Molt Limits Reveal Extent of Molt and Age in Black-capped Vireos

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ABSTRACT

I determined the extent of preformative and prealternate molt in the wing plumage of the Black-capped Vireo (Vireo atricapilla) by examining molt and molt limits in 619 individuals within the breeding range at Fort Hood Military Installation in central Texas. During the first molt cycle, these birds commonly replaced more secondaries and tertials than was previously known, typically four or five and as many as eight. A few individuals replaced outer primaries, primary coverts, and two alular quills during the first cycle which was also not previously known. Most of this molt occurred away from the breeding grounds as evidenced by hatching-year birds at Fort Hood which replaced no more than the tertials and one alular quill. The replacement of primary coverts during the first cycle has not been reported for other vireos and is also unusually extensive in this species (as many as five feathers) compared to other North American passerines. Second-year Black-capped Vireos replaced more wing feathers during their time away from the breeding grounds than after-second-years and the resulting molt limits in the secondaries, alula, primaries, and primary coverts provide additional characters for determining age. Previously known characters for determining the age of adults during the breeding season are rendered useless early in the prebasic molt by the loss of key feathers, but these new age characters allow ageing of many individuals for an additional month.

INTRODUCTION

With a typical mass of 8.2-9.5 g, the Blackcapped Vireo (*Vireo atricapilla*) is among the smallest of the vireos, smaller even than many wood warblers. The species nest in habitats characterized by patchy clumps of deciduous shrubs (Graber 1961) throughout its breeding range which extends from Oklahoma southward through Texas to the Mexican states of Nuevo León and Tamaulipas (Grzybowski 1995, Gonzáles-Rojas et al. 2014). These birds migrate to wintering areas on the Pacific slope of Mexico, mainly from Sinaloa south to Colima (Grzybowski 1995). Federally listed as endangered in 1987 (Ratzlaff 1987), the Black-capped Vireo was recently delisted in 2018 (United States Fish and Wildlife Service 2018) making it possible for more banders to study this species without the necessity of special permits.

Aspects of Black-capped Vireo life history on the breeding grounds are better known than those associated with migration or the wintering grounds (Grzybowski 1995), and this is also true of molt. Following the nomenclature of Humphrey and Parkes (1959) as amended by Howell et al. (2003), this species has a complex alternate molt strategy (Grzybowski 1995). The prebasic molt occurs on the breeding grounds (Butler et al. 2008). Understanding of the species' other molts is based on examination of small samples (<7; Graber 1961, Pyle 1997a). The preformative molt is thought to occur completely on the breeding grounds and to be restricted to replacement of body feathers, secondary coverts, tertials, and rarely the sixth secondary (Pyle 1997a, 1997b). The prealternate molt is thought to occur in wintering areas and include replacement of some secondary coverts, central rectrices, and as many as three tertials (Pyle 1997a, 1997b). The purpose of this investigation was to describe the extent of the preformative and prealternate molts of the Black-capped Vireo based on large samples with a particular focus on molt that occurs away from the breeding grounds. I use the phrase, "away from the breeding grounds" rather than "the wintering grounds" because it is unknown where these molts occur and it is possible that at least some feather replacement may occur at unknown stopover areas as is known for some

other North American passerines (Rohwer et al. 2005, Pyle et al. 2009). I limit descriptions to molt of wing feathers. I did not observe birds away from the breeding grounds, but instead observed growing feathers and molt limits on the breeding grounds to infer the extent of feather replacement that occurred elsewhere.

Molt limits form as a consequence of partial or incomplete molts in which only some feathers are replaced while others are retained (Jenni and Winkler 1994). These borders within the plumage can be recognized by the presence of relatively faded, worn feathers adjacent to others that are brighter, less worn, or that exhibit a different color pattern (Froehlich 2003). The presence and location of molt limits are not only useful characters for determining the age of birds (e.g., Mulvihill 1993, Jenni and Winkler 1994, Pyle 1997b), but also provide evidence of the extent of the molts in which they formed.

METHODS

From 2006 to 2017, I captured Black-capped Vireos at Fort Hood Military Installation (hereafter, "Fort Hood") in Bell and Coryell counties, Texas. This site included large areas of suitable habitat because disturbance from military training (unintended fires and maneuvering of heavy vehicles) and associated land management favors the early-successional, shrubby vegetation the species requires. Additionally, Brown-headed Cowbird (*Molothrus ater*) removal has increased reproductive success (Kostecke et al. 2005) so that Fort Hood's Black-capped Vireo population is among the largest known.

I captured Black-capped Vireos by luring them into mist nets with broadcasts of the vocalizations of conspecifics, the Eastern Screech-Owl (*Megascops asio*), or the scolding calls of the White-eyed Vireo (*Vireo griseus*) and Black-crested Titmouse (*Baeolophus atricristatus*). I recorded data on the molt limits in the right wings of 619 individual birds. Whenever a molt limit seemed unusual, I also checked the left wing. If the two wings differed by no more than one replaced feather, I recorded the pattern shown by the right wing. Otherwise, I did not include data from that bird Oct - Dec 2018 Jan - Mar 2019 North Ame in the sample (this was rare). I recognized molt limits by contrasts in wear and color between adjacent feathers or feather groups as described by Froehlich (2003). Because Black-capped Vireo wing feathers are primarily black or dark gray when new and fade to brown when old, most molt limits were distinct and easily discerned. Additionally, replaced feathers often had wider green edges than adjacent retained feathers. Molt limits within the primaries and alula, however, could be more subtle than elsewhere. For the primaries, differences between adjacent feathers in rachis color and the spacing of barbs along the rachis were helpful for identifying molt limits. It is possible that some of the apparent alular molt limits I recorded were caused by differential fading and wear rather than molt.

I searched for molt limits within the alulae, tertials, secondaries, primaries, and outer primary coverts of all age groups. Black-capped Vireos have nine visible primary coverts, and it is unclear whether an outermost tenth covert exists or is so small as to be difficult to distinguish from the marginal coverts. Consequently, I only considered the nine obvious quills when recording molt limits in this tract. When examining adults, I also searched for molt limits between the primary coverts and the adjacent carpal and marginal coverts of the hand (hereafter, "marginal coverts"). I followed Lucas and Stettenheim (1972) and considered the marginal coverts to be the small feathers between the leading edge of the wing and the bases of the primary coverts, those typically covered by the alula. I collected data concerning certain feather groups early in the project and only added others later as the project progressed. Consequently, samples differ among the various feather groups.

I recognized two age categories of adult Blackcapped Vireos, second-year and after-secondyear individuals (hereafter, "SY" and "ASY", respectively). I also examined hatching-year birds (hereafter, "HY"). The preformative molt of HYs begins about two weeks after fledging (Graber 1961). This molt had commenced for all of the HYs I examined, but it was unclear if it was finished. It was, therefore, impossible to know whether a given individual would replace additional feathers later and, consequently, my descriptions of molt limits of HYs likely underestimated the frequency that individual feathers were replaced. However, because I continued to examine HYs into late September when the last individuals would initiate southward migration, data from at least some should reveal the full extent of preformative molt that occurs on the breeding grounds.

The Black-capped Vireo replaces greater secondary coverts (hereafter "greater coverts") but not primary coverts during the preformative molt (Pyle 1997b). Accordingly, SYs should show a molt limit between the primary coverts and the greater coverts whereas ASYs should not. I previously examined the reliability of this character on 206 adults of known age. I could confirm the age of ASY individuals in this group because they were recaptured birds that I had originally banded as adults in a previous year. I could confirm the age of the SY birds because they were recaptured birds that I had originally banded as nestlings the previous year. For all of these birds, the presence or absence of the greater/primary covert molt limit correctly indicated age. For this investigation then, I used this reliable character as the basis for determining the age of all individuals captured for the first time.

I noted molt limits on Black-capped Vireos inhand and summarized each molt limit pattern as the percentage of the total sample of birds of that age. I recorded data on the plumages of HY Blackcapped Vireos from 17 Jun to 16 Sep. These data were necessary to determine whether additional feathers were replaced away from the breeding grounds. I collected data on adult Black-capped Vireos from the time they began arriving at Fort Hood in March and April to the time in July or August when prebasic molt eliminated the molt limits that existed previously. Because prebasic molt is complete (Butler et al. 2008), the resulting basic plumage has no molt limits. Thus, any molt limits in the plumage of ASY birds during the breeding season must result from feather replacement during the prealternate molt away from the breeding grounds.

I followed Pyle (1997b) by naming individual feathers by a lower-case letter indicating the feather tract followed by a number identifying the specific feather within that tract (see Fig. 1). The letters, "p", "s", and "a" denote "primary", "secondary", and "alula", respectively. I numbered the alular quills in the manner of Jenni and Winkler (1994) such that the proximal (and shortest) feather was "a1" and the distal (and longest) feather was "a3".

I tested whether birds that replaced more feathers in one tract during an incomplete molt also replaced more feathers in other tracts. To do this, I used data on the number of feathers replaced by SY Black-capped Vireos in three tracts, the alula, primaries, and secondaries. I treated the number of replaced alular quills and primaries as dichotomous categorical variables because replacement of more than one alular quill or of any primaries was uncommon. I then tested each pair of feather groups using either the Mann-Whitney or chi-square test following the methods described in Zar (1999).

RESULTS

Secondaries and Tertials. I examined the secondaries and tertials of 185 HY Black-capped Vireos and detected molt limits in 18% of this number. These birds replaced (or were actively replacing) s8 and s9, s9 only, s8 only, or s7-9 (8%, 7%, 3%, and 0.5% of HYs, respectively). Among adults, SYs replaced secondaries and tertials more frequently and more extensively than ASYs (Fig. 1). All 220 SYs showed a molt limit in this area and the most common patterns were for s6-s9 (45%) or s5-9 (29%) to have been replaced (see Fig. 2 for an example). The fewest number of replaced feathers in the SY group was two (s8 and s9, 5%) and the most was eight. The latter was by one individual that replaced s1 and s3-s9 on its right wing, but s2s9 on its left. In contrast, only 43% of 206 ASYs showed a molt limit in the secondaries and tertials. The most frequent pattern for this age group (34%)was for both s8 and s9 to have been replaced and the most extensive replacement was s7-s9 (6%). Replacement by ASYs of a single tertial only, either s9 or s8, was relatively rare, 2% and 0.5%, respectively.

Primaries and Primary Coverts. HY and ASY Black-capped Vireos (n = 185 and 206, respectively) had no molt limits within their primaries, but 7% (n = 227) of SYs did (Fig. 1). The replaced feathers consisted of a block of distal primaries usually including p10 (see Fig. 2 for an example). Two of the 17 birds showing this molt limit had apparently not replaced p10. The most common patterns were for p7-p10 (3%) or p5-p10 (2%) to have been replaced and the most extensive was p4-p10 (<1%).

Molt limits within the primary coverts were similar to those in the primaries. Only SY birds had a molt limit in this area, and it was uncommon in this age group (9% of 228 birds). All of the SY birds that had a molt limit in their primaries had another in their primary coverts. However, three that had a molt limit in their primaries. Replaced coverts always consisted of a block of the outermost of these nine feathers. I observed patterns in which three (6%), five (2%), or four (1%) coverts were replaced. Most of the birds that replaced primaries also replaced the corresponding primary coverts, but three retained the covert of the innermost replaced primary (see Fig. 2 for an example).

Alula. I detected an alular molt limit in 55% (n = 64) of HY Black-capped Vireos. In all cases, only al had been replaced or was growing. Alular molt limits were evident in 97% (n = 201) of the SYs, but its position varied. It was most common for al only to have been replaced (76%), but replacement of both al and a2 (14%) and both al and a3 (6%) also occurred (see Fig. 3 for an example). In contrast, few ASY individuals (1% of 207) showed an apparent molt limit in their alulae. Of the three ASY birds that had this molt limit, one replaced al and two replaced both al and a2.

Other Coverts. I found no molt limits between either the carpal covert or marginal coverts and surrounding feather groups of ASY Black-capped Vireos (n = 31). In contrast, all of the SY birds (n =33) showed fresh carpal and marginal coverts and faded and worn inner primary coverts. Although I did not look for molt limits among these coverts in HY birds, I did observe that all the marginal coverts and the carpal covert were growing on many individuals indicating that these feathers were being replaced during the preformative molt on the breeding grounds.

Comparison Among Tracts. SY Black-capped Vireos showed molt limits in several alar tracts and, there was evidence that individuals that replaced the greatest numbers of feathers in one tract also replaced more feathers in another. For example, those that replaced primaries had replaced a greater number of tertials and secondaries than birds that replaced no primaries (U = 408, P < 0.001). The median number of tertials and secondaries replaced by these two groups differed by one. Similarly, SYs that had replaced two alular quills also replaced more tertials and secondaries than those that replaced al only. In this case, the difference in medians was also one (U = 1572, P < 0.001). Additionally, 11% of SYs that replaced two alular quills also replaced some primaries compared to only 1% of those that replaced only a1 ($X_1^2 = 5.42$; P = 0.02).

DISCUSSION

Molt limits indicate that SY Black-capped Vireos replace more wing feathers during their time away from the breeding grounds than ASYs. Indeed, more than half of ASYs I examined showed no molt limits at all, indicating no wing feather replacement had occurred since the last prebasic molt on the breeding grounds. Those that did show molt limits had replaced only one to three tertials. In contrast, all SYs showed molt limits in their wings. These indicated replacement of a variable number of tertials and secondaries, primaries, primary coverts, and alular quills. Given that I observed HYs replacing only tertials and a1 on the breeding grounds, these birds replace as many as seven proximal tertials and secondaries, seven distal primaries, and one alular quill sometime after they depart the breeding grounds and before they return as SYs the following spring.

The Black-capped Vireo is most closely related to the Bell's (*V. bellii*) and White-eyed Vireos (Murray et al. 1994, Slager et al. 2014), and its first cycle feather replacement is more similar to these species than to other vireos. For example, Black-capped Vireos frequently replace a total of four or five tertials and secondaries, much like Bell's and White-eyed which can replace as many as five (Pyle 1997a, 1997b). Other vireos replace fewer: up to four (Gray Vireo [V. vicinior]), up to three (Blue-headed Vireo [V. solitarius], Cassin's Vireo [V. cassinii], Plumbeous Vireo [V. plumbeus], Yellow-throated Vireo [V. flavifrons] Warbling Vireo [V. gilvus], and Cuban Vireo [V. gundlachii]), one (Hutton's Vireo [V. huttoni]), zero (Philadelphia Vireo [V. philadelphicus], Redeyed Vireo [V. olivaceus], Yellow-green Vireo [V. flavoviridis], and Black-whiskered Vireo [V. altiloguus]) (Pyle 1997b, Voelker and Rohwer 1998, Voelker 2000, Pyle et al. 2004). Previous to this study, Bell's and White-eyed Vireos were the only vireos known to replace primaries during the first molt cycle and thus show molt limits in this tract as SYs (Lloyd-Evans 1983, Pyle 1997b). The eccentric preformative molt pattern of these two species (Pyle1997b) results in molt limits similar to those I observed in some Black-capped Vireos. This similarity may stem from shared ancestry, but could also be associated with the sunny, shrub-dominated habitats that all three species inhabit where feather wear would be accelerated (Willoughby 1991, Jenni and Winkler 1994).

Although the molt limits of ASY Black-capped Vireos must result from a partial prealternate molt, the origins of SY molt limits remain uncertain. One possibility is that they result entirely from the preformative molt. Although I did not observe HYs replacing more than the tertials and al on the breeding grounds, this molt could be suspended during migration and resumed at stopover areas or on the wintering grounds. Alternatively, SY molt limits could result from the combination of preformative and prealternate molt. Black-capped Vireos clearly undergo prealternate molt to some extent as evidenced by HY males that leave breeding areas with mostly gray formative head plumage and return the following spring with mostly black head plumage (and often a clear molt limit at the back of the head between black and gray areas). In this scenario, any replacement of feathers for the first time would be considered to be preformative molt whereas replacement for a second time would

be considered to be prealternate molt. Thus. the replacement of primaries, primary coverts, a2, and a3 would almost certainly result from preformative molt. Replacement of tertials away from the breeding grounds would be considered prealternate molt for any birds that had already replaced them once on the breeding grounds or for any others that had replaced them twice away from the breeding grounds. Similarly, replacement of secondaries would be considered preformative molt unless these feathers were replaced twice away from the breeding grounds. The idea that some tertials are replaced twice during the first molt cycle is supported by one female I examined in which s1-4 were old (juvenile), s5-7 were newer, and s8-9 newer still. Further clarification would require further study, such as observation of molt on the wintering grounds or determination of the isotope signatures of various feathers in a manner similar to the studies of Pérez and Hobson (2006) and Quinlan and Green (2011).

This study revealed that Black-capped Vireos often replace more feathers during the first molt cycle than previously reported. Pyle (1997b) indicated that this species replaces up to three tertials and "occasionally" s6 during the first cycle. Thirty-five percent of the SY birds I examined had replaced more than these four feathers and, indeed, only 20% had replaced fewer than four. My results for the ASY age group more closely agree with Pyle (1997b), who indicated that the prealternate molt of ASY birds involves the replacement of one to three tertials in about 75% of individuals. My observations confirm that the maximum extent is limited to three tertials but that only 43% of ASYs replaced any of these feathers.

This investigation is also the first to report the replacement of primaries by Black-capped Vireos during the first molt cycle. Furthermore, it is the first to document the replacement of primary coverts or either of the two larger alular quills by any North American vireo during the first molt cycle. The number of replaced primary coverts (3-5, not counting a possible reduced covert that may be associated with p10) is also unusual among all North American passerines. Of 54 species documented by Pyle (1997a) as having partial molts



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during their first cycle in which some primaries are replaced, 43 replaced fewer than 4 primary coverts. An additional species, Field Sparrow (*Spizella pusilla*), can replace all of its primary coverts during its preformative molt (Small et al. 2013). Another unusual observation in this study was that some Black-capped Vireos replaced both a1 and a3 but not a2. The only other documentation of this pattern that I am aware of is by an SY Woodchat Shrike (*Lanius senator*; clearly depicted in Jenni and Winkler 1994, Fig. 36).

Differences in the molt limits of SY and ASY Black-capped Vireos provide useful and previously unknown characters for determining the age of adults during the breeding season. It was already known that the presence of a molt limit between the primary and greater coverts is a reliable means of distinguishing between these age groups (Pyle 1997b) and I confirmed this with known-age birds. I also found that molt limits indicating the replacement of more than the three tertials also reliably indicates age SY and that a lack of a molt limit in this area or one indicating the replacement of only s9 or s8 reliably indicates age ASY. Additionally, nearly all SY birds had an alular molt limit whereas nearly all ASYs did not, so that this character alone identified age with an acceptably low potential for error. Furthermore, molt limits in the primaries or primary coverts, although uncommon, reliably indicate age SY. The addition of these three age characters not only improves the reliability of age determination for this species, but extends the period during which the age of adults can be determined. The greater coverts of this species are shed almost simultaneously early in the prebasic molt (pers. obs.). After the loss of these feathers, it is impossible to determine age based on contrasts between the primary and greater coverts. However, the alula and s4-s6 are among the last feathers to be replaced in this molt and so age characters based on these feathers extends the period during which one can separate SY and ASY Black-capped Vireos by approximately one month.

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Black-capped Vireo photo byDavid Cimprich