THE MECHANISM OF FEATHER REPLACEMENT DURING NATURAL MOLT

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Most ornithological reference books state that natural molt is a two-part process entailing loss of old feathers, "ecdysis," and subsequent growth of new feathers, "endysis" (Stresemann, 1927; Mayaud, 1950; Wing, 1956; Van Tyne and Berger, 1959). Furthermore, investigators who have studied molt in penguins, cassowaries, and emus state or imply that they are aberrant, since, in these birds, the old feathers are pushed out attached to the tips of the feathers of the incoming generation and are later abraded or are pulled off by the bird (Bartlett, 1879; Lowe, 1933; Friedmann, 1949; Rand, 1950). The evidence to be presented in this paper, very briefly reported earlier by Watson (1963), indicates, however, that this latter mechanism of feather replacement is more widespread among birds than previously believed and that natural molt is actively concerned only with the incoming generation. This finding is of significance for relating molts to plumages, especially in view of the current controversy over their nomenclature (Humphrey and Parkes, 1959, 1963; Miller, 1961, 1962; Stresemann, 1963).

During the course of early development in birds, the natal downs are carried out on the tips of the incoming juvenal feathers in the first molt, but are soon abraded. For this reason, some authors have maintained that down should not be considered a separate generation, but merely the modified tips of the juvenal feathers (Jones, 1907). Furthermore, plucking a definitive feather usually stimulates regeneration (Lillie and Juhn, 1932; but see Morton, 1962). The distal portion of the papilla is torn away in plucking but the papilla begins healing over at once and usually an entire new feather is grown (Cohen and 'Espinasse, 1961). The regeneration of plucked feathers has received much attention, especially from developmental biologists interested in regulation and morphogenesis (see review by Lillie, 1942). Their findings have been interpreted to reinforce the view that loss of feathers in molt stimulates growth of the new feathers. The mechanism of replacement of feathers during natural molt, however, has been little investigated.

Materials and Methods

Observations on molt in living birds were made on 6 hand-reared Rhode Island red chickens, 20 Chukar Partridges (*Alectoris chukar*), and 20 Japanese Quail (*Coturnix japonica*). Most of these were incubator-hatched, but 7 chukars and 5 quail were incubated by a domestic hen. The birds were kept in wire cages and fed commercial chick starter (protein 28 per cent) supplemented with fresh lettuce or grass; dry soil and eggshells were available for dusting and grit. Until the birds were able to thermoregulate, they were brooded under a 100-watt incandescent bulb. Many of the birds were handled daily and examined for molt while they were developing. All juvenal feathers dropped by one chukar were collected every other day.

Nonliving material consisted of five birds. An adult male Chukar Partridge, which died while molting at the Highland Park Zoo in Pittsburgh, and an adult male House Sparrow (*Passer domesticus*), picked up dead in Arlington, Virginia, were examined in the flesh. Flat skins of two molting Greater Scaup ducks (*Aythya marila*) were examined immediately after preparation. A wild Ruddy Sheld-Duck (*Casarca ferruginea*), preserved in formalin in 1960, was studied two years later.

Molting feathers were examined and photographed, when possible, on the living bird. Others were plucked, and examined or dissected while fresh, under a binocular dissecting microscope. A few molting feathers were preserved in Bouin's or Carnoy's fluids and examined after fixation.

In order to investigate growth rate during the development of early feather generations, Richard J. Hart, a student at Yale University, made daily measurements under my direction on the innermost primary (number 1) in female "Hall Cross" Rhode Island red preserved embryos and living chicks. For each day of incubation (days 11 through 20) he measured at least five specimens. Five chicks were raised for 32 days under the same conditions as the other live birds under observation. Measurements taken with calipers on the visible portion of the feather were recorded to the nearest 0.1 mm in the embryos and 0.5 mm in the live chicks.

Acknowledgments

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Observations and Results

A Rhode Island red chick in its fifth week provided the first evidence that the two-step sequence of molt might not be a reality. The bird had fully grown the inner juvenal primaries on both wings, but some of the more distal remiges were still in growth. Because the primaries were to be saved for work on pigmentation, they were pulled. When the innermost primary was plucked, the break came well below the inferior umbilicus at the collar, that part of the papilla in which new growth was taking place. Firmly attached to the base of the calamus of the old feather was 10 mm of new feather sheath. The feather was not easy to dislodge and the force applied was considerable.

The calamus of the juvenal primary is entirely keratinized and contains a series of dry pulp caps. The outer wall of the new feather sheath appears to be continuous with the keratinized calamus of the old feather and there is no apparent constriction at their juncture (Figure 1A). Within the new sheath, barbs have begun to form but the vascularized pulp still reaches almost to the calamus of the old feather. The pulp caps have not closed the inferior umbilicus as they do in later feather generations (Lil-

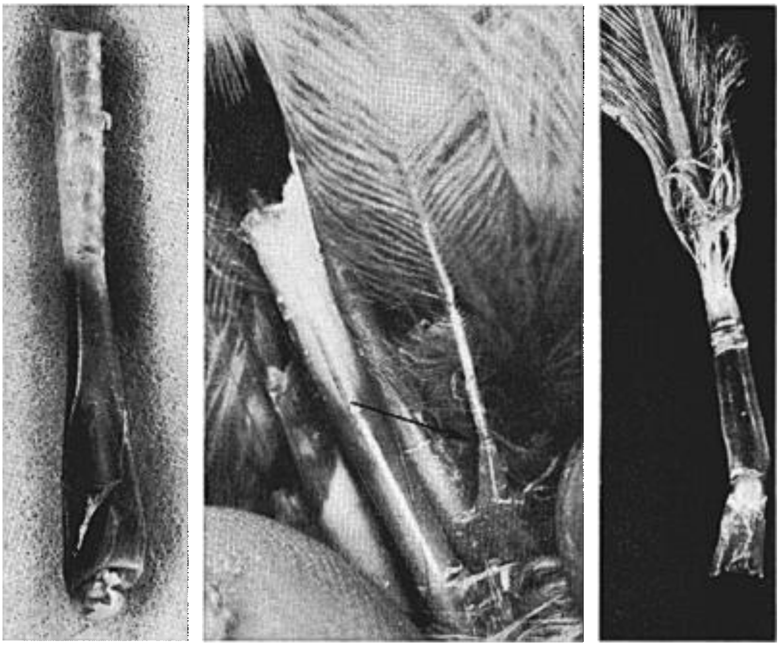

Figure 1. A. Zone of juncture between base of calamus (light area) of juvenal innermost primary and tip of sheath (dark area) of first basic primary in five-week-old Rhode Island red chick. Total length of preserved specimen, 18 mm. B. Juvenal flank feather (arrow) of living Chukar Partridge pushed out of follicle still attached to tip of incoming basic feather sheath. Other basic feathers already breaking sheaths. Photographer's fingers at bottom and left. C. Shed breast feather of adult Ruddy Sheld-Duck with broken-off cap of keratinized new feather sheath attached to base of calamus.

lie, 1940). The new sheath has not yet become fully keratinized and hard, even near its tip.

Every molting bird subsequently investigated in detail has shown this same mode of feather replacement in all molts and in most feather tracts.

The new feather sheath may push the base of the calamus of the old feather well beyond the end of the follicle so that the point of attachment of the two feather generations is visible externally (Figure 1B). Often there is a constriction at the zone of juncture between the two generations, but the outer layers of the calamus and sheath appear continuous. In the live bird, the calamus of the old feather is translucent and whitish but the vascularized pulp and barbs of the incoming feather make the new sheath appear dull, dark purple.

When the old feather, thus carried out on the tip of the sheath of the incoming feather, breaks off, part of the keratinized tip of the new sheath comes away attached to the inferior umbilicus of the old feather (Figure 1C). This may help the sheath of the new feather to start breaking open.

Most of the attached feathers were found during the first prebasic molt, but attached feathers were also present in later molts. This phenomenon was observed in the hackles, wing coverts, and alulae of Rhode Island red cockerels undergoing the subsequent molt when more than six months old. A year-old Chukar Partridge and an adult House Sparrow examined soon after death showed several first basic feathers which had been carried out on the tips of sheaths during the second prebasic molt.

Observations by Dr. Milton B. Trautman (letter), on a captive Mottled Duck (*Anas fulvigula*) in 1953 suggest that the same process takes place in the wing quills of year-old ducks:

> On June 18 at 11 a.m. "Fulvi" lost his first primary. That primary and all his other flight feathers were still firmly attached at 9 o'clock that same morning when I carefully jerked at some of the primaries. By 1 p.m. the next day (i.e. within 26 hours) he had lost all flight feathers. By early morning of the 19th, less than 24 hours after the first primary was dropped, some of the new primaries were one quarter inch out of the follicles. . . . When a feather was dropped, I could see the tip of the sheath of the new feather in the follicle.

Definitive breast feathers were also found attached to the tips of incoming feather sheaths in preserved flat skins of wild Greater Scaup ducks and in a whole specimen of Ruddy Sheld-Duck preserved in formalin. The connections between the two feather generations in the skins of the scaup had survived manual washing in detergent and benzene and subsequent drying in sawdust and a forced air stream.

Most of the connections between generations of pennaceous feathers were found during the first prebasic molt, which appears to follow directly on completion of growth by the juvenal generation. Daily measurements were therefore made on the innermost primary during the succession of down, juvenal, and first basic feathers in five Rhode Island red chicks in order to demonstrate whether there was a noticeable cessation of growth between these early feather generations. The innermost primary is the first juvenal feather to be replaced in the first prebasic molt of this breed. Measurements on the innermost primaries of five Rhode Island red embryos gave the following averages for days 11 through 20 of incubation: 0.9, 2.5, 7.5, 8.5, 8.8, 9.1, 9.4, 9.4, 13.0, and 15.3 mm. These measurements suggest that there is a two-day cessation of growth (days 17 to 18) in the embryo between down and juvenal generations (also found by Watterson, 1943, who only measured preserved embryos) and those in Table 1 show another cessation of five to nine days or more, commencing around day 46, between the end of juvenal growth and initiation of growth by the first basic generation. I suspect it is during this period that the new collar is formed. During three days of growth, one such juvenal feather was pushed out on the tip of the basic feather sheath a distance of 15 mm before it was lost (Figure 2). Thus, although there is a cessation of

TABLE 1

DAILY MEASUREMENTS (MM) OF INNERMOST PRIMARY IN FIVE FEMALE RHODE ISLAND RED CHICKS

Day*	Chick number					Day*	Chick number				
	1	*2*	*3*	*4*	*5*		*1*	*2*	*3*	*4*	*5*
21	17.0	22.0	22.5	20.5	20.8	37	73.0	78.5	74.0	76.0	75.0
22	21.0	28.0	27.5	25.0	23.5	38	73.0	79.0	74.0	77.0	77.0
23	25.0	33.0	32.5	31.0	30.0	39	74.0	81.5	75.0	79.0	78.0
24	30.5	38.0	39.0	35.0	34.0	40	76.0	84.0	76.0	81.0	79.0
25	34.5	41.5	43.0	40.0	36.5	41	77.0	86.0	76.5	83.0	79.5
26	39.0	45.5	46.5	44.5	43.0	42	78.0	86.5	77.0	83.0	81.0
27	44.5	51.0	51.0	49.5	47.5	43	81.0	87.0	77.0	86.5	—
28	50.0	54.0	55.0	54.0	52.5	44	81.5	90.5	80.0	87.5	86.5
29	51.5	59.0	58.0	57.0	56.0	45	81.5	91.5	82.5	88.0	87.0
30	55.0	60.0	60.0	59.0	61.0	46	81.5	91.5	82.5	90.0	88.0
31	56.0	61.5	62.5	62.0	61.5	47	81.5	92.0	82.5	90.0	90.0
32	60.0	67.0	63.0	64.0	64.0	48	81.5	92.0	83.0	90.0	90.0
33	62.5	68.5	66.0	66.5	67.0	49	81.5	92.0	83.0	90.0	90.0
34	65.0	71.5	68.0	70.0	69.0	50	81.5	92.0	85.5	90.0	90.0
35	68.0	75.0	69.5	72.5	71.0	51	81.5	92.0	92.5	90.0	90.0
36	70.0	76.0	72.5	73.5	72.0	52	81.5	92.0	98.0	90.0	90.0

* After start of incubation.

growth in the papilla between the two generations, the calamus of the old feather is firmly attached to the tip of the new feather sheath.

In the adult specimens (Mottled Duck mentioned in Dr. Trautman's letter, Chukar Partridge, and House Sparrow) there had been no feather growth for at least 10 months and the calami of the old feathers were completely keratinized. Even so there were full connections between the two feather generations.

The preliminary results of some experiments bearing on the mechanism of feather replacement were reported by Jacobs (1935). Pigeons were fed a thyroid hormone ("Elityran") tablet in order to stimulate feather growth. When the new feather germs were sectioned in the follicles, the old calami were found attached to the tips of the new sheaths and were being pushed out by them. Jacobs reports that the epidermal lining of the follicle, which is continuous with the outer surface of the feather sheath and in turn with the epidermis between the follicles, was being shed simultaneously. He attributed release of the feather to the breaking of the hold of this follicular lining. This experimental work was never pursued further.

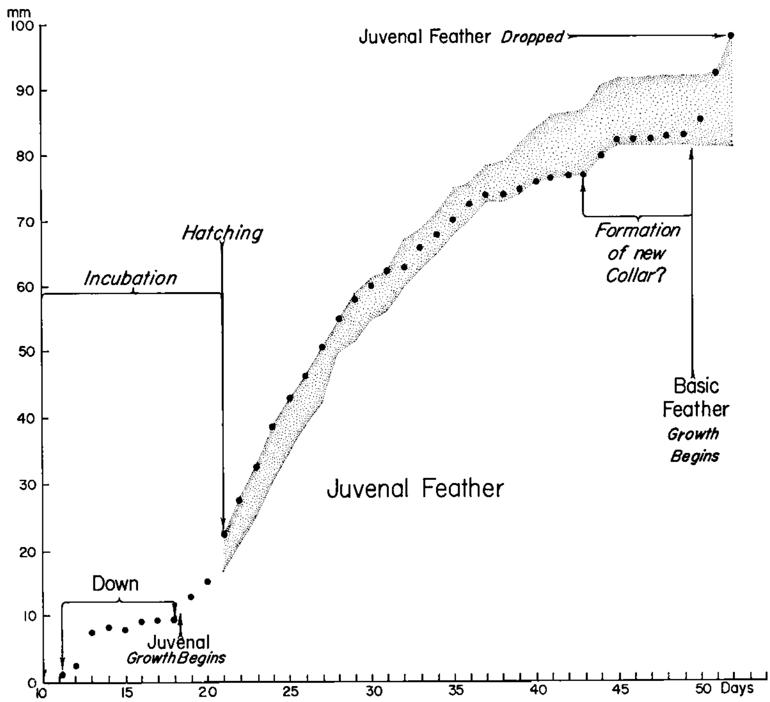

Figure 2. Graph of feather elongation during incubation and 31 days post-hatching showing cessation of growth between generations. Data from Table 1; chick 3 in dots and range of measurements of all chicks in stippling.

DISCUSSION

Feathers of one generation adhering to the tips of growing feather sheaths of the subsequent generation have been reported in a shorebird (Bonhote, 1907), a pigeon (Jackson, 1913), a parrot and a magpie (Kleinschmidt, 1903), and a New World sparrow (Sutton, 1941).

Thus, during molt in some members of at least eight diverse orders of birds (Sphenisciformes, Casuariiformes, Anseriformes, Galliformes, Charadriiformes, Columbiformes, Psittaciformes, and Passeriformes), the old feathers are pushed out on the tips of the new feather sheaths. The connection between the new and old feather generations is not usually as strong as it was in the case of the first primary of the chicken here reported. Almost as soon as the junction emerges beyond the end of the follicle, the old feather is broken off or is pulled out by the bird itself during preening. This probably coincides with the time of full keratinization of the tip of the new sheath. Remiges and rectrices are usually lost (but not necessarily alula quills nor greater wing coverts) before the base of the old feather is pushed out of the follicle. This tenuous and short-lived connection is probably the major reason why this mechanism of feather replacement has not been observed more frequently in active wild birds.

Loss of feathers by being pushed out of the follicles by the incoming generation cannot account for the dropping of feathers in "shock molt," which Dathe (1955) suggests may be brought about either by involuntary contraction or relaxation of the dermal muscles, nor for the loss of ventral feathers in preparation for the brood patch (Bailey, 1952), nor for seasonal differences in the number of contour feathers found by Wetmore (1936) and Staebler (1941). Feathers dropped under these conditions or artificially plucked may not be replaced immediately (Juhn, 1957; Bailey, 1952; Wetmore, 1936; Morton, 1962), showing that feather loss is not necessarily a stimulus for regeneration.

Several points about the mechanism of feather replacement remain to be investigated further.

The connection between the two feather generations is most probably of primary origin and not secondarily induced by the pressure of new feather growth from below. The outer cell layer appears continuous from the calamus of the old feather through the tip of the sheath of the new feather. Tearing of the tip of the inactive papilla during plucking is further evidence that these sheaths are continuous even before growth of the new generation begins (see photographs in Cohen and 'Espinasse, 1961).

It is not clear, however, whether during natural molt the tip of the papilla produces cuticle which separates the cavity of the old feather from the vascular pulp of the growing feather. Jacobs' description and drawings suggest that it does; Lillie's (1940) description of the relationship of pulp to feather is inconclusive; and my own preliminary observations suggest that it does not, at least in the first prebasic molt. During regeneration of plucked feathers, cuticular overgrowth from the dorsal part of the papilla covers the bared tip before a new collar forms (Cohen and 'Espinasse, 1961). If dorsal epidermis also contributes in the same proportion to the new feather in natural molt as the evidence presented by Cohen and 'Espinasse (1961) suggests, then growth of dorsal epidermis over the tip of the papilla would be the first indication of molt. Jacobs' observations on the thickening of cuticle at the tip of the papilla early in molt further suggest that this is true. Formation of the new collar in preparation for natural molt, therefore, needs to be further investigated.

The observations of Greite (1934) and Jacobs (1935) on the loss of the follicular lining during plucking and molt should be verified. Although this might be an artifact of fixation or sectioning, it would be reasonable to expect shedding of the entire cuticular layer of the skin during molt. Whether the cuticular lining of the follicle and possibly the dermal muscles serve to hold the mature feather in the follicle is unknown and needs investigation.

CONCLUSION

In the repeated molt cycle of many, if not all birds, the dropping of the old generation of feathers is brought about by the initiation of growth in the new generation which pushes the old feathers passively out of the follicles. Molt in birds is consequently a single growth process actively concerned only with the production of the new generation of feathers. This new growth causes the passive loss of the old generation of feathers. Molt nomenclature should reflect in some way this natural relationship between the growth process, the generation of feathers it produces, and the generation lost.

At present two methods are available for naming molts. In the system devised by Dwight (1900), the molt is ambiguously named either for the time of its occurrence in the life cycle of the bird and/or for the plumage shed (e.g., postnuptial molt produces winter plumage) or for the plumage gained (prenuptial molt produces nuptial plumage). In the recently proposed system of Humphrey and Parkes (1959) in use in the *Handbook of North American birds* (Palmer, 1962), the molt is consistently named for the incoming plumage (e.g., prebasic molt produces basic plumage, prealternate molt produces alternate plumage). The fundamental principle of this system is that energy is expended for the production of incoming feathers and not for shedding old feathers. In this respect, the new system of molt nomenclature reflects more closely the natural relationship between molts and plumages.

SUMMARY

1. Observations of feather replacement in live and preserved specimens of several species of birds during natural molt demonstrate that old feathers are actively pushed out of the follicles attached to the tips of the sheaths of the incoming feathers. 2. There may be a constriction at the zone of juncture but the outer layer of the calamus of the old feather and the sheath of the new feather are apparently continuous. 3. The old feathers are broken off when the new feather sheath becomes keratinized. 4. The physical connection is still present when growth is renewed in a papilla which has been dormant 10 months. 5. This mechanism of feather replacement has been observed in eight diverse orders of birds. 6. Molt

consequently appears to be a single growth process actively concerned only with the new generation of feathers. The old generation is passively shed. 7. Molt nomenclature should reflect this natural relationship between the growth process and the generation of feathers it produces.

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