

MOLT OF THE GRAY VIREO¹

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Abstract. Using museum specimens, I document the molt cycles and molting grounds of the Gray Vireo (*Vireo vicinior*). During prebasic molts, adult female Gray Vireos replace their primaries in 57 days, whereas adult males take 70 days; all body plumage is replaced during this molt. Prebasic molts occur almost exclusively on the breeding grounds; just 3 of 41 specimens replacing primaries were collected away from breeding grounds. No molting specimens were collected from wintering areas. Prealternate molt occurs on the wintering grounds, and appears limited to the replacement of innermost secondaries and a limited molt of body plumage. By performing prebasic molt on breeding grounds, the Gray Vireo differs from several other western breeding passerine species that use desert regions of the southwestern United States and northwestern Mexico to exploit late summer food resources. The areas of these southwestern desert regions used by other species form a small portion of the breeding grounds, and encompass the entire wintering grounds, of Gray Vireos. I hypothesize that this contrast in molting regions is not due to differences in the general timing of prebasic molts among these species; rather, the contrast may be due to constraints imposed on Gray Vireos by a dietary shift to fruit during winter and the need to defend winter territories.

Key words: Gray Vireo, molt, plumage, *Vireo vicinior*.

INTRODUCTION

Molt is an integral part of the avian annual cycle, and recent studies have documented interesting life-history tradeoffs in the scheduling of annual molts (Thompson 1991, Voelker and Rohwer 1998). In passerines, these tradeoffs generally involve the scheduling of fall molts relative to fall migration. For instance, many eastern North American breeding species replace flight feathers while still on their breeding grounds, perhaps because winter ranges are typically much smaller than are breeding ranges, which could increase competition for the resources necessary to support the high energetic costs of molt (Rohwer 1971, Voelker and Rohwer 1998).

In contrast to eastern birds, adults of many western breeding species of North American passerines begin fall migration prior to commencing fall molts. This would allow these species to avoid the late-summer droughts typical for much of western North America (Baldwin 1973), and an associated lack of food resources. A taxonomically diverse set of these western breeding species appear to stop during fall migration to commence molt in the Sonoran and Chihuahuan desert regions of the southwestern United States and northwestern Mexico; in sev-

eral species, these desert regions do not form part of either the breeding or wintering range. It has been argued that this stopover is performed in order to take advantage of food flushes produced by late summer rains (Rohwer and Manning 1990, Young 1991, Voelker and Rohwer 1998).

This molt-migration stopover raises an interesting question with regard to food resource productivity on the breeding grounds versus non-breeding grounds: do birds that breed in the xeric western/southwestern U.S., but that winter farther south, also take advantage of this late-summer increase in resources? If so, we should expect to find that molting birds are predominately found in the molt-migration stopover region, in species with disjunct breeding and wintering ranges that do not include this area. Or, we should find that molting birds are found predominately in one portion of either the breeding or wintering range, specifically the molt-migration area, for species whose breeding or wintering range includes this area.

In this paper, I begin to address this question by describing the molts and documenting the molting grounds of the Gray Vireo (*Vireo vicinior*). This species breeds throughout arid regions of the western/southwestern U.S., including part of the molt-migration area described for other species, and winters primarily along the Gulf of California.

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METHODS

SPECIMENS

I examined 178 specimens from 28 museums (see Acknowledgments). I requested from each museum any specimen collected between 1 July and 30 April, up to 10 adult specimens from May and up to 10 from June, and any juvenile specimen from May and June. I followed Pyle (1997) by referring to birds as either Hatching Year (HY; birds in their first calendar year) or After Hatching Year (AHY; birds in at least their second calendar year). Sex was established from museum labels.

SCORING MOLT

I generally followed Rohwer (1986) to determine whether molt was adventitious. I did, however, score asymmetrical primary feather molt if one to several contiguous primaries on one wing, but not the other, had been dropped, so long as primary one was included in this set of feathers. I did this because primary feather molt is often not synchronized between wings, and thus it is possible for one wing to start replacing feathers slightly ahead of the other wing.

In examining specimens for molt, I used a 3× magnifying lamp lighted with a 22-W fluorescent bulb, and a small forceps to lift feathers and quantify molt. For body molt, I estimated the percentage of feathers growing in each of five regions: chin and throat, breast, belly, head, and back (definitions in Rohwer 1986). I used Rohwer's (1986) scale of 0, 10, 30, 50, 70, and 90% of feathers in development. An overall body molt score was calculated for each specimen by averaging the scores of the five body regions.

For scoring flight feather molt, I generally followed Rohwer's (1986) practice of estimating the fraction of full length (by 0.1 intervals) attained by each growing feather, but used N to designate new feathers, which allowed a score of zero to be used for missing feathers (Voelker and Rohwer 1998). Gray Vireos have a total of 20 primaries, 18 secondaries, and 12 rectrices. I scored both sides of each specimen for flight feather condition.

All regression models for estimating molt duration are flawed. However, Pimm's (1976) regression method to estimate average duration of molt in individual birds is less flawed because the method overcomes the problem of heteroscedasticity in molt data (Underhill and Zucchini

1988), and I use it here. A more accurate method apparently exists for estimating molt duration (Underhill and Zucchini 1988), but is not readily available. Furthermore, it is unclear whether a basic assumption of this method, that observations constitute a random sample from the relevant population, could be appropriately applied to specimen-based data, or for that matter to any data set where a "relevant population" can not be unambiguously defined.

I followed the molt terminology of Humphrey and Parkes (1959). Following Langston and Rohwer (1996), I define a molt series as a set of flight feathers that are replaced by a single set of rules. Yuri and Rohwer (1997) should be consulted for a detailed explanation of the rules of feather replacement and the identification of molt series. Briefly, to identify the feathers of a series and the rules by which they are replaced, each growing (focal) feather is placed in one of three categories based on its stage of replacement and the stage of replacement of adjacent feathers. Nodal feathers are those feathers replaced first in a molt series and these are always more fully grown than adjacent feathers. Terminal feathers are those feathers replaced last in a molt series and these are always less fully grown than adjacent feathers. Other growing feathers provide directional information, showing whether replacement proceeds proximally to distally, or distally to proximally. In the simplest possible scenario for primary replacement, P1 would be nodal (dropped/replaced first), subsequent primaries would be dropped in order with P2 longer than P3, P3 longer than P4, and so on until P10 was reached. This sequence would indicate proximal to distal replacement of primaries, and, because P10 was dropped last, would indicate that P10 was the terminal feather in the series. More complex scenarios would involve multiple series in a single feather tract, and would be evidenced by multiple nodal feathers, multiple directional waves, and multiple terminal feathers (Langston and Rohwer 1995).

BREEDING AND WINTERING RANGES

Gray Vireos breed from southern California, southern Nevada, southern Utah, western and southeastern Colorado, and northwestern and central New Mexico south to northwestern Baja California, central and southeastern Arizona, southern New Mexico, western Texas, and northwestern to central Coahuila (Phillips 1991,

TABLE 2. Average start and completion dates of primary molt for adult male and female Gray Vireos, based on regressions of date on primary molt scores.

	<i>n</i>	Start date	Completion date	Days in molt	<i>r</i> ²	<i>P</i>
Males	29	3 July	11 September	70	0.93	<0.001
Females	10	14 July	10 September	57	0.72	0.002
Males + females	39	6 July	11 September	67	0.87	<0.001

to S5 and S6 to S9, or in three series, S1 to S5, S6, and S7 to S9. Without question, the outer series of secondaries is being replaced distally to proximally (S1 to S5; Table 1). S1 is replaced when P5–P6 is the outermost growing primary, and the S1 to S5 series is completed at the same time as the primary series, or shortly thereafter. S6 was longer than S5 in all cases where both feathers were growing simultaneously. This means that S6 was dropped prior to S5, and implies that S6 is not part of the S1–S5 series.

For the S7–S9 series in Gray Vireos, S8 is most typically nodal, with either S7 or S9 being dropped next in the series. In one of five cases

where S7 and S8 were being replaced simultaneously, S7 was longer than S8. This would imply that S7 may have been nodal, and this resulted in one S8 being categorized as distal to proximal replacement. Clearly, there does not appear to be a firm set of rules in the S7–S9 series, if indeed this set of feathers can be correctly called a series. Despite the obvious inconsistency, I retain the term series for this group, as they are often in other species replaced together in prealternate molts, where other secondaries are most often not replaced. S7 to S9 were being replaced when P1–P5 were the outermost growing primaries.

S6 may either be part of the S7–S9 series, or may perhaps more likely constitute a series by itself. In only 1 of 12 cases was S6 growing concurrently with S7 such that S6 could be viewed as the terminus of the inner molt series. In the other 11 cases, S6 was scored as a terminal feather but S7 was new and fully grown. In about half of these cases, S6 was quite short which suggests that it may have been dropped after S7 was fully grown. This implies that S6 may be an independent series, because in most molts, adjacent feathers are dropped before the preceding feather in a series completes growth.

Rectrices appear to be divided into two molt series: R1–R5, and R6. Feather replacement proceeds from R1 to R5 in the inner series (Table 1). R6 was scored as terminal in nine cases (shorter than R5) which would suggest that it was likely part of a single rectrix series, R1–R6. However, R6 was scored as nodal in three cases (longer than R5); to be considered nodal, R6 must have been dropped prior to R5, and thus R6 constitutes a separate molt series. Replacement of the rectrices commences at about the same time as does the replacement of the inner secondary series, and is completed just prior to the completion of the inner secondary series.

Definitive prebasic body molt begins soon after primary molt begins and appears to be occurring in all tracts by the time P4–P5 are being

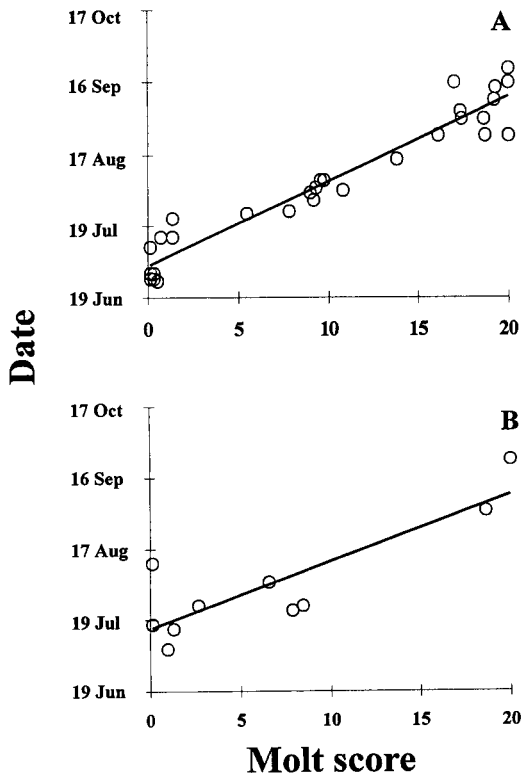


FIGURE 1. Regression of date on primary molt score for the Gray Vireo. A = males, B = females.

TABLE 3. Prealternate molt in Gray Vireos.

Date	n	% in molt	Mean body molt score	% replacing secondaries	% with fresh secondaries	% replacing rectrices	% with fresh rectrices
1 to 15 March	2	100	36	50	0	0	0
16 to 31 March	1	0	0	0	0	0	0
1 to 15 April	12	17	18	17	8	0	8
16 to 30 April	12	25	6	25	25	0	0
1 to 15 May	17	12	2	6	18	6	0

replaced. Body molt is completed at about the same time as the primary series is completed.

DEFINITIVE PREALTERNATE MOLT

Of 45 specimens collected between 1 March and 15 May, only 20% (n = 9) were molting body feathers, flight feathers, or both (Table 3). Body molt was not very intense on any specimen; no specimen had more than a 40% total body molt score, and just two specimens were simultaneously replacing feathers in all tracts. Just one specimen was replacing rectrices, and another had some fresh rectrices (Table 3). Seven specimens were replacing S7 to S9. Seven other specimens, collected in April and May, had fresh-appearing S7 to S9, and fresh body plum-

age in all tracts (Table 3). Five banded specimens of 35 trapped in March and April from the wintering grounds each showed a light to moderate amount of ventral molt (S. Russell, unpubl. data). These data combine to suggest that prealternate molt may be generally limited to the replacement of S7 to S9 and at least a limited replacement of body feathers.

MOLT IN RELATION TO MIGRATION

Definitive prebasic molt appears generally to be both initiated and completed on the breeding grounds. Of 41 AHY specimens undergoing this molt, 93% (n = 38) were replacing flight feathers on the breeding grounds, and 24% (n = 10) of these were replacing P10, which suggests that most birds are completing the prebasic molt on the breeding grounds.

Of the three molting specimens collected away from the breeding grounds, none had yet reached probable wintering areas (Fig. 2). Two of these were taken in Sonora in late September (15, 30), and had nearly completed the molt, whereas the third was taken in Durango on 13 August and had just dropped P1-P2; these three collection dates were later than the normal initiation and completion dates (Table 2). This suggests that these birds finished breeding later than usual and were forced to initiate migration prior to initiating molt.

DISCUSSION

MOLT PATTERNS

Gray Vireos replace their primaries according to the rules followed by most passerines. Under the assumption that multiple nodal feathers indicate multiple series, three specimens suggest that rectrices are being replaced in two series, R1-R5 and R6; this pattern has been documented in several other species (Jenni and Winkler 1994, Yuri and Rohwer 1997, Voelker and Rohwer 1998) and may be a general pattern among pas-

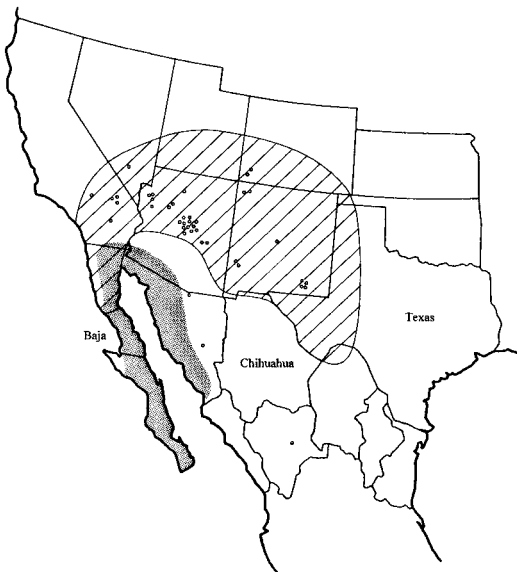


FIGURE 2. Geographic distribution of molting Gray Vireo specimens (open circles). The cross-hatched area denotes the approximate breeding range. The stippled area denotes both the approximate wintering range of Gray Vireos, and the distribution of elephant tree (*Bursera microphylla*).

serines as more detailed molt studies are conducted. Data from several specimens that had S6 longer than S5, suggest that S6 is either part of the inner series of secondaries (i.e., S6–S9) or constitutes a molt series by itself. If S6 is part of the S7–S9 series, then this is not a novel result among passerines; individuals of several Old World species have been found to drop S6 prior to S5 (Jenni and Winkler 1994), meaning that in these individuals, S6 is not part of the S1–S5 series. Indeed, in several species, all individuals show a similar “convergent” pattern of secondary replacement proximally from S1 and distally from S6, such that S6–S5 and perhaps S6–S4 are replaced as a series (Jenni and Winkler 1994). I have assumed that there is no individual variation in replacement patterns, and that therefore each feather must belong to a specific molt series. But the available molt data does not preclude the possibility that S6 can be replaced in any series, depending on the individual bird. However, variation in flight feather replacement within many species seems to involve the number of feathers replaced (due to time constraints), rather than the pattern in which feathers are replaced.

A lack of quantitative molt data from most other vireo species currently precludes a general comparison of molt patterns across the family. However, I find no evidence to suggest that Gray Vireos are replacing body feathers during migratory flights, as do western Warbling-Vireos (*Vireo swainsonii*; Voelker and Rohwer 1998); nor do Gray Vireos exhibit the replacement of outer, but not inner, primaries exhibited by White-eyed Vireos (*V. griseus*; George 1973, Lloyd-Evans 1983). Gray Vireos replace some, but apparently not all, of the juvenile secondary coverts during first prebasic molt, thus differing from Eastern Warbling-Vireo (*V. gilvus*), which replaces all secondary coverts, as well as differing from Western Warbling-Vireo and Hutton's Vireo (*V. huttoni*) which appear to retain their buffy secondary coverts (Davis 1995, Pyle 1997, Voelker and Rohwer 1998).

TIMING OF MOLT AND MIGRATION

Like most other north-temperate vireos, Gray Vireos undergo prebasic molt on the breeding grounds. This species does not perform a molt-migration, that is, migrating to a nonbreeding, nonwintering area to commence prebasic molt. Performing molt-migration might allow Gray

Vireos to take advantage of food flushes associated with late summer monsoons in southwestern United States and northwestern Mexican deserts (Szarek 1979, Nielson 1986). Four other western North American species that breed in arid, or in dry, riparian habitats perform such a molt-migration (Bullock's Oriole *Icterus bullockii*, Rohwer and Manning 1990; western Painted Bunting *Passerina ciris pallidior*, Thompson 1991; Lazuli Bunting *Passerina amoena*, Young 1991; Western Warbling-Vireo, Voelker and Rohwer 1998).

Prior to examining specimens, I had predicted that Gray Vireos would be taking advantage of the late summer food flush by moving away from northern and eastern portions of their breeding range where resource productivity presumably drops in late summer. Thus, I had expected to find that molting birds were either collected only in the southwestern portion of the breeding range (i.e., the Sonoran and Chihuahuan deserts), or that molting specimens had been taken there as well as farther south into Sonora, to include the wintering grounds. This does not appear to be the case, although collection localities of molting specimens in Figure 2 would seem to suggest that a late summer distribution shift has occurred such that most Gray Vireos are concentrated in the southwestern desert portion of their range similar to Bullock's Orioles (Rohwer and Manning 1990). Instead, this effect is the result of large numbers of breeding-grounds specimens having been collected in Arizona versus other states (i.e., less than 10 specimens each from Texas, Colorado, Utah, and Nevada).

One possible reason for not migrating prior to molting is that abundant, or at least sufficient, resources may be available late in the summer throughout the breeding range of Gray Vireos such that molt-migration would not provide a benefit. This argument has been used to explain why western breeding Hermit (*Dendroica occidentalis*) and Townsend's Warblers (*D. townsendi*) do not perform a molt-migration. These two species breed in montane forest habitats which are surely more productive in late summer than are lowland habitats west of the Rocky Mountains which several molt-migration species occupy during the breeding season (Jackson et al. 1992).

Another possible reason may be that, given the very short distance between breeding and

wintering ranges, Gray Vireos simply have sufficient time available to perform prebasic molt after breeding, and prior to migration. By comparison, species which migrate farther may lack sufficient time to molt on breeding grounds, and are thus constrained to molt elsewhere. Generalized time-constraints hypotheses are widely applied to trans-Saharan migration systems, although there are complex tradeoffs, such as environmental predictability, that vary considerably between species and which result in exceptions to generalized patterns (Jenni and Winkler 1994). Because ecological comparisons between breeding and wintering grounds are often unexplored (Jenni and Winkler 1994) for individual species, unique species- or group-specific patterns may be going unnoticed.

The reasons why Gray Vireos are not exploiting food resources in the southwest are not due to the general timing of the prebasic molt as compared to molt-migrating species; Gray Vireos, and all four species that exhibit molt-migration, undergo prebasic molt from July to September–October. That Gray Vireos and molt-migration species do not differ in the general timing of prebasic molt raises an interesting question with regard to the prebasic molt durations of western breeding passerine species that undergo molt-migration as compared to western breeding species which do not. Namely, does performing molt-migration to exploit late summer resources simply facilitate molt by providing resources, or, can performing molt-migration also increase the rate at which molt can be accomplished?

By comparing the prebasic molt duration of Gray Vireos to those of molt-migration species, it appears that by stopping in southwestern deserts, molt-migrating species may in fact be increasing the rate at which prebasic molt can be accomplished. Whereas Gray Vireos, as a species, appear to take 67 days to complete prebasic molt, molt-migrating species take only about 55 days to complete the molt (54–57 days; Thompson 1991, Young 1991, Voelker and Rohwer 1998). Just one of these previous studies (Thompson 1991) had sufficient molting specimens to document that males and females were molting at the same rate. It is unclear why female Gray Vireos appear able to complete prebasic molt faster than males (Table 2), at a rate similar to that of molt-migrating species. One possibility is that during second broods (Bent

1950) males may be able to begin molting while females rear young; however, limited evidence suggests that both sexes of Gray Vireos are equally involved in parental care (Bent 1950).

Finally, it is apparent that Gray Vireos are not performing any portion of the prebasic molt on wintering grounds. No specimens from this study were replacing flight feathers after arriving on wintering grounds, nor were 60 banded birds that were checked for molt while on wintering grounds (Bates 1987; S. Russell, unpubl. data). This lack of prebasic molt on the wintering grounds may be due to constraints imposed by winter ecology and diet. During winter, both males and females defend territories dominated by elephant trees (Bates 1992b) (Fig. 2). Gray Vireos undergo a dietary shift from being primarily insectivorous on the breeding grounds (Chapin 1925, Barlow 1978) to having a heavy reliance on elephant tree fruits during winter. Winter territoriality and frugivory imply several things. First, if the defended resource is seasonal, it may not pay to migrate early. And, indeed, Gray Vireos do not arrive on wintering grounds until late September, just after *Bursera microphylla* bears fruit (Bates 1992a). Second, although *Bursera* fruits have a high caloric content, they may be unable to meet the demands for increased protein, iron, and calcium required for successful molt (Murphy and King 1992). If so, undergoing molt on the breeding grounds would be a better strategy for Gray Vireos. Third, if birds must defend winter territories, it would be reasonable to do so while not simultaneously constrained by the need to replace feathers.

Similar to Gray Vireos, White-eyed Vireos on the Yucatan Peninsula have a heavy reliance on *Bursera* fruit during winter, and both sexes vigorously defend foraging territories from conspecifics as well as congeners (Greenberg et al. 1993, 1995). This species also appears to molt on its breeding grounds (Pyle 1997), and there appears to be a close connection between the time it spends on the Yucatan Peninsula portion of its wintering grounds and the fruiting of *Bursera* trees (Greenberg et al. 1993, 1995). Furthermore, White-eyed Vireos which do not winter in areas with *Bursera* show a heavy reliance on other fruits (Barlow 1980). This presents the interesting possibility that White-eyed Vireos may also be following a strategy of molting on

breeding grounds while waiting for a seasonal resource.

A number of other vireo species, such as Philadelphia (*V. philadelphicus*) and Yellow-throated (*V. flavifrons*) have a similar heavy reliance on fruits during winter (Skutch 1980); it is not clear whether these species, like Gray and White-eyed Vireos, defend this resource. Because modern molt studies have not been done on these other vireo species, it is unclear whether a possible connection between the timing of molt and fruiting of tropical trees can be inferred. An added obfuscating factor is that, in eastern North America, there are abundant late-summer food resources (insects). This food flush has been hypothesized as a major factor influencing breeding ground molts in eastern birds (Voelker and Rohwer 1998).

My study presents yet another example of the evolutionary lability of the fall molt and migration schedules of North American passerines in general, and of vireos in particular. Because a phylogeny of vireos is available (Murray et al. 1994), as more molt studies of vireos are conducted comparisons of the molt patterns among vireo species in a phylogenetic context will be possible; such a comparison could help clarify the evolutionary history of these patterns.

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