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GROWTH AND PLUMAGE DEVELOPMENT OF
DUCKLINGS IN INTERIOR ALASKA.

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GROWTH AND PLUMAGE DEVELOPMENT OF DUCKLINGS
IN INTERIOR ALASKA

A
THESIS

Presented to the Faculty of the
University of Alaska in Partial Fulfillment
of the Requirements
for the Degree of
MASTER OF SCIENCE

By

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May, 1965

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GROWTH AND PLUMAGE DEVELOPMENT OF DUCKLINGS
IN INTERIOR ALASKA

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ABSTRACT

The rates of growth and plumage development of Mallard, Canvasback, Lesser Scaup, and Bufflehead ducklings were determined at Tetlin, Alaska, from daily field observations of known-age broods and weekly measurements of weight and length of the culmen, the tarsus, the 9th primary, the 6th secondary, the longest tertial, the middle rectrix, and the longest scapular. The rates of increase of weight, culmen length, and tarsus length were similar to those at lower latitudes. Measurements of birds of different ages overlapped sufficiently to prevent their use as criteria for more precise age determination than is possible with a plumage classification system. The greatest variation in plumage development occurs at the age at which the first teleoptiles emerge. This variation occurs within broods as well as between broods and may cause errors of two weeks or more when the age of ducklings is estimated from their stage of plumage development. The rate of body feathering is controlled by the sequence of feather emergence, time of emergence of specific feathers, and the rates of growth of these feathers. Once feathering begins, the sequence and time of emergence appear to be constant for all members of a species at all latitudes. The rate of growth of individual feathers varies directly with the length of daylight. Latitudinal differences in daylight are such that of the individuals studied, Mallards feathered faster, Canvasbacks slightly faster,

and Lesser Scaups slower in the North than at lower latitudes. Early and late hatching broods at the same latitude also show different rates of feathering. Latitudinal differences in rates of plumage development are not reflected in Class I and are greatest in Classes IIB and IIC. Because the primaries emerge at a set time after the first teleoptiles emerge, birds with faster rates of body feather growth may spend more time in Class III than birds with slower rates of body feather growth, and differences in the age at which flight is attained are not as great as differences in rates of feather growth.

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
STUDY AREA	5
METHODS	6
APPRAISAL OF RESULTS	
Factors Affecting Sample Size and Survival of Ducklings	14
Plumage Development.	16
Mallard	18
Canvasback	21
Lesser Scaup	27
Bufflehead	27
Feather Growth	28
Growth of Body Parts	36
DISCUSSION	
Individual Variation in Plumage Development	41
Sexual Differences in Rates of Plumage Development	47
Value of Measurements as Criteria for Determining the Age of Ducklings in the Hand	48
Difference in Rates of Plumage Development	
Between Tetlin Ducklings and Those at Lower Latitudes	50
Possible Causes of Differences in Rate of Feather Growth at Different Latitudes	58
LITERATURE CITED	66

LIST OF TABLES

Table	Page
1. Development of a wild duckling viewed under ideal conditions	12
2. Average age span (in days) for each plumage subclass at Tetlin, Alaska, and in the Northern United States	17
3. Age span (in days) for each plumage subclass of individual Canvasbacks	42

LIST OF FIGURES

Figure		Page
1.	The holding pond used in 1964 showing the location of the drive trap	9
2.	Plumage development of the Mallard	19
3.	Plumage development of two Canvasbacks showing some of the individual variation	23
4.	Plumage development of two Canvasbacks showing some of the individual variation (continued from Fig. 3).	24
5.	Plumage development of two Canvasbacks (continued from Figs. 3 and 4)	26
6.	Early plumage development of the Lesser Scaup	29
7.	Later plumage development of two Lesser Scaups showing some individual variation.	30
8.	Feather growth of the Mallard	31
9.	Feather growth of the Canvasback	33
10.	Feather growth of the Lesser Scaup	34
11.	Growth of the 9th primary of seven individual Lesser Scaups showing similar rates of growth despite different times of emergence.	35
12.	Mean increase of weight, tarsus length, and culmen length of the Mallard	37

Figure		Page
13.	Mean increase of weight, tarsus lengths, and culmen length of the Canvasback . . .	38
14.	Mean increase of weight, tarsus length, and culmen length of the Lesser Scaup	39
15.	Average span of the pre-flight development at various latitudes and the maximum possible duration of daylight on the 15th of each month at those latitudes	60

INTRODUCTION

A need for reliable methods of estimating reproductive success of ducks has arisen in recent years. When a number of species is involved, it is frequently necessary to make several brood counts over one area in one season, so that very early and very late broods will be counted. A method of determining the age of duck broods in the field is necessary to establish the best times for repeat counts and to prevent duplication by eliminating those broods which were on the area during the first count. In addition, a standardized method of age determination can be useful to gain a better understanding of production by providing a means of estimating hatching peaks from regular brood data and of determining survival at various ages.

Experienced workers have been able to estimate ages of broods after gaining familiarity with the species involved. However, a need has existed for a standardized system which could be employed by personnel with little experience and which would enable comparison of data collected by different individuals. The most logical criterion for such a system is the degree of feathering of ducklings when they are viewed under field conditions. Several systems have been used. Most plumage classification systems have at least three basic classes: downy, partially feathered, and fully feathered. Some of these systems employ several subclasses for each major class. Determining the actual ages

of ducklings in these plumage classes has been a problem because insufficient numbers of wild, known-age broods have been studied throughout their pre-flight development.

Hochbaum (1944) described the plumage development of hatchery reared Canvasbacks (Aythya valisineria) and listed the approximate ages of flying for several other species. However, he did not attempt to apply any classification system to this information. Blankenship (1952) determined the rates of plumage development of several species of dabblers in the wild. Southwick (1953) studied the plumage development of several species of both divers and dabblers using artificially reared birds hatched from eggs collected in the wild. Blankenship, et al. (1953) compiled most of the available information and applied it to a practical classification system which could be used for age determination. Weller (1957) presented a detailed study of the plumage development of hatchery reared Redheads (Aythya americana) and included some information on wild birds for comparison. Mendall (1958) published observations on the development of the Ring-necked Duck (Aythya collaris). Dzubin (1959) made a comparatively complete study of the pre-flight development of wild Canvasbacks. While these last three papers have been published since 1954, Gollop and Marshall (1954) included the basic plumage development information from them when they revised Blankenship and his co-workers' work.

At present, Gollop and Marshall's work remains the best summary of the available information and is the most widely used system

for age determination today. The system utilizes seven subclasses and gives the approximate ages of several species of birds in these subclasses.

A number of problems is encountered when this system is applied to actual field conditions. Among these problems are varying conditions of visibility, differences in observers, and variation in the rates of plumage development of individual ducklings. The system assumes "...deliberate observation of a brood at 50 to 75 yards under excellent light and other climatic conditions." Under poor conditions of visibility remnants of down or beginning feathers are not as noticeable as they are under ideal conditions. Birds in the hand usually appear to be in a different subclass than when observed on the water. In addition, it is common for several observers to place the same brood into different subclasses even when the broods are observed under the same conditions of visibility.

Another source of error, encountered when the stage of plumage development is used for age determination, is the variation in rates of plumage development of individual ducklings. Individuals of the same brood may reach a given stage of plumage development at different ages. It has also been suggested that ducklings at higher latitudes require less time to go through their pre-flight plumage development. Hochbaum (1944) states that each year juvenile Canvasbacks and Lesser Scaups are shot at Delta, Manitoba, which are more advanced than the local

birds. These more advanced birds have brown stainings on their breasts which is characteristic of birds from certain northern areas. Gollop and Marshall (1954) state that U. C. Nelson found newly-hatched Pintail broods in northern Alaska only 4 weeks before freeze-up and suggest that the birds would have to be flying in half the time required by South Dakota birds if the population were to be maintained without recruitment from other areas.

The present study, conducted during the summers of 1963 and 1964 at Tetlin, Alaska, was undertaken to determine the rates of plumage development for ducklings of various species in interior Alaska and to compare these rates with those which have been determined by other investigators for ducklings at lower latitudes.

STUDY AREA

The area selected for the study is immediately east of Tetlin Lake near Tetlin, Alaska, and lies approximately 15 air miles or 55 river miles south of Tetlin Junction, Mile 1302 on the Alaska Highway. No definite boundaries were set for the study area; the most intensively studied region lies roughly between $63^{\circ}06'$ and $63^{\circ}08'$ N. Lat. and between $142^{\circ}32'$ and $142^{\circ}40'$ W. Long. This area was selected because it was accessible from the Tetlin River and was close to the camp site previously established by the U. S. Fish and Wildlife Service on Tetlin Lake near the outlet to the Tetlin River. In 1964 most of the ponds within 0.5 miles of the east shore of Tetlin Lake were searched for nests.

This area is predominantly spruce forest with numerous cave-in lakes and ponds formed by the thawing of permafrost. Murray (1961) has described the nature of the Tetlin area in more detail.

METHODS

Nests were located by systematically searching along borders of ponds, the Tetlin River, wet meadows, and other likely areas. Nests of dabbling ducks were scattered throughout the entire area and, therefore, were more difficult to find than those of diving ducks which tended to be more concentrated in the sedge borders of the ponds. As a result, more diving duck nests than dabbling duck nests were located. A 6-or 7-foot flushing stick frequently was used, but the nature of the area made the use of any other flushing device impractical.

In 1963 known-age ducklings were allowed to remain under completely natural conditions. When a nest was found, the date of hatching of the eggs was estimated by candling the eggs with a short length of radiator hose using the method described by Weller (1956). At some time prior to hatching, preferably within 2 or 3 days, the eggs were injected with dye. The clutches were allowed to hatch normally; and the colored, known-age ducklings were observed as frequently as possible.

Eggs were injected with dye using the technique described by Evans (1951). Crocein Scarlet MOO, Fast Green FCF, and Brilliant Blue FCF were used to dye the ducklings. All dyes used colored the ducklings satisfactorily. However, Brilliant Blue gave a greenish color which in most cases was indistinguishable from Fast Green.

Best results were obtained when the eggs were injected after the head and bill had become visible in the airspace when the eggs were candled. In all of five clutches injected more than 1 week prior to hatching, some mortality occurred. However, no mortality occurred in the six clutches injected within 4 days of hatching. On the other hand, when eggs were injected after pipping had begun, the color did not take as well as in those injected 1 or 2 days earlier.

Because of poor hatching success and brood mobility, only a few broods were observed throughout their entire pre-flight development in 1963. Therefore, in 1964 it was decided to restrict the movements of the broods. A pond of approximately 2.7 acres was fenced in 1964. This pond was selected because it was close to the base camp, was of a reasonable size from the standpoint of cost of fencing, and in 1963 was used more extensively by the species being studied than any of the other ponds in the area, indicating that it produced a good supply of food for both divers and dabblers.

The depth of the pond varied from about 1 to 2.5 feet. This pond was typical of the area, was surrounded by spruce forest, and had a sedge border which varied from about 5 to 30 feet in width. The border was largely Carex sp. with Scirpus validus located at the edge of the water. Clumps of Carex, separated from the shore, provided nest sites for some Lesser Scaups and also served as loafing spots.

The fence was 3 feet high and made of 1-inch-mesh poultry netting. Posts were cut from local spruce. As much of the sedge border as possible was included in the enclosed area. Frequent inspection was necessary to make sure no openings under the fence were large enough to allow ducklings to escape.

A drive trap, made from the same materials as the fence, was constructed on the north side of the pond (see Figure 1). This trap consisted of a pen, about 6 x 10 feet, near the shore with a short wing extending along the shore and a long wing extending out past the middle of the pond to form a funnel. An opening, large enough to allow one duckling at a time to enter the pen, was located at the vertex of the funnel. A dropping gate, activated by pulling a string from a point in the funnel, closed the opening after the ducklings had entered the pen.

To obtain ducklings, a nest trap of the type described by Coulter (1958) was placed on the nest during egg-pipping, and it was sprung when the ducklings had hatched. This technique required perfect timing so as to catch both the hen and the newly hatched ducklings before they left the nest. The frequent visits to the nest increased the chance of desertion and predation.

In addition, a 150-egg, oil-operated, hot water incubator was used so that eggs could be hatched artificially in cases when the first method failed due to desertion by the hen.

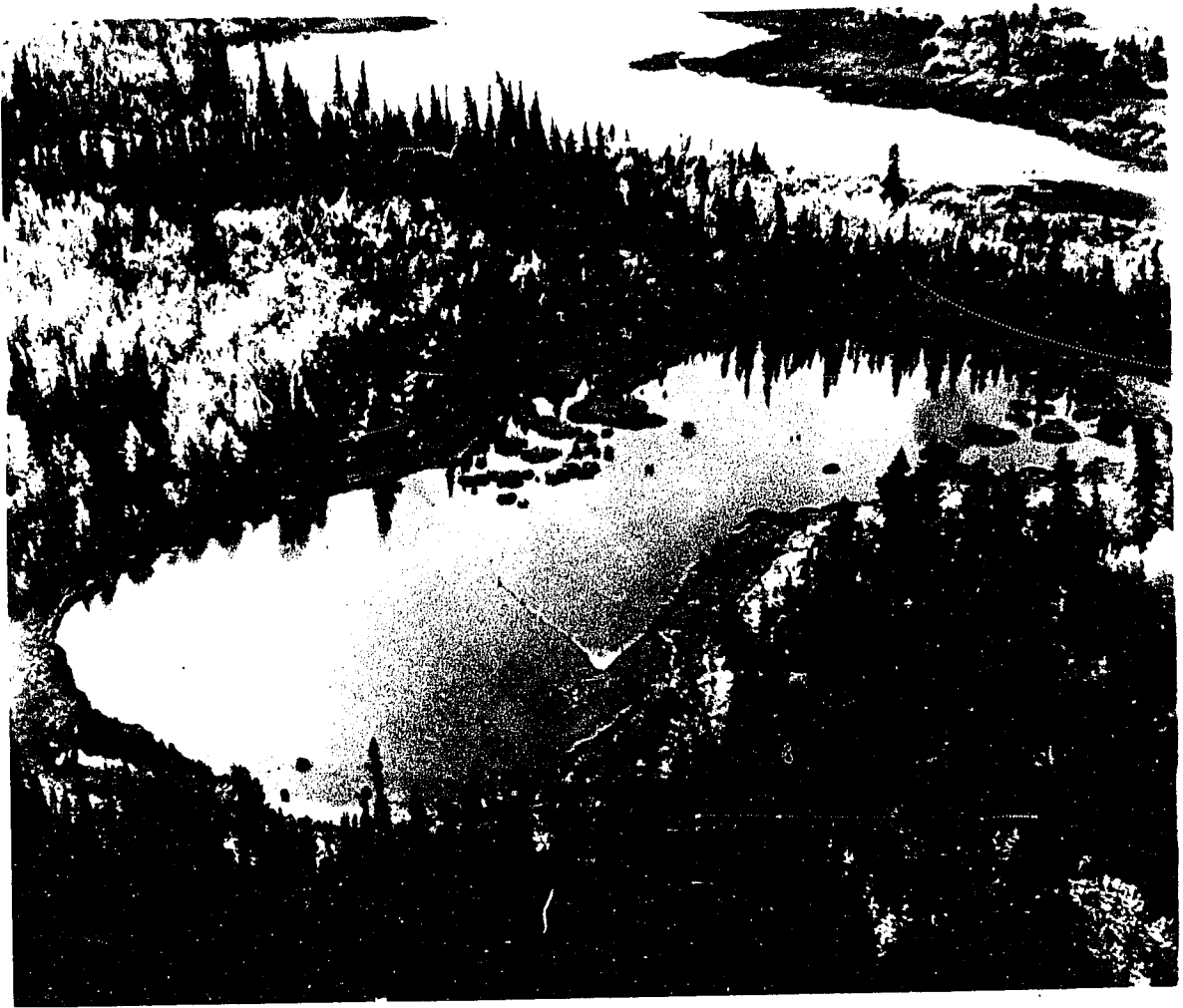


Fig. 1. The holding pond used in 1964 showing the location of the drive trap.

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Early attempts to catch a hen and brood on a nest failed, either because the hen escaped from the trap or because the eggs did not hatch as soon as expected. The eggs were then collected and hatched in the incubator, and the ducklings were released on the holding pond. Early survival of the captive ducklings proved to be good, so henceforth, we collected the eggs from all nests found, thus eliminating the loss to nest predators and flooding.

Because the incubator had to be kept in a tent, it was not possible to completely eliminate temperature variations. At first, the incubator temperature fluctuated from 85 F to 102 F because of wind and the fluctuations of the outside temperature. By covering the inside of the tent near the incubator with cardboard and by adjusting the flame and thermostat several times a day, it was possible to keep the temperature between 98 F and 100 F. The fluctuations did not appear to affect embryo survival.

The eggs were turned by hand twice a day. A moisture tray failed to keep the humidity above 35%, so the eggs were sprinkled with warm water each time they were turned.

The ducklings were held in the incubator for at least a day after hatching. No artificial feeding of the ducklings was done as it was desirable to keep conditions as natural as possible.

Some of the eggs were injected with dye so that individuals of various ages could be distinguished from a distance. On the basis of color, it was not possible to identify individuals of the same species which had hatched on the same day.

In order to be able to identify specific individuals in the hand, a No. 1 fingerling tag was fastened to the web of the right foot of each duckling (Grice, 1960). These were attached by piercing the web twice, looping the tag through both holes, and clamping it shut with pliers. With some exceptions, these tags worked well. No. 1 tags appeared somewhat large for small ducklings such as day-old Buffleheads and teal. Occasionally a tag would rip loose. In most of these cases, the ducklings were large enough to be re-marked with a numbered plastic leg band and replacement of the web tag was not necessary.

The ducklings were classified daily by deliberate observation at 50 to 75 yards with 7 x 35 binoculars using Gollop and Marshall's (1954) system of seven plumage subclasses (see Table 1). When light conditions were not good, compensation was made by observing the ducklings at a closer range. In order to determine the time of emergence of certain feathers with more precision, daily observations with a 20X spotting scope and weekly observations of birds in the hand were made. These observations often revealed the presence of feathers or down which were not visible with binoculars.

Table 1

Development of a Wild Duckling as Viewed Under Ideal Conditions
(from Gollop and Marshall, 1954)

Plumage Class	Sub-Class	Description
I	A	" <u>Bright ball of fluff</u> ". Down bright. Patterns distinct (except diving ducks). Body rounded; neck and tail are not prominent.
<u>Downy Young</u> No feathers visible	B	" <u>Fading ball of fluff</u> ". Down color fading, patterns less distinct. Body still rounded; neck and tail are not yet prominent.
	C	" <u>Gawky-downy</u> ". Down color patterns faded. Neck and tail becomes prominent. Body itself becomes long and oval.
II	A	" <u>First feathers</u> ". First feathers show on side under ideal field conditions. Stays in this class until side view shows one-half of side and flank feathered.
<u>Partly Feathered</u> as viewed from the side	B	" <u>Mostly feathered</u> ". Side view shows one-half of side and flank feathered. Primaries break from sheaths. Stays in this class until side view shows down in one or two areas only (nape, back or upper rump).
	C	" <u>Last down</u> ". Side view shows down in one or two areas only (nape, back or upper rump). Sheaths visible on erupted primaries through this class. Stays in this class until profile shows no down.
III <u>Fully Feathered</u> in profile		" <u>Feathered-flightless</u> ". No down visible. Primaries completely out of sheaths but not fully developed. Stays in this class until capable of flight.

Once a week the ducklings were captured in the drive trap for weighing and measuring. One person would beat the shore, while another guided the ducklings into the trap with the aid of a 14-foot, canvas-covered "rat" canoe. The trapped ducklings were caught in a dip net and placed in a holding box.

Weights were taken on a triple beam balance with the ducklings confined in a cloth bag to minimize movement. The weights were recorded to the nearest 0.1 g., however this degree of precision is not warranted as the ducklings frequently defecated before and after weighing. Measurements were taken of the exposed culmen; tarsus, including the tarsometatarsus and condyles of the tibiotarsus and digits; 9th primary; 6th secondary; longest tertial; middle rectrix; and, in the case of the Lesser Scaup, the longest scapular. Measurements were taken with a plastic rule to the nearest 0.5 mm; however, errors of 1 or 2 mm probably occurred due to the structure of the feathers.

All weights and measurements were taken between noon and 2:00 PM Alaska Standard Time to minimize the effect of any diurnal variations in weight such as found by Baldwin and Kendeigh (1938) and in rate of feather growth as found by Lillie and Wang (1940).

APPRAISAL OF RESULTS

Factors Affecting Sample Size and Survival of Ducklings

A number of factors controlled the numbers and species of ducklings which were studied. The number of nests found in 1964 was well below what was expected. Due to an extremely late spring, many pairs of early nesting species apparently made no attempt to nest. The most common species of dabbling ducks on the study area were Mallards (Anas platyrhynchos), Pintails (Anas acuta), Green-winged Teal (Anas carolinensis), and Baldpates (Mareca americana). Of these, Baldpates were the most common in 1963. In 1964, however, no Baldpate and only one Green-winged Teal, two Pintail, and four Mallard nests were found.

A total of 150 ducklings was released on the holding pond. This number included 1 Pintail, 15 Mallards, 25 Canvasbacks, 16 Buffleheads (Bucephala albeola), 5 Green-winged Teal, and 88 Lesser Scaups (Aythya affinis). Of these, only two Mallards, four Canvasbacks and six Lesser Scaups survived until they attained flight. A number of other individuals, however, survived long enough to furnish additional data. Several known-age broods of Buffleheads and Canvasbacks which were not on the holding pond, but which were observed throughout their pre-flight development, provided information on rates of plumage development. No measurements were obtained from these latter birds.

The primary causes of mortality of the ducklings on the holding pond were exposure and predation. Survival was usually good until there

was a wet, cool, windy night. In the absence of maternal care, the ducklings tended to spread out. Those ducklings which remained in groups had a much higher rate of survival. Clumps of Carex were such that the ducklings could swim into them and be protected to some degree by the overhanging vegetation. The summer of 1964 was unusually wet and cold at Tetlin, particularly at the time most of the Lesser Scaups were being released on the pond. Presumably, survival would have been better under more favorable weather conditions.

Mew Gulls (Larus canus) preyed heavily on Class IA ducklings. This was particularly true when the Lesser Scaups were being released on the pond as there were more ducklings to attract the gulls. Ducklings of all ages are believed to have been taken by Goshawks (Accipiter gentilis), Great Horned Owls (Bubo virginianus), and mink. One Class IA Mallard was killed when it was struck in the neck by a Horned Grebe (Podiceps auritus) when the duckling approached the latter's nest.

Veselovsky (1951, 1953) states that the uropygial gland does not function in ducklings until feathering begins and that downy ducklings normally pick up oil by brushing against the feathers of the female. Without this source of oil, he believes that ducklings up to 2 weeks old become soaked and will drown. There was no evidence of such wetting on the ducklings which were released on the holding pond at Tetlin, and they never had contact with an adult.

Food apparently was not a limiting factor from the standpoints of survival or rate of growth. The number of ducklings on the pond was

never great. The ducklings tended to form "broods," however these groups never exceeded 13 individuals, and they normally spread out over a section of the pond while feeding. Therefore, it seems unlikely that competition existed due to too many individuals feeding in one area. The pond was used by adults of several species of ducks throughout the summer. In fact, more ducks used this pond than any of the other ponds in the area, indicating that an abundance of food was available on the holding pond throughout the brood season.

Plumage Development

The rates of plumage development of Mallards, Canvasbacks, Lesser Scaups, and Buffleheads observed at Tetlin and at lower latitudes are given in Table 2. These rates are averages and, with the exception of the ages at which flight is attained, do not take into consideration individual variation. This will be discussed in detail later.

The following descriptions and photographs (see Figures 2 through 7) of the plumage development of each species are presented as aids to more precise placement of ducklings within specific subclasses. These descriptions are based on observations which were made with a 20X spotting scope and with birds in the hand as well as with binoculars under average field conditions.

Table 2

Average Age Span (in days) for Each Plumage Subclass at Tetlin, Alaska,
and in the Northern United States and Southern Canada

Species	Area	IA	IB	IC	IIA	IIB	IIC	III	Flying
Mallard	Tetlin	1-6	7-11	12-26	27-32	33-37	38-41	42-62	61-64
	South Dakota ¹	1-6	7-12	13-18	19-25	26-35	36-45	46-55	52-60
Canvasback	Tetlin	1-9	10-17	18-30	31-39	40-45	46-55	56-66	62-71
	Manitoba ²	1-9	10-18	19-25	26-32	33-42	43-53	54-65	56-68
Lesser Scaup	Tetlin	1-6	7-12	13-20	21-30	31-35	36-47	48-56	53-61
	South Dakota ¹	1-6	7-13	14-20	21-28	29-33	34-42	43-50	47+
Bufflehead	Tetlin	1-6	7-12	13-19	20-24	25-28	29-34	35-45	45+
	Washington ³	1-12	13-19	19-26	27-36	37-47	48-53	54-63	64+

¹ Gollop and Marshall (1954).

² Dzubin (1959).

³ Crouch (pers. comm.) includes one individual taken from the Tetlin study area.

Mallard

Classes IA and IB -- There is no sharp dividing line between these two classes and, under varying light conditions, individual ducklings may appear to be in either subclass. There is a gradual increase in size through both subclasses, with the body becoming more elliptical and the color of the down fading.

Class IC -- Birds in this subclass are more readily separated from those in other subclasses. The color of the down is very faded and the body and neck are distinctly longer than those of Class IB birds (see Figure 2A). The rectrices become visible in this subclass. The feathers on the side, just below the wing become visible with the bird in the hand about 4 days before the bird enters Class II. When these feathers become visible under field conditions, the bird enters Class IIA.

Class IIA -- Individual body feathers appear rapidly and some individual birds appear to be much more advanced than others. At 29 days all birds showed small patches of feathers around the wings when viewed from the side (see Figure 2B). On some individuals most of the breast feathers also were visible, while none were visible on others. The head and neck take on a mottled appearance as feathers begin to appear there during the later stages of Class IIA. When the body, viewed from the side, is half feathered the bird is placed in Class IIB.



A. 22 days (Class IC)



B. 29 days (Class IIA)



C. 36 days (Class IIB)



D. 43 days (Class III)



E. 50 days (Class III)



F. 57 days (Class III)

Fig. 2. Plumage development of the Mallard.

Class IIB -- By the time the bird reaches this class, the breast is completely feathered; the tail is well developed; small remnants of down remain on the neck; and the back and rump are downy. The birds progress through this subclass rapidly. In fact, a noticeable change may occur within a few hours, primarily due to the growth of the scapulars which cover most of the down on the back. The flight feathers have not yet started to develop (see Figure 2C). The sheaths of the tertials appear in the later stages of Class IIB and those of the primaries and secondaries appear during the last stage of this subclass. At this time, only a small patch of down is visible on the rump when the bird is viewed under field conditions. The back is still downy under the scapulars, but the down is visible only in the hand.

Class IIC -- Feathers on the rump appear near the tail first. As the more anterior rump feathers appear, the scapulars and tertials grow back until no down is visible while the bird is sitting on the water. Ducklings enter Class III at this point. A large downy area, however, still remains on the back, and therefore, an early Class III bird may be placed in Class IIC if viewed in the hand.

Class III -- The primaries and secondaries break their sheaths at the end of Class IIC or the beginning of Class III. The secondaries

usually break their sheaths a day or so earlier than the primaries (see Figure 2D). The feathering of the back requires more time than that of the rest of the body, and some down remains here midway through Class III. The wing feathers grow rapidly, but the primary sheaths remain visible when the wing is extended even under field conditions (see Figure 2E) until the primary coverts cover them 4 or 5 days before flight is attained. The birds remain in this class until they are able to fly.

Canvasback

Class I -- Most Canvasbacks proceed through Classes IA, IB, and into IC at approximately the same rate. As in the Mallard, there are gradual changes in size and shape with the body becoming more elliptical. The rectrices are the first feathers to appear and the tail becomes noticeable under field conditions late in Class IC. The first body feathers to appear are the contour feathers on the side below the wing. They are visible in the hand 3 or 4 days before they become visible under field conditions. When these side feathers are visible under field conditions, the bird enters Class IIA.

Class IIA -- The scapulars appear 1 or 2 days after the first contour feathers. Once feathering begins, the breast feathers rapidly. The head and neck appear mottled as the feathers replace the

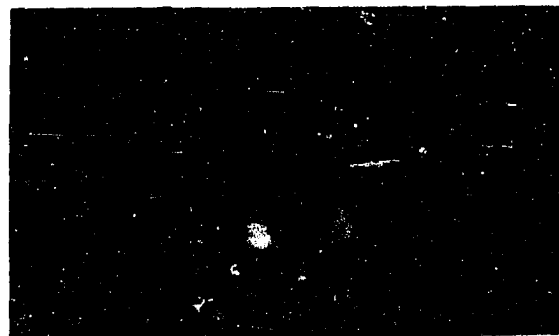
down. This mottled appearance first becomes evident about 3 days after the bird enters Class IIA (see Figure 3E). The feathering extends up the sides of the body back to the legs. The scapulars become large enough to cover the wings which have not yet started to develop. The head and neck become almost completely feathered with only small remnants of down visible (see Figure 4A). At this stage, the bird enters Class IIB.

Class IIB -- The sheaths of the tertials appear at about the same time the bird enters Class IIB. Within a day or two, the sheaths of the primaries and secondaries appear and the tertials break their sheaths (see Figure 4B). Feathering of the body continues up the side of the rump. The back is still downy, but it appears feathered under field conditions because the scapulars cover most of the down. The sheaths of the primaries are visible under field conditions when the bird stretches its wing during the last 2 or 3 days of this subclass (see Figure 4C). When only a small patch of down is still visible on the rump, the bird enters Class IIC. No down remains on the head, neck, or breast. The primaries and secondaries are about to break their sheaths.

Class IIC -- In most cases, the secondaries break their sheaths on the first day of this class, and the primaries break their sheaths a day later (see Figure 4D). This time at which the primaries



A. 19 days (Class IC)



B. 18 days (Class IC)



C. 26 days (Class IC)



D. 25 days (Class IC)



E. 33 days (Class IIA)



F. 32 days (Class IIA)

Fig. 3. Plumage development of two Canvasbacks showing some of the individual variation.



A. 40 days (Class IIA)



B. 39 days (Class IIB)



C. 47 days (Class IIB)



D. 46 days (Class IIC)



E. 54 days (Class IIG)

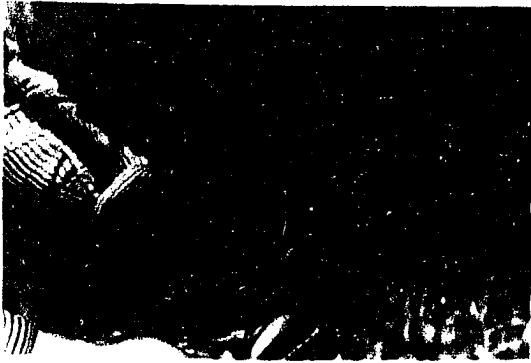


F. 53 days (Class III)

Fig. 4. Plumage development of two Canvasbacks showing some of the individual variation (continued from Fig. 3).

break their sheaths is in contrast to the Mallard where the primaries break their sheaths at the start of Class III. The feathers above the tail emerge forming a triangular pattern on the rump. At the same time the scapulars and primaries extend posteriorly so that only an inverted "V" of down can be seen on the rump when viewed from the rear (see Figure 4E). The upper wing coverts begin to come in at this point. Eventually, the "V" of down disappears and the coverts cover most of the remaining sheaths on the flight feathers. At this point, the bird appears fully feathered while sitting on the water and enters Class III.

Class III -- A large patch of down which remains on the back is hidden by the wings and scapulars while the bird is sitting on the water, but is visible with the bird in the hand. As a result, early Class III birds, classified while in the hand, are frequently placed in Class IIC. Three or 4 days after the bird enters this class, the center of the back is feathered, leaving two small strips of down under the wings. Within a week after entering Class III, the body is completely feathered and the wings are near full size, although remnants of the sheaths are left on the primaries (see Figure 5B). It is sometimes possible to see these remnants under excellent field conditions when the bird stretches its wing. Some remnants are still on the outer primaries at the time the



A. 61 days (Class III)



B. 60 days (Class III)



C. 68 days (Class III)



D. 67 days (Class III)

Fig. 5. Plumage development of two Canvasbacks (continued from Figs. 3 and 4).

bird makes its first flight, usually from 10 to 14 days after it enters Class III.

Bufflehead

The plumage development of the Bufflehead follows the same general sequence as that of the Canvasback, although the rate of plumage development is considerably faster. The primaries break their sheaths at the start of Class IIC as in the case of the Canvasback. However, there are some important differences in the sequence of plumage development. Because of their small size and rounder shape, even Class IC birds resemble a "ball of fluff," which is the term used by Gollop and Marshall (1954) to describe IA and IB ducklings. Once a worker becomes familiar with the species, he has little trouble classifying the ducklings. Class IIB Buffleheads differ from Canvasbacks in the same class in that the head and neck are still downy. The color pattern of the Class I duckling's head remains evident into mid-Class IC, when the cheek patch of the juvenal plumage becomes evident as the head and neck feathers appear.

Lesser Scaup

The sequence of plumage development of the Lesser Scaup is intermediate between those of the Canvasback and Bufflehead (see Figures 6 and 7). The differences mentioned above for the Bufflehead exist for the Lesser Scaup, although not to

the same degree. Because there is relatively little contrast in the color patterns of downy Lesser Scaup, the fading of down is not as noticeable as in most species, particularly in poor light. Also, the birds always have a rounded appearance as in the Bufflehead. As a result, it is difficult to place Class I ducklings in the correct subclass. The tendency is to underestimate the age. There is also less contrast between the color of the down and the feathers than in many species. As a result, feathers may not be noticeable in early Class IIA, and some down may not be noticeable in late Class IIC when light conditions are less than ideal.

As in the case of the Bufflehead, the head and neck of the Lesser Scaup feather later in the sequence of plumage development than those of Canvasbacks and Mallards. Feathers do not begin to appear on the head and neck until the bird is well into Class IIB. The cheek usually appears noticeably mottled on the 3rd or 4th day of that subclass, indicating that the feathers have just emerged. The last of the down disappears from this area within 2 or 3 days after the bird enters Class IIC.

Feather Growth

The mean rates of growth of the 9th primary, 6th secondary, longest tertial, and middle rectrix are given for the Mallard in Figure 8,



A. 9 days (Class IB)



B. 16 days (Class IC)



C. 23 days (Class IIA)

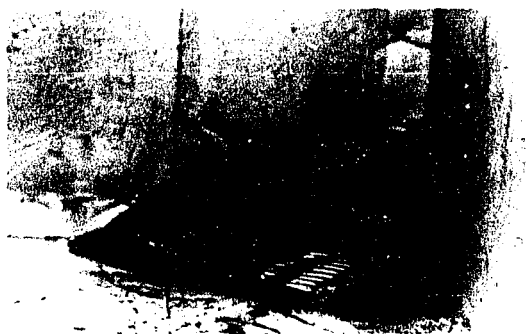


D. 30 days (Class IIA)

Fig. 6. Early plumage development of the Lesser Scaup.



A. 37 days (Class IIC)



B. 37 days (Class IIC)



X C. 44 days (Class IIC)



D. 44 days (Class IIC)



E. 51 days (Class III)



F. 51 days (Class III)

Fig. 7. Later plumage development of two Lesser Scaups showing some individual variation.

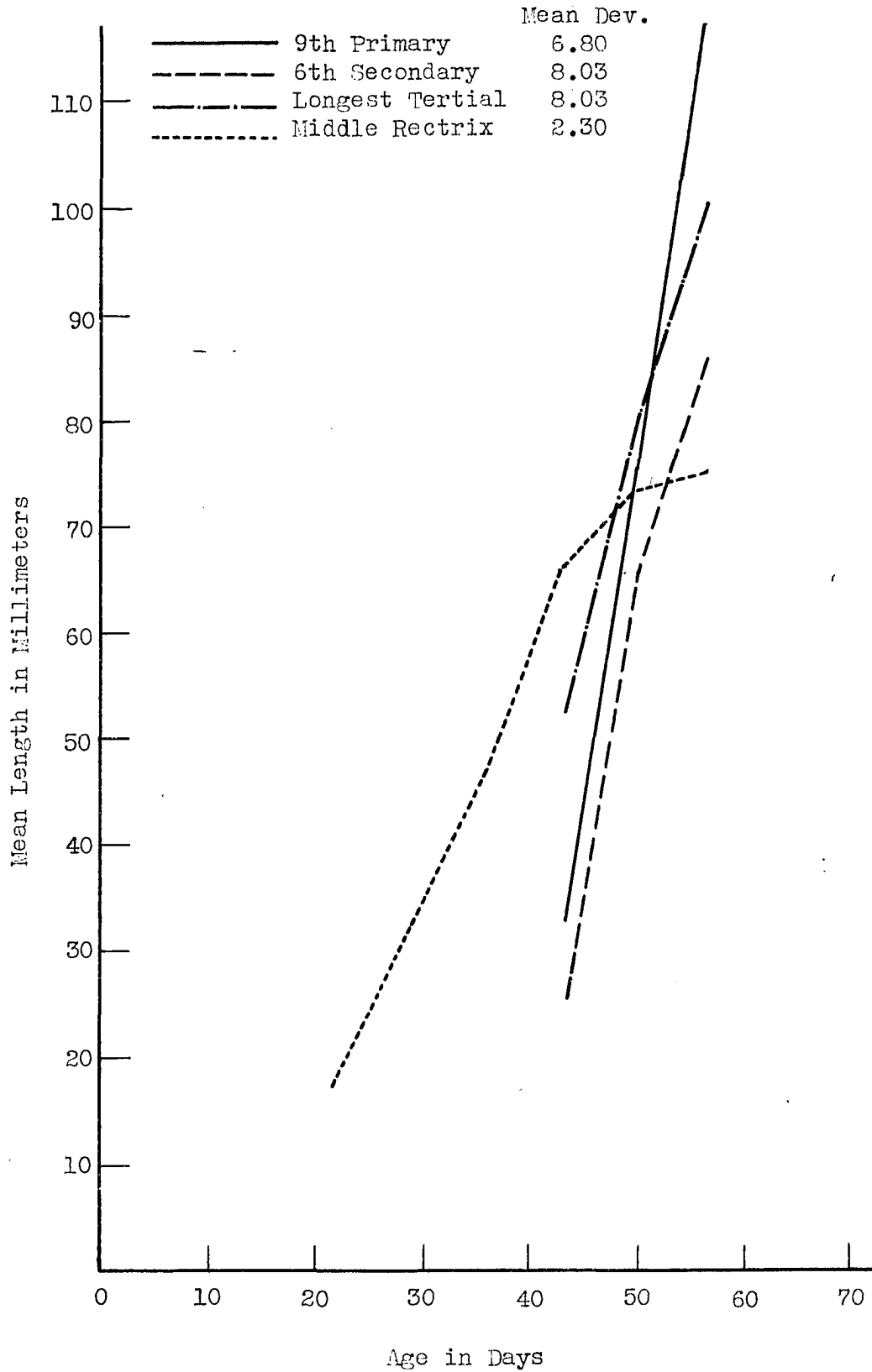


Fig. 8. Feather growth of the Mallard.

for the Canvasback in Figure 9, and for the Lesser Scaup in Figure 10. The rate of growth of the longest scapular of the Lesser Scaup is also given in Figure 13. This latter measurement was not taken on the Canvasback and Mallard because its importance was not realized until most of the ducklings of these species were able to fly. Veselovsky (1951) found that the rate of growth of the primaries of hatchery-reared Tufted Ducks (Nyroca fuligula) varied from day to day, ranging from 0 to 10 mm per day. It seems likely that some evidence of this daily variation would be found even with weekly measurements. All measurements taken at Tetlin indicate that individual feathers grew at a constant rate from day to day; diurnal variations would not show up as all measurements were taken at the same time of day.

While in some individuals certain feathers emerged a week or more before the same feathers in other individuals of the same species, there was little individual variation in the rates of growth once the feathers emerged. This lack of variation in the post-emergence growth rates of individual feathers was particularly evident in the primaries (see Figure 11), secondaries, and tertials. There was more variation in the individual rates of growth of middle rectrices and the longest scapulars. Part of the apparent variation in the growth curves of the rectrices may be due to the tips of the feathers breaking off. This breakage occurs on most of the rectrices, but does not occur uniformly.

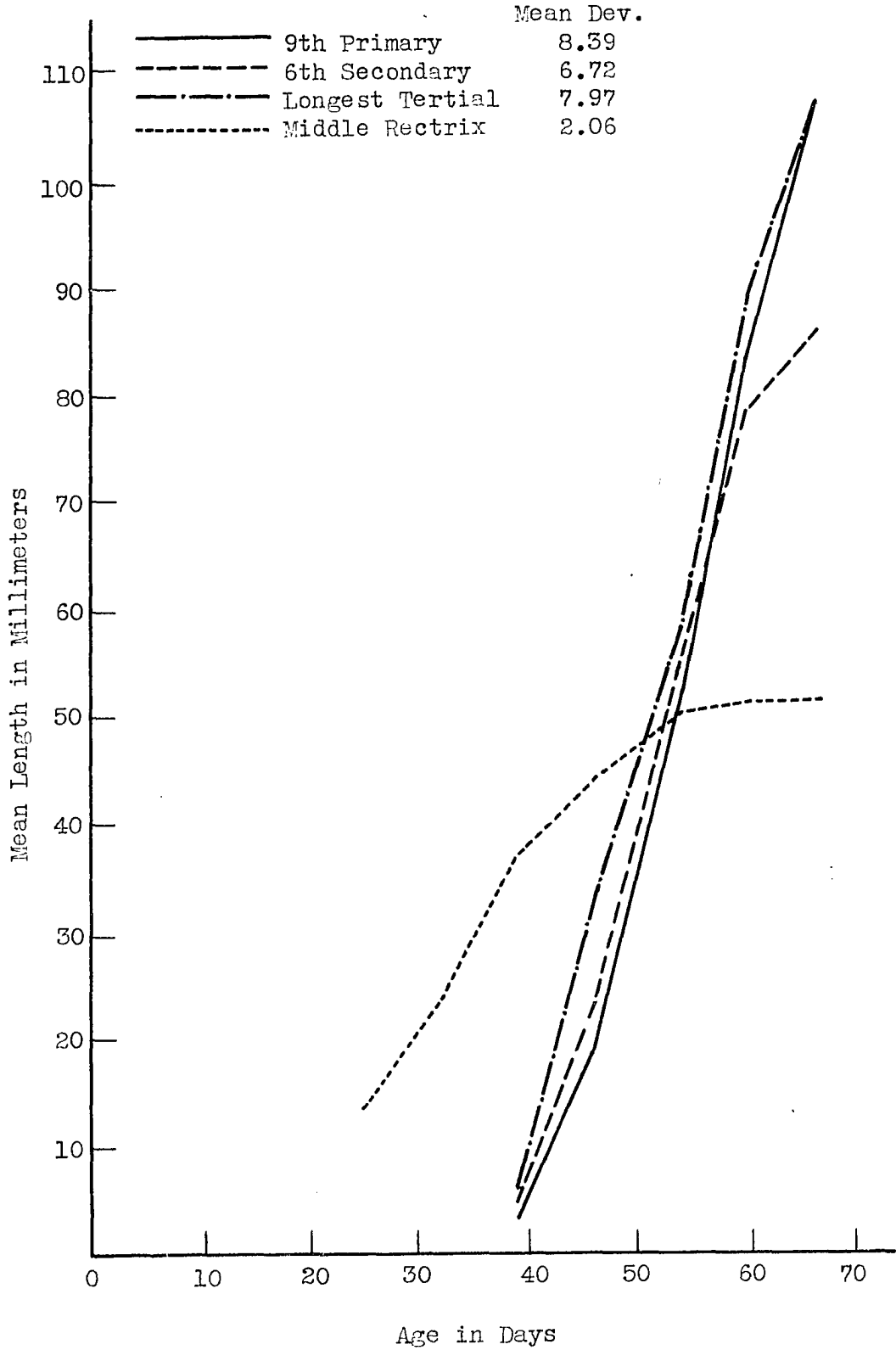


Fig. 9. Feather growth of the Canvasback.

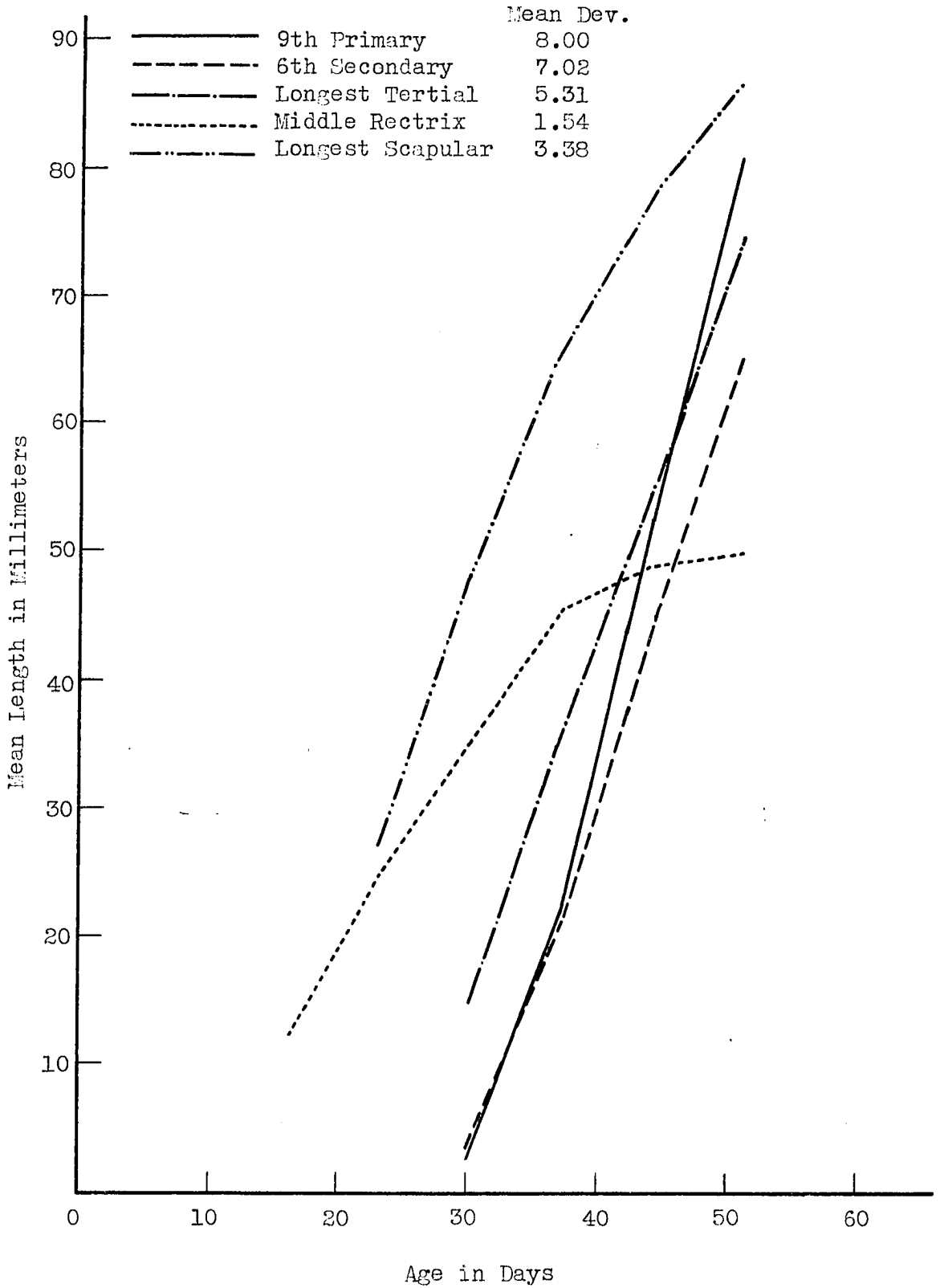


Fig. 10. Feather growth of the Lesser Scaup.

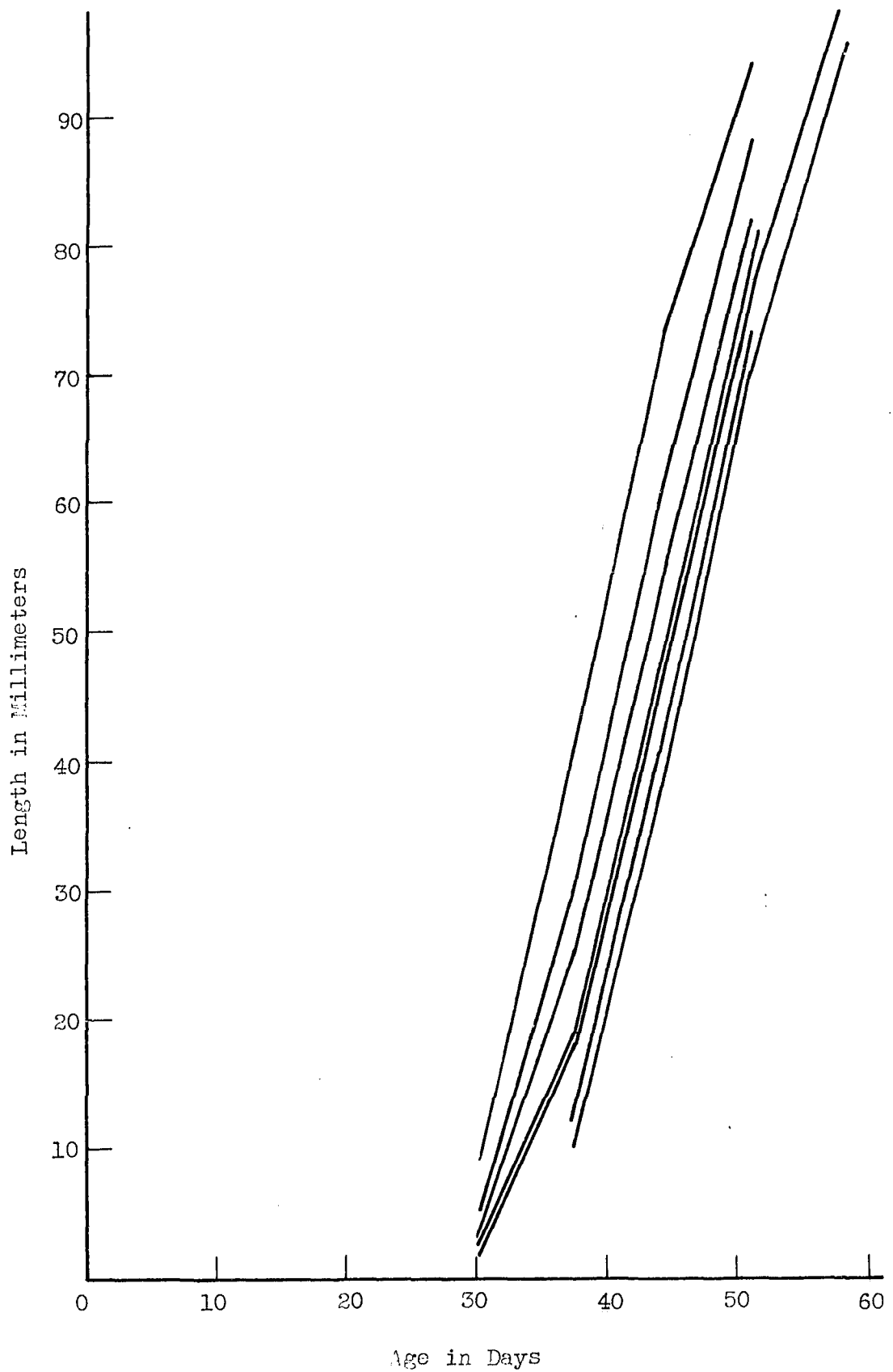


Fig. 11. Growth of the 9th primary of seven individual Lesser Scaups showing similar rates of growth despite different times of emergence.

The scapulars are more difficult to measure accurately than the other feathers measured, and errors in measurement may have been responsible for some of the apparent variation in their individual growth curves.

Precise comparative information on the rates of growth of feathers of Canvasbacks at lower latitudes is available (Dzubin, 1959), but the investigator averaged all birds in a plumage subclass, making it difficult to separate individuals of a specific age. Satisfactory comparative information for the Mallard and the Lesser Scaup was not found. The southern growth rates for the Canvasback appear to be similar to those at Tetlin, although the individual feathers did not emerge as early on most of the individuals studied at Tetlin.

Growth of Body Parts

The mean rates of growth as expressed by body weight, culmen length, and tarsus length are given for the Mallard in Figure 12, for the Canvasback in Figure 13, and for the Lesser Scaup in Figure 14.

There was considerable individual variation in the rates of weight increase, although the general shape of the curves was essentially the same for all individuals of a species. There appears to be a period during the first few days after hatching when no increase in body weight or in the length of the tarsus occurs. This period is particularly noticeable in the Canvasback, which is the only species which was weighed

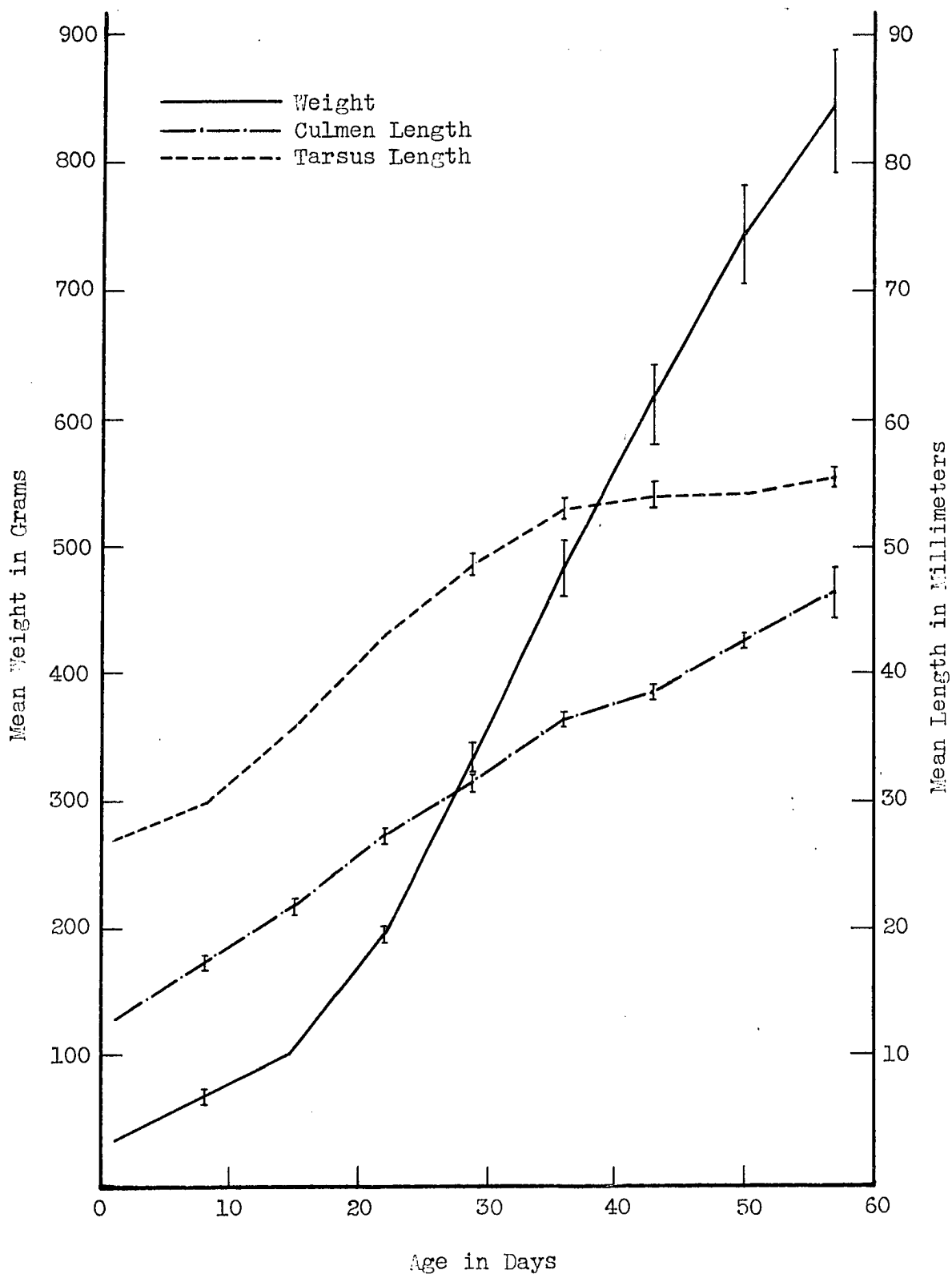


Fig. 12. Mean increase of weight, tarsus length, and culmen length of the Mallard. Vertical bars show the measurement error.

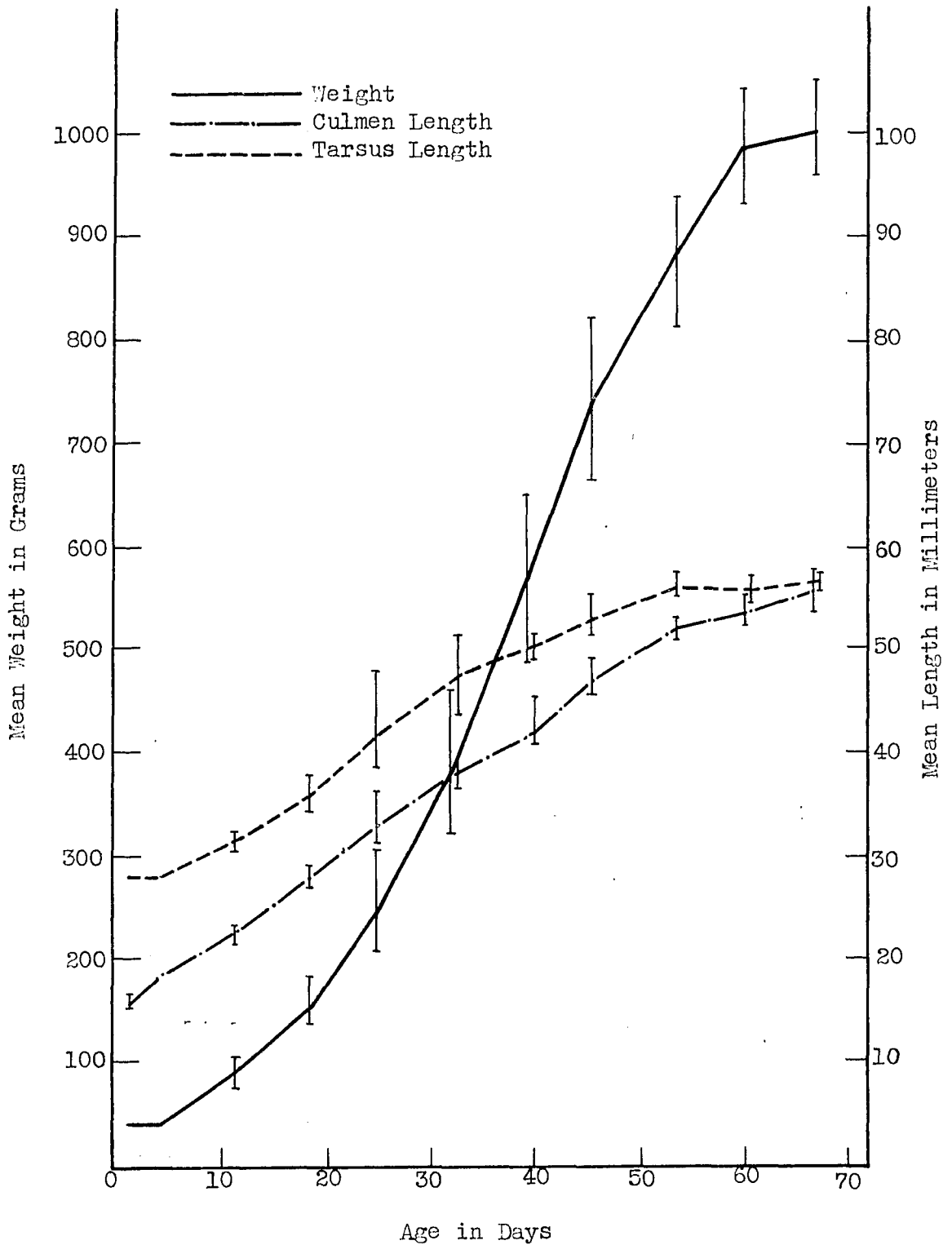


Fig. 13. Mean increase of weight, tarsus length, and culmen length of the Canvasback. Vertical bars show the measurement range.

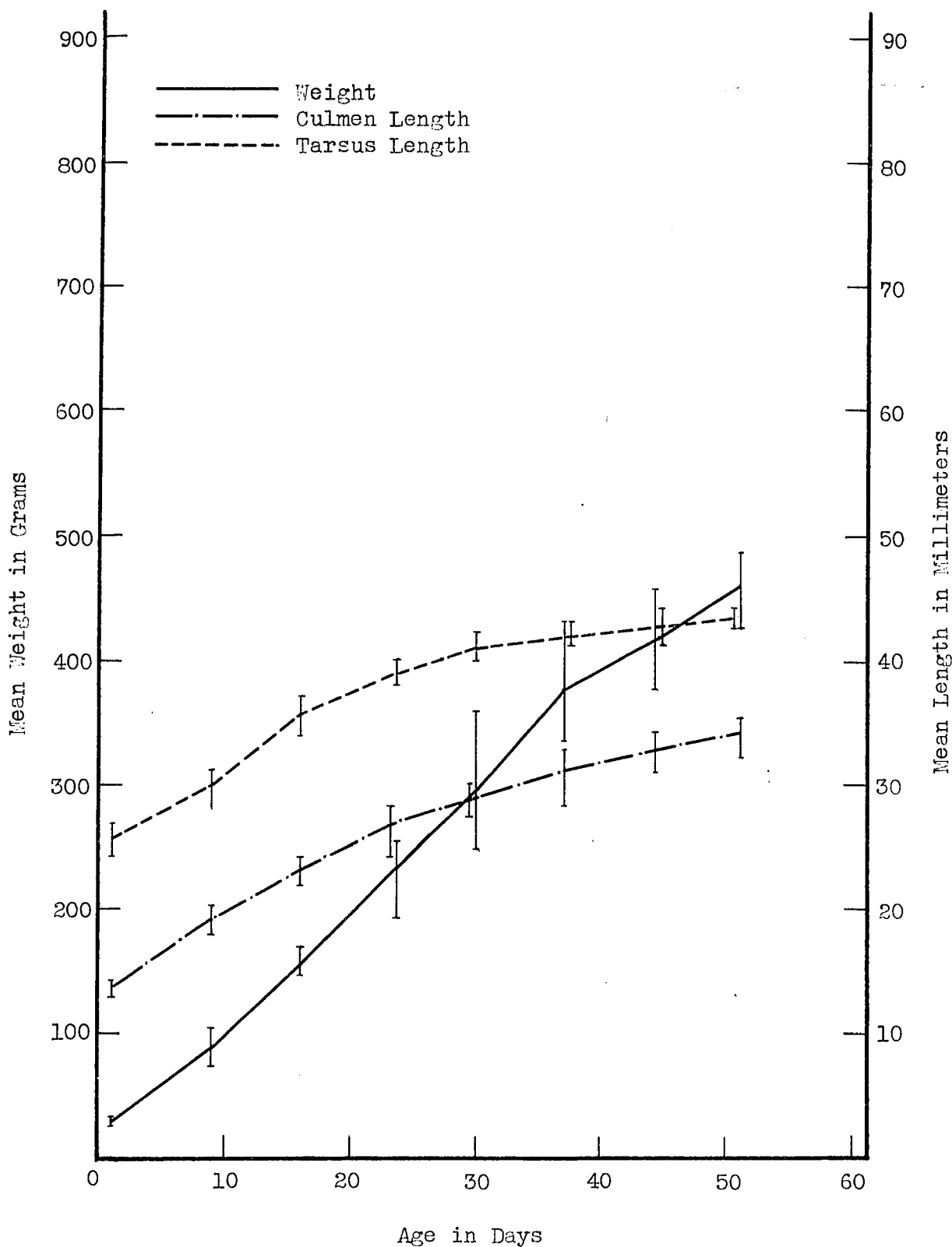


Fig. 14. Mean increase of weight, tarsus length, and culmen length of the Lesser Scaup. Vertical bars show the measurement range.

and measured more than once during the first 3 or 4 days, but there is some indication that a period of no increase in weight and tarsus length also occurred in the Mallard and the Lesser Scaup. Growth of the culmen in all three species appears to continue from the day of hatching.

The Canvasback's weight curve showed a marked leveling-off after the 60th day. This leveling-off occurred just before flight was attained, when they were near full adult weight. It is possible that continued measurements would have shown the same leveling-off for Mallards and Lesser Scaups, but all individuals of these species were able to fly from the pond before it occurred. Veselovsky (1953) found a similar leveling-off in the weight curve in several species of duck in Europe. He also found another plateau or even a drop in weight at the time when the first flight feathers were beginning to grow. This latter plateau occurred in some of Weller's (1957) Redheads and was evident in Southwick's (1953) data. All three of these studies were conducted on hatchery-reared birds. Dzubin (1959) did not find this plateau in wild Canvasbacks, but thought that a larger sample might show one. At Tetlin, however, even regular measurements of the same individuals failed to show any leveling-off of the weight curve at the time of major growth of the flight feathers in any of the species studied.

From the available information, the rates of increase of weight for all three species and of the length of the culmen and tarsus for the Canvasback are similar at both northern and southern latitudes.

DISCUSSION

Individual Variation in Plumage Development

There was considerable apparent variation in the rates of plumage development among individuals of the same species and sometimes among individuals of the same brood. The lengths of time spent in each subclass by a number of individual Canvasbacks are shown in Table 3. The variation was not as great in the other species studied, but the samples were too small to be expected to show the complete range of variation that exists in the population of those species.

"Rate of plumage development" is a poor term to use because it indicates that the plumage develops at a continuous rate from hatching to flying, which is not true. It is better to divide this pre-flight period into two portions, one covering the time prior to the emergence of the first juvenal feathers and the other covering the time during which the juvenal feathers are coming in. Class I corresponds roughly to the period prior to the emergence of the first teleoptiles, although the rectrices do appear in this class. The period of feathering corresponds to Classes II and III. A look at Table 3 will show that the length of time spent in Class I varies greatly, while the period of feathering is relatively constant for all individuals.

While the overall length of time different individuals spent in Classes II and III did not vary greatly, the length of time they spent in

Table 3

Age Span (in days) for Each Plumage Subclass of Individual Canvasbacks at Tetlin

Brood Number	No. of Individuals	IA	IB	IC	IIA	IIB	IIC	III	Flying
27A	1	1-8	9-15	16-30	31-40	41-47	48-58	59-68	69
	1	1-8	9-17	18-26	27-38	39-42	43-50	51-67	68
24H	1	1-8	9-17	18-31	32-29	40-47	48-56	57-70	71
	1	1-8	9-17	18-33	34-42	43-48	49-56	57-70	71
24A	4*	1-10	11-18	19-25	26-32	33-37	38-50	51-61	62-64
27F	5*	5	12	?-18	19-25	26-34	35-45	46-?	?

* All members of brood developed at same rate.

each subclass did vary. Certain individuals require less time to pass through Class IIA and more time to pass through Class IIB than other individuals. It is necessary to look at all the factors which determine the rate of feathering in order to understand why these differences exist, because they are a result of slight differences in several factors rather than great differences in any one factor.

1. Judgement of the Observer -- Some of the variation is undoubtedly due to errors in the judgement of the observer as a result of varying conditions of visibility. When possible, an attempt was made to compensate for poor conditions by making observations at closer range or by using a spotting scope. However, in cases where the criteria for separating two subclasses are not well defined, some errors probably did occur.
2. Variation in Time of Sloughing off of Neossoptile -- The down feather or neossoptile is pushed out and remains on the end of the teleoptile until it is sloughed off. Because this sloughing is a mechanical action and may depend on the activity of the bird, the neossoptile may remain on some birds longer than others, making them appear downy for a longer period of time.
3. Rate of Growth of Individual Feathers -- The rates of growth of individual feathers, as determined by weekly measurements of single feathers, were fairly constant for all individuals. This lack of variation in rates of feather growth was particularly

true for flight feathers (see Figure 11). However, there were slight individual variations, particularly in the rates of growth of the scapulars, tertials, and rectrices.

4. Sequence of Feather Emergence -- Weekly observations of birds in the hand and daily field observations indicated that little variation existed in the sequence of feather emergence within each species, although slight individual differences may have occurred.

5. Time of Emergence of Individual Feathers -- While the time at which feathers began to emerge varied, the length of time between the emergence of any two specific feathers appeared to be relatively constant. Relative differences in the time between the emergence of the first feathers on the side of the body and the emergence of the primaries can be demonstrated by comparing the time between the first day of Class IIA and the day the primaries break through their sheaths. In all Canvasbacks studied, this period was either 17 or 18 days. Therefore, it appears that the primaries and possibly all feathers emerge at a set time after the first feathers emerge, regardless of the age at which the first feathers emerge. Here again, there may be slight individual variations.

The individual effects of the judgement of the observer and the sloughing-off of the neossoptile are obvious; however, the rate of

growth, sequence of emergence, and relative time of emergence of individual feathers act together. A section of the body will appear feathered under field conditions if many short feathers emerge at once or if a few long feathers grow back and cover the down. The length of time spent in a given plumage subclass with the exception of IA and IB is controlled by the time and sequence of emergence and the rate of growth of specific feathers. Each factor, however, is not equally important in each subclass. The length of time spent in Class IC depends primarily on the time of emergence of the first feathers on the side. Because down obscures feathers until several days after they first emerge, the rate of growth of the feathers will have a slight effect on the time the feathers become visible under field conditions and, hence, will affect the age of entry into Class II. The time required to go through Class IIA depends on the sequence of feather emergence and the length of time between the emergence of the first feathers and the feathers of the breast, sides, head, and neck. The time spent in Class IIB depends on the time and sequence of emergence of the feathers on the rear of the body but is also dependent on the rate of growth of the scapulars which grow back and cover the down on the back long before any feathers emerge there. The rates of growth of the scapulars and tertials are also the major factors regulating the length of time spent in Class IIC. The length of time spent in Class III depends on

the time of emergence of the flight feathers with respect to the other feathers and on the rate of growth of the flight feathers. Therefore, if all the feathers on two birds have the same rates of growth but the time between the emergence of certain feathers is less for one bird, this latter bird will require less time to go through the various subclasses, but the differences will be greater in Class IIA than in Class IIB. With slight individual variations in all three factors, one would expect a situation similar to that shown in Table 2 where one individual might spend more time in one subclass and less time in another subclass than another individual of the same species.

From the foregoing discussion it is evident that the most important variation of plumage development among individuals of the same species occurs at the time that the first feathers emerge. However, if variations occur at this stage, there will be equal variation in the ages of birds at all later stages of plumage development. Therefore, errors may occur when an attempt is made to determine the age of individual ducklings using the average rates of plumage development, and investigators using this system of age determination should be aware of this limitation. When applied to large groups of ducklings, the system can be a useful tool; but when applied to individuals, it cannot be relied upon to give more than a rough estimate of age.

Sexual Differences in Rates of Plumage Development

The Lesser Scaup was the only species studied for which both sexes were known to be represented throughout their entire pre-flight development. The sex was not determined for any Buffleheads and for most Canvasbacks. Those Canvasbacks for which the sex was determined were females, and all of the Mallards were females. In the case of the Lesser Scaups, the four females feathered faster than the three males; however, there was no distinct gap between the sexes and the sample was small. Body growth, as expressed by weight increase, was also faster for females than for males. However, Dzubin (1959) found that male Canvasbacks averaged heavier than females in the later plumage subclasses, although there was considerable overlap. Weller (1957) found a similar situation for the Redhead. Therefore, there is a good possibility that the situation found in the Lesser Scaups studied at Tetlin is actually the reverse of what is true of the species as a whole. The sexual differences in the rate of plumage development of scaups at Tetlin may also be the opposite of what exists in the population as a whole, because those individuals which exhibited a faster rate of body growth also tended to exhibit a faster rate of plumage development. It would take a much larger sample to determine whether sexual differences in rate of plumage development actually exist. It seems unlikely, if differences do exist, that they would be great enough to cause

any problems beyond those presented by the individual variation mentioned previously.

Value of Measurements as Criteria for Determining the Age of Ducklings
in the Hand

Originally, it was hoped that the measurements of certain feathers and body parts could be used as criteria for more precise age determination of ducklings in the hand than is possible with the plumage classification system which is being used here. Unfortunately, the great variation in the age at which feathers first appear, which limits the usefulness of the plumage classification system, also limits the usefulness of feather measurements as age determination criteria. The value of weight measurements is likewise limited as there tends to be as much or more correlation between weight and stage of plumage development as there is between weight and age, particularly at the start of Class IIA. Canvasbacks showed the greatest individual variation in rates of weight increase and in the time of the emergence of the first feathers. All four of the individuals which were weighed at the start of Class IIA weighed between 300 and 350 grams, although there was a difference of up to a week in age. There is some indication from the two specimens collected from brood 24F (see Table 3) that the members of this brood, which entered Class IIA almost 2 weeks before the average, weighed about the same as the other ducklings at the same stage of plumage development. Therefore, the weight of a bird is of

no greater value for age determination than is the plumage subclass.

The culmen and tarsus growth curves appear to be more constant among individuals than the weight curves, but the rates of growth of these parts are slow so that considerable overlap in measurements occurs among birds with a week difference in age and, therefore, these measurements cannot be relied upon for accurate determination of ages, particularly in the later stages of pre-flight development. It is important to note that the individual variations in the growth curves are greater for those species which were represented by more individuals in the study. Obviously the samples are too small to determine the range of variability that might be expected to exist in the population as a whole. Therefore, the overlap in weight, culmen, and tarsus measurements of different age groups is probably even greater than indicated.

The growth rates of feathers are faster than those of the culmen and tarsus so there should be less overlap between age groups than with the culmen and tarsus. However, there are other limitations. The rectrices appear earlier than the other feathers, but they also attain their full length earlier and are subject to breakage. The period of fastest growth of a rectrix lasts for only 20 to 25 days and, even during this time, they are unreliable for age determination because of the breakage of the tips.

Because of the rapid growth rates, little overlap occurred in the lengths of the 9th primary, 6th secondary, and the longest tertial between birds of a week or more apart in age. Unfortunately, these can be used only in the last 3 weeks before flight is attained.

The length of the longest scapular would probably be the most reliable single criterion for age determination, as it maintains a relatively fast rate of growth over a longer period of time than most other feathers. Even with this measurement, there is probably some overlap between birds a week or more apart in age. Accurate measurements of the scapulars are difficult to obtain because of the structure of the feather. Also, little information on the growth of the scapulars of the Mallard and Canvasback was obtained in the present study.

It is evident that none of the measurements taken in the present study provide a method of age determination of birds in the hand which would be any more reliable than the plumage classification system used on birds under field conditions. With experience, however, workers should be able to estimate the age of most ducklings to within a week of their correct age, using a combination of measurements and the stage of plumage development.

Differences in Rates of Plumage Development Between Tetlin Ducklings and Those at Lower Latitudes

A comparison of the average rates of plumage development of

ducklings observed at Tetlin in the present study with the average rates observed in southern Canada and northern United States by other investigators (see Table 2) does not substantiate the idea that northern ducklings have faster rates of plumage development than southern ducklings of the same species. The rate of feathering of northern birds, apparently, can be faster, slower, or the same as that of southern birds. For the purposes of this discussion, the rate of plumage development is considered to be the time between hatching and attainment of flight. The rate of body feathering is considered to be the time from the first appearance of juvenal feathers on the side of the body to the time when no down is visible under field conditions. In other words, the rate of plumage development involves Classes I, II, and III, whereas the rate of feathering involves only Class II.

The plumage development information presented in Table 1 was determined by a number of different individuals and under different conditions. How these varying conditions affect the rates of growth and plumage development is difficult to determine. The information gathered at Tetlin in the present study was from observations under field conditions of wild birds either under completely natural conditions or semi-natural conditions where they were restricted to one pond without maternal care. Most of the information on southern birds presented in Table 2 was obtained from wild ducklings. The Canvasbacks were

classified in the hand. The information on Buffleheads from Washington was collected from birds reared under hatchery conditions. These Buffleheads were from eggs collected in the wild in British Columbia and included one collected from the Tetlin study area.

It has been assumed that no great differences in rates of growth and plumage development exist between hatchery reared birds and wild birds. Southwick (1953) suggests that down might wear off wild birds somewhat faster than hatchery birds. Weller (1957) found little difference when he compared the rates of plumage development of a few wild Redheads with those he had reared in a hatchery. Hochbaum's observations of Canvasbacks at Delta, Manitoba, indicate that little difference exists in plumage development between hatchery and wild birds. However, Dzubin (1959) found that his wild Canvasbacks were 200-300 grams heavier at 6 weeks than Southwick's (1953) hatchery reared birds and that they were somewhat more advanced in the later stages of plumage development, probably due to faster wearing off of down. Gollop and Marshall (1954) point out that variations between hatchery and wild birds may be greater in some species due to differences in temperament of species and differences in hatchery techniques. In most cases, the differences in rates of plumage development are not great. The Bufflehead appears to be an exception to this. The differences in plumage development shown in Table 2 are much greater than one would expect

from differences in latitude, as will be shown later. What weight information is available indicates an equal difference in rates of body growth. According to Dennis Crouch (pers. comm.) who provided comparative information, Buffleheads have proved to be difficult to propagate in captivity, indicating that they do not adapt to captivity as well as many other species. This lack of adaptation could be responsible for the differences in rates of growth and plumage development. Because of the likelihood that the Seattle rates are not representative of what occurs in the wild, the following discussion will be based on the information gained from the Mallard, Canvasback, and Lesser Scaup, but not the Bufflehead.

While the length of time required to attain flight for Mallards was similar for both Tetlin and South Dakota, the rate of body feathering of the Tetlin birds was considerably faster. Once the first feathers appeared, South Dakota birds required 27 days to become completely feathered when viewed under field conditions while Tetlin birds required only 15 days. Canvasbacks in Manitoba required 28 days to pass through Class II while those at Tetlin required 25 days. Lesser Scaups in South Dakota required 22 days while those at Tetlin required 27 days.

The samples of all groups of ducklings were small. Therefore, it is difficult to draw definite conclusions from the available information. However, certain aspects are surprisingly consistent and fit into a logical pattern. The fact that Tetlin Mallards required slightly more time to attain flight, even though they feathered faster, is due to the

longer period spent in Class IC and III. Judging from the information on individual variation obtained from Canvasbacks (see Table 3), it is possible that the Mallards studied at Tetlin spent a longer than average time in Class IC. However, if the case of the Canvasback holds true for the Mallard, the rate of development through Class II and III would be relatively constant for all individuals in a given area at a given time, and those studied at Tetlin should be representative of the population at Tetlin for this period.

As stated in the discussion of variation in rates of plumage development among individuals, the main factors controlling the rate of feathering are the sequence of feather emergence, the time between the emergence of the first feathers and of other specific feathers, and the rate of growth of individual feathers. The sequences of feathering described for birds at lower latitudes (Southwick, 1953; Dzubin, 1959) are essentially the same as those observed at Tetlin. The time between the appearance of the first body feathers and the breaking of the primary sheaths can be used to determine the relative length of time between the emergence of these feathers. Gollop and Marshall (1954) state that the primaries of South Dakota Mallards break their sheaths on about the 35th day which is 17 days after the average bird enters Class II, the time when the first feathers appear on the side of the body. The primaries of the Tetlin birds broke their sheaths on about the 43rd day which is also 17 days after they entered Class II.

As previously stated, the primaries of all Canvasbacks at Tetlin broke their sheaths either 17 or 18 days after the first body feathers appeared. Those of Gollop and Marshall's (1954) average Canvasback duckling broke their sheaths 17 days after the appearance of the first body feathers. No information has been located concerning the age at which Lesser Scaups' primaries break their sheaths at lower latitudes. However, for the Mallard and the Canvasback, the time between emergence of the first body feathers and the emergence of the primaries (and possibly all other feathers) is not only relatively constant for all individuals of a species in a given area, but it is also relatively constant for individuals in both northern and southern areas. If the sequence and time of feather emergence are constant, the rate of feather growth would have to be the variable factor causing the differences in rate of feathering.

A comparison of the length of time northern birds spend in each subclass within Class II with the length of time southern birds spent in these subclasses gives further indication that the rate of feather growth is the factor controlling the rate of feathering. As pointed out previously, the rate of feather growth is of minor importance in Class IIA, of more importance in IIB, and of major importance in IIC. Therefore, a difference in rate of feather growth should be more noticeable in Classes IIB and IIC than in IIA, all other factors being equal. The differences are greater in Classes IIB and IIC than in Class IIA, as shown in Table 2.

Mallards from both areas required about the same time to go through Class IIA, but those from Tetlin went through Classes IIB and IIC twice as fast as those from South Dakota. Tetlin Canvasbacks required a little less time to go through IIB than Manitoba Canvasbacks and about the same time to go through IIC. Lesser Scaups at Tetlin required more time to go through Class IIC than those in South Dakota, while they required about the same time for Class IIB and slightly more for IIA. The above information suggests that the rate of body feather growth of northern birds is faster than that of southern birds in the Mallard, about the same for the Canvasback, and somewhat slower for the Lesser Scaup.

There also appear to be differences in the age at which feathers first appear, but individual variation is so great that the differences in averages may be due to the small samples. It is possible that some individual Mallards at Tetlin spend as much as 10 days less in Class I than those studied. Assuming that these faster individuals would require the same length of time to go through Classes II and III as the individuals studied, they would attain flight at an earlier age than the individuals studied at both Tetlin and South Dakota.

The constant time between the emergence of the first body feathers and the emergence of the primaries places limits on the age at which flight is attained. The age at which the primaries emerge is

more or less fixed, the only important variable being the age at which the bird begins to feather. The age at which flight is attained is determined by this fixed length of time plus the time required for the primaries themselves to reach full length. The length of this pre-flight period is independent of the length of time required for the body to become feathered. This is why the primaries of the Mallards at Tetlin broke their sheaths at the start of Class III, whereas those of the South Dakota birds broke through at the end of Class IIB, and it is also the reason why the Tetlin Mallards spent more time in Class III than those from South Dakota. The bodies of the northern birds feathered faster, but the primaries of both groups emerged at the same time with respect to the start of feathering. The combined times of Classes II and III did not differ greatly for either group of birds.

A comparison of the length of time between the breaking of the primary sheaths and the attainment of flight should indicate the relative growth rates of the primaries of the northern and southern birds of each species. For Mallards, this time averaged 19 days for Tetlin birds and 20 days for South Dakota birds. The average times for Canvasbacks were also 19 days at Tetlin and 20 days in Manitoba.

Actual measurements of the primaries of hatchery reared Lesser Scaups in southern Manitoba taken by J. P. Rogers of the Gaylord Memorial Laboratory in Puxico, Missouri, (pers. comm.) showed that

these birds had almost identical rates of primary growth as those studied at Tetlin. However, Rogers noted that wild Lesser Scaups were flying 10 days to 2 weeks before his hatchery reared birds. Therefore, the wild birds in Manitoba must have had faster rates of primary growth than wild birds at Tetlin.

The similar rates of growth of primaries of Mallards at both northern and southern latitudes would appear to contradict all the previously presented evidence. It has been suggested that the rates of growth of body feathers, particularly scapulars of Mallards, were faster for northern birds, but now the information suggests that the primaries grow at about the same rate. Actually, this situation is exactly what should be expected; however, a discussion of the probable causes of variation in feather growth rate is necessary to demonstrate why this is true.

Possible Causes of Differences in Rate of Feather Growth at Different Latitudes

There are several factors which may cause a variation in feather growth rate at various latitudes. These factors may be either genetic or environmental. The idea of a genetic difference seems unlikely. There are fast- and slow-feathering alleles in chickens and theoretically similar alleles could exist in wild ducks; however, the migratory habits of ducks make it unlikely that two separate populations, one with each genotype, would develop. Dennis Crouch (pers. Comm.) raised one

Bufflehead from an egg collected at Tetlin along with a number of others from eggs collected in British Columbia. The duckling from Alaska demonstrated rates of body growth and of plumage development which were close to the average of the other ducklings, suggesting no genetic difference.

The two main environmental factors which have been suggested as possible direct or indirect causes of a latitudinal variation in growth are temperature and duration of daylight. Karplus (1952) has suggested that in areas having lower average temperatures, homiothermic birds require more energy to maintain their body temperature and that this might affect growth rates. However, northern birds would require more energy to maintain their body temperature and this would tend to slow the rate of feather growth rather than speed it up. All indications are that Mallards at Tetlin had a faster rate of body feather growth, indicating that temperature had little effect. Duration of daylight is the most commonly suggested cause of differences in rates of plumage development, and the evidence indicates that a direct correlation exists. Figure 15 shows the approximate, maximum possible duration of daylight and the span of the pre-flight development of the "average duckling" of each species for each of the areas from which data are available. The exact time of hatching of the ducklings used in other studies is not known, so the average times listed by Hochbaum (1944) for

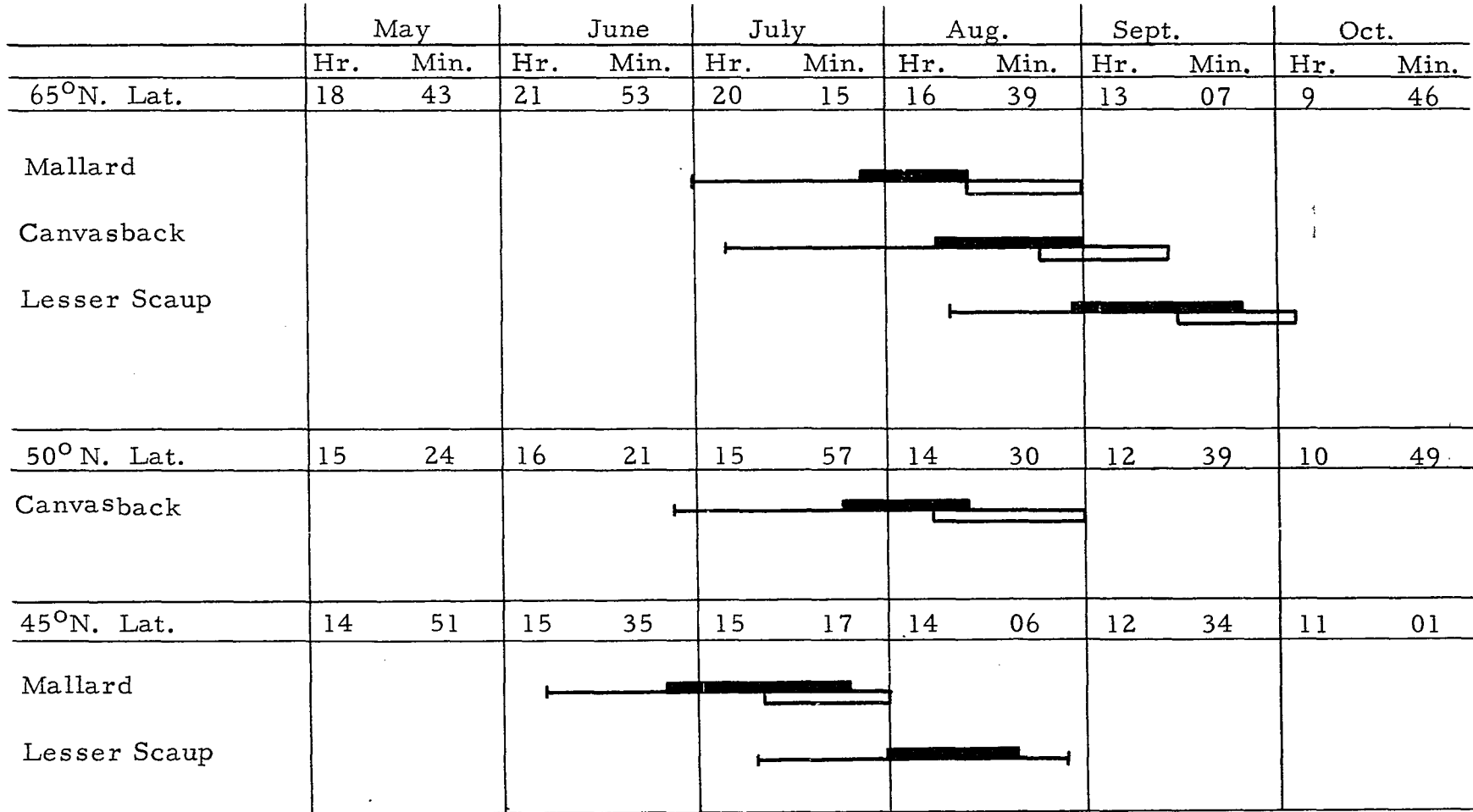


Fig. 15. Average span of the pre-flight development at various latitudes and the maximum possible duration of daylight on the 15th of each month (Thomas, 1953) at those latitudes. The total pre-flight period is represented by , Class II by , and the period of growth of the primaries by .

Manitoba were used. As can be seen, there are large differences in the duration of daylight between the northern and southern areas. While there is more daylight in the North throughout most of the brood season, the difference is not uniform throughout this period and by late September and October there is actually less daylight. Also, the brood season in the North is sufficiently delayed to complicate the situation further.

There was an average of about 15 1/4 hours of daylight in South Dakota at the time of major body feather growth of the average Mallard. At the time of major body feather growth of the Mallards studied at Tetlin, there was an average of over 18 hours of daylight. However, at the time of growth of the primaries, there was an average of 15 1/2 hours of daylight at Tetlin and 15 hours in South Dakota. In the case of the Canvasback, there was an average of about 15 hours in Manitoba and 15 1/2 hours at Tetlin during their respective times of major body feather growth. There was an average of about 14 1/2 hours of daylight during the time that the primaries were growing in both areas. Lesser Scaups feathered under an average of 14 1/4 hours of daylight in South Dakota and an average of 13 hours at Tetlin. There was only an average of 12 1/4 hours of daylight during the time of growth of the Scaups' primaries at Tetlin and probably about 14 hours in South Dakota.

Mallards, therefore, had a greater rate of body feather growth in the North under a greater duration of daylight than in the South. But,

the primaries grew at about the same rate under roughly the same amount of light. Canvasbacks at Tetlin had a slightly faster rate of body feather growth under slightly more daylight and about the same rate of primary growth under the same length of daylight. Lesser Scaups at Tetlin, on the other hand, had slower rates of body feather and primary growth than those in South Dakota and Manitoba, which follows with the greater duration of daylight in the latter area at the time that the birds were feathering. All differences in growth rates of feathers appear to be roughly proportional to the differences in daily duration of daylight.

If early nesting species have faster rates of feather growth in the North than in the South and late nesting species have slower rates in the North than in the South and if the varying conditions can influence the rate of growth of body feathers of a duckling to a greater degree than the rate of growth of the primaries of the same individual, then it is reasonable to assume that individuals which hatch early will exhibit more rapid rates of feather growth than individuals of the same species in the same area which hatch later in the season. Hochbaum (1944) has noted a faster rate of development in early broods at Delta, Manitoba. This difference should be even more noticeable at higher latitudes where the variation in length of daylight is much greater. The spring of 1964 was exceptionally late, and the first hatching dates

were almost 2 weeks later than normal. Of the birds studied at Tetlin that year, the Mallards hatched later than normal, the Canvasbacks at about the normal time, and the Lesser Scaups later than any other broods observed in the area. Therefore, the information presented in this study does not necessarily represent the average that could be expected from year to year. Mallards which hatched 2 weeks earlier than those studied probably would have had a greater rate of primary growth and would have been flying at an earlier age. Also, there is more daylight at higher latitudes than Tetlin, and a faster rate may occur in these areas. However, at some point there may be a limit beyond which added daylight would not influence the rate of feather growth.

If this correlation between duration of daylight and rate of feather growth is valid, it raises the question as to whether the duration of daylight is a direct cause or an indirect cause. There is a possibility that daylight stimulates hormone production which might affect feather growth. It has been shown many times that the effect of length of daylight on hormone production is a factor in inducing molting in adult ducks. Another possibility is that longer daylight induces longer feeding periods and that faster rates of feather growth are due to greater daily food intake. A greater quantity of food would yield more energy and could support a more rapid rate of feather growth without sacrificing body growth.

Lillie and Wang (1940) have demonstrated a nocturnal reduction of growth rates of certain feathers on Brown Leghorn capons. They found that for saddle feathers, 30% of the daily growth occurred between noon and 6:00 PM, 29% between 6:00 PM and midnight, 6% between midnight and 6:00 AM, and 35% between 6:00 AM and noon. They attributed this nocturnal reduction in feather growth to the normal diurnal depression of the rate of metabolism as evidenced by a depression of body temperature and oxygen consumption. This depression normally occurred between 6:00 and 9:00 PM, so there is a 6-hour lag before it became evident in the reduction of feather growth rate. By reversing the periods of light and dark, the daily growth curve was reversed, indicating that this drop in metabolic rate was initiated by a lack of light. However, in birds that are normally nocturnal, the curve was reversed and the depression occurred during the day, indicating that the light did not affect this depression directly, but had some other indirect effect. A complete interruption of feather growth at night has been demonstrated in wild ducks (Veselovsky, 1951).

It is possible that the period of darkness at lower latitudes exceeds the minimum sleep requirement of the birds, but that feeding activity is limited by light conditions. Therefore, the birds are not devoting the maximum possible time to feeding activity, but under greater duration of daylight they would feed more and take in a greater quantity of food each day. This longer period of activity might bring

about a reduction of the period of slower feather growth and result in more growth per day.

Moultrie, et al. (1955) and many others have found no differences in rate of feather growth of domestic fowl and ducks at various lengths of daylight. This lack of difference in rates has been attributed to the fact that food is easily available and the birds can get enough food to grow at the maximum rate even in a short day. Judging from the rates of plumage development of Southwick's (1953) ducklings, the feathers of wild ducks reared under hatchery conditions do not grow at their maximum rate, possibly because of behavioral differences.

There is probably a limit to the quantity of food that a wild duckling under natural conditions can obtain or utilize in a single day. This limit might be reached by ducklings subjected to less than 24 hours of daylight, so that beyond the amount of daylight at which this limit is reached there may be no increase in rate of feather growth as the duration of daylight is increased.

The effects of feeding behavior, total food consumption, and quality of food consumed on rates of feather growth of ducklings exposed to different lengths of daylight need further investigation. Studies of this nature would require frequent measurements of individual feathers, preferably every 3 hours. Such frequent measurements would require that the project be carried on under hatchery conditions. A greater knowledge of the effects of these conditions on the rates of growth of ducklings would be necessary to evaluate these results.

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