

INTERRELATION OF VARIABLES IN POSTJUVENAL MOLT OF CARDINALS

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Within single-brooded passerine species, the juveniles hatch almost concurrently, generate juvenal plumage, and later molt into sexually-stereotyped first-winter (= Basic I) plumage (Welty, 1962; Pettingill, 1970). In double-brooded species, the scheme is more complex, yet the interval and pattern of postjuvinal (= Prebasic I) molt are relatively standardized. In the multi-brooded species, these events occur in complex patterns.

This paper reports data taken from live, free Cardinals (*Cardinalis cardinalis*), a multi-brooded species, showing that hatching dates, discontinuation of the molt season, and the components—initiation, duration, rate, and sequence—and results of postjuvinal molt are variables that are imperfectly interrelated. Juveniles hatched over a five-month period. Immediately after hatching, the postnatal molt (the only constant event) was started and subsequently completed in seven weeks. Following this, the young may or may not have rested (i.e., a time of essentially no molt) between the two molts. Initiation dates for postjuvinal molt spanned three months. Duration of molt varied recessively from 17 to six weeks, the rate varied from leisurely to accelerated, and the sequence of flight feather molt was contingent upon duration and rate of molt. Cessation of molt occurred some time in November. In response to the other variables, the results ranged from a complete molt to the molt of only the body feathers.

METHODS

In 1967-1972, during weekly sessions of general banding at the Cincinnati Nature Center and in Ft. Thomas, Kentucky (similar equipment was used; Wiseman, 1975), birds were trapped and quickly processed. Individuals were identified by their U. S. Fish and Wildlife Service band numbers, a cumbersome series of eight digits (as in Figure 2). In the text, the last three digits and the banding location are combined so that #C-501 is a Cincinnati Nature Center bird banded with #72-199501 and #K-501 is a Kentucky bird banded with #75-157501.

At every capture throughout the year, I examined each Cardinal and, on tape (Wiseman, 1972), collected data on bill colors, injuries, the regeneration of accidentally lost feathers, feather wear, and molt. On each molt record, the major flight feathers (rectrices and remiges) were listed by number (see Figure 2) and recorded as: old (= retained juvenal feathers), missing, developing, or new (= completed first-winter feathers). The size, i.e., growth to date, of each developing feather was estimated as a percentage of the length of an adjacent mature feather. All other feathers, including the wing coverts, were studied in groups using a similar scheme.

Excluding the first year when I developed my procedures, I recorded details of molt from 659 juveniles captured 1,407 times between 4 June (the earliest date) and mid-November (when molt

ended) distributed as follows: in June, 52 captures, July 305, August 376, September 290, October 253, and before 20 November, 131 captures. In addition, 125 of these birds and another 168 juveniles (new bandings) were taken within two-three months after the end of molt, affording data on the outcome of their molt.

Terminology.—The following terms are used with specific meaning. "Molt" refers only to normal conditions, i.e., not to accidentally lost feather replacements. A "partial molt" indicates the retention of one or more flight feathers, whereas a "complete molt" indicates the replacement of all flight feathers but not necessarily all minor feathers. The plural forms of these terms refer to and include all of the various degrees, results, or durations of postjuvenal molt—e. g., "The partial molts, which on various individuals lasted from six to 11 weeks and resulted in the retention of from 1 to 24 (all) flight feathers, were . . .," is paraphrased to, "The partial molts were . . ."

For the ending of partial molts, "cessation of molt" indicates (1) that, while in progress, evidence of a premature discontinuation of molt was (or might have been) detected, or (2) the time this event occurred or could be expected to occur, whereas "terminated" means that all evidence of molt had disappeared.

Determining age of juveniles.—On very young birds, age could be judged by the characteristics of juvenal plumage and by bill color, which at first was totally dark but gradually faded as the orange-red (adult) color developed. Bill color could be used safely until only small patches of dark remained, at which time it could be confused with adults that had a dark discoloration on their bill (possibly due to injury), particularly along and to each side of the culmen.

When these features were doubtful, age was ascertained by the degree of skull pneumatization using a 10X hand-lens (Wiseman, 1968). Of the juveniles first captured in summer and which had completed their postjuvenal molt, 10 to 15 birds were completely pneumatized in November but another 40-50 were not fully pneumatized until December. When the postjuvenal molt had been partial, pneumatization was usually not completed until January or February, but on these young the age could usually be judged by plumage as follows.

Determining the age of feathers.—On most juvenile males, all juvenal feathers were distinctively brownish whereas first-winter feathers were reddish, so with practice I could determine the age of most feathers by characteristic color. However, on some males the two plumages were nearly the same color, so the body feathers could not be distinguished and only by careful examination could I determine if some flight feathers had been retained. A comparison of feathers between two individuals was worthless.

On the females, the age of the flight feathers could be determined by colors similar to those on the males, but the body feathers did not differ in color between the two plumages. However, my data on active molt showed that the sexes were identical in all aspects of molt.

The age of flight feathers was also indicated by their size. In a sample of 30 males captured both before and after a complete postjuvinal molt, I found the wing chord measurement (bend to tip) was greater after molt by an average of 4.9 mm (range 2-7 mm) and the tail measurement (central base to tip) was longer by 5.6 mm (range 4-11 mm). Hence, after a partial molt, an adult remex or rectrix was longer and slightly broader than an adjacent juvinal feather. When the remiges were molted but the entire tail was retained, the wing measurement increased but the tail (except for wear) remained the same. When all or most juvinal primaries were retained, all rectrices were retained, so neither measurement changed. Because individuals varied in size (wing chord range: 85-94 mm before and 89-99 mm after molt; tail range: 89-105 mm and 97-110 mm), only comparisons on the same bird were deemed valid.

Scott (1967) found that Cardinal rectrices were pointed in juveniles and blunt in adults and suggested these shapes be used to identify retained juvinal feathers. However, I used this scheme cautiously because I had noticed that when adults lost a feather(s) outside the molt period, the replacement feather(s) were atypical. For study, I plucked and saved adult rectrices and found that 157 matured replacements were 2-11% short of the original feathers, and were often closer in color, size, and shape (sometimes pointed) to juvinal rectrices. When the replacements were collected, the loss of characteristics on the second replacement was even more obvious. Therefore, I used Scott's scheme only if several apparently juvinal rectrices were present in symmetrical patterns and, even so, in about 5% of these the rectrices were intermediate in color, shape, and size.

When the postjuvinal molt had been prematurely terminated, all feathers were retained until the postnuptial molt of the following year. (In spring all Cardinals shed their downy feathers but none molted contour feathers until breeding was complete.) Between these annual molts, flight feathers retained most of their characteristic color, shape, and size, but feather wear was consistently more severe on the juvinal feathers. By these attributes, I could determine which birds had retained juvinal feathers and, thereby, that these were young Cardinals.

RESULTS

Figure 1 shows, for the first 100 juveniles banded in 1969 at the Cincinnati Nature Center, the distribution and frequency of 244 captures, the outermost primary being molted at each capture, and, for some birds, the duration and/or results of the postjuvinal molt. A perusal shows the molt was not synchronized; thus, on the same day, e. g., 24 August, some birds were not yet molting, some were initiating molt, and others were well into molt. Of the birds captured after cessation of molt, some had completed the molt but others had retained various flight feathers. For this variation, Palmer (1972:81) wrote, "The 'population' method of studying molt is complex in multi-brood species. Flocks contain

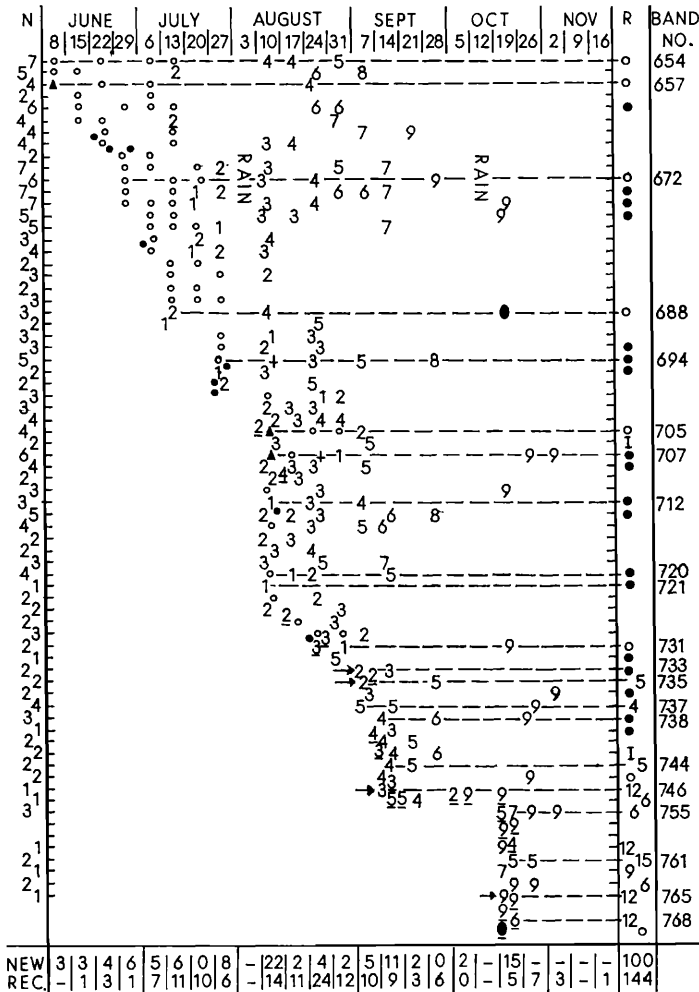


FIGURE 1. The distribution and frequency of captures, degree of primary molt, and (for some) results of postjuvinal molt for the first 100 juveniles banded (Cincinnati Nature Center) in 1969. N = number of captures per individual during molt period, single captures excluded but "1" indicates recapture after molt. R = results: ○ = complete molt indicated at last capture; ● = captured after complete molt; I = irregular loss, results uncertain; numerals = number of flight feathers retained as suggested at last capture or known by recapture. KEY TO DATED CAPTURES: ○ = no molt, see text. ● = no molt, single capture. ▲ = ending of postnatal molt. + = postjuvinal body molt prior to loss of flight feathers. Numerals = outermost primary lost or growing, underscored = single capture. Dash line connects captures (arrow = numeral starting line) with results and band of individuals discussed in text. ● = ending of complete postjuvinal molt. At bottom, sample sizes by date of new bandings and recaptures of these bandings.

early- to late-hatched individuals and, since their variation in age is reflected by differences in molting and other functions, the general picture for the sample may mask the desired information about an individual." I believe Figure 1 amply demonstrates this "masking" effect and the "complex" nature of this study.

Among the factors not shown in Figure 1 are the degree of primary growth (from missing to the loss of the next primary), the timing and sequence of secondary and rectrix molt, which feathers (if any) were retained, and the sequence of retention. To comprehend these intricate details for each individual, I plotted data for 18 right remiges and six retrices on simple work charts (Fig. 2).

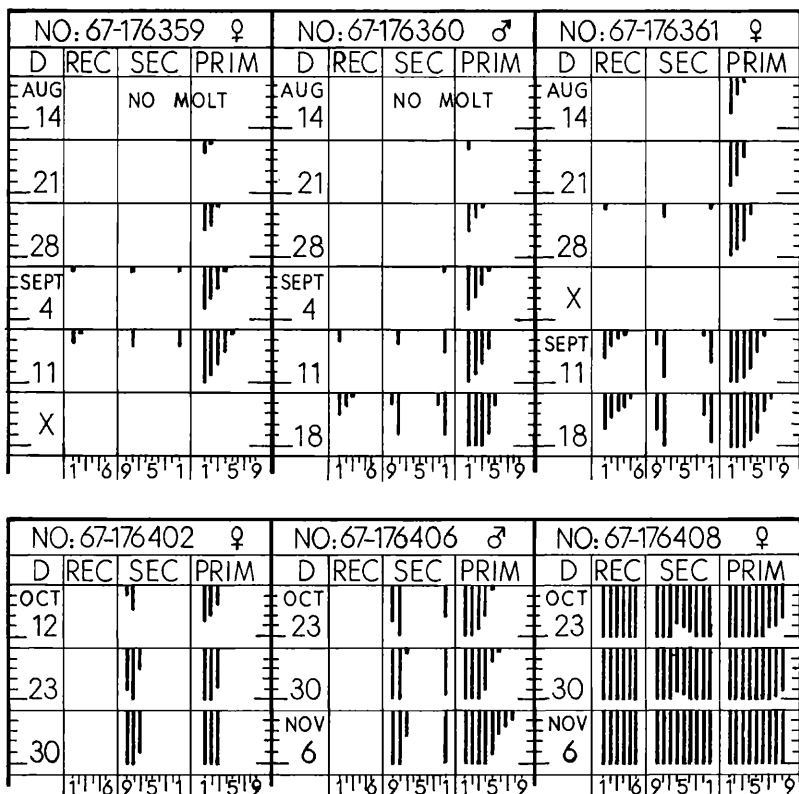


FIGURE 2. Six examples of work charts recording the postjuvinal molt on young captured almost weekly. Vertical bars indicate start, timing, sequence, and rate of growth of adult flight feathers (juvinal feathers assumed to be present). Upper charts, start of complete molts; lower charts compare partial molts of two birds while third completes all flight feathers. U. S. F&WS band number and sex are at top; position and number of each right rectrix, secondary, and primary at bottom; and percentage of growth on sides (longer line = 100%). D = date of capture, X = not captured. Dates are not identical or consecutive in all charts.

On recaptured birds, I compared the charted data to determine the onset, sequence, duration, and rate of molt of the flight feathers. No one bird provided details for its entire molt cycle, but hundreds of molting juveniles were repeatedly scrutinized within limited periods or at protracted intervals spanning the entire period (Fig. 1, 2). By combining two or more appropriate charts, e.g., # K-361 and 408 (Fig. 2), and comparing this composite to charts of various individuals taken over a long period, I formed a comprehensive overview of the molt cycle. This work showed that individuals followed numerous patterns (Fig. 2) which varied in sequential and temporal alignment and results, and that, infrequently, individualistic anomalies occurred on apparently healthy birds.

Because of the multiplicity of "normal" patterns, the variables of captures, anomalies, and the results of molt and the basic complexities of molt, exact sample sizes cannot be given for specific events, e. g., the loss of primary 1. In a sense, every bird was a sample of one or, at best, each day of the breeding season afforded a new sample.

Concept of available time versus molt.—The rationale for the multiplicity of results eluded me until I conceived the hypothesis that juvenal molt was circumscribed by the hatching date and the

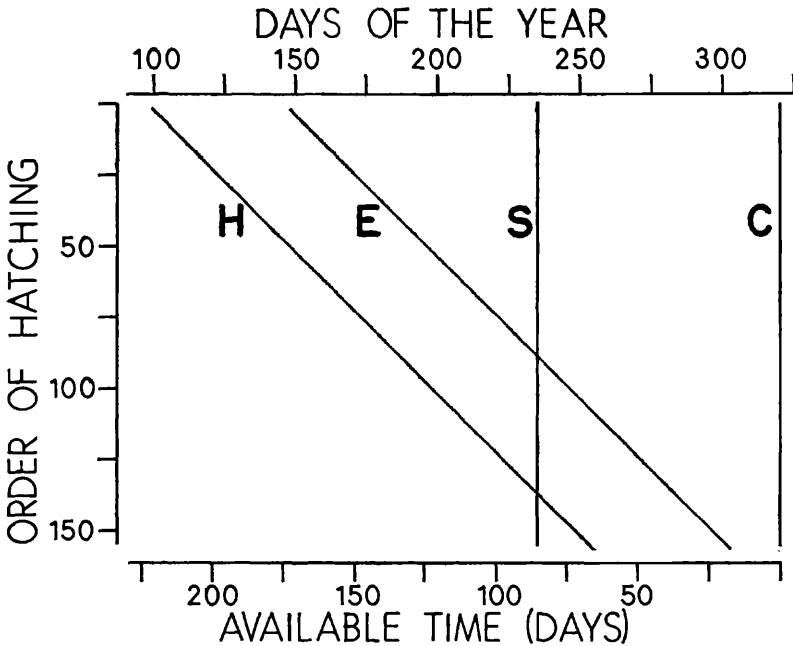


FIGURE 3. Conceptual alignment of pertinent factors which suggest that time limitations (increasingly) preclude late-hatched young from completing (some or much) postjuvinal molt. Line H = hatching dates, E = end of postnatal molt, S = final day for start of complete postjuvinal molt, and C = cessation of molt.

cessation of molt, and, as these factors came into close proximity, the reduction in available time forced a reduction in molt. To depict this, in Figure 3 the numerical days of the year (1-365) were set on the horizontal axis, the serial order of hatching (first, second, third, etc.) was set on the vertical axis, and the intersect points of these were connected (line H). Then, since each juvenile required about seven weeks to complete the postnatal molt, 49 days were added to each hatching date to determine the completion dates and these points were connected (line E). Next, the cessation of molt (line C) was arbitrarily fixed on day 319 (15 November) and the theoretically final day (line S) for the start of the complete postjuvinal molt (i. e., starting at a later date would reduce the available time to less than the 12 weeks required for completion) was set on day 235 (day 319 minus 84 days).

The intersect of lines E and S suggests that over 50% of the young should complete postnatal molt and then have time to complete the postjuvinal molt, which agrees with my findings that 58% of the young accomplished this (Table 1). For the remaining young, it suggests that—as the hatching date closely approaches the cessation of molt—regressively less molt would be possible. This agrees with my findings that the flight feathers were cumulatively retained in progressively larger numbers (Table 1). When I aligned my data on this basic sketch, nearly all data sets fell into place as suggested in Figure 4.

An overview of the molt season.—Figure 4 diagrams the chronology of the episodes of the molt season relative to five first-of-month hatching dates and cessation of molt. In each, postnatal molt immediately followed hatching and was always completed in about seven weeks. When hatching occurred about 1 May, a prolonged period of rest preceded the leisurely postjuvinal molt. Later hatching (e. g., 1 June) resulted in the shortening of both periods until, about 1 July, no time was available for a rest and the postjuvinal molt was greatly accelerated in order to be completed. Because the postjuvinal molt could not be completed in less than 12 weeks, hatching after early July usually resulted in partial molt. When hatched about 1 August, the young retained all rectrices and some secondaries. When hatched very late (about 1 September), only a few flight feathers were replaced. In each case, body molt was continued and very nearly completed regardless of the hatching dates. The duration and results of postjuvinal molts for intervening dates can be extrapolated. Each of the above episodes and their relationships are discussed and evidenced below in chronological order.

Nesting, hatching, and fledging.—Cardinals hatched from 4 April through 10 September, a span of five months. In four nests, eggs were laid daily until a clutch of three was completed, then incubation started. After 12 to 14 days, all young hatched within 2 to 12 hours and were naked except for a scant covering of light grayish down on the dorsal regions. Fledging occurred about day 10 but, in disturbed nests, on day 8. These findings agree essentially with those reported in Bent (1968).

TABLE 1.

Results¹ of postjuvénal molt for 196 juvenile Cardinals banded in 1969² at the Cincinnati Nature Center.

R ³	B ⁴	R	B	R	B	R	B
1	0	7	2	13	2	19	1
2	3	8	7	14	1	20	0
3	0	9	2	15	1	21	0
4	10	10	2	16	3	22	1
5	14	11	4	17	1	23	1
6	18	12	7	18	0	24	2
45 ⁵		24		8		5	
(23%) ⁶		(12%)		(4%)		(2.5%)	

¹Number of birds that retained a specific number of flight feathers. In addition, 114 (58%) had completed the molt.

²April through November only.

³Number of feathers retained.

⁴Number of birds.

⁵Column totals: First column = rectrices only; second column = rectrices and first six secondaries; third column = rectrices, first six secondaries, and some primaries; fourth column = all rectrices, most secondaries, and most primaries.

⁶Percentage of total sample.

Postnatal molt.—At hatching, the remiges appeared as dark spots in the skin along the posterior margin of the wing. These erupted en masse on day 2 or 3 and were fully formed in about four weeks. All rectrices erupted about a week after hatching and matured in about six weeks. On the head, the dorsal feathers erupted shortly after hatching, but the lateral and ventral feathers did not emerge until six to 10 days later. Body feathers developed in irregular patterns and numbers within each tract. For example, on the spinal tract about 10-15% of the feathers, essentially in the middle rows, erupted just after hatching. As these grew, a few quills scattered through the tract emerged every few days, gradually adding to the number of incoming feathers. Because these small feathers matured in 7 to 14 days, the number of growing feathers was held to 20-30% of all the feathers in the tract. On the ventral tract, a similar pattern was followed but about a week later. The apteria remained naked throughout the summer.

Final vestiges of postnatal molt were found on each side of the body in three small, irregular patches of feathers. Two were on the ventral tract: (1) in the lateral edges of the upper breast, i. e., under each wing, and (2) at the posterior end of the flank element (see Clench, 1970:658). The third was on the spinal tract in the posterior row of the mid-back (saddle element of Clench, p 659).

Hatching dates and the duration of the postnatal molt.—The difficulties of attracting banded fledglings from scattered nests to my trapping area severely limited my data on exact hatching dates and the duration of the ensuing postnatal molt. Three young were

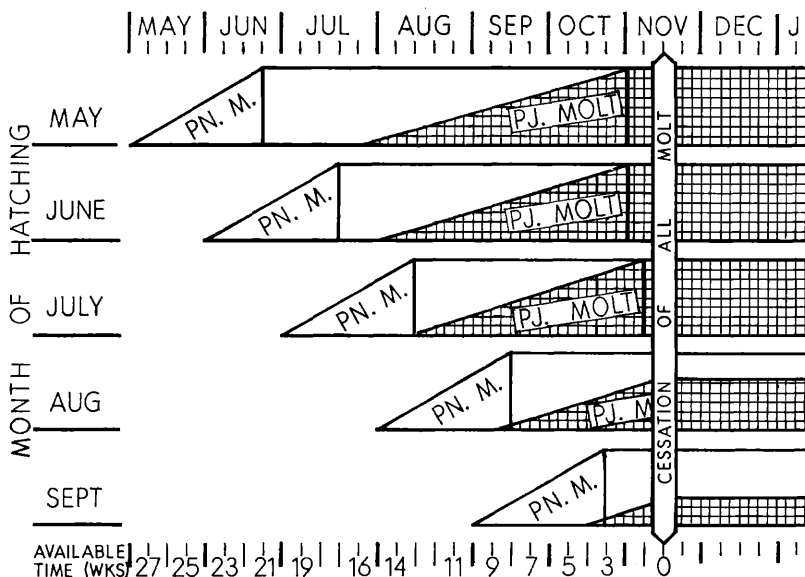


FIGURE 4. Sequence and chronology models of postnatal molt (PN. M.) and postjuvinal molt (PJ. MOLT) as related to first-of-month hatching dates and cessation of molt. Open triangles and bars indicate juvenile plumage, cross-hatched = first winter adult plumage, and mixture (as at lower right) suggests fraction of each plumage present during or after molt. Slope of triangle indicates cumulative percentage of molt completed and vertical side = completion. Months (top) are arranged as 4-5 weeks regardless of actual days.

hatched on the trapping area on 4 July 1970 and remained nearby, so each was captured five times during their first eight weeks. At seven weeks, all three were completing their postnatal molt and, concurrently for 3-5 days, starting postjuvinal molt. (Apparently to conserve time as suggested in Fig. 4, the two molts were overlapped, i. e., as the juvenile feathers (postnatal molt) were being completed laterally, the adult feathers (postjuvinal molt) were erupting centrally in the tracts.) Twelve other nestlings, hatched on 3, 6, and 20 June and 2 August, were closely studied until fledged and all 15 birds started postjuvinal molt immediately upon hatching. Four from the June nests were captured at three (2 birds), four, five (2), seven, and 14 weeks. Weights and measurements of these 15 young concurred on growth and molt rates, showing that all young apparently complete the postnatal molt in about seven weeks.

Further evidence of postnatal molt duration was provided by the 15-20 young captured in early June. By subtracting seven weeks from the capture dates, approximate hatching dates of 10-20 April can be retrospectively determined. These would be early hatching dates and longer postnatal molts would, illogically, require extreme dates. Furthermore, considering the energy required for body and feather growth (Payne, 1972), a faster molt

rate would seem unreasonable and, because the young are restricted in flight and food gathering capabilities, thus demanding parental care throughout this molt period, I see no biological advantage for a slower rate.

Therefore, I have assumed that seven weeks is required for the postnatal molt throughout the season. By using this figure when the young were captured as they completed postnatal molt, approximate hatching dates were assigned to 35-40 young captured at various times. In Figure 1, both #C-705 and 707 were trapped on 10 August showing traces of postnatal molt, indicating they hatched about 20 June.

The rest period.—Over 100 juveniles captured in June, July, and/or August were found to be in a "Rest Period," i. e., a period when absolutely no molt could be found on any area of the bird. I found this Rest Period, lasting from the end of postnatal molt until the start of postjuvenal molt, diminished in duration from about seven weeks to zero. As examples, #C-654 (Fig. 1) had completed postnatal molt on 10 June, was not molting on three recaptures, and the status of his molt on 10 August suggested postjuvenal molt started about 20 July; hence, he had rested at least seven weeks. #C-657, banded with traces of postnatal molt, probably started postjuvenal molt about 1 August after resting six to seven weeks. On 10 August, #C-705 was completing postnatal molt, then rested about three weeks before starting postjuvenal molt at the end of August, and #C-707 rested just two weeks. In contrast, the three young hatched on 4 July overlapped the two molts and had no Rest Period. As these and others in Figure 1 suggest, the reduction in the duration of Rest Period was directly correlated with later hatching dates. The Rest Period did not include all possible time—the earliest-hatched birds completed their postjuvenal molt two or three weeks prior to the cessation of molt (e. g., #C-688).

The complete postjuvenal molt.—In 50-60 observations, the postjuvenal molt started concurrently in three symmetrical areas: (1) all median secondary coverts, (2) a small number of feathers in the anterior scapular region, and (3) several feathers scattered through the middle rows of the ventral tract on the upper breast. A few days later, P1 (= Primary #1) was dropped and the other primaries followed at about weekly intervals in serial order (Figs. 1, 2) from the wrist outward. As indicated in Figure 2, each had grown about 25% of its length before the next primary was dropped.

The loss of three other flight feathers, S1 (= Secondary #1), S8, and R1 (= Rectrix #1), was closely associated with the start of P4 (#K-359, 360, and 361, Fig. 2). Each feather represented a distinct section of the flight feathers which followed a specific pattern. In these, S1-6 developed in serial order inwardly in slow rotation, but S8, S9, and S7 grew rapidly in that order and (being smaller feathers) matured before S1-3. Concurrently, the rectrices erupted serially, outwardly, and rapidly and were completed before the primaries. S5 and S6 were the last flight feathers to be completed.

Reese (1975:306) reported a different sequence of flight feather molt for Maryland Cardinals, but wrote, "Some HY birds were well into the molt sequence when trapping began on 1 September. Therefore, the information (reported) should be used with discretion until late summer trapping can be carried out." I suggest that Figure 1 indicates the need for summer trapping and that Reese, by pooling both complete and partial molts, may have (in Palmer's words) "masked the desired information about an individual."

On the head and body, the pattern of the postjuvinal molt roughly duplicated that of the postnatal molt. Thereby, (1) the juvinal feathers that developed first were replaced first, (2) final traces of the two molts were found in similar locations, and (3) each follicle was rested between molts even without a Rest Period as described above. Payne (1972) suggested that this rest may be essential as a refractory period for the follicles.

Regarding this molt, Blake (1971:269) stated, "The postjuvinal molt begins in the pectoral region just about the time that the juvinal primaries are completely formed. . . . The primary molt begins about one month after the body molt begins (and) is still in process long after the completion of body molt." I suggest that in the first instance Blake had observed the last of the postnatal molt and, therefore, I question these statements. I found that body molt was often "hidden" by matured feathers. To ascertain if body feathers were growing, I blew strongly on the contour feathers and found that tiny quills were erupting centrally or laterally in the tracts and/or that full feathers had traces of sheathing. In over 50 cases, (e. g., # C-688 in Fig. 1), I found that body molt was being completed a week or more after all flight feathers were completed. From Blake's data (p 272), by allowing seven weeks for the postnatal molt and one week for each primary, I suggest hatching occurred about 28-30 April and seven weeks later (10 June) postnatal molt was being completed. After a four- or five-week Rest Period, postjuvinal molt started 10-15 July and was completed 14 weeks later in mid-October.

The duration of the complete postjuvinal molt, like the Rest Period, was pliable and correlated to the available time (Fig. 4). Apparently, # C-688 (Fig. 1) started molt about 1 July and completed it 26-30 October, thus molting for about 17 weeks. # C-654, 655, and 657 would fit this sequence also. However, # C-694 (and 712, 720, and 721) started molt about 10 August and completed it in 15 weeks maximum. Others, with just 12-13 weeks available, e. g., # C-705, 707, and 731, expedited the molt to fit this available time.

To conform with the duration, the rate of molt was variable. In leisurely molts (17 weeks), the primaries were dropped at eight- to 10-day intervals and body feathers were initiated in small numbers. As time decreased (14 weeks), primaries were lost at six- to seven-day intervals and numerous body feathers were concurrently generated. When time was very short (12 weeks), several other time and energy conserving procedures were employed by

various individuals. Among those more easily detected were the overlapping of the two molts (up to 10 days) found on 25-30 young, the loss of P1 while the median secondary coverts were erupting rather than nearing completion, and/or the loss of P1-3 within one week rather than spread over two weeks. Toward the end of these molts, several flight feathers were dropped in rapid succession, particularly P8-9 and S4-6. Reese (1975) reported finding similar almost concurrent flight feather molt on some juveniles.

Other methods of accelerating the molt were for the young to retain the upper lesser secondary coverts (on the patagia, Pettin-gill, 1970) and most or all underwing coverts (I found both regions were replaced during leisurely molts). This lack of molt was not easily detected because these small feathers showed little color change and were completed in only 8 to 12 day, thus demanding weekly observations. However, on 10-12 birds that were late in starting molt (after 15 August) and were retrapped weekly, I observed this retention. Additionally, some body feathers were retained, primarily those on the breast and back (the last to molt), which I estimated (on colorful males) to be 2-3% of the body feathers. Except for these few feathers (less than 1-2% of the total plumage), the molt was rapidly completed. Technically, these were partial molts, but when all flight feathers were molted, it would be difficult to detect this condition in the field or on museum skins.

Even when all methods of molt acceleration were employed, 12 weeks was apparently the minimum period necessary for a complete postjuvinal molt. When less time was available, I found the results invariably included the retention of some flight feathers.

Complete versus partial molts relative to hatching dates.—Scott (1967:45) stated, "Birds hatched before the fourth week in July underwent a complete molt Birds hatched later than (that had a partial molt)." My data disagree with the precision and timing suggested by Scott. I found that hatching dates were a devious base for predication of either complete or partial molts.

Figure 1 shows that on #C-731, 733, and 735, molt was initiated 25-30 August and prior to that time on #737, 738 and 744. Apparently, all hatched before mid-July, yet three of these birds, as shown, completed molt and three (two of which started earlier) retained four or five rectrices. My notes indicate that #731 was rapidly generating feathers until the end of November and, thereby, completed molt. However, #737 apparently molted for a shorter period of time at a slower rate and was ceasing molt by early November, i.e., on 26 October, R1-2 and the head molt were completed, the remiges were nearing completion, and body molt was generating a reduced number of feathers; and on 24 November, all feathers were completed but R3-6 were juvenal feathers. At least 25-30 other juveniles provided similar, relatively complete data for the duration of molt. These suggest that when inception of molt (and thus hatching dates) were so closely aligned as to produce either type of molt, the primary determinants were the duration and rate of molt. Therefore, my best projection is that, of the young hatched in July, later hatching reduces the probability of a complete molt.

Partial postjuvinal molts.—As the duration varied, the results of these molts also varied. When considerable time (about 11 weeks) was available, all but a few flight feathers were molted but, conversely, when time was severely restricted (about six weeks), all flight feathers were retained. Meantime, the accelerated head and body molt progressed to virtual completion regardless of what occurred elsewhere on the birds. This was not a failure to complete the normal molt. Explicitly, the molt sequence was prematurely and selectively modified so as (1) to end in November and (2) to conform specifically with the available time. For example, prior to 23 October, #K-406 (Fig. 2) did not (but should have) initiate rectrix molt; he then retained S2-6, but continued to molt the primaries and body plumage into November. Many other individuals (e. g., Fig. 5) showed this “regionally-limited” termination of molt (in spite of the continuance of molt in other regions) which progressed as follows.

26 OCTOBER				2 NOVEMBER				9 NOVEMBER			
N-R	REC	SEC	PRIM	N-R	REC	SEC	PRIM	N-R	REC	SEC	PRIM
771	∞			795				814			
0,9,9				0,0,0				0,9,9			
777				800				815			
0,9,9				0,2,5				0,3,9			
782				801				819			
2,9,9				1,9,9				0,7,9			
783			o	804	∞			827			
0,1,7				4,9,9				0,3,8			
786	o			811	o			831			
2,9,9				2,9,9				0,2,0			
790				812			o	834			
0,2,8				0,3,9				0,5,9			
		1 6 9 5 1 1 5 9				1 6 9 5 1 1 5 9				1 6 9 5 1 1 5 9	

FIGURE 5. Eighteen work charts for juveniles captured at Cincinnati Nature Center in late stages of partial molt on three dates in 1969. N-R are, for each bird, band number (top) and results of molt (bottom), i. e., the total number of rectrices, secondaries, and primaries (respectively) later found to have been molted. o = accidentally, asymmetrically lost feathers. Other symbols as in Figure 2.

When the period of molt was only 10-11 weeks, molt was initiated normally in all areas. At some point, one rectrix failed to drop and (while all remiges were molted in normal sequence) that rectrix and all sequential rectrices were retained. As examples, if R5 failed to drop, R5-6 were retained (#C-804, Fig. 5); if R3 did not drop, R3-6 were retained (#782); or if R1 was retained, all rectrices were retained (#777). The retention sequence was, cumulatively, R6, 5, 4, 3, 2, and 1. Column 1 (Table 1) shows that about 23% of the juveniles retained some rectrices. I suggest that when only one (R6) to three (R4-6) rectrices might have been retained, these

rectrices were sometimes lost accidentally in the field (Fig. 5 shows asymmetrical loss on #804). I frequently noticed that when the central rectrices were molting and thus short, the remaining full-length rectrices extended abnormally outward and were highly vulnerable to loss. Therefore, I used extreme caution while handling the birds to prevent the loss of these rectrices and, because mist nets caused feather losses, I did not use them in this study. My experience indicates that Cardinals lose flight feathers more often than do other species (Fig. 5 shows some natural asymmetrical losses), but I cannot explain how or why.

When time was two or three weeks short, all rectrices and some remiges were retained as evidenced in Figure 5. These remiges were always S1-6 in the sequence of S6, 5, 4, 3, 2, and 1. Thus all rectrices and the first secondary that failed to drop plus all sequential secondaries were retained, e. g., on # K-406 (Fig. 2) S2 did not drop so S2-6 and R1-6 were retained. # C-812, S15, 827, and 834 (Fig. 5) exhibit other examples. Column 2 in Table 1 lists the occurrence of these retentions for one season, indicating that about 12% of the juveniles suffer these partial molts.

When further confined by available time, juveniles retained R1-6, S1-6, and some primaries in serially descending order, i. e., the first primary not lost and all sequential primaries, e. g., # K-402 (Fig. 2). Additionally, the upper greater primary coverts overlying each retained primary were also retained. On several occasions, a few were retained even when the underlying primaries were molted. Body molt progressed at an accelerated rate.

A detailed record of these restricted molts was best provided by a male, # C-123 (not shown), trapped on 20, 27 September, 4 October, 15 and 22 November 1970. At first, the postnatal molt was developing in all areas and, concurrently, postjuvenal body molt was just starting. A week later, postnatal molt, many adult body feathers, and P1-2 were progressing. On the third capture, (postnatal molt was complete) P1-3 and large numbers of feathers in each body tract were developing. On 15 November, P1-4 and S8-9 were matured, P5-6 and S7 had sheathing, but no new feathers were erupting anywhere, so cessation of molt was recorded. On 22 November, some body feathers had traces of sheathing but all others had matured. Thus, this male presumably hatched 15-20 August and overlapped the two molts for more than a week. After nine weeks maximum, postjuvenal molt was terminated, only P1-6 and S7-9 were adult (but right primary covert #6 and left #3 were old), and only a few body feathers appeared to be juvenile.

In these restricted molts, the cumulative retention sequence of R1-6, S1-6, and then some primaries was constant—no deviations were ever observed. However, the retention of S7 was unpredictable in that it was interjected into the sequence at any point after R1-6 and S1-6 had been retained, i. e., with or prior to the retention of P9 or any sequential primary. In the majority of observations, S7-9 were molted while a few or most (P4-9) primaries were retained, e. g., the molt of S7-9 and P1-3 (# K-402, Fig. 2) was observed on 12 to 15 birds during this study. However, of all restricted molts, 20-30% retained S7 at some point (# C790 and 800, Fig. 5), pre-

sumably while an additional primary was molted. Therefore, S7 may or (as was most frequently observed) may not be included at any level of column 3 of Table 1, but S7 is included in column 4.

So few individuals were trapped while replacing less than six flight feathers (column 4) that the retention sequence is doubtful. Two birds in five years molted S8-9 and P1-3 and a third bird replaced S8-9 and P1. About six birds molted only S8-9 (e. g., #C-831, Fig. 5), and a like number molted only S9. These data suggest that S7, P3, 2, 1, S8 and (lastly) S9 are retained in that order. Since S8 begins the molt of S7-9, it is surprising that S9 would be the last flight feather retained. Another 10-11 birds retained all flight feathers (e. g., #C-795) but molted the body feathers at an intense rate.

Apparently, all birds with partial molts replaced nearly all body plumage except those same few feathers retained during the accelerated complete molts. One male did not—when first captured in February, he had obviously retained about 40% of the juvenal head and body plumage; the face mask contained, in that ratio, both black (adult) and brown (juvenile) feathers in striking contrast. Also, right P5 and S9 (the pair) were adult, but this may have been accidental. (A year later, he was a bright red male.)

The importance of regeneration of the body plumage is enhanced by the fact that nearly all Cardinals, regardless of age or degree of molt, developed downy feathers on the apteria in September when the temperature was falling. The exceptions were the young hatched in August-September; they had not yet started the postjuvenal molt. These birds began developing downy feathers shortly after initiating the molt and had feathered the apteria long before the cessation of molt.

Cessation of molt.—In November, I found that some juveniles had completed or were just finishing postjuvenal molt whereas others were discontinuing molt before its completion. This cessation of molt was recorded explicitly when all incoming feathers were maturing but none of the sequential juvenal feathers had yet been lost. Of the juveniles mentioned in Figure 5, none were discontinuing molt (new feathers were erupting) until 9 November when #C-815, 819, 827, 831, and 786 (a recapture) were ceasing molt.

The earliest and latest occurrences of cessation of molt were recorded the first and last weeks of November, respectively, with one bird still molting on 12 December. For the majority, cessation occurred 10-20 November, so I have used mid-November (15 November in Fig. 3) as a convenience. Both Scott (1967) in Ontario and Reese (1975) in Maryland reported that all molt was terminated about this time. Cincinnati temperatures (August-November) averaged 3-5° C higher than those listed for Ontario by Scott.

DISCUSSION

The unique variability of the components of the molt season suggests that several beneficial adaptations may have evolved in the Cardinal. First, the multiple small clutches and the extended breeding season suggest provisions for offsetting a low rate of

fledging success and a high mortality rate, neither of which have, to my knowledge, been reported. However, at the Nature Center the frequency of kills (remains found) suggests high mortality. As evidenced by distress calls, the number of conflicts with avian (e. g., Blue Jay, *Cyanocitta cristata*), mammalian, and reptilian predators and the number of victimized nests found empty in spring suggest a reduction in fledging success, particularly in April-June nests when predators were rearing young. The initiation of post-natal molt immediately after hatching suggests this molt was completed forthwith, to free the parents for reneating. Nevertheless, those surviving from early nests provided a reserve of young that may have completed postjuvenile molt later.

The Rest Period seems to be little more than a convenience of variable duration filling the interim between the two molts. Apparently, on early-fledged birds the inception of postjuvenile molt was delayed until foods were plentiful and temperature was optimal. Harrison (1964) suggests that light, temperature, nutrition, etc. influence the molt cycle. Thereby, the energy required for molt was easily acquired while thermoregulation demands were minimal. The prolongation (when possible) of the postjuvenile molt suggests that energy demands were dispersed whereas the acceleration (when necessary) of the molt provided for the completion of all but the least important feathers.

The sequence of retaining the flight feathers has been selected, logically, to provide for the replacement of the most important feathers, which in turn allows survival of the greatest number of young. Being a colorful, moderate-sized species with slow, straight flight, the Cardinal seems (as suggested above) to be an easy target for predators. It follows that the development of the adult primaries improves flight and escape possibilities and are, therefore, the most important of the flight feathers for survival. Scott (1967) suggested that because Cardinals spend much time foraging on the ground, much wear to the old rectrices probably results. I agree but suggest that this wear does not significantly impair flight or escape, at least not to the degree as would the retention of the smaller juvenile primaries. Although the young that retain the primaries are possibly subject to greater mortality (I have not studied this nor have I noted an obviously higher loss), this group possibly serves as a buffer, i. e., a group to be sacrificed, to protect those that have completed the molt.

It has been suggested (King and Farner, 1961:246-248) that molt restrictions may conserve the energy expended to generate new feathers for utilization in thermoregulation. My findings support this idea because body feathers were developed even when the flight feathers were not. Furthermore, the development of down feathers on the apteria in September-October as temperature and day-length decreased, regardless of molt, attests to the importance of the body plumage for survival.

The variability of these molt components suggests a variety of responses to temporally aligned stimuli. Harrison (1964), King and Farner (1961), Payne (1972), and others agree that extrinsic (environmental) factors influence the molt cycle by inducing in-

trinsic (hormonal) changes. It seems logical that, as the season progresses, these external cues vary in direction and intensity (i.e., longer vs. shorter days) which, in compliance with current internal conditions, influence the various responses in young Cardinals. Payne (1972) theorizes that the follicles, which vary through time in response to hormonal changes, establish the sequence (e. g., the "wave" of molt through the flight feathers) by local events and interactions of developing neighboring follicles. As yet, no one has addressed the recessive variations of molt as seen in juvenile Cardinals, House Finches (*Carpodacus mexicanus*) (Michener and Michener, 1940), Indigo Buntings (*Passerina cyanea*) (Blake, 1965), and other species.

The climatic factors could be properly evaluated only in an environmental chamber and would probably show that a spring-hatched Cardinal would experience a partial molt when subjected to fall conditions and vice versa. Although remote, such experiments may reveal that part of the answer lies with the female that, having laid several clutches, had exhausted or diminished certain vital elements, or, responding to changes in photoperiod, etc., suffers an hormonal imbalance. If so, birds from late clutches may then be predestined to partial molts even under optimal conditions.

SUMMARY

Cardinals were trapped in weekly banding sessions, and 1,407 molt records from 659 juveniles provided details of postnatal and postjuvinal molt. Cessation of molt occurred in November regardless of molt conditions. The variations in available time, i.e., between hatching and cessation of molt, produced variations in the chronology, duration, and sequence of the postjuvinal molt of the flight feathers.

Evidence presented indicates that immediately after hatching all young completed the postnatal molt in about seven weeks. Following this, those birds from early nests had time for a Rest Period and then completed the postjuvinal molt in 14-17 weeks. Young from mid-season nests (about 1 July) had no Rest Period, overlapped the two molts, and accelerated the postjuvinal molt to complete it in just 12 weeks. Young from late nests retained one or more pairs of flight feathers including, cumulatively, the rectrices, the distal six secondaries, and some distal primaries. Those hatched last (in September) molted only a few remiges or, occasionally, no flight feathers at all.

Of 196 juveniles banded in one season, 58% completed the postjuvinal molt, 23% retained some rectrices, 12% retained all rectrices and some secondaries, and 7% retained most or all flight feathers. In all instances, nearly all body feathers were molted. The environmental factors that influenced these variations are discussed briefly.

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