THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

# BREEDING BIOLOGY AND MOLTS OF THE GADWALL, *Anas strepera* Linnaeus

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

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Norman, Oklahoma

1966

BREEDING BIOLOGY AND MOLTS OF THE GADWALL,

*Anas strepera* Linnaeus

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## ACKNOWLEDGEMENTS

I am especially indebted to George M. Sutton, University of Oklahoma, and to H. Albert Hochbaum and the entire staff of the Delta Waterfowl Research Station for invaluable assistance throughout the course of my study. Financial aid was provided by the Delta Waterfowl Research Station and the National Institutes of Health. William B. Lemmon graciously provided pens and feed for my ducks in Oklahoma. Richard E. Phillips was kind enough to section papillae of primary feathers and to read a portion of the manuscript critically. Were it not for the assistance of Dan Tucker, John Farrand, and my wife Kay, this study would never have been completed. I also wish to thank the following persons for advice during some portion of the study: Norman H. Boke, Charles W. Dane, Richard A. Goff, George J. Goodman, Ralph S. Palmer, Miles D. Pirnie, Carl D. Riggs, J. Teague Self, Ari van Tienhoven, and Milton W. Weller.

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# BREEDING BIOLOGY AND MOLTS OF THE GADWALL

## *Anas strepera* Linnaeus

## INTRODUCTION

The gadwall, originally the gaddel (Merrett, 1666, in The Oxford English Dictionary, 1961), and variously known as the gadwale, gadwell, or grey duck, is a well known breeding bird throughout the north temperate zone. Linnaeus (1758) based the scientific name *Anas strepera* (noisy duck) upon his own experience despite the fact that the species had been referred to repeatedly in the literature for nearly a hundred years prior to his description.

Though the gadwall has been the subject of numerous writings, certain phases of its life history have been neglected. The growth of juveniles and weight changes of both young and mature birds have gone unreported. Schiøler (1925) and Witherby *et al.* (1948) attempted to describe thoroughly the plumages of the species but these authors did not work with live birds nor did they have available skins of birds whose ages or breeding histories were known.

Little attempt has been made to correlate molts with other phenomena in the life cycle. Gadwall breeding biology has recently been described in detail (Gates, 1962) from Utah, but similar information is not available from elsewhere in the species' range.

Using the fine facilities of the Delta Waterfowl Research Station at Delta, Manitoba, I have been able to hatch, rear, and breed gadwalls in captivity. I have studied the molts of these birds and correlated molts with features of the breeding cycle; I have been able to compare molts and breeding biology of these captive birds with those of wild gadwalls; and I have described growth and weight change from embryonic life through two years of age.

## SUMMER BIOLOGY

The summer season began several weeks later in the Delta Marshes in 1964 than it did in Utah in 1961 (Gates, 1962). At Delta, in 1964, the first gadwalls appeared in mid-April and the peak arrival of residents did not develop until early May; in Utah, in 1961, the species arrived in early March and the peak arrival of residents developed in mid-April. At Delta most birds were paired on arrival, though yearling drakes were still trying to win mates; the peak arrival of residents was 23 days earlier than the average date of nest initiation -- i.e., laying of the first egg. In Utah, in 1961, 28 days elapsed between arrival and nest initiation -- 17 between arrival and territory establishment plus 11 between territory establishment and nest initiation (Gates, 1962).

### Nest Initiation

At Delta in 1963 and 1964 nests were begun about three weeks later than in Utah (Gates, 1962). Clutches were begun in nine wild nests in 1963 an average of two days earlier

than 21 wild nests in 1964. Captive nests in 1964 were begun about the same time as those in the wild that year (Table 1).

Table 1. Nest Initiation

| | 1963<br>9 Wild Nests | 1964<br>21 Wild Nests | 1964<br>9 Captive Nests |
|---|---|---|---|
| Average | 26 May | 29 May | 28 May |
| Extremes | 22 May - 1 June | 24 May - 6 June | 17 May - 4 June |

## Nest-sites

Nests were usually on well-drained ground such as a dike or slight rise in the marsh. Island and peninsula sites were above flood level. Twenty-nine of 33 (88%) wild nests at Delta were within 50 yards of water as compared to 94% of 156 nests observed by Gates (1962) in Utah. Twenty-one of 33 (64%) were within 10 feet of a conspicuous landmark such as the edge of a clump of reed (Phragmites communis) or cattail (Typha latifolia); 32 of 33 (97%) were within 60 feet of such a landmark.

Green vegetation was already 8-15 inches tall when egg laying started. At that time, live and dead vegetative matter were in approximately equal proportion within

18 inches of the centers of nests. By the time eggs hatched, green matter was 18-36 inches tall and it dominated the aspect of nest-sites. The most common green plants at nest-sites were nettle (Urtica gracilis), whitetop grass (Scolochloa festucacea), and Canada thistle (Cirsium arvense). Early nests were usually surrounded by nettle. Thistle and whitetop grass came up later. Other live plants around nests, in descending order of abundance, included goldenrod (Solidago spp.), Kentucky bluegrass (Poa pratensis), freshwater cordgrass (Spartina pectinata), mint (Mentha arvensis var. canadensis), awnless bromegrass (Bromus inermis), reed, sow-thistle (Sonchus uliginosus), and knotweed (Polygonum spp.). Whitetop grass was by far the most common dead plant near nests. Dead reed, thistle, goldenrod, nettle, and cordgrass were also common. Twenty-nine of 31 (93%) nests were shaded by a canopy of vegetative matter, mainly dead, 8-12 inches above them. In a few cases, hens made the canopy by bending or pulling plants over the nest.

In captivity, nests were as close as eight feet apart in a pen one-seventh acre in size as long as they were initiated 10-15 days apart. Such chronological spacing of nests allowed the aggression peak of one drake to subside before that of another developed. This may be of great

importance in dense island populations such as those observed by Hammond and Mann (1956) in North Dakota. In captivity a few nests were built in abnormal places such as a plywood nesting box and a reed basket but most nest sites were typical of those in the wild.

## Clutch Size

First clutches of the season were larger in the wild in 1963 than in 1964, and larger both years in the wild than in captivity in 1964 (Table 2). The difference between the sizes of initial clutches in the wild in 1963 and those in 1964 was significant at the 5% level according to an unpaired-T test. The difference between all initial clutches in the wild and those in captivity was significant at the 1% level as determined by the unpaired-T test. I believe the difference in wild clutch sizes was due to my having collected most of the hens in the study area in 1963. Most of my 1964 sample were therefore yearlings. Dane (1965) has shown that yearling blue-winged teal (Anas discors) lay smaller clutches than do older birds. The smallness of clutches in captivity may be a direct result of crowded conditions. The average clutch size of 92 gadwall nests which Gates (1962) considered initial was 11.1 -- a figure not significantly different from the combined average of my 26 nests.

Table 2. Clutch Size

| | Average | Range |
|---|---|---|
| Delta, 1963<br>8 Wild Nests | 11.75 | 8-14 |
| Delta, 1964<br>18 Wild Nests | 10.05 | 8-12 |
| Delta, 1963-64<br>26 Wild Nests | 10.57 | 8-14 |
| Utah, 1956-57<br>92 Wild Nests<br>(Gates, 1962) | 11.10 | ---- |
| Delta, 1963-64<br>4 Re-nests | 8.25 | 6- 9 |
| Utah, 1956-57<br>24 Re-nests<br>(Gates, 1962) | 7.80 | 5-10 |
| Delta, 1964<br>9 Captive Nests | 8.67 | 5-11 |

His assumption that all nests with 10 or more eggs were initial and that all with nine or fewer eggs were re-nests may have raised his average a little.

Of 43 nests found in the wild at Delta, four were re-nests and two others may have been. Gates (1962) found a significantly greater proportion of re-nests in Utah. This may be explained by the fact that the entire breeding cycle was three weeks earlier there and the birds therefore had more time in which to nest following predation or desertion. Dane (1965) and Gates (1962) have shown that second clutches are smaller than initial ones. The differences I have observed between initial and re-nest clutch sizes were, according to an unpaired-T test, significant at the 1% level. There is probably a relationship between the size of re-nest clutches and the stages at which the initial nests were abandoned or destroyed. This remains to be proved.

Limited data from captives suggest that eggs were normally laid between 0900 and 1100 hours. Hens sat on nests four to six hours each day of the laying period. The earliest a hen was known to leave a nest without being disturbed and after having laid an egg was 1115 hours. No hen spent the night on the nest during the laying period.

## Incubation Period

In 1964, incubation periods of eggs at the hatchery were compared to those of eggs incubated by hens -- both captive and wild (Table 3). Hatchery incubators were kept at 99° F. and 90-100% relative humidity. Variables pertinent to incubation period are discussed on pages 26 and 32. Incubation periods were shorter in the hatchery than they were out-of-doors. The difference, as determined by an unpaired-T test, was significant at the 1% level.

Table 3. Incubation Period

| | In Hatchery 50 Eggs in 6 Clutches | With Female 69 Eggs in 8 Clutches |
|---|---|---|
| Average | 24.00 | 25.75 |
| Range | 22-26 | 24-27 |

## Seasonal Variation in Gonad Size

Sowls (1955) collected six female pintails (Anas acuta) which were searching for nest-sites and found their largest ova to be 5-7 mm. in diameter. Phillips and van Tienhoven (1962) discussed the development of pintail ova only from the 6 mm. stage on (development past the time of yellow yolk's first appearance) since most ovaries contained many

ova smaller than 6 mm. but only a few ova larger than 6 mm. Both hen pintails (Phillips and van Tienhoven, 1962) and hen gadwalls collected prior to nest initiation had an average of six ova larger than 6 mm. in the ovary. These species lay an egg a day. About seven days are required for ova to develop from the 6 mm. stage to the 33-37 mm. stage at ovulation. Benoit (1950) estimated the period of total ovarian development to be 5-13 days in chickens (Gallus gallus), 14 days in pigeons (Columba livia), and 10-13 days in domestic ducks (Anas platyrhynchos). At ovulation, gadwall ova measured 33-37 X 31-33 mm. During the three days preceding ovulation, ova measured 21-28 X 15-27 mm.; 16-20 X 16-19 mm.; and 10-12 X 10-12 mm. Ova were more or less spherical except during the two days prior to ovulation when they assumed a more oblong shape.

Males arrived on the breeding grounds with somewhat enlarged testes. Three drakes collected while they were chasing unmated hens had testes averaging 26 X 10.3 mm. (left) and 18.3 X 8 mm. (right). Fourteen males attending hens had testes averaging 34.4 X 16.4 (left) and 27.2 X 13.5 mm. (right). In 16 of 17 drakes, the left testicle was larger than the right by an average of 6.6 X 2.4 mm. Two not-yet-flightless adult drakes collected from a post-breeding aggregation each had testes less than 8 mm. long.

The testes of 27 flightless adult drakes were all between 6 and 15 mm. long.

## Hatching, Predation, and Desertion

Of 30 wild nests containing eggs, 14 (46%) produced one or more chicks, 11 (37%) were depredated, and 5 (17%) were deserted. Gates (1962) reported 45% hatching success, 41% predation, and 14% desertion for 106 nests observed in Utah.

Six nests at Delta were apparently depredated by ground squirrels (*Citellus* spp.), four by raccoons (*Procyon lotor*), and one by a striped skunk (*Mephitis mephitis*). Many nests were on dikes, and these were especially subject to predation by ground squirrels since the squirrels used dikes as runways. Remains of eggs destroyed by squirrels were found at great distances from the nest; shells often had scratch marks. Skunks and raccoons destroyed total nests. Near four of five nests that were totally destroyed were raccoon tracks or droppings. Absolute determination of cause and rate of predation is virtually impossible, especially with a large sample. I recognize the possibility that my finding a nest and the departing hen's defecation may have caused a substantial increase in predation. It is significant that no instances of avian predation were recorded. Crows

(Corvus brachyrhynchos) have been exterminated from the Delta area and no gulls (Larus spp.) bred nearby. In Utah, California gulls (L. californicus) and striped skunks were the only important predators (Gates, 1962).

Two cases of desertion were apparently due to storms, two to human disturbance, and one to predation. A nest containing 11 eggs that I found 8 July 1964 had no eggs the following day. After clearing the area, I found five eggs containing live embryos in three widespread places, all about 10 feet from the nest. Another nest (9 eggs) located near a construction site was deserted the day I found it. Two nests were deserted in the midst of heavy rains. One held a full clutch, the other two eggs. A nest that contained five eggs when I found it, contained a broken egg when I visited it later.

I took the eggs from 3 of my 10 captive nests. Another was destroyed by a raccoon. Two of the remaining six were deserted, one on the night of a very severe storm eight days after the start of incubation, the other between the fourth and ninth day of incubation. The remaining four nests hatched a total of 27 young.

## Pair Bond Dissolution

In captivity, pair bonds were broken at various stages

of the breeding cycle (Table 4). One male left his mate just after she had laid her fifth egg to chase another female whose nest had just been robbed. All other males (7) whose mates incubated eggs, remained with them during some portion of the incubation period. One drake remained until the 23rd day of incubation -- the day before the eggs hatched. All of the males (9) deserted their mates between 12 and 22 June. In a pen where six pairs bred, one pair bond was dissolved on 13 June, four 15 June, and one 18 June. Two of the 15 June dissolutions represented nests from which I took the eggs 11 June, at which time the pair bonds were still intact. One of the two pairs just mentioned joined a postbreeding group together; the female of the second pair was won over by a male with whom she had not previously associated.

Gates (1962) observed similar variability in desertion times. He felt that although drakes usually left the hens early in the season, before the middle of incubation, some remained until hatching -- precisely what I observed in captivity. In my opinion, the sight of postbreeding groups may hasten the breaking of pair bonds. In early June, few such groups -- all small -- are extant. Later, large aggregations are common.

Table 4. Stages of Breeding Cycle and Dates at which Pair Bonds were Broken

| Stage | Date |
|---|---|
| *5 eggs laid on . . . . . | 15 June |
| 9 eggs laid when nest was robbed, bond broken four days later on . . . . . | 15 June |
| 2-8 days incubated on . . . . . | 12-18 June |
| *4 days incubated on . . . . . | 13 June |
| *4 days incubated when nest was robbed, bond broken seven days later on . . . . | 18 June |
| 8 days incubated when nest was deserted, bond broken one or two days later on . . . . . | 21-22 June |
| *13 days incubated on . . . . . | 15 June |
| 16 days incubated on . . . . . | 15 June |
| *18 days incubated when nest was robbed, bond broken four days later on . . . . . | 15 June |
| *23 days incubated on . . . . . | 15 June |

*One of six nests in one pen

I watched the dissolution of one pair bond closely. Early in the incubation period whenever the hen was flushed from her nest or left it for a break, she immediately joined her mate. He responded by frequent quacks and head bobs. By the 10th day of incubation the drake still accepted the hen and chased nearby males but he no longer quacked and his head bobs were infrequent. On the 15th day of incubation the hen, when flushed from the nest, joined her mate immediately, following him down the ditch. She was still aggressive toward foreign birds and chased them from the territory, but the drake ignored strangers and no longer paid attention to her. On the following day (16th day of incubation) I saw the pair together but the male was not in the least aggressive toward other birds and he exhibited no courting activity. By the 19th day of incubation the hen made no attempt to join her mate. The attraction between the two was permanently severed.

## Postbreeding Season

All captive drakes were still with their mates the first week in June. Harrying flights were frequent though most males were rapidly molting their body feathers. By 5 June, four of seven drakes in one pen had bred and all were obviously molting. A fifth, which later became the

last in the pen to breed, had molted considerably fewer feathers than the four mentioned above. The two remaining drakes in that pen were unsuccessful in their attempts to mate. They had no visible feathers of the basic plumage until 20-22 June.

By the end of June harrying flights had ceased; hens were deserted. Molting concentrations which had been increasing for several weeks were at maximum size. During most of July, wild and captive birds spent most of each day sitting along shorelines preening or sleeping. Most feeding was restricted to the early morning and late evening hours. Not until 23 July did I actually observe a flightless gadwall, but on that date 10-15% of the birds that I saw were flightless; many that I saw or collected had just dropped their remiges; and a drake that I collected was almost ready to fly again. By 23 July no adults in any of my breeding pens had dropped their remiges. In two large enclosures housing nonbreeding birds, 3 of 14 wing-clipped females (21%) and 8 of 10 (80%) wing-clipped drakes had dropped their remiges. In other words, 54% of a nonbreeding population had become flightless, a percentage substantially greater than my estimate of the flightless portion of the wild population. By 5 August, about 50% of the wild adult males were flightless but I saw no flightless females. On

that same day, 9 of 10 (90%) nonbreeding captive males and 6 of 14 (44%) nonbreeding captive females were flightless.

Yearling males are less likely to breed than older birds. In pens where all drakes were yearlings there was little breeding and very few pairs formed. Most two-year-old captive males, on the other hand, bred. Of 15 wild males shot while they accompanied their mates in June (14) and July (1), only three (20%) were yearlings. I have collected just three unpaired drakes in June; all were yearlings. Gates (1962) stated that the first gadwalls to arrive in Utah in spring were unmated yearling drakes. The drake mentioned above which had almost full grown wings 23 July 1964 may have been just such a yearling which never became involved in courtship. In my opinion, there are a few wild gadwalls, primarily yearling males, that never partake in courtship activities and these few birds are the first to form postbreeding groups and to molt their remiges.

A few completely nonbreeding birds or birds thwarted very early in their nuptial efforts are probably the first gadwalls to drop their flight feathers. These are followed by early breeding males, by later breeding drakes, by non-breeding drakes which were not thwarted in their sexual efforts until the season was well along, by early breeding hens, and finally by late breeding hens.

One of my captive breeding males became flightless during the third week in June due to badly worn feathers. When these feathers became wet, they absorbed water, and the drake was as incapable of flight as he would have been had he dropped his remiges. Several other males in the pen likewise had badly worn primaries and were able to rise from the water only at very gradual angles. I have, on three occasions, taken ducks in the wild showing this same condition. One, an adult female lesser scaup (Aythya affinis), was so obviously flightless on the water that I didn't realize she actually had a full complement of flight feathers until some time after I had shot her. Another hen scaup that I caught by hand was alert and in fine bright plumage but the flight feathers of her right wing were almost completely devoid of barbs. A flightless male gadwall that I collected had many broken flight feathers though none had fallen out. Various degrees of wear in primary feathers are shown in Fig. 8.

In my breeding pens only 2 of 21 drakes were flightless by 5 August and neither of these had bred. This may well have been due to the fact that I pruned the vegetation of these pens in late July -- at about the time the birds would normally have dropped their remiges. The disturbance and

lack of suitable cover for hiding may have been responsible for failure of the birds to molt at the normal time. Dense concealing vegetation is, I believe, as essential for the suitability of a molting area as are water and proper food. In the Delta Marshes, molting areas all contained dense stands of bulrush (Scirpus spp.) or cattail. Freedom of movement may also be essential. In the large pens where adequate vegetation was available and freedom of movement was guaranteed, birds molted normally. Hochbaum (1944) states that the suitability of a marsh as a haven for flightless dabbling ducks depends upon its providing food, cover, and isolation.

The activity schedule of captives in one pen was studied on 7 August when my assistant and I took turns watching continuously from a blind from 0430 (1-1/2 hours before sunrise) to 2230 hours (1-1/4 hours after sunset). A few days later we watched these same birds from 2100 to 0200 hours. Only 2 of 13 adults fed during the early morning hours. Starting at 0630 there was a half hour period of rapid, nervous swimming back and forth. Otherwise the flock preened and slept until 0815 hours. Feeding picked up markedly during the middle of the day and reached a peak in early evening. At dark, the nervous swimming recurred. The flock swam back and forth, crawled onto

land, re-entered the water, and occasionally flew to the opposite side of the pen only to swim rapidly back to the starting point. There was no evidence of feeding between 2300 and 0200 hours.

Perhaps the nervousness exhibited by these captives at dawn and dusk was indicative of "Zugunruhe" or migratory unrest. True, these captives still had old remiges but adults in the wild were testing new wings by mid-August. The wild flocks too were restless, moved about a great deal, and fed throughout the middle of the day.

During the remainder of August and in early September, gadwall flocks increased greatly in size. These flocks were wary, but they fed throughout the day if undisturbed. Their favorite feeding grounds were areas in which fruit-clusters of pondweed (Potamogeton spp.) were numerous. By mid-September gadwalls were leaving the Delta marshes; by the end of the month they were rare.

## Weight Variation

Although weights of gadwalls have been included in numerous writings, no one has attempted to correlate weight changes during the breeding season with the various phenomena which affect ducks nutritionally. In Illinois during the southbound migration adult males averaged 990 grams,

juvenile males 908 grams, adult females 849 grams, and juvenile females 808 grams (Bellrose and Hawkins, 1947). Leopold (1919, 1921) reported that gadwalls (sex and age classes combined) averaged about 850 grams during fall and winter in New Mexico and Texas. Kortright (1942) stated that drakes averaged 908 grams (extremes of 709-1135) and females 823 grams (596-1021) but he did not mention what season or seasons his data represented. Tables 5 and 6 categorize, according to stages of the breeding cycle, 82 wild gadwalls (47 males, 35 females) taken in southern Manitoba. Drakes gained weight rapidly after deserting their mates. Their weight then remained relatively constant until the final stages of wing-molt at which time they lost about 75 grams. Hens lost a great deal of weight during the incubation period but regained weight rapidly while rearing their broods. Females probably lose a good deal of weight while growing new wing feathers but the loss could not be determined from my data. Table 7 presents weight averages for both sexes for the summer months. These averages reflect the normal activities of gadwalls during these months (see Tables 5 and 6 for correlation of weight with activities).

Table 5. Weights of Male Gadwalls at Various Stages of Breeding Cycle

| Stage of Annual Cycle | Sample Size | Extremes (in grams) | Average (in grams) |
|---|---|---|---|
| Paired, 2+ yrs. old | 2 | 866-1039 | 952.5 |
| Unpaired, yearlings | 2 | 744- 771 | 757.5 |
| With laying or incubating females | 12 | 688- 908 | 822.1 |
| In postbreeding flock before wing molt | 2 | 930- 965 | 948.5 |
| In midst of dropping remiges | 2 | 874-1038 | 956 |
| With 9th primary 1-50 mm. | 9 | 869-1006 | 914.4 |
| With 9th primary 51-100 mm. | 8 | 840-1004 | 912.4 |
| With 9th primary 101-122 mm. | 10 | 753- 935 | 839.3 |

Table 6. Weights of Female Gadwalls at Various Stages of Breeding Cycle

| Stage of Annual Cycle | Sample Size | Extremes (in grams) | Average (in grams) |
|---|---|---|---|
| Not yet laying (ova less than 38 mm.) | 4 | 751- 962 | 842.75 |
| Laying -- full sized egg in duct | 3 | 852-1031 | 929.3 |
| With eggs incubated 1-12 days | 8 | 625- 757 | 682.5 |
| With eggs incubated 13+ days | 5 | 574- 685 | 631.2 |
| With brood 7 days old or less | 5 | 655- 786 | 695.6 |
| With brood 8-14 days old | 4 | 730- 803 | 759.5 |
| With brood 15+ days old | 4 | 695- 789 | 738.75 |
| Flightless; brood deserted | 2 | | |
| with 9th primary 33 mm. long | 1 | | 796 |
| with 9th primary 91 mm. long | 1 | | Unknown |

Table 7. Weights of Gadwalls during Summer Months

| Sex | Month | Sample Size | Extremes (in grams) | Average (in grams) |
|---|---|---|---|---|
| ♂ | May | 4 | 744-1039 | 855 |
| ♂ | June | 11 | 674- 908 | 821 |
| ♂ | July | 17 | 831-1038 | 937 |
| ♂ | August | 15 | 753- 931 | 849 |
| ♀ | May | 1 | | 962 |
| ♀ | June | 14 | 603-1031 | 765 |
| ♀ | July | 18 | 574- 803 | 698 |
| ♀ | August | 4 | 658- 796 | 731 |

## GROWTH, MOLTS, AND PLUMAGES OF THE GADWALL

The following discussion is based upon analysis of 42 embryos and 283 skins as well as upon repeated examination of about 250 additional live birds. Eggs from incomplete clutches were considered "fresh." Such eggs were placed in incubators immediately after being collected; heat in the incubators was usually maintained at 99.5° F. but was raised to 101° F. when eggs were hatching. Relative humidity, though variable, was always kept high. Two embryos were preserved in 10% 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. This method enabled me to examine papillae as well as feathers. Of the total, 185 specimens were captives of known age and 98 were wild adults. Captive specimens dated 1 October 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 8 contains 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 included in Table 9. The exponential growth curves of embryos in Fig. 1 and of juveniles in Fig. 2 are similar to those described by Weller (1957) for the redhead (Aythya americana). Rapid weight-gain ceased by seven or eight weeks. Both males and females had fully developed tarsi and culmens by about five weeks. Growth during the first six weeks is illustrated in Fig. 3. The molts and plumages of a modal male and female are diagramed in Fig. 9.

## Prenatal Development of Feathers

Descriptions of prenatal feather development in ducks have been limited previously to domestic strains of the mallard (Lamont, 1921; Hosker, 1936; Koecke, 1958). Since the incubation period of these strains averaged 28 days, as compared to 24 days for the gadwall, a chronological description of feather development in the embryonic gadwall is needed.

Though all gadwall eggs were "fresh" when put into incubators, rate of development varied. This may have been due to variation of conditions in the incubators; to

Table 8. Growth of Embryos

| Days Incubated | Length mm. | Culmen mm. | Tarsus mm. | Weight gm. |
|---|---|---|---|---|
| 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 |

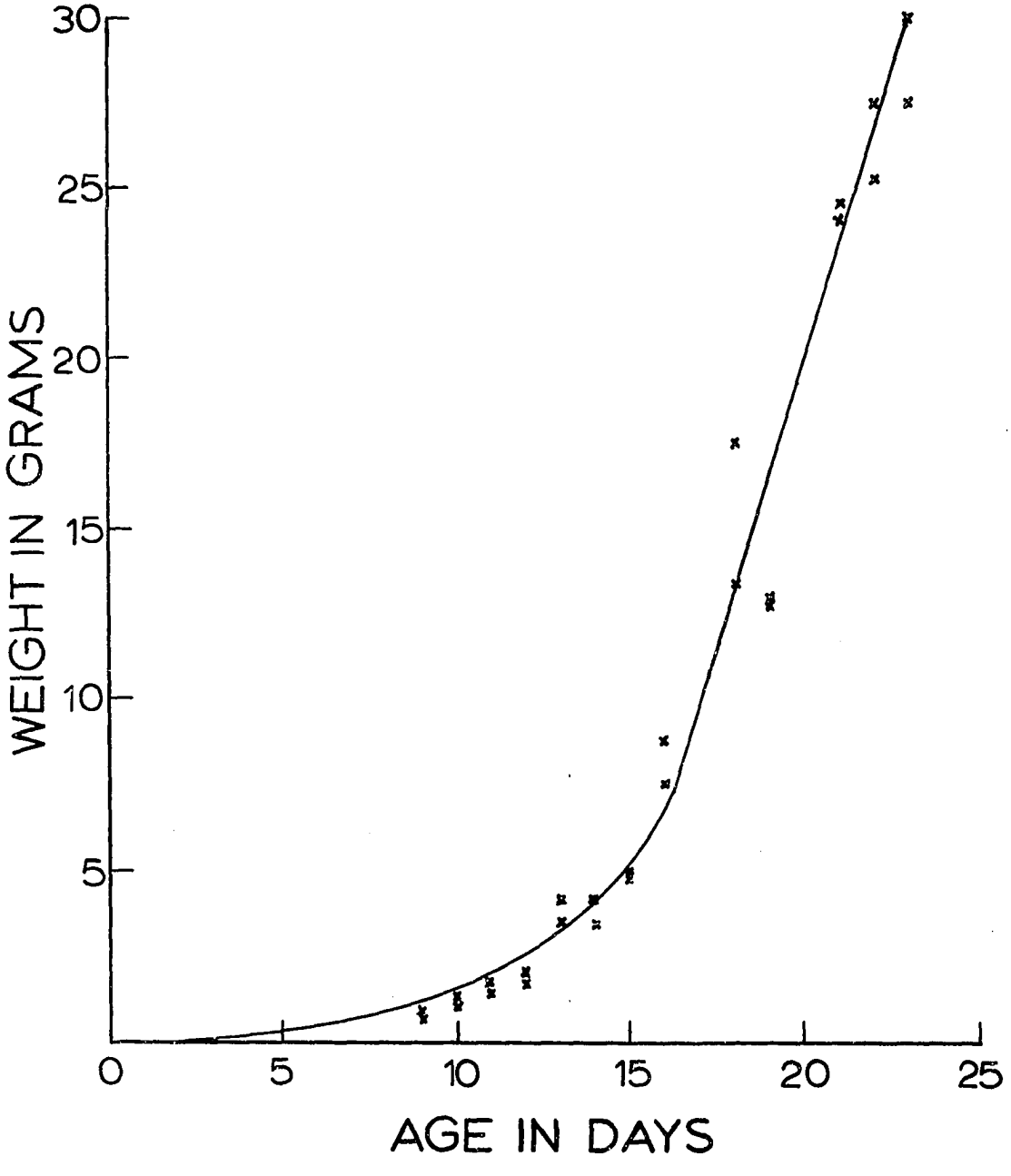


Figure 1. Weights of Embryonic Gadwalls.

Table 9. Growth of Juveniles

| Age | Weight gm. ♂ | Weight gm. ♀ | Culmen mm. ♂ | Culmen mm. ♀ | Tarsus mm. ♂ | Tarsus mm. ♀ |
|---|---|---|---|---|---|---|
| 1 Day | 28 | 29 | 13.5, 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 | 39.5 |
| 7 Weeks | 661 | 565 | 40.5 | 39 | 39.5 | 38 |
| 8 Weeks | 577, 677 | 671, 635 | 47 | 40 | 41 | 40 |

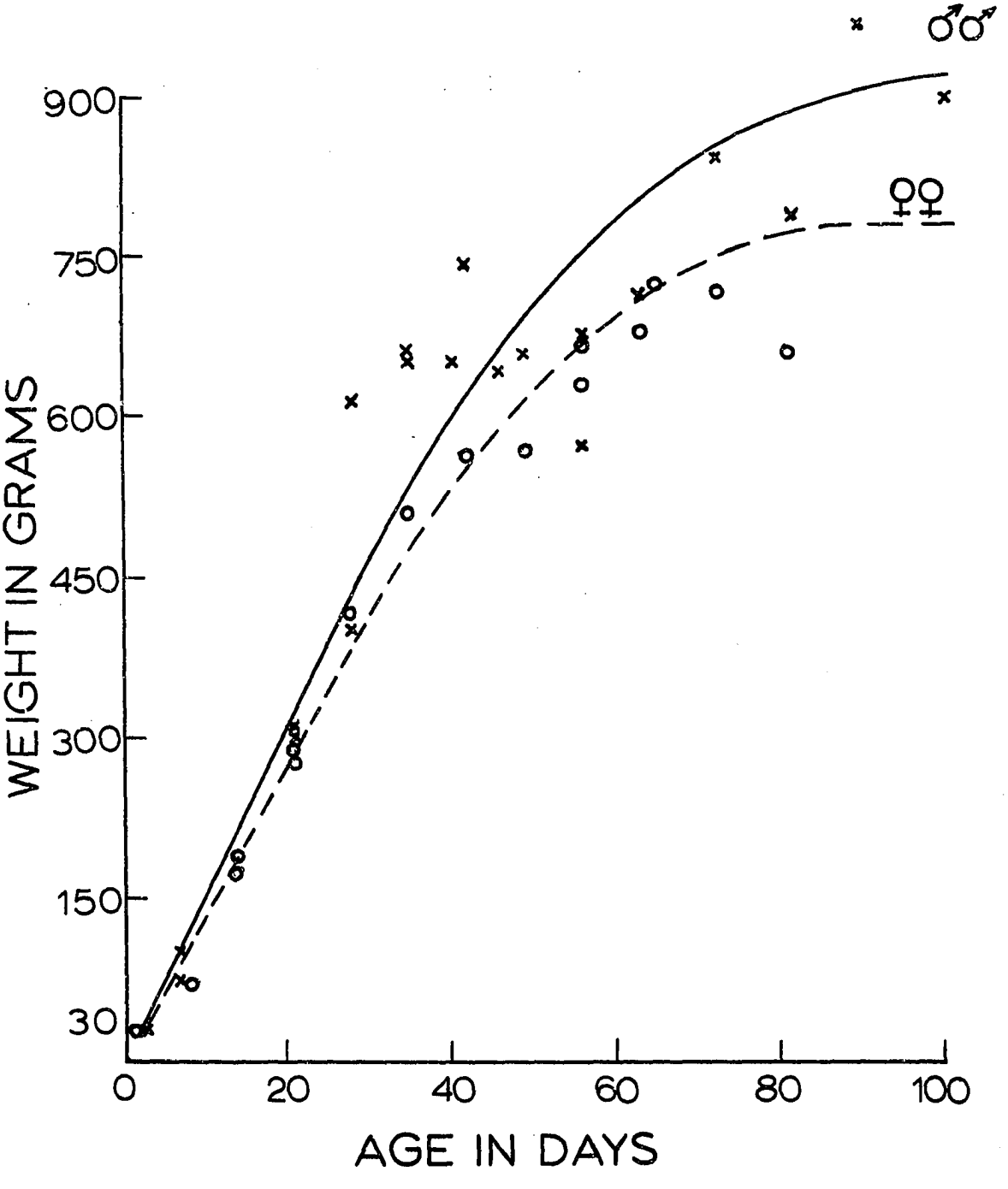


Figure 2. Weights of Juvenile Gadwalls.

Figure 3. Gadwalls 1 Day and 1 - 6 Weeks Old.

Figure 4. Venters of Juvenile Gadwalls (birds pictured are females though similar variation occurs in males).

variation in factors inherent in the eggs; to differences in length of time the eggs were retained in the uterus; to differences 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 gadwalls (24.0 day average). However, Khaki Campbell and Indian Runner domestic mallards have an incubation period of 28 days (Koecke, 1958; Lamont, 1921). Gadwalls as well as wild and domestic mallards have nearly parallel embryological development for at least the first 18 days of incubation. These first 18 days in the domestic mallard apparently represent a recapitulation of ancestral developmental stages. The increased time beyond 18 days required for completion of embryological development is seemingly an adaptation to recently derived conditions of increased body weight (Khaki Campbell variety) and upright posture (Indian Runner variety).

When two embryos of the same age differ considerably in size, I refer to them as the "smaller" and "larger." At the beginning of my descriptions for days 5-18 (see below), I list the comparable stage or stages for the domestic duck (Koecke, 1958) and the chick (Hamburger and Hamilton, 1951).

Beyond 18 days such comparisons probably are meaningless. Descriptions below deal primarily with the gadwall. All references to Koecke (1958) pertain to the "domestic duck" since he lumped all data from the Khaki Campbell and Indian Runner varieties. References to Lamont (1921) pertain only 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.

5 days: 5-day domestic duck; stages 22-23 chick.

6 days: 6-day domestic duck; stage 25 chick.

7 days: 6- to 7-day domestic duck; stage 27 chick.

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

9 days: 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 as 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 the spinal and femoral tracts and on the sides of the tail, where they formed a double ridge (Lamont, 1921). In Khaki Campbell embryos the first indications of natal down appeared on the spinal and femoral tracts but the sites of "feather embryos" were visible microscopically at 8 days (Hosker, 1936).

10 days: 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 half way 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].

11 days: 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; pigment was not visible.

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

13 days: 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 1/3 of cornea, as reported for duck at 12 days (Koecke, 1958). Both upper and lower eyelids covered with 2 to 3 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.

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

15 days: 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 it does 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.

16 days: 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 1/4 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.

17 days: No sample available.

18 days: 18-day domestic duck; stages 39-40 chick. Tarsal scales overlapping for more than 1/3 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.

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

20 days: No sample available.

21 days: 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.

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

23 days: 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.

24 days: 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. In addition, they are more than twice as thick as any other natal feathers.

## Natal Plumage

The prepennae of anatids are protoptiles rather than mesoptiles, as made clear by Ewart (1921). They correspond to the first of the two down coats in penguins (Spheniscidae). In the gadwall I have found well developed mesoptiles 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. In the mallard Ewart (1921) found mesoptiles on the secondaries and greater upper secondary coverts, here and there among the body plumage, and also on the outer pair of rectrices. The irregular arrangement and variable size of mesoptiles indicates that they have been, or are being, suppressed in the Anatidae.

According to Witherby et al. (1948) gadwalls at hatching are sepia or brownish black on the crown, nape, mantle, back, rump, uropygial tufts, the patch on the side of the body, and the back of the thigh; the "long filaments tinged cinnamon-buff..., most pronounced in region of upper mantle; cream-buff eye-stripe extending well onto sides of crown; light patches [two pairs] on upper-parts cream-buff..., cheeks, sides of neck, chin, throat and fore-neck cream-buff..., paler on breast and belly." Posterior margin of wings cinnamon-buff. The sharply pointed egg tooth, which falls off during the first day, is creamy white. It is located at the tip of the much larger and almost circular nail. The nail is tawny, the maxilla medium gray, the maxillary edge and mandible buffy yellow, and the iris dark brown. Dorsal and ventral parts of the legs and feet, the middle of the webs, and the proximal parts of the nails are medium gray. The sides of the legs and toes, the web adjacent to the toes, and the distal parts of the nails are buffy yellow. The inner digit is yellower than the others.

The faint 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 eight or nine days. Nowhere among anatids is it more

evident than in bright yellow downy young such as those of the redhead.

To date no one has extracted and analytically identified pigments from gadwall natal down. The granular nature of the dark filaments is, however, 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 which have been out-of-doors appear more faded than birds of similar age which have lived in the hatchery. Under the microscope, down from one- and two-day-old faded skins appears structurally identical to that from unfaded skins. In view of the fact that this fading occurs among birds which have not been exposed to water and which have no visible feather wear, carotenoid auto-oxidation catalized by heat and light seems to be the most plausable 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 which 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 stage are truly gray. The grayness does not change noticeably until juvenal pennae are evident during the third week.

## Prejuvenal Molt

By four days of age, follicles of both down and pennae are active in most feather tracts. Since 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 sixth day. At seven days juvenal down pushes through the skin along the sides and in the posterior part of the back. By eight days the natal rectrices have pushed out a few millimeters. By nine days prepennae of the side feathers have also pushed out. The pushing out of natal rectrices by incoming juvenal quills has long been known (Kortright, 1942), but only recently has the normal mechanism of feather ecdysis as a pushing out of the old by the new been recognized (Watson, 1963).

Despite its precocial beginning, the juvenal plumage is not readily noticeable until the duckling is about two weeks

old. Now, a parting of the prepennae reveals a mass of incoming down and pennae. Ensheathed tertials are first visible at about 17 days. At three weeks some birds are completely covered below with pennae, while others continue to look down-covered. In every bird under observation at this stage pennae were obviously growing over the whole body and remiges were plainly visible. At 3-1/2 weeks greater coverts and axillars become visible. By four weeks every one of my captive birds was well covered with juvenal plumage, the principal wing feathers were all visible, mesoptiles were well developed on the secondaries and upper greater secondary coverts, and the oil gland tufts were full grown. Lesser and median under wing coverts become apparent by 4-1/2 weeks. During the fifth week many body feathers and rectrices clear and there is a sudden surge of wing-growth. By six weeks, juvenal rectrices, scapulars, and side feathers are completely grown and down of the first alternate plumage is apparent along the mid-ventral line. Most of my captive birds first flew at between 50 and 56 days. 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 first alternate 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 first alternate down is pushing through the skin for the first time. Captive birds older than 10 weeks all had a considerable number of first alternate feathers. Rectrices, scapulars, and flank feathers are fully grown by six weeks, secondaries by seven weeks, primaries and tertials by seven or eight weeks.

I repeatedly handled 50 juvenile gadwalls (26 ♂♂, 24 ♀♀) 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 (see Weller, 1957, for a detailed description of the primary-clearing phenomenon). 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 puddle ducks. No 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 there was no apparent difference between males and females. My data agree closely with those of

Hochbaum (1944), who ascertained that hatchery-reared gadwalls first fly at between 49 and 63 days.

Table 10. 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 |

I have no comparable data for wild birds. I did, however, keep track of a brood of four hatched 16 June 1964 in a large pen containing lush vegetation and marsh water. The brood fed almost exclusively upon natural food. All four birds were observed flying on 3 August -- 48 days after hatching (data not included in Table 10). One male and one female were caught that day and both had four partially clear primaries. Several other birds reared in a large flight pen were observed to fly at 46 days (data not

included in Table 10). Ten drake mallards that 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. It appears then that gadwalls first fly at an age somewhat intermediate between the first flying age of their two closest relatives. For a résumé of the times at which 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. Members of the other group hatched between 10 and 13 July. The groups were kept in separate brooders in the hatchery and were fed at first only turkey "prestarter." After two weeks they were fed a mixture of wheat, barley, and "prestarter." At 51 days, 7 of 19 early-hatched birds and 12 of 19 late-hatched birds flew. By 56 days, the early birds averaged five clear primaries, the late 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. In other words, the birds which hatched 16-19 days later, matured to flying 2.58 days more quickly than did early-hatched birds. Using an unpaired-T test, this

difference is significant at the .5% level. Smart (1965) and Dane (1965) observed a similarly different rate of maturation among redheads. Smart (1965) attributed the discrepancy to the fact that warm temperatures tend to decrease thyroxine output and therefore to slow feather growth. Stahl et al. (1961) have shown that decreased tempertures increase thyroxine output and Premachandra et al. (1959) have shown 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 in early- and late-hatched blue-winged teal.

## Juvenal Plumage

MALE: Crown brownish black, each feather edged with dark brown. Nape brownish black, each feather edged with buff. Mantle feathers and scapulars dark brown (occasionally tinged with olive), edged with buff and sometimes marked with broad straight or V-shaped bars. Back and upper rump feathers black, edged with brownish black. Lower rump feathers and upper tail coverts dark brown (sometimes tinged with olive), edged and marked with buff. Indistinct brown streak from base of maxilla through eye to nape. Cheeks, sides of head, chin, throat, and foreneck light

buff, narrowly streaked with dusky brown, the streaking least heavy on the throat. Upper breast sepia, each feather tipped with buff and irregularly marked with buff, cream, or white (see Fig. 5). Rest of breast and belly white to buff, feathers usually spotted or streaked or both -- the maculation, which is always lightest on the belly, sometimes approaching the double-spotting found in some juvenile females (Fig. 4). Sides (see Fig. 6) and flanks sepia, feathers edged and sometimes marked with buff. Under tail coverts sepia, each edged and marked with white to buff. Femoral feathers dusky brown, edged with buff. Oil gland tufts brownish black. Rectrices (each notched at tip where natal down was attached) sepia, usually edged with buff. Primaries mouse-gray, paler on inner webs and shading to white at base. Distal secondaries dark mouse-gray tipped with white, the more proximal ones tipped with white and with black outer webs, the innermost with white to pearl-gray outer webs. Tertials mouse-gray, usually tipped with buff. Greater primary coverts mouse-gray, the inner three sometimes with much white on outer webs. Alula and median coverts mouse-gray, the latter lightly marked with buff. Lesser primary coverts mouse-gray spotted and edged with buff and cream. Greater

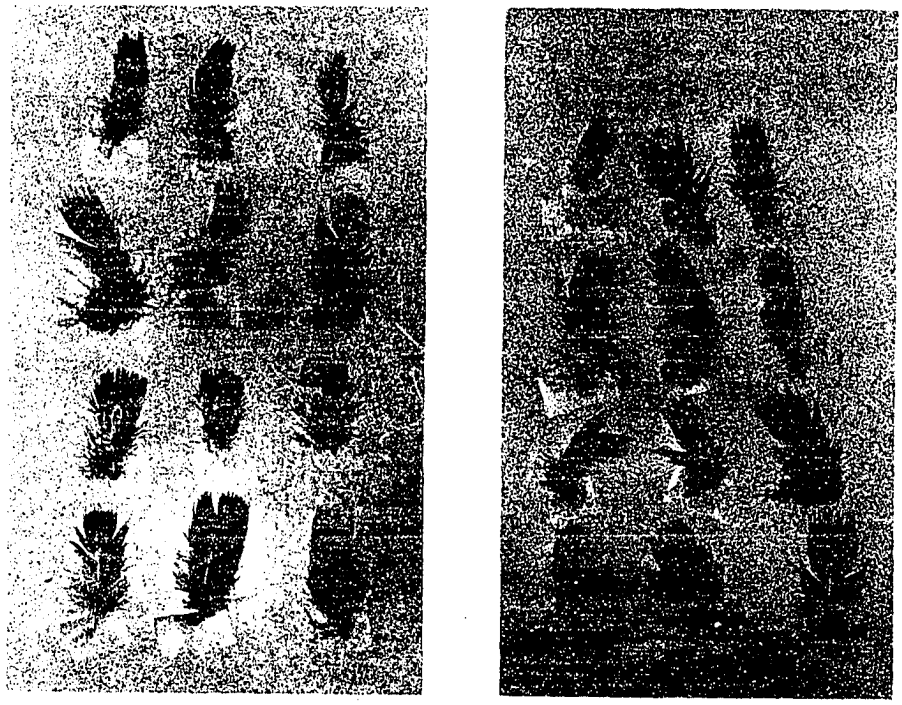

Figure 5. Breast Feathers of Male (left) and Female (right) Gadwalls (top to bottom: juvenal, first basic, first alternate, second basic).

Figure 6. Side Feathers of Male Gadwalls (left to right: juvenal, first basic, first alternate, second basic).

Figure 7. Median Upper Wing Coverts of Male Gadwalls (juvenal above, adult below).

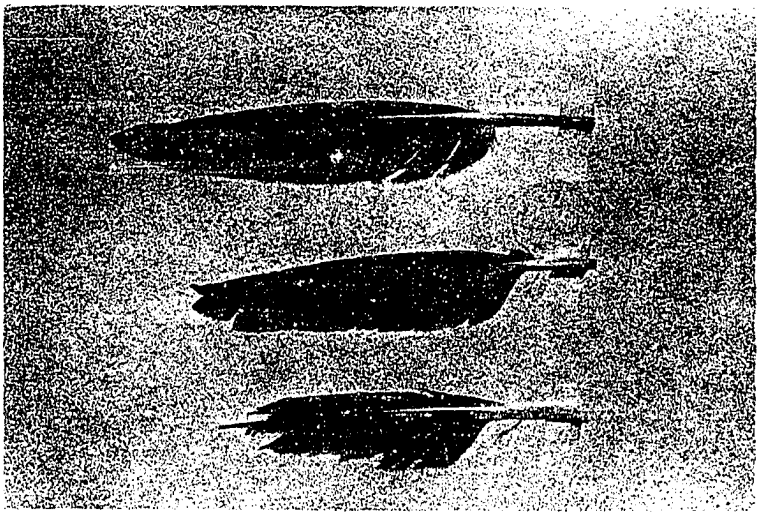

Figure 8. Seventh Primaries of Gadwalls in Summer Illustrating Variation in Feather Wear.

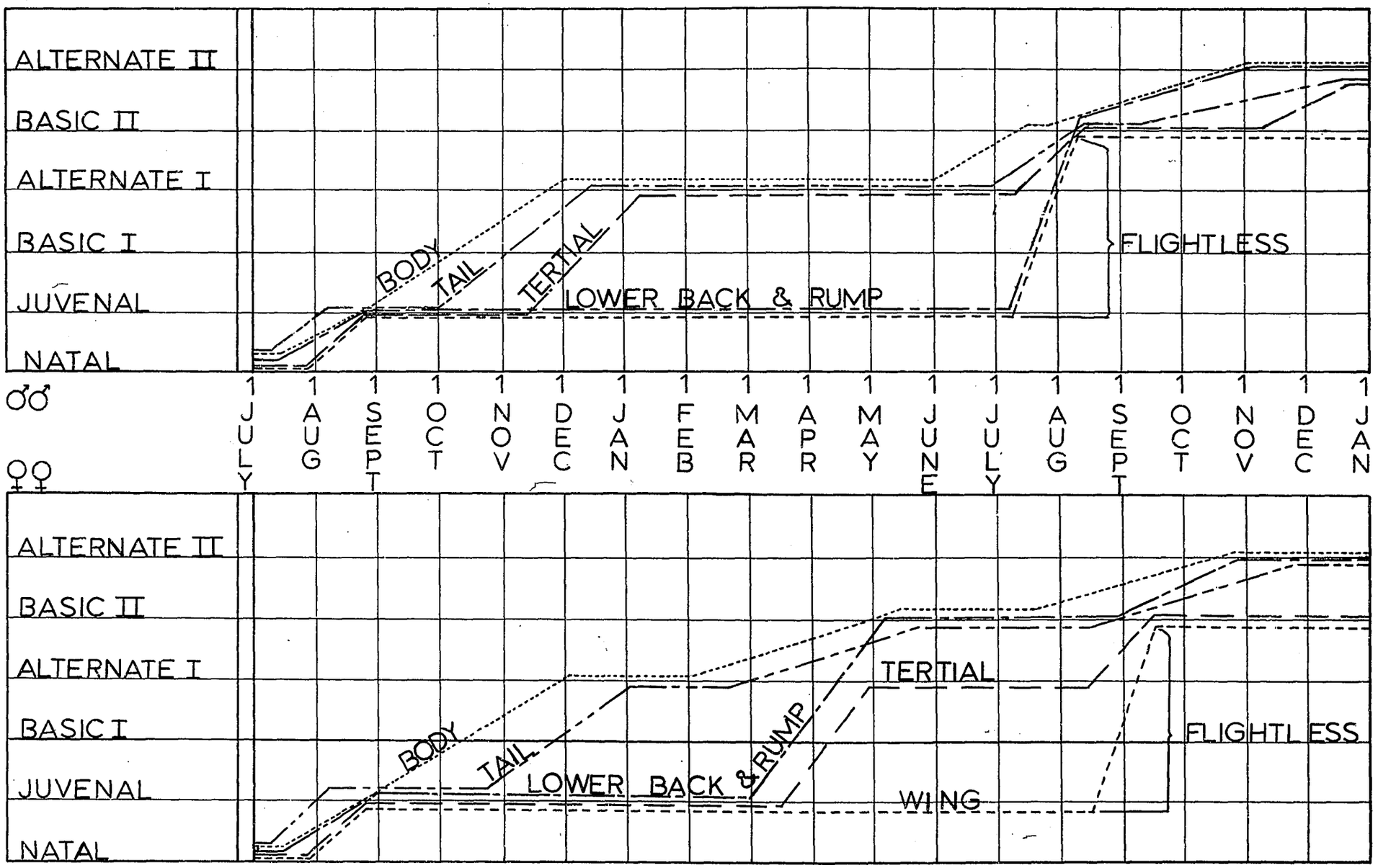


Figure 9. Sequence of Molts and Plumages in a Modal Male and Female Gadwall.

secondary coverts black, the outer ones mouse-gray, some tipped with chestnut and more or less bordered with black on the outer webs, the inner ones tipped with buff and mouse-gray on the inner webs. Lower series of median coverts mostly black or chestnut, tipped with black; upper series and distal lower series chestnut; proximal median coverts mouse-gray spotted and flecked or barred with cream, markings bolder than in adults (see Fig. 7). Lesser coverts mouse-gray edged and usually heavily barred with buff, markings nearly always bolder than in adults. Axillars white, rarely flecked with light gray. Greater under primary and secondary coverts white to pearl-gray. Median under coverts white. Lesser under coverts white variously marked with dusky brown. Distal 2/3 of down light gray grading through pale gray to white basally. Bill "pomeranian-yellow," legs "saffron-yellow" (Witherby et al., 1948). Iris brown.

FEMALE: Like male but mantle feathers and scapulars less barred as a rule; back and rump lighter -- dark sepia edged with buff; belly feathers sometimes double-spotted, rarely immaculate or nearly so (variation in venters illustrated in Fig. 4, breast feathers in Fig. 5). Tail frequently more extensively marked with buff. Wing duller -- less black, white, and chestnut. Outer webs of middle

secondaries with narrower black borders or wholly without black, inner secondaries white to light gray on outer webs. Greater coverts olive-brown tipped and edged with cream, middle ones more or less black on outer webs. Median coverts olive-brown edged with cream, most of them marked with a buff bar, those bordering the greater coverts being more or less black and without chestnut or with chestnut only on tips. Lesser coverts olive-brown fringed with buff. Down white to pearl-gray. Soft parts as in male -- bill may or may not have a few small black spots.

## First Prebasic Molt

Juvenal plumage is partially replaced during the first prebasic molt. Follicles of the first basic plumage can be seen beneath the skin on the chest and along the sides as early as 56 days of age. The molt is not readily detectable exteriorly, however, until 65-80 days. In some individuals this molt continues as late as early November. In both sexes, it occurs only on the chest and sides.

## First Basic Plumage

Schiøler (1925), reporting on anatine ducks, described a previously overlooked plumage which he termed the post-juvenal or first adult plumage. Because this plumage was

variable 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 available only a small number of skins and by not being able to view the inside of such skins as he did have. This perhaps explains why he did not find a partial plumage in hens comparable to the first adult plumage in drakes and why, therefore, he homologized the first adult (here first basic) plumage in the drake with the first alternate plumage of the hen. Such an oversight is understandable in view of the similarity of the hen's several plumages.

As part of the present study, I have prepared as flat skins 17 male and 18 female gadwalls between the ages of 56 and 132 days (25 August to 3 November). I have found no differences between the patterns of molt in males and females prior to assumption of the first alternate plumage. Because the existence of a first basic plumage is necessary if Humphrey and Parkes' (1959) hypothesis of plumage homologies is to be accepted for anatine ducks, I have paid special attention to plumages during the first few months of life. Not only have I found the first basic plumage to be present on the chest and sides 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 first alternate plumages.

MALE: Similar to definitive basic plumage but breast feathers are more complex (see Fig. 5). Each dark brown breast feather is edged with buff and crossed distally by a broad tan horizontal bar and proximally by one or more white markings. Tan bars sometimes curve toward base of feathers laterally, thus being "horse-shoe shaped" (Schiøler, 1925). Side feathers as in definitive basic plumage (see Fig. 6).

FEMALE: Similar to juvenal or first alternate plumage, exhibiting the same range of variability as that of those plumages (see Fig. 5).

## First Prealternate Molt

A few papillae destined to produce down of the first alternate plumage become active at between 35 and 46 days (late July to early September). First alternate 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) first alternate down is apparent on the outside of the skin. This gray down

grows rapidly; in about a month little of it is still growing. It continues to grow, however, until the onset of the second prebasic molt. The prealternate 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 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 molt. Head and neck pennae, rectrices, and tertials (retained until spring in the female) are the last to molt. First alternate 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 3-4 weeks for renewal of

tertials. Eight of 12 captive males and 5 of 21 captive females first molted one of their middle rectrices; five males molted both middle rectrices first as did four females. None of the above mentioned 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 which 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. (1948), females, as well as males, retain juvenal back and upper rump feathers. On just two birds, a male and a female, did I find any evidence of dorsal molt posterior to the wings prior to the assumption of the first alternate plumage. I quite agree with Witherby et al. (1948) that the female juvenal tertials are not renewed before assumption of alternate plumage. As regards tail molt, my findings also concur with those of Witherby et al. (1948) for I have found 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 a great deal of rectrix wear and it is often impossible to determine to which plumage certain feathers belong.

## First Alternate Plumage

MALE: Similar to definitive alternate plumage (first alternate breast and side feathers illustrated in Figs. 5 and 6 respectively). In some individuals, dusky flecking at tips of feathers gives lower breast and belly a spotted appearance; in others lower breast and belly are white; nearly all individuals have some vermiculation on lower belly and vent (variation illustrated in Fig. 10). Juvenal lower back and upper rump feathers (black edged with brownish black) as well as juvenal wing feathers (exclusive of tertials and tertial coverts) are worn simultaneously with the first alternate plumage.

FEMALE: Similar to definitive alternate plumage (first alternate breast feathers shown in Fig. 5). Feathers of lower breast and belly usually white, but occasionally spotted or streaked with brown (variation illustrated in Fig. 10). Juvenal lower back and upper rump feathers, as well as wing feathers, are worn simultaneously with the first alternate plumage. Juvenal tertials are present until about the beginning of the second prebasic molt of body

feathers; they are then replaced by first alternate tertials which have more rounded tips and more extensive buff edges and are occasionally marked or barred with buff.

## Second Prebasic 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. Occasionally, however, a drake begins its prebasic molt in April and is in full basic dress by late May or early June. Some drakes are still in complete alternate plumage (with no papillae producing basic follicles) late in 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 pre-alternate 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, however, 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 2-1/2 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 3-1/2 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 one day after the remiges. Lesser and median coverts are pushed out about three 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 molted as early as the first week in July and as late as the first week in August -- but

usually they are dropped 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.

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 second week in February and the molt is complete by early May. Of five birds which 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: the body feathers are molted in spring but all the wing feathers are retained until after the breeding season (see Fig. 9). 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 six weeks after their young hatch. The discontinuity of the prebasic molt in hens is, apparently, an adaptation which frees the critical egg laying-and-incubation period of such stress as molt imposes.

## Second Basic Plumage

MALE: Upper parts resemble juvenile male more than adult female (in either plumage), upper mantle being barred, but under parts usually not narrowly streaked or spotted as in juvenile. Head and neck as in adult female. Mantle dark brown, feathers with broader and more semicircular buff bars than in juvenile. Scapulars dark brown, edged with cinnamon-olive, edges of feathers lighter brown than in juvenile. Upper tail coverts as in adult female. Cheeks, sides of neck, chin, and throat more heavily streaked than in juvenile. Feathers of upper breast whitish, barred with dark brown and tipped with cinnamon-buff (see Fig. 5). Side and flank feathers as in adult female but with V-shaped buff markings (see Fig. 6). Rest of breast, belly, and vent white, spots on feathers being larger and not as numerous as in juvenile. In four specimens at hand the venter is heavily marked; in three it is lightly marked; and in seven it is immaculate (see Fig. 10). Under tail coverts white, marked irregularly with sepia. Oil gland tufts brownish black. Tail as in alternate plumage. Primaries mouse-gray, on inner webs paler and shading to white at base. Outer secondaries dark mouse-gray tipped with white, adjacent ones with outer webs black, inner ones with outer webs white.

Primary coverts mouse-gray, spotted and edged with cream. Distal greater coverts mouse-gray, some of them tipped with chestnut and more or less bordered with black on their outer webs; proximal greater coverts mouse-gray throughout. Lower series of median coverts mostly black or chestnut tipped black but distal feathers chestnut as a rule; upper series of median coverts chestnut or mouse-gray, spotted and flecked with cream. Lesser coverts mouse-gray vermiculated and spotted with cream. Axillars and under wing coverts white. Tertials shorter and less tapered at tip than those of alternate plumage, and tinged with brown. Bill slate gray. Legs and feet grayish yellow (occasionally straw-yellow or dusky).

FEMALE: Like alternate plumage but general appearance buffier or yellower, and upper parts more extensively edged and marked with buff (for pattern of breast feathers see Fig. 5). Chin white. Throat usually white but sometimes streaked with dusky brown. Feathers of sides and flanks as in alternate plumage but edging and barring of a lighter shade of buff. Tail markings usually buff or cream but sometimes as white as in alternate plumage. Wing mouse-gray but middle secondaries with outer web gray bordered with black. Greater coverts black but not so intense or extensive as in male, outer ones mouse-gray tipped with

white, inner ones with inner webs olive-brown. Lower series of median coverts mostly black or chestnut tipped with black, but sometimes olive-brown with no chestnut. Inner median coverts and upper series olive-brown edged with cream, a patch toward center being washed with chestnut. Lesser coverts olive-brown edged with light buff. Axillars and under wing coverts white. Tertials and their coverts olive-brown faintly tipped with cream and occasionally marked with buff. According to Witherby et al. (1948) heavily spotted appearance of hens in summer is a result of plucking of feathers for nest lining. According to my observations, however, about a third of the hens are heavily streaked or spotted on the under parts before feather-plucking begins (see Fig. 10). Spotting on under parts is ashy brown, thus being grayer than that of alternate plumage. Down usually dusky brown, but sometimes dark gray, and frequently tipped with white. Bill may or may not have a few small blackish brown spots during early stages of incubation; the spotting increases rapidly after the eggs hatch.

### Second Prealternate Molt

MALE: Soon after the prebasic molt of each body papilla is completed, its prealternate molt begins. Indeed, prealternate 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 which I handled weekly, seven molted all of their basic rectrices, one retained one basic rectrix, and the other three each retained two basic rectrices.

FEMALE: The onset of this molt is directly related to the hen'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 two weeks old do the hen's pennae papillae gather pulp. Pulp-filled papillae first appear on the sides, then on the venter, and later in the scapular, flank, and femoral regions. By the time the young are two or three 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 2-1/2 months to be 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.

## Second Alternate Plumage

MALE: Crown and nape brownish black, feathers tipped and barred with various amounts of cinnamon. Back black or olive-brown, feathers usually finely flecked and vermiculated with cream. Most scapulars grayish black vermiculated with cream, but some mouse-gray edged with buffy brown, the long ones sometimes mouse-gray throughout and sometimes vermiculated with buff. Rump feathers and upper tail coverts glossy black. Feathers of forehead, lores, cheeks, side of neck, chin, throat, and foreneck light buff, spotted and barred with dusky. Feathers of upper breast (Fig. 5) with brownish black and white bars toward tip, terminal ones crescent-shaped (variations in relative thickness of bars causes a variety of patterns). Rest of breast, belly, and vent white or faintly (sometimes heavily) flecked,

vermiculated, or barred with dusky brown (see Fig. 10). Feathers of sides and flanks, and short under tail coverts vermiculated as in mantle (see Fig. 6). Rest of under tail coverts black. Oil gland tufts brownish black. Tail ashy brown, sometimes with blackish borders, outer feathers paler, edged and occasionally marked with buff. Tertials mouse-gray, elongated, and tapered at tips. A few basic upper and under tail coverts, scapulars, femorals, and feathers of the flanks and chest sometimes present. Down light-gray distally grading through pale gray to white basally. Bill and feet as in basic plumage.

FEMALE: Crown glossy brownish black, feathers streaked and edged with warm buff. Nape dusky brown, feathers edged with light buff. Mantle, scapulars, and upper tail coverts dark brown tinged with olive, most feathers with broad fringes and usually V-shaped markings and barrings of buff. Long scapulars olive-brown faintly tipped with white. Back and rump sepia glossed with olive, feathers edged and usually barred with buff. Indistinct dark brown streak from base of maxilla through eye to nape. Cheek, side of neck, chin, throat, and foreneck light buff narrowly streaked with dusky brown, the throat sometimes nearly immaculate, sometimes streaked with dusky brown. Upper breast warm buff, marked with dark

brown (see Fig. 5). Remainder of breast, belly, and vent white. Three of twelve specimens at hand are spotted on the belly and vent, one of these with double spots (see Fig. 10). Feathers of sides and flanks as well as under tail coverts sepia, fringed and marked with buff (some under tail coverts are white marked with sepia). Oil gland tufts brownish black. Tail ashy brown with irregular buff markings. Tertials olive brown, edged and irregularly barred and marked with buff and white. Inner greater secondary coverts dark brown similarly barred and marked. Median secondary coverts with dark brown centers and broadly edged with buff. Down medium gray distally grading through pale gray to white basally. Bill dusky with dull orange or yellow sides. Bill spotting increases in late stages of incubation and during rearing of young -- heaviest from late July through September but fading after October. Legs and feet straw-yellow to orange-brown, webs dusky.

## Variation

Anyone who handles a large number of gadwalls will come to realize how variable the species is. I have tried to take this variation into account in the discussions above but certain facts demand emphasis. In general, juveniles are dark below, adults white below. But dark

bellied juveniles vary greatly -- some are streaked below, some spotted, some double spotted (Fig. 4). A few juveniles are almost or quite immaculate below. Similarly, not all adults have white venters. About half of my specimens that are in basic plumage -- both males and females -- have ventral spots or streaks (Fig. 10). And I have specimens of two-year-old birds of both sexes in alternate plumage with fully spotted bellies and vents (Fig. 10). Such variation appears to be due solely to individual genetic differences. Ralph S. Palmer (in letter) has observed similar variation among male specimens in basic plumage (Institute of Zoology, Alma-Ata, Kazakhstan, U.S.S.R.) and in alternate plumage (University of Moscow, Moscow, U.S.S.R.).

Too, there is considerable variation in the amount and distribution of black and chestnut in the greater and median coverts, in the amount of white tipping in the secondaries, and in the whiteness of the speculum. In general, adult males have the brightest wings followed in descending order of brightness by immature males, adult females, and juvenile males. Occasionally, however, an immature female may be brighter than an adult female, an adult female brighter than a juvenile male, or a juvenile male brighter than an adult male. Rarely a juvenile female

is brighter than a juvenile male. Variation within the various age and sex classes is illustrated in Fig. 11.

Rectrices not only show a good deal of variation in the extent of buff markings but in their total number. Of 55 birds whose tail feathers were counted repeatedly, 46 (86%) had 16 rectrices, three had 15, three had 17, two had 14, and one had 18. I have handled a specimen apart from this group which had 19 rectrices.

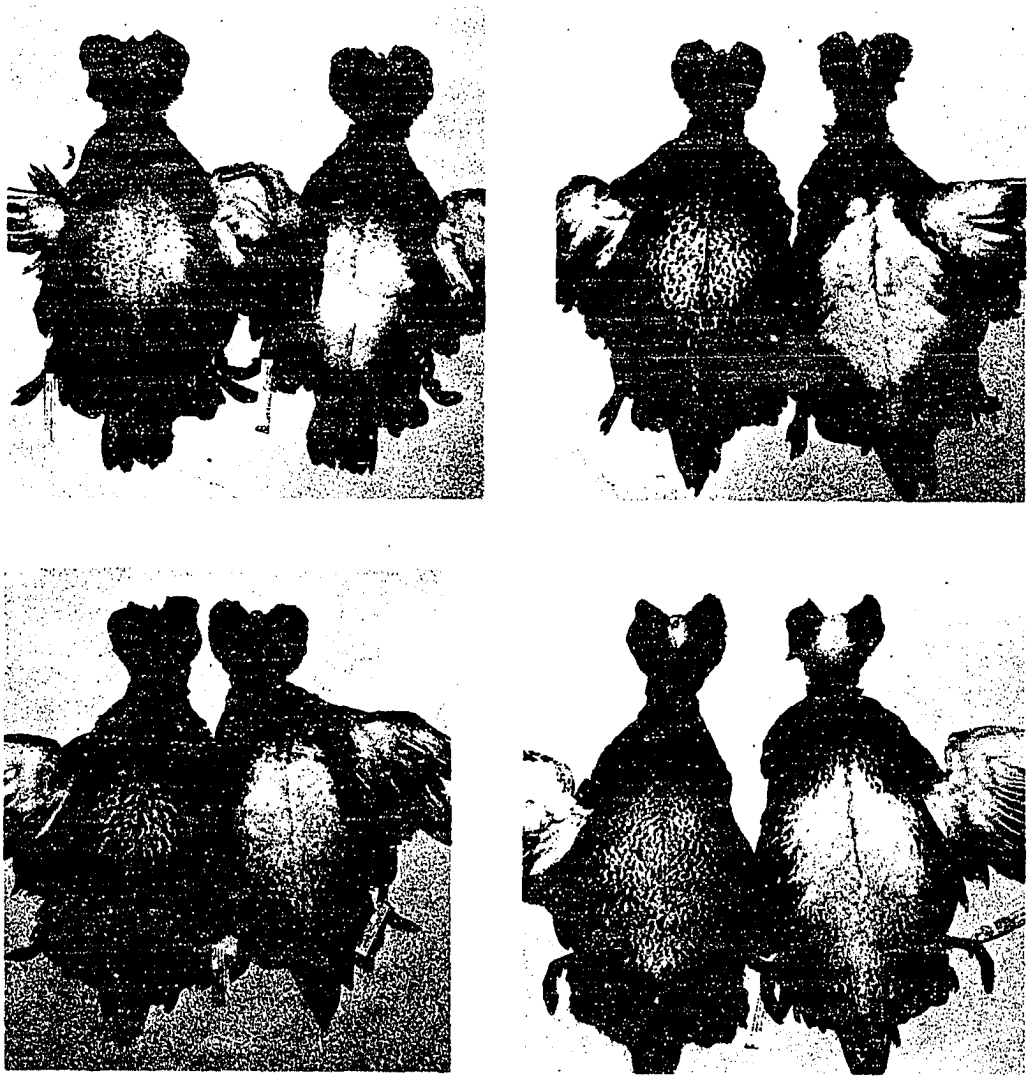

Figure 10. Variation in Venters of Adult Gadwalls (upper left, male second alternate; upper right, female second alternate; lower left, male third basic; lower right, female third basic).

Figure 11. Variation in Brightness of Gadwall Wings (upper left, adult male; upper right, adult female; lower left, juvenile male; lower right, juvenile female).

## FACTORS AFFECTING MOLT

In the fowl, molt has been initiated experimentally by administration of many substances, primarily hormones, including thyroxine (Larionov and Kusmina, 1931, in Juhn and Harris, 1955; Juhn and Barnes, 1931; Van der Meulen, 1939; Juhn and Harris, 1955; Tanabe and Katsuragi, 1962; Juhn, 1963), progesterone (Shaffner, 1955; Juhn and Harris, 1956, 1958; Tanabe and Katsuragi, 1962; Juhn, 1963), 17-oxyprogesterone-7 caproate (Kobayashi, 1958), prolactin = LTH (Juhn and Harris, 1956, 1958; Tanabe and Katsuragi, 1962), pregnant mares' serum = PMS (Juhn and Harris, 1956; Tanabe and Katsuragi, 1962), follicle stimulating hormone = FSH (Juhn and Harris, 1956), luteinizing hormone = LH (Juhn and Harris, 1956), desoxycorticosterone acetate = DCA (Juhn and Harris, 1956; Tanabe and Katsuragi, 1962), enheptin (Tanabe and Katsuragi, 1962), epinephrine (Tanabe and Katsuragi, 1962), and testosterone proprionate = TP (Juhn and Harris, 1956, 1958). Estrogen inhibits normal autumnal molt in hens (Tanabe and Katsuragi, 1962).

The amount of thyroxine (Van der Meulen, 1939) or progesterone (Harris and Shaffner, 1957) needed to induce molt in the fowl decreases as the normal time of molt approaches. Tanabe and Katsuragi (1962) found that thyroxine, progesterone, and PMS would induce molting of feathers "within 6 months of death," while LTH, epinephrine, and DCA were effective only on "old feathers after 6 months of death." Feather aberrations occur with dosages of thyroxine (Juhn and Barnes, 1931) and of progesterone (Shaffner, 1955) far below those necessary to induce molt. Since 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." Since ducks molt twice a year, but only one of these molts

(the postbreeding) seemingly is controlled endocrinologically, and since 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 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 reaction 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 three weeks later than breeding drakes, my reason being that data from my gadwalls indicate that some nonbreeding males are among the very first birds to molt. In the gadwall, some drakes which 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. There exists, however, another group of nonbreeding birds which never become involved in courtship, and in this group, which may include members of either sex, are birds which are the very first to molt. The gonads of these birds never

enlarge. This 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, DCA, PMS, FSH, and LH) which 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 in some way to my pruning of the vegetation in July. This pruning 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 of my captive gadwalls which 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

Richard E. Phillips. In Dr. Phillips' opinion, the presence of any pigment at all in these sections probably meant that some new follicular growth had occurred since "feathers showing no signs of cellular proliferation showed no pigment" (Phillips, in letter). In all eight birds the primary papillae had undergone some new cellular activity, but in six the pigment collar was less than 1 mm. in length. In these six birds the formation of new primary follicles seemingly had begun but growth had been 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, in letter). The other individual had 5 mm. of pigmented cells in each of the primary follicles and the barbs were well formed. This was the most advanced growth stage. In both of the more advanced birds new primaries were, apparently, actively forming. According to Rawles (1960), once papillae are activated, feathers rapidly reach maximum size and do not exhibit interrupted growth such as I have observed.

The molt of body feathers and rectrices was not delayed abnormally in any of these eight birds. Two of the eight specimens had tertials about an inch long when collected. Since 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 the primary pigment collar 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 and presumably it is produced in sufficient quantity to alter pigment patterns only during the height of testicular activity. In the blue-winged teal, I found that about two weeks are required for ingrowing breast, cheek, and flank feathers to reappear externally after plucking, and about 3-1/2 weeks for them to become full-grown. Melanin granules are deposited soon after feather cells are formed. In feathers which require 3-1/2 weeks to mature, granules are deposited during about the first two weeks of development. The extreme dates of pigment deposition for a particular molt can thus be approximated by subtracting two weeks from the first date and 1-1/2 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. True, by 1 July the testes (both germinal and interstitial cells) have usually regressed, but 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.

In late August there is a brief period during which there is no molt 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 during late August (18 to 31 August) and from 1 September to 5 May or later, are alternate. Such feathers are produced during <u>testicular eclipse</u>. The fact that the drake's "high" 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, there is not, as yet, a satisfactory physiological explanation 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, to me, indicates 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. It is obvious that 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.

## SUMMARY

Gadwalls arrived, selected nest-sites, and started laying eggs about three weeks later in southern Manitoba in 1963-64 than they do in northern Utah. In Manitoba nest-sites were almost always on dry ground, surrounded by green vegetation, and near water as well as some conspicuous landmark. Clutches were larger in the wild than in captivity, and first clutches were larger than re-nest clutches. Incubation periods were shorter in the hatchery than they were out-of-doors. In the wild, 46% of 30 nests were successful, 37% were depredated, and 17% were deserted. In captivity, pair bonds were severed at stages varying from just after laying of the fifth egg to the 23rd day of incubation. Nearly all pair bonds of captives were broken between 12 and 22 June. Pair bond dissolution was gradual. All captive drakes were with their mates during the first week of June. At that time harrying flights were common and most males were already molting. By the end of June, no pairs were intact and molting concentrations had reached maximum size. Wild flightless adult gadwalls were first

noticed 23 June. Nonbreeding males that were never active in courtship molted before breeding drakes did, whereas males which did not breed but which attempted to court, molted after breeding drakes molted. By mid-summer some birds became flightless, or nearly so, as a result of badly worn remiges. Disturbance coupled with lack of cover inhibited wing-molt of captives. Once wild adults regained flight in late August or early September they became wary and formed large flocks. By mid-September such flocks were leaving the Delta region.

Wild male gadwalls were heaviest just before dropping their primaries. They lost 75 grams or more during the flightless period. Wild females were heaviest while laying. They lost weight during the incubation period but gained weight during the brood-rearing period. I was unable to measure weight change of females during wing-molt.

About six days were required for ova to develop from the 6 mm. stage to ovulation. Testes of mated drakes were larger than those of unmated drakes that were chasing hens. Testes regressed rapidly once drakes deserted their hens.

Gadwall embryological development closely parallels that of the domestic mallard for at least the first 18 days. Papillae first 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. On the 24th day ducklings emerge -- their wet down ensheathed. Prepennae are protoptiles. True mesoptiles develop primarily on the wings. At hatching, gadwalls are cream-buff below and sepia above (except for four light spots), some individuals being yellower in tone than others. The faint yellowish tinge is probably due to carotenoids. Fading probably is the result of carotenoid auto-oxidation catalized by heat and light. Feather wear also alters down color.

Follicles destined to produce juvenal feathers are evident beneath the skin of the duckling 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 young birds fly at 50 to 56 days of age. Late-hatched gadwalls fly at a younger age than do early-hatched birds -- a fact perhaps explainable by the increase in thyroxine output which accompanies a decrease in temperature. Juvenal body and tail feathers are dark brown in both sexes, characteristically edged and barred with buff. Juvenal wing feathers generally have less white, black, and chestnut than do wing feathers of older birds and many juvenal lesser and median upper wing coverts have distinct horizontal bars of buff which

are absent in older birds. Gadwalls in juvenal plumage can best be identified by the square-tipped rectrices, narrow body feathers, and dull wing-color. Though the venters of both juvenile males and juvenile females usually have brown spots or streaks, immaculate-bellied juveniles of both sexes are occasionally found.

Feathers of the transitory and highly variable first basic plumage are worn from mid-August through December. These first appear just before the juvenal plumage is completed, and they are soon replaced by feathers of the first alternate plumage. They are present principally in the breast and sides. In the male, they may be told from juvenal feathers by their broadness and from first alternate feathers by their buff or brown bars (as opposed to the gray and white pattern of the alternate plumage). In the female, they differ from juvenal feathers by their broadness, but they do not differ from first alternate feathers in any significant way and are therefore difficult to identify.

A few follicles destined to produce first alternate down are active beneath the skin as early as 35-46 days of age. A few follicles of first alternate pennae are growing by 63 days. By 72 days, alternate pennae and down are evident exteriorly on the venter. Head and neck pennae, rectrices, and tertials of the first basic plumage are the

last to drop out. First alternate 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 in both sexes and other feathers often are. These juvenal feathers, together with juvenal wing feathers (except the tertials which are molted twice per year), are worn simultaneously with the first basic plumage and the first alternate plumage. Male alternate plumage is characterized by sharply contrasting patterns of dark gray and white. Breast feathers are gray barred with white. Venters are usually white though occasionally they are spotted or vermiculated with gray. Side and flank feathers are vermiculated with gray and white. Under tail coverts are black. A head crest is usually prominent. In the female in alternate plumage the feathers of the upper parts are dark brown narrowly edged with buff; the throat and chin are dark; and the venter, while nearly always immaculate, is sometimes spotted with brown.

The second prebasic molt of drakes usually begins in late May or early June. Breast and side feathers are the first to molt. 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 feathers generally are molted a few days after the tertials. The second prebasic molt of hens (body and tail) occurs from January to May but is heaviest in March and April. The black venter down appears in late April and May after the pennae are grown. Wing feathers are not molted until after the breeding season -- usually when the young are about six weeks old. The second basic plumage of the male is dull brown. The upper parts are barred as in the juvenile male and the breast has dark brown spots that are larger, but less numerous than those of the juvenal plumage. About half the birds have such markings also on the venter. Females in second basic plumage are similar to those in alternate plumage except that the chin and throat are buff and the body feathers are broadly edged with buff. As in the male, females in second basic plumage often have spotted bellies.

Molt has been induced by numerous substances, especially hormones, many of which cause feather abnormalities. The sensitivity of feathers to such substances varies with the age of the feathers. It seems likely that normal molt is an autonomous process controlled within the feather papillae and that 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.

## GLOSSARY

Adult down: Teleoptiles with no vane and with short or vestigial rachis.

Alternate plumage: Name of plumage when there are two or more plumages per annual cycle. If there are two, they are basic and alternate -- alternate being more derived. In ducks includes contour feathers and down.

Aylesbury: Large, white domestic mallard weighing 8-9 lbs.

Basic plumage: Name of plumage when there is one plumage per cycle. When there are two or more plumages per cycle, basic is the more primitive. In ducks includes contour feathers and down.

Calamus: Shaft of feather proximal to rachis.

Clear feathers: Feathers with hard, translucent calami.

Contour feathers: Outer feathers of head, neck, body, and limbs including flight feathers. Pennae.

Culmen: Ridge or upper border of maxilla.

Down: Small, soft feathers, without vane and with very short or vestigial rachis. Includes natal and adult down.

Filaments: Embryonic feathers with appearance of thin threads.

Fresh eggs: Eggs prior to beginning of incubation; any egg taken from an incomplete clutch presumably is fresh.

Harrying flights: Pursuits in which several drakes chase and attempt to copulate with a nesting hen.

Indian Runner: Domestic mallard, usually white, with relatively long legs and upright carriage and weighing 4-4½ lbs.

Juvenal plumage: The first covering of true (sometimes modified) contour feathers and adult down.

Khaki Campbell: A large, light-colored domestic mallard.

Mesoptiles: Feathers in the second of two successive coats of nestling down.

Molt: Collective loss and replacement of an entire generation of feathers, whether this includes all or only a portion of bird. Molts are named in relation to following or incoming plumage, e.g., prebasic, prealternate, etc. A molt may be limited in time, protracted, or even interrupted.

Natal down: Protoptile with short or vestigial rachis and no vane.

Neossoptiles or Neoptiles: Nestling feathers, consisting of prepennae, prefiloplumulae, and preplumulae.

Papillae: Small, pimple-like protuberances on the skin.

Pennae: Contour feathers (plumae), as distinguished from down feathers (plumulae).

Plumage: A single generation of feathers (whether it includes all those worn at one time or not). Plumages are named juvenal, basic, and alternate. Many birds wear more than one plumage simultaneously.

Plumage cycle: In an adult bird, runs from a given plumage or molt to next occurrence of same plumage or molt.

Plumae: Contour feathers or pennae.

Plumulae: Down feathers.

Prefiloplumulae: Nestling down feathers preceding filoplumes.

Prepennae: Nestling down feathers preceding contour feathers.

Preplumulae: Nestling down feathers preceding future definitive down feathers.

Protoptiles: Feathers in first of two successive coats of nestling down.

Primaries: Flight feathers (remiges) attached to the manus (hand).

Rachis: The vane-bearing shaft of a feather.

Rectrices: Tail feathers.

Remiges: Primaries and secondaries.

Secondaries: Flight feathers with proximal portions abutting on ulnae; distal to tertials..

Teleoptiles: Adult-type feathers; pennae or down which succeed neossoptiles. Some authors (Ingram, 1920) use teloptiles for pennae only.

Tertials: Innermost wing feathers with proximal end adjacent to elbow; often distinguished from secondaries by size, shape, and color.

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