

MOLT CYCLES OF THE ORANGE-CROWNED WARBLER

MERCEDES S. FOSTER

Studies of the timing and extent of molt in congeneric species of migratory birds have revealed striking interspecific differences that reflect molt adaptation at the specific level (for example, see Johnson, 1963). However, with the exception of Miller's (1928) work on the Loggerhead Shrike (*Lanius ludovicianus*), little attempt has been made to explain intraspecific variation in the timing and extent of molt in a migratory species in terms of adaptations at the subspecific level. The Orange-crowned Warbler (*Vermivora celata*) is a suitable species for such a study because it includes four well-marked geographic races which vary greatly in the extent and location of the breeding range, in the distance and period of migration, and in the timing of breeding.

V. c. celata occupies a wide longitudinal range from central Alaska and the Alaskan peninsula eastward across Canada to western and central Ontario. *V. c. orestera* and *V. c. lutescens*, in contrast, occupy extensive latitudinal ranges. However, *lutescens*, which is found from southeastern Alaska to southern California, breeds along the Pacific coast and in the coast ranges, while *orestera*, an inland race, breeds in the Rocky Mountains and mountains of the Great Basin. *V. c. sordida* is restricted to the Channel Islands off the coast of southwestern California and to limited coastal areas on the adjacent mainland (ranges in all subspecies, A.O.U. Check-list, 1957).

Furthermore, with the exception of an investigation of the Yellowthroat (*Geothlypis trichas brachidactylus*) by Stewart (1952), there has been, to my knowledge, no detailed study of molt in a parulid. Therefore, a study of the extent, sequence, and timing of the molt in the Orange-crowned Warbler was undertaken to determine the type and degree of possible interracial differences and to see if these differences represented adaptations at the subspecific level.

METHODS AND MATERIALS

A total of 2155 museum specimens taken in all months of the year and from a wide range of breeding and wintering localities were examined. Included were 331 specimens of *V. c. celata*, 452 *V. c. orestera*, 940 *V. c. lutescens*, and 436 *V. c. sordida*. Of these, 494 were in some stage of molt, defined here as the cyclic loss and replacement of part or all of the plumage, excluding noncyclic, accidental loss. Molt was signified by the presence of feathers with sheaths. To expose the bases of the feathers for close examination, the feathers were parted or gently lifted with a dissecting needle. A fluorescent magnifying lamp facilitated observation. Designations of feathered regions and age classes are based on criteria published previously (Foster, 1967).

POSTJUVENAL MOLT

Extent of molt. The postjuvenile molt in the Orange-crowned Warbler was studied previously by Dwight (1900). He was concerned primarily with the extent of plumage replacement and states that there is "a partial postjuvenile molt which involves the body plumage and wing coverts, but not the rest of the wings nor the tail." From this rather general statement, it is difficult to determine which, if not all, of the wing coverts are included, as well as whether or not the tail coverts are included. In the present study, in which 353 skins of birds actually in the process

TABLE 1
EXTENT OF REPLACEMENT OF CERTAIN FLIGHT FEATHERS DURING THE POSTJUVENAL MOLT

Secondaries											
Sex	Number examined	Symmetric replacement		Replacement of 8-8		Replacement of 9-9		Replacement other		Replacement of > 1 pair	
		N	%	n	%N	n	%N	n	%N	n	%N
♂ ♂	378	6	1.59	2	—	3	—	2	—	1	—
♀ ♀	322	13	4.04	8	—	6	—	4	—	3	—
??	54	4	—	2	—	3	—	1	—	1	—
Total	754	23	3.05	12	52.17	12	52.17	7	30.43	5	21.73

Rectrices											
Sex	Number examined	Symmetric replacement		Replacement of 6-6		Replacement of 1-1		Replacement other		Replacement of > 1 pair	
		N	%	n	%N	n	%N	n	%N	n	%N
♂ ♂	378	31	8.20	23	74.19	10	32.25	4	12.90	9	29.03
♀ ♀	322	20	6.21	15	75.00	7	35.00	3	15.00	3	15.00
??	54	8	—	6	—	1	—	2	—	1	—
Total	754	59	7.82	44	74.57	18	30.50	9	15.25	13	22.03

of the postjuvénal molt were examined (*celata*, 52; *orestera*, 90; *lutescens*, 186; *sordida*, 25), both the upper and under tail coverts were observed to molt, as were all the wing coverts except the upper greater primary coverts.

In addition, it was noted that juvenal rectrices and remiges were frequently missing or in the process of renewal both during the body molt, and shortly after its completion. Records were kept of individual renewal in order to determine its extent and significance. Only symmetric replacement was considered to represent molt, with asymmetric replacement the result of adventitious loss. Symmetric replacement after the completion of the body molt was regarded as part of the postjuvénal molt until 31 October. This date was chosen because the majority of individuals have completed the body molt by this time. Of the birds examined, only four replaced a symmetric pair of flight feathers in October, none after 16 October. Because no differences in number or location of feathers replaced were recorded among the four races, their values were combined. Numbers of feathers replaced were converted to percentages of the sample for purposes of comparison where sample sizes were sufficient to warrant consideration (table 1).

Of the entire sample, only two birds were replacing symmetric pairs of primaries, a female renewing 1-1, and a bird of indeterminate sex renewing 5-5. It can be assumed, therefore, that replacement of primaries is not a regular feature of the postjuvénal molt. In contrast, there does seem to be a definite, though not very widespread, molt of certain secondaries, with 3.05 per cent of the individuals replacing symmetric pairs. Secondaries 8-8 and 9-9 were replaced more frequently than any of the others, although secondaries 1-1, 2-2, and 4-4 were each replaced by one individual, and 6-6 and 7-7 by two individuals. There is no significant difference between the percentages of males and females replacing secondaries.

The number of rectrices molted, as well as the predominance of replacement

of rectrices 6-6 and 1-1, is equivalent in males and females. Other rectrices replaced included 3-3 in two individuals, 4-4 in three individuals, and 2-2 and 5-5 in four individuals. The deviation from 1-1 and 6-6 is not as high as these figures seem to indicate, since they include data from two females that replaced the entire tail.

Of the 754 birds considered, only 76 individuals, or 10.08 per cent, showed evidence of symmetric replacement of any flight feathers. Of these, 36 were males, 29 were females, and 11 were of indeterminate sex, which indicates no significant difference between the sexes. Specimens were taken from a wide range of localities, from Alaska to Baja California and from the Channel Islands to Idaho, and span a period from 4 June until 16 October. However, the number of individuals molting, as well as the region and extent of the molt, do not vary according to geographic area or date, factors commonly causing much variation (Pitelka, 1945; Selander and Giller, 1960). Although there is no difference between the sexes in the number of birds molting, there is a difference in the extent of the molt. The majority of the birds molting flight feathers were found to be molting only primaries, only secondaries, or only rectrices. Eight individuals, or 10.5 per cent of those molting, were replacing symmetric pairs in more than one area. Five of these were females, which means that 17.2 per cent of the molted females molted in more than one area. Only one male, or 2.8 per cent of those which had symmetric replacement, molted in more than one area. This indicates a significant difference between the amount of molt in the sexes (SE of % difference [S_P] = 1.99; $P < 0.05$). Also differing between the sexes is the amount of molt within one area. The one male that was molting both rectrices and secondaries was molting only one pair of each, and no male molted more than two pairs of rectrices or two pairs of secondaries at one time. Of the females that were molting in more than one area, several were replacing more than one pair in each area. In addition, two individuals molted all six pairs of rectrices as well as secondaries 8-8, and 7-7, 8-8, and 9-9, respectively. It may be significant that both of these birds were taken in the San Jacinto Mountains of California, at an elevation of 8000 feet, one on 14 July 1895, and one on 29 July 1908.

Although the number of birds molting flight feathers was small, I believe that some such renewal is a regular part of the postjuvinal molt. Presumably, as Miller (1928) found, this replacement is "an adaptation for the purpose of reinforcing the most vulnerable parts of the plumage." Those feathers involved (rectrices 1-1 and 6-6, secondaries 8-8 and 9-9) occupy the most exposed portions of the wing and tail. A similar situation has been noted in the Pine Warbler (Norris, 1952) and Northern Water-thrush, *Seiurus noveboracensis* (Eaton, 1957), two species whose molt had been reported to include only the body plumage and wing coverts (Dwight, 1900).

Interrupted molt. Five specimens were examined in which molt had progressed through a degree equivalent to stage one (table 2) of the postjuvinal molt and then apparently had ceased. Included were the following: *orestera*, taken 19 June; *lutescens*, taken 1, 13, 17, and 20 June. One *orestera*, taken on 10 August, had replaced plumage equivalent to that replaced in stage two (table 2) of the postjuvinal molt, prior to the cessation of molt. All of the *lutescens* showed obviously new feathers in the spinal and ventral tracts. The feathers were fully grown, and there was no evidence of sheaths or of any other feathers molting. The two *orestera* showed comparable amounts of new feathers with no trace of sheaths. However, there was evidence in both of small numbers of sheath tips just barely breaking the skin in the spinal tract, and thus indicating a resumption of the molt. These specimens lend

support to the assumption that molt, rather than being curtailed, was merely interrupted. In addition, no immature individuals which have retained any juvenal body feathers have been found at any other time of the year.

Sutton (1935), in a study of the juvenal plumage and postjuvenal molt of sparrows, found in several species what appeared to be a separate, intermediate, incomplete plumage that differed from both the juvenal and first winter plumages. In the Cardinal (*Richmondia c. cardinalis*) nearly all the body plumage is involved, although in most species replacement involves only the scapular and back regions. In view of the limited extent of the molt in Orange-crowns, the small number of individuals exhibiting this phenomenon, and the occurrence of a replacement sequence identical to that of the postjuvenal molt, it appears that the renewed feathers do not represent an interposed "postjuvenal plumage," but rather that there has been an interruption of the postjuvenal molt and that the renewed feathers are part of the future immature plumage.

Cases of interrupted molt have been reported also for the Andean Sparrow, *Zonotrichia capensis* (Miller, 1961), the Black Noddy, *Anous tenuirostris atlanticus* (Ashmole, 1962), and the Sooty Tern, *Sterna fuscata* (Ashmole, 1963, 1965). All these instances, however, involved the postnuptial molt in adults. In each, the suppression of molt was correlated with the onset of breeding activities, indicating presumably the mutually exclusive nature of the two events. There is no such possible explanation in the Orange-crown, as the birds are juveniles and would not be breeding.

Sequence of molt. Molt may first occur in the central dorsal region of the spinal tract, in the sternal-axillary regions of the ventral tract, or in the marginal coverts on the leading edge of the patagium. It usually begins in only one region, but is so closely followed by molt in the other regions that initiation in the three may be considered to be simultaneous. In the spinal and ventral tracts, molt proceeds anteriorly, posteriorly, and laterally, spanning the rest of the molt in duration. Molt of the marginal coverts spreads posteriorly over the patagium and distally along the edge of the wing. When molt is well established in these areas, the tail coverts are dropped and replaced quite rapidly; the underwing coverts and the upper lesser secondary coverts followed by the greater secondary coverts and then the lesser primary coverts are renewed. Almost simultaneously, replacement begins in the antero-dorsal crural region spreading ventrally. Sheath tips also begin to appear in the central-anterior frontal region and central-posterior occipital region with molt spreading anteriorly, posteriorly, and laterally in the capital tract.

Because of this consistency in pattern of feather replacement, the coincident occurrence among several tracts of particular steps in the progression of each tract can be recognized. It was possible, therefore, to define arbitrarily five molt stages (table 2) applicable to both sexes of all races. With the use of intermediate designations, effective classes were increased by five.

These stages apply exclusively to molt of the body plumage, as molt of the flight feathers is somewhat erratic in timing. The independence of the rectrix molt is illustrated by four individuals taken in stage 4 of the body molt. All were replacing rectrices 1-1. In one of these four, the rectrices were less than one-quarter grown and were completely ensheathed; in another, they were one-third grown; in a third, one-half grown; and in the fourth, three-fourths grown. Such variation is also found in the timing of the replacement of the other rectrices. Similar irregularities are present in the molt of rectrices of flickers, *Colaptes* spp. (Test, 1945), in which rectrices 6-6 may molt in any sequence in relation to the other five pairs.

TABLE 2
ARBITRARY STAGES OF THE POSTJUVENAL MOLT IN *Vermivora celata*

Tract	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
Spinal	Either juvenal or some replacement in anterior pelvic and posterior dorsal regions.	Replacement advancing into interscapular region.	Replacement beginning in central cervical region. Extensive in other areas.	Few juvenal feathers in extreme lateral, anterior areas. Some ensheathed elsewhere.	Few ensheathed feathers in lateral and anterior areas. Growth otherwise complete.
Ventral	Either juvenal or replacement beginning in central sternal region.	Replacement advancing through cervical, axillary, and abdominal regions.	Replacement advancing through central submalar and interramal regions.	Few juvenal feathers in lateral, anterior areas. Extensive molt elsewhere.	Ensheathed feathers in extreme lateral and anterior areas. Growth otherwise complete.
Alar	Either juvenal or replacement of marginal coverts at bend of wing.	Lesser and greater secondary and lesser primary coverts dropped.	Middle secondary coverts juvenal. Extensive molt of other coverts.	Growth of marginal coverts complete. Other coverts ensheathed.	Few secondary coverts with sheaths. Growth otherwise complete.
Humeral	All juvenal feathers.	All juvenal feathers.	Replacement beginning anterodorsally.	Extensive replacement. Few juvenal feathers.	Growth complete. Few feathers ensheathed basally.
Crural	All juvenal feathers.	All juvenal feathers.	Replacement beginning centrally.	Scattered juvenal feathers ventrally.	Growth complete.
Caudal	All juvenal feathers.	Upper tail coverts dropped.	Upper and under tail coverts one-half grown.	Upper and under tail coverts three-fourths grown.	Growth complete or with basal sheaths.
Capital	All juvenal feathers.	All juvenal feathers.	Replacement beginning in frontal, coronal, and occipital regions.	Replacement advancing in postauricular, auricular, superciliary, loreal, and malar regions.	Ensheathed feathers in ocular, superciliary, auricular, and malar regions. Growth otherwise complete.

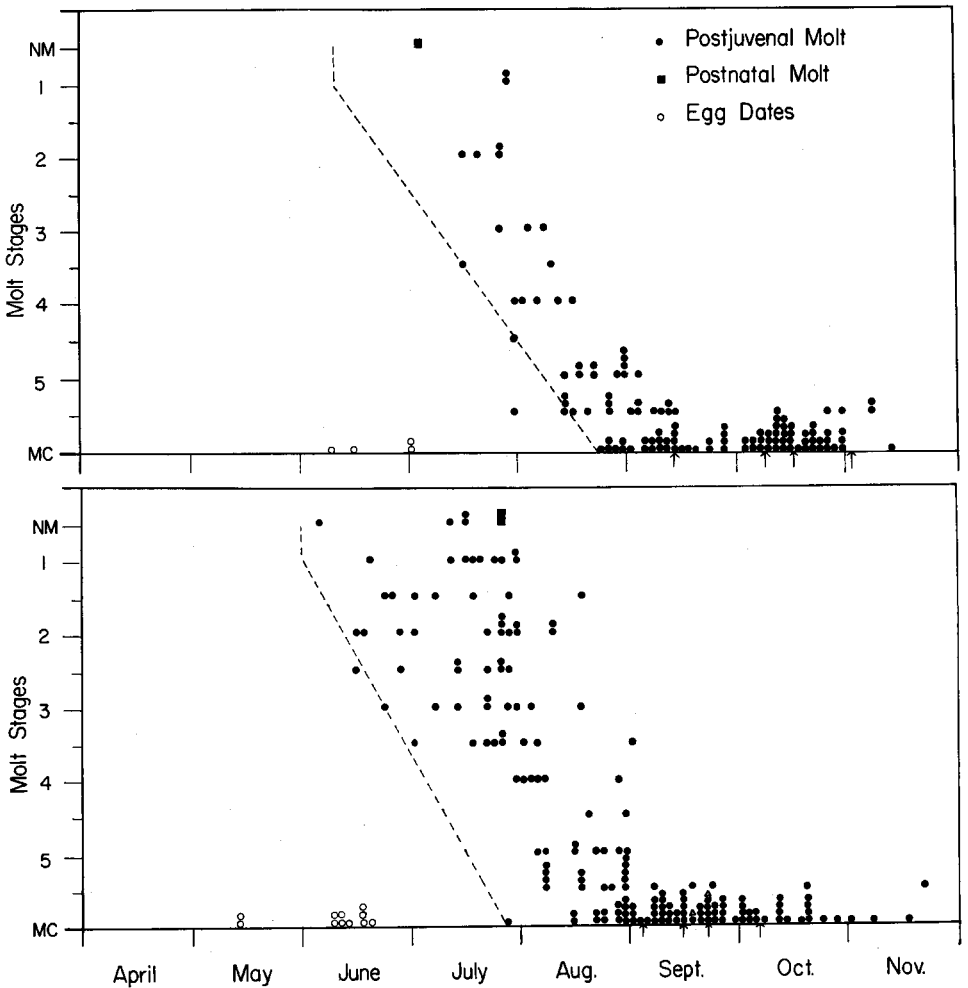


Figure 1. Timing of the postjuvenile molt in *V. c. celata* (above) and *V. c. orestera* (below). Arrows indicate molt completion by (from left to right) 25, 50, 75, and 100 per cent of the sample over the 70-day period of molt completion. Dotted line signifies the projected period of molt for the first individual to complete the molt. Sexes not separated. Δ indicates five individuals.

Only two sets of secondaries were replaced often enough to give any indication of pattern of molt. Of the 23 individuals replacing any of the secondaries, only one replaced them before stage 3, when individuals that have dropped secondaries begin to appear in number. No individuals with secondaries actually in stages of growth appear until stage 4. However, after stage 4, there is no correlation between stage of the body molt and amount of growth in the secondaries. For example, an individual taken in stage 4-5 shows slight growth of secondaries 9-9, while two individuals taken in stage 5 show these same secondaries just dropped, and in the final stages of growth, respectively. Three individuals taken during stage 5 of the body molt are replacing secondaries 8-8. In one they have been dropped; in another they are

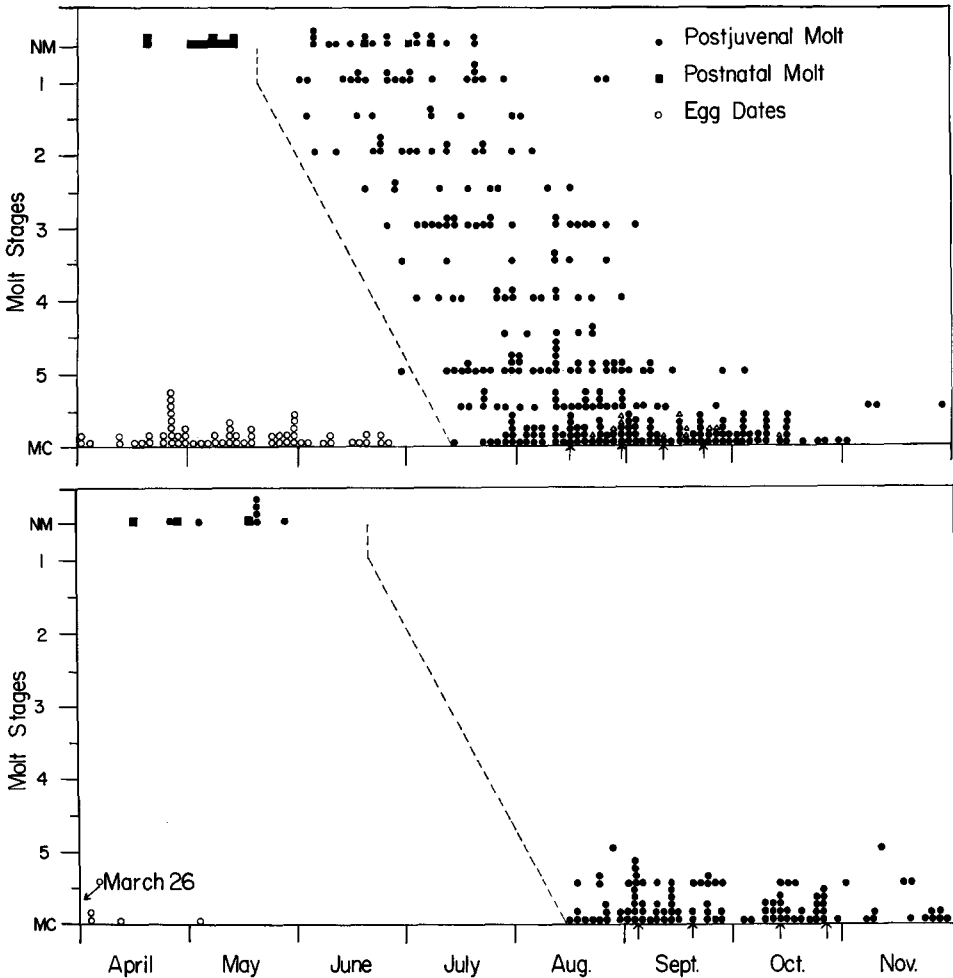


Figure 2. Timing of the postjuvenile molt in *V. c. lutescens* (above) and *V. c. sordida* (below). Arrows indicate molt completion by (from left to right) 25, 50, 75, and 100 per cent of the sample over the 70-day period of molt completion. Dotted line signifies the projected period of molt for the first individual to complete the molt. Sexes not separated. Δ indicates five individuals.

one-third to one-half grown; in the third they are almost completely grown with just a basal sheath. There is no apparent correlation of this variation with date or geographic area. The latter two birds in the above example were taken within two days of each other at the same locality.

Period and timing of molt. From figures 1 and 2 in which the timing of the molt for the various subspecies is plotted, it is possible to gain some ideas concerning the duration of the molt and its various stages. In *lutescens* molt takes approximately eight to nine weeks for one individual (no time is allotted for passage from "no molt" to stage 1, as a bird showing any sign of molt is included in stage 1). This also appears to be the period required in *orestera*. Dividing this figure by the five molt stages one would expect approximately 12 days to be passed in each

TABLE 3
TIMING OF CERTAIN ASPECTS OF THE POSTJUVENAL MOLT

Subspecies	First recorded egg date ^a	Onset of molt ^a	First MC ^b	25%-MC ^a	50%-MC ^a	75%-MC ^a	100%-MC ^a
<i>V. c. lutescens</i>	2 April	19 May	14 July	15 Aug.	29 Aug.	11 Sept.	22 Sept.
<i>V. c. orestera</i>	13 May	2 June	28 July	4 Sept.	15 Sept.	22 Sept.	6 Oct.
<i>V. c. celata</i>	10 June	29 June	24 Aug.	13 Sept.	8 Oct.	16 Oct.	1 Nov.
<i>V. c. sordida</i>	26 March	21 June	16 Aug.	4 Sept.	19 Sept.	13 Oct.	28 Oct.

^a See text for method used in determining dates.

^b MC = Molt completed.

stage. In *lutescens*, the only subspecies in which the sample is large enough for analysis, the median individual of those taken in each stage falls on the following dates (fig. 2): stage 1, 30 June; stage 2, 3 July; stage 3, 22 July; stage 4, 30 July; stage 5, 11 August; molt completed, 29 August (the manner in which this latter date was determined will be discussed subsequently). It is noted that the date for the median individual in stage 2 is very close to that of stage 1, and correspondingly far from that of stage 3. If the dates for median individuals in stages 1-2 and 2-3 are considered, it is found that they fall on 10 July and 14 July, respectively, and consequently 3 July probably does not accurately represent the true median date for stage 2. Therefore, for the purpose of discussion, 12 July will be used as the value for this stage. It is then noted that the spacings of the dates of the median individuals of each stage are 12, 10, 8, 12, and 18 days, respectively. This last figure may indicate a slowing in the rate of the final stage of molt. Presumably a larger sample would show an equal shortening of the periods of the other four stages to 10 or 11 days, rather than a more rapid passage through stage 3 only. The suggestion of a prolongation of molt after the completion of the first four stages is supported by the presence of individuals of all races in stages 5 or 5-MC as late as 28 November, despite the absence of correspondingly late individuals in the other stages. In *sordida*, in addition to the late November individuals recorded (fig. 2), two specimens taken in December still show signs of the postjuvinal molt (♂, 16 December, early stage 5; ♀, 6 December, stage 5-MC).

In *lutescens* the duration of each molt stage for the subspecies as a whole is surprisingly uniform. In the majority of cases birds representing any one molt stage are found for only 10 weeks, and thus the entire molting period for the subspecies encompasses approximately 18 weeks. In order to derive a meaningful way of comparing the timing of the molt among the subspecies, in view of the lack of adequate samples of the other races, 10 weeks was taken as the time necessary for each stage of molt to be completed by all members of each of the subspecies. The 10-week period for molt completion was defined as the first 70 days after the appearance of the first individual to have completed the molt. The presumed date of onset of molt in each race was calculated by subtracting 56 days (eight weeks) from the date of the first individual to complete the molt. The date of completion of the molt by one-quarter, one-half, and three-quarters of all the individuals of a race included within the 70-day span was also recorded (table 3). Molt in *lutescens* presumably begins as early as 19 May and is completed by 22 September. However, molting of individuals is not equally spaced within that time. Seventy-five per cent of the individuals complete the molt between 15 August and 22 September, a period of 38

days. If molt were distributed equally, this period should extend for 52.5 days. The same situation is found in *orestera*, which presumably begins molting on 2 June and completes the molt on 6 October. Seventy-five per cent of the individuals complete the molt in the final 32-day period. In *celata* and *sordida* molt is more equally distributed.

A comparison among the subspecies of the timing of completion of the molt by various percentages of the population reveals some significant differences. Because *lutescens* molts the earliest, it will be used as the basis for comparison. The average lag of *orestra* behind *lutescens* is 15 days, although this delay increases to 20 days before 25 per cent of the individuals have completed the molt. This indicates that the postjuvinal molt in *orestera* is somewhat later in starting than in *lutescens*. In *celata* and *sordida* the lag is 36 and 32 days, respectively. This delay is reduced markedly in one instance, since 25 per cent of the individuals in each of the latter subspecies finish the molt earlier than would be expected in relation to *lutescens*. However, such decreases are expected because of the more equitable distribution of molting individuals within the 70-day period in *celata* and *sordida*.

DISCUSSION OF TIMING OF POSTJUVENAL MOLT

Individuals presumably must reach some minimum level of maturation before molt begins. The only available data concerning the length of the incubation period in the Orange-crown are observations made by Linsdale and Hubbard on a single nest at the Hastings Natural History Reservation. The eggs were incubated for 10 days; the young left the nest nine days after hatching. Such data are scarce for other species of *Vermivora* as well. In the Golden-winged Warbler (*Vermivora chrysoptera*) the incubation period is 10 days (Jacobs, 1904), the nestling period is 10 days (Jacobs, 1904; Crosby, 1912), and the young begin to molt approximately one month after leaving the nest (Faxon, 1911). In the Blue-winged Warbler (*Vermivora pinus*), incubation may last 10 or 11 days, with the young staying in the nest from eight to 10 days after hatching (Burns, in Chapman, 1907). The Nashville Warbler (*V. r. ruficapilla*) incubates from 11 to 12 days, and nestlings leave after eight (Kendeigh, 1952) or 11 (Knight, 1908) days. No information concerning the length of time elapsing after hatching before the onset of the postjuvinal molt is available for the Orange-crown. Assuming, for lack of better evidence, that the molt begins 30 days after they leave the nest, as in the Golden-winged Warbler, then a period of 49 days or seven weeks elapses between the time of laying and the onset of molt. In *lutescens*, 47 days elapse between the first egg date and the projected date of onset of molt. At least one of the sets of eggs taken on 2 April was marked "incubation started." In *celata* and *orestera* only 19 and 20 days, respectively, elapse between the first egg date and the onset of molt, presumably because of the lack of an adequate sample of egg dates. Nests containing eggs of *sordida*, an extremely early breeder, have been recorded as early as 26 March, which means that 87 days or 12½ weeks elapse between the first recorded egg date and the calculated time of onset of molt, a period nearly double that expected.

It also is of interest that there are no specimens of *sordida* in molt stages 1 through 5 during June, July, and early August; this cannot be explained entirely on the basis of lack of collecting in appropriate areas. Although only one Orange-crown has been taken from the Channel Islands in July, this is not true for May, June, or August. In May, 14 Orange-crowns have been collected from the Channel Islands. Several specimens were taken in each of three years; in six other years, only one

specimen was taken. Twelve of these were adult, breeding birds. As the peak of egg laying is presumed to fall in late March and early to middle April, numerous juveniles should have been in evidence. Neither of the two juveniles taken showed any signs of the postjuvinal molt. In June nine adult and no juvenile Orange-crowns have been taken. Seven of these were taken within five days in one year. In August three birds have been taken, two within three days in the same year. Only one was a juvenile. This collecting record does not account for the absence of juvenile specimens from the islands during these periods but suggests the probability that many of the juveniles leave the islands not long after hatching. It has long been known that some *sordida* winter on the Channel Islands but that many if not most of them migrate to the mainland (Grinnell and Miller, 1944; Bent, 1953), appearing as early as mid-July (Grinnell, 1898). It seems reasonable to postulate that many of the juvenal birds which migrate to the mainland do so before the postjuvinal molt.

Although there is no direct evidence available to support this postulate, several lines of circumstantial evidence suggest that it is reasonable. The lack of juvenal birds on the islands during the molting period, as well as their absence from other areas, could be explained as follows: juvenal *sordida* and *lutescens* are indistinguishable on the basis of plumage characteristics and cannot be separated on the basis of tail and wing measurements (Ridgway, 1902; Foster, unpublished data). The length of the bill, which is the most reliable measurement for separating the two groups, cannot be used since the bills are not fully grown in juveniles. Immature birds, which share the plumage characteristics of the adults, can easily be separated. C. H. Townsend (1890), in describing the race, said of *sordida*: "Adult male: Entire plumage decidedly darker than *H. celata lutescens*. Feet and bill larger; wings slightly shorter. There is an appearance of grayness about the upper plumage, owing to a leaden tinge on ends of feathers. Throat and under parts slightly streaked." These differences are obscured in birds with a mixture of two plumage generations (juvenile and immature) and in birds with large portions of their feathers in sheaths. I feel, therefore, that it is probable that many juvenal *sordida* migrate to the mainland in their juvenal plumage and there undergo the postjuvinal molt. Juvenal or molting specimens are assumed to be *lutescens* because of geographic distribution rather than racial characteristics. Toward the end of the molt, enough of the immature plumage is revealed to allow the proper identification of these specimens, and one sees a tremendous increase in the number of available *sordida*. At the present time I am unable to propose any characteristics that adequately serve to separate juvenal *sordida* and *lutescens* before or during the postjuvinal molt.

It is also significant that the two individuals of *sordida* taken in a molt stage other than 5-MC were both taken from the mainland. One, a male in early stage 5, was taken in Palo Alto, California, on 12 November; the other, a female also in stage 5, was taken on Wilson's Peak, Los Angeles County, California, on 28 August.

Additional evidence pointing to the migration of *sordida* before it molts is the delay in the timing of its molt. The presumed lag of five weeks in the onset of molt undoubtedly has several causes and is adaptive to many features of the life cycle of *sordida*. However, an added passage of time for both migration and the replacement of energy reserves used during migration before molt could occur might contribute to such a delay.

Apparently, the suitability of the various Channel Islands decreases as the summer season progresses. Grinnell (1897), in an early-spring visit (28 March until 3 April 1897) to San Clemente Island, found that *sordida* was "quite numerous in the weed-patches and brush along the ravines nearly to the beaches." However, during a stay later in the spring (28 May until 7 June) "when most of the plants were dry and dead, they were confined to the cherry thickets along the canons [sic]." Grinnell later (1898) stated that *sordida* "is probably a visitant to the mainland from the neighboring islands of San Clemente and Santa Catalina at a season when the latter are dry and uninviting." It would appear to be advantageous for a portion of the birds, in this case the young, to migrate before the subspecies enters a period of molt so as to decrease the total demand for suitable habitat and food during the molt period.

Thus, the geographic separation of the postjuvinal and postnuptial molts would have an effect comparable to the separation of the molts in time, the situation found by Pitelka (1958) in the nonmigratory Steller Jays of the Queen Charlotte Islands in British Columbia, in which the diminished period of overlap decreased the total demand for food at any one time. Such a delay of the postjuvinal molt until after migration would probably be adaptive in terms of wear since individuals of *sordida* hatch extremely early in the season and yet undergo no prenuptial molt in the following spring. In addition, molt after migration would explain the persistence of individuals in the late stages of molt through November and early December, since molts that occur after migration tend to be protracted (Johnson, 1963).

Timing of molt in the other races apparently is influenced by the timing of the fall migration. In *V. c. celata* the extreme dates of migration in Alaska fall in early July and late September, while the peak of movement occurs in August and early September (Bent, 1953; Gabrielson and Lincoln, 1959). Individuals are migrating through British Columbia from August until early September (Munro and Cowan, 1947), and in Washington, California, and Arizona in September and October (Grinnell and Miller, 1944; Jewett *et al.*, 1953; Phillips *et al.*, 1964). The schedule of molt, based on a 10-week period from the date of completion of molt by the first individual, extends to the end of October. This and the fact that specimens in stage 5 or 5-MC have been collected outside the breeding range indicate that some migration may occur before the completion of the molt. I do not think, however, that this indicates that a large proportion of *celata* are molting during the migration. Most of these specimens were taken in areas adjacent to known breeding localities, and displacement is probably the result of a period of late-summer vagrancy similar to that reported for *lutescens* (Grinnell and Miller, 1944). In addition, it is probable that the timing of the molt would shift to an earlier period in a larger sample in view of the fact that the majority of the present sample has completed stage 5-MC by the end of the second week in September.

The fall migration of *lutescens* spans a long period, from mid-August through October (Gabrielson and Jewett, 1940; Grinnell and Miller, 1944; Munro and Cowan, 1947; Bent, 1953; Jewett *et al.*, 1953; Gabrielson and Lincoln, 1959; Phillips *et al.*, 1964). *V. c. orestera* leaves British Columbia between 6 August and 15 September (Munro and Cowan, 1947), arriving in Washington to winter by 1 September (Jewett *et al.*, 1953), and passing through California and Arizona from late August to mid-October (Grinnell and Miller, 1944; Phillips *et al.*, 1964). Molt in both *orestera* and *lutescens*, assuming a period of 70 days, is completed before migration during these months.

PRENUPTIAL MOLT

In agreement with Dwight (1900), I found that the nuptial plumage is acquired by a "partial prenuptial molt which involves chiefly the anterior part of the head and the chin." Specifically the areas most commonly involved are the frontal, coronal, superciliary, malar, interramal, and submalar regions. A few birds molt, in addition, the auricular, ocular, and loreal regions, and a few molt the extreme anterior portion of the ventral cervical region. Five individuals (of 525) replaced varying amounts of the spinal and ventral tracts, and in one instance the crural tract. In contrast, an equally limited number of birds molted only the coronal and frontal regions, and a few, only the submalar and interramal regions. Further variation occurred in the degree to which each region molted. Occasionally molt was concentrated in one

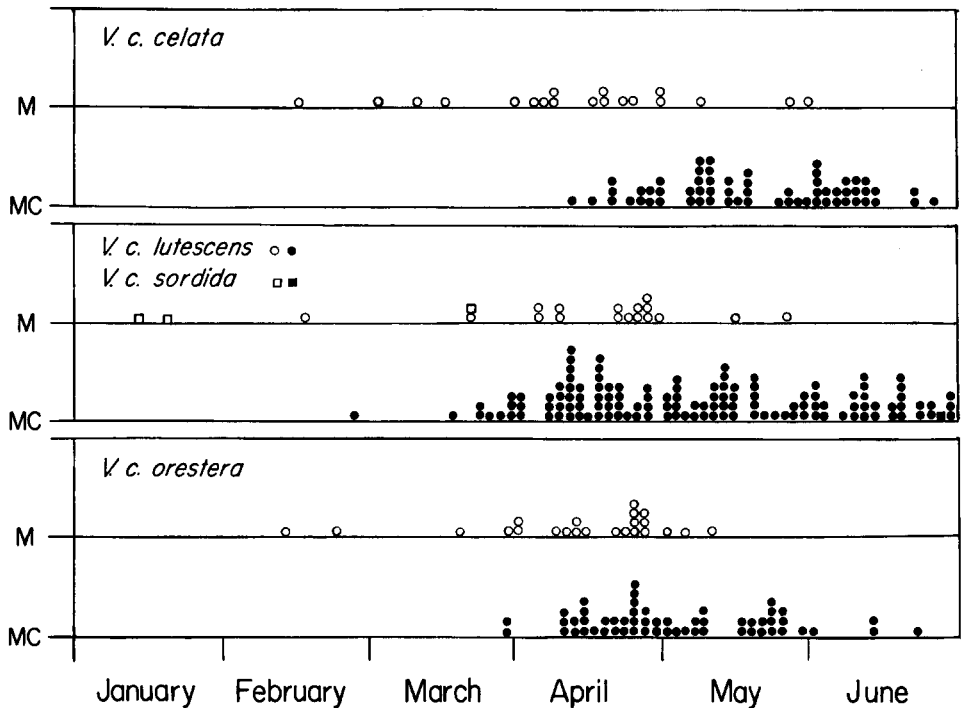


Figure 3. Timing of the prenuptial molt in the Orange-crowned Warbler. Sexes not separated. M = molting; MC = molt completed.

portion of an area, *e.g.*, anterior or posterior, but more commonly, with the exception of the coronal region in which the anterior central was nearly always molted, variation involved the number of feathers replaced, with a fairly even distribution of them throughout the region. There was no correlation between the number of tracts molting and the extent of the molt within each tract, or between either of these and the sex, age, subspecies, geographic distribution, or date of the molt of the individuals.

Of more than 200 specimens of *sordida* collected in January through July, only four individuals showed evidence of molt. For two of these taken in January the designation of the molt as prenuptial is questionable. I conclude, therefore, that a prenuptial molt is not a regular feature of the life cycle of *sordida*, as it is of the other subspecies.

Sequence of molt. It is difficult to make accurate statements concerning the sequence of the molt because the areas molted are so limited. It often appears that molt has begun simultaneously in all regions. In those individuals in which it is possible to discern some sequence of replacement, the sequence is extremely variable. It appears, however, that in the majority of the birds, molt begins in the anterior interramal region from which it spreads posteriorly and laterally to the submalar and cervical regions. Shortly after the inception of molt in the ventral tract, it begins in the posterior frontal region of the capital tract, proceeding posteriorly to the coronal, superciliary, and ocular regions and anteriorly through the frontal and loreal

regions. Molt moves laterally from all these areas to the malar and auricular regions. Because of the limited nature of the prenuptial molt and the variation in its sequence, no attempt was made to define stages of completion of the molt in the individual.

Timing of molt. The period of active molt and its completion are plotted for each subspecies in figure 3. Data for individuals that have not begun to molt are omitted because large numbers of birds never undergo a prenuptial molt. No data were available on the duration of molt in the individual. Although there is undoubtedly much individual variation, it is difficult to believe that it could be as extensive as indicated by comparing the date of appearance of the first individual in molt and the first individual to complete the molt in each of the subspecies.

Although the sample of molting birds is small, some generalizations about the timing of the molt are possible. It appears that molt begins at approximately the same time in each of the three races, but ends slightly earlier in *orestera* than in *lutescens* and *celata*. These differences may be correlated with the differences in time of breeding and migration among the subspecies.

V. c. celata, which breeds in Alaska and eastward across Canada, migrates in April and May, arriving in numbers on its breeding territory in middle and late May (Chapman, 1907; Gabrielson and Jewett, 1940; Grinnell and Miller, 1944; Munro and Cowan, 1947; Bent, 1953; Jewett *et al.*, 1953; Gabrielson and Lincoln, 1959; Phillips *et al.*, 1964). Breeding occurs from late May until early July. *V. c. orestera* breeds over a great latitudinal range in the Rocky Mountains and the mountains of the Great Basin. Spring migration begins very early in April and lasts through May (Chapman, 1907; Munro and Cowan, 1947; Bent, 1953; Jewett *et al.*, 1953; Gabrielson and Lincoln, 1959; Phillips *et al.*, 1964). Breeding, however, may occur as early as late April in the southern part of the breeding range, although being delayed to mid-May in the northern portion. In *lutescens* migration begins in March. Some birds take up their spring and summer residence in California in this same month (Grinnell and Miller, 1944), and consequently eggs may be found in early April in California. Northward, the breeding dates are progressively later (Gabrielson and Jewett, 1940; Munro and Cowan, 1947; Jewett *et al.*, 1953); in Alaska, they extend from early June to early July (Bent, 1953; Gabrielson and Lincoln, 1959).

Thus we see in *celata*, which migrates and breeds the latest, the latest extension of the molt period. In *orestera* we see the early completion of the molt in keeping with the earlier breeding season. The molt period in *lutescens* extends slightly later than in *orestera*, presumably a result of the late-breeding and late-migrating birds of Alaska.

VARIATION IN THE PRENUPTIAL MOLT

In addition to the variation in timing of molt, there is much variation among the subspecies, and within each subspecies, in the number of individuals undergoing the molt. This may be correlated with sex-age groups, geographical or latitudinal differences in the breeding range, and differences in the timing of the molt. In order to determine the extent of the variation between various sex, age, subspecific and geographic units, comparisons were made between samples of each. These samples were composed entirely of birds taken after 15 May. Since only three birds taken after 15 May were still undergoing the prenuptial molt (in the very last stages), it was assumed for the sake of comparison that all birds taken after that date which had not molted would not have done so. In order to eliminate contamination of geo-

TABLE 4
EXTENT OF THE PRENUPTIAL MOLT

Sex and age categories	<i>V. c. celata</i>			<i>V. c. lutescens</i>			<i>V. c. orestera</i>		
	No.	No. with molt	% with molt	No.	No. with molt	% with molt	No.	No. with molt	% with molt
Adult ♂ ♂	21	14	66.67	28	13	46.43	27	4	14.81
First-year ♂ ♂	17	14	82.35	57	29	50.88	48	12	25.00
Adult ♀ ♀	2	1	—	17	7	41.18	4	1	—
First-year ♀ ♀	10	7	70.00	28	9	32.14	14	7	50.00
Total	50	36	72.00	130	58	44.61	93	23	24.73
SE of per cent difference (S_p) ^a			/-----	3.30-----	/-----	3.07-----	/-----		/-----
			/-----	5.53-----	/-----		/-----		/-----

^a $P = 0.05$ for $S_p \geq 1.962$; $P = 0.01$ for $S_p \geq 2.578$.

graphic units by migrants, birds were included only if they were within the known breeding range of the subspecies, or if they were labeled as breeding birds or carried gonad data which would verify this.

Subspecific variation. There is variation in each sex-age group in the number of individuals which undergo the molt. The degree of variation and its direction vary also, among the subspecies (table 4). The first-year females have the fewest molting birds of any sex-age group in *lutescens* while in *orestera* they have the highest and in *celata* the second highest percentage. On the basis of present small samples, statistical analysis of variation among many of the categories within a subspecies is not possible. In addition, in those categories where some analysis is possible, differences are not significant, although in many instances the 5 per cent confidence limit is approached (e.g., *lutescens*: first-year ♂ ♂ vs. first-year ♀ ♀, $P = 0.10$). It is possible that the significance of these differences would increase if a larger sample were obtained. However, as no significant differences were evident in the present sample, the values for the sex-age groups were combined within each subspecies, and the percentage of molt for each subspecies was compared. If the actual difference between the proportions molting divided by the standard error of the difference between them [$S_p = \sqrt{pq/(n_1 + n_2)}$, where p = proportion of one attribute, $q = 1 - p$, and n_1 and n_2 = sample sizes in the two classes] gave a value of 1.962 or more, differences were considered to be significant at the 95 per cent level; values of 2.578 or more were considered significant at the 99 per cent level. Each of the subspecies was different from the others at the 99 per cent level ($P \leq 0.01$; table 4).

Intraracial variation. In addition to the variation between the races, there were differences within each race in the number of molting individuals at various latitudes. To compare the geographic variation within races, the breeding samples were divided arbitrarily into populations on a north-south axis (fig. 4). The sex-age composition of each population is listed with molt data in table 5.

Because of a lack of adequate samples from more areas, it was possible to define only one population of *celata*. It was possible to define five geographic samples of *lutescens*. When the amount of molt is compared between adjacent populations in a north-south direction (table 6), it is seen that IB and IIB are the same but differ quite strikingly ($P < 0.01$) from populations IIIB, IVB, and VB, which

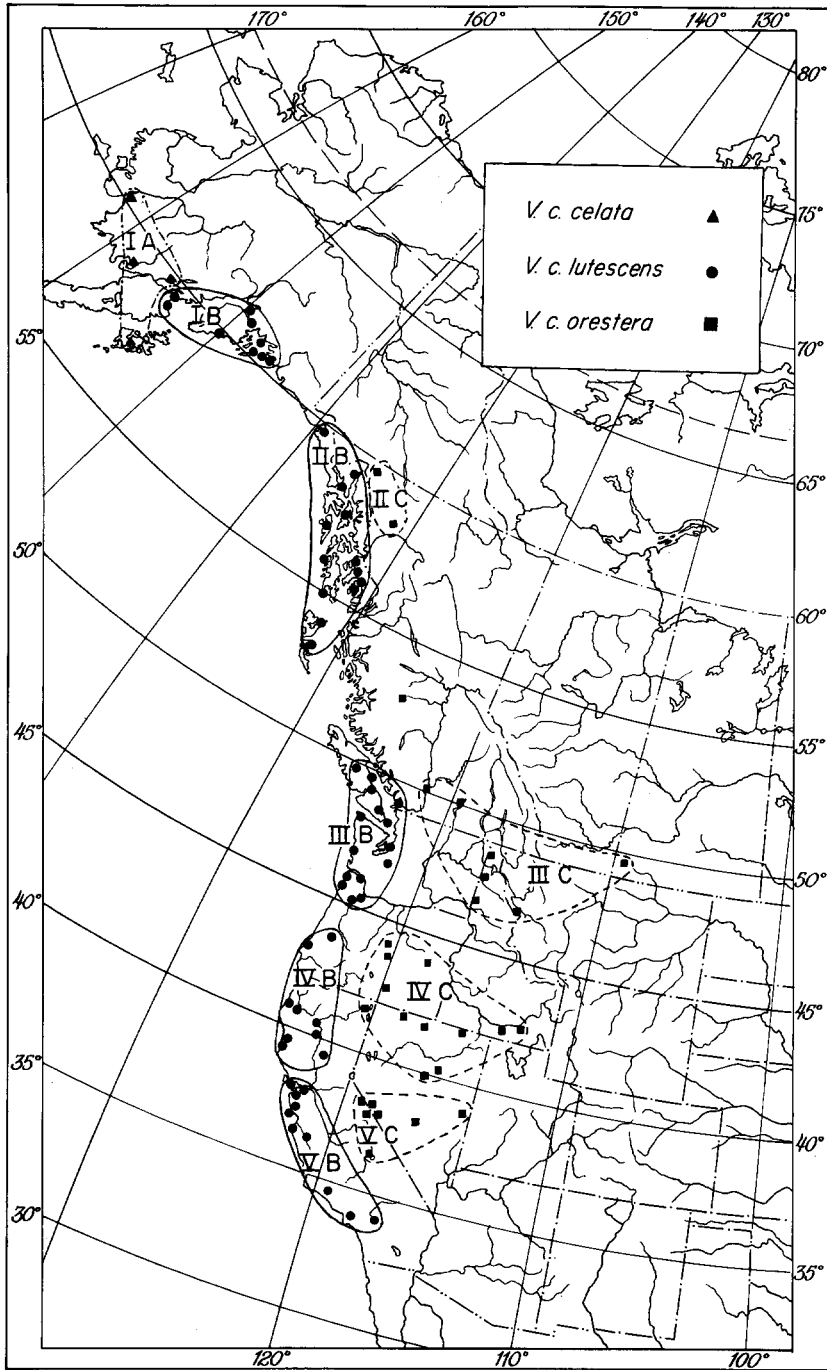


Figure 4. Selected breeding populations of the Orange-crowned Warbler. Each symbol represents one breeding locality, or several breeding localities within a 20-mile radius.

TABLE 5
SEX-AGE COMPOSITION AND EXTENT OF PRENUPTIAL MOLT IN GEOGRAPHIC POPULATIONS OF THE
ORANGE-CROWNED WARBLER

Population	No.	No. with molt	% with molt	Adult males		First-year males		Adult females		First-year females	
				No.	No. M ^a	No.	No. M	No.	No. M	No.	No. M
<i>V. c. celata</i>											
IA	26	19	73.08	15	11	2	2	2	1	7	5
<i>V. c. lutescens</i>											
IB	33	29	87.88	10	8	19	18	3	2	1	1
IIB	18	14	77.78	4	3	7	5	4	4	3	2
IIIB	33	7	21.21	4	1	12	1	5	1	12	4
IVB	17	2	11.76	4	0	6	1	2	0	7	1
VB	26	3	11.53	5	0	11	2	3	0	7	1
<i>V. c. orestera</i>											
IIC	23	12	52.17	4	2	10	5	1	1	8	4
IIIC	11	4	36.36	2	0	5	2	0	0	1	0
IVC	46	7	15.22	16	1	26	4	1	0	3	2
VC	12	2	16.66	4	1	6	1	1	0	1	0

^a M = Molting.

also are statistically the same. Despite the lack of significance of the differences in number molting among all of these populations, there is an evident decrease in the percentage molting as one progresses southward (table 5). It is possible that the significance of the differences would increase with larger samples since this would allow for the separation of sex-age groups and, therefore, a more meaningful comparison between populations. In addition, no compensation has been made for the differences in sex-age composition among the populations, and even though the difference in amount of molt between these categories may not prove to be significant, differences do exist which cannot help but influence the molt value for the population.

V. c. orestera was divided into four populations approximately parallel to but inland from the populations of *lutescens*. The number of individuals molting in the northernmost population, IIC, does not differ significantly from the number in its adjacent population, IIIC. However, it does differ significantly from populations IVC ($P < 0.05$) and VC ($P < 0.01$), although IIIC does not (table 6). Again there is an apparent north-to-south decrease in the number of individuals molting.

Variation in the prenuptial molt has been reported in several other species of birds. In the Harris Sparrow, *Zonotrichia querula*, immatures of both sexes undergo a more extensive prenuptial molt than do the two-year-old adults, which, in turn, molt more extensively than older birds (Swenk and Stephens, 1929). In several species of parulids extent of molt is dependent upon both age and sex differences. Differing climatic conditions may also result in molt variation, at least among populations of the Rock Ptarmigan, *Lagopus mutus* (Salmonsens, 1939). In the northern subspecies of the Bobwhite, *Colinus virginianus* (Watson, 1962), molt is much less extensive than in southern subspecies. In the White-crowned Sparrow, *Zonotrichia leucophrys* (Grinnell, 1928; Blanchard, 1941; Banks, 1964), the reverse is true.

TABLE 6
COMPARISON OF EXTENT OF PRENUPTIAL MOLT IN ADJACENT NORTH-SOUTH POPULATIONS
OF *Vermivora celata*^a

<i>V. c. lutescens</i>		<i>V. c. orestera</i>	
Populations	S_p	Populations	S_p
IB vs. IIB	0.95 ^b	IIC vs. IIIC	0.86 ^b
IIB vs. IIIB	3.92	IIC vs. IVC	2.98
IIIB vs. IVB	0.26	IIC vs. VC	2.04
IVB vs. VB	0.02	IIIC vs. IVC	1.60
		IVC vs. VC	0.13

^a Confidence levels were not calculated between populations where values were more divergent than those already shown to be significantly different. For example, population IB was more different from population IIIB than was population IIB. Therefore, since populations IIB and IIIB were significantly different, it was assumed that populations IB and IIIB were also significantly different. Statistics also were not calculated between populations where values were less divergent than those already shown to be statistically indistinguishable.

^b $P = 0.05$ for $S_p \geq 1.962$; $P = 0.01$ for $S_p \geq 2.578$.

Molt is more extensive in northern races, a condition which may be correlated with differences in the timing of the molt (Michener and Michener, 1943).

Less frequently reported is variation between subspecies with respect to the presence or absence of the prenuptial molt. It has been reported, however, in various sylviid warblers such as *Prinia subflava* (Chapin, 1953) and members of the genus *Cisticola* (Lynes, 1930), as well as in *Lalage sueurii*, a campephagid Triller (Mayr, 1940), and in *Anas castanea* (Ripley, 1942). In each instance the race with the prenuptial molt occupies the temperate portion of the range of the species, while those lacking the molt are found nearer the equator in tropical areas. In *Anas castanea*, at least, and possibly in the others, this results from differences in climatic characteristics between the two areas. The temperate climate, with contrasting seasons, favors a definite breeding season and a cycle of molts. The tropical climate does not, and these subspecies are in near-breeding condition throughout the year (*op. cit.*). This explanation is not applicable to the Orange-crown in which all subspecies are subject to a seasonal temperate climate.

It is possible that the differences in numbers of individuals undergoing the molt are dependent on the timing of molt in relation to the timing of migration. In more southerly areas the breeding season begins earlier than in the more northerly regions, presumably due to the earlier appearance of suitable climatic and other environmental conditions. Early breeding requires an early spring migration, and consequently residence on the wintering grounds terminates earlier in the spring. I feel that this early departure from the wintering grounds may explain the presence of a less extensive molt in the more southerly populations. Molt apparently must be completed before migration and yet cannot be so rapid as to cause excessive energy drain. This presumably is possible despite the limited nature of the molt, since numbers of individuals molting during migration is insignificant. In the southern populations it may be assumed that too short a time elapses between the appearance of the stimulus for molt and the appearance of the stimulus for the spring migration to allow for the completion of the molt before migration. Therefore, only the late-migrating members of southern populations undergo a molt. This would explain the extremely high proportion of molting individuals of *celata* and of the northern populations of *lutescens*.

TABLE 7
 EXTENT OF THE PRENUPTIAL MOLT AMONG SEX-AGE GROUPS IN ADJACENT NORTH-SOUTH POPULATIONS

Population	Number	Number molting	Per cent molting	Number	Number molting	Per cent molting
		Adult males			First-year males	
I	25	19	76.00	21	20	95.23
II	8	5	62.50	17	10	58.82
III	11	1	9.09	21	2	9.52
IV	13	1	7.69	23	4	17.39
V	9	1	11.11	17	3	17.64
		Adult females			First-year females	
I	5	3	—	8	6	75.00
II	5	5	—	11	6	54.54
III	6	1	—	13	4	30.76
IV	2	0	—	7	3	42.85
V	4	0	—	8	1	12.50

Variation by sex-age class. In order to elucidate further the facts concerning the differential amount of molt between the sex-age classes, each category within each of the larger "latitudinal" populations (I, II, III, IV, V) was compared with the adjacent northerly and southerly populations (tables 7 and 8). The combination in this way of populations IA and IB, and so on, served to enlarge sample sizes. However, samples of adult and first-year females were still not large enough for statistical treatment. Even many of the male samples were of dubiously adequate size, but they were treated for the sake of discussion. The results are greatly influenced by the fact that data for the subspecies were combined since the differences between them are significant (table 4).

Within both age groups of the male populations, there was a north-to-south decrease in the number of individuals molting. In the adult males, however, populations I and II were not significantly different from each other although they were significantly different from populations III, IV, and V, which were also statistically the same. In the first-year males, populations I and II and II and III were statistically different although populations III, IV, and V were not (table 8). Within the populations of females, the same trend is apparent in the absolute values (table 7).

The differences in amount of molt between various sex-age groups can be correlated with the physical features of the bird, whose name is derived from the presence of a rich-orange crown patch. It may be assumed that this is flashed by the males during encounters with other males over territorial possession and during courtship displays. Finley (1904) observed that the crown feathers are raised when these warblers become alarmed. The Myrtle Warbler, *Dendroica coronata* (Forbush, 1929; Smith, 1955), Chestnut-sided Warbler, *Dendroica pennsylvanica* (Kendeigh, 1945; Lawrence, 1948; Ficken and Ficken, 1962), and Ovenbird, *Seiurus aurocapillus* (Gibbs, 1885; Nice, 1931), all of which have distinctive crown markings, flash their crowns when alarmed, and also in courtship displays. In addition, crown raising has been reported (Hoffman, 1927) as part of the courtship displays of the Lucy Warbler, *Vermivora luciae*, a species with a distinctive crown patch, and the American Redstart, *Setophaga ruticilla* (Ficken and Ficken, 1962).

Although these observations refer primarily to males, females of some species

TABLE 8
COMPARISON OF EXTENT OF PRENUPTIAL MOLT AMONG CERTAIN SEX-AGE GROUPS IN ADJACENT
NORTH-SOUTH POPULATIONS^a

Adult males		First-year males	
Populations	S_p	Populations	S_p
I vs. II	0.84	I vs. II	2.80
II vs. III	2.52	II vs. III	3.25
III vs. IV	0.12	III vs. IV	0.76
IV vs. V	0.27	IV vs. V	0.02

^a See footnotes, table 6.

also display, although less vigorously (Kendeigh, 1945). It would appear advantageous, then, for males to possess a large, distinct crown patch, whereas in females, this would seem to be less important.

The feathers composing the crown patch are gray basally and then banded successively with orange, bright yellow-green, and finally, a dark gray-green at the tips of the feathers. In those females that lack the orange band, the crown feathers, all of which are gray basally, may be a nearly uniform gray-green or uniform bright green in their outer portions, depending upon the rest of the body coloration. In a large proportion of females, however, and particularly in the adults, the crown feathers are a bright green in the midregion and have distinctly gray-green tips. This is especially widespread in *celata* and gives the birds the appearance of possessing a distinct bright green crown in place of the orange one.

An attempt was made to determine the amount of correlation between possession of a crown patch and the extent of the prenuptial molt. The frequency of the orange crown in the various sex-age groups of each subspecies was determined for a period beginning with the end of the postnuptial and postjuvenile molts and continuing through 30 December (table 9). No attempt was made to segregate individuals according to populations since territorial ties may be broken early and followed by a period of late-summer vagrancy (Grinnell and Miller, 1944). Not only was the presence or absence of the crown patch noted, but to a minor degree, its extent. The two classes distinguished were (1) crown patch covering an appreciable portion of the coronal region, and (2) extremely limited in extent or very pale and barely distinguishable from adjacent feathers or both.

Adult males of all races possess a full orange crown. Therefore, variation in the number of adult males that undergo a prenuptial molt is not a factor affecting the proportion of them which have an orange crown. Furthermore, the brightness of the crown is not necessarily increased by the molt because new feathers have unworn gray-green tips which may conceal the orange band. In heavily worn birds the crown patch is often exceedingly bright and conspicuous.

Among the first-year males the highest proportion of individuals with a crown patch (including those with limited amounts) is found in *V. c. sordida* in which the prenuptial molt is absent. In contrast, in *V. c. celata* in which the proportion of fall first-year males with an orange crown is the lowest of any subspecies, the highest proportion undergoes a prenuptial molt. Consequently, in a spring sample of *celata* taken after 15 May, all first-year males had an orange crown. In *lutescens*, in which an intermediate proportion of birds molt, the frequency of the orange crown patch

TABLE 9
 FREQUENCY AND EXTENT OF THE ORANGE CROWN PATCH BEFORE AND AFTER THE PRENUPTIAL MOLT

Subspecies and extent of crown patch	Premolt		Postmolt		Premolt		Postmolt	
	No.	%	No.	%	No.	%	No.	%
	Adult males				First-year males			
<i>V. c. celata</i>								
full	12	100.0	21	100.0	28	62.22	17	100.0
limited	—		—		8	17.78	—	
absent	—		—		—		—	
Total	12		21		45		17	
<i>V. c. orestera</i>								
full	15	100.0	27	100.0	55	76.39	44	91.67
limited	—		—		8	11.11	3	6.25
absent	—		—		9	12.50	1	2.08
Total	15		27		72		48	
<i>V. c. lutescens</i>								
full	50	100.0	28	100.0	108	83.07	54	94.74
limited	—		—		12	9.23	1	1.76
absent	—		—		10	7.70	2	3.50
Total	50		28		130		57	
<i>V. c. sordida</i>								
full	38	100.0	7	100.0	61	91.04	23	100.0
limited	—		—		4	5.97	—	
absent	—		—		2	2.99	—	
Total	38		7		67		23	
	Adult females				First-year females			
<i>V. c. celata</i>								
full	3	18.75	—		12	17.39	1	10.00
limited	3	18.75	2		6	8.70	6	60.00
absent	10	62.50	—		51	73.91	3 (2) ^a	30.00
Total	16		2		69		10	
<i>V. c. orestera</i>								
full	5	29.42	—		9	18.75	7	50.00
limited	2	11.76	2		8	16.67	3	21.42
absent	10	58.82	2		31	64.58	4 (1)	28.58
Total	17		4		48		14	
<i>V. c. lutescens</i>								
full	30	61.22	10	58.82	41	36.94	6	21.44
limited	11	22.44	5	29.42	14	12.61	8	28.57
absent	8	16.34	2 (1)	11.76	56	50.45	14 (4)	49.99
Total	49		17		111		28	
<i>V. c. sordida</i>								
full	16	55.17	1		26	37.14	3	33.33
limited	3	10.35	—		9	12.86	1	11.11
absent	10	34.48	—		35	50.00	5	55.56
Total	29		1		70		9	

^a Numbers in parentheses indicate individuals which underwent a prenuptial molt and lack a crown patch.

in the spring and the fall varies only slightly, although it is greater in the spring. In addition there is a reduction in the number of birds with a limited crown patch. In *orestera*, despite the low percentage of molt, nearly all spring first-year males have an orange crown. It is of interest that the one bird that did not have an orange crown had undergone a prenuptial molt.

In the adult females significant data are available only for *lutescens* in which there is not an appreciable difference between the fall and spring samples in the percentage with orange crowns. In the first-year females of *lutescens* and *sordida* this is also the situation. In *celata*, in which there were fewer fall first-year females with an orange crown than in any of the other races, there is a high proportion of individuals molting. Coincident with this is the marked increase in the spring of the proportion of first-year females with the orange crown. *V. c. orestera*, in which there is also a marked increase in the spring of the proportion with the orange crown, shows a high percentage of molt.

Influence of migration. If length of stay on the winter range is a factor influencing the number of molting birds, then another possible cause for the differences between the groups would be a differential timing of spring migration among them. "In the spring, the two sexes [of a species] may migrate together, but the males are usually the first to arrive in the north. They select the territory in the nesting area, defend it against invasion by other males, and act as hosts to the females when they arrive" (Dorst, 1962). Specific examples of this have been noted in the Prairie Warbler, *Dendroica discolor discolor* (Nolan and Mumford, 1965), in which the adult males arrive before the adult females, first-year males, and first-year females. A similar situation occurs in the Hammond Flycatcher, *Empidonax hammondi*, in which the adult males precede the adult females and first-year males, both of which in turn precede the first-year females (Johnson, 1965). Brewer and Ellis (1958) noted a similar occurrence in several additional species.

If there is a differential timing of spring migration in the Orange-crown (no relevant data are available at present), it would be expected that the adult males would have the lowest proportion of molting birds, followed in sequence by higher proportions of adult females and first-year males, and then first-year females. Such a sequence is found only in the subspecies *orestera*, in which the small sample sizes limit analysis to only three classes. In addition, no differences were found in the timing of molt in those birds actually undergoing the molt or in the appearance of birds which had completed the molt, among the various sex-age groups. The north-to-south decrease in number of birds molting (table 7) affects all sex-age classes. However, in all races, more of the first-year than adult males molt. This would correlate with an earlier migration time of the adult males. In the females there is no such correlation, presumably because they are not under the same pressure as are the males to undergo a molt, *i.e.*, to acquire an orange crown.

If the prenuptial molt results, in first-year birds, in the acquisition of characteristics already present in the adult which are advantageous in territorial defense and mate selection, and if the occurrence or lack of molt is related to the length of stay on the wintering grounds, then presumably it is advantageous for first-year birds to delay the migration. Although this speculation has obvious implications in the male, it is less applicable to females in which there is as yet no known advantage in having an orange crown.

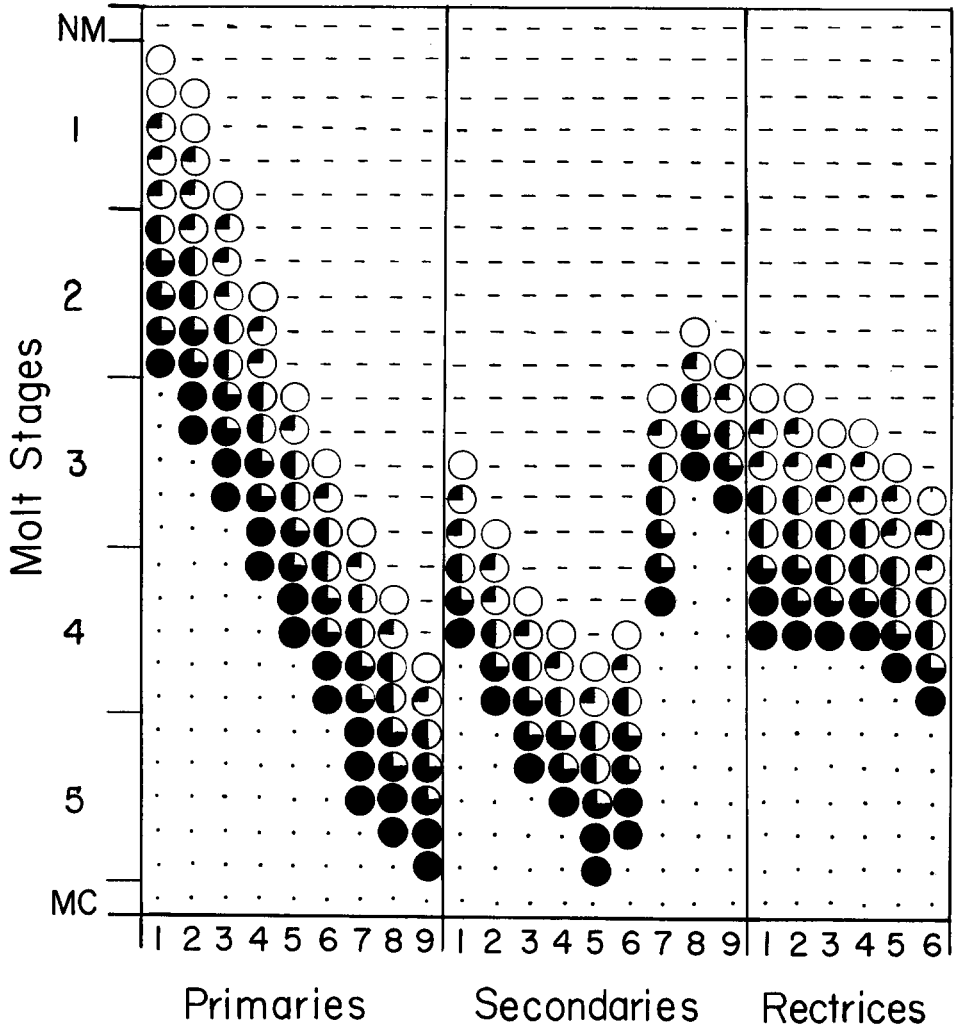


Figure 5. Arbitrary stages of the postnuptial molt in the Orange-crowned Warbler: - = feather old; ○ = feather dropped; ◐ = feather breaking the skin to $\frac{1}{4}$ grown; ◑ = feather $\frac{1}{4}$ to $\frac{1}{2}$ grown; ◒ = feather $\frac{1}{2}$ to $\frac{3}{4}$ grown; ◓ = feather $\frac{3}{4}$ to fully grown; ● = growth completed.

POSTNUPTIAL MOLT

Of the birds examined, 66 were in the postnuptial molt, in which all the flight feathers and the body plumage are replaced. The molt most commonly begins with the loss of the first or innermost pair of primaries. Replacement continues in sequence from one through nine with the feathers being dropped at fairly regular intervals. The vestigial tenth primary drops with primary 9. In the majority of individuals the molt of the primaries spans the molt in all other areas. The exceptions retain sheathed feathers in the lateral interramal and submalar regions and the auricular region after the primaries are fully grown. Because of the limited nature of this post-primary molt, molt stages were based entirely on the molt of the

primaries (fig. 5). These stages were established on an arbitrary basis. Each stage will not necessarily span the complete range of variation to be found in the degree of growth of each primary in relation to that of the others.

A program for the molt of the secondaries and the rectrices in relation to the molt of the primaries has also been determined (fig. 5). These schedules, however, are quite variable and do not always occur in synchrony with the expected condition in the primaries. Therefore, I attempted to map the program in such a way that any variation would fall within the limits of the molt stage to which the specimen had been assigned. The molt of the secondaries in relation to the primaries is much more variable than is the molt of the rectrices.

Despite the variability in timing, the sequence of replacement in both these areas is constant. The rectrices are always replaced in order from 1 through 6. This molt is quite rapid and often appears to be nearly simultaneous. It is difficult to believe that such a rapid molt does not to some degree impair flight. Molt of the secondaries begins with number 8, which usually drops after the first four primaries have been molted. It is followed by numbers 9 and then 7. These three feathers reach a fairly advanced stage of growth before the next secondary, number 1, is dropped. Numbers 2 and 3 are lost at fairly regular intervals after 1. Numbers 4 and 6 molt nearly simultaneously and are followed very shortly by number 5, although occasionally numbers 5 and 6 will drop simultaneously after number 4.

The three alular feathers are molted in an anterior-posterior sequence. They are dropped in early, middle, and late stage 4, respectively, and usually have completed growth by late stage 5. Although the greater primary coverts are dropped with their respective primaries, none of the other alar coverts nor the tail coverts are replaced with regard to the replacement of their corresponding flight feathers. Instead, they molt in sequence with the body plumage exactly as they did in the postjuvinal molt. The replacement of the rest of the body plumage also follows the same sequence in both molts. However, the molt stage numbers of the two molts do not correspond. Always the first and second, and often the first three primaries are growing in before the body molt begins, although the latter is completed with or only shortly after the completion of the molt of the primaries.

Only three exceptions to the above sequence were noted. In one individual, secondaries 7, 8, and 9 on each side had completed approximately one-sixth of their growth and rectrices 1-1 half of their growth although all of the primaries were old. In another, body molt had begun in the central areas of both the spinal and ventral tracts with no accompanying molt of the flight feathers. In the third, although the primaries were only in late stage 2, the rectrices were all new and approximately one-eighth grown.

Timing. The timing of the molt according to the designated molt stages is illustrated in figure 6. Because the specimens of birds actually in the process of molt were few in number, it was necessary to combine the data for all the races. However, individuals prior and subsequent to the molt are separated according to subspecies. The combined molt data show that molt requires approximately two months in the individual while in the species it spans a period of four months, from mid-June to mid-October.

It may be assumed that molt begins in the individual some minimum length of time after breeding, since no breeding birds taken have shown evidence of molt. If this interval is fairly constant in the species, then the time after which birds that have not yet begun the molt may no longer be found should bear a relationship to the

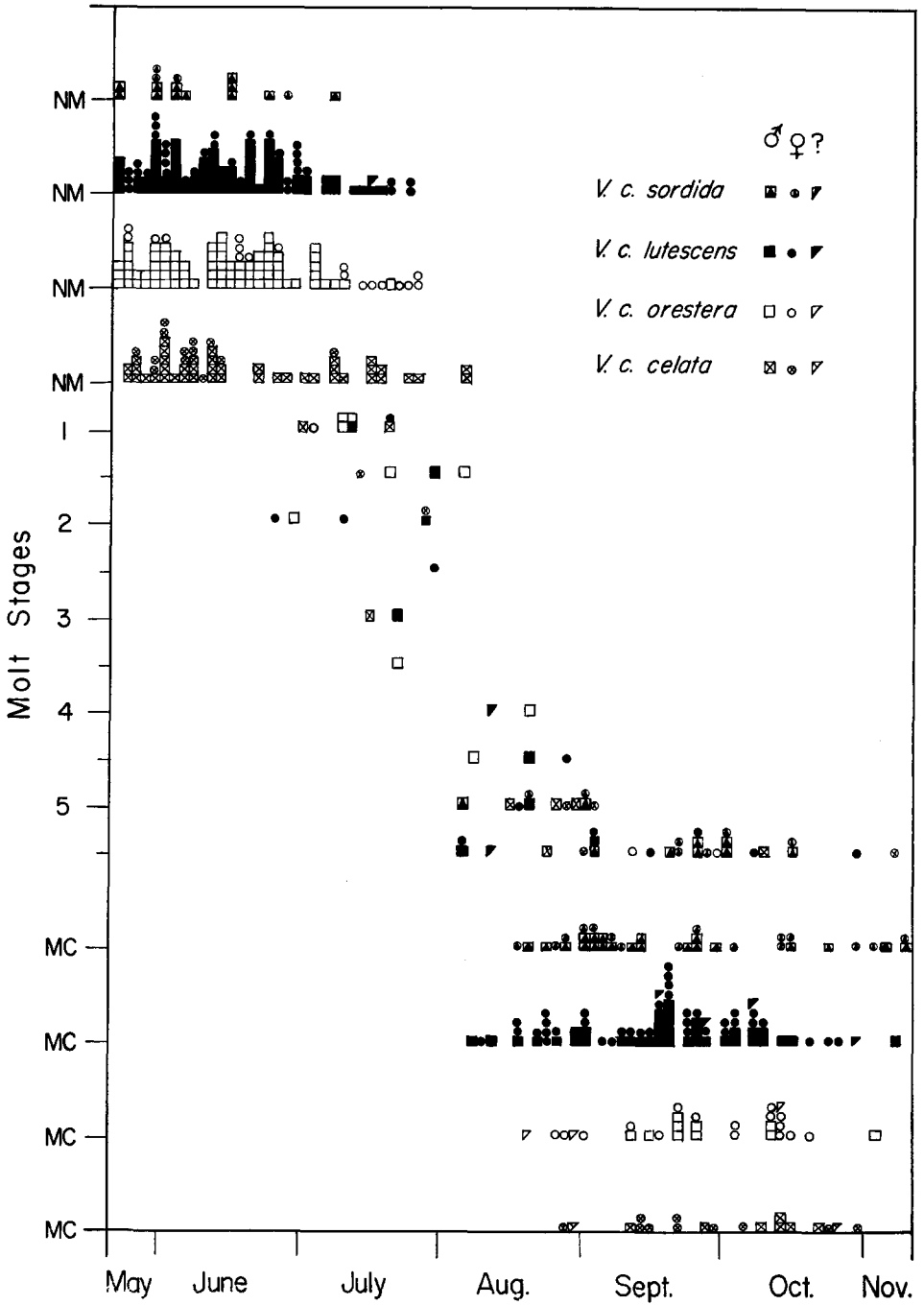


Figure 6. Timing of the postnuptial molt in the Orange-crowned Warbler.

time of breeding. In *sordida*, which breeds the earliest of the four races, all individuals taken after 8 July have started the postnuptial molt. *V. c. orestera* begins breeding later than *sordida* and consequently nonmolting individuals have been found until 5 August. Because the breeding season begins early and is prolonged in *lutescens*, molting individuals would be expected to appear nearly as early as they do in *sordida*, and nonmolting individuals to disappear as late as they do in *celata*. The unexpected absence, from the present sample, of nonmolting birds taken after 24 July may be explained best by the lack of a meaningful sample from all parts of the breeding range, particularly the more northern areas.

The timing of the appearance of birds that have completed the molt conforms to the expected in three of the subspecies. Such individuals of *lutescens* appear on 8 August, individuals of *orestera* approximately two weeks later on 20 August, and individuals of *celata* approximately three weeks later on 28 August. Although they presumably begin the molt before the other subspecies, individuals of *sordida* that have completed the molt do not appear until 10 days after *lutescens*. Apparently, molt proceeds more slowly in *sordida* in the absence of a strong migratory pressure, since many do not migrate, and those that do travel only a short distance to the mainland and northward. Presumably this subspecies operates under conditions not unlike those of a sedentary species in which the molt tends to be more protracted than in those with an extensive fall migration.

If a period of 60 days is allowed for the completion of the molt in an individual, it is possible to determine the approximate date upon which molt should be completed in all members of the subspecies by adding 60 days to the date of the latest individual found which has not yet entered the molt. In *sordida*, the projected date would be 8 September. However (fig. 6), an extremely high proportion of the birds in molt stage 5-MC are *sordida*, taken after 8 September. The projected date for *lutescens* would be 24 September, and for *orestera* 26 September. Only three specimens of *lutescens* and one of *orestera* taken after these dates were molting, and all of them are in the stage 5-MC. Two of these are within three days of the proposed completion date. Only two individuals of *celata* taken after the projected completion date of 6 October still show signs of molt.

Because no difference was noted in the timing of the molt between first-year and adult birds, the data for each were combined. In addition, there was no apparent difference in the timing between the sexes in *orestera*, *lutescens*, and *sordida*. In *celata*, however, the females appear to enter the molt several weeks before the males; also, numbers of females that have completed the molt appear sooner than do the males. However, the samples, especially of birds completing the molt, are so limited that no conclusive statement may be made at this time. This may be contrasted with the situation in the Clark Nutcracker (*Nucifraga columbiana*), in which the males appear to enter the molt sooner than the females (Mewaldt, 1958).

SURVEY OF MOLT IN THE PARULIDAE

The extent to which the plumage of the Orange-crowned Warbler is replaced during each of its molts agrees with that reported for other warblers. Apparently, molt patterns are fairly consistent among the Parulidae. As was expected, all have complete postnatal and postnuptial molts. In addition, only four of many North American species considered (table 10) have been reported to undergo a complete postjuvenile molt. One of these, the Yellow-breasted Chat (*Icteria virens*), may not be a parulid (Bent, 1953; Eisenmann, 1962; Ficken and Ficken, 1962).

TABLE 10
 OCCURRENCE OF THE CROWN PATCH AND EXTENT OF POSTJUVENAL AND PRENUPTIAL MOLTS IN
 NORTH AMERICAN MEMBERS OF THE FAMILY PARULIDAE

Species ^a	Post-juvinal molt	Pre-nuptial molt	Crown patch	Authority
<i>Mniotilta varia</i>	P	B	-	Dwight (1900)
<i>Protonotaria citrea</i>	P	-	-	Bent (1953); Dwight (1900)
<i>Limnothlypis swainsonii</i>	P	-	-	Dingle (1953); Dwight (1900)
<i>Helmintheros vermivorus</i>	P	-	-	Bent (1953); Dwight (1900)
<i>Vermivora chrysoptera</i>	P	-	-	Dwight (1900)
<i>Vermivora pinus</i>	P	-	-	Bent (1953); Dwight (1900)
<i>Vermivora bachmanii</i>	P	H	x	Dingle (1953)
<i>Vermivora peregrina</i>	P	1) H 2) B	-	1) Bent (1953); Dwight (1900) 2) Dickey and van Rossem (1938)
<i>Vermivora celata</i>	P ¹	H or -	x	Present study
<i>Vermivora ruficapilla</i>	P	H	x	Bent (1953); Dwight (1900)
<i>Vermivora virginiae</i>	?	H	x	Bent (1953)
<i>Vermivora crissalis</i>	?	B?	x	Bangs (1925)
<i>Vermivora luciae</i>	P	-	x	Bent (1953)
<i>Parula americana</i>	P	H	-	Dwight (1900)
<i>Parula pitiayumi</i>	?	?	-	
<i>Parula graysoni</i>	?	?	-	
<i>Peucedramus taeniatus</i>	?	-	-	Bent (1953); George (1962)
<i>Dendroica petechia</i>	P	B ¹	x	Bent (1953); Dickey and van Rossem (1938); Dwight (1900)
<i>Dendroica magnolia</i>	P	B ¹	-	Dwight (1900)
<i>Dendroica tigrina</i>	P	B	-	Bent (1953); Dwight (1900)
<i>Dendroica caerulescens</i>	P	H	-	Bent (1953); Dwight (1900)
<i>Dendroica coronata</i>	1) P 2) C	B ¹	x	1) Bent (1953); Dwight (1900) 2) Phillips <i>et al.</i> (1964)
<i>Dendroica auduboni</i>	1) P 2) C	P	x	1) Bent (1953); Swarth (1926) 2) Phillips <i>et al.</i> (1964)
<i>Dendroica nigrescens</i>	P	1) H? 2) -	-	1) Bent (1953) 2) Forbush (1929)
<i>Dendroica townsendi</i>	P	B?	-	Bent (1953)
<i>Dendroica virens</i>	P	H	-	Dwight (1900); Forbush (1929)
<i>Dendroica chrysoparia</i>	P?	?	-	Bent (1953)
<i>Dendroica occidentalis</i>	?	B?	-	Bent (1953)
<i>Dendroica cerulea</i>	P	B or H	-	Dwight (1900)
<i>Dendroica fusca</i>	P	B ¹ or H	x	Dwight (1900)
<i>Dendroica dominica</i>	P	-	-	Dwight (1900)
<i>Dendroica graciae</i>	P	1) - 2) H to P?	-	1) Bent (1953) 2) Webster (1961)
<i>Dendroica pensylvanica</i>	P	B	x	Bent (1953); Dwight (1900)
<i>Dendroica castanea</i>	P	B	x	Dwight (1900)
<i>Dendroica striata</i>	P	B ¹	x	Dwight (1900); Gross (1953)
<i>Dendroica pinus</i>	P ¹	-	-	Dwight (1900); Norris (1952)
<i>Dendroica kirtlandii</i>	P	B	-	Bonhote (1903); Mayfield (1960); Van Tyne (1953)
<i>Dendroica discolor</i>	P	H	-	Dwight (1900)
<i>Dendroica palmarum</i>	P	H-B	x	Dwight (1900)
<i>Seiurus aurocapillus</i>	P ¹	-	x	Dwight (1900)

TABLE 10 (Continued)

Species ^a	Post-juvinal molt	Pre-nuptial molt	Crown patch	Authority
<i>Seiurus noveboracensis</i>	P ¹	H?	-	Dwight (1900); Eaton (1957)
<i>Seiurus motacilla</i>	P ¹	-	-	Dwight (1900); Eaton (1957)
<i>Oporornis formosus</i>	P	H	x	Dwight (1900)
<i>Oporornis agilis</i>	P	H	-	Dwight (1900)
<i>Oporornis philadelphia</i>	P	H	-	Dwight (1900)
<i>Oporornis tolmiei</i>	P	B	-	Bent (1953); Dickey and van Rossem (1938)
<i>Geothlypis trichas</i>	C	H	-	Stewart (1952)
<i>Geothlypis beldingi</i>	P	-	-	Bent (1953)
<i>Chamaethlypis poliocephala</i>	?	?	-	
<i>Icteria virens</i>	C	-	-	Dwight (1900)
<i>Euthlypis lachrymosa</i>	P	-	-	Dickey and van Rossem (1938)
<i>Cardellina rubrifrons</i>	P	-	-	Bent (1953)
<i>Wilsonia citrina</i>	P	-	-	Dwight (1900)
<i>Wilsonia pusilla</i>	P	H	x	Dwight (1900); Tyler (1953)
<i>Wilsonia canadensis</i>	P	H	-	Bent (1953); Dwight (1900)
<i>Setophaga ruticilla</i>	P	H or -	-	Dwight (1900); Gross (1953)
<i>Setophaga picta</i>	P	?	-	Bent (1953)

^a Sequence follows the A.O.U. Check-list (1957): P = molt including the body plumage, tail coverts, alar coverts except the greater primary coverts, but neither the wings nor the tail; C = complete molt; B = molt in which varying amounts, but not all of the body feathers are replaced; H = molt restricted to all or parts of the head, chin, and throat; x = with a crown patch; - = no molt or without an orange crown patch; ? alone = no information available; ? with data = authority cited designated his conclusions as questionable; 1 = some evidence of limited renewal of flight feathers.

Particularly surprising, however, was the report (Phillips *et al.*, 1964) of a complete postjuvinal molt in the Audubon Warbler (*Dendroica auduboni*) and Myrtle Warbler (there designated as the Yellow-rumped Warbler, *Dendroica coronata*), since in no other members of this genus has such an extensive molt been noted. A cursory examination of the molting juveniles of this species in the collection of the Museum of Vertebrate Zoology revealed no evidence of a complete molt. However, no examination was made of individuals that had completed the postjuvinal body molt. It is possible, although there is no statement to this effect, that the molt of the flight feathers occurs after the completion of the body molt and was, therefore, overlooked. Nevertheless, the designation of this molt as complete must remain, at best, questionable, until a more thorough study is undertaken to determine its extent. This leaves the Northern Yellow-throat as the only certain North American parulid with an unquestioned complete postjuvinal molt.

A partial postjuvinal molt, *i.e.*, one including the body plumage, tail coverts, alar coverts except the greater primary coverts, but neither the wings nor the tail, has been reported for all of the other species considered. In the majority of these species, data have been compiled from Dwight (1900) and Bent (1953), both of whose work was at times necessarily superficial in view of the quantity of material covered and the limited availability of specimens. Therefore, in several species in which the molt has been studied more thoroughly, evidence of the limited renewal of certain flight feathers has been found. It is probable that detailed reexamination of molt in other species will reveal the common occurrence of a limited molt of some flight feathers.

The prenuptial molt is much more variable among the warblers. Although no birds

were reported to undergo a complete molt, variation included Type 1—no molt; Type 2—molt restricted to all or parts of the head, chin, and throat; Type 3—molt in which varying amounts, but not all, of the body feathers are replaced in addition to the head plumage; and Type 4—molt including the body plumage, tail coverts, alar coverts except the greater primary coverts, but neither the wings nor the tail.

It was thought that it might be possible to correlate the presence or absence of the prenuptial molt with the presence or absence of a crown patch, a common characteristic among the Parulidae. Difficulties were at once encountered over the definition of "crown patch." It was decided arbitrarily that those birds in which the coronal feathers stand out in contrast to the adjacent frontal, occipital, and superciliary feathers would be designated as having a crown patch (table 10). This would eliminate such forms as the Golden-winged Warbler and the Yellow-throat, which have a contrasting, distinctive "forehead" rather than a crown patch.

Seventeen of the species were considered to have crown patches. These include the Yellow Warbler (*Dendroica petechia*) since a crown patch is present in certain of the numerous subspecies. In three of these 17 species, no prenuptial molt has been recorded. In the Hooded Warbler (*Wilsonia citrina*) this absence is surprising, since both the Wilson Warbler (*W. pusilla*) and the Canada Warbler (*W. canadensis*) do molt. Of even greater interest is the absence of the molt in the Lucy Warbler. Reportedly, this species is most closely related to the Nashville, Virginia, and Colima warblers (Mengel, 1964). All four forms possess a similar crown patch. Molt has been observed in the Nashville Warbler and Virginia Warbler (*V. virginiae*). Its occurrence in the Colima Warbler (*V. crissalis*), in which the fall plumage has been reported to differ from the spring plumage in several aspects (Bangs, 1925), can be inferred, although it is possible that such differences are the result of wear. The Ovenbird lacks a prenuptial molt as do its congeners, the Northern and Louisiana waterthrushes (*Seiurus noveboracensis* and *S. motacilla*, respectively).

It appears, therefore, that molt is adaptive at the specific rather than the generic level and, consequently, does not always reflect generic relationships defined by other criteria.

SUMMARY

The present study of molt in the Orange-crowned Warbler (*Vermivora celata*) is based on 2155 museum specimens taken in all months of the year and from a wide range of breeding and wintering localities.

The partial postjuvinal molt usually replaces only the body plumage, tail coverts, and alar coverts except the greater primary coverts. However, evidence of limited replacement of certain flight feathers also was found. Most commonly renewed are rectrices 6-6 and 1-1, and secondaries 8-8 and 9-9, which occupy the exposed portions of the tail and wings and are, therefore, most vulnerable to wear. The molt occurs on the breeding grounds before the fall migration in all races except *sordida*. In the latter subspecies, evidence suggests that molt occurs after migration. For example, *sordida* in early stages of molt are almost entirely absent from the sample. This would be expected if migration to the mainland takes place prior to the molt, since juvenal and molting *sordida* are indistinguishable from juvenal and molting *lutescens*, and all mainland specimens (including both *sordida* and *lutescens*) probably are assigned to the latter race on geographic grounds. Molt in an individual usually takes approximately two months. In each subspecies, the postjuvinal molt takes approximately 18 weeks.

The prenuptial molt, which most commonly involves only areas of the head and chin, is completed in the species by mid-May, although all individuals have not necessarily undergone the molt. There are significant differences among the races in the proportion of individuals undergoing a prenuptial molt. The percentage is greatest in *celata*. *V. c. sordida* has no prenuptial molt. In *lutescens* and *orestera* there is a statistically significant decrease from north to south in the proportion of individuals molting. The more northerly populations of the species presumably migrate the latest, spending more time on the wintering grounds and, therefore, having a longer period in which to molt. Variation in the number of individuals in each sex-age group that undergo a prenuptial molt may be correlated with the variation in frequency of occurrence of the orange crown patch. Categories with the lowest proportion of individuals with orange crowns before the molt have the highest proportion of molting birds.

The postnuptial molt is complete and occurs on the breeding grounds between the time of breeding and the fall migration. It takes approximately two months in an individual. Evidence suggests that females of *celata* may begin the molt prior to the males.

A survey of species of Parulidae from North America revealed that the extent of the postnatal, postjuvinal, and postnuptial molts is quite uniform in the family, but that the extent of the prenuptial molt varies considerably. Such variation appears to be adaptive at the species level and hence does not always reflect generic relationships defined by other criteria.

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Egg dates were obtained from the collections and records at the Museum of Vertebrate Zoology and from the Western Foundation of Vertebrate Zoology, through Ed N. Harrison. Information on incubation, obtained by Jean M. Linsdale and Douglass Hubbard at the Hastings Natural History Reservation, was provided by John Davis.

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Museum of Vertebrate Zoology, University of California, Berkeley, California.
(Present address: Department of Biology, California State Polytechnic College,
Pomona, California.) 20 December 1965.