J. Field Ornithol., 54(1):50–57

INCOMPLETE MOLT OF JUVENILE WHITE-EYED VIREOS IN MASSACHUSETTS

By Trevor L. Lloyd-Evans

A long history of uncertainty from Stone (1896) to George (1973) is documented in the literature on the postjuvenal (first prebasic) molt of the White-eyed Vireo (*Vireo griseus*). This history is clearly and concisely presented in the latter paper. On the basis of at least 5 molting juvenile birds, George postulates "... first, that young White-eyed Vireos in southern Illinois typically replace most and probably all major flight feathers during juvenile life, and second, that certain specimens or populations in the midwestern prairie region possibly retain some or all juvenile flight feathers until the second prebasic (first postnuptial) molt." The present paper provides information on the postjuvenal molt of the species in Massachusetts and particularly documents an incomplete wing molt involving only the distal 5 primary feathers, the 3 tertials (also known as proximal secondaries 7–9), and occasionally the proximal secondary (no. 6). This partial flight feather molt has not been previously demonstrated for the species. Clearly, it could be of considerable physiological significance for successful migration and pre-migratory fat deposition.

In Massachusetts the White-eyed Vireo is at the extreme northeast of its present range. Griscom and Snyder (1955) described it as "locally common" prior to 1880, since then it has rapidly declined. Recently (1950's) there has been a northward re-establishment of the breeding range in the state, where it is still far from common.

METHODS

Birds were banded at 2 sites in Plymouth County, Massachusetts, by staff of the Manomet Bird Observatory from 1973–1978. Netting sites were either near breeding territories or within the limits of post-fledging dispersal prior to migration. Age of first-year birds was determined by their incomplete skull ossification and/or gray, not white, iris (Wood 1969).

Molt information on 47 captures of juvenile birds was recorded on British Trust for Ornithology molt cards, see Snow (1967); Snow's numbering, sequences, and definitions are used. Following the British molt score system used by Evans (1966) old remiges and rectrices were scored 0; feathers absent or in pin, 1; stages of growth, 2, 3, or 4; and complete new feathers, 5. Birds with all unmolted primary feathers thus score 0, and fully molted birds 50, when the small, distal no. 10 primary is included. By convention the right wing only is considered in scores, assuming that the normal course of molt is to show almost exact symmetry (Snow 1967). The primary, secondary, tertial, or tail scores can be plotted against date on scatter diagrams to indicate speed and timing of molt (Newton 1967, Snow 1969). Repeat captures of the same banded bird will indicate whether primary molt is approximately linear. Regression analysis can be used for initial captures only, to ensure independent observations (see Evans 1966). Greater covert, carpal covert, and alula molt were recorded for each feather on the right wing as old, molting or missing, or new. Contour feather molt was summarized for lesser and median coverts, underwing, upperparts, underparts, and head. In all cases a code was available for full-grown feathers of uncertain age; this is particularly a problem in the White-eyed Vireo where the greenish-gray color makes it difficult to distinguish "old" juvenal, from "new" first basic feathers.

Twenty-six cards were completed showing molt of major flight feathers on 20 birds. Banded individuals were recorded on 21 other occasions as having either all juvenal or all first-basic flight feathers. Two individuals were caught twice and 2 caught 3 times during active primary molt with cards completed 6–16 days apart.

RESULTS AND DISCUSSION

Primary molt.—Even though the proximal primaries are shown not to have molted (see later), they are credited with a score of 5 (new feather), for the purposes of plotting molt scores. The primary score should thus be regarded as an index of completion, since this standardized presentation of the molt is being used in an unusual case. In the upper data set of Figure 1, I have graphed the primary score (y) against the number of days from the end of July (x). Thus 15x = 15 August and 50x = 19 September. A bird showing active primary molt on successive dates has the scores joined (4 individuals). From these repeating birds I conclude that the progress of molt was roughly linear. All were caught at Manomet Bird Observatory in 1974. A linear regression analysis (see Evans 1966) of the 11 initial captures only, gave the upper line $y = 18.46 + .60x$ with a correlation coefficient r of .8. Thus 64% ($r^2 \times 100$) of the variation in y is attributable to a linear change in x (time). This figure jumps to 96.3% if only the 4 repeating birds are used, but the observations are then non-independent.

No birds ever showed active molt in primaries 1–5. However, 5 out of 6 August (early molt) birds showed active molt in primary 6. In addition, the theory that molt started with the 6th or later primary is strengthened in Table 1, where 7 birds were examined twice each; once before any active primary molt, and later showing such molt. Lines parallel to the multiple capture lines were applied to each active plot of the primary score to obtain a best estimate for the last dates of score 0 (10 old feathers), and also score 25 (in effect 5 retained old proximal feathers). These dates thus represent 2 possible alternatives for the start of primary molt.

If the molt were linear, no bird could have replaced *all* the primaries on these dates. However, the first 5 birds could have started with primary 6 and the last 2 would have to have started with primary 7. The only other possibilities to account for the above are extremely unlikely.

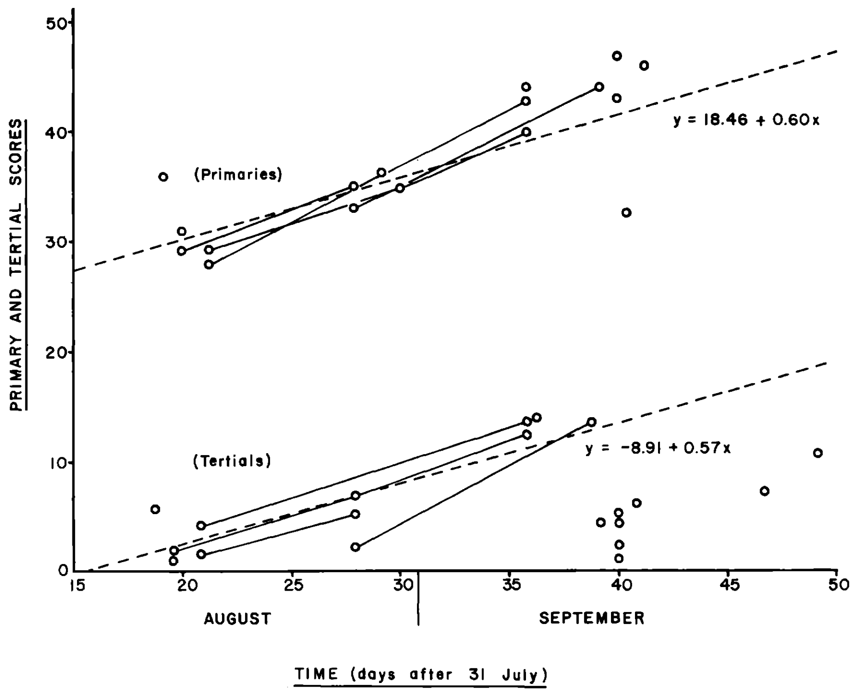

FIGURE 1. White-eyed Vireo postjuvenal primary and tertial molt against time. (Regression lines are calculated from initial captures only although all captures are shown on the figure; see text.)

There could be a very rapid early molt of the proximal primaries after fledging in July, then a pause until resumption in mid-August; second, the proximal primaries could molt nearly simultaneously and by chance no such birds were caught in mist nets since they would be almost flightless. The time available to bird no. 7 to complete the molt of 6 primaries under the latter regime would be a highly unlikely 6 days!

It thus seems that primary molt starts in mid-August in Massachusetts, progressing distally from primary 6 or more distal feathers, while the juvenal proximal feathers are retained. This was admitted as one possibility by George (1973) for certain specimens or populations in the midwestern prairie region. He did not observe molt in primaries 1–4 and neither did Thompson (1973) in another very small sample of birds from Monroe County, Indiana. It is tempting to suggest that the retention of the juvenal primary 5 in Massachusetts, as opposed to its renewal in at least some more western populations, may indicate a geographic difference in molt strategy. More data are obviously needed. The earliest date of primary molt observed in Massachusetts was bird no. 6 on 19 August 1974. Few juveniles were caught before this date, (4 from

TABLE 1. Calculated duration of primary molt in White-eyed Vireos. See text. (Based on 7 individuals captured twice each at Manomet Bird Observatory, Massachusetts.)

Day (1 = 1 Aug.)	Primary Score	Bird Number	Calculated Last Date of Score 0	Calculated Last Date of Score 25
02 20	0 31	1	−21 (11 Jul.)	12 (12 Aug.)
07 28	0 33	2	−14 (18 Jul.)	16 (16 Aug.)
12 20	0 29	3	−14 (18 Jul.)	16 (16 Aug.)
15 21	0 29	4	−14 (18 Jul.)	16 (16 Aug.)
15 21	0 28	5	−14 (18 Jul.)	16 (16 Aug.)
12 19	0 36	6	−25 (07 Jul.)	05 (05 Aug.)
34 40	0 33	7	−05 (27 Jul.)	28 (28 Aug.)

1974–1978), the earliest 26 July 1978. None of these early birds were replacing primaries.

Bailey (1955) and Forbush (1929) give the Massachusetts nesting season for White-eyed Vireos as the last week of May to the third week of June. At Manomet Bird Observatory unpublished fall data on 150+ banded birds (1966–1976) indicated a post-fledging dispersal into the area, followed by migration. This activity spanned the period of late August to the first week of October (see also the 2 above mentioned authors and Griscom and Snyder 1955). The best estimate of the duration of primary molt from Figure 1 is mid-August to mid-September with 2 early birds complete by 8 September. The line for multiple capture birds suggests that an approximate duration for molt of 10 primaries would be 60 days, the entire time from the end of nesting to the start of movement. Primaries 5–10 would take approximately 36 days, 6–10 ca 30 days, and 7–10 ca 24 days. When primary molt was well under way, 3 or 4 feathers, occasionally 5, were seen in active molt at the same time.

For 7 birds primary 10 was observed in active molt; nothing in the pattern of renewal suggested retention of any old, juvenal, distal feathers in any other birds. This presents an intriguingly different case from the Red-eyed Vireo (*Vireo olivaceus*) in which the juvenile has a complete postjuvenal molt, while the adult has an arrested and irregular molt of the flight feathers, which is completed 6 months later as part of the prenuptial molt on the wintering grounds (Baird, pers. comm.)!

Secondary molt.—Secondaries are taken as the 6 major flight feathers proximal to the 10 primaries, and are numbered centripetally, i.e., distal no. 1 to proximal no. 6. George (1973) suggests "complicated but probably sequential renewal of the secondaries," but only saw one secondary feather *sensu stricto* in active molt (no. 2). Forty-seven cards for Massachusetts birds showed only 3 with active molt of secondary no. 6, one bird on the right wing only. Dates were between 28 August and 5 September, with no other molt of this tract in any earlier or later observations. These scanty data suggest that secondaries, with a few minor exceptions, were not normally molted in Massachusetts.

Tertial molt.—Tertials, the proximal secondaries of Thompson (1973) and other authors, are taken as the 3 major flight feathers proximal to the secondaries and numbered 7 distal to 9 proximal. The score 0–15 is plotted in Figure 1 as the lower set of data. Active molt was observed on 21 occasions for 16 individuals. As with the primaries, the same 4 repeating birds showed roughly linear molt. A linear regression analysis of the 7 initial captures gave the lower line $y = -8.91 + .57x$ with a correlation coefficient r of .8. Thus 64% ($r^2 \times 100$) of the variation in y is attributable to a linear change in x (time). As with the primaries, this figure jumps to 89.0% when only the 4 repeating birds are used. It was obvious that a greater individual variation in timing was demonstrated by the tertials, so that the earliest molt (score 1 on 6 August, not figured) predates all primary molt. Similarly, although only 3 feathers are involved on each wing, the last active molt (score 12 on 18 September) postdates all primary molt. On individual birds all 3 tertials were often in active molt at the same time. The best estimate of average duration was 22 days, this from the lines of the repeating birds. Order of molt of the tertials followed Dwight (1900) in his general remarks on passerines. Where it was possible to compare stages of growth on the same bird, tertial no. 8 was observed to molt first on 14 occasions, no. 9 second on 9 occasions, and no. 7 last on 15 occasions. No deviation was observed from this order although some pairs of tertials on the same wing often appeared equal in development.

Tail molt.—Rectrices molted completely and centrifugally or simultaneously. This rapid molt was widely variable in dates of onset and completion. Although 13 cards on 7 birds recorded active tail molt, plotting of the scores and their analysis proved not to be significant. The best estimate of duration was 26 ± 5 days for one individual recorded at scores 5, 13, and 24 out of the maximum 30. The period of tail molt was well documented, being from 19 August, with several very low scores, to the second week of September, 10 subsequent cards showing apparently new tails. In a correlation with primary molt, all tail molt was completed at primary score 45, which represents 8 or 9 new feathers.

Wing covert molt.—Primary coverts molted with their corresponding primary. All greater (upper secondary) coverts were replaced almost synchronously (both also confirmed by George 1973), the latter feathers being completed before primary score 40. Median, lesser, and underwing covert molt was completed at approximately the same time as that of the primaries and appeared to encompass all feathers. Alula molt did

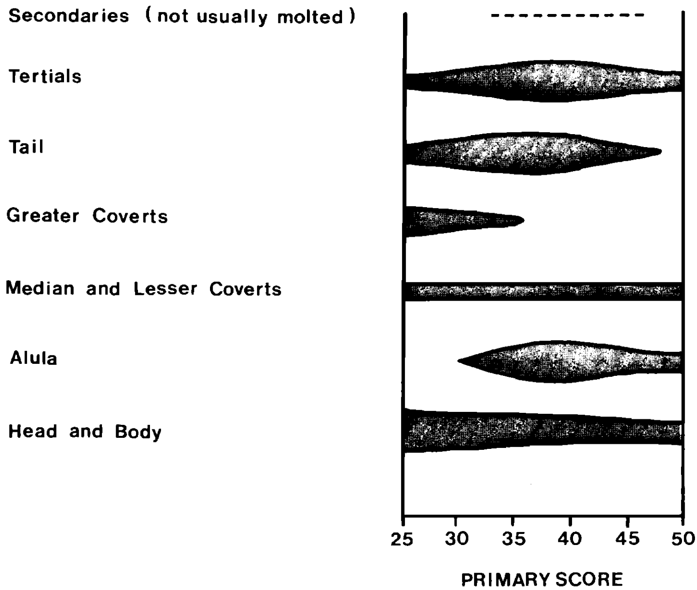

FIGURE 2. White-eyed Vireo postjuvenal molt compared with primary scores of 25–50. (The peak of molt activity within each tract is represented by the widest section of the bars.)

not start until primary score 35 and was complete, finishing with, or slightly after the primaries. It was thus the latest tract to commence molting with an earliest date of 28 August.

Head and body molt.—This appeared to be complete, having started before any birds were caught, and being well under way on the earliest bird recorded, 6 August 1973. These tracts continued to show active molt after completion of the outermost primary with a latest date of 18 September.

Figure 2 contrasts molt of the other tracts against primary score to eliminate variations in the date of onset. Peak molt for any one tract is represented by the thickest part of the figure. Data were summarized from 47 molt cards taken on 41 birds. The more important feather tracts suffer the same compression in time shown by the abbreviated primary molt.

In their breeding range, White-eyed Vireos differ from all other eastern Vireonidae in the greater extent of the first prebasic primary, tertial and rectrix molt. The latter species have not been shown routinely to molt juvenal remiges and rectrices, with the exception of tertial molt in the Red-eyed Vireo (Dwight 1900, Manomet Bird Observatory unpublished data). The more extensive first prebasic molt of the White-eyed Vireo cannot be completely explained as a preparation for fall migration, since the northern portion of its wintering range is less distant from its breeding range than is the case in the Yellow-throated (*Vireo flavifrons*), Red-eyed, Philadelphia (*V. philadelphicus*), and Warbling (*V. gilvus*) vireos. Possible explanations for the adaptive advantage of the White-eyed Vireo's unique first prebasic molt include replacement of worn feathers, increase in wing area, and reduction of nest predation. Data presented by George (1973) strongly indicate an increase in wing area after this molt to equip young birds with an adult-sized wing prior to migration. The species nests in thickets and low shrubs, while other eastern Vireonidae generally nest higher and in less dense vegetation; thus the juvenal plumage of White-eyed Vireos may suffer more abrasion (Dwight 1900). Although there is no clear evidence of unusually rapid fledging in the White-eyed Vireo, the rapid attainment of the reduced juvenal wing area may allow rapid dispersal of the young from nest sites which are more at risk from predation by snakes and mammals.

SUMMARY

In Massachusetts the White-eyed Vireo is at the extreme northeast of its breeding range and although increasing in abundance, it is still considered uncommon. The postjuvenal molt is described and is shown to be incomplete prior to fall migration. It involves, at most, the distal 5 primaries, all 3 tertials, an occasional secondary, the tail, and contour feathers. Date and duration of the molt are discussed on the basis of 47 captures of banded birds. It is suggested that an abbreviated molt allows replacement of the most critical worn feathers prior to fall migration, without the delay inherent in a complete postjuvenal molt.

ACKNOWLEDGMENTS

The data presented in this paper originate from the banding program at Manomet Bird Observatory and thus represent the efforts of staff, students, and volunteers. I am grateful to the observatory for supporting the work, to James M. Loughlin who originally discovered the molt at Manomet, and assisted with the analysis, and particularly to James Baird who critically reviewed the manuscript.

LITERATURE CITED

Bailey, W. 1955. Birds in Massachusetts. The College Press, South Lancaster, Massachusetts.

Dwight, J. 1900. The sequence of plumages and moults of the passerine birds of New York. Ann. New York Acad. Sci. 13:73–360.

Evans, P. R. 1966. Autumn movements, moult and measurements of the Lesser Redpoll (*Carduelis flammea cabaret*). Ibis 108:183–216.

Forbush, E. H. 1929. Birds of Massachusetts and other New England States, part 3. Massachusetts Dept. Agr.

George, W. G. 1973. Molt of juvenile White-eyed Vireos. Wilson Bull. 85:327–330.

Griscom, L., and D. E. Snyder. 1955. The birds of Massachusetts. Anthoensen, Portland, Maine.

Newton, I. 1967. Feather growth and moult in some captive finches. Bird Study 14: 10–24.

SNOW, D. W. 1967. A guide to moult in British Birds. British Trust for Ornithology Field Guide No. 11.

———. 1969. The moult of British thrushes and chats. Bird Study 16:115–129.

STONE, W. 1896. The moulting of birds with special reference to the plumages of the smaller land birds of eastern North America. Proc. Phil. Acad. Nat. Sci. 108–172.

THOMPSON, C. F. 1973. Postjuvenal molt in the White-eyed Vireo. Bird-Banding 44:63–65.

WOOD, M. 1969. A bird-bander's guide to determination of age and sex of selected species. College of Agriculture, The Pennsylvania State University, University Park, Pennsylvania.

Manomet Bird Observatory, Box 936, Manomet, Massachusetts 02345. Received 17 May 1982; accepted 22 Aug. 1982.