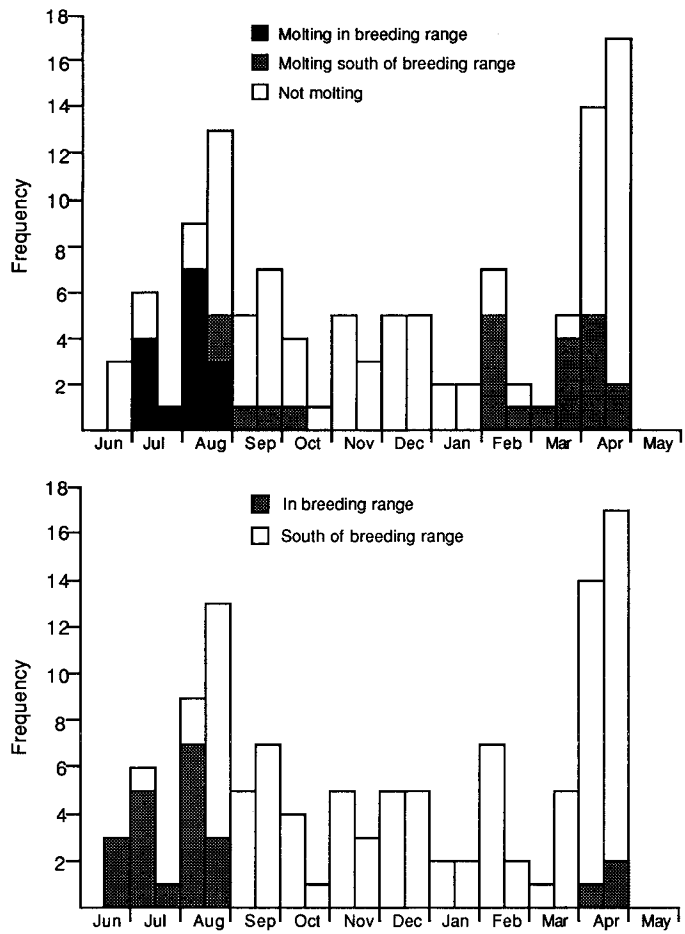

FIGURE 4. Top graph: Frequency distribution of adult Hermit Warblers molting in the breeding range, molting south of the breeding range, or not molting per time period. Bottom graph: Frequency distribution of adult Hermit Warblers collected in the breeding range or south of the breeding range per time period.

MOLT AND MIGRATION

We did not discover any specimen molting its secondary wing coverts or its rectrices during the prealternate molt. The 20 birds molting their wing or tail feathers were all doing so from early July through late August, following breeding. Thus, the aging criteria we developed based on the appearance of these feathers allowed us to age spring birds accurately.

TABLE 1. Number of Townsend's and Hermit Warblers scored for molt that were aged by each aging criterion.

Aging criterion	Townsend's Warblers	Hermit Warblers
Throat color/feather wear	161	137
Tail spot size/shaft streaks	90	66
Shape of rectrices	11	8

The four species-and-age groups exhibited similar molt schedules (Figs. 2–5). All birds were in body molt, except for two adult Townsend's Warblers and one adult Hermit Warbler that were only molting their primaries. It is clear that prealternate molt essentially is completed by the time birds reach the breeding range (Figs. 2–5).

The major portion of the prebasic molt probably is completed before birds begin migrating southward, although we did discover several specimens in prebasic molt south of the breeding range. However, several observations suggest that these latter birds are in the final stages of molt. First, 19 of the 20 birds in wing or tail molt were

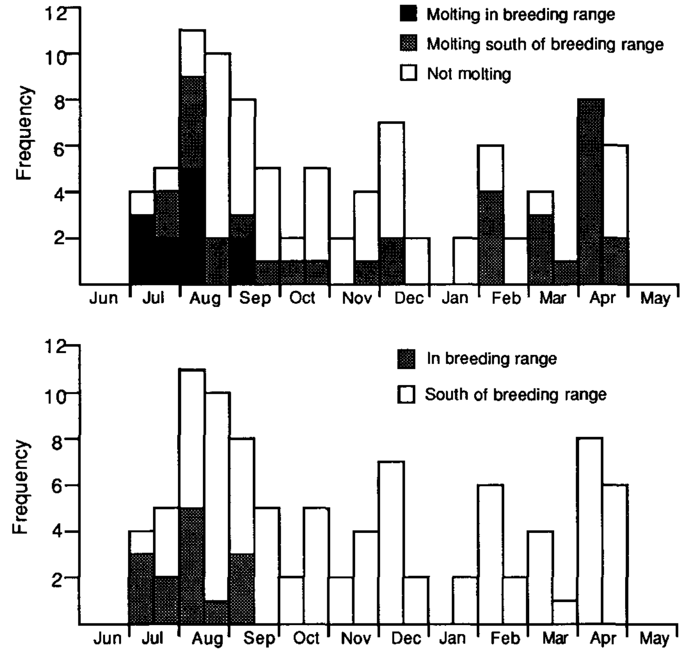

FIGURE 5. Top graph: Frequency distribution of immature Hermit Warblers molting in the breeding range, molting south of the breeding range, or not molting per time period. Bottom graph: Frequency distribution of immature Hermit Warblers collected in the breeding range or south of the breeding range per time period.

collected in the breeding range. The remaining bird (an adult Townsend's Warbler collected on 30 August in New Mexico) had essentially completed the molt, but still had some sheath present at the base of the outermost primary on each wing.

A second piece of evidence that the major portion of the prebasic molt is completed by the time birds reach the wintering grounds comes from examining the extent of the prebasic molt in birds in the breeding range vs. south of the breeding range from 1 July through 30 October. We combined the four species-and-age groups for this analysis because the sample sizes for individual groups were small. The proportion of birds in moderate-to-heavy molt was significantly higher for birds in the breeding range (21 of 43, or 49%) than for birds south of the breeding range (3 of 23, or 12%) ($G = 9.12$, df $= 1$, $P < 0.005$). By moderate-to-heavy molt, we mean birds molting >20% of the feathers in at least two body areas or 10–20% of the feathers in at least three body areas.

In addition, no immatures that were collected south of the breeding grounds had any juvenal plumage (the plumage immediately preceding the first basic plumage). Thus, immatures must complete most of the first prebasic molt before leaving the breeding grounds. Finally, we examined the 15 adult Townsend's and 24 adult Hermit Warblers collected south of the breeding range in August and September. All were in fresh plumage. Thus, adults also complete most of the prebasic molt before they depart the breeding range.

Several birds were discovered in molt in November and December. The four adult Townsend's Warblers in molt in the end of November were all in light molt in just one body area (either the face or the throat). The six immature Townsend's Warblers molting in late November were in light molt in one or two body areas (usually the face and throat). The 3 immature Hermit Warblers in molt in late November and early December were in light molt on the face. Thus, all birds molting during this time of the year are in light molt and presumably just beginning the prealternate molt because the prebasic molt seems completed by this time.

DELAYED PLUMAGE MATURATION

Immature Townsend's Warblers had a significantly greater percentage of yellow feathers in their throats than did adult Townsend's Warblers (Table 2). While the majority of immatures had

TABLE 2. Plumage scores (mean and minimum–maximum) for adult males, immature males (from 1 February–30 April) and females by species. Differences between adult males and immature males for each species are analyzed with the normal approximation of the Mann-Whitney *U*-Test, corrected for ties.

	Townsend's			
Plumage character	Adults (n = 35)	Immatures (n = 49)	Z	Females (n = 16)
Percentage yellow in throat	0.37 (0–5)	16.39 (0–80)	4.71**	60.47 (2–100) (n = 15)
Streaking on mid-flanks	5.51 (0–7)	4.86 (4–6)	4.33**	2.56 (2–4)
Streaking on lower-flanks	7.29 (6–8)	6.27 (5–7)	5.62**	4.69 (3–6)
Extent of yellow down breast	26.71 (20–36)	26.51 (18–34)	0.36	19.00 (14–23)
Intensity of yellow on breast	6.69 (6–7)	6.04 (5–7)	5.75**	5.00 (4–6)
Size of bib corner	7.80 (6–10)	6.25 (3–8)	6.10**	3.80 (2–7) (n = 15)
Amount of yellow in crown	8.00 (8)	8.00 (8)	0.00	8.00 (8)
Streaking on back	5.49 (3–8)	7.06 (5–9)	5.15**	9.81 (9–10)
Color of back	7.20 (7–8)	7.00 (7)	3.25*	6.19 (5–7)

* $P < 0.005$.
** $P < 0.001$.
NA, Not applicable.

black throats, many had throats containing greater than 5% yellow feathers, and a few had throats that were over half yellow (Fig. 6). In Hermit Warblers, immatures did not have throats that contained a significantly greater percentage of yellow feathers than did adults (Table 2).

Of the 32 immature Townsend's Warblers from the molt study that had yellow throats and that were in prealternate molt, 9 were growing yellow feathers in the throat. We also discovered immature Hermit Warblers growing yellow feathers in the spring. Four of the 12 yellow-throated birds in prealternate molt were doing so.

Immature Townsend's Warblers differed from adults in several other plumage characters in addition to throat color (Table 2). Immatures had less streaking on the mid-flanks, lower-flanks, and back than did adults. They also had smaller bib corners, duller breasts, and grayer backs. For all of these characters, immatures sported female-like plumage to varying degrees (Table 2). Immature Hermit Warblers differed from adults in only one character: immatures had less streaking on the backs than did adults (Table 2). We did not examine whether the female-like plumage was retained from the first basic plumage, or was newly acquired during the prealternate molt.

DISCUSSION

The aging criteria we developed based on tail-spot size and the presence or absence of shaft streaks on the secondary wing coverts were very

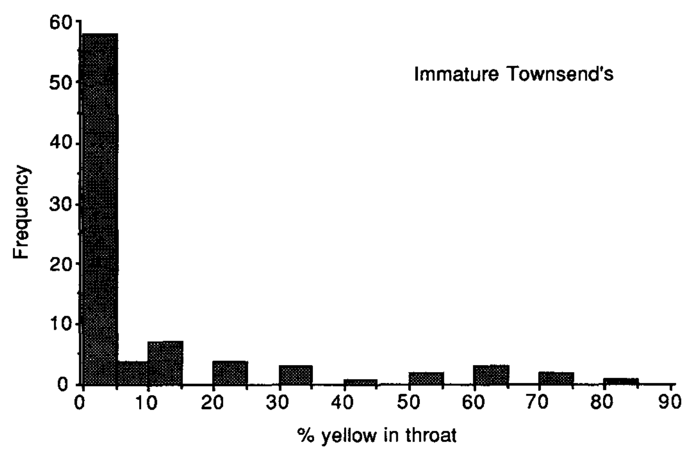

FIGURE 6. Frequency distribution of percentage of yellow in throat for immature Townsend's Warblers (1 February–30 April).

TABLE 2. Extended.

Hermit			
Adults (n = 51)	Immatures (n = 21)	Z	Females (n = 5)
0.343 (0–5)	0.33 (0–5)	0.21	68.00 (50–90)
NA			
NA			
NA			
NA			
1.28 (0–3)	0.86 (0–2)	1.82	1.60 (0–2)
2.26 (0–5)	2.48 (0–5)	0.53	6.20 (5–7)
3.18 (0–7)	5.05 (2–8)	3.61**	9.40 (9–10)
1.20 (0–4)	1.14 (0–2)	0.20	0.40 (0–1)

accurate; we correctly aged 99% of birds whose age we could determine independently on the basis of throat color. In addition, the tail spot/shaft streak criteria and the throat color criterion allowed us to assign the vast majority of birds (96%) to one of the two age cohorts. We used a third criterion, based on the shape of the rectrices, to age the remaining 4% of the birds. Only 1% (6 of 479) of birds could not be aged with any of these three criteria. Thus, this method of aging birds will prove useful in investigations of selection against Hermit-Townsend's Warbler hybrids over their first winter. Estimates of the relative frequency of the two age classes should be accurate because the percentage of birds that we will be unable to age is so small.

We found no major differences in the molt schedules between the two species. Birds essentially complete the prealternate molt on the wintering grounds before they begin the migration to the breeding grounds. Both species also complete the majority of the prebasic molt before migrating southward, although some birds appear to complete the final stages of molt on the wintering grounds. Because the two species have similar molt schedules, hybrids will not suffer from recombinations of conflicting molt schedules. The relatively large hybrid zone of these two species may be a reflection of this.

In contrast to the situation in warblers, differing molt schedules pose potential sources of selection against hybrids in several other hybridizing species pairs. For example, Bullock's Orioles (*Icterus galbula bullockii*) either complete the fall migration before beginning the prebasic molt or make an extended stopover in the American Southwest to molt before continuing on to their wintering areas (Rohwer and Manning 1990), while Baltimore Orioles (*I. g. galbula*) complete the majority of the prebasic molt on the breeding grounds (Sealy 1979, Rohwer and Manning 1990). Bullock's Orioles also almost entirely lack a prealternate molt, while Baltimore Orioles undergo a prealternate molt to varying degrees, depending on age and sex (Rohwer and Manning 1990). These major differences in the molt schedules of these two races may explain why the hybrid zone between these taxa is relatively narrow and why there may have been a recent drop in the frequency of hybrids (Corbin and Sibley 1977). Likewise, Indigo Buntings (*Passerina cyanea*) complete the first and later prebasic molts before migrating southward (Rohwer 1986), while both adult and recently fledged Lazuli Buntings (*P. amoena*) migrate to the American Southwest and Baja California to undergo this molt (Young 1991). Here, too, this difference may help explain why these two species hybridize only sporadically (Sibley and Short 1959). Finally, in Painted Buntings (*L. ciris*), eastern birds undergo their prebasic molts on the breeding grounds, while in western birds this molt takes place either on a migratory staging ground or on the wintering grounds (Thompson 1991).

A contrast emerging between east-west species pairs of North American passerines is for birds breeding in the west in dry, riparian habitats to begin migrating before initiating the prebasic molt and for birds breeding in the east to complete the majority of the prebasic molt on the breeding grounds. The examples noted above fit this pattern: Bullock's Orioles and Lazuli Buntings breed in the west, while Baltimore Orioles and Indigo Buntings breed in the east. Because molt is an energetically demanding activity (King 1981, Walsberg 1983), if the breeding grounds are significantly depleted of resources, birds may have to migrate at least part way to find a habitat that can provide their increased nutrient requirements. Birds breeding in dry habitats are more likely to be faced with this situation as illustrated by Bullock's Orioles and Lazuli Buntings and suggested by Foster (1967) for the Channel Island race of the Orange-crowned Warbler (*Vermivora celata*). Hermit and Townsend's Warblers, despite breeding in the west, also fit this pattern. Townsend's Warblers breed exclusively in moist, montane habitats and Hermit Warblers that breed in the lowlands are found in humid areas where nutrients still may be abundant following breeding.

Finally, we detected several yellow-throated, immature males of both species growing yellow throat feathers in the prealternate molt. In addition, SY males can be distinguished from ASY males during the breeding season on the basis of other plumage characters in both species, but especially in Townsend's Warblers, where year-old males often have yellow feathering in their throats. Thus, it is likely that the answer to why immature males look like females during their first potential breeding season will be found among the Summer Hypotheses for delayed plumage maturation. Two explanations that may apply to warblers are first, that immature males mimic females to avoid aggression by adult males, thereby deceptively gaining access to territories and mates (the female-mimicry hypothesis; Rohwer et al. 1980) and, second, that immature males signal their competitive inferiority, thereby reducing the amount of energy they spend in fights and reducing their risk of injury (the status-signalling hypothesis; Rohwer 1975, Rohwer and Ewald 1981, Lyon and Montgomerie 1986).

The acquisition by immature males of female-like plumage in the spring has been documented for only one other species, Painted Buntings (Thompson 1991). Immature males grow male-like plumage in the prealternate molt in the remaining species for which this type of data has been collected: Indigo Buntings (Rohwer 1986); Lazuli Buntings (Young 1991); and Baltimore Orioles (Rohwer and Manning 1990). Painted Buntings differ from Hermit and Townsend's Warblers in that the prealternate molt is extensive in the warblers, while it is limited in the buntings (although at least some individuals may have extensive molt (Thompson, pers. comm.). Thus, the reasons for growing female-like feathers may be different in the two cases. Because buntings have a limited molt, they can only change their appearance by a limited amount. If growing only a few male-like feathers does not affect, for example, an individual's status signal, then growing female-like feathers may be a best-of-a-bad-situation strategy if there is any cost to growing these male-like feathers. Because warblers can change their appearance substantially during the prealternate molt, and yet all individuals do not do so as much as possible, the acquisition of female-like feathers may be, in fact, superior to growing exclusively adult male-like feathers.

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