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MOLT SCHEDULING OF WESTERN NEOTROPICAL MIGRANTS AND UP-SLOPE MOVEMENT OF CASSIN'S VIREO

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Abstract. We investigate the effects of body mass and breeding habitat use on the timing and location of the fall molt of western Neotropical migrant passerines. Most western migrants that molt within their breeding ranges breed in coniferous forests, while most that move south before molting breed in low elevation broadleaf or open habitats. We show that larger passerines take longer to molt than smaller passerines and that larger species are more likely to migrate south before molting, whereas smaller species are more likely to molt in their breeding ranges, presumably because their molts take less time. To test our habitat results, we surveyed Cassin's Vireos (*Vireo cassinii*) during their breeding and molting season in Washington to assess up-slope movements. Vireos that bred in low elevation coniferous forest (usually ponderosa pine [*Pinus ponderosa*] or Douglas-fir [*Pseudotsuga menziesii*]) moved up-slope at least 300 m to molt in wetter, high-elevation Douglas-fir forests.

Key words: molt and elevation, molt-migration, molt rate, size and up-slope movement, Vireo cassinii.

Cronología de la Muda en Aves Migratorias Neotropicales del Occidente y Movimientos Altitudinales de *Vireo cassinii*

Resumen. Investigamos el efecto de la masa corporal y del hábitat de anidación sobre el momento y lugar en que sucede la muda en aves paserinas neotropicales. La gran mayoría de las especies de paserinos migratorios occidentales que mudan dentro de su ámbito de anidación lo hacen en bosques de coníferas, mientras que muchas de las especies que migran hacia al sur antes de mudar, anidan a elevaciones menores en hábitats abiertos o en bosques caducifolios. Encontramos que en los paserinos más grandes el tiempo de muda es mayor en comparación con las especies de menor tamaño. Además, las especies de mayor tamaño tienden a migrar hacia al sur antes de la muda, mientras que los paserinos pequeños tienden a mudar en el mismo sitio de anidación, probablemente debido a que el tiempo de muda es más corto. Para poner a prueba nuestros resultados acerca del hábitat de anidación, realizamos censos de *Vireo casiini* durante la temporada de anidación y de muda en el estado de Washington para evaluar los movimientos altitudinales. Los individuos que anidaron a elevaciones bajas en los bosques de confieras se desplazaron por lo menos 300 m cuesta arriba a finales del verano, para mudar en bosques de coníferas más húmedos de alta elevación.

Migratory birds must make two annual migrations, breed, and replace their feathers (molt) each year. Spring migration and breeding are fixed in the annual cycle because early fledging is associated with high survival of young (Lack 1968). This leaves flexibility only in the scheduling of molt relative to the fall migration.

Comparative studies of Neotropical migrant passerines have revealed striking east-west contrasts in the timing of molt relative to the fall migration. Most migrants that breed in the east molt within their breeding ranges before migrating because the east remains productive in late summer. In contrast, about half of western breeding migrants migrate to northwestern Mexico before molting (Rohwer et al. 2005), while other western migrants complete their molts within their breeding ranges. Western species that migrate before molting are thought to be "pushed" away from their breeding range by late summer aridity and to be "pulled" to the region of the Mexican monsoon, where abundant food is available to support the energetic demands of molting (Rohwer et al. 2005). The "push-pull" hypothesis helps understand the east-west contrast, but it offers little insight into why nearly half of western Neotropical migrants molt within their breeding ranges.

An alternative to molting in the region of the Mexican monsoon is moving up-slope to molt. High elevation habitats remain wetter during late summer and presumably continue to produce food throughout the late summer molting season. Moving up-slope to molt is currently documented only for Nashville Warblers (*Vermivora ruficapilla*) in California (Greenberg et al. 1974), but such movements are also suggested for juvenile Western Tanagers (*Piranga ludoviciana*), which are frequently collected at high elevations in late summer (Butler et al. 2002). Up-slope movements of the Nashville Warbler suggest that other western species that molt within their breeding ranges may also move up-slope to molt, especially if these movements do not require habitat changes.

The purpose of this paper is three-fold. First, we show that most western species that molt within their breeding ranges breed in coniferous forest, which presumably enables them to move up-slope for molting without experiencing dramatic habitat changes. Second, using body mass as a measure of size for

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The Condor, Vol. 110, Number 2, pages 365–370. ISSN 0010-5422, electronic ISSN 1938-5422. © 2008 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/cond.2008.8321

these same species, we show that western passerines that molt within their breeding ranges are smaller and therefore require less time to molt than western passerines that move to the region of the Mexican monsoon to molt. Third, we examine upslope movements in Cassin's Vireo (*Vireo cassinii*), a small western breeding bird of coniferous forest that molts within its breeding range.

METHODS

CATEGORIZING SPECIES

We used Appendix 1 of Rohwer et al. (2005) to categorize western Neotropical migrants as breeding range– or as monsoon-molting birds (Table 1) and compared the breeding habitats used by these two groups of species. We excluded from our analyses several western species that molt on their winter ranges (south of the monsoon region) because we do not understand the forces favoring wintering-ground molts in North American passerines. Although the Gray Flycatcher (*Empidonax wrightii*) molts on its winter range, we included it because much of its winter range lies in the monsoon region of western Mexico (Sterling 1999, Johnson 1963) and because we have documented a number of molting adults in coastal Sinaloa, showing that it molts in the monsoon region. We also excluded transcontinental species with the exception of the "Western" Warbling Vireo (*Vireo gilvus swainsonii*); *V. g. swainsonii* was included because it molts after migration (unlike its eastern counterpart) and because it is strongly differentiated genetically from its eastern counterpart (Johnson et al. 1988; Murray el al. 1994). We excluded two Southwestern species, the Hepatic Tanager (*Piranga flava*) and Grace's Warbler (*Dendroica graciae*), because they are pine-oak specialists, and much of their breeding ranges overlap their winter ranges in the Mexican highlands. As outlined by Rohwer et al. (2005), we also excluded western emberizids because their winter ranges lie primarily in the southern United States. We excluded four western species: the Western Wood-Pewee (*Contopus sordidulus*), Say's Phoebe (*Sayornis saya*), Pacific-slope Flycatcher (*Empidonax difficilis*), and Cordilleran Flycatcher (*Empidonax occidentalis*). Each of these species molts on its winter range that lies mostly outside of the monsoon region. In three years of netting and collecting in the monsoon region of western Mexico, we have encountered but a single molting adult of either Pacific-slope or Cordilleran Flycatcher, so we presume their molt takes place south of the monsoon region.

To determine whether the breeding habitat of these 22 species included coniferous forest, we used the Birds of North America (Poole 2005) accounts. We categorized species as regularly breeding in coniferous forest or as regularly breeding in other habitats (mostly broadleaf or open habitats) and specified the Gray Flycatcher and Ash-throated Flycatcher (*Myiarchus cinerascens*) as arid coniferous breeding birds associated with pinyon pine (*Pinus* spp.) and juniper (*Juniperus* spp.). Species that breed in the Great Plains and move to the region of the Mexican monsoon to molt (Baird's Sparrow [*Ammodramus bairdii*], Voelker 2004; Lark Bunting [*Calamospiza melanocorys*], VGR, unpubl. data; Lark Sparrow [*Chondestes grammacus*], VGR unpubl. data; Painted Bunting [*Passerina ciris*], Thompson 1991) were not included in Table 1. Although plains species also face dry late-summer conditions, up-slope movements are less available to them; most breed far from mountains, and montane forests would be unsuitable for them for molting.

TABLE 1. Western Neotropical migrant passerines used to analyze the relationship between molt location (within the breeding range or in the Mexican monsoon region) and breeding habitat (scored as coniferous or broadleaf deciduous).

Species	Molt location	Use conifers
Hammond's Flycatcher (*Empidonax hammondii*)	Breeding range	Yes
Plumbeous Vireo (*Vireo plumbeus*)	Breeding range	Yes
Cassin's Vireo (*Vireo cassinii*)	Breeding range	Yes
Black-throated Gray Warbler (*Dendroica nigrescens*)	Breeding range	Yes
Townsend's Warbler (*Dendroica townsendi*)	Breeding range	Yes
Hermit Warbler (*Dendroica occidentalis*)	Breeding range	Yes
Western Tanager (*Piranga ludoviciana*)	Monsoon	Yes
Gray Vireo (*Vireo vicinior*)	Breeding range	No
Virginia's Warbler (*Vermivora virginiae*)	Breeding range	No
MacGillivray's Warbler (*Oporornis tolmiei*)	Breeding range	No
Gray Flycatcher (*Empidonax wrightii*)	Monsoon	No*
Ash-throated Flycatcher (*Myiarchus cinerascens*)	Monsoon	No*
Cassin's Kingbird (*Tyrannus vociferans*)	Monsoon	No
Western Kingbird (*Tyrannus verticalis*)	Monsoon	No
"Western" Warbling Vireo (*Vireo gilvus swainsonii*)	Monsoon	No
Lucy's Warbler (*Vermivora luciae*)	Monsoon	No
Black-headed Grosbeak (*Pheucticus melanocephalus*)	Monsoon	No
Lazuli Bunting (*Passerina amoena*)	Monsoon	No
Bullock's Oriole (*Icterus bullockii*)	Monsoon	No
Hooded Oriole (*Icterus cucullatus*)	Monsoon	No
Scott's Oriole (*Icterus parisorum*)	Monsoon	No
Lesser Goldfinch (*Carduelis psaltria*)	Monsoon	No

*Associated primarily with arid pinyon pine and juniper woodlands.

SIZE AND TIME REQUIRED TO MOLT

Pimm (1976) showed that the average time it takes an individual to replace its primaries can be estimated by regressing day of year on primary molt for comparable samples of birds (e.g., same age class or sex if molt varies by age or sex). We searched the Science Citation Index (Thomson Scientific, Philadelphia, Pennsylvania) and found "Pimm estimates" of time to replace primaries for 21 passerines from Europe and North America

TABLE 2. Data used for the regression of primary molt duration on body mass in Figure 1. All molt duration estimates follow Pimm (1976).

Species	Mass (g)	Primary molt duration (days)	Source
Ash-throated Flycatcher (*Myiarchus cinerascens*)	27.2	62	Butler et al. 2006
Western Kingbird (*Tyrannus verticalis*)	39.6	70	VGR, unpubl. data
Red-eyed Vireo (*Vireo olivaceus*)	16.7	78	Mulvihill and Rimmer 1997
"Eastern" Warbling Vireo (*Vireo gilvus gilvus*)	13.5	38	Voelker and Rohwer 1998
"Western" Warbling Vireo (*Vireo gilvus swainsonii*)	12.0	55	Voelker and Rohwer 1998
Rough-winged Swallow (*Stelgidopteryx serripennis*)	15.9	100	Yuri and Rohwer 1997
Tree Swallow (*Tachycineta bicolor*)	20.1	110	Stuchbury and Rohwer 1990
Willow Warbler (winter molt) (*Phylloscopus trochilus*)	9.6	74	Underhill et al. 1992
Willow Warbler (late summer molt) (*Phylloscopus trochilus*)	9.6	37	Underhill et al. 1992
Gray Catbird (*Dumetella carolinensis*)	36.9	49	Heise and Rimmer 2000
European Starling (*Sturnus vulgaris*)	83.0	102	Rothery et al. 2001
Virginia's Warbler (*Vermivora virginiae*)	7.8	42	Voelker and McFarland 2002
Lucy's Warbler (*Vermivora luciae*)	6.6	71	Voelker and McFarland 2002
Yellow Warbler (*Dendroica petechia*)	9.5	42	Rimmer 1988
Bullfinch (*Pyrrhula pyrrhula*)	30.0	72	Newton and Rothery 2000
Western Tanager (*Piranga ludoviciana*)	28.1	43	Butler et al. 2002
Black-headed Grosbeak (*Pheucticus melanocephalus*)	45.6	63	VGR, unpubl. data
Lazuli Bunting (*Passerina amoena*)	15.5	57	Young 1991
"Western" Painted Bunting (*Passerina ciris palidor*)	15.6	43	VGR, unpubl. data
Orange-breasted Bunting (*Passerina leclancherii*)	13.8	65	Thompson and Leu 1995
Baird's Sparrow (*Ammodramus bairdii*)	17.7	39	Voelker 2000

(Table 2). We included two species of swallows and present our analysis both with and without them because, as aerial foragers, they molt very slowly. We did not use the estimate of Thompson (1991) of Painted Bunting molt because it includes both western and eastern subspecies; our estimate is for only the western subspecies (*P. c. pallidior*). To show how the duration of primary molt is related to body size, we regressed these estimates on body mass. Masses were averages of the weights of five males and five nonlaying females from the University of Washington Burke Museum, collected in the breeding season, except for Baird's Sparrow whose weight came from Dunning (1984).

A CASE STUDY OF UP-SLOPE MOVEMENT

Cassin's Vireo is an ideal bird for assessing up-slope movement because males are vocal in both spring and fall. Cassin's Vireo is a commonly breeding species on the east slope of the Cascade Mountains of northeastern Washington and favors dry coniferous forest of ponderosa pine (*Pinus ponderosa*) or Douglas-fir (*Pseudotsuga menziesii*; Goguen and Curson 2002).

Our study site was in the Okanogan highlands of Okanogan County in eastern Washington, where continuous forested habitats suitable for vireos can be found from lower elevation ponderosa pine forests to higher elevation Douglas-fir forests. Continuous suitable habitat from low to high elevations was the primary reason for locating this survey in Okanogan County. Above the upper elevational distribution of Douglas-fir, we found mixed spruce (*Picea* spp.) and lodgepole pine (*Pinus contorta*) forests with no vireos in either spring or fall.

We conducted a single spring survey from the evening of 21 May to midafternoon of 23 May 2004, spanning an elevation range of 500–1600 m. We drove U.S. Forest Service roads through suitable habitat (i.e., pure pine forest, mixed pine and fir, pure fir forest; all of which had shrubby understories) and stopped every 0.3 km to listen for vireos. At each stop, we listened for two minutes and recorded the locations of singing vireos with a GPS receiver. On 22 May 2004, the weather varied from cloudy to light rain. We suspected that fewer vireos would be singing because of the rainy weather; thus on 23 May 2004 during sunny weather, we revisited all stops made on the 22 May survey. During this repeated survey, only one vireo was found that was not detected on 22 May; therefore, the light rain seemed to have little effect on our ability to find vireos. For each vireo found, we estimated percent Douglas-fir of the surrounding forest within a 100-m diameter around the singing vireo by visually assessing the abundance of Douglas-fir in comparison to other tree species (primarily ponderosa pine or spruce).

We conducted two kinds of surveys in the fall. From 18–21 August 2004, we repeated our spring survey by listening for vireos at each of the spring survey stops. Because Cassin's Vireos are considerably less vocal in the fall, we always listened for five min or more at places where vireos had been found in the spring; the locations of singing vireos were recorded with a GPS receiver. In addition, we expanded our fall surveys during 31 August–2 September 2004 to both higher and lower elevations, surveying an elevation range of 350–1750 m. For these dates, we made stops not only while driving, but also while walking potential habitat inaccessible by road. To make the data from our walking surveys comparable to our driving surveys, we determined that 15 min of walking was equivalent to every 0.3 km of road survey.

RESULTS

HABITAT AND MOLT LOCATION

Breeding habitat and molt location were associated among western Neotropical migrants (Fisher's exact test $P = 0.02$; Table 1). Six of the seven passerines that breed in coniferous forest molt within their breeding ranges. The exception, the adult Western Tanager, migrates to the region of the Mexican monsoon to molt. Twelve of the 15 passerines that breed in habitats other than tall coniferous forest (broadleaf, open, or arid pinyon pine and juniper habitats) depart their breeding ranges to molt in the region of the Mexican monsoon. The three exceptions, the Gray Vireo (*Vireo vicinior*), Virginia's Warbler (*Vermivora virginiae*), and MacGillivray's Warbler (*Oporornis tolmiei*), molt within their breeding ranges.

SIZE AND TIME REQUIRED TO MOLT

As predicted, body mass is correlated with the time required to replace the primaries (with swallows $P = 0.08$, $r^2 = 0.15$; without swallows $P = 0.007$, $r^2 = 0.35$, Fig. 1). Yet less than half of the variance in time required to molt is explained by body size, reflecting the likely importance of other ecological and life history variables affecting the duration of primary molt. Of the 22 western Neotropical migrants included in our comparative study (Table 1), the median mass for the nine western migrants that molt within their breeding ranges was 10.4 g, while the median mass for the 13 western migrants that migrate to the region of the Mexican monsoon before molting was 28.1 g—a significant difference (Wilcoxon test, $P = 0.02$).

UP-SLOPE MOVEMENT IN CASSIN'S VIREO

Differences in spring and fall survey data show that Cassin's Vireos move up-slope approximately 300 m in Washington to molt (Fig. 2). In the fall, vireos were largely absent from low elevation sites where they were breeding abundantly in spring. During spring surveys, we found 14 of 22 vireos below 1000 m, while we found only two of 24 vireos below 1000 m in the fall (Fisher's exact test, $P = 0.007$; Fig. 2). Further, the two vireos found at low elevations (640 m and 870 m) were on north-facing slopes dominated by Douglas-fir.

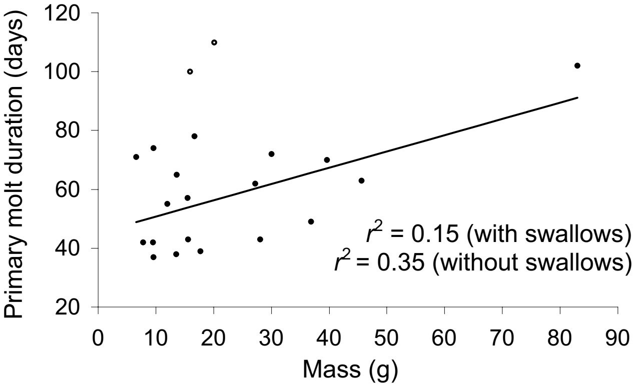

FIGURE 1. Pimm (1976) estimates of primary molt duration regressed on mass for 21 North American and European passerine species; estimates come from an online search of the Scientific Citation Index. Unfilled circles in the upper left quadrant are swallows. The time required to replace the primaries, which accounts for most of the time required for a complete molt, increases with body size.

In our fall surveys, we revisited each of the 22 stops where, in spring, we had found vireos. Of the 14 low elevation sites that had vireos in spring, just one had a vireo in the fall; of the eight high elevation sites that had vireos in spring, four had vireos in the fall. Although not significant (Fisher's exact test, $P = 0.14$), this trend further suggests that low elevation breeding habitats were not suitable for molting.

Using encounter rates to compare spring and fall vireo densities eliminates the bias of variable amounts of time spent surveying Cassin's Vireos in specific elevation categories. In the fall, few vireos ($n = 2$) were observed below 1000 m, despite greater survey effort in every elevational category in fall than spring. In fall, we made 20 stops per elevation category at low elevation sites (<1000 m) and 22 stops per elevation category at high elevation sites (>1000 m). Thus, the paucity of Cassin's Vireos at low elevation sites in the fall is not a product of biased survey effort.

We attribute the increase of vireo densities in fall at higher elevations (Fig. 2) to up-slope movements of individuals that bred at low elevations. Factors such as hotter temperatures at lower elevations and the presence of newly produced young likely did not affect our results. We conducted surveys in cool, morning temperatures when birds were active at low elevations. We also collected three individuals, all of which were singing adult males molting primaries (UWBM 38958, 84367, 84368); these specimens suggest our fall surveys reflect the presence only of adult males, as females and juveniles apparently are silent in the fall.

DISCUSSION

HABITAT AND MOLT LOCATION

Most western Neotropical migrants that breed primarily in coniferous forest remain within their breeding ranges to molt, likely because they can meet the energetic demands of molt (Murphy and King 1992, Lindström et al. 1993) by moving up-slope while

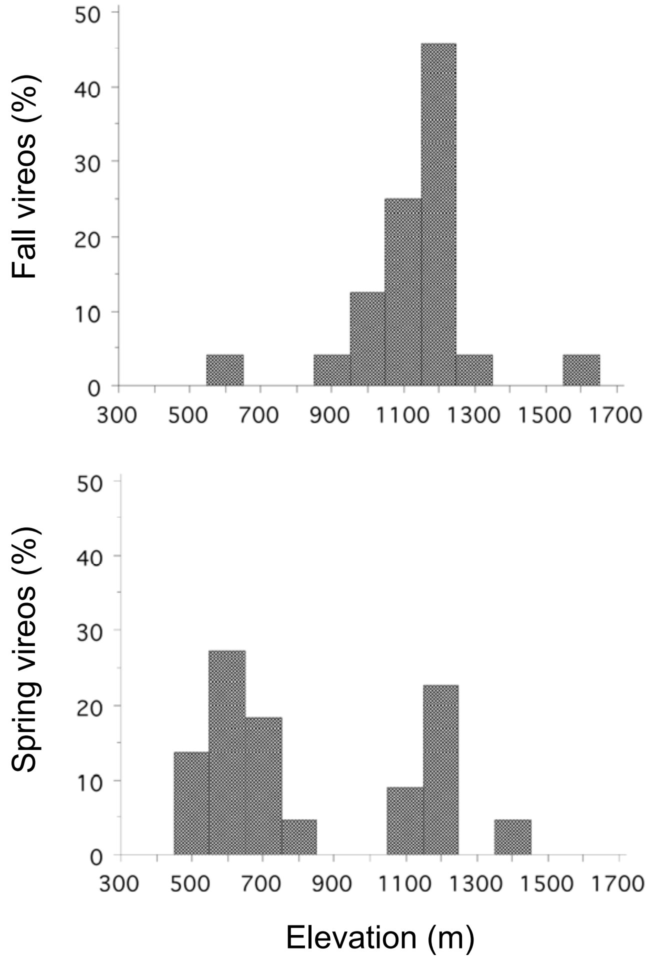

FIGURE 2. Plots of the percentage of Cassin's Vireos by elevation category found in surveys during the spring (22 singing males, most mated) and fall (24 singing individuals that were likely adult males) in Okanogan County, Washington, 2004.

remaining in predominantly coniferous habitat. Western species that complete their molts within their breeding ranges are typically small birds that require less time to molt. In contrast, most western passerines that breed in broadleaf or open habitats move to the region of the Mexican monsoon to molt. We suspect these species are better adapted for foraging in the tropical deciduous forests of the monsoon region than species that breed in coniferous forest, and can thus exploit the enormous food flush associated with the monsoon rains. Many are also larger species that might have difficulty finishing their molts within their breeding ranges.

Two complementary hypotheses may help explain why several western species molt within their breeding ranges and not on their wintering grounds or in the monsoon region. First, with the added energetic cost of molt, foraging in temperate coniferous forest may be more efficient than foraging in tropical forests of winter ranges. Coniferous forests are widespread in western North America and provide ample habitat suitable for molting. Although pine-oak woodlands dominate much of the Mexican highlands, migrants are likely deterred from molting in this region because pines are not favored foraging trees (Balda 1969, Franzreb 1978, Hutto 1985); pines seem to be avoided when alternative coniferous trees are available. Second, interspecific competition for resources would increase substantially if those western species that remain within their breeding ranges to molt also moved to the monsoon region to molt. This idea is supported by the fact that the winter ranges of Neotropical migrants are compressed to about 1/5 to 1/10 the size of their breeding ranges (Terborgh 1989, p. 79). These range compressions would be far greater if they were calculated on the basis of the land area in the monsoon region used by molt migrants.

Not all species in Table 1 fit our predictions based on breeding habitat. Western Tanagers often breed in coniferous forest, yet adults move to the monsoon region to molt, while juveniles remain within the breeding range, where they replace their body feathers (Butler et al. 2002). Because Western Tanagers are larger passerines and take longer to molt, adults that migrate south likely eliminate time constraints of molting within their breeding range. MacGillivray's Warbler molts within its breeding range but does not regularly use coniferous forest; rather, it uses riparian habitats and the deciduous understory of coniferous forest, both of which are available at higher elevations. Thus, we predict that MacGillivray's Warbler will be found to move up-slope to molt; unpublished data from MAPS banding stations support our prediction (P. Pyle, The Institute for Bird Populations, pers. comm.).

Two other species, the Gray Vireo and Virginia's Warbler, do not fit our habitat-based predictions; both are reported to molt within their breeding ranges (Voelker 2000, Voelker and McFarland 2002). Further analyses that account for collecting effort seem necessary for both of these species because they have southerly breeding ranges that make molt-related movements difficult to assess given that the monsoon region extends north into Arizona and New Mexico (Comrie and Glenn 1998). By not considering collecting effort, Voelker and McFarland (2002) failed to recognize Lucy's Warbler (*Vermivora luciae*) as a molt migrant (Rohwer et al. 2007). We specified Gray and Ash-throated Flycatchers as species that breed in pinyon-juniper habitats (Table 1) because they are often associated with pinyon pine or juniper over much of their breeding ranges. Gray Flycatchers also nest in arid, lower elevation coniferous forests, and Ash-throated Flycatchers are also common breeding birds in oak and mesquite woodlands. Although Black-throated Gray Warblers (*Dendroica nigrescens*) are associated with junipers and pinyon pine in the southern portion of their breeding range, they prefer Douglas-fir forest for breeding when this habitat is available (Guzy and Lowther 1997), unlike Gray and Ash-throated Flycatchers.

SIZE AND TIME REQUIRED TO MOLT

Western Neotropical migrant passerines that molt within their breeding ranges are significantly smaller than those that move to the region of the Mexican monsoon to molt. Because feathers grow at relatively constant rates (Prevost 1983, Rohwer 1999), and the summed length of all the primaries is much shorter for small than large birds, small passerines can complete their molts in considerably less time than can midsized passerines. Passerines that molt before migrating and those that move up-slope to molt are further time constrained by the earlier onset of cold fall weather in the mountains. Thus, we predict that moving up-slope for the fall molt would be more feasible for small than large species. This prediction needs direct assessment in more species than Nashville Warbler and Cassin's Vireo.

UP-SLOPE MOVEMENTS IN CASSIN'S VIREO

During spring and fall surveys, vireos were not found in higher elevation larch (*Larix* spp.) or lodgepole pine forest. The absence of Cassin's Vireos in these higher elevation habitats is not likely due to colder temperatures because, in the fall, we failed to find vireos in these habitats at places where they interdigitated with high elevation Douglas-fir forests. Instead, Cassin's Vireos appear to favor Douglas-fir forests over other coniferous habitats (such as larch or other *Pinus* spp.), probably because they prefer foraging in Douglas-fir.

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