

MOLT-MIGRATION IN WESTERN TANAGERS (*PIRANGA LUDOVICIANA*): AGE EFFECTS, AERODYNAMICS, AND CONSERVATION IMPLICATIONS

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ABSTRACT.—We describe timing and location of the prebasic molt in Western Tanagers (*Piranga ludoviciana*), focusing on age class differences in premolt movements. Most adults migrate south to the American Southwest where they stop to molt before moving on to their wintering grounds. Molting adults are found in southern mountain regions (Sierra Madres and southern Rockies) and in the Mexican monsoon region, where late summer rains cause a substantial increase in productivity. In contrast, juvenile Western Tanagers move to nearby montane habitats to molt before migrating, a previously undocumented strategy in western passerines that show molt-related movements. By molting in nearby montane habitats, juveniles avoid the aerodynamic cost of migrating in their “fluffy”, aerodynamically inefficient juvenal plumage. Western Tanagers are the fifth species known to use the Mexican monsoon region during the prebasic molt, further affirming the importance of that area to the conservation of Neotropical migrants that breed in western North America. Received 25 July 2001, accepted 8 July 2002.

RESUMEN.—Describimos el tiempo y localización de la muda prebásica en individuos de la especie *Piranga ludoviciana*, enfocándonos en las diferencias entre clases de edad de los movimientos anteriores a la muda. La mayoría de los adultos emigran al sur hacia el Sudoeste de Norte América donde se detienen para mudar antes de seguir a las tierras de invernada. Adultos que se encuentran mudando se han encontrado en las regiones montañosas del sur (Sierra Madre y Rocallosas del Sur) y en la región del monzón mexicano donde las lluvias de fines del verano causan un aumento sustancial en la productividad. Por el contrario, los juveniles de *Piranga ludoviciana* se desplazan a los hábitats montanos cercanos para mudar antes de emigrar, una estrategia previamente no documentada para aves paserinas occidentales que presentan movimientos relacionados a las mudas. Al mudar en los hábitats montanos cercanos, los juveniles evitan el costo aerodinámico de emigrar con su plumaje juvenil, “cubierto de pelusa” y aerodinámicamente ineficaz. *Piranga ludoviciana* es la quinta especie conocida en usar la región del monzón mexicano durante la muda prebásica, reafirmando la importancia de esta región para la conservación de las aves migratorias del Neotrópico que se reproducen en América del Norte occidental.

SCHEDULING OF THE annual molt is likely to be under intense selection pressure because it influences successful migration, reproduction, and social signaling (Berthold and Querner 1982, Butcher and Rohwer 1989, Rohwer and Manning 1990). Thus, evolution of molt schedules is critical to studies of avian life-history evolution and to avian conservation. Despite their general importance, species descriptions of molt for most North American birds are insufficient to support the comparative studies

needed for insight into the adaptive significance of molt scheduling.

In most migratory passerines of Europe and North America, adults replace body and flight feathers in the late summer, immediately following and rarely overlapping the energetically demanding breeding season (Jenni and Winkler 1994). Molt is usually temporally separated from breeding and migrating, and occurs when food is abundant at northern latitudes. In contrast, adults of the following six well-studied species of western North America depart the breeding grounds prior to the prebasic molt: Gray (*Empidonax wrightii*) and Dusky (*E. oberholseri*; Johnson 1963) flycatchers;

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Bullock's Oriole (*Icterus bullockii*; Rohwer and Manning 1990); Lazuli Bunting (*Passerina amoena*; Young 1991); western populations of Painted Bunting (*Passerina ciris*; Thompson 1991), and Western Warbling-Vireo (*Vireo gilvus swainsonii*; Voelker and Rohwer 1998). This unusual scheduling of molt and migration likely reflects multiple independent adaptations to breeding in the arid west, where most annual precipitation accumulates in winter and early spring (Rohwer and Manning 1990).

Most western species that undertake all or part of their fall migration before molting show age-class differences, with adults molting on their wintering grounds or at a stopover site, and juveniles molting in the north before migration. That age-class difference could be a consequence of the loose texture of the juvenal body plumage of some species, which may create sufficient drag to make molting before migrating the best option for juveniles (Rohwer and Manning 1990; M. Speidel and S. Rohwer unpubl. data). Thus, it is important to recognize that the costs and benefits of molting before migrating may differ for adults and juveniles.

To further investigate scheduling of molt and migration in western passerines, we studied molt scheduling in Western Tanagers (*Piranga ludoviciana*), an insectivorous long-distance migrant. This study was initiated to determine whether adult Western Tanagers use the American Southwest as a stopover site for molting, or whether they molt on their wintering grounds. Age-class differences were also emphasized in the scheduling and location of the fall molt, with the aim of understanding how juveniles may respond to the late summer aridity of the west without moving southward to molt. We examined the possibility that juvenile Western Tanagers hatched in the intermountain west move to more productive high elevation forests before molting. Because Western Tanagers feed primarily in coniferous forests, up-slope movement would take juveniles to habitats that are relatively productive in late summer without forcing them to leave coniferous forests.

Over 600 Western Tanager specimens were scored for body and flight-feather molt. To test for age-class differences and to illustrate post-breeding movements and molt locations, the collecting localities of juveniles and adults

were mapped. Sequence and timing of the pre-basic molt is also described for this species.

METHODS

Species range and habits.—Western Tanagers breed throughout western North America in open mid-elevation coniferous and mixed coniferous–deciduous forests. They nest as far north as southern Yukon Territory and as far south as western Texas (Hudon 1999). Their diet consists mainly of insects, with a smaller dependence on fruit (Hudon 1999). Nest building begins in May or early June, and egg-laying peaks in June throughout much of the range (Hudon 1999). Western Tanagers winter primarily from central Mexico south to Costa Rica, feeding mainly on insects and fruit (Stiles and Skutch 1989, Hudon 1999).

Study specimens.—Specimens were initially examined from the University of Washington Burke Museum and from seven other museums in the United States with large collections (see Acknowledgments). Loans were requested in 1998 for Western Tanagers collected from 1 July–30 April, excluding May and June specimens to minimize size of loans. Autumn adults and specimens collected south of the United States before January are scarce in museum collections. To obtain reasonable samples of molting adults, a second request was made to additional museums for birds collected between 1 August and 30 November (see Acknowledgments).

Geographical and temporal analyses.—To test the prediction that Western Tanagers move to more productive habitat to molt, the geographic distribution of specimens collected during the breeding season was compared to the geographic distribution of molting specimens. If Western Tanagers migrate southward before molting, then molting birds should be relatively uncommon in northern parts of the breeding range. To describe latitudinal patterns of molt, specimens were grouped into 5° latitudinal regions beginning with 50–46°N and continuing south to 20–16°N. That method includes all but one specimen in the samples (a nonmolting adult male collected at 59°N), and it summarizes the percentage of molting specimens collected in equal latitudinal increments.

If Western Tanagers leave the arid lowland west to molt, then molting birds should be rare in that region compared to the frequency of breeding birds. Very few specimens examined had elevation data, making direct comparison of breeding and molting elevations impossible. Instead, to delineate the intermountain west, an outline of the arid region was drawn bounded by the Cascade and Sierra Nevada mountains on the west, and the Rocky Mountains on the east, and excluding the monsoon region in southwestern America. That boundary provided a climatological and elevational standard for comparing the

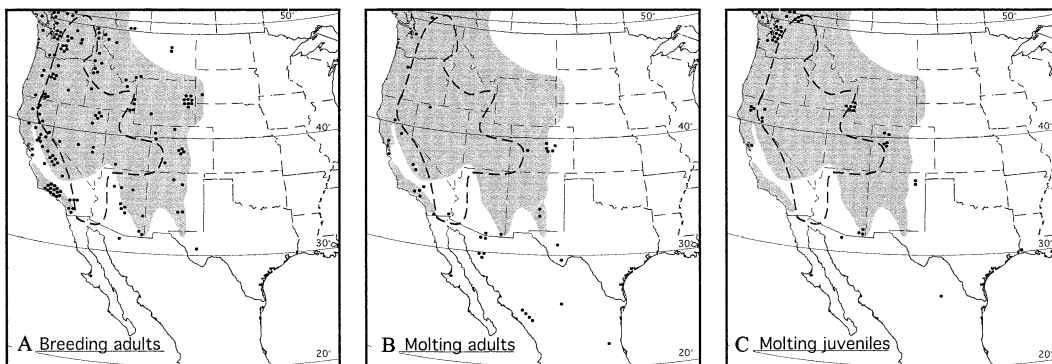


FIG. 1. Geography of molt in Western Tanagers relative to the Great Basin (heavy dashed line) and the breeding range (shaded area; Hudon 1999). (A) Adults used to estimate frequency of breeding Western Tanagers in the Great Basin (collected 1–15 July). (B) Adults molting flight feathers (collected 16 July–31 October). (C) Juveniles molting body feathers (collected 16 July–31 October). Map of the Great Basin drawn from PRISM 1961–1990 mean annual precipitation image prepared by the Spatial Climate Analysis Service, Oregon State University.

geographic distribution of Western Tanagers before and during the prebasic molt. The Great Basin constitutes most of the lower elevation region of the intermountain west, and Western Tanagers commonly breed in the coniferous forests of that region. Thus we use the term “Great Basin” throughout this article to describe the arid region delineated on our maps of western North America. To investigate possible movement of Western Tanagers out of lower elevation habitats prior to molting, frequency of specimens breeding in the Great Basin was compared to frequency of specimens molting there.

Unfortunately, loan requests were designed to target molting specimens and not to estimate the breeding distribution of Western Tanagers. Nonetheless, the distribution of breeding Western Tanagers could be estimated using specimens collected 1–15 July, during the final stages of incubation and early nestling phase (Hudon 1999). Those birds seemed to be breeders because (1) no hatching-year birds collected before 22 July were received, and (2) 89.2% of 158 adults collected 1–15 July were taken in the breeding range (Hudon 1999; Fig. 1), and none were molting. Thus, we are confident that nearly all of the 158 adults we examined from 1–15 July were taken before the onset of molt-related movements.

Most localities were precisely described, but ~2% were resolved only to county (United States) or state (Mexico). Those specimens were included by plotting them in the geographic center of their county or state. To describe timing of the molt, specimens were grouped into semimonthly periods from 1 July–31 October (e.g. 1–15 July, 16–31 July, etc.). The raw number of molting specimens is strongly biased by differences in collecting effort between northern and southern latitudes and among seasons. Thus, the

percentage of molting birds was used to compare geographic and temporal effects.

Scoring molt.—M. G. Donahue performed all molt scoring under a 2× magnifying lamp with a 60 watt incandescent bulb. Body molt was scored by lifting feathers at 5–7 points in each region using a dissecting probe, and scoring the percentage of developing feathers as: 0 = no feathers in development, 10 = 1–20% of feathers in development, 30 = 21–40% in development, and so on, so that the highest possible molt score for a given region (indicating the most intense molt) was 90 (Rohwer 1986). Molt scores of 10 were divided into four smaller categories of feather development: 10a = 1–2%, 10b = 3–4%, 10c = 5–6%, and 10+ = 6–20% of feathers in development (Rohwer 1986).

Small, asymmetrical patches of growing feathers of the same age were considered adventitious replacement and not scored as molt, and specimens with molt scores of 10a–c in only one region obtained a body molt score of 0. Thus we probably excluded a small number of specimens that were at the very beginning or very end of molt, but more error would be introduced if we considered all birds with very small amounts of growing body feathers to be “molting” specimens. Specimens with scores of 10a–c in two or more regions were treated as molting, and given a score of 10 for each area. That method slightly overestimates intensity of molt for specimens that are just beginning or in the final stages of molt, but it has the advantage of including birds at the end or beginning of body molt.

Individual flight feathers (primaries, secondaries, and rectrices) were recorded as new (growth complete, and without frayed edges), old (faded, edges worn), or molting. Growing feathers were scored on

a scale of 0.1 to 0.9, at 0.1 increments, representing the approximate percentage of the feather that was grown. Thus, 0.1 represented a feather ~10% grown, and 0.9 a feather ~90% grown. We assigned scores of 0 to missing feathers, and scores of 1.0 to newly replaced feathers with flakes of sheathing at their base.

The progression of flight-feather molt for each specimen was measured by the percentage of flight feathers replaced. Specimens that had not yet begun the molt were 0% complete and specimens with all new flight feathers were 100% complete. Percentage of flight feathers replaced was calculated as follows. (1) For each feather, we multiplied the score (0–1) by the average length (millimeters) of the feather when fully grown (feather length measurement described below) to obtain the millimeters of each feather that was new. (2) The millimeters of new feather were summed at every position to obtain the total millimeters of new feathers for each specimen. (3) We divided the total millimeters of new feathers by the total millimeters of a complete set of feathers to obtain the percentage of flight feathers replaced. Rectrix lengths were measured from study skins, and primary and secondary lengths were measured from extended wings. Females had slightly shorter feathers than males, so average feather lengths were calculated for each sex ($n = 5$ for each sex).

Specimens with highly asymmetrical flight-feather molt were excluded because they were likely replacing accidentally lost feathers. In some specimens in early primary molt, the position or length of growing primaries could not be scored without damaging the specimen. Thus, some molting specimens lacked precise molt scores, but no unscorable feathers were included in molt sequence analyses.

Describing flight-feather molt series.—To identify molt series, each growing (focal) flight feather was characterized as nodal, terminal, proximal to distal, or distal to proximal, on the basis of the condition of the neighboring feathers (see Yuri and Rohwer 1997). A feather that is more advanced in growth than adjacent feathers marks a site where molt was initiated in the current episode (a nodal feather). A feather that is less advanced than adjacent feathers marks a site where molt stopped in the current episode (a terminal feather). S9 and P9 can be compared with only one neighboring feather, and were classified as nodal or terminal. A growing feather that is more advanced than the adjacent distal feather, but less advanced than the adjacent proximal feather, indicates proximal to distal replacement. A growing feather that is more advanced than the adjacent proximal feather, but less advanced than the adjacent distal feather, indicates distal to proximal replacement.

Curve-fitting methods were used to describe relative scheduling of replacement among the different groups of flight feathers. Our curves were fit in STATVIEW (Abacus Concepts 1992) using Loess smoothing with tension set at 45.

Statistical analyses.—Fisher's exact test was used to compare the frequency of molting and nonmolting specimens in and out of the breeding range and the Great Basin. Regression analysis was used to test the possibility that adult Western Tanagers replace flight feathers while migrating. If they molt during the migration, then molt score for adults should be low at northern latitudes (molt recently begun) and high at southern latitudes (molt nearly complete), causing a significant relationship between flight-feather molt score and latitude. The G-test with Williams' correction (Sokal and Rolf 1995) was used for contingency analyses of age, feather class, latitude, and temporal differences in molt. For all statistical tests, statistical significance was accepted at $\alpha = 0.05$. We used Pimm's (1976) regression method to estimate duration of primary molt.

A potential sampling problem was comparison of the geographic distribution of breeding-season specimens from one set of museums to the geographical distribution of molting-season specimens from another, nonexclusive set of museums. It is possible that differences in sampling effort between those museum sets produced the differences found in the breeding and molting areas of Western Tanagers. However, our distribution of breeding-season specimens very closely matched the published breeding distribution of Western Tanagers (Hudon 1999; Fig. 1), so including the breeding-season specimens from museums used only in our molting-season analyses probably would have had little effect on our results. Throughout our analyses, we controlled for variation in museums and collecting effort by comparing rates rather than counts.

RESULTS

Description of rate and timing of feather replacement is important to comparative studies of molt, but lends itself poorly to discussion in single-species studies. Because we focus this paper on the ecological aspects of molt-migration, we briefly interpret the description of the prebasic molts as they are presented below.

Timing of molt in juveniles and adults.—All juveniles collected before 3 August were molting in three or more body regions ($n = 6$). No juvenile specimen examined was molting flight feathers. The percentage of juveniles in molt was highest in late July and declined through the end of September (Fig. 2A). The skewed distribution of Figure 2A suggests that juveniles begin replacing juvenile body feathers at or near the time of fledging.

The adult prebasic molt includes all body and flight feathers. Adults overlap the flight-

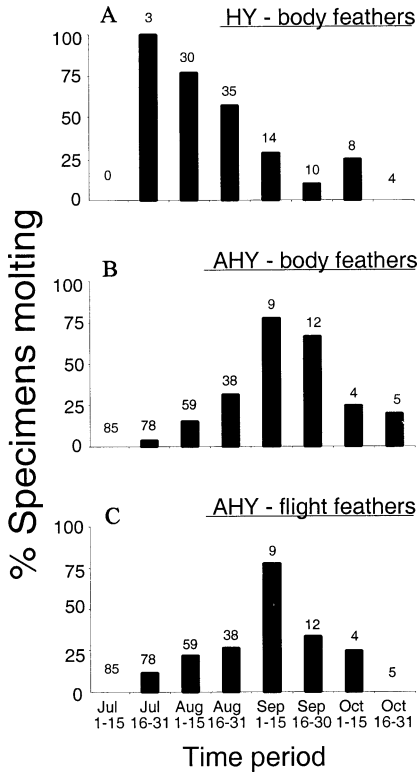


FIG. 2. Temporal distribution of molting Western Tanagers. Each histogram shows molting specimens as a percentage of all specimens collected in semi-monthly periods (sample sizes shown above bars). (A) Juvenile (hatching year) specimens molting body feathers. (B) Adults (after hatching year) molting body feathers. (C) Adults (after hatching year) molting flight feathers.

and body-feather molts temporally ($G_{adj} = 5.04$, $df = 6$, $P > 0.25$, Fig. 2B and C), rather than separating those molts as do some migratory passerines (Jenni and Winkler 1994, Pyle 1997). Adults replace their body feathers significantly later than juveniles, presumably because adults move southward before molting (Fig. 2A and B; $G_{adj} = 25.93$, $df = 5$, $P < 0.001$; our sample included only three juveniles collected 16–31 July, so that time period was excluded from this analysis).

Body-feather replacement occurs simultaneously in all body regions for both juveniles and adults (Fig. 3). Adults with molt intensities $>10\%$ are found from late July to mid-September, but adult body-molt scores $>10\%$ were mostly found in late August and early September. Body-molt scores for juveniles are highest

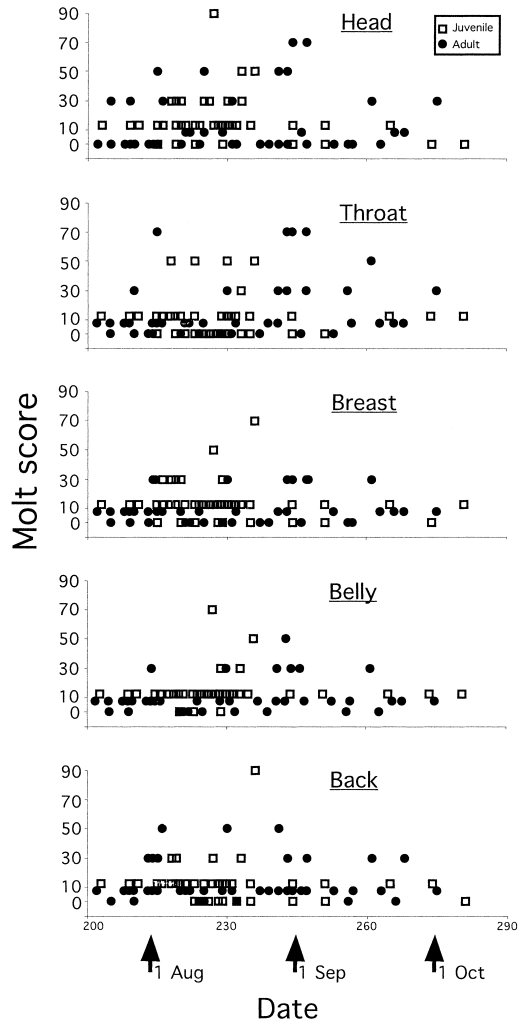


FIG. 3. Temporal distribution of body-molt scores for adult (closed circles) and juvenile (open squares) Western Tanager specimens (16 July–31 October). Peak juvenile molt intensities occur around mid-August, and peak adult molt intensities occur around early September. Symbols representing molt scores of 10 are separated by age class for readability.

in early August, illustrating the difference in the timing of the molt between the age classes (Figs. 2 and 3).

In some passerines of Europe, males molt earlier than females presumably because they cease parental care before females (Siikamaki et al. 1994, Svensson and Nilsson 1997, Hemborg and Merila 1998). We looked for that possibility in Western Tanagers in two ways. First, molt scores of males and females in body molt

TABLE 1. Frequency of feathers indicating molt sequence at each position in the wing (primaries and secondaries) or tail (rectrices). The primary molt begins at P1 and proceeds distally to P9; the secondary molt begins at S1 and proceeds proximally to S6; rectrix molt begins at R1 and proceeds laterally to R6.

	Primaries									Secondaries						Rectrices									
	9	8	8	7	6	5	4	3	2	1	6	8	1	1	2	3	4	5	6	1	2	3	4	5	6
Nodal					6								1 ^c				4								1 ^b
Proximal to distal										1 ^a							3				2				5
Distal to proximal	11	10	5	1	3	3	5				6	5	6	1			1								
Terminal										1 ^a		1 ^c					2								1 ^b
Ambiguous	14				1	2	3	1						2			1								1

^a S1 = 0.6 and S2 = 0.7, indicating that these feathers were lost at nearly the same time, but resulting in a terminal score for S1 (CMNH 164791).

^b R4 = new growth complete, R5 = 0.8, and R6 = 0.9, indicating that R5 was lost slightly before R6, and resulting in a terminal score for R5 and a nodal score for R6 (Moore 8553).

^c S1 = new, S2 = 0.4, and S3 = 0.6, resulting in a terminal score for S2, and a nodal score for S3 (UMMZ 172627).

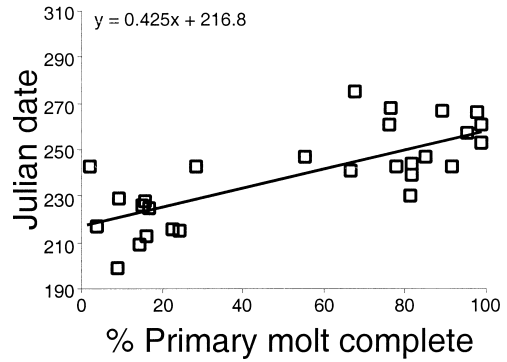


FIG. 4. Regression of Julian date on percentage primary feather molt complete in molting adult Western Tanagers (see Pimm 1976). Replacement of primaries requires ~43 days ($F = 32.37$, $df = 1$ and 23 , $r^2 = 0.585$, $P < 0.001$).

were compared during the first half of the adult molting period (July–August). There was no difference between males and females in a median test (Fisher’s exact test, $P = 0.99$; 9 of 19 males and 8 of 15 females above median). Second, the start dates of molt in males and females was compared by regressing Julian date on primary molt score for each sex (Pimm 1976). The mean start date for males was 7 August, eight days later than the mean of 30 July for females ($F = 0.68$; $df = 1$ and 24 , $P = 0.42$).

Description of the prebasic flight-feather molt.—As in most other passerines, primaries constitute a single molt series (as defined by Langston and Rohwer 1995) and are replaced proximally to distally, beginning with P1 (Jenni and Winkler 1994; Table 1). Replacement of primaries takes ~43 days (Fig. 4).

S1 through S6 was clearly a separate molt series from the primaries because S1 was always lost after primary replacement had proceeded distally through P5 being fully grown ($n = 15$). We note, however, that we have little evidence that S6 is the terminal feather in that series because our samples of specimens growing S5 or S6 is small (Table 1). We could not establish the sequence of replacement in the tertials (S7–S9) because we examined only three specimens replacing those feathers during the prebasic molt. Tertials typically constitute a separate secondary molt series in passerines (Jenni and Winkler 1994).

Rectrix molt begins at R1 and progresses laterally to R6 (Table 1). R6 was lost almost immediately after R5 in six of seven informative

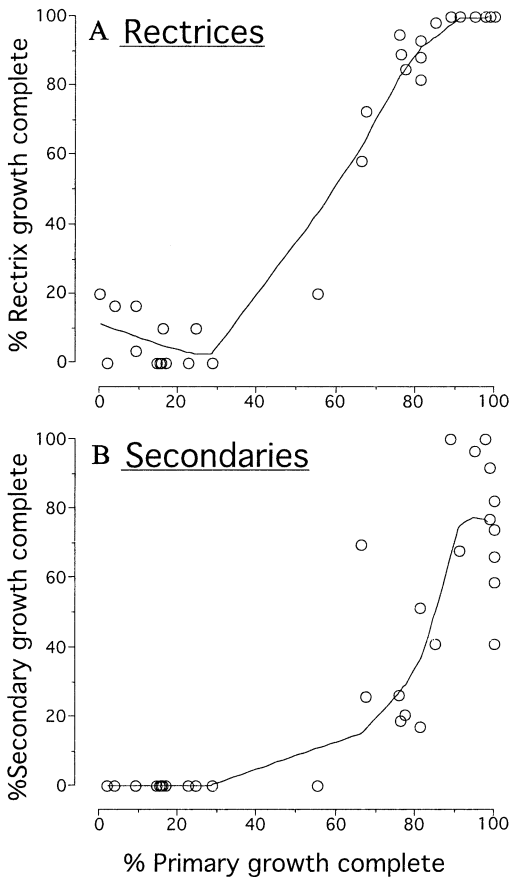


FIG. 5. Scheduling of (A) rectrix and (B) secondary replacement relative to primary molt in adult Western Tanagers (open circles). Lines represent the best-fit Loess curves.

specimens. Thus, no compelling evidence was found for Western Tanagers molting R6 as a separate series, as has been observed in several other passerines (Jenni and Winkler 1994, Yuri and Rohwer 1997, Voelker and Rohwer 1998).

To illustrate timing of rectrix and secondary replacement relative to primary replacement, percentage rectrix and percentage secondary replacement were plotted against percentage primary replacement using Loess curves (Abacus Concepts 1992). Rectrix replacement largely overlaps primary replacement and is always completed before primary replacement is complete (Fig. 5A). That scheduling results in little overlap between molt of rectrices and outer primaries, both of which are important to landing (Evans 1966). In contrast, replacement of S1–6 begins only after primary molt has progressed

through the loss of P8 or P9 (Fig. 5B). By that time, P5 was fully grown in these specimens ($n = 6$), so five fully grown inner primaries separated the gaps created by the simultaneous replacement of primaries and secondaries. That late scheduling of S1–6 replacement extends the overall duration of flight-feather molt.

Time added to the flight-feather molt was estimated by late replacement of S1–6 as follows. First, mean millimeters of S1–6 remaining to be replaced was calculated in birds that either had P9 more than half grown, or that had replaced all their primaries but were still growing secondaries (mean millimeters remaining to be replaced \pm SD = 80.9 ± 80.3 mm, $n = 9$). Second, the time required to grow this 80.9 mm of flight feathers was estimated using the growth band method (Rohwer 1999). Passerines grow their flight feathers at a mean rate of 3.2 mm day⁻¹ (Rohwer 1999), and Western Tanagers grow 2.3 ± 0.79 (mean \pm SD) secondaries while they are replacing S1–6. Thus, the late start of the replacement of S1–6 adds 11 days ($80.9/3.2 \times 2.3$) to overall duration of the flight-feather molt. Presumably that cost of extending the duration of the flight-feather molt is outweighed by the benefit of separating the gaps in the wing created by the loss of the outer secondaries and inner primaries (Jenni and Winkler 1994).

Molt and migration scheduling in adults.—Adult Western Tanagers depart the lowland west and migrate southward before beginning the prebasic molt (Fig. 1A and B). Twenty-five percent of 158 breeding adults (1–15 July in our sample) were found in the Great Basin, but only 7.7% of 39 molting adults were from the Great Basin (one-tailed Fisher's exact test, $P = 0.007$), suggesting that adults depart the lowland west before beginning the prebasic molt. Furthermore, 89.2% of 158 adults collected from 1–15 July were taken in the breeding range (Hudon 1999), but only 48.7% of 39 molting adults were found in the breeding range (Fig. 1A and B; one-tailed Fisher's exact test, $P < 0.0001$). Of the 20 molting adults from outside the breeding range, 75.0% were taken completely south of the breeding range, suggesting that adults move to the American Southwest before they begin the prebasic molt (Fig. 1B). The evidence for a southward movement of adults becomes even more convincing when collecting effort, indicated by variation in sample sizes across latitude, is considered. Far more Western Tan-

agers have been collected 16 July–31 October in the north than in the southwest, where most adults appear to molt (Fig. 1B). During that period, 68.8% of the 16 adults collected between 21°N and 30°N latitude were molting flight feathers, but only 20% of 175 adults collected north of 30°N were molting flight feathers ($n = 28$) or had a completely new set of flight feathers ($n = 7$; all other specimens had all old flight feathers).

The three northernmost molting adults were males from British Columbia (MVZ 105049, collected 18 August), Washington (UWBM 17486, collected 4 September) and Oregon (USNM 593567, collected 10 September). Two were more than halfway through primary replacement, and the third had finished primary replacement but was growing secondaries. On the basis of the duration of the primary feather molt (see above), the British Columbia specimen began the molt before any of the other specimens in our sample, thus it may have ceased breeding early enough that local conditions were still suitable for molting. The Washington and Oregon specimens began molt about the same time as birds farther south, and nothing on their labels suggested an explanation for them molting so far north. However, S. Rohwer collected the Washington specimen precisely because a molting adult was unexpected in Washington. There was no difference between the other 16 birds molting farther south in the breeding range and our sample of adults molting south of the breeding range in age, sex, Julian date, and percentage of flight-feather molt completed. Thus, we have no evidence that those birds are on a different molt schedule (e.g. due to early nesting, nest failure, or unsuccessful mating) than birds molting farther south.

Although adults clearly molt after migrating southward, no molting “hotspots” or stopover sites were found, as seen in other passerines that molt after a partial migration (e.g. Lazuli Buntings in Baja; Young 1991). Instead, molting adults are found throughout the Sonoran Desert and along the Sierra Nevada and Rocky Mountains from about 20 to 40°N, with the highest concentration of molting birds from 20 to 30°N (Fig. 1B). Adults molting in the southern part of the breeding range, but not in the productive Mexican monsoon region, were

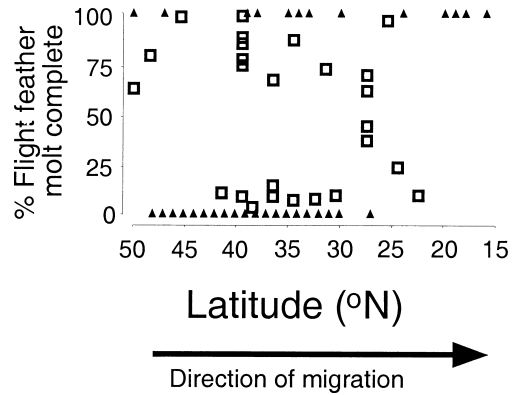


FIG. 6. Relationship between latitude and the progression of flight-feather molt in adult Western Tanagers collected 16 July–31 October. For birds in active molt there is no relationship between molt and latitude ($r^2 = 0.08$, $F = 2.04$, $df = 1$ and 30 , $P = 0.17$), indicating that adults do not molt while migrating. Triangles represent either specimens that had not initiated molt (0% complete) or specimens that had completed the molt (100% complete).

concentrated in montane regions surrounding the Great Basin (Fig. 1B).

Adult Western Tanagers did not appear to be molting and migrating simultaneously because there was no correlation between flight-feather molt score and latitude ($r^2 = 0.08$, $F = 2.04$, $df = 1$ and 30 , $P = 0.17$; Fig. 6). If Western Tanagers molted flight feathers as they migrated, flight-feather molt scores would increase continuously from north to south, resulting in a significant correlation between molt and latitude. Instead, specimens near the beginning and end of flight-feather replacement were found from 20–40°N (Fig. 6).

Most adults move south to the wintering grounds by late October. Only three of nine adults collected in November, all nonmolting, were found above 16°N (22°N, 24°N, and 25°N). Adults taken in December ($n = 21$) were from 14 to 19°N, with two exceptions (a male from Brownsville, Texas [Denver 5488], and a female from Seattle, Washington [UWBM 15397]).

Molt and migration scheduling in juveniles.—Molting adults are rare at northern latitudes and common at relatively southern latitudes, but the opposite is true for juveniles (Fig. 7). Most molting juveniles we examined were from British Columbia, Washington, Idaho, and northern California, and relatively few molting juveniles were taken in the American South-

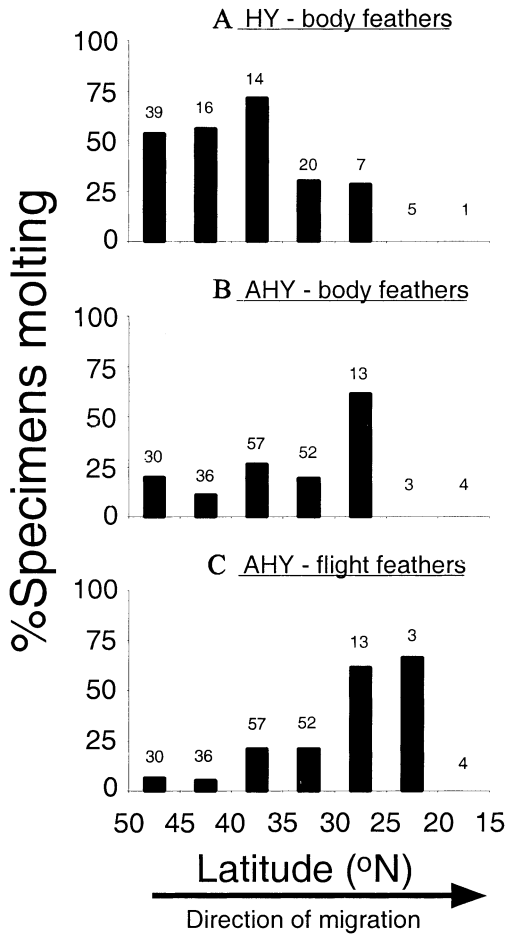


FIG. 7. Latitudinal distribution of molting Western Tanagers collected 16 July–31 October (most breeding occurs 35–50°N, Hudon 1999). (A) Juveniles in body molt. (B) Adults in body molt. (C) Adults in flight-feather molt. Sample sizes are shown above bars.

west (Fig. 1C). That age difference in molt location is clearly demonstrated by the latitudinal distributions of molting juveniles and adults (Fig. 7). Whereas peak adult molting occurs at 20–30°N, the highest frequencies of juvenile molting birds were at 35–50°N (latitudinal comparison of body molt: $G_{adj} = 22.47$, $df = 5$, $P < 0.001$). Eighty-two percent of 49 molting juveniles were found in the breeding range, closely matching the 89.2% of 158 adults collected in the breeding range 1–15 July, suggesting that juveniles do not migrate southward before molting (Fig. 7; one-tailed Fisher's exact test, $P = 0.21$).

How do juveniles respond to the dry conditions of late summer when they are molting? Figure 1C clearly shows a lack of molting juveniles in the Great Basin compared to surrounding areas. Only 18.4% of 49 molting juveniles were found inside the Great Basin, but that is not significantly lower than the 25% of birds that should have been produced there as estimated from the proportion of breeding adults from that region (one-tailed Fisher's exact test, $P = 0.34$). That similarity is largely due to five juveniles collected in mid-August in southern British Columbia, at the northern edge of the range of molting birds, and where late summer conditions are probably much less severe than would be the case farther south in the Great Basin. With those five specimens removed from the analysis, only 8.2% of molting hatching-year birds were collected in the Great Basin (one-tailed Fisher's exact test, $P = 0.01$). Therefore, we suspect that most juvenile Western Tanagers depart the Great Basin to perform their prebasic molt. This suspicion is strongly supported by the montane distribution of molting juveniles (Fig. 1C).

DISCUSSION

Molt-related movements in Western Tanagers.—Adults collected in the later stages of the breeding season were used to estimate the distribution of breeding adults and birds of the year. By comparing geographic distributions of breeding and molting specimens, we demonstrated a dramatic southward movement by adults prior to the molt, and we were even able to show that juveniles likely move relatively short distances out of the Great Basin to molt in surrounding mountains. Because most migratory passerines do not overlap breeding and molting, extensive loans of breeding specimens are rarely requested for museum-based studies of molt-related movements. The preceding comparisons, though based on small samples of specimens taken during the breeding season, clearly show that better samples from the breeding season would facilitate accurate description of even short-distance molt related movements. Loans should be planned accordingly!

The Western Tanager is the only migratory *Piranga* known to migrate before the prebasic molt. Because conditions are wet in eastern North America in late summer, Scarlet Tana-

gers (*P. olivacea*), as well as the eastern populations of Summer Tanager (*P. rubra*) would be expected to molt before migration, as reported by Pyle (1997). However, some parts of the range of the western race of Summer Tanagers (*P. rubra cooperi*; American Ornithologists' Union [AOU] 1957) lie north of the Mexican monsoon region, and we predict that individuals from that region will be found to move south into the Mexican monsoon region before molting. Because most of the northern breeding range of the Hepatic Tanager (*P. flava*) includes the area of the Mexican monsoon, we would not expect that northern migratory population to migrate before molting. Wintering ranges of all temperate migratory *Piranga* largely overlap, so variation in molt strategies among those tanagers is probably due largely to differences in suitability of their breeding grounds for molting.

Voelker (2000) proposed that monsoon molting birds benefit from a rapid flight-feather molt, noting that monsoon stopover species take ~55 days to complete the primary feather replacement (Thompson 1991, Young 1991, Voelker and Rohwer 1998), whereas Gray Vireos (*V. vicinior*), which molt north of the monsoon area, take ~67 days (Voelker 2000). Our findings support that hypothesis: Western Tanagers take ~43 days to complete the primary molt, the fastest yet reported for any of the Great Basin species, but comparable to some eastern American species (e.g. Gray Catbird [*Dumetella carolinensis*] in Vermont = 44 days; Dwyer-Heise and Rimmer 2000). None of the monsoon molting birds are strict aerial foragers, and thus they can afford to perform rapid, presumably aerodynamically costly flight-feather molt because they forage by foliage gleaning. In contrast, Western Wood-Pewees (*Contopus sordidulus*; Pyle 1997) and Dusky and Gray flycatchers (Johnson 1963) breed in the Great Basin and migrate southward around the time of the Mexican monsoons but do not stop to molt, possibly because their dependence on aerial foraging precludes them from a rapid, flight-limiting molt, and the benefit from molting in the southwest.

Age effects on the scheduling of molt and migration.—Unlike past studies of molt-related movements in western passerines, in this article we demonstrate that young birds hatched in the Great Basin, where the late summer

drought is particularly severe, likely move into nearby mountains before undergoing their first prebasic molt. We looked specifically for evidence of such movement in Western Tanagers because, as coniferous forest breeders, up-slope movements would take them to more productive habitats in the same biome.

In the first studies of molt and migration in western passerines, young birds in full juvenal plumage were shown to move southward with adults before undergoing their first prebasic molt (Gray and Dusky flycatchers, Johnson 1963; Bullock's Orioles, Rohwer and Manning 1990). In other species in which southward movement by adults has been documented, young birds undergo their first prebasic molt before the fall migration (Western Tanager, this study; Western Warbling Vireo, Voelker and Rohwer 1998; Lazuli Bunting, Young 1991). Those age-class differences promise to be challenging to interpret because hypotheses must address why juveniles of some species molt before migrating, whereas others do not.

Both adults and juveniles should be "pushed" southward by dry late summer conditions of the lowland west (Rohwer and Manning 1990). Similarly, both age classes may also be "pulled" southward before the molt to exploit the food flush produced by the Mexican monsoon (Rohwer and Manning 1990). Voelker's (2000) rapid-molt hypothesis cannot explain age-related differences in molt-migration to the Mexican monsoon region because juveniles of those species do not replace their flight feathers during the first prebasic molt. It is unlikely that juvenile Western Tanagers lack the energetic reserves, flying skills, or flight muscles to migrate southward in time for the monsoon in late August. They fledge approximately one month before the start of the monsoon rains and two months before peak adult molt. Physiological-constraints hypotheses must reconcile why juveniles have the flight skills and energetic reserves to depart lowland breeding areas and to support molt immediately after fledging, but lack migratory flight skills and energetic reserves one month later when they would presumably migrate to meet the monsoon rains.

Voelker and Rohwer (1998) proposed that age-class differences in body plumage texture could explain age-class differences in molt and migration. Following Rohwer and Manning

(1990), M. Speidel and S. Rohwer (unpubl. data) have shown that juvenal body feathers are measurably more loosely textured than adult body feathers in several families. Furthermore, those texture differences were minimal in species for which newly fledged young depend heavily on flight before the first pre-basic molt (e.g. Barn Swallow [*Hirundo rustica*]), suggesting that less fluffy body plumage reduces drag (M. Speidel and S. Rohwer unpubl. data). If fluffy plumage generates undue drag, then molting before migrating may be a better option for juveniles in species with relatively fluffy juvenal plumage, or in species for which other biomechanical factors make juvenal plumage exceptionally costly for small migrants (e.g. frictional drag during flight is a relatively more predominant force for smaller than larger birds; Pennycuik 1989).

In combination, those hypotheses make several predictions about molt movements worthy of future study. First is the need to look carefully for evidence of short-distance movements that take juveniles into more productive habitat for molting. For instance, juveniles of many species that breed in western riparian habitats may be "pushed" to molt elsewhere. However, if their juvenal plumage is aerodynamically inefficient, they may be unable to migrate to the wintering grounds or to the Mexican monsoon region. Other studies of riparian breeding birds in which juveniles molt on the breeding grounds have not examined that possibility (Young 1991, Voelker and Rohwer 1998). Second, adults and juveniles of species that mainly breed in high elevation western coniferous forests are not expected to move to the Mexican monsoon region for their fall molts. At least three western mountain breeding birds characteristic of wetter, higher elevation forests remain on their breeding grounds to molt: Hermit (*Dendroica occidentalis*) and Townsend's (*D. townsendi*) warblers (Jackson et al. 1992) and Hammond's Flycatcher (*Empidonax hammondi*; Johnson 1963). Within those species, individuals that breed or hatch at low elevations may move up-slope before molting, but no current data address that possibility.

Ecology of molt-migration in Great Basin passerines.—Rohwer and Manning (1990) first hypothesized that the premolt movement southward by Bullock's Orioles was a response to deteriorating foraging conditions in the low-

land west in late summer, and to a simultaneous food flush associated with the monsoons of northern Mexico and the southwest United States (the Mexican monsoon region; following Douglas et al. 1993). The same logic has been used to explain the movements of Lazuli Buntings (Young 1991), western populations of Painted Buntings (Thompson 1991), and adult Western Warbling Vireos (Voelker and Rohwer 1998), and was predicted but not found for Gray Vireos (Voelker 2000). This study of Western Tanagers adds yet another species to the list of Neotropical passerines that depend on the Mexican monsoon for suitable habitat during the fall molt.

Can geographical and temporal patterns of primary (photosynthetic) and secondary productivity explain molt-related movements of Great Basin passerines? The highest temperatures and lowest precipitation of the year occur in August in the Great Basin (Walter 1971), but we found no documentation of a concurrent decline in foraging conditions for insectivorous birds, despite an extensive literature search. Several insectivorous species are believed to molt in the upper Great Basin (see Pyle 1997), suggesting that, for at least some species, conditions are suitable for molting. Our understanding of molt strategies would benefit from detailed study of those species, and from study of elevational differences in food availability during late summer.

There is better evidence that the Mexican monsoon region provides suitable and even abundant food resources for insectivorous birds during the late summer. The link between rainfall, plant productivity, and herbivore abundance is well established on an ecological scale (Schowalter 2000, Ostfeld and Keesing 2000), and experimental variation in precipitation causes associated variation in arthropod abundance on the creosote bush (*Larrea tridentata*) in New Mexico (Schowalter et al. 1999). The most compelling evidence for a monsoon-related insect flush is the late summer breeding by several southwestern species, including the Curve-billed Thrasher (*Toxostoma curvirostre*; Short 1974), Rufous-winged Sparrow (*Aimophila carpalis*; Phillips 1951), Cassin's Sparrow (*Aimophila cassinii*; Ohmart 1966), and several insectivorous mammals (Reichert 1979).

Conservation implications.—Perhaps the most important result of this study is the discovery

of yet another Neotropical passerine that depends on the Mexican monsoon for the fall molt. In five species, one or both age classes migrate to that area for their prebasic molt: adult and juvenile Bullock's Orioles (Rohwer and Manning 1990), adult Lazuli Buntings (Young 1991), adults of western populations of Painted Buntings (Thompson 1991), adult Western Warbling Vireos (Voelker and Rohwer 1998), and adult Western Tanagers. Furthermore, studies of habitat use by Neotropical migrants have demonstrated a high diversity and abundance of species in mountainous and riparian areas of the American Southwest during the fall migration (Block et al. 1992, Leal et al. 1996, Yong and Finch 1996).

The meteorological nature of the Mexican monsoon presents a special challenge to the conservation of Neotropical migrants that depend on it for molting. The geographic area over which the rains may occur is enormous, from west Texas and Coahuila west to Arizona and Sonora, and southwest to Sinaloa (Douglas et al. 1993). Monsoon rains fall somewhere in that region every year between July and September, but the location of the rains is highly variable from year to year (Comrie and Glenn 1998). Thus, conserving riparian and montane habitats at any particular locality in that region will be insufficient to conserving the species that rely on those habitats to molt. Rather, riparian and montane habitats must be maintained throughout that region so that species that molt there can find an insect response to the rains wherever they occur in a particular year. The importance of scattering conservation areas over a wide region would be supported if birds were shown to "follow the rains" each year.

Whereas western riparian habitats are heavily used by migrants and molt-migrants (Leal et al. 1996, Yong and Finch 1996), conservation of those habitats has a distressing history. Ninety-five percent of western riparian habitat has been altered, degraded, or destroyed by humans over the last 100 years (Krueper 2000). Several western migratory passerines depend on that region to support one of the most important events of the annual cycle—the annual replacement of all plumage. These recent discoveries, together with the spatial unpredictability of the Mexican monsoon, strongly support the value of conserving riparian and

montane habitats throughout the southwest for Neotropical migrants.

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