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Ecology and Demography of East-West Differences in Molt Scheduling of Neotropical Migrant Passerines

AMONG NEOTROPICAL MIGRANT PASSERINES that breed in North America, adults of just five of 55 eastern breeders migrate in the fall before molting, whereas adults of at least 13 of 26 western breeders undertake all or part of their fall migration before molting, a difference that remains significant when limited to phylogenetically independent contrasts. Several recently studied species that begin migration before molting (Bullock's Oriole, Western Warbling Vireo, Lazuli Bunting, Western Tanager) have been shown to move to the region of the Mexican Monsoon, where they pause to molt before continuing on to their wintering areas. Two complementary environmental forces favor this scheduling of molt and migration in western passerines. Most of the lowland West is exceedingly dry and unproductive in late summer, but a late-summer food flush favorable for molting is generated by the Mexican Monsoon rains of New Mexico, eastern Arizona, and northern Mexico. Some authors have suggested that migrating before the fall molt is favored for defending winter territories, but we found no comparative support for this hypothesis. Just 18% of winter territorial species migrate before molting, whereas 33% of species that are not territorial in winter migrate before molting. Tyrannid flycatchers vary greatly in the scheduling of molt and migration, with several eastern and transcontinental species migrating before their fall molt. This variation is poorly understood, but two factors may be especially important for larger tyrannids: breeding-season time constraints (associated with prolonged parental care) and the need for slow flight-feather replacement to maintain maneuverability for capturing large insects. In some North American passerines juveniles molt before

migrating but adults molt after; in other species both juveniles and adults migrate before molting. Part of this variation may be explained by interspecific differences in the quality of the juvenile plumage. Species in which both juveniles and adults migrate before molting have better-quality juvenile plumage than species in which juveniles, but not adults, molt before migrating. Finally, passerines of the western Palearctic-African migration system differ from Neotropical migrants in that none (except swallows) delay molt of their body plumage until after migration. In contrast, many Palearctic-African migrant passerines delay replacement of their flight feathers until late in winter, and we argue that they do so because their African wintering habitats are more abrasive than the habitats used by North American passerines wintering in the Neotropics.

INTRODUCTION

Our goal in this chapter is to provide a synthetic overview of molt-migration scheduling in Neotropical migrant passerines that breed in North America. The impetus for this study is the recent discovery of an east-west contrast in the scheduling of the prebasic molt relative to the fall migration in a number of closely related east-west species pairs (Rohwer and Manning 1990; Young 1991; Voelker and Rohwer 1998). Surprisingly, the special scheduling of the fall molt of passerines breeding in western North America seems without precedent in European passerines that winter in sub-Saharan Africa.

Breeding, migrating, and molting place special energetic demands on birds and are often segregated in time. Given that environmental constraints appear to prevent winter breeding in all Palearctic and Neotropical migrants (hence, fixing the timing of migrations and breeding), only molt can vary with respect to its scheduling in the annual cycle. The complete annual molt in adults may occur on the breeding grounds before the fall migration or on the wintering grounds after the fall migration, or parts of it may occur in different places. To our knowledge, all Neotropical migrant passerine species that replace different components of their plumage in different regions replace body plumage on the breeding grounds but delay replacement of most flight feathers until after the fall migration (Jenni and Winkler 1994; Pyle 1997), although the reverse would be more difficult to document. In some species the molt is scheduled such that the fall migration is broken into two phases; the first phase takes these species to special stopover sites where they molt and the second phase takes them on to their final wintering area (Rohwer and Manning 1990; Young 1991; Jones 1995).

In the following analyses we use ecological and demographic variables to explain differences in the scheduling of the fall molt. We found it helpful to conceptualize these variables as “pushes” and “pulls.” Pushes are ecological or demographic characteristics that disfavor molting in that region. Thus pushes favor birds leaving a region to molt elsewhere. Pulls are ecological or demographic characteristics

of a region or population that favor individuals moving to that region before they begin a molt.

Large differences in precipitation and primary productivity in mid and late summer seem to drive differences in molt scheduling between eastern and western species. Remarkably, east-west differences between adults often do not apply to juveniles, and we suggest that species differences in the quality of the juvenile plumage, which may be a consequence of different rates of nest predation, may help explain these contrasts between age classes. We also propose that structural contrasts between the winter environments used by Palearctic and Nearctic migrants may explain continental contrasts in their molt scheduling better than previous hypotheses do. Finally, we make a special effort to identify weaknesses in the comparative data set for North American migrants and to identify species whose ecology or relationships make them particularly worthy of detailed study.

Scientific names of North American birds that are included in the Appendix to this chapter are omitted from the text.

EAST-WEST COMPARISONS

Categorizing Species

We base this analysis on the 115 migratory passerines (listed in the Appendix to this chapter) that breed in North America and mostly winter considerably south of the United States. We treated species as migratory if most individuals winter south of the United States (e.g., Lesser Goldfinch, Townsend's Warbler, Painted Bunting). Two groups were difficult to categorize with regard to migration—those species with only small parts of their breeding range in the United States and those few western breeders whose winter ranges scarcely extend south of Mexico. We excluded most migrant emberizids because they winter primarily north of Mexico. We further divided the 115 migratory species into four categories according to their breeding distributions: eastern, breeding largely east of the Rocky Mountains; western, breeding largely west of the Rocky Mountains; northern, having transcontinental ranges north of the arid intermontane region of western North America (hereafter the Great Basin); and continental, having more southern transcontinental ranges that include the Great Basin (Appendix to this chapter).

As is often the case in broad comparative studies, this one suffers from unevenness in the quality of the data. For some species the literature is conflicted on the timing and the location of the fall molt (e.g., Dickcissel [cf. Mengel 1965 and Pyle 1997]). For others there are simply no data, and differences among other close relatives caution against presumption. We used Pyle (1997) as our primary reference but provided additional citations (Appendix to this chapter) when we found better or updated references.

The fundamental question in this study was whether western passerines show multiple independent origins of

molting after initiating the fall migration. We scored all Neotropical migrants as molting body feathers *before* or *after* a substantial southward movement. We used “substantial southward movement” because several western species interrupt their southward migration to molt before continuing on to their wintering grounds. For characters that have few states and that are highly labile over evolutionary history, the reliability of node reconstruction diminishes as one moves deeper into a phylogenetic tree (Omland and Lanyon 2000). Because the East has more than twice as many Neotropical migrants as the West, our test of east-west differences using phylogenetically independent contrasts was limited mostly by the number of western species with close relatives in the East. Some western species had no eastern relatives, and two, Scott’s Oriole and Green-tailed Towhee, had such distant eastern relatives that we omitted them because of the uncertainty of correctly reconstructing internal nodes. Further, we excluded comparisons involving Least Flycatcher and Orchard Oriole because they had no close relatives in the West. With these restrictions we had 17 independent contrasts in molt-migration scheduling between eastern and western clades; all of these contrasts were comparisons of species in the same genus.

East-West Environmental Contrasts

Homogeneity and contrast characterize the late-summer molting environments encountered by eastern and western species, respectively. Annual precipitation is high in the East and low in most of the West. In the East, precipitation is evenly distributed throughout the year and primary productivity remains high in late summer. In contrast, most precipitation that results in primary productivity in the West comes as winter rain or snow (see rainfall maps in Espenshade 1991). Thus, throughout most of the West late-summer conditions are exceedingly dry. Variability in western environments is further augmented by the great topological relief of the region. Winter snow packs in the Pacific coastal ranges, the Cascades and, to a lesser extent, the Rockies and the Sierra Nevada Mountains, provide sufficient runoff for montane regions to remain productive into the late-summer molting season.

Late-summer conditions also vary substantially with latitude in the American West. To the south of the Great Basin, over a large arid region including New Mexico, eastern Arizona, and northern and western Mexico, most of the limited annual precipitation occurs in July, August, and September (hereafter the Mexican Monsoon, following Comrie and Glenn 1998). The flush in productivity that follows these rains has long been known to stimulate late-summer breeding in several southwest species including the Curve-billed Thrasher (*Toxostoma curvirostre* [Short 1974]), Rufous-winged Sparrow (*Aimophila carpalis* [Phillips 1951]), and Cassin’s Sparrow (*Aimophila cassinii* [Ohmart 1966]), and several other insectivorous animals (Reichert 1979).

Given the energy and protein demands of molting, aridity seems to create a strong “push” for insectivorous species

of the lowland West to depart their breeding grounds before molting. Many of these same species also seem to be “pulled” to more productive regions for molting. For example, various authors have suggested that the flush of productivity associated with the Mexican Monsoon constitutes a strong “pull” to the southwest for molting by various lowland western insectivorous birds (Rohwer and Manning 1990; Young 1991; Voelker and Rohwer 1998; Butler et al. 2002). In addition, species that breed at low elevations may be “pulled” to molt in more productive high-elevation habitats (Greenberg et al. 1974; Butler et al. 2002), whereas others may move directly to their Neotropical wintering grounds before molting (Johnson 1963).

EAST-WEST CONTRASTS IN MOLT SCHEDULING

Adult Prebasic Molts

Most eastern species molt in their breeding range. Just five of 55 eastern breeders (Yellow-bellied Flycatcher, Gray Kingbird, Eastern Wood-Pewee, Orchard Oriole, and central populations of Painted Bunting) are thought to leave the breeding range for the adult prebasic molt of body feathers (table 8.1A, Appendix to this chapter), and the categorizations of some of these five could change with more study. Orchard Orioles certainly leave without molting. East coast populations of Painted Bunting molt on the breeding grounds but central populations, which we considered eastern for consistency, move to the American Southwest before molting (Thompson 1991).

By contrast, adults of at least half of the 26 western breeders depart their breeding grounds before undergoing the prebasic molt (table 8.1A, Appendix to this chapter). It

Table 8.1 Breeding range and location of the adult prebasic molt of body feathers

A. Species counts without correction for relatedness ($p < 0.0001$ for East/West \times off/on)			
	Off	On	Totals
East	5	50	55
West	13	13	26
North	1	5	6
Continental	8	11	19
Southwestern	1	3	4
Totals	28	82	
B. Phylogenetically independent contrasts (one-tailed $p = 0.026$)			
	Off	On	Totals
East	2	15	17
West	9	8	17

is well established that several of these western species molt in the Mexican Monsoon region: Bullock's Oriole (Rohwer and Manning 1990), Lazuli Bunting (Young 1991), Western Warbling Vireo (Voelker and Rohwer 1998), and Western Tanager (Butler et al. 2002). Adults of several other species are known to depart the breeding grounds before molting, but whether they molt in the Mexican Monsoon region or on the wintering grounds requires further study (e.g., Western Kingbird, Western Wood-Pewee, Ash-throated Flycatcher, and Black-headed Grosbeak).

Independent Contrasts

The preceding summary of east-west contrasts included several groups of closely related species with similar scheduling of molt and migration. Thus, we used phylogenetically independent contrasts to explore whether the east-west differences in the full species list included enough independent changes to suggest adaptive change unequivocally. There are far fewer western than eastern species, so we matched each western species or each western clade having similar molt scheduling with its most closely related eastern species or clade. We then scored the molt scheduling of every species or clade as molting on or off the breeding grounds. For these comparisons we used the phylogenies of Klicka et al. (2001) for *Passerina*, Murray et al. (1994) and Cicero and Johnson (1998) for *Vireo*, Zink and Johnson (1984) for *Empidonax* and *Contopus*, Omland et al. (1999) for *Icterus*, Lovette and Bermingham (1999) and Lovette et al. (1999) for *Dendroica*, Burns (1998) for *Piranga*, and Zink et al. (2000) for *Vermivora*.

Phylogenetically independent contrasts revealed the same trend observed in the full data set, even though the number of species or clades that could be contrasted fell to 34 (Fisher's one-tailed $p = 0.026$ [table 8.1B]). We consider this analysis overly conservative because molt scheduling is sufficiently labile that close relatives with the same molt scheduling, which generate just one contrast, may represent replicates of species that could have changed but did not do so because their current molt scheduling is being maintained by stabilizing selection (Reeve and Sherman 1993; Hansen 1997). Several closely related east-west pairs show differences in molt scheduling (e.g., eastern and western Warbling Vireos, Black-headed and Rose-breasted Grosbeaks), and Painted Buntings even show population differences in molt scheduling between East Coast and Midwestern breeding populations (Thompson 1991). Furthermore, Western Tanagers feature variation among adults in molt scheduling, suggesting the presence of variation sufficient for rapid evolutionary changes in molt scheduling (Butler et al. 2002).

We may also explore whether phylogenetic constraints explain the exceptions to the general pattern described above. Specifically, are the few eastern species that depart their breeding ranges before molting closely related to western species that also migrate before molting? And are western species that molt on their breeding ranges closely

related to eastern species that also molt before migrating? This further exploration of phylogenetic constraints is especially important for western insectivores that are not high-elevation breeders. Thus we exclude from this analysis western species that breed in the mountains because phylogeny and environment could be pulling them toward the same molt scheduling.

Of the eight species that oppose the rule, east "on" and west "off," five had sister clades "pulling" them to be opposed to the rule and three did not. Thus, there is weak but nonsignificant evidence of phylogenetic constraint explaining these exceptions ($p = 0.36$; one-tailed binomial test). Note, however, that this comparison may be strengthened by asking how much potential constraint is seen in those western species that molt "off." There were eight such western clades, all of which had an eastern relative molting "on," suggesting no phylogenetic constraint ($p = 0.004$; one-tailed binomial test).

WHERE DO WESTERN SPECIES MOLT?

Some lowland western insectivores are apparently "pushed" away from their breeding range for molting by late-summer aridity, and some are also "pulled" to the Mexican Monsoon region. A recent series of papers treating Bullock's Oriole (Rohwer and Manning 1990), Lazuli Bunting (Young 1991), Western Warbling Vireo (Voelker and Rohwer 1998), and Western Tanager (Butler et al. 2002) shows that adults of these species mostly molt in the southwest monsoon region. Unfortunately, the early literature on molt-migration scheduling did not assess stopover molting in the Mexican Monsoon region (Johnson 1963, 1974). Johnson (1963) implies that Gray Flycatchers molt on their winter range, but he provides no data on the number of molting specimens examined or on their dates and localities of collection.

The Mexican Monsoon region is clearly an important area for the conservation of the several species that are known to molt there, but little is known about their ecology and behavior during their fall molts. Furthermore, several other western species need to be examined for the possibility of stopover molting in the region. These include Dusky Flycatcher, Western Wood-Pewee, Western Kingbird, Ash-throated Flycatcher, Cordilleran Flycatcher, Pacific Slope Flycatcher, Lesser Goldfinch, Black-headed Grosbeak, western populations of Summer Tanager, northern populations of Hepatic Tanager, and Hooded Oriole. Several of these species arrive at Southeast Farallon Island in July or early August (Pyle and Henderson 1991), suggesting departure from their breeding grounds before molting. Despite the paucity of late-summer specimens from the region of the Mexican Monsoon, museum studies will likely provide the best first approach to examining the possibility of stopover molting in this region for these species.

Western topography may explain why several western breeders molt on their summer range. Most western moun-

tain breeders that forage in conifers molt in their breeding range (Townsend's, Hermit, and Black-throated Gray Warblers, Hammond's Flycatcher, Audubon's Warbler). Other western species that breed in lower-elevation coniferous and riparian habitats and molt in their breeding range could easily move upslope in late summer for molting. For example, Black-throated Gray and Audubon's Warblers have populations that breed in relatively low-elevation coniferous forests of the Great Basin, and we suspect that they move upslope to molt in more productive habitats. Unfortunately, we know of few data addressing this issue of regional upslope movements for molting, though upslope movements have been documented for Nashville and Orange-crowned Warblers (Greenberg et al. 1974) and are implied for juvenile Western Tanagers (Butler et al. 2002).

Molt-migration patterns of other western species that molt on their breeding grounds can be explained by dietary differences, or are poorly studied. Like other migrant emberizids, Green-tailed Towhees molt on their arid western breeding grounds, where seeds are abundant in late summer. The remaining group of western species that apparently molt in their breeding range before moving south are poorly studied. At least two species, Orange-crowned and Nashville Warblers, are known to move upslope to more productive late-summer habitats for molting (Greenberg et al. 1974; Steele and McCormick 1995), and similar movements seem likely for additional species. Further, additional species are likely to be found to migrate to the region of the Mexican Monsoon before molting. Possibilities include Scott's Oriole, Hooded Oriole, Cassin's Vireo, Plumbeous Vireo, western populations of Summer Tanager, and northern populations of Hepatic Tanager.

WINTER TERRITORIALITY AND MOLT SCHEDULING

Several authors have suggested that winter territoriality "pulls" individuals to migrate before molting so they arrive early on their wintering grounds and benefit from site dominance (Alerstam and Högstedt 1982; Sealy and Biermann 1983; Lindstrom et al. 1993). This argument seems flawed on two counts. First, it ignores the cryptic behavior characteristic of molting birds because of the energetic and aerodynamic costs of molting and because of the risks of damaging soft, growing quills (Vega Riveria et al. 1998). Second, it is questionable that prior-residency advantages would be sufficient to enable early migrants molting on their winter territories to defend these territories from later migrants that could molt before migrating and, thus, be fully competitive upon arrival. Late-arriving birds in fresh plumage, unencumbered by energetic costs of molt and risks to growing feathers, should easily displace molting territory holders. Ironically, this use of the prior-residency argument is never applied to the breeding season, when it would be just as logical. That no passerine delays the spring molt until arrival on the breeding

grounds strongly argues against territoriality as a pull favoring molting after migrating.

The prior-residency hypothesis predicts that Neotropical migrants that are territorial during winter should be more likely to molt after migrating compared with species that do not hold winter territories. We found data on winter territoriality and molt scheduling for 112 Neotropical migrants (Appendix to this chapter). In contrast to the prior-residency hypothesis, 33.3% of the 48 non-territorial species molt on the wintering grounds, but only 18.5% of the 54 territorial species molt on the wintering grounds (Fisher's exact $p = 0.11$, but opposite the predicted direction).

BREEDING-RANGE TIME CONSTRAINTS AND MOLT SCHEDULING

As aerial foragers, swallows are forced to molt slowly, making it difficult to complete the molt on the breeding grounds. Regardless of their distribution in North America, swallows molt and migrate simultaneously during the overland component of their fall migration (Niles 1972; Stutchbury and Rohwer 1990; Pyle 1997; Yuri and Rohwer 1997). Swallows wintering far into the Southern Hemisphere replace few flight feathers before arriving on their wintering grounds and arrest their molt before crossing the Gulf of Mexico. Those with more northern wintering distributions replace their flight feathers in late summer and fall, and eastern populations of Northern Rough-winged Swallows pause at the coast to complete flight-feather molt before crossing the Gulf of Mexico (Yuri and Rohwer 1997). Because swallows should molt slowly, time constraints likely favor most of the fall molt occurring after migration in those that are transequatorial migrants.

For North American passerines there are three general rules of molt-migration scheduling: eastern species molt before migration; western arid species molt after migration; and aerial foragers molt during overland migration. Tyrannids stand out as generating the most exceptions to these rules. Two eastern tyrannids molt their body and flight feathers after arriving on the winter range (Eastern Wood-Pewee and Gray Kingbird) and additional eastern tyrannids (Least Flycatcher, Great Crested Flycatcher, and, possibly, Yellow-bellied Flycatcher [Hussell 1982]) molt their body feathers (or at least begin this molt) before migrating, but delay replacement of their flight feathers until arrival on their winter grounds. A suite of transcontinental and western tyrannids also leaves its breeding range before molting (Eastern Kingbird, Willow Flycatcher, Alder Flycatcher, Olive-sided Flycatcher, Western Kingbird, Scissor-tailed Flycatcher).

As with swallows, something seems to be special about flycatchers. Both groups catch prey in the air, and they likely replace flight feathers as slowly as possible to maintain aerial efficiency (Johnson 1963). Because swallows forage while flying and migrate during the day, there should be little cost

to molting during overland migrations. In contrast, tyrannids sally to forage and mostly migrate at night, making molting while migrating unlikely. Johnson (1963) observed that molts occurring after the fall migration tend to be protracted, citing data for tyrannids and swallows, but this idea has not been well tested in a comparative context. Two predictions might be examined. First, tyrannids should replace flight feathers much more slowly than gleaners and, possibly, even more slowly than swallows because they take larger prey that require greater maneuverability in flight. For this test it will be important to eliminate the confounding influence of day length by comparing tyrannids with other passerines molting after the fall migration. For temperate molters, decreasing day length in the fall is well known to accelerate the rate of molt (see Dawson 1994). Second, time constraints, driven by how early the eggs are laid in spring and in the length of post-fledging care, might explain additional variation within tyrannids. For example, post-fledging care is prolonged in Eastern Kingbirds, with young being fed several times an hour for nearly a month after fledging (Morehouse and Brewer 1968). This suggests that tyrannids may have longer periods of fledgling dependency than foliage-gleaning insectivores, presumably because acrobatic aerial foraging requires much time to learn. Temperate phoebes (*Sayornis*) molt on their breeding range, unlike other medium-sized tyrannids. Perhaps they have time to molt because they nest relatively early, and because they are smaller than kingbirds.

AGE CLASS CONCORDANCE

This section treats the scheduling of the first prebasic molt of body feathers by considering concordance between adults and yearlings. For 110 species the scheduling of both the adult (or definitive prebasic) molt and the first (post-juvenile) prebasic molt is known. Of these, 103 species feature age class concordance, and only seven do not (table 8.2). Moreover, every case of nonconcordance is a result of adults migrating *before* they molt and young migrating *after* they molt; thus, there are no “on-off” species featuring adults molting before migration and juveniles migrating southward in juvenile plumage before molting (table 8.2). The “off-on” group (adults off, juveniles on) includes two

eastern species, four western species, and one transcontinental species. The “off-off” group (adults off, juveniles off) includes three eastern species, nine western species, and nine transcontinental species (Appendix to this chapter).

This summary of age class concordance suggests that there may be important reasons for the contrast between “off-off” species (in which both adults and young depart the breeding range before molting) and “off-on” species (in which adults molt after departing the breeding range, while young remain behind to molt on the breeding range before migrating). Why do the young of some species migrate southward in juvenile plumage and then molt *after* migrating (like adults), whereas juveniles of other species remain in their breeding range and molt *before* migrating (*unlike* adults)? In the following section we develop a hypothesis based on variation in quality of juvenile plumages to explain this age class discordance in molt scheduling.

FEATHER QUALITY AND ADULT-YEARLING DISCORDANCE

Ornithologists have long known that birds in juvenile plumage can often be recognized by the loose texture of their body plumage (Göhringer 1951; Dwight 1900). Juvenile feathers often have fewer barbs per unit of rachis and reduced connectivity between adjacent barbs, even on the distal, most vanelike, portion of their feathers (Rohwer and Manning 1990; Speidel and Rohwer, unpubl.). The functional significance of this difference is largely unexplored, but contrasts between species are striking (Butler et al., unpubl.). Juveniles with highly “decomposed” barbs give the impression of having grown cheap feathers that facilitate rapid fledging, perhaps because of intense nest predation.

Thus, small passerines may have two counts against undertaking the fall migration in juvenile plumage. First, aerodynamic drag is due in part to frictional forces between the air and the surface of the body (skin friction). The relative contribution of skin friction to overall aerodynamic drag increases as body size decreases. For species with equally decomposed juvenile plumage, therefore, smaller species should suffer more from frictional aerodynamic drag than larger species. Second, as body size decreases, the risk of nest predation likely goes up, because larger birds are more capable of nest defense. Thus, small species not only experience more of their total drag as skin friction, but they also may be more likely to grow cheap “decomposed” juvenile feathers to facilitate rapid fledging. By this logic nestling predation drives the quality of the juvenile plumage, which entrains things like how long this plumage is worn and whether adults feed fledglings while they undergo their first prebasic molt of body feathers.

The preceding speculation about juvenile plumage quality suggests that “decomposed” juvenile plumages “hold back” juveniles from migrating with adults. To explore this question we compared feather quality in species that were off-off concordant with those that were off-on discordant

Table 8.2 Concordance between adults and yearlings on the location of the prebasic molt of body feathers

		Yearlings		Totals
		Off	On	
Adults	Off	21	7	28
	On	0	82	82
	Totals	21	89	110

(having adults that migrate before molting and juveniles after molting [table 8.2]). To assess feather quality we counted barbs on flank feathers of adults and juveniles. For each species, we measured three to five juvenile specimens and three to five adult specimens, with similar proportions of each sex in each age class. For each specimen, we counted the total number of barbs (medial and lateral side of each feather) on the distal 1 cm of three flank feathers, starting within 2–3 mm from the tip of the feather, at the point where barbs began being regularly spaced. Mean barb counts were computed for each specimen and used to compute age class means for each species. All barb measurements were made by LKB using a lighted, 10× magnifying glass.

To correct for species differences in mean barb number we compared $(C_a - C_j)/C_a$, where C_a is the adult barb count and C_j is the juvenile barb count. Values above 0 characterize species for which adults have higher-quality feathers than juveniles, and values below 0 would represent species for which adults have lower-quality feathers than juveniles (fig. 8.1).

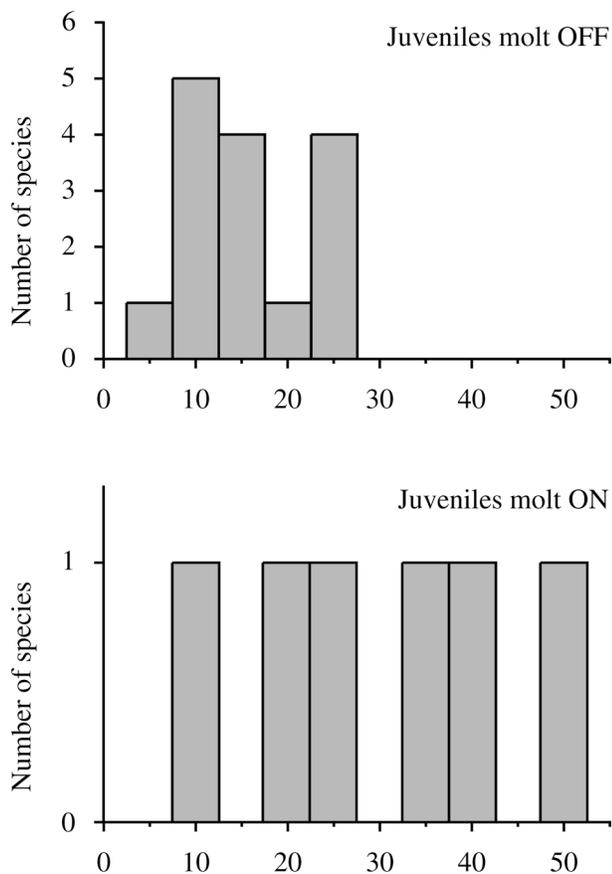


Fig. 8.1. Quality contrasts between the adult definitive basic and the juvenile body plumage for species in which adults migrate before they molt. The top graph contrasts these plumages for species in which juveniles molt after they have migrated in juvenile plumage; the bottom graph contrasts species in which juveniles remain behind to replace their body plumage on the breeding grounds and migrate in first basic plumage.

Unfortunately, the list of comparisons we were able to make is limited because there are few off-on species (table 8.2), so phylogenetically independent contrasts could not be attempted. Nonetheless, those species characterized by discordance (adults molting after migration, juveniles molting before migration) have barb count differences significantly greater than species in which juveniles migrate with adults before molting ($P[\text{AQ1}] = 0.003$, t -test [fig. 8.1]). Further exploration of this comparative contrast will require incorporating migrants from other parts of the world with age contrasts in molt scheduling (if any exist!), because there are so few Neotropical migrants with age class discordance. Nevertheless, the success of this comparison suggests that feather quality merits further exploration: Will drag forces be higher in species with more decomposed juvenile plumages? Does a highly decomposed juvenile plumage reflect the demography of nesting success, or is it related to something entirely different, such as thermoregulation?

COMPARISONS WITH PALEARCTIC MIGRANTS WINTERING IN AFRICA

Does the Push of Aridity Apply to Trans-Saharan Migrants?

The contrast in molt scheduling between eastern and western Neotropical migrant passerines prompted us to ask how general might be the “push” of late-summer aridity. Thus, we asked if the subset of trans-Saharan migrants having predominantly Mediterranean breeding distributions in Europe and western Asia tended to molt after their southward migration. We examined the 51 species listed in table 8.2 of Jenni and Winkler (1994) for this comparison. Other than swallows, all of the Palearctic migrants included in their table renew body plumage before migrating. Thus, the only comparison relevant to the Nearctic migrants of western North America was the scheduling of flight feather replacement.

To our surprise, species that breed in the Mediterranean region were no more likely to molt after migrating than species that are more widely distributed in the eastern Palearctic. For the 16 species with breeding ranges restricted to the Mediterranean region, 43.8% molted their flight (and body) feathers after the fall migration. For the 35 species with larger breeding ranges in the western Palearctic, 42.9% molted after the fall migration. Although late-summer aridity is far more severe and affects a much larger region of western North America than is true of the Mediterranean region of Europe, this result weakly suggests that the “pull” of the Mexican Monsoon may be as important as the “push” to depart a drying breeding range for passerines of the American West.

Molt Scheduling in Trans-Saharan Migrants

Trans-Saharan migrants of the western Palearctic generally molt body plumage in the breeding range, but they are re-

markedly variable in the timing of their primary molt relative to the fall migration (Moreau 1972; Alerstam and Högstedt 1982; Jenni and Winkler 1994; Jones 1995; Svensson and Hedenstrom 1999). In contrast, Neotropical migrants typically molt their body and flight feathers together in the fall.

Using *Phylloscopus* warblers, Svensson and Hedenström (1999) showed seven to ten independent origins of body and flight feather molt being separated by migration. Evolutionary lability in molt scheduling is strongly supported, but there is little consensus about ecological and demographic causes. As has been suggested for North American species (Sealy and Biermann 1983), winter territoriality is sometimes suggested as favoring departure from the breeding range before molting (Alerstam and Högstedt 1982; Lindstrom et al. 1993), but we are unaware of comparative tests of this hypothesis for Palearctic migrants. Time constraints are suggested by two associations. First, delaying molt until winter is significantly associated with longer migrations in *Phylloscopus* (Svensson and Hedenström 1999). Second, in some Eurasian species, multibrooding is associated with a delay in replacement of flight feathers until arrival on their African wintering grounds, where the birds spend most of the year (Alerstam and Högstedt 1982; Jones 1995).

Insights from Nearctic-Palearctic Comparisons

The hypothesis that winter territoriality favors molting after migration is based on unlikely assumptions and, as shown above, it fails empirically for Neotropical migrants. Time constraints must be important for molt scheduling, particularly for the flight feathers of large birds (Pietiäinen et al. 1984; Langston and Rohwer 1995, 1996; Rohwer 1999). Given the low variability in the rate of flight feather growth in birds of all sizes (Rohwer 1999), time constraints on molt scheduling should be minimal for most small passerines because the summed length of their primaries is small. However, in Arctic breeding passerines the molt is often so accelerated that birds in heavy molt are nearly flightless (see Jenni and Winkler 1994). Time constraints are important for aerial foragers that must molt slowly to minimize foraging costs. Indeed, time constraints may be serious enough for Chuck-will's-widows (*Caprimulgus carolinensis*) that they cannot forage during very intense late stages of their molt (Sutton 1969; Rohwer 1971; Mengel 1976). Among Nearctic and Palearctic migrants, time constraints seem particularly likely to apply to larger tyrannids and bee-eaters, which replace their flight feathers after arriving on the winter range.

Although distance of migration is associated with multiple origins of winter flight feather molt in Palearctic migrants (Svensson and Hedenström 1999), we doubt that migratory distance is a primary cause. Among Nearctic migrants, eastern breeders generally migrate much farther than western breeders, yet western species often delay their molt until after the fall migration. That nearly all eastern Nearctic migrants molt before migration seriously challenges migration distance as a causal variable for winter flight feather replacement in Palearctic migrants.

Winter Habitat and Molt Scheduling

Is there a general hypothesis that can explain the differences in molt scheduling between the long-distance migrants of North America and Eurasia? We propose that differences in exposure to sun and in the abrasiveness of winter habitats may be the primary cause of contrasts between Nearctic and western Palearctic migrants. In both of these migration systems, species inhabiting grasslands or reed beds have two complete or near-complete molts each year because of excessive abrasion of their plumage by siliceous deposits in grasses and sedges (e.g., sedge wrens [*Cistothorus*] and *Ammodramus* sparrows of North America [Woolfenden 1956], and some *Locustella* and *Acrocephalus* warblers of Eurasia [Svensson and Hedenström 1999]). These molts seem to be driven solely by plumage abrasion because these species do not change color seasonally and several migrate only short distances.

Most trans-Saharan Palearctic migrants live in harsher, more exposed, and more abrasive winter habitats than do Neotropical migrants. Eurasian migrants wintering in sub-Saharan Africa are strongly concentrated in thorn scrub and acacia savannas of the Sahel, Sudan, East Africa, and southern Africa (Moreau 1972; Jones 1995). Such habitats are more likely to abrade plumages than Neotropical forests, and prolonged exposure to UV light in African savannas likely renders feathers brittle and easily damaged (Bergman 1982). Almost no western Palearctic migrants winter in the tropical forests of Central and West Africa, presumably because of intensive competition from forest residents (Moreau 1972). In contrast, temperate forest breeders of the New World typically winter in tropical forests with more shade and softer foliage. Interestingly, except for Bobolinks, no passerine migrant to the Neotropics replaces its primaries twice a year, something that the trans-Saharan migrant *Phylloscopus trochilus* does, as do three other open-country Palearctic migrants that winter in Africa or Asia, *Lanius cristatus*, *L. tigrinus*, and *Pericrocotus divaricatus*. Environmental abrasion seems minimal during winter for forest-dwelling Neotropical migrants, because these species show minimal wear of their flight feathers when they arrive in North America in the spring, despite having carried these feathers throughout the winter.

We propose that contrasts in vegetation structure and exposure to sun between the winter habitats of western Palearctic and Nearctic migrants result in dramatic differences between these groups in abrasion of their flight feathers during winter. If, as we suggest, flight feathers deteriorate rapidly in the harsh and sunny winter habitat occupied by Palearctic migrants to Africa, this feather wear may favor late-winter flight feather replacement in trans-Saharan migrants. This hypothesis is consistent with the following observations:

- Several long-distance *Phylloscopus* migrants that winter in Asian forests (*P. inornatus*, *P. proregulus*, *P. fuscatus*) replace their flight feathers before, rather than after, migrating (Svensson and Hedenström 1999).

- Trans-Saharan migrants appear to delay replacement of the flight feathers until as late in winter as foraging conditions allow. Many move to the Sahel and Sudan, where food conditions are good for 1 to 2 months after their arrival. Those that remain in these northern regions for the winter molt their flight feathers early because these areas become dry and unproductive later in winter. However, many other species stop here for a month or so and then, instead of molting, fatten and perform a second migration to meet the rains in eastern and southern Africa. Those species that proceed farther southward in this second movement do not molt until late winter (Jones 1995).

Comparative tests of habitat-related differences in the rates of feather wear would be informative. An obvious test would be to look for differences in rates of feather damage caused by abrasion and exposure to sunlight between migrants to the Neotropics and Palearctic migrants to sub-Saharan Africa.

METHODOLOGICAL RECOMMENDATIONS

Our experience attempting to document molt-migration scheduling from museum specimens prompts us to offer several suggestions for improving such studies. On the one hand, museum specimens offer comprehensive and directly comparable data from throughout breeding, migratory, and winter ranges. This is a huge advantage. On the other hand, collecting effort varied enormously throughout the year with the effect that, although birds may be abundant in particular times and places, museum specimens from those times and places may be sparse. This is strikingly true of North American migrants in the Neotropics from September to December (see Rohwer 1986 for Indigo Buntings). Such collecting biases are also apparent for July, August, and September from the Mexican Monsoon region. Furthermore, throughout much of its history, most collecting in North America targeted breeding birds for the description of geographic variation. Collectors also avoided molting birds, and the extreme heat and humidity during the Mexican Monsoon has resulted in little fieldwork in this region at exactly the time when it is used as a stopover site for molting.

Shortages of specimens taken during the late summer and fall in the American Southwest and the Neotropics are further exacerbated by the relative abundance of specimens from late summer from areas to the north, where more late-summer and fall collecting and salvage take place. For example, although most adult Western Tanagers depart the North to molt in the Southwest, nearly as many adults in primary feather molt come from the breeding range as from the American Southwest (Butler et al. 2002). In this case establishing that most adults move before molting was easy for two reasons. First, although molting adults collected on the breeding grounds in late summer are relatively uncommon,

there are hundreds of molting juveniles in collections from this region. These young birds, as well as many additional nonmolting adults from the north, assure us that molting adults are not missing from this region simply because collectors were not active. Second, if a period when most adults are in molt is defined (16 July–31 October for the Western Tanager), it then becomes possible to compare the proportion of adults taken in this period from the breeding range and from the Southwest that are in molt. Although few adults have been collected in the Southwest during this period, most are in molt. The converse is true for areas to the north, suggesting that nonmolting late-summer birds taken in the North are mostly late breeders that would still have left before molting (Butler et al. 2002).

Because of systematic collecting biases, researchers should use molt rates (e.g., percent specimens in molt by region and time period) or measures of collecting effort (e.g., [adults]/[adults + young]) to reliably evaluate whether most birds leave their breeding area to molt. More general measures of collecting effort should now be possible with data from increasing numbers of collections being available online. For example, the total number of specimens of other species collected can be used as an index of collecting effort for a selected region and time period. Incorporating measures of collecting effort should greatly increase the likelihood of detecting subtle molt-related movements.

The common practice of targeting only molting-season specimens minimizes the possibility of distinguishing short-distance molt-related movements. For example, Western Tanager juveniles hatched in the Great Basin appear to disperse to nearby high-elevation forests to molt. The departure of juveniles out of the Great Basin could not have been established without comparing the geographical distribution of molting juveniles with the distribution of “hatchling” juveniles, which was measured by the distribution of breeding adults (Butler et al. 2002). Thus, studies of molt-related movements should consider the distribution of breeding-season specimens, which are normally excluded to reduce the size of specimen loans.

Finally, we note that the importance of the Mexican Monsoon region as a molt stopover site for other species could be evaluated by using stable isotopes from the huge numbers of specimens available from the breeding grounds. However, this methodology depends on whether the Mexican Monsoon region has a unique isotope signature (Marra et al. 1998; Hobson 1999).

FUTURE DIRECTIONS

Molt is among the most important activities driving the evolution of avian life histories. Despite its high energetic costs (Murphy and King 1992), implications for survival (Nilsson and Svensson 1996; Dawson et al. 2000), and enormous time requirements (Rohwer 1999), few avian biologists have explored the relevance of molting to avian life history evolution. Every section of this chapter reveals serious short-

comings in our understanding of the scheduling of molt and migration in migrant passerines. Only recently have we discovered the importance of the region of the Mexican Monsoon as a molting ground for Neotropical migrant passerines. Future collection-based studies of molt scheduling in individual species should raise the bar for data quality by using on-line data bases to generate powerful interspecific indices of collecting effort. With such indices we expect that additional species with breeding ranges that include the region of the Mexican Monsoon, but that also extend well north of this region, will be added to the list of species that rely on this region for their fall molt. Indeed, this could even include Lark Sparrows, which we recently encountered in this region in August and September in numbers far beyond breeding densities.

With our growing awareness of the importance of this region for molting, we badly need to understand the ecology of species that move there to molt (Leu and Thompson 2002). How many are using riparian corridors, which have been seriously degraded by agriculture and the invasion of salt cedar (*Tamarix*)? Our recent (and inconclusive) survey suggested that molt migrants were mostly using lowland acacia flats, a habitat that seemed less degraded than riparian corridors, but is heavily affected by grazing and efforts to make pastures more productive. Exactly which habitats in this region so many North American birds are using to molt remain unknown, mainly because no one has looked for them.

Similarly, we know little of the ecology of molting for those western species (or age classes) that breed in arid regions and that do not move to the monsoon region to molt. In an extensive search of the literature we found just two references (Greenberg et al. 1974; Steele and McCormick 1995) documenting upslope movements for molting. Surely there are good data residing in banding files for numerous MAPS stations that could be used to explore such movements for additional species.

Finally, for all the importance of feathers in the lives of birds, the avian literature is remarkable for its absence of papers interpreting the significance of structural variation among contour feathers. As we have shown here, lax juvenile plumages may prevent juveniles in some species from migrating before they molt in the fall. Studies of the significance of variation in feather quality have the potential of becoming career research programs. Similarly, studies of how rates of wear vary across habitats and, thus, how differences in wear could affect the scheduling of molt between western Palearctic-African migrants and Neotropical migrants will likely be elucidating.

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APPENDIX: CATEGORIZATIONS OF SPECIES USED IN THE COMPARATIVE ANALYSES OF ROHWER, BUTLER, AND FROEHLICH AND FROEHLICH, ROHWER, AND STUTCHBURY

This table provides a list of how we categorized species with respect to the location of their breeding grounds, molts winter territoriality. The data on molt mostly came from Pyle (1997); better or updated references that change Pyle's categorizations are listed in the text of Rohwer et al. (2003), but are not flagged in this appendix. Because there are few detailed studies of Neotropical migrants on their wintering grounds, the classification of species with regard to winter

territoriality is difficult. For this reason we have provided a list of the references we consulted in making these decisions. Many of these references were also used in the analyses by Froehlich et al. (Chap. 25, this volume). To avoid duplication, we have presented the complete list of references on winter territoriality here. Scientific names follow the AOU Checklist (1998), except that we treat eastern and western populations of Warbling Vireo as separate species.

Common name	Species	Breeding grounds	Adult prebasic molt	First-year prebasic molt	Winter territorial	Winter territoriality references
Olive-sided Flycatcher	<i>Contopus cooperi</i>	Continental	Winter	Winter	Yes	Meyer de Schauensee et al. 1978; Ridgely & Tudor 1994; Stiles & Skutch 1989; Nickell 1968
Western Wood-Pewee	<i>Contopus sordidulus</i>	Western	Winter	Winter	Yes	Bemis & Rising 1999
Eastern Wood-Pewee	<i>Contopus virens</i>	Eastern	Winter	Winter	Yes	Fitzpatrick 1980; Willis 1966
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	Eastern	Winter	Breeding	Yes	Rappole & Warner 1980; Stiles & Skutch 1989; Dickey & van Rossem 1938
Acadian Flycatcher	<i>Empidonax virescens</i>	Eastern	Breeding	Breeding	Yes	Willis 1966; Morton 1980; Stiles & Skutch 1989; Ridgely & Gwynne 1989
Alder Flycatcher	<i>Empidonax alnorum</i>	Northern	Winter	Winter	Yes	Ridgely & Tudor 1994; Lowther 1999;
Willow Flycatcher	<i>Empidonax traillii</i>	Continental	Winter	Winter	Yes	Gorski 1969; Ridgely & Tudor 1994
Least Flycatcher	<i>Empidonax minimus</i>	Eastern	Breeding	Breeding	Yes	Ely 1973; Rappole & Warner 1980
Hammond's Flycatcher	<i>Empidonax hammondi</i>	Western	Breeding	Breeding		
Gray Flycatcher	<i>Empidonax wrightii</i>	Western	Winter	Winter	Yes	Sterling 1999
Dusky Flycatcher	<i>Empidonax oberholseri</i>	Western	Winter	Winter		
Pacific-Slope Flycatcher	<i>Empidonax difficilis</i>	Western	Winter	Winter	Yes	Hutto 1987; Lowther 2000;
Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	Western	Winter	Winter	Yes	Hutto 1987; Lowther 2000;
Eastern Phoebe	<i>Sayornis phoebe</i>	Eastern	Breeding	Breeding		
Say's Phoebe	<i>Sayornis saya</i>	Western	Breeding	Breeding		
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	Western	Stopover/ winter	Stopover/ winter		
Great-crested Flycatcher	<i>Myiarchus crinitus</i>	Eastern	Breeding	Breeding	Yes	Willis 1966; Morton 1980
Cassin's Kingbird	<i>Tyrannus vociferans</i>	Western	?	?		
Western Kingbird	<i>Tyrannus verticalis</i>	Western	Winter	Winter	No	Stiles & Skutch 1989; Gamble & Bergin 1996; Dickey & van Rossem 1938
Eastern Kingbird	<i>Tyrannus tyrannus</i>	Continental	Winter	Winter	No	Fitzpatrick 1980; Morton 1980; Ridgely & Tudor 1994
Gray Kingbird	<i>Tyrannus dominicensis</i>	Eastern	Winter	Winter	No	Meyer de Schauensee et al. 1978
Scissor-tailed Flycatcher	<i>Tyrannus forficatus</i>	Eastern	?	?	No	Stiles & Skutch 1989; Regosin 1998
Purple Martin	<i>Progne subis</i>	Continental	Winter	Winter	No	Ridgely & Tudor 1989; Brown 1997;
Tree Swallow	<i>Tachycineta bicolor</i>	Continental	Migration	Migration	No	Ridgely & Gwynne 1989; Howell & Webb 1995;
Violet-green Swallow	<i>Tachycineta thalassina</i>	Western	Migration	Migration	No	Dickey & van Rossem 1938; Bent 1942
N. Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>	Continental	Migration	Migration	No	Dejong 1996
Bank Swallow	<i>Riparia riparia</i>	Continental	Winter	Winter	No	Garrison 1999
Cliff Swallow	<i>Hirundo pyrrhonota</i>	Continental	Winter	Winter	No	Ridgely & Tudor 1989

Common name	Species	Breeding grounds	Adult prebasic molt	First-year prebasic molt	Winter territorial	Winter territoriality references
Barn Swallow	<i>Hirundo rustica</i>	Continental	Winter	Winter	No	Brown & Brown 1999
Gray Catbird	<i>Dumetella carolinensis</i>	Eastern	Breeding	Breeding	Yes	Nickell 1968; Rappole & Warner 1980
Veery	<i>Catharus fuscescens</i>	Eastern	Breeding	Breeding	No	Willis 1966
Gray-cheeked Thrush	<i>Catharus minimus</i>	Northern	Breeding	Breeding	No	Willis 1966
Bicknell's Thrush	<i>Catharus bicknelli</i>	Eastern	Breeding	Breeding	Yes	Rimmer, pers. comm.
Swainson's Thrush	<i>Catharus ustulatus</i>	Continental	Breeding	Breeding	No	Willis 1966
Hermit Thrush	<i>Catharus guttatus</i>	Continental	Breeding	Breeding	Yes	Brown et al. 2000
Wood Thrush	<i>Hylocichla mustelina</i>	Eastern	Breeding	Breeding	Yes	Morton 1980; Rappole & Warner 1980; Rappole et al. 1992; Winker et al. 1990; Willis 1966
Blue-gray Gnatcatcher	<i>Poliptila caerulea</i>	Continental	Breeding	Breeding	No	Hutto 1994
White-eyed Vireo	<i>Vireo griseus</i>	Eastern	Breeding	Breeding	Yes	Barlow 1980; Rappole & Warner 1980
Bell's Vireo	<i>Vireo bellii</i>	Continental	Breeding	Breeding	Yes	Barlow 1980
Black-capped Vireo	<i>Vireo atricapillus</i>	Eastern	Breeding	Breeding	Yes	Barlow 1980
Gray Vireo	<i>Vireo vicinior</i>	Western	Breeding	Breeding	Yes	Barlow 1980; Bates 1992; Barlow et al. 1999
Yellow-throated Vireo	<i>Vireo flavifrons</i>	Eastern	Breeding	Breeding	Yes	Barlow 1980; Morton 1980; Stiles & Skutch 1989
Plumbeous Vireo	<i>Vireo plumbeus</i>	Western	Breeding	Breeding	Yes	Barlow 1980
Cassin's Vireo	<i>Vireo cassinii</i>	Western	Breeding	Breeding	Yes	Barlow 1980
Blue-headed Vireo	<i>Vireo solitarius</i>	Eastern	Breeding	Breeding	Yes	Barlow 1980; James 1998
Eastern Warbling Vireo	<i>Vireo gilvus</i>	Eastern	Breeding	Breeding	No	Dickey & van Rossem 1938; Meyer de Schauensee et al. 1978; but see Barlow 1980
Western Warbling Vireo	<i>Vireo swainsonii</i>	Western	Stopover	Breeding	No	Hutto 1994
Philadelphia Vireo	<i>Vireo philadelphicus</i>	Eastern	Breeding	Breeding	No	Barlow 1980; Dickey & van Rossem 1938; Wetmore et al. 1984; Moskoff & Robinson 1996; Tramer & Kemp 1980; Stiles & Skutch 1989; but see Loftin 1977
Red-eyed Vireo	<i>Vireo olivaceus</i>	Eastern	Breeding	Breeding	No	Barlow 1980
Black-whiskered Vireo	<i>Vireo altiloquus</i>	Eastern			No	Barlow 1980
Lesser Goldfinch	<i>Carduelis psaltria</i>	Western	Stopover	Stopover	No	Howell & Webb 1995
Blue-winged Warbler	<i>Vermivora pinus</i>	Eastern	Breeding	Breeding	Yes	Morton 1980
Golden-winged Warbler	<i>Vermivora chrysoptera</i>	Eastern	Breeding	Breeding	Yes	Morton 1980; Tramer & Kemp 1980; Stiles & Skutch 1989
Tennessee Warbler	<i>Vermivora peregrina</i>	Northern	Breeding	Breeding	No	Morton 1980; Tramer & Kemp 1980; Stiles & Skutch 1989; Ridgely & Gwynne 1989; Dickey & van Rossem 1938; Meyer de Schauensee et al. 1978; but see Thurber & Villeda 1976
Orange-crowned Warbler	<i>Vermivora celata</i>	Continental	Breeding*	Breeding*	Yes	Rappole & Warner 1980
Nashville Warbler	<i>Vermivora ruficapilla</i>	Continental	Breeding*	Breeding*	No	Hutto 1994; Beebe in Bent 1953
Virginia's Warbler	<i>Vermivora virginiae</i>	Western	Breeding	Breeding	No	Curson et al. 1994; Olson & Martin 1999; but see Howell & Webb 1995
Lucy's Warbler	<i>Vermivora luciae</i>	Southwestern	Breeding	Breeding	No	Howell & Webb 1995; Johnson et al. 1997
Northern Parula	<i>Parula americana</i>	Eastern	Breeding	Breeding	No	Faaborg & Arendt 1984; Staicer 1992; but see Diamond & Smith 1973
Yellow Warbler	<i>Dendroica petechia</i>	Continental	Breeding	Breeding	Yes	Morton 1980; Rappole & Warner 1980; Greenberg & Salgado-Ortiz 1994; Warkentin & Hernandez 1996; Hutto 1981a
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>	Eastern	Breeding	Breeding	Yes	Gradwohl & Greenberg 1980; Morton 1980; Greenberg 1984
Magnolia Warbler	<i>Dendroica magnolia</i>	Eastern	Breeding	Breeding	Yes	Rappole & Warner 1980; Morton 1980; Greenberg & Salgado-Ortiz 1994; Greenberg 1979
Cape May Warbler	<i>Dendroica tigrina</i>	Eastern	Breeding	Breeding	Yes	Eaton 1953; Staicer 1992; Latta & Wunderle 1996
Black-thr. Blue Warbler	<i>Dendroica caerulescens</i>	Eastern	Breeding	Breeding	Yes	Holmes et al. 1989; Wunderle 1995; Wunderle & Latta 2000

Common name	Species	Breeding grounds	Adult prebasic molt	First-year prebasic molt	Winter territorial	Winter territoriality references
Audubon's Warbler	<i>Dendroica coronata</i>	Western	Breeding	Breeding	No	Rappole & Warner 1980; Latta & Wunderle 1996; Howell 1972; Greenberg 1979
Myrtle Warbler	<i>Dendroica coronata</i>	Northern	Breeding	Breeding	No	Rappole & Warner 1980; Latta & Wunderle 1996; Howell 1972; Greenberg 1979
Black-thr. Gray Warbler	<i>Dendroica nigrescens</i>	Western	Breeding	Breeding	No	Curson et al. 1994
Golden-cheeked Warbler	<i>Dendroica chrysoparia</i>	Eastern	Breeding	Breeding	Yes?	Vidal, R. M. et al. 1994; King & Rappole 2000; Ladd & Gass 1999
Black-thr. Green Warbler	<i>Dendroica virens</i>	Eastern	Breeding	Breeding	Yes	Skutch in Bent 1953; Rappole & Warner 1980; Latta & Wunderle 1996; Tramer & Kemp 1980; Greenberg 1979; but see Dickey & van Rossem 1938
Townsend's Warbler	<i>Dendroica townsendi</i>	Western	Breeding	Breeding	No	Froehlich, unpub. data; Curson et al. 1994; Dunn & Garrett 1997; but see Tramer & Kemp 1980 and Thurber & Villeda 1976
Hermit Warbler	<i>Dendroica occidentalis</i>	Western	Breeding	Breeding	No	Curson et al. 1994
Blackburnian Warbler	<i>Dendroica fusca</i>	Eastern	Breeding	Breeding	No	Chipley 1980; Ridgely & Tudor 1989; but see Stiles & Skutch 1989
Yellow-throated Warbler	<i>Dendroica dominica</i>	Eastern	Breeding	Breeding	Yes	Howell 1972; Curson et al. 1994; Howell & Webb 1995; but see Hall 1996
Grace's Warbler	<i>Dendroica graciae</i>	Southwestern	Breeding	Breeding	No	Curson et al. 1994; Howell & Webb 1995
Kirtland's Warbler	<i>Dendroica kirtlandii</i>	Eastern	Breeding	Breeding	Yes	Mayfield 1992
Prairie Warbler	<i>Dendroica discolor</i>	Eastern	Breeding	Breeding	Yes	Staicer 1992; Latta & Wunderle 1996; Diamond & Smith 1973
Palm Warbler	<i>Dendroica palmarum</i>	Eastern	Breeding	Breeding	No	Eaton 1953; Ridgely & Gwynne 1989; but see Howell 1972
Bay-breasted Warbler	<i>Dendroica castanea</i>	Eastern	Breeding	Breeding	No	Greenberg 1984
Blackpoll Warbler	<i>Dendroica striata</i>	Northern	Breeding	Breeding	No	Meyer de Schauensee et al. 1978; but see Sick 1971
Cerulean Warbler	<i>Dendroica cerulea</i>	Eastern	Breeding	Breeding	No	Meyer de Schauensee et al. 1978; Robbins et al. 1992;
Black-and-white Warbler	<i>Mniotilta varia</i>	Eastern	Breeding	Breeding	Yes	Morton 1980; Rappole & Warner 1980; Rappole et al. 1992; Latta & Wunderle 1996; Wunderle & Latta 2000; Ornat & Greenberg 1990
American Redstart	<i>Setophaga ruticilla</i>	Eastern	Breeding	Breeding	Yes	Rappole & Warner 1980; Latta & Wunderle 1996; Holmes et al. 1989; Ornat & Greenberg 1990; Marra et al. 1993; Warkentin & Hernandez 1996; Wunderle & Latta 2000
Prothonotary Warbler	<i>Protonotaria citrea</i>	Eastern	Breeding	Breeding	No	Morton 1980; Lefebvre et al. 1994; Warkentin & Hernandez 1996
Worm-eating Warbler	<i>Helmitheros vermivorus</i>	Eastern	Breeding	Breeding	Yes	Rappole & Warner 1980; Rappole et al. 1992; Diamond & Smith 1973
Swainson's Warbler	<i>Limnothlypis swainsonii</i>	Eastern	Breeding	Breeding	Yes	Eaton 1953; Diamond & Smith 1973; Brown & Dickson 1994
Ovenbird	<i>Seiurus aurocapillus</i>	Eastern	Breeding	Breeding	Yes	Rappole & Warner 1980; Rappole et al. 1992; Faaborg & Arendt 1984; Eaton 1953; Warkentin & Hernandez 1996
Northern Waterthrush	<i>Seiurus noveboracensis</i>	Northern	Breeding	Breeding	Yes	Rappole & Warner 1980; Morton 1980; Warkentin & Hernandez 1996; Schwartz 1964
Louisiana Waterthrush	<i>Seiurus motacilla</i>	Eastern	Breeding	Breeding	Yes	Eaton 1953; Rappole & Warner 1980; Robinson 1995; Eaton 1953; Morton 1980

Common name	Species	Breeding grounds	Adult prebasic molt	First-year prebasic molt	Winter territorial	Winter territoriality references
Kentucky Warbler	<i>Oporornis formosus</i>	Eastern	Breeding	Breeding	Yes	Morton 1980; Rappole & Warner 1980; Mabey & Morton 1992; Rappole et al. 1992; Willis 1966
Connecticut Warbler	<i>Oporornis agilis</i>	Eastern	Breeding	Breeding	Yes	Meyer de Schauensee et al. 1978; Pitocchelli et al. 1997; Curson et al. 1994
Mourning Warbler	<i>Oporornis philadelphia</i>	Eastern	Breeding	Breeding	Yes	Meyer de Schauensee et al. 1978; Morton 1980; Dunn & Garrett 1997; Stiles & Skutch 1989
Macgillivray's Warbler	<i>Oporornis tolmiei</i>	Western	Breeding	Breeding	Yes	Hutto 1981a; Stiles & Skutch 1989; Dunn & Garrett 1997
Common Yellowthroat	<i>Geothlypis trichas</i>	Continental	Breeding	Breeding	Yes	Hutto 1981a; Ornat & Greenberg 1990; Rappole & Warner 1980
Hooded Warbler	<i>Wilsonia citrina</i>	Eastern	Breeding	Breeding	Yes	Rappole & Warner 1980; Rappole et al. 1992; Ornat & Greenberg 1990
Wilson's Warbler	<i>Wilsonia pusilla</i>	Continental	Breeding	Breeding	Yes	Skutch in Bent 1953; Hutto 1987; Tramer & Kemp 1980; Hutto 1981a; Loftin 1977; Rappole & Warner 1980; Rappole et al. 1992
Canada Warbler	<i>Wilsonia canadensis</i>	Eastern	Breeding	Breeding	Yes	Greenberg & Gradwohl 1980; but see Willis 1966
Yellow-breasted Chat	<i>Icteria virens</i>	Continental	Breeding	Breeding	Yes	Diamond & Smith 1973; Stiles & Skutch 1989; Rappole & Warner 1980
Hepatic Tanager	<i>Piranga flava</i>	Southwestern	Breeding	Breeding	No	Meyer de Schauensee et al. 1978; Howell & Webb 1995; Stiles & Skutch 1989
Scarlet Tanager	<i>Piranga olivacea</i>	Eastern	Breeding	Breeding	Yes	Ridgely & Tudor 1989; Mowbray 1999; Howell & Webb 1995; but see Stiles & Skutch 1989
Summer Tanager	<i>Piranga rubra</i>	Continental	Breeding	Breeding	Yes	Morton 1980; Rappole & Warner 1980; Stiles & Skutch 1989; Howell & Webb 1995
Western Tanager	<i>Piranga ludoviciana</i>	Western	Stopover	Breeding ^a	Yes	Stiles & Skutch 1989; Howell & Webb 1995
Green-tailed Towhee	<i>Pipilo chlorurus</i>	Western	Breeding	Breeding	No	Dobbs et al. 1998
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	Eastern	Breeding	Breeding	No	Loftin 1977; Stiles & Skutch 1989; Howell & Webb 1995
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	Western	Stopover	Breeding	No	Howell & Webb 1995
Blue Grosbeak	<i>Guiraca caerulea</i>	Continental	Winter	Breeding	No	Howell 1972; Stiles & Skutch 1989; Howell & Webb 1995
Lazuli Bunting	<i>Passerina amoena</i>	Western	Stopover	Breeding	No	Howell & Webb 1995; Greene et al. 1996
Indigo Bunting	<i>Passerina cyanea</i>	Eastern	Breeding	Breeding	No	Nickell 1968; Rappole & Warner 1980; Payne 1992; Stiles & Skutch 1989; Howell & Webb 1995
Painted Bunting (E. coast)	<i>Passerina ciris</i>	Eastern	Breeding	Breeding	Yes	Froehlich, pers. obs.
Painted Bunting (Central)	<i>Passerina ciris</i>	Eastern	Stopover	Stopover	No	Rappole & Warner 1980; Howell & Webb 1995
Dickcissel	<i>Spiza americana</i>	Eastern	Breeding	?	No	Meyer de Schauensee et al. 1978; Ridgely & Gwynne 1989; Basili 1998
Bobolink	<i>Dolichonyx oryzivorus</i>	Eastern	Breeding	Breeding	No	Ridgely & Tudor 1989
Hooded Oriole	<i>Icterus cucullatus</i>	Southwestern	Winter	Winter	No	Howell & Webb 1995
Baltimore Oriole	<i>Icterus galbula</i>	Eastern	Breeding	Breeding	No	Morton 1980; Stiles & Skutch 1989; Howell & Webb 1995
Bullock's Oriole	<i>Icterus bullockii</i>	Western	Stopover	Stopover	No	Howell & Webb 1995
Orchard Oriole	<i>Icterus spurius</i>	Eastern	Winter	Winter	No	Greenberg & Salgado Ortiz 1994; Stiles & Skutch 1989; Dickey & Van Rossem 1938; Nickell 1968; Morton 1980; Howell & Webb 1995
Scott's Oriole	<i>Icterus parisorum</i>	Western	Breeding	Breeding	No	Howell & Webb 1995

^aIndividuals of these species generally move upslope to higher elevations in the intermontane West after breeding or fledging.

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