MOLT IN FLIGHT FEATHERS OF FLICKERS

By FREDERICK H. TEST

Molt in flickers has been described by Stone (1896:112-115, 117, 128, 130) and, in part, by Friedmann (1930), but my findings are contradictory to some of those of the former investigator and provide certain additional information. The data given below were gathered in the course of examination of about 1250 study skins, 150 living birds (some held in captivity for several months), and a small number of alcoholics. The principal objective of this examination was a study of coloration, and no record was kept of the number of molting birds, which is now estimated to be about one-tenth of the above figures. It was felt at the time of the original study that enough birds had been examined to make well-founded the conclusions reached. Subsequent work with an additional 1200 specimens has shown this belief to be correct.

The majority of birds seen belong to the species *Colaptes cafer,* but *C. auratus, C. chrysocaulosus, C. chrysoides,* and *C. mexicanoides* are also represented by sufficient numbers to indicate any striking differences.

In this paper the customary method of numbering the flight feathers is followed. The sequence of primaries is from proximal to distal ends of the manus, whereas the most distal secondary is number one, and number twelve is nearest the body. Burt, in his study of woodpecker pterylography (1929:439), records only eleven secondaries, but there are definitely twelve. Rectrices are numbered from the central pair outward on each side.

TIME AND SEQUENCE OF MOLT

Newly hatched flickers are without down, and it is some time before the papillae of the juvenal plumage appear above the surface of the skin. All appear at about the same time, and their rates of growth remain fairly equal, at least within the same type of feather. This being true, the shorter feathers, as the inner secondaries, inner primaries, and primary ten, attain their full lengths before the longer feathers do. Juvenal primaries one and two are considerably weaker than the other primaries. Number two is only about two-thirds the size of primary three, which is about 85 mm. long, and number one is even smaller. This contrasts with the condition in adult plumage, in which primaries one and two are approximately as strong as number three and only a few millimeters shorter (about 15 mm. and 10 mm., respectively).

The time of inception of the postjuvenal molt varies considerably in different individuals, probably in the main because of differences in time of nesting of different pairs of adults. The first feathers molted apparently are lost about the time the bird leaves the nest (as found in European woodpeckers by the Heinroths [1931, vol. 4]) and at least sometimes (perhaps always) before the longest juvenal remiges and rectrices are mature. This date of first loss of feathers may be, in different individuals, from the early part of June to the last of July in *auratus* and *cafer*, in March or April in *chrysocaulosus*, from May to July in *mexicanoides,* and in May in *chrysoides.*

The first feathers lost are the weak primaries, one and two, in that order, but not far apart in time. After a somewhat longer interval, number three is dropped, then number four, and so on consecutively, through ten. I have not recorded the molt in number eleven; it probably follows primary ten. As in most species of birds, molt and subsequent regeneration are approximately symmetrical on the two sides of the body in primaries, secondaries, and rectrices. One of a pair of feathers may, however, be a few millimeters ahead of the other in growth, and sometimes the disparity is even greater. I have seen instances in which an adult primary was half-grown, while the corresponding feather in the other wing was an unmolted juvenal.

Usually, no postjuvenal molt takes place in the series of secondaries, the juvenal feathers being retained until the first annual molt late in the following summer. This is directly contradictory to statements in the literature regarding molt in woodpeckers in general (Stone, 1896; Dwight, 1907; Heinroth and Heinroth, 1931) and in flickers in particular (Palmer, 1901; Bent, 1939). These authors state that a complete postjuvenal molt occurs. Possibly some of the above authors who did original work on the problem were misled by finding growing secondaries present simultaneously with the growth of the inner adult primaries. This is a result of the short time that juvenal primaries one and two are held before their early loss, as noted above. My work has uncovered no evidence for anything approaching a complete loss of secondaries in the postjuvenal molt of flickers. Infrequently, however, a few of the proximal secondaries are molted. This was watched in a captive *auratus*, in which secondaries ten and eleven in one wing and nine, ten, and eleven in the other wing were molted and replaced in the order given. The same thing is indicated by several study skins in which a few proximal secondaries have a more intense carotenoid color (red or yellow) than does the rest of the series. A pale carotenoid color is characteristic of juvenal plumage. Another point of importance is shown by the same captive *auratus*: where molt is irregular in occurrence it is frequently not symmetrical on the two sides.

Molt of the rectrices usually begins when that of the primaries is about half completed. The small rectrix six is usually shed first, but its loss is somewhat irregular in time, and apparently it may be shed in almost any sequence with regard to the others, even to being the last one lost. In the large rectrices, however, the sequence appears to be invariable; it is, as noted by Stone (1896), Friedmann (1930), and others: 2, 3, 4, 5, 1. Numbers two, three, and four are apparently shed and regenerated in that order in rapid succession, especially two and three. Five follows at about the time two, three, and four are one-fourth or one-third grown. Number one follows number five at a similar time interval.

The whole postjuvenal growth of flight feathers is usually completed in September or October, primary ten (eleven?) or rectrix one being the last to reach maturity.

The annual molt of adults does not differ greatly from the postjuvenal molt except that the secondaries are always involved. In *auratus* and *cafer* the molt apparently begins about the middle of June with the loss of primary one. The other primaries follow consecutively, two to ten (eleven?) at rather long intervals. An irregularity was found in one specimen of *cafer*, in which number one was regenerated late, with number seven.

Molt of the secondaries begins about the time primary three is shed. It is somewhat irregular in extent and in exact sequence, but the order is usually: 8, 9, 7, 6 or 10, 1 or 2, 3 or 11, 5, 4. Diagramed, it may be represented thus:

(a) (b)

← —————— —————— → ← ——————

11 10 9 8 7 6 5 4 3 2 1

Here, molt and replacement are initiated in secondary eight and proceed both distally and proximally at the same time. Soon after secondaries six and ten have been lost, number one (usually) is molted, from which point molt and regeneration move proximally. It appears that the molt wave initiated in secondary eight never proceeds distally beyond number five, and molt started in secondary one never gets beyond four.

This molt of the secondaries is different from that recorded by Stone (1896:113), apparently for birds in general, but is of the convergent type, as stated by Heinroth (1898). It is similar to that of the Loggerhead Shrike (Miller, 1928) in the presence and location of the two molt centers, but differs slightly in the point at which the molt waves from these centers meet. A greater difference occurs in the sequence of feather loss as a result of the late origin in flickers of the wave beginning in secondary one.

As Miller (1928:415) has suggested for shrikes, there is probably a significant relation between the presence of a distal and a proximal molt center in the secondaries and the double embryonic origin of the series of secondaries as revealed by Steiner (1918). Steiner found that the first four secondaries are derived from papillae originally in series with papillae which produce greater undercoverts in the region proximal to secondary four. As embryonic development proceeds, the distal end of this longitudinal row of feather fundaments migrates to the posterior edge of the wing, thus coming in line with the feather germs of proximal secondaries, which develop in their original positions. It is not strange, therefore, that these two groups of secondaries should have separate centers in which molt is initiated. Likewise, it is not surprising that the approaching molt waves from these centers should not proceed beyond the interval between feathers four and five, which is the site of union of the two ontogenetic groups of secondaries.

In the light of this knowledge it is indeed interesting that the four distal secondaries are so like the rest of the secondary series in form and pigmentation. These two characteristics would appear, in the light of Steiner's work, to be dependent upon position on the wing and induced by surrounding influences. In contrast, the factors controlling place of initiation and extent of molt waves (perhaps those postulated by Miller [1941: 115]) seem to be inherent in the feather papillae—determined before their migration to the posterior edge of the wing. Skin-grafting experiments by Danforth (1929) indicate that in the chicken the form and coloration of feathers is fixed (except for sexual differences) by time of hatching.

In a considerable proportion of birds the molt waves from secondaries eight and one do not meet, leaving one or more feathers to be retained an additional period. This phenomenon is indicated by the presence in many birds taken in late fall, in winter, and in spring, of a fourth secondary that shows a much greater degree of wear and a more faded carotenoid color than does the rest of the series. Secondary three is almost as frequently retained and secondary two only a little less often. Numbers one and five also are sometimes found to be those of the year before.

There is excellent evidence for believing that the unshed secondaries in the region of number four frequently are not kept for an entire additional year. Instead, they may be lost and regenerated at some time between annual molts. Differences in degree of abrasion and fading and differences in size, as discussed below, form part of this evidence. The rest is based on color differences, which will be taken up in detail in another paper. The length of time for which off-season regenerants are retained is not known. It is probable that they are not held through the next annual molt.

The rectrices are shed and regenerated in the same sequence as occurs in the postjuvenal molt except that number six is more irregular. The order usually is: 2, 3, 4, 5 or 6, 1.

The time of completion of the annual molt varies with individual birds, falling between the middle of September and the latter part of October for *cafer* and *auratus*. The duration of the molt period for any single bird is thus about three months. Apparently, either the primaries or the rectrices are the last of the flight feathers to complete molt.

No spring molt of flight feathers occurs in *Colaptes*, but at almost any time of year one or a few feathers may be lost and regenerated. This latter fact is abundantly illustrated by the presence in many birds taken in fall, winter, and spring, of feathers that are growing or that show less wear than the other members of the series. The phenomenon is sometimes symmetrical on the two sides of the body, sometimes not. What causes these feathers to drop at an off-season, I do not know. Some are probably knocked out by predators, but it is difficult to account for all by this means, especially in instances of symmetrical loss. It is probable that much of it is a response to internal stimuli. Regeneration apparently follows this off-season molt almost invariably, most of the new feathers being slightly shorter and narrower than feathers regenerated following normal molt. This usually can be shown by comparing the new feather with the older one on the other side of the body. The few examples given in the following table indicate the usual magnitude of difference. The newer (less worn) feathers are starred.

Table 1

Measurements in Millimeters of Flight Feathers Grown in Off-season (*) and at Annual Molt in *Colaptes cafer*

Specimen	Feather	Width Left	Width Right	Length Left	Length Right
No. 69375, Mus. Vert. Zool., May 26, 1936	rectrix 5	*14.9	18.9	*84	97
	rectrix 4	21.6	21.0	109	107
Field no. 687, F. H. Test Coll., April 8, 1938	rectrix 6	9.0	9.0	40.5	41.0
	rectrix 5	17.6	*18.0	107.6	*97.0
	rectrix 4	21.5	*21.1	108.4	*105.5
	rectrix 3	21.9	*21.2	112.0	*110.5
	rectrix 2	22.7	*22.3	112.8	*110.0
	rectrix 1	18.2	*17.8	114.0	*113.0
	secondary 4	21.8	*21.6	93.6	*95.0

Actual dates of off-season losses of feathers are difficult to determine unless the new feather is found while still growing. Usually the only certain indication that a particular feather has been grown at a time other than that of the annual molt is the difference in wear between it and the rest of the series. However, I have records of 21 specimens in which new feathers were actually being grown at the time of collection and after the bird had completed its normal molt program. The dates range through every month between annual molts. Mature, off-season feathers have been found in many other specimens.

RATE OF GROWTH OF INDIVIDUAL FEATHERS

Several flickers kept in captivity for studies of coloration afforded opportunity for learning something of the speed of growth of flight feathers. It is recognized that, for some purposes, studies of this sort made on captive birds are not as valuable as they would be if free-living subjects were used. However, studies on captives are important in interpreting *other* kinds of experimental data obtained from captive birds. This was true in the present situation.

The birds used were hand-fed in a small cage for one or two weeks until they learned to feed themselves, when they were released into an indoor flight cage measuring 12 × 3 × 8 feet. They were fed on a mixture compounded in the following proportions: pheasant meal, 450 gm.; crissel, 150 gm.; ant "eggs" (= pupae), 50 gm.; dried "flies" (= ostracods or aquatic hemipterans), 50 gm.; rendered suet, 112 gm.; cod liver oil, 19 cc.; calcium lactate, 4 gm.; boiled potato or grated raw carrot root equal to about one-half the volume of the preceding constituents. This mixture is modified from one kindly provided by Dr. G. B. Happ of Principia College. When uninjured and with relatively few ectoparasites, the flickers kept in good condition on this food.

A number of individuals, mostly *C. cafer collaris*, were used in measuring growth rate. Because of the birds' wildness, measurements were made at intervals of several days (usually three or four) and the rate per day for each interval computed on an average basis. Some measured feathers were grown in the course of normal molt; others regenerated following plucking. Only one feather had stopped growth at or before the time of the last measurement. It is a primary, to be identified in the following table by having the last two measurements equal.

Table 2

Measurements in Millimeters Showing Growth of Primaries in Captive *Colaptes*

Birds and feathers	Dates and measurements						
C. cafer collaris, ad. ♂, 34-307551	Mar. 7		9		20		25
Primary right 7	60		67		93		96
Rate of growth		3.5		2.4		0.6	
C. cafer collaris, ad. ♂, 34-307556							
Primary left 8	....		69		93		
Rate of growth				2.2			
C. cafer collaris, ad. ♂, No. 2	July 30				Aug. 3		7
Primary left 8					13		35
Rate of growth						5.5	
Primary left 7	56				77		95
Rate of growth			5.3			4.5	
Primary right 7	50				73		91
Rate of growth			5.8			4.5	
Primary right 6	116				126		126
Rate of growth			2.5			....	
C. cafer collaris, ad. ♀, No. 4							
Primary left 5	33				60		75
Rate of growth			6.8			3.8	
Primary left 4	90				100		108
Rate of growth			2.5			2.0	
Primary right 5	35				60		76
Rate of growth			6.3			4.0	
Primary right 4	96				104		110
Rate of growth			2.0			1.5	
C. cafer collaris, ad. ♀, 34-307553	Aug. 30				Sept. 3		10
Primary left 7	45				63		90
Rate of growth			4.5			3.9	
Primary right 7	56				....		97
Rate of growth				3.7			
C. auratus luteus, juv. ♀, "Blue"	Aug. 28				Sept. 9		
Primary left 7	15				77		
Rate of growth			5.2				
Primary right 7	11				74		
Rate of growth			5.3				
C. auratus luteus, ad. ♀	Sept. 25				Nov. 10		
Primary left 7	34				77		
Rate of growth			0.9				

The data in table 2 show that the rate of growth of primaries is greatest at first and gradually decreases as the feather becomes longer. The same thing is shown more clearly in figure 11, in which points are plotted from growth rates listed in table 2. In preparing figure 11, only those growth rates were used which had been determined from measurements made at intervals of five days or less; most of the intervals are three or four days. A long interval would tend to mask changes in rate. There is apparent a straight-line decrease in growth rate with increase in length of the feather. In the early part of its growth a primary grows at a rate of about 6.7 mm. per day, with the rate decreasing to about 4.2 mm. per day at mid-length and to 1.2 mm. per day just before maturity is reached.

In general, difference in rate at the same stage of growth is relatively small among the middle primaries, even of different individuals. Some of the variation which is ap-

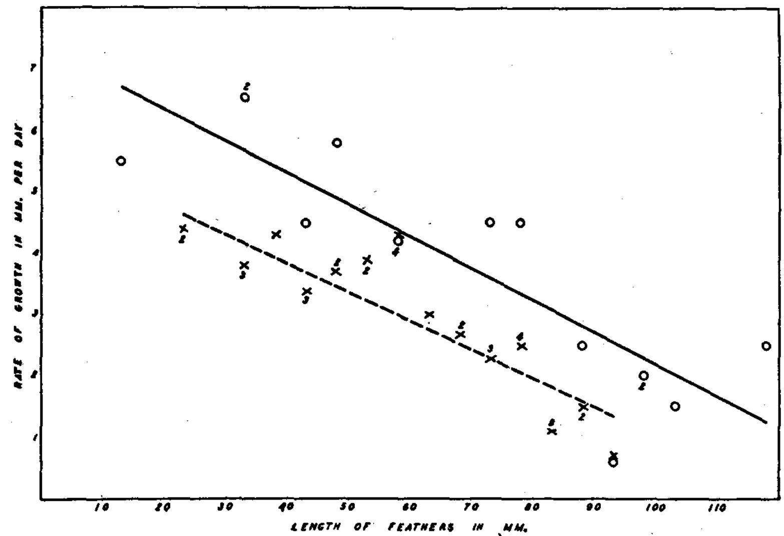

Fig. 11. Relation between rate and stage of growth in flight feathers of *Colaptes cafer collaris*. Circles and solid line, primary wing feathers; crosses and broken line, secondaries. Numerals beside points indicate number of data (different feathers) averaged in calculating each. Only rates of growth determined from measurements at intervals of five days or less are included.

parent probably is caused by differences in inherent factors, although sex seems not to be a cause. The data are too few to permit determination of this latter point. The birds differed in their states of health, to which can probably be attributed part of the variation in growth rate of their feathers.

Table 3

Measurements in Millimeters Showing Growth of Secondaries in Captive *C. cafer collaris*

Birds and feathers	Dates and measurements								
34-307556, ad. ♂					Mar. 9		Mar. 20		
Secondary right 2					62		84		
Rate of growth						2.0			
No. 2, ad. ♂	Apr. 24		27		May 1		July 30		Aug. 3
Secondary left 2	24		36		56		....		....
Rate of growth		5.0		4.3					
Secondary right 5	35		49		65		....		....
Rate of growth		4.7		4.0					
Secondary right 1	....		....		....		78		92
Rate of growth								3.5	
No. 4, ad. ♀									
Secondary left 5	21		32		45		....		....
Rate of growth		3.7		3.3					

The data given in table 3 are not complete for any single feather and were taken at various stages of growth. Table 4 shows nearly the complete growth of four secondaries regenerated after plucking.

Table 4
Measurements in Millimeters of Growth of Secondaries, Following Plucking, January 23, in Two Captive *C. cafer collaris*

Birds and feathers	Dates and measurements								
No. 2, ad. ♂	Feb. 5	14	17	21	24	28	Mar. 1	4	6
Left 4	6	42	53	70	78	88	94	93	....
Rate		4.0	3.0	4.3	2.7	2.5	2.0		
Right 5	10	46	56	73	80	89	91	93	93
Rate		4.0	3.3	4.3	2.3	2.3	1.0	0.7	
No. 4, ad. ♀									
Left 4	3	35	45	62	71	80	83	88	88
Rate		3.6	3.3	4.3	3.0	2.3	1.5	1.7	
Right 5	6	42	53	67	75	84	85	88	88
Rate		4.0	3.0	3.5	2.7	2.3	0.5	1.0	

Measurements of secondaries (tables 3 and 4) show a decreasing rate of growth similar to that of primaries. A slower growth rate throughout is indicated for secondaries (figure 11). It appears to be about 4.5 mm. per day near the beginning, decreasing to 3.5 mm. at mid-growth, and being about 1.5 mm. in the last couple of days of growth.

Measurements of rectrices (table 5) are few and mostly taken at such long intervals as not to show a true picture of their rates of growth at different stages. They suggest, however, a slower growth than in flight feathers of the wing. This lower rate may result from inherent physiological differences, or might be caused, at least in part, by the bird's frequent and strenuous use of these feathers for support while they are growing. Growing wing feathers are, indeed, used in flight, but they usually are partially supported by adjacent feathers, whereas the pressure on the tail feathers is against the tip of each and is transmitted longitudinally to the growing and dividing zones of the feather and its papilla. The sudden and large changes in pressure and probable tearing effects in this region might have a direct, slowing effect on growth.

Table 5
Measurements in Millimeters of Growth of Rectrices in Captive *Colaptes*

Birds and feathers	Dates and measurements			Birds and feathers	Dates and measurements		
C. cafer collaris	March 9		20	*C. cafer collaris*	Sept. 3		10
34-307551, ad. ♂				34-307553, ad. ♀			
Left 2	57		65	Left 5	41		60
Rate of growth		0.7		Rate of growth		2.7	
34-307556, ad. ♂				Right 5	57		74
Right 2	55		77	Rate of growth		2.4	
Rate of growth		2.0		*C. auratus luteus*	Sept. 9		Oct. 4
Left 3	57		82	"Blue," juv. ♀			
Rate of growth		2.3		Left 5	25		50
Left 4	53		78	Rate of growth		1.0	
Rate of growth		2.3		Right 5	3.3		50
				Rate of growth		1.9	

Measurements of rate of feather growth appear to be rather scarce in the literature, and I have found none at all for woodpeckers. Sumner (1933) studied the growth of the juvenal sixth primary, first secondary, a tail feather, and the upper covert of each, in the Pacific Horned Owl (*Bubo virginianus pacificus*), Golden Eagle (*Aquila chrysaëtos canadensis*), and Barn Owl (*Tyto alba pratincola*). His histograms for single individuals show that the growth rate of all the coverts steadily decreased. A less rapid decrease took place in all the larger feathers except the rectrix of the owl and the rectrix and primary of the eagle. These latter feathers held a nearly steady rate for the entire period of growth. Fragmentary data by the same author (1929) on the juvenal fifth primary of the Golden Eagle, Sparrow Hawk (*Falco sparverius*), and Pasadena Screech Owl (*Otus asio quercinus*) show a similar variation. The growth rate greatly decreased in the screech owl, decreased slightly in the eagle, and held about the same throughout the period of measurement in the hawk. It should be emphasized that these data refer to feathers of the first teleoptile (juvenal) plumage. My measurements on flickers were all of *regenerating* feathers (of postjuvenal or later generations).

Juhn, Faulkner, and Gustavson (1931) have published data on regenerating breast, back, and saddle feathers in the adult fowl (*Gallus domesticus*) following plucking. In the back and saddle feathers there was a remarkably uniform rate in each type. Breast feathers had a relatively uniform rate up to the period between 50 and 60 days of age, when their growth rate in the male decreased somewhat.

That actual rate of growth often is different between species, sexes, individuals, and types of feather is shown by the sets of data referred to above. The actual rates given by Sumner (1929) for the early growth of the fifth primary in the juvenal screech owl and sparrow hawk—species with body weights similar to that of the flicker—are about the same (a little lower) as those recorded here for the flicker. Juhn, Faulkner, and Gustavson (*loc. cit.*) found a significant sexual difference in rate of growth in the common fowl in feather regions where there is sexual dimorphism.

SUMMARY

Study of about 2500 flickers—living, dead, and as study skins—has shown certain previous conclusions regarding molt in these birds to be incorrect and has provided additional information.

Postjuvenal molt of primaries is complete and is initiated in the small, weak primary one, proceeding distally through the other primaries, in order. This process begins about the time the birds are fledged and before all feathers of the juvenal plumage are fully grown. The time of inception of molt differs between species and between individuals, depending probably upon the time of nesting of the adults. The annual (fall) molt of adults follows the same order as the postjuvenal molt; variations from that sequence are rare.

Despite assertions to the contrary, there is little or no postjuvenal molt of secondaries. The infrequent replacement which does occur at this time involves only a few proximal secondaries. This irregular molt is apt to be asymmetrical. Annual molt of secondaries begins about the time primary three is shed and usually follows the order: 8–9–7–6 or 10–1 or 2–3 or 11–5–4, but variation is frequent. Thus, molt is initiated in two centers—secondaries eight and one—with molt waves spreading both ways from the former and proximally from the latter. Approaching molt waves do not extend beyond the space between secondaries four and five and frequently do not meet, resulting in retention of one or more secondaries for an additional period beyond the usual twelve months. The molt wave from secondary one more commonly lags, with secondary four most commonly retained and numbers one and five least likely to be held over.

It is thought that the presence of two molt centers in the secondaries and the point of meeting of the approaching molt waves are causally related to the double embryonic origin of these groups of feathers. If this be true, there is here indicated an earlier embryonic determination of molt response than of feather type.

Molt of the rectrices usually begins when that of the primaries is about half completed. The sequence in the large feathers is 2–3–4–5–1. The small outer rectrix (num-

ber six) usually is shed first in postjuvenal molt but may be inserted anywhere in the series; in annual molt it is even more irregular in position in the molt sequence.

Colaptes has no regular spring molt of flight feathers, but a few feathers may be lost and regenerated at any time of year. Some of this loss probably is caused by forcible removal, but much of it appears to be a response to internal stimuli. Regenerants grown at these times are usually shorter and more narrow than normal.

Measurements of growing feathers have been made on captive flickers following postjuvenal and annual molt and experimental plucking. Primaries and secondaries show a steady decrease in growth rate as the feather lengthens; satisfactory data are not at hand for rectrices. Early growth rate in primaries is between five and seven millimeters per day, in secondaries between four and five millimeters per day. That of rectrices appears to be somewhat lower than in secondaries. Comparable data for other species are scarce but indicate differences dependent upon potentialities inherent in the species, sex, individual, age, and type of feather. Some feathers in other species have been shown by previous workers to have a relatively constant growth rate.

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