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GROWTH, MOLTS, AND PLUMAGES OF THE GADWALL

LEWIS W. ORING

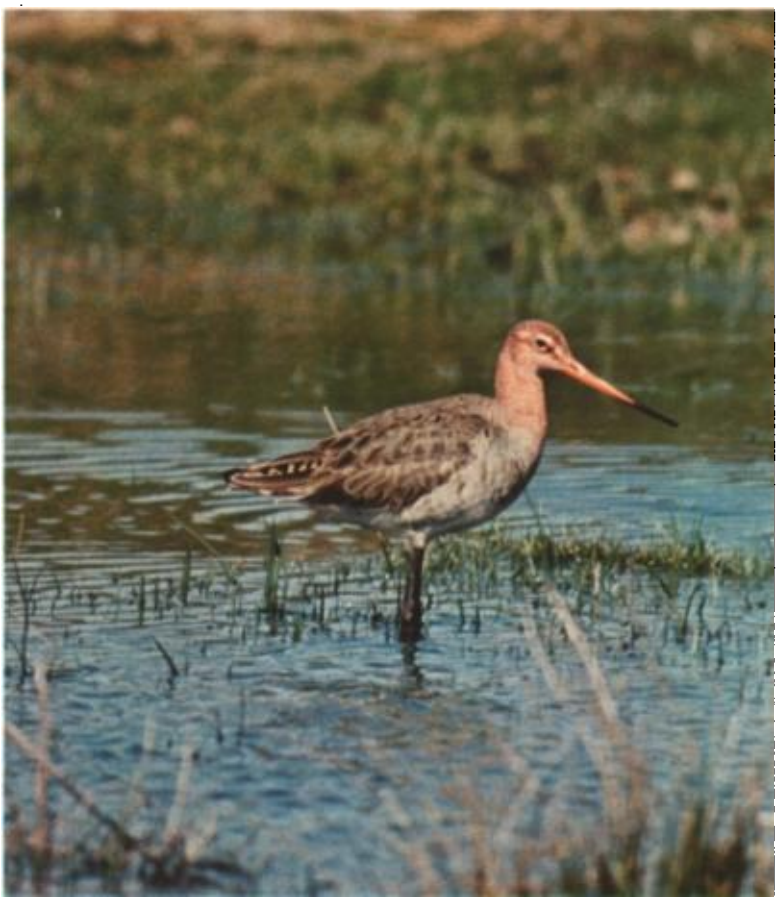
DESPITE the wealth of literature on waterfowl, the molts and plumages of few species have received adequate attention. Classical works such as those of Millais (1913), Phillips (1922–26), Schiøler (1925–26), and Witherby *et al.* (1939) described the plumages of many species mainly from museum material. M. D. Pirnie (1928) studied various forms from both living birds and skins. The works of Sutton (1932), Salomonsen (1941, 1949), and Stresemann (1948) on the complicated molts of the Old Squaw (*Clangula hyemalis*), indicate the need for similar detailed studies of other species.

Schiøler (1925), Witherby *et al.* (1939), and others included in their works descriptions of Gadwall (*Anas strepera*) plumages but none worked with living birds or with skins of birds of known ages and breeding histories. Using the fine facilities of the Delta Waterfowl Research Station at Delta, Manitoba from 1962–64, I was able to hatch, rear, and breed Gadwalls in captivity and study them in the wild. Here and in a concurrent study of breeding biology, I have attempted to correlate molts and plumages with environmental and physiological factors.

PRENATAL AND POSTNATAL DEVELOPMENT

The following discussion is based upon analysis of 42 embryos and 283 skins and repeated examination of about 250 live birds. Eggs from incomplete clutches and considered "fresh" were placed in incubators immediately after collection. The incubators were usually maintained at 99.5°F but were raised to 101°F when eggs were hatching.

Relative humidity, though variable, was always kept high. Two embryos were preserved in 10 per cent formalin on each of 21 of the 23 days prior to hatching. None was stained and no slides were prepared. Nearly all of the 283 specimens were skinned from the back and made into flat skins, which allows examination of the papillae as well as the feathers. Of the total, 185 specimens were captives of known age (1 day to 27 months) and 98 were wild adults. Captive specimens dated 1 October



Black-tailed Godwit in Dartmouth, Massachusetts. Photographed 30 April 1967 by Severyn S. Dana. (See page 500)

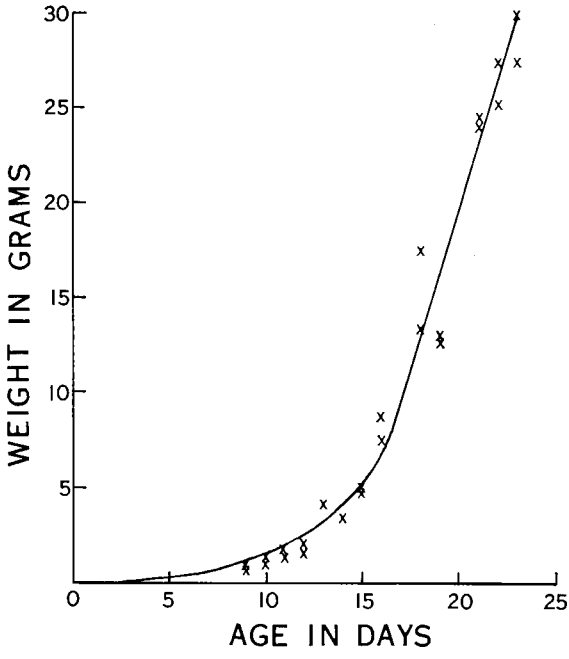


Figure 1. Weights of embryonic Gadwalls.

to 30 March were killed at Norman, Oklahoma, while those from 1 April to 1 September were killed at Delta, Manitoba. All wild specimens were collected from 1 May to 31 August at Delta.

Table 1 shows weights of embryos as well as measurements of total length, culmen, and tarsus of embryos at various stages of development (after Weller, 1957). Weights of juveniles and measurements of juvenile culmens and tarsi are given in Table 2. The exponential growth curves of embryos in Figure 1 and of juveniles in Figure 2 are similar to those described by Weller (1957) for the Redhead (*Aythya americana*). I have described in detail all Gadwall molts. Except for the controversial Basic I plumage, only the diagnostic features of plumages are given. For more complete plumage descriptions see Oring (1966). The molts and plumages of a modal male and female are diagrammed in Figure 3.

Embryonic development.—Descriptions of prenatal feather development in ducks (Lamont, 1921; Hosker, 1936; Koecke, 1958) have been limited to domestic strains of the Mallard (*Anas platyrhynchos*). As the incubation period of these strains averages 28 days, as compared with 24 days for incubator-hatched Gadwalls (Oring, 1966), a chronological description of feather development in the embryonic Gadwall is needed.

TABLE 1
GROWTH OF EMBRYOS

Days incubated	*Length (mm)*	*Culmen (mm)*	*Tarsus (mm)*	*Weight (g)*
9	54	3.2	3.0	.80
9	56	3.5	3.0	.85
10	61	4.0	4.0	1.15
10	66	4.5	4.0	1.30
11	66	4.9	4.8	1.55
11	76	5.0	4.9	1.90
12	70	5.0	4.5	1.80
12	71	5.0	5.0	2.10
13	86	6.0	6.5	3.60
13	92	6.0	7.0	4.20
14	88	6.0	6.0	3.50
14	92	7.0	8.0	4.25
15	101	7.5	8.0	5.00
15	102	8.0	8.0	5.00
16	100	8.2	10.0	7.55
16	105	10.0	10.5	8.90
18	119	10.0	13.0	13.40
18	132	10.0	15.0	17.50
19	104	10.0	13.0	12.85
19	111	10.0	13.5	12.90
21	140	11.0	18.0	24.00
21	145	11.0	18.0	24.50
22	137	11.0	18.0	25.25
22	143	11.5	19.0	27.50
23	170	12.0	19.5	27.50
23	174	12.0	20.0	30.07

Though all Gadwall eggs were "fresh" when put into incubators, rate of development varied. This may have been due to variation of incubation conditions, to factors inherent in the eggs, to differences in length of time the eggs were retained in the uterus or in the amount of time hens spent on the nest during the laying period, or to variation in environmental temperature during laying.

The 22–24-day incubation period of wild Mallards (Hochbaum, 1944) is similar to that of incubator-hatched Gadwalls (24.0 day average), but Mallards of "Khaki Campbell" and "Indian Runner" strains have an incubation period of 28 days (Koecke, 1958; Lamont, 1921). Gadwalls, domestic Mallards, and, almost certainly, wild Mallards have nearly parallel embryological development for at least the first 18 days of incubation which, in the domestic Mallard, apparently represents a recapitulation of ancestral developmental stages. The increased time beyond 18 days required for completion of embryological development may have evolved along with recently derived increased body weight (Khaki Campbell variety) and upright posture (Indian Runner variety).

In the following descriptions of Gadwall embryos at 1-day intervals, I list the comparable stage or stages for the domestic duck (Koecke, 1958)

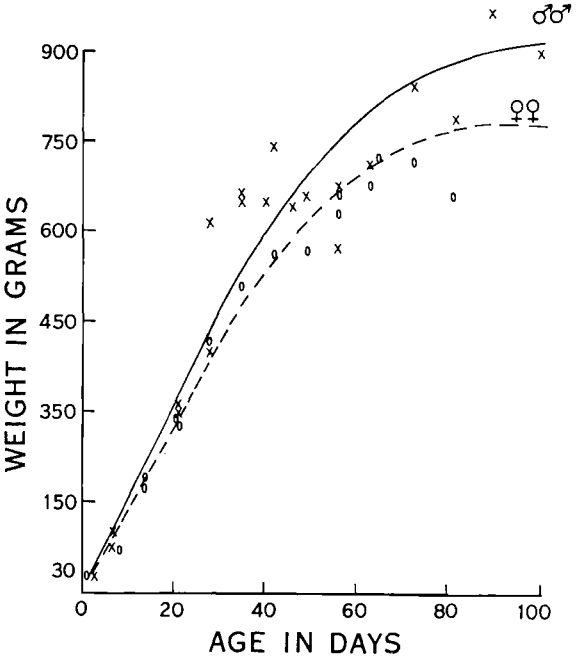


Figure 2. Weights of juvenile Gadwalls.

and the chick = fowl (Hamburger and Hamilton, 1951) for days 5–18. Beyond 18 days such comparisons probably are meaningless. When two embryos of the same age differ considerably in size, I refer to them as the "smaller" and "larger." All references to Koecke (1958) pertain to the "domestic duck" as he lumped all data from the Khaki Campbell and the Indian Runner varieties. References to Lamont (1921) pertain only

TABLE 2
GROWTH OF JUVENILES

Age	*Weight (g)*		*Culmen (mm)*		*Tarsus (mm)*	
	♂	♀	♂	♀	♂	♀
1 day	28	29	14, 14	13	19, 20	18, 18
1 week	75, 103	75	21, 20	—	25, 25	21
2 weeks	—	179, 193	—	25	—	33, 31
3 weeks	330, 318	295, 299	30	30	36, 38	36, 38
4 weeks	406, 618	420	36, 38	36	39, 41, 45	40
5 weeks	655, 666	516	40	—	41, 44	40, 41
6 weeks	747	562	40	38	40	40
7 weeks	661	565	41	39	40	38
8 weeks	577, 677	671, 635	47	40	41	40

to the Indian Runner while those to Hosker (1936) pertain to the Khaki Campbell unless otherwise stated. In evaluating comparison of my findings with those of Lamont (1921) it must be kept in mind that his samples skipped from 10 days to 11 days 7 hours, to 14 days 7 hours, to 17 days 7 hours, to 21 days 7 hours, to 24 days 10 hours, and finally to hatching at 28 days.

Day 5: 5-day domestic duck (Koecke, 1958), stages 22–23 chick (Hamburger and Hamilton, 1951).

Day 6: 6-day domestic duck, stage 25 chick.

Day 7: 6- to 7-day domestic duck, stage 27 chick.

Day 8: 7-day domestic duck, stages 28–29 chick. Mouth slit distinct, egg tooth not yet formed, no papillae present.

Day 9: 9-day domestic duck, stage 34 chick. Embryo resembles bird. Beak present with egg tooth on maxilla, webbing on feet apparent. Nictitating membrane visible for first time in Gadwall, though apparent in 8-day duck (Koecke, 1958). Embryo has pimpled appearance. Prepennae papillae obvious on spinal, femoral, and humeral tracts. Two rows of papillae cross caudal end where they ultimately will form rectrices and upper tail coverts. Papillae of under tail coverts visible but not bulging nearly so much as those of rectrices and upper coverts. Papillae of secondaries just appearing in larger embryo. Ring of osseous scleral papillae complete; in larger embryo papillae just appearing above and in front of eye. Neck papillae barely perceptible dorsally in both embryos and faintly visible ventrally (especially posteriorly) in larger embryo. Papillae of large side feathers visible. Ventral papillae visible in larger embryo but not yet elevated above surface of skin. In 9-day (61 mm) Indian Runner embryos papillae were visible only on spinal and femoral tracts and on sides of tail, where they formed a double ridge (Lamont, 1921). In Khaki Campbell embryos first indications of natal down appeared on spinal and femoral tracts, but sites of "feather embryos" were visible microscopically at 8 days (Hosker, 1936).

Day 10: 10-day domestic duck, stages 35–36 chick. Claws not yet visible on toes, first finger and fourth toe free from rest of limb. Papillae of spinal and femoral tracts as well as of rectrices considerably elongated. Tibial region covered with papillae. In Redhead (Weller, 1957), rectrices not enlarged until 12th day, spinal and femoral feathers until 14th. Upper and under tail covert papillae well developed by 10 days in Gadwall. Pigment obvious in papillae of rectrices and upper tail coverts of larger embryo. Lamont (1921), Hosker (1936), and Koecke (1958) did not note pigment until after 10 days. Secondaries and greater upper secondary covert papillae barely visible in smaller embryo. Secondaries and three rows of upper secondary coverts easily seen in larger embryo. Tertials, two rows of upper tertial coverts, and primaries barely visible in larger embryo. Papillae visible on top and back of head and around ear, but absent from throat. Nictitating membrane visible halfway between osseous scleral papillae and cornea. Numerous rows of papillae present between upper eyelid and mid-coronal line. Dorsal side of neck covered with papillae. Raised papillae apparent throughout venter. Lamont (1921) found at 10 days (62 mm) papillae of the ventral and humeral tracts, rectrices, and upper tail coverts. Hosker (1936) reported at 10 days feather germs visible over entire body—in Aylesbury Mallard depressed, in Khaki Campbell elevated as in Gadwall.

Day 11: 11-day domestic duck, stages 35–36 chick. In larger embryo much melanin apparent dorsally—pigment concentrated in spinal tract but also present in humeral and femoral tracts. Mid- and lower back darkest. In smaller embryo all but two

pairs of outer rectrices and three outermost pairs of upper tail coverts pigmented. In larger embryo all rectrices and upper tail coverts pigmented, rectrices up to 2 mm long. In smaller embryo papillae of secondaries, tertials, and three rows of upper wing coverts visible. In larger embryo papillae of primaries, upper greater primary coverts, secondaries, tertials, upper greater secondary coverts, four rows of median coverts, and two rows of lesser coverts clearly visible, axillar and alular papillae barely visible. No papillae on throat or upper third of foreneck in either embryo. Papillae visible (perhaps preplumulae) directly under wing on trunk of both embryos—more developed posteriorly. Flanks of both embryos covered with fine papillae. Lamont (1921) noted that at 11 days 7 hours (65 mm) papillae protruded well above the skin, and that papillae were visible on the head, especially above the eye; he found no papillae on the wing; no pigment was visible.

Day 12: 11-day domestic duck, stage 36 chick. Intermediate between the two 11-day embryos.

Day 13: 13-day domestic duck, stage 37 chick. Papillae of tarsal scales and of middle toe barely visible. No scale papillae on other toes or around ankle joint. Lamont (1921) noted that at 17 days 7 hours (120 mm) scale papillae were first visible. In Gadwall all feather tracts apparent by this stage. Many papillae so elongated they could be called feather filaments. Filaments expanded slightly at base and tapered gradually to fine point. Longitudinal ridges of developing barbs and centrally located blood vessels visible on dorsum. Marginal coverts visible for first time. Pigmented prepennae included: (1) crown and auricular region (entire capital tract in larger embryo), (2) nape, (3) extreme posterior ventral tract between leg and yolk stalk, (4) side feathers, (5) femoral tract, (6) rectrices and upper and under tail coverts, (7) secondaries, greater upper secondary coverts (two rows of upper coverts in the larger embryo), and few humerals (all tertials and humerals as well as primaries and greater primary coverts in larger embryo). Alula well developed but papillae not pigmented. Upper eyelid nearly to cornea. Lower eyelid covering about ⅓ of cornea as reported for duck at 12 days (Koecke, 1958). Both upper and lower eyelids covered with two to three rows of papillae similar to 15-day duck (Koecke, 1958). Preplumulae visible but variable in size and arrangement in both Gadwall embryos, and containing some pigment in larger embryo. Lamont (1921) first noted pigmented preplumulae at 17 days 7 hours. Larger Gadwall embryo had body filaments of 2–15 mm, rectrices of about 6 mm, and secondaries of 2–3 mm. Lamont (1921) noted at 14 days 7 hours (112 mm) trunk filaments up to about 8 mm, and tail filaments up to 6 mm, and at this stage he first saw melanin, evidence of barb formation, blood vessels, and preplumulae.

Day 14: No advancement beyond the 13-day embryos.

Day 15: 15-day domestic duck, stages 37–38 chick. Scales present on total surface of tarsus and dorsal surface of toes as in 14-day duck (Koecke, 1958). Webs comparable to those of 13-day duck (Koecke, 1958) in that they are not serrated along edges. Upper eyelid reaches cornea for first time as in 14-day duck (Koecke, 1958). Almost entire dorsum dark. All feathers that eventually will have melanin pigmented. Oil gland not protruding but 10 tuft papillae visible. Prefiloplumulae visible dorsally alongside prepennae for first time. Body filaments up to 15 mm long, rectrices to 8 mm, and secondaries to 7 mm. Lamont (1921) first observed prefiloplumulae at 17 days 7 hours. He then observed delicate strands of muscle forming a mesh between prepennae, but this I did not see.

Day 16: 16-day domestic duck, stages 38–39 chick. Scales present on webs dorsally, on toes ventrally as in 17-day duck (Koecke, 1958). Some scale overlap on front

of tarsi similar to that in 17-day duck (Koecke, 1958). Edges of webs serrated for first time as in 14-day duck (Koecke, 1958). Feather "Anlagen" of eyelids containing a little pigment and in late papillae stage. Lower eyelid covering less than ¼ of cornea as in 14-day duck (Koecke, 1958). Oil gland protruding from skin and containing at least two rows of 10 tuft feathers; all plumes of anterior row containing some melanin.

Day 17: No sample available.

Day 18: 18-day domestic duck, stages 39–40 chick. Tarsal scales overlapping for more than ⅓ their length. Eyes open only as tiny slits. Oil gland tufts well developed and pigmented. Filoplumes projecting to short but sharp peak. Prefiloplumulae up to 4 mm long. Body filaments up to 22 mm, rectrices to 18 mm, secondaries to 17 mm. Embryo was at 21 days 7 hours (158 mm) when Lamont (1921) observed preplumulae and body filaments; the former measured 5–7 mm, the latter 20–26 mm.

Day 19: No advancement beyond the 18-day embryos.

Day 20: No sample available.

Day 21: Plumes of oil gland still receiving blood and surrounded by continuous skin sheath. Body filaments up to 23 mm, rectrices to 25 mm, secondaries to 19 mm. Lamont (1921) noted prepennae almost ready to burst from sheath at 24 days 10 hours (176 mm). By drying and teasing out, he then caused them to burst at tip.

Day 22: No advancement beyond the 21-day embryos.

Day 23: Prepennae clear at base for first time. Body filaments up to 29 mm long, rectrices to 28 mm, secondaries to 25 mm, and primaries to 19 mm.

Day 24: Gadwall fresh from shell wet, with down still enclosed in sheaths; sheaths fall off rapidly during drying process; by end of first day, usually within 12 hours, duckling is dry and fluffy. It is then covered by three different types of "down": (1) prepennae—long dominant filaments arranged in regular diagonal rows, (2) preplumulae—shorter filaments of irregular size and arrangement, and (3) prefiloplumulae—still smaller filaments found alongside prepennae. Shafts of all down feathers except rectrices translucent, indicating that they are no longer growing. Shafts of rectrices still contain pulp. Long continued development of tail despite its early beginning is, I believe, explainable by the fact that natal rectrices have by far the greatest volume of all neossoptiles. At hatching, rectrices when plucked are over 26 mm long as opposed to 14 mm for primaries and 20 mm for secondaries, and are also more than twice as thick as any other natal feathers.

Natal plumage.—Gadwall prepennae, for the most part, represent a single generation of epidermal tissue. On the wings, mainly among the secondaries and greater upper secondary coverts (see Prejuvenal molt), and also scattered here and there in the body plumage, is a restricted second prepennae generation. Ewart (1921) found a similar feather generation in the Mallard on the secondaries and greater upper secondary coverts, scattered among the body feathers, and also on the outer pair of rectrices.

At hatching Gadwalls are cream-buff below and sepia above (except for four light dorsal spots), some individuals being yellower than others. The yellowish tinge present at hatching fades within a day or two. In some a cinnamon tinge becomes apparent on the chest. This slight fading continues for at least 8 or 9 days. Nowhere among anatids is it more evident than in bright yellow downy young such as those of the Redhead.

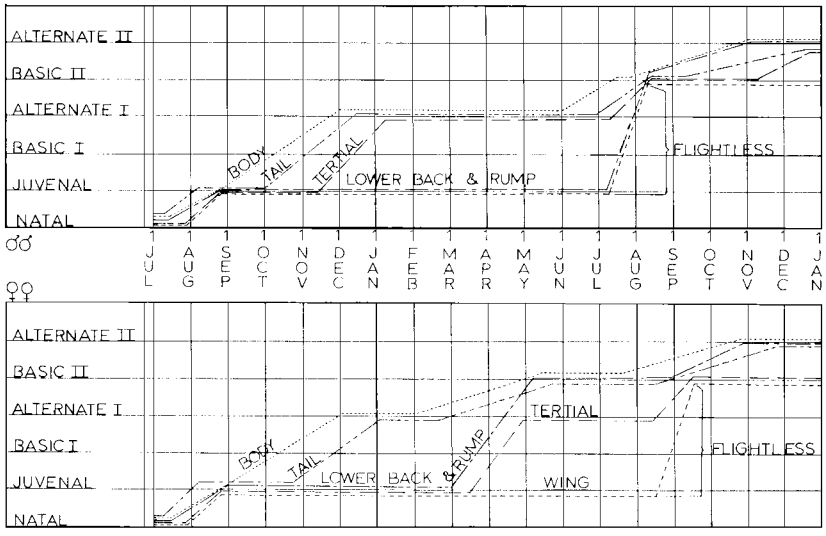


Figure 3. Sequence of molts and plumages in a modal male and female Gadwall. Diagonals represent inclusive periods of feather-growth as viewed from both inside and outside skin. At the termination of a given diagonal, the particular part (tail, wing, etc.) is at completed stage.

So far as I know, no one has extracted and analytically identified pigments of waterfowl down. The granular nature of the dark Gadwall filaments is indicative of melanin. The faint yellow color at hatching is almost certainly due to a carotenoid. It is known that in teleoptiles of the flicker (*Colaptes*) yellow carotenoids oxidize rapidly whereas melanins are relatively inert (Test, 1940). In comparing Gadwall ducklings of known age it is apparent that dark parts change color but little, whereas light parts fade rapidly, even among birds kept in an incubator. Day-old ducklings that have been out-of-doors appear more faded than birds of similar age kept in the hatchery. Under the microscope, down from 1- and 2-day-old faded skins appears structurally identical to that from unfaded skins. In view of the fact that this fading occurs among birds that have not been exposed to water and that have no visible feather wear, carotenoid auto-oxidation catalyzed by heat and light seems to be the most plausible explanation.

Other factors affect their color as the downy young grow older. At one week the Natal down is not yet badly worn, but the same number of feathers that cover the duckling at hatching now cover a much larger area. Gray feather bases are visible. By 9 or 10 days many prepennae shafts and barbs are broken, revealing still more gray bases, and preplumulae pushed out by ingrowing down become visible. Gadwalls at this

TABLE 3
AGES AT WHICH CAPTIVE GADWALLS FIRST FLEW

Age	*Number flying*	*Percentage*
48 days	1	2
49 days	1	2
50 days	5	10
51 days	25	50
53 days	6	12
56 days	11	22
63 days	1	2

stage are truly gray. The grayness does not change noticeably until Juvenal pennae are evident during the 3rd week.

Prejuvenal molt.—By 4 days of age follicles of both down and pennae are active in most feather tracts. As down growing at this time accompanies the Juvenal plumage, I have called it Juvenal down. Juvenal pennae of the oil gland, with Natal down attached to their tips, push through the skin on the 6th day. At 7 days Juvenal down pushes through the skin along the sides and in the posterior part of the back. By 8 days the Natal rectrices have been pushed out a few millimeters. By 9 days prepennae of the side feathers have also pushed out. Not only are Natal rectrices of waterfowl pushed out by incoming Juvenal quills (Kortright, 1942), but the normal mechanism of feather ecdysis is a pushing out of the old by the new (Khvatov, 1935 and Voitkevich, 1934 *in* Voitkevich, 1966; Watson, 1963).

Despite its precocial beginning, the Juvenal plumage is not readily noticeable until the duckling is about 2 weeks old, when a parting of the prepennae reveals a mass of incoming down and pennae. Ensheathed tertials are first visible at about 17 days. At 3 weeks some birds are completely covered below with pennae, while others appear down-covered. In every bird under observation at this stage pennae were obviously growing over the whole body and remiges were plainly visible. At 3½ weeks greater coverts and axillars become visible. By 4 weeks every one of my captive birds was well covered with Juvenal plumage, the principal wing feathers were all visible, a second coat of down (mesoptiles of Ewart, 1921) was well developed on the secondaries and upper greater secondary coverts, and the oil gland tufts were fully grown. Lesser and median under wing coverts become apparent by 4½ weeks. During the 5th week many body feathers and rectrices clear and wing growth suddenly surges. By 6 weeks Juvenal rectrices, scapulars, and side feathers are completely grown and down of the Alternate I plumage is apparent along the mid-ventral line. Most of my captive birds first flew at between 50 and 56 days (see Table 3). At 56 days only a very few Juvenal feathers are still partly

ensheathed—on the lower belly, sides, under tail coverts, and lower back. Primaries, secondaries, and tertials are fully grown. Some Natal down remains on the back of the neck and under the wings while down of the Alternate I plumage continues to grow beneath the skin. During the 10th week, partly ensheathed Juvenal feathers are to be found only on the flanks and under the wings, and Alternate I down is pushing through the skin for the first time. Captive birds older than 10 weeks all had a considerable number of Alternate I feathers. Rectrices, scapulars, and flank feathers are fully grown by 6 weeks, secondaries by 7 weeks, primaries and tertials by 7 or 8 weeks.

I repeatedly handled 50 juvenile Gadwalls (26 males, 24 females) in an effort to determine the age at which they first were capable of flight and to coordinate this stage with the clearing of primaries (for a detailed description of the primary-clearing phenomenon see Weller, 1957). Only birds that became airborne when chased were considered truly able to fly. Admittedly, this method is time- and space-consuming, but I believe it to be accurate for dabbling ducks. None of these Gadwalls flew before three primaries were clear; all flew by the time five were clear. All but three birds first flew between the 50th and 56th day. Data for both sexes are lumped as no differences were apparent between males and females. My data agree closely with those of Hochbaum (1944), who found that hatchery-reared Gadwalls first fly at between 49 and 63 days.

I have no comparable data for wild birds. I did, however, keep track of a brood of four that hatched 16 June 1964 in a large pen containing lush vegetation and marsh water and fed almost exclusively upon natural food. All four birds were seen flying on 3 August—48 days after hatching (data not included in Table 3). One male and one female caught that day both had four partially clear primaries. Several other Gadwalls reared in a large flight pen were seen to fly at 46 days (data not included in Table 3). Ten drake Mallards I raised all flew first at between 55 and 59 days (average 56.6 days). Five drake Pintails I reared averaged 45.8 days when they first flew; five hen Pintails averaged 40.8 days. Gadwalls apparently first fly at an age intermediate between the first flying ages of these two close relatives. For a résumé of time when various other anatids first fly see Weller (1957).

Among the 50 juveniles I studied were two special study groups of 19 birds each. All the birds of one group hatched 24 June, those of the other between 10 and 13 July. The groups were kept in separate brooders in the hatchery and were fed at first only turkey "prestarter." After 2 weeks they were given a mixture of wheat, barley, and prestarter. At 51 days 7 of the 19 early-hatched birds and 12 of the 19 late-hatched birds flew. By 56 days the early birds averaged five clear primaries, the late

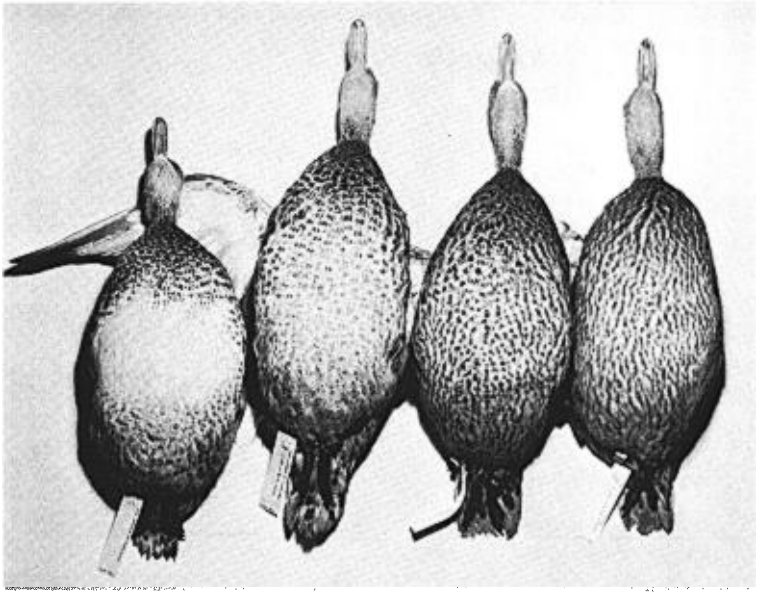


Figure 4. Juvenal plumage of female Gadwalls viewed ventrally (similar variation occurs in males).

birds seven, and all members of both groups flew. The average age at first flight was 53.89 days in the early-hatched group, and 51.31 days in the late-hatched group. Thus the birds that hatched 16–19 days later matured to flying 2.58 days more quickly than the early-hatched birds did. Using an unpaired t-test, this difference is significant at the .5 per cent level. Smart (1965) and Dane (1965) report a similarly differential rate of maturation among Redheads, which Smart attributes to the fact that warm temperatures tend to decrease thyroxine output and therefore to slow feather growth. Stahl *et al.* (1961) show that decreased temperatures increased thyroxine output and Premachandra *et al.* (1959) show that increased thyroxine rates increase slightly the growth rate of chickens. Dane (1965) found no difference in the amount of time required for primary feather maturation between early- and late-hatched Blue-winged Teal (*Anas discors*).

Juvenal plumage.—Characterized by square-tipped rectrices, narrow body feathers, and dull wing color. Dorsal body and tail feathers are dark brown, edged and barred buff. Though venters usually have brown spots (single or double) or streaks, immaculate-bellied juveniles of both sexes are found occasionally (see Figure 4). Juvenal breast and side feathers are compared to those of other plumages in Figures 5 and 6 respectively. Lesser and median upper secondary coverts of many males have distinct horizontal bars of buff that are absent in older birds (Figure 7). Females can be told from males by their generally smaller size, less barring on mantle feathers

and scapulars, lighter back and rump, buffier tail, and almost always by their duller wings (see Figure 8). In male, distal ⅔ of down is light gray grading through pale gray to white basally; in female, down is white to pearl-gray.

Prebasic I molt.—Juvenal plumage is partially replaced during the Prebasic I molt. Follicles of the Basic I plumage can be seen beneath the skin on the chest and along the sides as early as 56 days of age, but the molt is not readily detectable exteriorly until 65–80 days. In some individuals this molt continues as late as early November. I have detected this molt on the chest, sides, and lateral upper back in both sexes—precisely where Schiøler (1925) found such feathers in young males.

Basic I plumage.—Schiøler (1925) described a previously overlooked plumage in anatines that he termed postjuvenal or first adult. Because this plumage varied in extent as well as in pattern, and because of its transitory nature, Schiøler considered it suppressed or selected against.

Schiøler was handicapped by having only a few Gadwall skins and by being unable to view their insides. This perhaps explains why he did not find a partial plumage in hens comparable to the transitory first adult (here Basic I) plumage in drakes and why, therefore, he considered the extensive plumage acquired by hens in late winter or early spring to be their Basic I plumage. The oversight is understandable in view of the similarity of the hen's several plumages.

In the present study I prepared as flat skins 17 male and 18 female Gadwalls between the ages of 56 and 132 days (25 August to 3 November). I found no differences between the patterns of molt in males and females prior to assumption of the Alternate I plumage. Because the Basic I plumage must be accounted for if Humphrey and Parkes's (1959) hypothesis of plumage homologies is to be accepted for anatines, I paid special attention to plumages during the first few months of life. Not only have I found the Basic I plumage present on the chest, sides, and upper back of both male and female Gadwalls, but I have found a comparable generation of feathers on the heads and necks of both male and female Mallards and Redheads. This plumage is worn simultaneously with parts of the Juvenal and Alternate I plumages.

MALE: Breast feathers are dark brown, edged with buff, and crossed distally by a broad tan horizontal bar and proximally by one or more white markings (Figure 5). Tan bars sometimes curve toward base of feathers laterally, thus being "horse-shoe shaped" (Schiøler, 1925). Side feathers are dark brown with tan markings that tend to cross laterally rather than longitudinally (Figure 6). Gray-brown lateral feathers of the upper back are stippled and barred variously with tan.

FEMALE: Exhibits same range of variability as comparable feathers in Alternate I plumage. Breast feathers are illustrated in Figure 5.

Prealternate I molt.—A few papillae destined to produce down become active at between 35 and 46 days (late July to early September). This down, despite its succeeding Juvenal down, is apparently part of the Alternate I plumage for it is shed simultaneously with Alternate I pennaceous feathers. Alternate I oil gland plumes are visible by 38 days. By 56 days the inside of the skin is covered with active down papillae. At about 65 days (late August to early October) Alternate I down is apparent on the outside of the skin. It grows rapidly; in about a month little of it is still growing, but it continues to grow until the onset of the Prebasic II molt.

The Prealternate I molt of pennae is a little later than that of down, but most feathers are renewed by the end of November (approximately 150 days). Some of my females continued to lose Juvenal feathers as late as 6 January and some of my

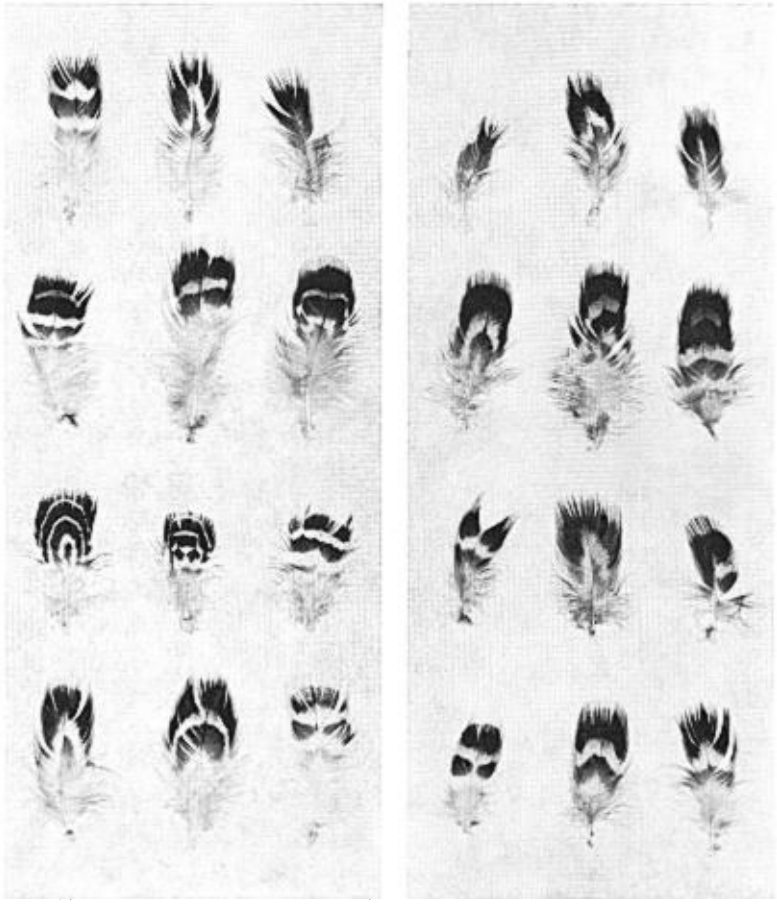


Figure 5. Breast feathers of male (left) and female (right) Gadwalls (top to bottom: Juvenal, Basic I, Alternate I, and Basic II).

males as late as 22 March. A few pennae papillae contain pulp by 63 days. Scapulars, as well as chest and vent feathers, push through the skin by 72 days. These are soon followed by other trunk feathers except those of the back and upper rump which are retained until the Prebasic II molt. Head and neck pennae, rectrices, and tertials (retained until spring in the female) are the last to molt.

Alternate I head and neck feathers can be seen on the outside of the skin at between 81 and 83 days. Juvenal oil gland tufts are molted at between 38 and 132 days. In my captive birds the Juvenal tail was renewed from mid-September (83 days) to early February in males, from late October to mid-January in females. Female tertials are not molted until sometime between 1 February and 4 June (usually between 1 March and 1 May). Males renew their tertials between late November and early February. Individual birds require 12–15 weeks for renewal of rectrices and

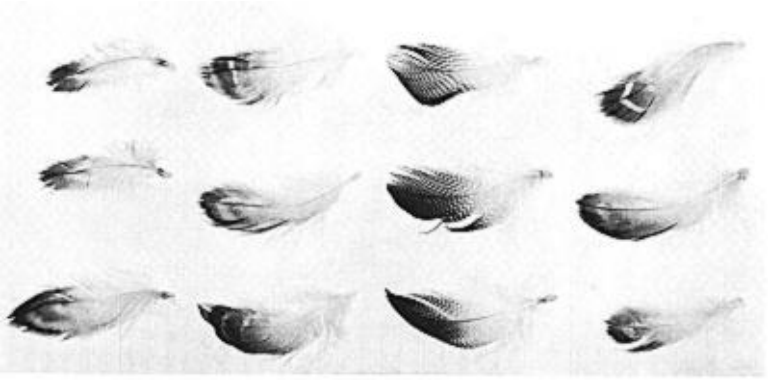


Figure 6. Side feathers of male Gadwalls (left to right: Juvenal, Basic I, Alternate I, Basic II).

3–4 weeks for renewal of tertials. Eight of 12 captive males and 5 of 21 captive females molted one of their middle rectrices first; 5 males molted both middle rectrices first as did 4 females. None of these 33 birds molted their entire tail symmetrically, nor have I ever handled a bird whose entire tail was molting symmetrically.

In addition to the Juvenal lower back and rump feathers that are not molted, the most commonly retained Juvenal feathers are those of the sides, scapulars, flanks, and upper back, and the upper tail coverts. Retained less often are feathers of the chest, vent, and under tail coverts.

The above résumé pertains to both sexes. It should be noted that, contrary to the findings of Witherby *et al.* (1939), females as well as males retain Juvenal back and upper rump feathers. On just two birds, a male and a female, did I find evidence of dorsal molt posterior to the wings prior to the assumption of the Alternate I plumage. I quite agree with Witherby *et al.* (1939) that the female Juvenal tertials are not renewed before assumption of Alternate I plumage and that females occasionally retain Juvenal rectrices until the following spring whereas males do not. It should be borne in mind, however, that captive birds suffer so much rectrix wear it is often impossible to determine to which plumage certain feathers belong.

Alternate I plumage.—MALE: Similar to Alternate II plumage (Alternate I breast and side feathers illustrated in Figures 5 and 6 respectively). Lower breast and belly are more often spotted and less often vermiculated than in Alternate II plumage. Juvenal lower back, upper rump, and wing feathers (exclusive of tertials and tertial coverts) are worn simultaneously with Alternate I plumage.

FEMALE: Similar to Alternate II plumage (Alternate I breast feathers shown in Figure 5). Juvenal lower back, upper rump, and wing feathers are worn simultaneously with Alternate I plumage. Juvenal tertials and tertial coverts are present until about beginning of Prebasic II molt of body feathers. They are then replaced by Alternate I tertials which have more rounded tips, more extensive buff edges, and are occasionally marked or barred with buff.

Prebasic II molt.—MALE: During March and April, perhaps as a result of accidental feather loss, a few Alternate body feathers are usually growing. As a rule the papillae do not begin to produce Basic follicles until late May, but occasionally a drake begins its Prebasic molt in April and is in full Basic dress by late May or early

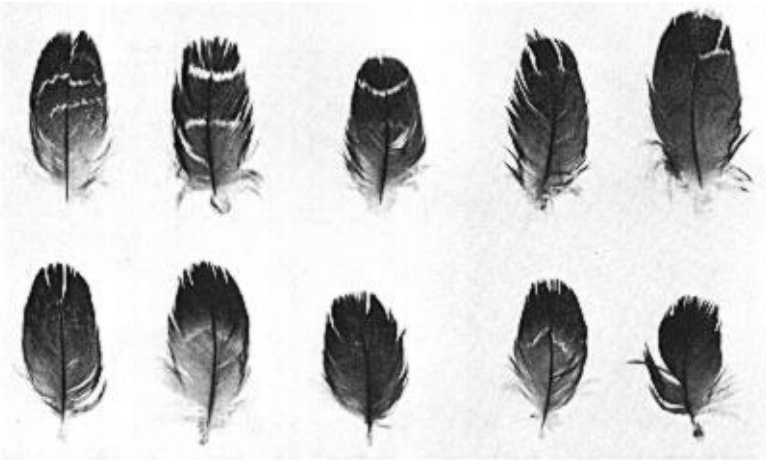


Figure 7. Lesser median upper secondary coverts of male Gadwalls (juvenile above, adult below).

June. Some drakes are still in complete Alternate plumage (with no papillae producing Basic follicles) in late June. Alternate feathers of the lower back and rump, which are among the very last to molt, usually do not begin to drop out before late July. Some of these may not, indeed, drop out before the Prealternate molt in the fall.

Molt of the Alternate plumes of the oil gland and of the cloacal ring parallels that of Alternate body feathers, though it sometimes begins earlier in the spring. Alternate tail feathers usually are not replaced until mid-July just before the birds become flightless. New tails are then complete by the end of August. I have handled a few birds in June that were missing tail feathers, and occasionally a bird does not complete its new tail until early October. The molt of rectrices requires about 2½ months to be completed.

Alternate tertials usually fall out in July a few days before any other wing feathers do. Between 8 July and 9 September, and rarely as late as 1 October, I have handled specimens whose Basic tertials were just coming in, but normally new Basic tertials are clear by the end of August. Tertials are renewed in 3½ to 4 weeks. The remaining wing feathers are molted in the same order as in the Prejuvenal molt except that the lesser and median under coverts molt simultaneously with the lesser and median upper coverts. Remiges are usually molted a few days after the tertials; they may all be pushed out at once or they may require a full day to drop out. Alulars are pushed out at the same time as, or shortly after, the remiges. All greater coverts and axillars are pushed out about 1 day after the remiges. Lesser and median coverts are pushed out about 3 days after the remiges, but they become translucent before the remiges do.

By September nearly all drakes have completed their new tails and wings. Captive birds completely renew their wings in 35–40 days, but can fly in about 25 days. In the wild, wing feathers are dropped as early as the 1st week in July and as late as the 1st week in August, but usually they fall out during the first half of July. The molt of down is, in general, closely allied to the molt of pennae. It is heaviest in July and early August.

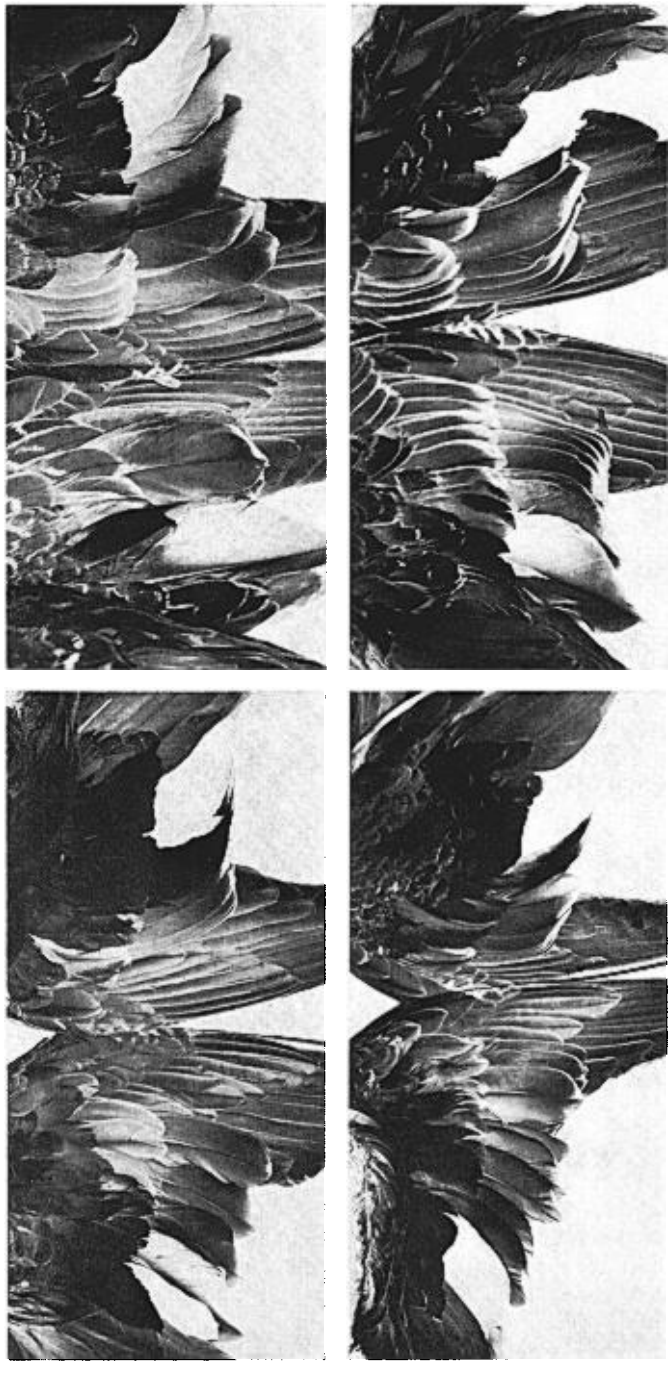


Figure 8. Variation in brightness of Gadwall wings (upper left, adult male; upper right, adult female; lower left, juvenile male; lower right, juvenile female).

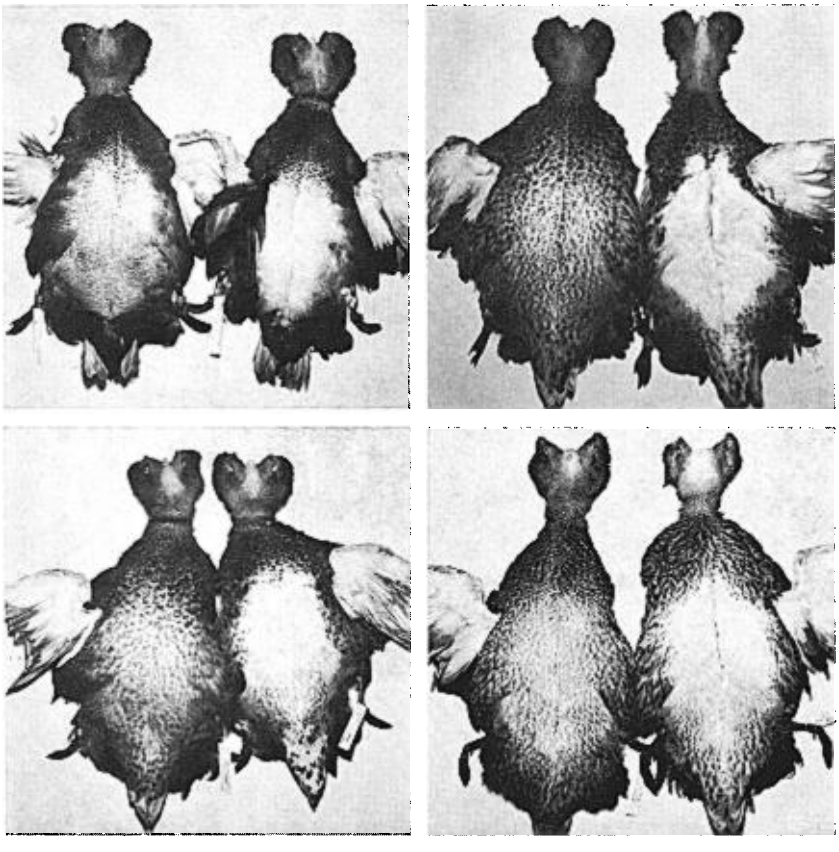


Figure 9. Variation in venters of adult Gadwalls (upper left, male Alternate II; upper right, female Alternate II; lower left, male Basic III; lower right, female Basic III).

FEMALE: Alternate body feathers are replaced from January to late May. Molt is heaviest in March and April. The belly and vent are renewed last. Renewal of black venter down follows renewal of the venter pennae—usually in late April and May. Rectrices begin molting sometime after the 2nd week in February and the molt is complete in early May. Of five birds that I handled repeatedly, one molted all of its rectrices, two retained three, one retained five, and one six. I believe this molt to be discontinuous: body feathers are molted in spring but all the wing feathers are retained until after the breeding season (see Figure 3). Basic tertials are acquired as early as 5 August and as late as early October. The rest of the wing feathers usually are molted a few days after the tertials. Adult females shed their wing feathers about 6 weeks after their young hatch. The time required for renewal of remiges is similar to that in males. The discontinuity of the Prebasic molt in females is apparently an adaptation that frees the critical egg-laying-and-incubation period of such stress as molt imposes.

Basic II plumage.—MALE: Dull brown upper parts are barred as in Juvenal plumage. The breast has dark brown spots that are larger and therefore appear less numerous than those of Juvenal plumage. In four specimens at hand the venter is heavily marked, in three lightly marked, and in seven immaculate (see Figure 9). R. S. Palmer (pers. comm.) reports similar variation in specimens at the Institute of Zoology, Alma-Ata, Kazakhstan, U.S.S.R. Basic II breast and side feathers are illustrated in Figures 5 and 6 respectively. Lesser upper wing coverts are vermiculated and spotted with cream rather than being barred as in Juvenal plumage (Figure 7). Tertials are shorter and less tapered at the tip than those of Alternate plumages. Wings have more boldly contrasting pattern of black, chestnut, and white than in any female and than in nearly all Juvenal males (Figure 8). This plumage is complete. Down is as in Alternate plumage.

FEMALE: Chin and throat are buffier and body feathers more broadly edged with buff than in Alternate or Juvenal plumages. According to Witherby *et al.* (1939), the heavily spotted appearance of hens in summer is a result of plucking feathers for nest lining. According to my observations, however, about a third of the females are heavily streaked or spotted ventrally before feather-plucking begins (see Figure 9). The ashy brown spotting on the underparts is grayer than that of Alternate plumage. Breast feathers are compared to those from other plumages in Figure 5. Tail markings usually are buff and cream but sometimes are as white as in Alternate plumage. Wings are duller than in all adult males and almost all Juvenal males, but brighter than in nearly all Juvenal females (Figure 8). This plumage is complete. Down usually is dusky brown but sometimes is dark gray and is frequently tipped with white.

Prealternate II molt.—MALE: Soon after the Prebasic molt of each body papilla is completed, its Prealternate molt begins. Indeed, Alternate body feathers are visible before the wings are fully grown. Late in August drakes are a mass of growing pennae and down papillae, all tracts molting practically at once. By the end of October most birds are in full Alternate dress, down and pennae. Basic tertials are molted between 10 November and 14 December or later. Basic rectrices are molted from 3 September to 6 December, rarely as late as 6 January. Of 11 birds handled weekly, 7 molted all their Basic rectrices, 1 retained one Basic rectrix, and the other 3 each retained two Basic rectrices.

FEMALE: The onset of this molt is directly related to the female's breeding cycle. Incoming Alternate plumage first becomes visible as dark down papillae on the inside of the skin on the 20th or 21st day of incubation (22 June to 22 July). The oil gland tufts molt at the same time as the venter down. When the eggs hatch only venter down and oil gland papillae are active. Not until the chicks are about 2 weeks old do the hen's pennae papillae gather pulp. Pulp-filled papillae first appear on the sides, then on the venter, and later on the scapular, flank, and femoral regions.

By the time the young are 2 or 3 weeks old (mid-July at Delta), the hens are in general body molt. Alternate body plumage is completed in late October or early November. Basic rectrices are molted as early as 1 July and as late as mid-December—rarely to 6 January, the tail of each individual requiring about 2½ months to be renewed. I did not handle all my captive females early enough to be certain whether or not all Basic rectrices were renewed. Usually the new Alternate tails are complete by mid-November. The molt is discontinuous in that the tertials are not dropped until some time between 6 January and late March. They are always completely renewed by early May. See Prebasic molt for discussion of wing molt.

Alternate II plumage.—MALE: Feathering is predominantly dark gray and white.

Feathers of the upper breast have brownish black and white bars toward tip, variations in relative thickness of bars causing a variety of patterns. Venters are usually white though occasionally spotted, vermiculated, or barred with gray or dusky brown (Figure 9). R. S. Palmer (pers. comm.) reports similar variation in specimens at the University of Moscow, U.S.S.R. Breast (Figure 5) and side feathers (Figure 6) are compared to those from other plumages. A few Basic upper and under tail coverts, scapulars, femorals, and feathers of flanks and chest are sometimes worn simultaneously with Alternate plumage. A head crest, varying in color from gray to brown is usually present. Tertials are elongated and tapered at the tip. This plumage includes all body feathers, rectrices, and tertials but no other wing feathers. Down is as in Juvenal plumage but has less light gray and more pale gray and white.

FEMALE: Feathers of upper parts are dark brown narrowly edged with buff; the throat and chin are usually darker than in the Basic plumage. The venter is nearly always immaculate, but 3 of 12 specimens at hand are spotted brown—1 of these with double spots (see Figure 9). Breast feathers are compared to those from other plumages in Figure 5. This plumage includes all body feathers, rectrices, and tertials but no other wing feathers. Down is medium gray distally grading through pale gray to white basally.

Variation in number of rectrices.—Of 55 birds whose tail feathers were counted repeatedly for more than a year, 46 (86 per cent) had 16 rectrices, 3 had 15, 3 had 17, 2 had 14, and 1 had 18. I examined a specimen apart from this group that had 19 rectrices.

Soft parts.—DOWNY YOUNG: The maxilla is medium gray, the maxillary edges and mandible buffy yellow. The sharply pointed egg tooth, at the tip of the much larger almost circular, tawny-colored nail, is creamy white; it falls off during the first day. Dorsal and ventral parts of legs and feet, middle of webs, and proximal parts of nails are medium gray. Sides of the legs and toes, the web adjacent to toes, and distal parts of toenails are buffy yellow. The inner digit is yellower than others. The iris is dark brown.

JUVENILE MALE: The bill is gray with yellowish edges. Adult condition is gradually attained by first winter. Legs are grayish yellow; iris dark brown.

JUVENILE FEMALE: As in male. Bill may or may not have a few small brown spots.

ADULT MALE: Bill is slate gray, occasionally with orange or pale yellow sides. Legs and feet are grayish yellow (occasionally straw-yellow or dusky); iris dark brown.

ADULT FEMALE: Bill is dusky with dull orange or yellow sides prior to and during early stages of incubation, with or without a few small blackish brown spots. Bill spotting and brightness of orange or yellow increases slowly in late stages of incubation and rapidly after eggs hatch. Spotting is heaviest in late July through September, fading after October. Legs and feet are straw-yellow to orange-brown; webs dusky. Iris is dark brown.

FACTORS AFFECTING MOLT

Molt has been initiated experimentally in birds, primarily the fowl, by administering a number of different hormones and other substances (see Juhn and Barnes, 1931; Van der Meulen, 1939; Shaffner, 1955; Juhn and Harris, 1955, 1956, 1958; Harris and Shaffner, 1957; Kobayashi, 1958; Tanabe and Katsuragi, 1962; Juhn, 1963; and Voitkevich, 1966). Normal autumnal molt is inhibited by estrogen (Tanabe and Katsuragi, 1962). Feather aberrations occur with dosages of thyroxine (Juhn and Barnes,

1931) and of progesterone (Shaffner, 1955) far below those necessary to induce molt. As similar aberrations have not been observed in feathers grown under normal conditions, it is unlikely that thyroid surges, whether induced via progesterone (as proposed by Assenmacher, 1958, but discounted by Juhn, 1963) or not, can be the normal physiological trigger for molt in the fowl. Tanabe and Katsuragi (1962) concluded that activation of the thyroid could not be responsible for normal autumnal molt in hens, but that this molt was caused by decreased ovarian activity together with senile deterioration of the feather's follicular structure. More recently Juhn (1963) has proposed that "molt is an entirely autonomous process, the primary seat of the cyclical renewals being the feather papillae proper." As the susceptibility of a feather to molt-inducing substances varies with the age of the feather, Juhn's hypothesis appears sound. Further work should be done with prolactin = LTH, especially to determine if, as has been proposed (Juhn and Harris, 1958; van Tienhoven, 1961), the drake's circulatory level of this hormone rises in sympathetic response to the incubating hen. Determination of factors involved in testicular collapse may also shed light on the molt-control mechanisms of drakes (van Tienhoven, 1961).

Hochbaum (1955) is, in my opinion, only partially correct in stating that nonbreeding Mallard drakes molt about 3 weeks later than breeding drakes, because some of my nonbreeding male Gadwalls were among the very first birds to molt. Some Gadwall drakes that enter into courtship activities but do not breed do indeed molt very late. Such birds, primarily yearlings, retain enlarged testes later in the season than do breeding birds. Among another group of nonbreeding birds that never become involved in courtship, and that may include members of either sex, are birds that are the very first to molt. The gonads of these birds never enlarge, which leads me to believe that some factor(s) intimately associated with gonadal development and breeding may inhibit the autonomous molt-controlling mechanism discussed by Juhn (1963). A similar situation apparently is present in the fowl where factors (progesterone, desoxycorticosterone acetate = DCA, pregnant mares' serum = PMS, follicle stimulating hormone = FSH, and luteinizing hormone = LH) that inhibit laying are known to induce molt (Juhn and Harris, 1956).

Drake Gadwalls in the wild usually begin to molt their remiges sometime in July and hens in mid-August. In 1964 several of my captive Gadwalls did not molt their flight feathers as early in the season as expected. I cannot explain this postponement, but I suspect that it was related to my pruning the vegetation in July, which not only destroyed vital cover but may have caused a psychological disturbance. The wariness of ducks increases greatly following the breeding season. Lack of high protein food

or of an adequate water supply is known to inhibit molt of remiges (Hochbaum, 1955), but my Gadwalls had all the food and water they needed.

Eight captive Gadwalls that had not started to molt by 19 August I killed between 19 August and 9 September (two males and a female 19 August, two females 31 August, two females and one drake 9 September). Papillae of the primary feathers from these adult birds were sectioned by R. E. Phillips, who writes me (pers. comm.) that the presence of any pigment at all in these sections probably means that some new follicular growth has occurred, as "feathers showing no signs of cellular proliferation showed no pigment." In all eight birds the primary papillae had undergone some new cellular activity, but in six the pigment collar was less than 1 mm long. In these six birds new primary follicles seemingly began to form, but growth was arrested at a very early stage. One of the remaining two birds "showed 1–2 mm of pigment and the beginning of barb development in the follicle" (Phillips, pers. comm.). The other individual had 5 mm of pigmented cells in each primary follicle and the barbs were well formed. This was the most advanced growth stage. In both the more advanced birds new primaries apparently were forming actively.

The molt of body feathers and rectrices was not delayed abnormally in any of these eight birds. Two of them had tertials about 2.5 cm long when collected. As tertials are usually molted several days before remiges, it was not surprising to find that in one of the two specimens the pigment collar of the incoming primaries was over 5 mm long. In the other bird it was less than 1 mm long.

Factors Affecting Pigmentation

Partially grown Basic feathers are most often found on drake Gadwalls taken from 1 June to 31 July (exceptionally 5 May to 9 August). According to Caridroit (1938) the pattern of the Basic feather in the Mallard is brought about by the presence of estrogen. The same control mechanism almost certainly exists in the Gadwall. Estrogen is produced in the testes presumably in sufficient quantity to alter pigment patterns only during the height of testicular activity.

In the Blue-winged Teal I found that about 2 weeks are required for ingrowing breast, cheek, and flank feathers to reappear externally after plucking, and about 3½ weeks for them to become full-grown. Melanin granules are deposited soon after feather cells are formed. In feathers that require 3½ weeks to mature, granules are deposited during about the first 2 weeks of development. The extreme dates of pigment deposition for a particular molt can thus be approximated by subtracting 2 weeks from the first date and 1½ weeks from the last date on which incompletely grown feathers are observed.

Applying this method to the Prebasic molt of the Gadwall, extreme dates of pigment deposition for the Basic plumage can be approximated as 15 May and 20 July. Certainly the peak of testicular activity falls between these dates. Although the testes (both germinal and interstitial cells) have usually regressed by 1 July, the system may still contain sufficient estrogen to bring about the pattern of the Basic feather. It is possible that estrogens as well as progestins are produced by the collapsing testes. It is also possible that at the time of testicular collapse, estrogen has already activated the genes responsible for the production of pigment-producing enzymes. Levels of circulating estrogen must now be determined for drakes early in July.

During a brief period in late August no molt is in progress other than that of wing feathers. At this time the testes are minimal in size and they remain so during winter and early spring. In the Gadwall feathers grown from 18 August to 5 May or later are Alternate. Such feathers are produced during testicular eclipse. The fact that the drake's brightest plumage is produced during testicular eclipse and that his eclipse plumage is produced at the peak of testicular activity, is in itself sufficiently confusing to warrant elimination of the word "eclipse" from plumage terminology.

The slight differences evident in the hen's two plumages might also be brought about by hormonal fluctuations, but this has not been demonstrated experimentally. Similarly, no satisfactory physiological explanation has yet been offered for the differences in feather patterns apparent in the various plumages young birds wear during their first few months of life.

On 5 June 1963 I plucked Alternate cheek, breast, and flank feathers from seven adult Blue-winged Teal drakes that were housed in a pen without females. All feathers that replaced the plucked ones were Basic in pattern. None of these birds began normal molting before 1 July, and one bird showed no signs of self-induced molt until 15 July. In other words these birds were physiologically ready to produce Basic feathers (presumably their testes were enlarged and active) 25–40 days before the Prebasic molt actually started. This suggests that the mechanisms controlling feather pigmentation and those controlling the onset of molt are not the same, and further, that these mechanisms are not normally synchronous. Partially grown Basic feathers were present in the teal as late as 19 August. Most feathers plucked 12 May were renewed in Alternate pattern though a few feathers plucked as early as 28 April were renewed in Basic pattern. All feathers plucked 19 May were renewed in Basic pattern. The period of Basic plumage pigment deposition in the Blue-winged Teal is approximately 19 May to 8 August. Obviously the peak of testicular activity

normally falls within these dates. Alternate feathers were first seen 2 September. All growing feathers from 2 September to 17 April were Alternate, as were nearly all feathers growing from 17 April to 19 May.

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SUMMARY

Gadwall embryological development parallels that of the domestic Mallard for the first 18 days. Papillae appear at 9 days and some pigment is visible by 10 days. At 13 days embryos are covered with papillae and filaments, and tarsal scales are visible. Ducklings emerge after 24 days. At hatching Gadwalls are mostly cream-buff below and sepia above. The yellowish tinge is probably due to carotenoids. Fading most likely is the result of carotenoid auto-oxidation catalyzed by heat and light. Feather wear also alters down color.

Follicles destined to produce Juvenal feathers are evident beneath the skin at 4 days. Juvenal down pushes through the skin at 7 days, Juvenal rectrices at 8 days. Side feathers also appear early. All wing feathers are among the last to grow. Most birds fly at 50 to 56 days of age. Late-hatched Gadwalls fly at a younger age than do early-hatched birds. Juvenal plumage is characterized by square-tipped rectrices, narrow body feathers, and dull wing color. Venters of both sexes usually have brown markings.

Feathers of the Basic I plumage, present principally on the breast and sides, are found from mid-August through December. They first appear just before the Juvenal plumage is completed, and are soon replaced. They may be told from Juvenal feathers by their broadness.

A few follicles destined to produce Alternate I down are active beneath the skin by 35–46 days of age. A few follicles of Alternate I pennae are

growing by 63 days. By 72 days, ventral Alternate pennae and down are evident exteriorly. Head and neck pennae, rectrices, and tertials of the Basic I plumage are the last to drop out. Alternate I tail feathers grow in males from mid-September to early February, in females from late October to mid-January. Males renew their tertials from late November to early February, females from 1 February to 4 June. Juvenal back and upper rump feathers are almost always retained; others often are. Retained Juvenal feathers, together with Juvenal wing feathers (except tertials), are worn simultaneously with the Basic I and Alternate I plumages. Male Alternate plumage is characterized by sharply contrasting patterns of dark gray and white. Venters are usually immaculate. In the female dorsal feathers are dark brown narrowly edged with buff, the throat and chin are dark, and the venter is nearly always immaculate.

The Prebasic II molt of drakes usually begins in late May or early June. Breast and side feathers molt first. Lower back and rump feathers are among the last to molt and some may be retained. Tail feathers are usually molted from mid-July to late August, tertials from early July to late August. The rest of the wing generally is molted a few days after the tertials. The Prebasic II molt of hens (body and tail) occurs from January to May but is heaviest in March and April. Dusky venter down appears in late April and May after pennae are grown. Wing feathers are retained until the young are about 6 weeks old. The male's dull brown Basic II plumage is similar to the Juvenal plumage but the breast has larger dark spots. About half the birds have dark venter markings. Females in Basic II plumage are similar to those in Alternate II except that the chin and throat are buffier and the body feathers are broadly edged with buff. Females in Basic II plumage also are broadly edged with buff.

The sensitivity of feathers to molt-inducing substances varies with the age of the feathers. Probably normal molt is an autonomous process controlled within the feather papillae and some factor(s) associated with gonadal development inhibit(s) this process. Feather development can be arrested during the early phases of follicular growth by abnormal environmental conditions. The dull pattern of the male's Basic plumage is probably induced by estrogens produced by the testes. In drake Gadwalls Basic feathers have been found growing from 15 May to 20 July. Pigment deposition during the rest of the year produces an Alternate pattern.

LITERATURE CITED

ASSENMACHER, I. 1958. La mue des oiseaux et son determinisme endocrinien. Alauda, **26**: 241–289.

CARIDROIT, F. 1938. Recherches expérimentales sur les rapports entre testicules, plumage d'eclipse et mues chez le Canard sauvage. Sta. Zool. Wimereux, **13**: 47–67.

DANE, C. D. 1965. The influence of age on the development and reproductive capability of the Blue-winged Teal (*Anas discors* Linnaeus). Unpublished Ph.D. dissertation, West Lafayette, Indiana, Purdue, Univ.

EWART, J. C. 1921. The nestling feathers of the Mallard, with observations on the composition, origin, and history of feathers. Proc. Zool. Soc. London, 1921: 609–642.

HAMBURGER, V., AND H. L. HAMILTON. 1951. A series of normal stages in the development of the chick embryo. J. Morphol., **88:** 49–92.

HARRIS, P. C., AND C. S. SHAFFNER. 1957. Effect of season and thyroidal activity on the molt response to progesterone in chickens and pigeons. Poultry Sci., **36:** 1186–1193.

HOCHBAUM, H. A. 1944. The Canvasback on a prairie marsh. Washington, D. C., Amer. Wildl. Inst.

HOCHBAUM, H. A. 1955. Travels and traditions of waterfowl. Minneapolis, Univ. Minnesota Press.

HOSKER, A. 1936. Studies on the epidermal structures of birds. Phil. Trans. Roy. Soc. London, **226:** 143–188.

HUMPHREY, P. S., AND K. C. PARKES. 1959. An approach to the study of molts and plumages. Auk, **76:** 1–31.

JUHN, M. 1963. An examination of some interpretations of molt with added data from progesterone and thyroxine. Wilson Bull., **75:** 191–197.

JUHN, M., AND B. O. BARNES. 1931. The feather germ as an indicator for thyroid preparations. Amer. J. Physiol., **98:** 463–466.

JUHN, M., AND P. C. HARRIS. 1955. Local effects on the feather papillae of thyroxine and of progesterone. Proc. Soc. Exp. Biol. Med., **90:** 202–204.

JUHN, M., AND P. C. HARRIS. 1956. Responses in molt and lay of fowl to progestins and gonadotrophins. Proc. Soc. Exp. Biol. Med., **92:** 709–711.

JUHN, M., AND P. C. HARRIS. 1958. Molt of capon feathering with prolactin. Proc. Soc. Exp. Biol. Med. **98:** 669–672.

KOBAYASHI, H. 1958. On the induction of molt in birds by 17-oxyprogesterone-7 caproate. Endocrinology, **63:** 420–430.

KOECKE, H. 1958. Normalstadien der Embryonalentwicklung bei der Hausente (*Anas boschas domestica*). Embryologia, **4:** 55–78.

KORTRIGHT, F. 1942. The ducks, geese, and swans of North America. Washington, D. C., Wildl. Mgmt. Inst.

LAMONT, A. 1921. On the development of the feathers of the duck during the incubation period. Trans. Roy. Soc. Edinburgh, **53:** 231–241.

MILLAIS, J. G. 1913. British diving ducks. 2 vols. London, Longman's Green.

ORING, L. W. 1966. Breeding biology and molts of the Gadwall, *Anas strepera* Linnaeus. Unpublished Ph.D. dissertation, Norman, Univ. of Oklahoma.

PHILLIPS, J. C. 1922–26. A natural history of the ducks. 4 vols. Boston, Houghton Mifflin Co.

PIRNIE, M. D. 1928. The plumage changes of certain waterfowl. Unpublished Ph.D. dissertation, Ithaca, New York, Cornell Univ.

PREMACHANDRA, B. N., G. W. PIPES, AND C. W. TURNER. 1959. Study of growth in New Hampshire chickens with varying thyroid status. Poultry Sci., **38:** 795–798.

SALOMONSEN, F. 1941. Mauser und Gefiederfolge der Eisente (*Clangula hyemalis* (L.)). J. f. Orn., **89:** 282–337.

SALOMONSEN, F. 1949. Some notes on the moult of the Long-tailed Duck. Avicult. Mag., **55:** 59–62.

SCHIØLER, E. L. 1925–26. Danmarks Fugle, med Henblik paa de i Grønland, paa Faerøerne og i Kongeriget Island forekommende Arter, 2 vols. Copenhagen, Nordisk Forlag.

SHAFFNER, C. S. 1955. Progesterone induced molt. Poultry Sci., **34:** 840–842.

SMART, G. 1965. Development and maturation of primary feathers of Redhead ducklings. J. Wildl. Mgmt., **29:** 533–536.

STAHL, P., G. W. PIPES, AND C. W. TURNER. 1961. Time required for low temperature to influence thyroxine secretion rate in fowls. Poultry Sci., **40:** 646–650.

STRESEMANN, V. 1948. Eclipse plumage and nuptial plumage in the Old Squaw, or Long-tailed Duck. Avicult. Mag., **54:** 188–194.

SUTTON, G. M. 1932. Notes on the molts and sequences of plumages in the Old-Squaw. Auk, **49:** 42–51.

TANABE, Y., AND T. KATSURAGI. 1962. Thyroxine secretion rates of molting and laying hens, and general discussion on the hormonal induction of molting in hens. Bull. Natl. Inst. Agr. Sci., Series G, **21:** 49–59.

TEST, F. H. 1940. Effects of natural abrasion and oxidation on the coloration of flickers. Condor, **42:** 76–80.

VAN DER MUELEN, J. B. 1939. Hormonal regulation of molt and ovulation. Proc. 7th World's Poultry Congr., p. 109.

VAN TIENHOVEN, A. 1961. Reproductive endocrinology of birds. *In* Sex and internal secretions, vol. 2 (W. C. Young, ed.). Baltimore, Williams and Wilkins Co.

VOITKEVICH, A. A. 1966. The feathers and plumage of birds [Transl. from Russian]. New York, October House.

WATSON, G. E. 1963. The mechanism of feather replacement during natural molt. Auk, **80:** 486–495.

WELLER, M. W. 1957. Growth, weights, and plumages of the Redhead (*Aythya americana*). Wilson Bull., **69:** 5–38.

WITHERBY, H. F., F. C. JOURDAIN, N. F. TICEHURST, AND B. W. TUCKER. 1939. The handbook of British birds, vol. 3. London, H. F. & G. Witherby, Ltd.

Department of Zoology, The University of Oklahoma, Norman, Oklahoma 73069. Present address, Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455.