TIMING AND EXTENT OF THE MOLTS OF ADULT RED-EYED VIREOS ON THEIR BREEDING AND WINTERING GROUNDS[1]

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Abstract. The molt of adult Red-eyed Vireos (*Vireo olivaceus*) on their breeding grounds was studied at three widely separated sites in northeastern North America: North Point, James Bay (NPJB), Ontario; Vermont Institute of Natural Science (VINS), Woodstock, Vermont; and Powdermill Nature Reserve (PNR), Rector, Pennsylvania. Unlike other North American vireos and most other North American passerines, adult Red-eyed Vireos undergo an incomplete molt on the breeding grounds. This molt typically replaces most or all of the body plumage, about half of the wing coverts, the tertials, and the central rectrices. Extent of molt did not differ among localities; however, timing of the molt was 1–2 weeks earlier and onset of molt occurred over a longer period at PNR than at VINS or NPJB. Based on examination of museum specimens, flight feathers not molted on the breeding grounds are replaced on the wintering grounds beginning in early January; average duration of primary molt on the wintering grounds is 78 days. It is unclear whether or not feathers molted on the breeding grounds are molted again at this time. This issue needs to be resolved before Humphrey-Parkes terminology can be applied to breeding and wintering ground molt episodes in this species. Selective advantages associated with a protracted nesting season and with early onset of migration both may have had a role in shaping the molt strategy of adult Red-eyed Vireos. Rapid onset of fall migration following nesting in this seasonally frugivorous species may have been influenced by the phenology of fruit availability and abundance en route to and especially on its Amazonian wintering grounds.

Key words: Vireo olivaceus, Red-eyed Vireo, molt cycle, breeding grounds, wintering grounds, migration timing, molt terminology.

INTRODUCTION

Most adult passerines undergo a complete molt following nesting and before migrating to their wintering grounds (Dwight 1900, Pyle et al. 1987, Jenni and Winkler 1994); however, various other passerine molt strategies have been described. For example, in many North American flycatchers (Tyrannidae), adults do not molt any flight feathers until after they have arrived on their wintering grounds (Johnson 1963, Hussell 1980). Flight feather molt by adults of several species of swallows (Hirundinidae) and Old World warblers (Sylviidae) typically begins on the breeding grounds but is suspended during migration and later completed on or near the wintering grounds (Niles 1972, Pyle et al. 1987, Jenni and Winkler 1994). In a few species that

ordinarily have a complete molt on the breeding grounds, some individuals may suspend this molt prior to completion and resume molting at a migratory stopover site or after arrival on the wintering grounds (e.g., Rose-breasted Grosbeak *Pheucticus ludovicianus,* Cannell et al. 1983, Painted Bunting *Passerina ciris,* Thompson 1991).

The molt of adult Red-eyed Vireos (*Vireo olivaceus*) on their breeding grounds was long assumed to be complete, like that of most other passerines (Dwight 1900, Tyler 1950). The first observation that this might not be the case apparently was made by James Baird, who documented a variable pattern of incomplete molt in 13 fall migrant adult Red-eyed Vireos in Massachusetts from 1958–1970 (J. Baird, unpubl. data). Pyle et al. (1987:125) stated that the molt of adult Red-eyed Vireos "appears to be suspended over migration, with some flight feathers not renewed" until the species reaches its

wintering grounds, and "should be further in-vestigated." Cramp and Perrins (1994:446) pro-vided some quantitative data on the incomplete molt of 10 fall migrant Red-eyed Vireos, but nonetheless characterized the "adult post-breeding" molt as "perhaps occasionally com-plete . . . on the breeding grounds."

More importantly, no completely accurate and detailed description of molt in adult Red-eyed Vireos has been published, and the molt strategy of this species remains poorly known. We undertook this study to determine the tim-ing, sequence and extent of molt in adult Red-eyed Vireos on breeding grounds in northeast-ern North America and on wintering grounds in northwestern South America.

MATERIALS AND METHODS

We examined the molt of adult Red-eyed Vireos at three widely separated sites in northeastern North America: North Point, James Bay (NPJB), Ontario, Canada (51°29′N, 80°27′W); Vermont Institute of Natural Science (VINS), Woodstock, Vermont (43°36′N, 72°32′W); Powdermill Nature Reserve (PNR), 4.5 km SSW of Rector, PA (40°10′N, 79°16′W). Molt data were collected between July and Septem-ber from 1981–1984 at NPJB ($n = 35$), 1986–1995 at VINS ($n = 75$), and 1987–1995 at PNR ($n = 174$). Birds used in the study were cap-tured in mist nets and marked with U.S. Fish and Wildlife Service bands. Adult Red-eyed Vireos (AHY, or after hatching year) in the sum-mer and fall are easily distinguished from juve-niles (HY, or hatching year) on the basis of eye color (juveniles have brown irides); we did not routinely separate yearling (SY, or second year) from older adults (ASY, or after second year). The sex of some vireos caught during the early stages of molt was determined based on physi-cal evidence of recent breeding condition (e.g., brood patch or refeathering brood patch in fe-males; cloacal protuberance in males), but samples of known-sex birds were too small for assessing differences in the timing or extent of molt between males and females.

We used a conventional molt scoring system (Ginn and Melville 1983) that assigns each re-mex and rectrix a score of 0 to 5 as follows: 0 = old feather not dropped; 1 = feather miss-ing or in pin; 2 = feather at "brush" stage or up to one-third grown; 3 = feather one-third to

two-thirds grown; 4 = feather two-thirds to nearly full-grown; 5 = new feather fully grown and unsheathed. Molt of body feathers and wing coverts was simply recorded as present or ab-sent; quantitative data on the number of wing coverts replaced during the molt were not taken in every case. We used only birds in the last stages of molt (i.e., all remex and rectrix molt scores ≥ 4) for our description and analyses of molt extent. In our analyses of molt timing, onset of wing molt was defined as the date when at least one flight feather had been assigned a molt score of "1" and none had a molt score >1; molt completion was defined as the date when all molted flight feathers were scored ≥ 4. We statistically compared the tim-ing and rate of molt among geographical samples by regressing date on molt score for secondary 8 feather for actively molting birds. We limited our analysis to secondary 8, which is the first flight feather dropped during the course of the breeding ground molt, because it was the only one molted in common by all birds in our samples. By using date as the dependent variable, the resulting regression can be used to estimate average molt parameters for individual vireos in each sample (see Pimm 1976 for sta-tistical methodology).

In order to determine the timing and extent of molt by Red-eyed Vireos on or near the win-tering grounds, Mulvihill examined specimens of adult *V. olivaceus* taken in Panama, Colom-bia, Venezuela, Ecuador, Brazil, and French Guiana in the collections of the Carnegie Mu-seum of Natural History (CMNH; $n = 8$) and the U.S. National Museum (USNM; $n = 6$). Ad-ditional molt notes for the USNM specimens and data from specimens in the collection of the American Museum of Natural History (AMNH; $n = 5$) were supplied to us by J. Baird. Rel-evant material for our study of wintering ground molt in this species was lacking in several other museum collections that we surveyed. To esti-mate mean dates of molt onset and completion for vireos on the wintering grounds, we again followed the methodology of Pimm (1976) and regressed date on total primary molt score for one wing (maximum total = 45), using data from molting specimens collected between 15 January and 14 April. Onset and completion of primary molt delimits virtually the entire molt period in most passerines (Jenni and Winkler 1994).
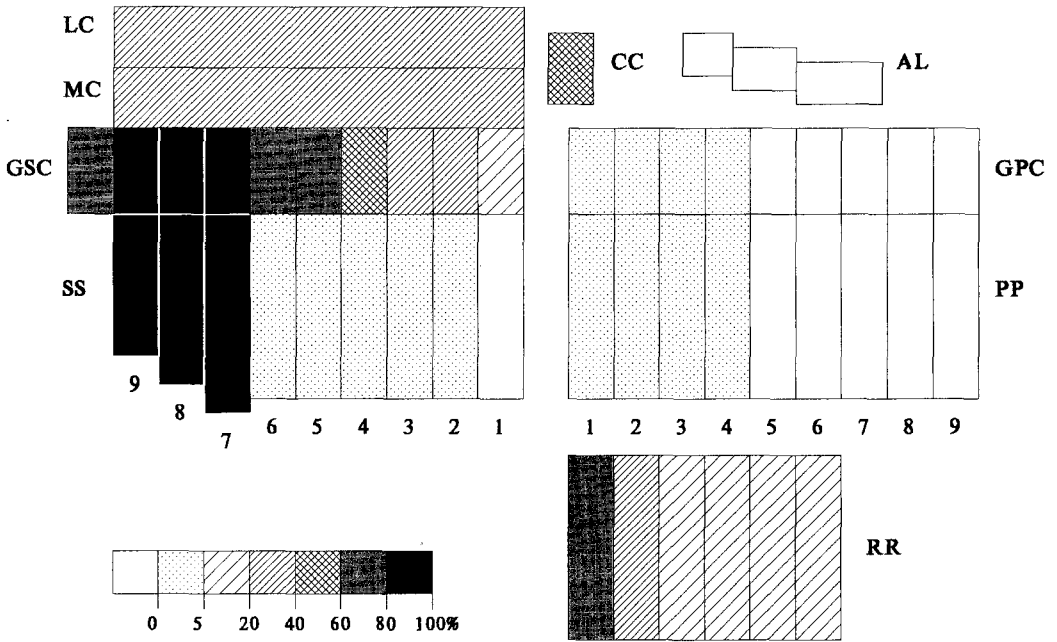
FIGURE 1. Schematic representation of the feathers of the right wing and right half of the tail showing variation in the extent of molt by adult Red-eyed Vireos on the breeding grounds. The analysis is based on molt data for vireos that had completed or nearly completed molting ($n = 95$; see Methods). Shading indicates the percent of birds that molted the following feathers: greater secondary coverts (GSC), carpal covert (CC), alula (AL), greater primary coverts (GPC), secondaries (SS), primaries (PP), and rectrices (RR). Shading in the boxes representing lesser coverts (LC) and median coverts (MC) should be interpreted to mean that most adult vireos retained at least a few coverts in these groups.

Differences in molt extent among localities were assessed with ANOVA and significance of the molt score regressions was assessed with independent, two-tailed t-tests, in both cases using SYSTAT (Wilkinson 1990). Elevations and slopes of the calculated regression lines also were compared using independent, two-tailed t-tests (Zar 1984).

RESULTS

EXTENT AND SEQUENCE OF MOLT ON THE BREEDING GROUNDS

Molt by adult Red-eyed Vireos on the breeding grounds is variable but always incomplete (Fig. 1). It ordinarily includes most or all of the body feathers, some number (usually less than all) of the lesser, median and greater secondary coverts, 0–3 (usually 3) tertials, and 1–6 (usually one) pairs of rectrices. There were no significant differences among the three localities in molt extent (one-way ANOVAs: greater secondary coverts, $F_{2, 74} = 0.91$, $P = 0.41$; tertials,

$F_{2, 92} = 0.06$, $P = 0.94$; rectrices, $F_{2, 92} = 1.09$, $P = 0.34$; Table 1).

Based on our data, the overlapping sequence of molt on the breeding grounds begins with feathers on the head (capital tract), followed shortly by feathers in the other body tracts. After the onset of body molt, wing molt begins with the middle tertial (secondary 8) and some number of inner greater secondary coverts, followed by molt of scattered lesser and or median coverts. If the molt proceeds further, the next feathers shed usually are the central rectrices and, at about the same time, secondary 9 followed shortly by secondary 7. From this point, any additional rectrices are shed centrifugally.

Rarely, the molt on the breeding grounds may be very limited in extent, including only some body plumage, none to a few lesser, median, and greater secondary coverts, and the middle tertial. Five PNR and two VINS birds had completed a molt this limited in extent. In addition,

TABLE 1. Descriptive statistics showing variation in the number of feathers molted by adult Red-eyed Vireos at three localities in northeastern North America. Acronyms used throughout the text to identify the banding sites are given in parentheses.

| Geographic locality | Feather groups[a] | | |
	Greater secondary coverts	Rectrices	Tertials
James Bay, ONT (NPJB)			
n	6	7	7
mean ± SD	5.0 ± 3.0	2.3 ± 2.6	2.7 ± 0.8
median	6	1	3
min.-max.	0–8	0–6	1–3
Woodstock, VT (VINS)			
n	16	18	18
mean ± SD	5.9 ± 3.2	1.2 ± 1.6	2.7 ± 0.7
median	6	1	3
min.-max.	0–10	0–6	1–3
Rector, PA (PNR)			
n	55	70	70
mean ± SD	6.5 ± 2.9	1.2 ± 1.8	2.7 ± 0.6
median	7	1	3
min.-max.	0–10	0–6	1–3

[a] Maximum possible number of feathers molted in each group: greater secondary coverts (10), rectrices (6), tertials (3).

a PNR vireo banded on 14 September 1991, about two weeks later than the date of latest onset of molt observed at PNR (Table 2), showed no signs of any active molt or recently grown plumage, suggesting the possibility that a few individuals may not initiate any molt while on the breeding grounds.

We observed molt of remiges other than tertials in four vireos at PNR and two at VINS. One PNR bird had replaced secondaries 2–6 and primaries 1–4 and the associated primary coverts on both wings, in addition to all of its tertials and the central pair of rectrices. The breeding ground molt of another vireo, observed in successive years at PNR, included symmetrical replacement of primaries 1 and 2, the associ-

ated greater primary coverts, and at least two pairs of rectrices in one year, but no primaries or rectrices in the previous year. Because these two PNR birds had nearly finished molting when they were examined, we cannot determine when in their molt sequence the additional remiges were replaced. However, molt scores for three vireos that were actively, although asymmetrically, replacing primary 2 and or primary 1 and their coverts indicated that primary 1 was dropped at about the same time or shortly after the middle tertial. A vireo banded at PNR on 9 September 1987 that was still actively molting secondary 6 (molt score of "4") on each wing had completed the molt of its tertials, rectrices and greater secondary coverts. We did not observe molt of any alular feathers by adult Red-eyed Vireos on the breeding grounds.

ONSET AND DURATION OF MOLT ON THE BREEDING GROUNDS

Dates of earliest onset and completion of molt were similar for NPJB and VINS; however, vireos from these more northerly areas began and completed molting about two weeks later than vireos caught at PNR (Table 2; Fig. 2). In addition, date of latest onset was 5–10 days later at PNR than at NPJB and VINS. Vireos showing signs of active flight feather molt were observed as late as 4 September at NPJB, 13 September at PNR, and 22 September at VINS. The late-molting birds at VINS and PNR may have been migrants rather than local breeding birds (Cannell et al. 1983, Parkes 1988); the PNR bird had maximum subcutaneous fat deposits, rating a "3" on a scale of 0–3 (none to fat mounded; Leberman 1967).

Regressions of date on molt score for secondary 8 were significant for all three samples (PNR: $r^2 = 0.14$, $t_{96} = 3.99$, $P < 0.001$; VINS: $r^2 = 0.24$, $t_{51} = 3.98$, $P < 0.001$; NPJB: $r^2 =$

TABLE 2. Variation in the timing of molt of adult Red-eyed Vireos at three localities in northeastern North America. Acronyms used throughout the text to identify the banding sites associated with each geographic locality are given in parentheses.

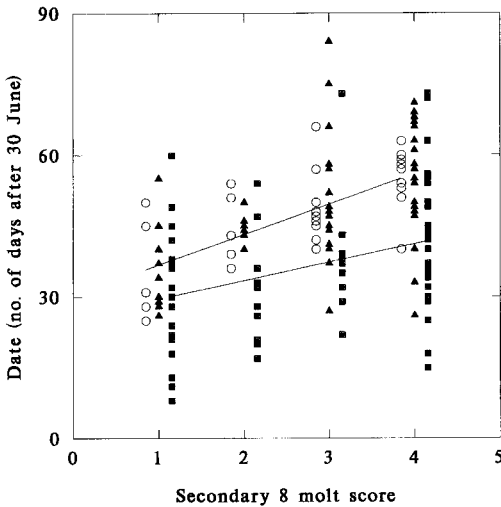| Locality	Earliest onset	Earliest completion	Latest onset	Range of molt onset
James Bay, ONT (NPJB) 51°29′N	25 July	19 August	19 August	26 days
Woodstock, VT (VINS) 43°36′N	26 July	16 August	24 August	30 days
Rector, PA (PNR) 40°10′N	8 July	4 August	29 August	53 days

FIGURE 2. Regressions of capture date on molt scores for secondary 8 of molting Red-eyed Vireos from NPJB (circles) and VINS (triangles) (common regression: $Y = 30.67 + 6.07X$), and PNR (squares) ($Y = 26.34 + 3.85X$).

FIGURE 3. Regression of date on total primary molt score for one wing of molting Red-eyed Vireos collected on the wintering grounds ($Y = 36.89 + 1.78X$).

0.47, $t_{30} = 5.18$, $P < 0.001$; Fig. 2). There was no difference between the regressions for NPJB and VINS (slope: $t_{81} = 0.26$, $P < 0.50$; elevation: $t_{82} = 0.10$, $P > 0.50$); the PNR regression was significantly different in elevation, and marginally different in slope, from a common regression of the NPJB and VINS samples (slope: $t_{179} = 1.55$, $0.10 < P < 0.20$; elevation: $t_{180} = 6.23$, $P < 0.001$) (Fig. 2). Based on these regressions, the average date of flight feather molt onset was about one week earlier at PNR (30 July) than at VINS or NPJB (7 August); average date for completion of molt of secondary 8 was two weeks earlier in vireos at PNR (15 August) than at the other sites (30 August). Given the lack of significant differences in extent of molt among sites, differences in the timing of molt of secondary 8 likely are proportional to average differences among sites in overall timing of the breeding grounds molt.

MOLT ON THE WINTERING GROUNDS

Eight Red-eyed Vireo specimens collected on or near the species wintering grounds between late August and mid-December showed no signs of active molt. Eleven specimens taken from 15 January–14 April were in molt. All of these appeared to be in the process of completely replacing their remiges and rectrices in a more or less typical sequence for passerines (Jenni and
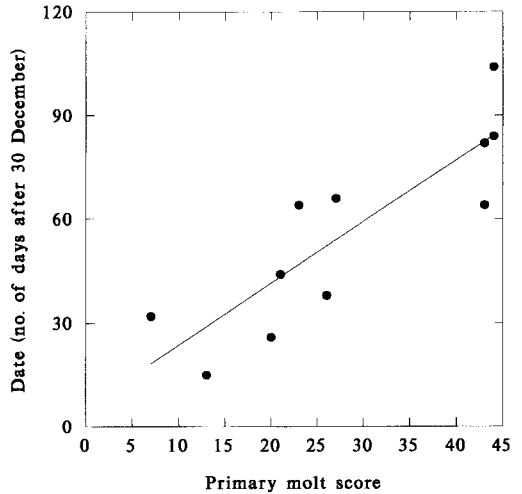
Winkler 1994), and all were undergoing a general, low intensity body molt (i.e., scattered molting feathers recorded in all body tracts). Four of the eleven specimens showed active molt of secondary 8, a feather that was replaced by all 284 vireos examined by us on the breeding grounds.

Regression of date on total primary molt score for the 11 molting specimens was statistically significant ($r^2 = 0.74$, $t_9 = 5.03$, $P = 0.001$; Fig. 3). Average dates of onset and completion of primary molt estimated from this regression were 9 January and 27 March, respectively, giving an average primary molt duration of 78 days.

A few specimens were suggestive, but none was conclusive, regarding the possibility that Red-eyed Vireos actually resume molting on the wintering grounds from the point where their molt was suspended on the breeding grounds. The best evidence in support of this possibility was provided by AMNH specimen #183566 collected on 7 March 1924 in Ecuador—its central two rectrices were fully grown and appeared "old" (i.e., replaced on the breeding grounds prior to migration), at the same time that all other rectrices were in molt and no more than 1/4 grown (J. Baird, unpubl. data). Additional evidence came from vireos examined by us during spring migration at PNR and VINS—some

of these showed marked differences in wear among tertials, rectrices and or greater secondary coverts consistent with the idea that wing and tail molt is resumed on the wintering grounds from the point where it was suspended on the breeding grounds 3–4 months earlier. These differences, however, are difficult to interpret because they also can result from the differential exposure to wear of *same-generation* feathers, depending on their position in the plumage (Hasselquist et al. 1988, Lindström et al. 1993).

DISCUSSION

Adult Red-eyed Vireos undergo an incomplete and very limited molt on the breeding grounds, in contrast to most North American passerines and other North American vireos (Pyle et al. 1987, Mulvihill and Rimmer, unpubl. data). This molt typically replaces only the body feathers, some number of inner greater secondary coverts, the tertials, and the central rectrices—the feathers of a bird's plumage that are most subject to wear (Svensson 1992). The pattern and extent of the breeding ground molt of adult Red-eyed Vireos actually is more similar to that seen in immature rather than adult passerines (Mulvihill 1993). This, together with the long-held assumption that adult Red-eyed Vireos have a complete molt on the breeding grounds like most other North American passerines, apparently resulted in their molt sometimes being mistaken for the incomplete *first* prebasic molt of the species, which, although strictly limited to the body plumage and wing coverts (Mulvihill, unpubl. data), has been described as often (Dwight 1900) or sometimes (Pyle et al. 1987, Cramp and Perrins 1994) including the tertials.

Molt of the tertials by immature Red-eyed Vireos has never been observed at PNR. In fact, the species appears to be characterized by a highly uniform first prebasic molt that replaces all of the juvenile body feathers and upper wing coverts (excluding the greater primary coverts) and the proximal feather of the alula in >90% of individuals (Mulvihill, unpubl. data). Molt limits within the wing feathering resulting from this incomplete first prebasic molt are discernible in SY vireos in the spring and early summer (Mulvihill 1993, unpubl. data). This contradicts the conclusion reached by Cramp and Perrins (1994) that immature Red-eyed Vireos

apparently undergo a complete "first prebreeding" molt on the wintering grounds.

A factor contributing to the confusion over molts in this species may be the fact that Red-eyed Vireos have an unusually slow rate of cranial pneumatization compared to other passerines. Whereas most passerines complete the pneumatization process in much less than a year (Winkler 1979, Jenni and Winkler 1994), the skulls of Red-eyed Vireos often show large unpneumatized areas for a year or more, like those typically associated with immature birds; some vireos may retain smaller unpneumatized skull "windows" for more than three years (Leberman and Mulvihill, unpubl. data). Adults (birds >1 year old) with incompletely pneumatized skulls may be mistakenly labeled as being immature (<1 year old) birds, especially in the case of museum specimens.

TIMING OF MOLT IN ADULT RED-EYED VIREOS

Geographical differences in timing of the incomplete molt by adult Red-eyed Vireos on the breeding grounds are consistent with the generalization of an earlier and more protracted molting period for birds nesting at more southerly latitudes (e.g., Dwight 1900, Miller 1933). Such differences can arise from earlier onset of nesting, later departure from the breeding grounds, or some combination of the two in southern populations (Miller 1933, Mewaldt et al. 1968, Mewaldt and King 1978, Jenni and Winkler 1994 and references therein). The shorter period of time generally available to northern nesting birds for molting compared to birds of the same species nesting at more southerly latitudes sometimes is compensated for by a reduction in molt extent and/or a decrease in molt duration (Jenni and Winkler 1994). Given that there were no significant differences among the three sites in molt extent, and that the marginally significant differences in estimated molt duration between PNR and the two northerly sites were not in the expected direction, Red-eyed Vireos from northern populations evidently have not evolved these compensatory mechanisms. In long-distance migrant species like the Red-eyed Vireo that must fit molt into a comparatively short period of time, physiological and other constraints may have prevented further increases in molt rate (Rimmer 1988, Jenni and Winkler 1994).

Molt-breeding and molt-migration overlap also can partly compensate for a shorter interval between breeding and migration in northern populations (e.g., *Dendroica aestiva,* Rimmer 1988). There is some evidence that Red-eyed Vireos from northern populations may effectively lengthen their molt period through molt-breeding overlap (Lawrence 1953) and by moving south of the breeding grounds prior to or while molting (Cannell et al. 1983, Parkes 1988). Molt-migration overlap (in particular, substantial movement away from the breeding grounds prior to onset of molt) also has been observed in Tennessee Warblers (*Vermivora peregrina,* Baird 1967, Rimmer and Mulvihill, unpubl. data), Swainson's Thrushes (*Catharus ustulatus,* Cherry 1985, Mulvihill and Rimmer, unpubl. data), Painted and Lazuli Buntings (*Passerina ciris,* Thompson 1991, *P. amoena,* Young 1991), and several European passerines (Jenni and Winkler 1994). The comparatively protracted molt period for vireos caught at PNR, where the latest date of molt onset was observed, therefore may be due partly to delayed molt onset of vireos from more northerly populations.

Feathers not molted by Red-eyed Vireos on the breeding grounds (the majority of flight feathers) are molted 3–4 months later on the wintering ground. The average duration of primary molt in Red-eyed Vireos (78 days) is typical for similar-sized European passerines that molt their primaries on the wintering grounds (ca. 65–90 days; Ginn and Melville 1983, Jenni and Winkler 1994) and considerably longer than that seen in species that undergo a complete molt on the breeding grounds prior to migration (ca. 40–60 days; Ginn and Melville 1983, Jenni and Winkler 1994, Mulvihill and Rimmer, unpubl. data).

HUMPHREY-PARKES TERMINOLOGY APPLIED TO THE MOLTS OF ADULT RED-EYED VIREOS

Molt data from available winter specimens and apparent differences in wear among wing feathers in spring Red-eyed Vireos do not clearly indicate whether feathers replaced during the incomplete molt on the breeding grounds are molted again on the wintering grounds. This issue needs to be resolved before the number of molts per cycle in this species can be determined and before the Humphrey-Parkes (1959)

system of molt terminology can be applied correctly.

In the simplest of a number of possible molt scenarios, the molt of adult Red-eyed Vireos on the wintering grounds may be exactly complementary to the incomplete molt on the breeding grounds. This would mean that adult Red-eyed Vireos have one complete, temporally divided molt—an interrupted definitive prebasic molt, using Humphrey-Parkes (1959) terminology—similar to that seen in several species of swallows (Pyle et al. 1987, Jenni and Winkler 1994). If, on the other hand, adult Red-eyed Vireos actually undergo a complete molt on the wintering grounds that eclipses the incomplete molt observed on the breeding grounds, a pattern that has been reported for European passerines (Ginn and Melville 1983, Svensson 1992, Jenni and Winkler 1994), then by definition the species has two molts per cycle (Humphrey and Parkes 1959), and determining the correct names for these molts is less straightforward.

In species that have two molts per cycle, one complete and one incomplete, the former is at least provisionally called the definitive prebasic molt, and the latter is the definitive prealternate molt (Humphrey and Parkes 1959). However, adherence to this rule cannot violate the concept of homology, which must take precedence in order for the Humphrey-Parkes (1959) system to be applied correctly (Rohwer et al. 1992, Thompson and Leu 1994). Decisions concerning molt homology are based on a comparison of the number, timing and extent of molts, and of any ensuing plumage color changes, both among age-sex classes within a species and among closely related species (Rohwer et al. 1992, Thompson and Leu 1994). Because the Red-eyed Vireo is seasonally and sexually monochromatic, changes in plumage color associated with its molts are not helpful for determining homology.

Homology of the Red-eyed Vireo's incomplete breeding ground molt with the complete definitive prebasic molt of most other passerines, including all other species of North American vireos, is supported by its timing—immediately following or slightly overlapping breeding and prior to or slightly overlapping migration—and by the rare replacement during this molt of 1–4 proximal primaries and 1–5 dis-

tal secondaries in a more or less typical sequence for a complete prebasic molt.

Homology of the possibly complete wintering ground molt with the incomplete definitive prealternate molt of most other species also would be supported by timing. To begin with, molt by Red-eyed Vireos on the wintering grounds begins 3–4 months after they arrive there, whereas in species that delay or interrupt the definitive prebasic molt until they reach their wintering grounds, this molt ordinarily begins within a month after arrival (e.g., *Empidonax minimus*, Hussell 1980). Furthermore, the wintering ground molt of Red-eyed Vireos occurs during the same period (January–March) when congeneric *V. flavifrons* (Wetmore et al. 1984) and *V. gilvus* (Dickey and Van Rossem 1938), as well as many other passerines (e.g., *Passerina* spp; Thompson 1991, Young 1991), undergo an incomplete prealternate molt. The possibility of this sort of reversal to the usual homology of incomplete and complete molts within a two-molt cycle was anticipated by Humphrey and Parkes (1959).

In order to determine if the incomplete flight feather molt by Red-eyed Vireos on the breeding grounds is simply the first stage of a complete molt that is continued on the wintering grounds after an unusually long hiatus, we will need either more data from molting birds on the wintering grounds or an unequivocal means for distinguishing feathers molted on the wintering grounds from those molted 3–4 months earlier on the breeding grounds. Recent studies have shown that isotopic variation in feather material can be used to identify seasonal dietary shifts (e.g., Thompson and Furness 1995). Assuming that feathers replaced by Red-eyed Vireos on their temperate breeding grounds have a different isotopic signature than feathers grown on their tropical wintering grounds, a possibility that is strengthened by the species' seasonal shift from insectivory to frugivory (see below), we suggest that this method could be applied to the study of molt in Red-eyed Vireos and perhaps also to other species that have complex or enigmatic molt cycles.

POSSIBLE FACTORS AFFECTING THE EVOLUTION OF DELAYED FLIGHT FEATHER MOLT IN RED-EYED VIREOS

The molt cycle of adult Red-eyed Vireos represents a departure from that of other North American vireos and so may be an evolutionarily derived trait. Several adaptive hypotheses have been suggested to explain why some north temperate breeding birds delay molting most or all of the flight feathers until after arrival on the wintering grounds, while other closely related species do not (reviewed in Holmgren and Hedenström 1995). These include possible selective advantages of: (1) increased reproductive output made possible by a protracted nesting season (i.e., additional broods or replacement clutches in lieu of a complete molt; Rohwer and Manning 1990), (2) earlier onset of migration and earlier arrival on the wintering grounds in long-distance migrants, particularly winter-territorial species (Sealy and Biermann 1983, Rohwer and Manning 1990, Lindström et al. 1993), and (3) molting in an area with more abundant or higher quality food resources than the breeding grounds, especially in species that nest where predictable late summer food shortages occur (Rohwer and Manning 1990, Thompson 1991, Young 1991, Jenni and Winkler 1994). The last hypothesis, which has been offered as a possible explanation for delayed molt strategies in birds of the midwestern and western United States that experience drought conditions following nesting, is unlikely to be a factor in the delayed molt of Red-eyed Vireos.

Although Red-eyed Vireos are only occasionally double-brooded, they commonly make 1–2 renesting attempts following an initial nest failure, and the success rate for these second and third attempts is high (Lawrence 1953). Their nesting season, which often extends into August, is later than that of any other vireo in northeastern North America (Laughlin and Kibbe 1985, Andrle and Carroll 1988, Brauning 1992). Despite this, the median fall passage of adult Red-eyed Vireos at PNR occurs 2–6 weeks *earlier* than other *Vireo* species, before the end of August (Leberman and Clench 1969, Leberman and Mulvihill, unpubl. data). Earlier timing of fall migration by Red-eyed Vireos compared to several congeners also is evident in coastal Louisiana (Remsen et al. 1996).

Rapid onset of migration following nesting in this species may be related to its migration and wintering ecology. Red-eyed Vireos feed increasingly on fruits from late summer through fall (Tyler 1950, Martin et al. 1951) and may be largely frugivorous on their Amazonian wintering grounds (Morton 1977, Barlow 1980). If

the timing of their fall migration is tied to the availability and abundance of fruits en route to and on their wintering grounds, as has been suggested for the Yellow-green Vireo (*V. flavoviridis,* Morton 1977), then a longer post-nesting delay in migration onset for the purpose of undergoing a complete molt might be disadvantageous.

We therefore conclude that advantages associated both with a longer nesting season in the north temperate region and with earlier migration and earlier arrival on the wintering grounds in this seasonally frugivorous species, may have been key selective factors in the evolution of the Red-eyed Vireo's unusual molt strategy compared to other North American vireos. However, the possibility that some aspects of the molt of North American *V. olivaceus* also may reflect its close phylogenetic relationship with austral members of the *V. olivaceus* superspecies complex (e.g., *V. o. chivi*; Johnson and Zink 1985, Johnson et al. 1988) should not be overlooked. Although none were examined for the present study, South American *V. olivaceus* presumably undergo a complete molt following nesting and prior to migration, during the southern hemisphere's late summer and early fall seasons (January–March), or during the same period when North American Red-eyed Vireos are undergoing their extensive wintering ground molt. A comparative study of breeding, molt, and migration schedules in the closely related South American taxa would be helpful for correctly determining molt homologies and for evaluating possible selective factors affecting the timing and pattern of molt observed in North American Red-eyed Vireos.

ACKNOWLEDGMENTS

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