HATCHING AND THE HATCHING MUSCLE IN SOME NORTH AMERICAN DUCKS

HARVEY I. FISHER
Southern Illinois University, Carbondale

ABSTRACT.—The pre- and early post-hatching development of the hatching muscle, M. complexus, is described for eight species of ducks. Its pattern of change in conformation and mass is similar to that known for other birds. The time of occurrence of certain events in development appears to be correlated with length of incubation period rather than with biomass. Movement of lymph into and out of the hatching muscle constitutes the major factor in the changes in bulk of the muscle. Actual weight of the muscle at the time of pipping is roughly correlated with thickness of egg shell in ducks, as it is in grebes, but these correlations exist only within closely related phylogenetic lines in birds. It is suggested that genetic background and factors such as humidity and composition of the shell are also significant in the history of the hatching mechanism.

The time required for a single egg to hatch (from pip to emergence) is highly variable with species, season, chronological position in the clutch and, in American Coots at least, with the number of eggs in the clutch. Hatching time of a clutch (time from pip of first egg to emergence of last duckling) appears to be specifically and seasonally variable, as is emergence time (period of emergence from first to last duckling), but the latter time is much shorter in precocial species.

The hatching mechanism in the Ruddy Duck (Oxyurinae) shows major differences from that in the Anatinae and the Aythyinae in which it is similar.

The hatching muscle in birds was first considered to be the caput part of the M. cucullaris of Fürbringer (1888:1056). Since it is a true skeletal muscle in its own right and has been called M. complexus, George and Berger (1966:272) favor retention of the latter name. I agree.

Early modern studies of M. complexus aroused a minor controversy about its function. Rosenstadt (1912) regarded it as a relict with no functional significance, but Keibel (1912) believed that it furnished the power to thrust the egg-tooth of the embryo against the inner surface of the egg shell and thus effect the first break in the shell. Pohlman (1919:101) stated that the muscle was ". . . relaxed at the time of picking through the shell," and consequently the muscle could not be a functional part of the hatching mechanism.

In a series of studies in 1958, 1961, and 1962, H. I. Fisher suggested that: 1) M. complexus was indeed the power for the egg-tooth; and 2) it was likely that lymph, infiltrating the muscle just before hatching, carried nutrients for the temporarily high energy requirements of the muscle.

Driver (1960) working with the Common Eider (*Somateria mollissima*), the Oldsquaw (*Clangula hyemalis*), and the Redbreasted Merganser (*Mergus serrator*) reported that the "upward nod" was the most obvious movement of the head in the immediate pre-hatch stage and that this "nod" did bring the egg-tooth against the shell in typical pipping motions.

In 1963 George and Iype found lipase activity and a high glycogen content in M. complexus of the chick at the time of hatching, as well as in the pectoralis muscles. Their conclusion was that the hatching muscle powered the pipping process and aided in the final emergence from the shell but that the pectoralis muscles probably were the primary factor in the actual emergence of the chick.

Embryos of all avian species must in some way escape from the heavy, calcified shell, but all the experimental studies of hatching have thus far concerned themselves only with the domestic chicken. The presence of a hatching muscle with a developmental history that would make possible a contribution to hatching has been demonstrated only in the: domestic chicken (H. I. Fisher, 1958); American Coot (*Fulica americana*) (J. R. Fisher, 1962); Franklin's Gull (*Larus pipixcan*), Common Tern (*Sterna hirundo*), and Black Tern (*Chlidonias niger*) (H. I. Fisher, 1962); and in five species of North American grebes (Family Podicipedidae) (H. I. Fisher, 1961).

When the mechanical and physiological aspects of hatching become known in more species of birds, we shall undoubtedly discover considerable variation. As yet we are in no position to generalize — as is indicated by the observations of Wetherbee and Bartlett (1962) who found in the American Woodcock (*Philomena minor*) and the Willet (*Catoptrophorus semipalmatus*) that the neural processes of the cervical and thoracic vertebrae formed a ridge that ripped the shell longitudinally.

Consequently, it remains desirable to study additional groups of birds to determine the method of emergence, the occurrence of the muscle and the gross features of its development, with particular emphases on the time of maximum size and on the amount and period of infiltration of lymph.

The purpose of this paper is to report investigations of the embryological features of the hatching muscle in some North American ducks and, as adjuncts of the study, to present information on the thickness of the egg shell at hatching, hatching times for clutches and for single eggs, body weights at hatching, fertility and hatchability.

METHODS AND MATERIALS

Duck eggs collected for this study included: Mallard 44, Gadwall 39, Pintail 43, Blue-winged Teal 123, Shoveler 57, Redhead 182, Canvasback 3, and Ruddy Duck 69. The actual number of each species used for each aspect of the investigation is indicated in the figures and tables. Canvasbacks were rare and no attempt was made to secure an adequate series. Although Redheads were also scarce and extensive collecting thus undesirable, it was possible to obtain a significant number of eggs from "dump nests," eggs deposited by several females and which represented reproductive "losses" in any event since they are usually not incubated. The collections were made in the marshes at the south end of Lake Manitoba between the villages of Delta and St. Ambroise, Manitoba, Canada, and in the "Pothole Country" near Minnedosa, Manitoba.

Methods and conditions employed for incubation of eggs and study of the size of the hatching muscle were the same as those employed by H. I. Fisher (1961). At the time of this study in 1960 the possible effects on hatching time of physical contact between the eggs of a clutch (Vince, 1964) or of vocalizations (Vince, 1966) had not been postulated. The duck eggs of a clutch were arranged in linear fashion in a single trough in the incubator and, although there was no contact with eggs of other clutches of the same or other species, eggs of several clutches were at times within the audio range of sounds made by various ducklings.

Since study of synchronization of hatching within a clutch was not an objective of this investigation and since the only possible effects yet attributed to contact and sound are reported to occur in the 24 hours prior to hatching, it seems likely that the random contacts and sounds produced, if anything, only an increased variability in the ratios of hatching muscle to body weights.

The thickness of the shell was measured in ten thousandths of an inch with machinist's dial calipers. Each shell was measured immediately after hatching. The thickness was determined by averaging the measurements of three randomly-selected areas at the "pip end" of the egg; variation between these three thicknesses was less than 10%, but it is recognized that the shells may have thinned during incubation.

Computation of the "lymph area" was made by multiplying greatest length by greatest width. Since the width was variable, and the glands often roughly triangular in shape, "area" simply represented a convenient and approximate composite index to size rather than an accurate measurement of space covered.

Weights of ducklings "at hatching" were made before 10 hours of age. Since intruded yolk was included at hatching and not with any embryos before hatching, the apparent increase between pipping and hatching weights was not real.

Information on the hatching process, particularly the time span between the first pipping of an egg and the emergence of the duckling and the time between emergence of the first and last ducklings in a brood, was obtained by continuous observation of the clutch after the first egg pipped. Time was not available to watch all clutches used in this study. Our conclusions were based on watching the process in: 4 clutches of Ruddy Duck eggs, 4 of Redheads, 7 of Blue-winged Teals, 1 of Shovelers, and 2 of Pintails. Observations were also made on 15 clutches of Franklin's Gulls, *Larus pipixcan* (H.I. Fisher, 1962) and of 5 clutches of the American Coot, *Fulica americana* (J.R. Fisher, 1962).

Incubation of clutches of the same species, laid at different times, made feasible a few observations on possible seasonal differences in hatchability and hatching time.

Data on fertility and hatchability were kept on all clutches. All eggs were candled before being put in the incubators, but all were incubated for a week before any were discarded as infertile.

OBSERVATIONS ON THE HATCHING MUSCLE

General features.—M. complexus in all species investigated was a three-segment, occasionally four-, paired muscle on the dorsal aspect of the neck (Figs. 1,2). Most anteriorly it spread laterally and ventrally to cover a bit of the side of the neck in the region of vertebrae 1 and 2. It was superficial to the biventor cervicis and spinalis muscles. Without exception, each muscle of the pair was widest anteriorly where it inserted fleshily on the posterior, parietal crest of the skull between the origins of the two depressor mandibularis muscles and between the most dorsal tips of the hyoid apparatus.

The origin of the muscle was, for the most part, tendinous and from the dorsal surfaces of the transverse processes of cervical vertebrae 3 and 4, but there was some fibrous attachment to the lateral surfaces of the neural spines of these vertebrae.

Segmentation.—Segmentation of the muscle was first indicated by a transverse line between segments 1 and 2; in all species this occurred when body weight reached 5 to 9 grams. Within a species the time of first appearance of segmentation was even more uniform—for example, between 6 and 8 grams in the Redhead and 5 to 7 in the Blue-winged Teal and Gadwall.

Segment 3 showed when body weight became 1 or 2 grams greater (7 to 11 grams) except in the Mallard in which it appeared with a 13-gram body weight.

It was only at the prepip stage that the fourth segment (not found in the Ruddy Duck) became visible in the Mallard, Shoveler, and Gadwall. In the Blue-winged Teal and Redhead, segment 4 showed only after hatching, but it was present at the prepip and just-hatched stages in the Pintail.

Segmentation was faint or completely masked, temporarily, at the time of pip-

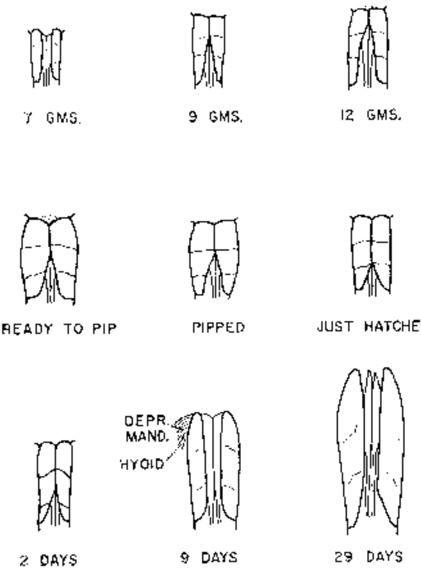

FIGURE 1. Sketches of dorsal views of hatching muscles in Blue-winged Teals of different ages. X⅔. (Weights indicated are body weights.)

ping, reappeared during hatching, and became progressively obscure (Fig. 1, Blue-winged Teal) or absent within 30 days after hatching (Fig. 2, Mallard). In the Shoveler, segments were not visible after 6 days of age, and many of the Blue-winged Teals showed no segmentation after 9 days.

Relative sizes of the segments for the Blue-winged Teal are illustrated in Figure 1; they are typical of all the ducks studied. Segment 4, when present, was a much-attenuated structure no more than half the size of segment 3 (Fig. 2, Redhead).

Although there was little or no change in this relative size of the segments during development, the segments increased in absolute size (Fig. 1). The expansion was in all dimensions, but primarily in width and in thickness.

The most easily observed indication of this rapid growth was the degree of medial extension and the extent to which the segments hid from view the underlying Mm. biventer cervices.

In the Blue-winged Teal, a typical species in these developments, embryos of 3 grams total weight possessed hatching muscles consisting of two thin bands lying side by side and touching each other throughout their length. Between the 4- and 6-gram stages the muscle bands began to separate from one another, and they were usually completely apart at 7 grams of body weight. Within the span of a day or so, and an increase of one or two grams in body weight, the anterior ends of the pair of muscles were again in contact along their medial edges (Fig. 1). Contact between the muscles continued progressively caudad until the pipping and hatching stages when, in more than half the embryos, the inner edges touched throughout their length. In the fourth or fifth day of age the muscles

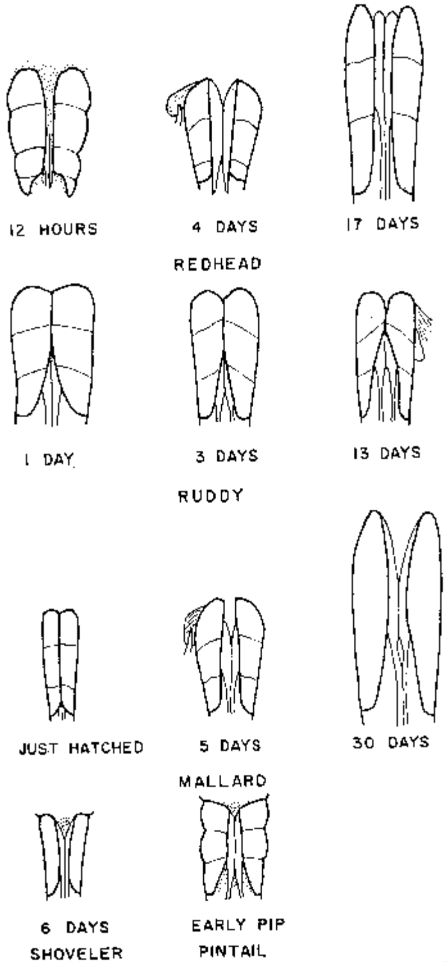

FIGURE 2. Sketches of dorsal views of hatching muscles in five species of ducks. X¾.

of the two sides separated permanently; this dissociation began at the posterior end and proceeded anteriorly to the junction of segments 1 and 2 while a slower disengagement was initiated at the anterior end. The process is shown for the Ruddy Duck in Figure 2.

The Shoveler's development in this regard was the same as the Blue-winged Teal's except that medial contact between the two sides was initially lost at 9 grams of body weight, and final separation took place 2 days after hatching. The only variation between the Teal and the Pintail was that the body weight in the latter was approximately 12 grams when the muscles first separated. Embryos of the Gadwall exhibited great individual variation in the degree of contact between the two sides, but in all instances the contact was less than in the other species.

In the Redhead the initial, complete separation was found in only a few specimens; most maintained contact in the middle third of the muscles' length. Another major variation from the pattern of the Blue-winged Teal was that the muscles of the two sides became distinct and completely separate entities within hours after hatching (Fig. 2), and occasionally even before hatching.

Neither the Mallard nor the Ruddy Duck exhibited the first separation of the muscles and a greater degree of contact was maintained for a longer, post-hatching period. In the Ruddy, even at 13 days, the muscles still touched each other.

Infiltration of lymph. — Indications of the presence of lymph were several: A change in the color of the muscle from dark pink to yellow-pink to straw-yellow; an increase in the number of "lymph areas"; greater size of the areas; and finally, to be discussed later, enlargement of the muscle masses as measured by weight and turgidity.

The presumed, immediate source of this lymph was a gland, roughly triangular in shape, that laid along the lateral edge of either muscle and a lymph spot that appeared between the separated anterior ends of the Mm. biventer cervices and deep to the hatching muscle. In all the species the lateral lymph areas were present, though small, at the time the hatching muscles became distinct to the unaided eye.

The first intimation of actual movement of lymph into the muscle was a change in the color of segment 1. This happened in the various species at the following body weights: Blue-winged Teal, 7-8 grams; Shoveler and Pintail, 9-10 grams; Gadwall, 13-14; Mallard, 10-12; Redhead, 15-20; and Ruddy Duck, 20-25 grams.

The medial lymph spot appeared in each species when body weights were 2 to 5 grams greater than those just given. With increased age the spot elongated and broadened and extended posteriorly between Mm. biventer cervices and Mm. complexi. For example, in the Blue-winged Teal it sometimes formed a band 2 mm. by 6 to 10 mm. at the prepipping maximum. It disappeared near the end of the pipping activity, during hatching, or within 36 hours of hatching.

Extraordinarily rapid changes in the lateral lymph areas also took place. Those changes in the Redhead were fairly typical. Data in Table 1 illustrate the continuous and quick increments in size through the prepip stage. What was not evident in this species, but was true of all others, was that the decline in lymph area began during pipping of the egg. In the Ruddy Duck the areas did not exhibit the continuous buildup prior to pipping; most of the increase occurred as body weight increased 5 grams in the prepip stage. The areas in just-hatched ducklings of all species were significantly smaller than in ducklings sampled during pipping. In the week following hatching the areas decreased rapidly, but in the second week they began a second surge of growth observed to continue, at least in the Blue-winged Teal and Mallard, through 30 days of age.

The Ruddy Duck was again an exception. By all relative and absolute standards the areas of lymph in it were very significantly greater than in any other species. Further, the lateral areas invaded the region beneath the outer edges of the hatching muscle just prior to hatching. But, by the fourth or fifth day after hatching, yellow fat replaced most of the lymph and covered the remainder.

Changes in muscle mass. — The data presented for the Redhead (Table 1) were representative of the changes in absolute weights of the hatching muscle and also in the relative weights shown in Figures 3, 4, and 5.

Absolute weights increased during development through the prepip stage, dropped significantly during hatching (particularly in the pipping stage), declined for 3 to 8 days after hatching, and increased thereafter. In the two

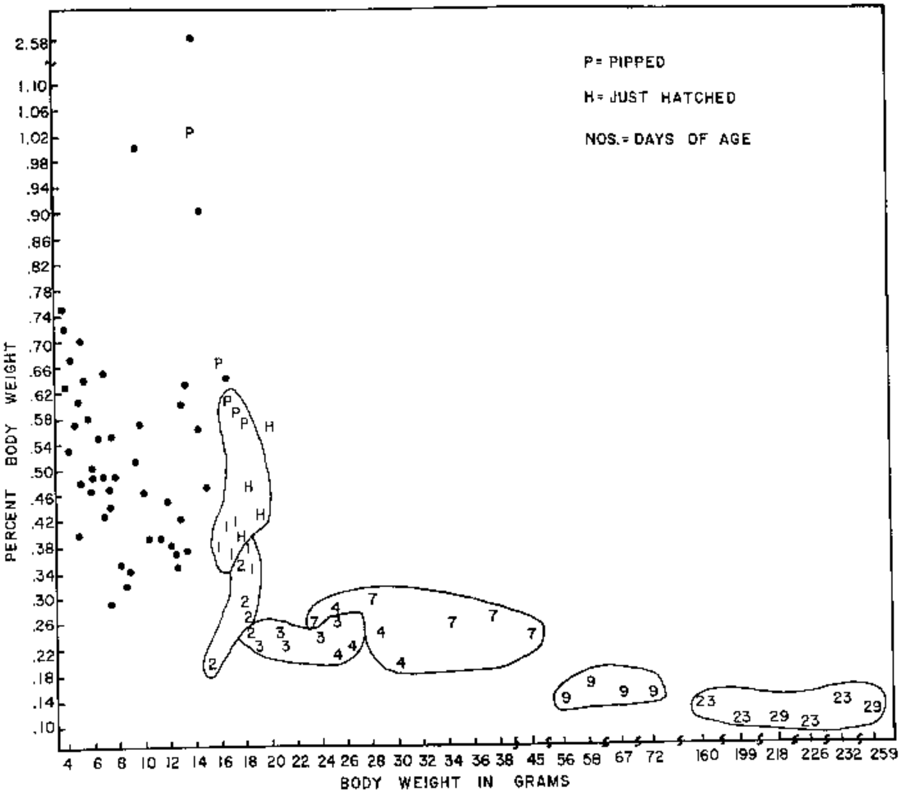

FIGURE 3.—Scattergram showing changes in size of hatching muscles relative to body weights of Blue-winged Teals. (Each encircled group represents a single brood.)

species kept as long as a month after hatching, the muscle was 2.5 times heavier than at pipping in the Blue-winged Teal and twice as heavy in the Mallard. But in the Ruddy Duck at 13 days of age the muscle weight was slightly less than half that at pipping.

The pre-hatching increases were neither steady nor uniform, and they were greater than the relative increments in body weight. Between average body weights in the Redhead of 18 and 23 grams (increase of 28%), muscle weights gained 49%, and when average body weight increased 22% (23- to 28-gram stages) muscle weights went up 55%. The major gains took place during the prepip phase; body weight went up 25% and the muscle weight advanced 129%!

A third of the muscle mass was lost before 24 hours of age and another third in the next 24-hour period. The decline in the next few days was slight and even, but by the end of the first week, in the Redhead, the process was reversed and the daily gain in muscle weight was about 15%. The post-hatching loss of weight was slower in the Ruddy Duck; not until 4 or 5 days did the muscle reduce to a third of its mass at pipping.

The relative size of the muscle was studied in two ways: compared to lymph area and to body weight. When muscle weight was plotted against lymph area, it became obvious that the two increased in a straight-line relationship during the period the embryo gained half its hatching weight. However, body weight increased twice as fast as lymph area in the latter part of the incubation period. The post-hatching regression of lymph and muscle was again directly and uniformly correlated, but the fol-

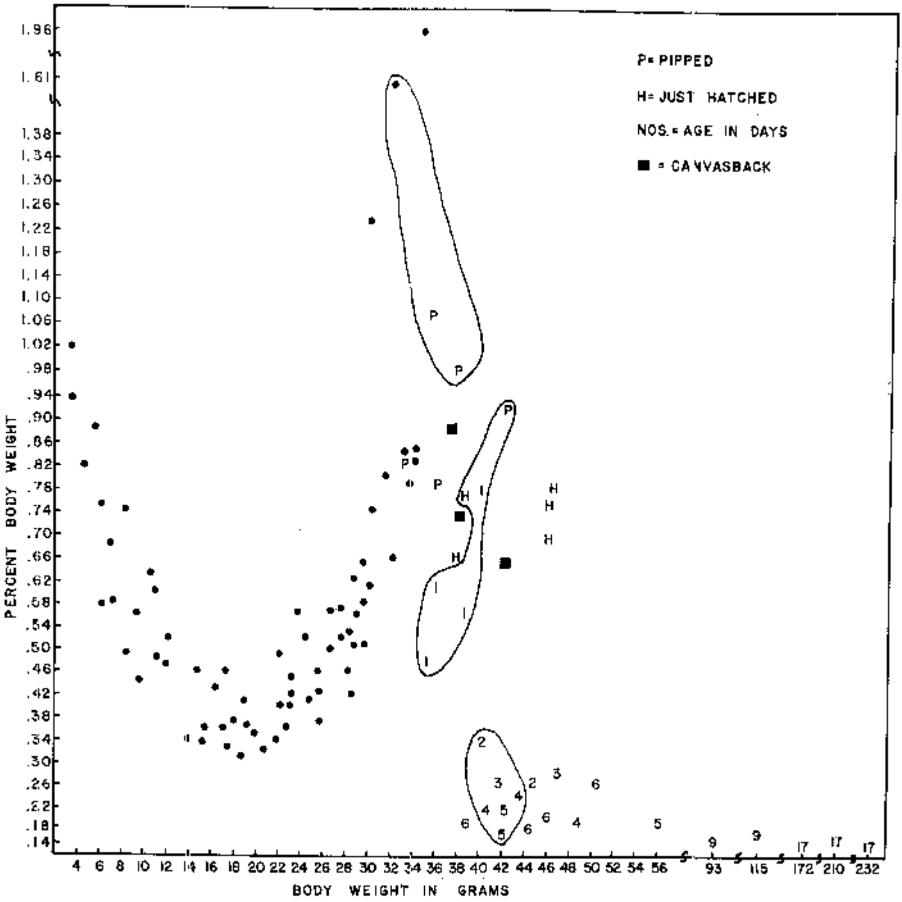

FIGURE 4.—Scattergram showing changes in size of hatching muscles relative to body weights of Redheads. (Each encircled group represents a single brood.)

lowing recrudescence of muscle was much more rapid than that of the lymph area (Fig. 6).

The data in Figures 3, 4, and 5 and Table 1 revealed that, despite a constant, pre-hatching increase in muscle mass, there was in all species a period of decline in the relative size of the muscle that continued until half the hatching weight had been attained. Thereafter the gain in muscle weight was relatively much more rapid than the gain in body weight.

Without exception the greatest relative mass of the muscle was present in the prepip and early pipping stages (Table 2). It was also evident in Table 2 that relative muscle weight dropped markedly during the hatching process in most species, but significant variations did occur in the percentage decrease between the pipping and just-hatched stages. Shovelers and Pintails showed declines during hatching of 48 and 43%, respectively, the Blue-winged Teals 36%, and Mallards and Redheads 22 and 28%. The muscle in the Ruddy Duck did not exhibit this regression between pipping and emergence.

The data indicated that relative muscle size decreased greatly during pipping, at least in some species. (See Pintail, Blue-winged Teal, and Ruddy Duck in Table 2.)

When the gain in relative size of the hatching muscle, from its lowest pre-hatching level to its mass at the combined pipping and pre-pipping stages, was compared for the species studied, major diversities were revealed (Table 3, top). Gains ranged from 26 to 221%! When percentage increase in relative size was calculated simply as the gain from least to greatest (Table 3, bottom), a similar degree of variation was demonstrated.

Considerable uniformity was exhibited (Table 3), however, in the least relative sizes of the muscle before hatching (0.33-0.43% of body weight) except for the Ruddy Duck (0.59%) and in the relative sizes immediately after hatching (Table 2, 0.44 to 0.54% of body weight) with the exceptions of the Redhead (0.73%) and the Ruddy Duck (0.77%).

The similarity between greatest relative weights of the hatching muscle was not so evident (Table 3); these weights ranged from 0.89% of body weight in

TABLE 1. Quantitative Changes in the Hatching Muscle and Lymph Areas During Development in the Redhead.

N	Body wt. (gms.) or stage	Muscle wt. (gms.)	Ratio, muscle: body wts.	Lymph area (mm²)
8	6–10	0.047 (0.037–0.063)	0.62 (0.46–0.77)	15
7	11–15	0.062 (0.050–0.070)	0.52 (0.36–0.65)	36
11	16–20	0.068 (0.052–0.082)	0.39 (0.33–0.48)	66
11	21–25	0.101 (0.071–0.137)	0.44 (0.34–0.58)	90
18	26–30	0.157 (0.101–0.231)	0.55 (0.39–0.76)	96
8	Pre-pip	0.360 (0.216–0.655)	1.11 (0.68–1.96)	118
5	Pipping	0.348 (0.282–0.394)	0.94 (0.81–1.10)	121
5	Just hatched	0.308 (0.225–0.375)	0.73 (0.63–0.79)	103
4	1 day	0.241 (0.174–0.322)	0.63 (0.50–0.80)	86
2	2 days	0.137 (0.128–0.145)	0.32 (0.29–0.36)	57
2	3 days	0.129 (0.119–0.139)	0.30 (0.29–0.30)	78
3	4 days	0.106 (0.096–0.116)	0.24 (0.22–0.27)	41
3	5 days	0.101 (0.084–0.120)	0.22 (0.20–0.24)	25
4	6 days	0.128 (0.080–0.140)	0.23 (0.19–0.28)	25
2	9 days	0.181 (0.152–0.210)	0.17 (0.16–0.18)	63
3	17 days	0.300 (0.239–0.335)	0.14 (0.14–0.15)	75

TABLE 2. Ratio of Weight of Hatching Muscle to Body Weight.

	Pre-pip		Pip		Just-hatched	
	N	Mean	N	Mean	N	Mean
Mallard	3	0.63	6	0.89	4	0.54
Gadwall	6	0.37	2	0.51	1	0.44
Pintail	5	1.24	2	0.89	4	0.51
Blue-winged Teal	4	1.17	5	0.69	5	0.44
Shoveler	4	0.74	4	0.92	2	0.48
Redhead	8	1.11	5	0.94	6	0.73
Ruddy Duck	7	1.03	4	0.73	3	0.77

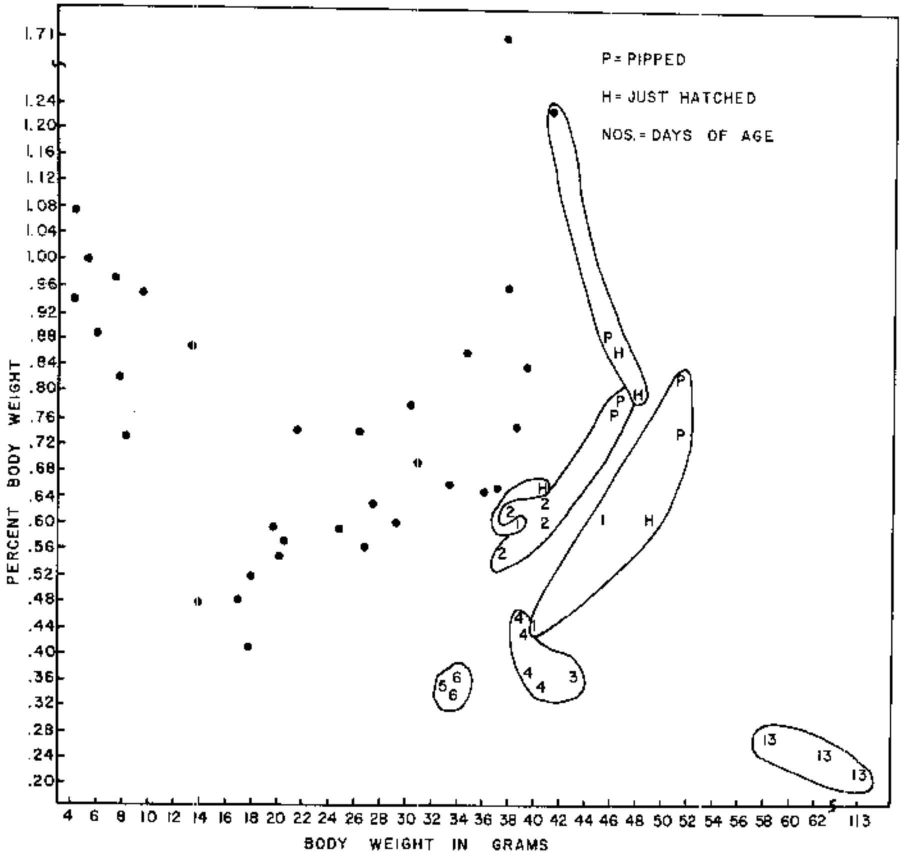

Figure 5.—Scattergram showing changes in size of hatching muscles relative to body weights of Ruddy Ducks. (Each encircled group represents a single brood.)

the Mallard to 1.24% in the Pintail, if one discounted the 0.51% in the Gadwall as being based on an inadequate sample.

Within a day or so after hatching, the relative weight of the muscle was at or below its lowest pre-hatching level. The mass of the muscle continued to lose relative size at least for a month in some species. At the end of this time it was down to approximately 0.10% of body weight.

The decline in relative size of the muscle during the hatching process and later was further substantiated by sampling of members of the same clutch or brood which constituted samples that could be expected to be more genetically uniform (Figs. 3, 4, and 5). All 14 broods or clutches of ducks sampled at two or more stages exhibited the decrease.

Body Weight at Time of Pipping and Hatching

The data are in Table 4. It was not possible to attach any significance to increases in weight between the pipping and hatched stages; inclusion of yolk with the latter ducklings may have been responsible for these differences. It was noteworthy that the Mallard and Ruddy Duck exhibited no increase despite the inclusion of the yolk. During sampling it was observed that yolk sacs of the Redhead were much heavier than those of any other species. Weights of 5 from the Redhead averaged 7.3 grams compared to 4.9 for 5 of the Mallard and 5.4 grams for 4 sacs taken from Ruddy Ducks. The data may mean a slower and later intrusion of yolk in the Redhead and may suggest that these weight relationships of the Redhead should be considered similar to those in the Ruddy and Mallard.

THICKNESS OF EGG SHELL AT HATCHING

The data are in Table 5. The shell in the Ruddy Duck was significantly thickest of the species investigated; that of the Redhead was next thickest. The shell in the Mallard was intermediate to these two species and the Shoveler. There was no significant difference between the Pintail and the Blue-winged Teal which had the thinnest shells.

HATCHING TIME OF SINGLE EGGS

Blue-winged Teal: Of 68 eggs of 7 clutches the shortest time between pipping and emergence was 4.0 hours and the longest was 35.5 hours (mean, 9.0± 1.8).

TABLE 3. Gain in Relative Size of the Hatching Muscle During Incubation.

	Per cent muscle is of body weight at:				
	N	Pre-pip + pip stages	N	Lowest pre-hatch stage	Per cent of gain
Mallard	6	0.63	6	0.39	62
Gadwall	4	0.44	13	0.35	26
Pintail	4	1.06	6	0.33	221
Blue-winged Teal	9	0.90	8	0.42	114
Shoveler	8	0.85	10	0.43	98
Redhead	10	1.03	11	0.39	164
Ruddy Duck	11	0.92	5	0.59	56

	N	Greater, pre-pip or pip stage	N	Lowest pre-hatch stage	Per cent of gain
Mallard	6	0.89	6	0.39	128
Gadwall	2	0.51	13	0.35	46
Pintail	5	1.24	6	0.33	276
Blue-winged Teal	4	1.17	8	0.42	179
Shoveler	4	0.92	10	0.43	114
Redhead	8	1.11	11	0.39	185
Ruddy Duck	7	1.03	5	0.59	75

TABLE 4. Body Weights in Grams at Pipping and Hatching.

	Pipping			Hatched		
	N	Mean	Range	N	Mean	Range
Mallard	5	36.6	35.5–38.3	4	36.4	34.1–39.2
Gadwall	2	25.8	24.0–27.6	1	26.1	....
Pintail	2	24.9	20.8–25.1	4	27.9	24.5–30.5
Blue-winged Teal	5	16.1	13.6–17.5	5	18.5	17.3–19.8
Shoveler	6	19.3	17.5–21.8	2	22.1	20.1–24.2
Redhead	5	36.9	33.0–42.1	6	41.8	36.0–46.3
Ruddy Duck	4	48.2	46.3–51.3	3	44.8	40.5–47.8

Redhead: Forty-one eggs showed a mean time of 26.4± 3.1 hours (11-48) from pip to hatch.

Ruddy Duck: Seventeen eggs, in two fresh clutches taken June 10, had a mean time from pip to hatch of 5.6± 0.30 hours (2.5-9.0). Two clutches, incubated less than one week and collected June 23, showed in their 19 eggs a variation from 5.5 to 40.0 hours (mean 12.4± 1.8). In Table 6 is the chronology of a clutch collected on June 23. It illustrated the great diversity in hatching time between eggs of the same clutch and the longer mean hatching time late in the season.

Shoveler: The mean time between pipping and hatching of an egg in a sample of 11 from one clutch was 10.8± 1.1 (7.9-12.2) hours.

Pintail: From pip to hatch required a mean of 12.6± 1.3 hours (8.6-14.1) among 19 eggs of 2 clutches collected in mid-June.

Franklin's Gull: The 20 eggs in the 2-egg clutches showed a mean time from pip to emergence of 8.6 hours (5.5-17.0); in the 3-egg clutches (15 eggs) it was 7.9 hours (5.5-14.5). There was no significant difference in time between first and second or first and third eggs in a clutch.

American Coot: Mean hatching time of 60 eggs was 9.3 hours but the range was very great—4.5 to 20 hours. Eggs in the 8-, 10-, and 11-egg clutches averaged 11.6 hours; in the 14- and 17- egg clutches the mean was 7.9 hours. In all clutches the last half of the number of eggs to pip had significantly shorter hatching times than the first eggs that pipped.

HATCHING OF ENTIRE CLUTCHES

Blue-winged Teal: Seven clutches had a mean time of 31.4 hours (21.5-38.5) between pipping of the first egg and hatching of the last duckling (hatching time), but all ducklings in a clutch emerged within a span of 11.6±1.3 hours (8.0-16.5) (emergence time).

Redhead: One clutch of 8 hatched within 31 hours. The three other clutches showed times of 39 (12 eggs), 61 (10 eggs), and 72 hours (11 eggs). The ducklings of the first clutch (early June) emerged within a 10-hour period, the second set in a 24-hour span, the third set within 46 hours, and the time from first to last emergence in the last clutch (third week of June) was 60 hours. In Table 7 are data indicating that in a clutch the hatching was quicker in eggs which start the process later.

Ruddy Duck: Four clutches with a total of 36 eggs showed a mean hatching timespan of 18.4±2.1 hours (10.5-40.0) between pipping of the first egg and emergence of the last duckling. However, if the clutch with the 40-hour span was eliminated, the data were: mean, 14.6±0.8; range, 10.5-22.0. The two clutches (17 eggs) of June 10 showed a mean time of 13.6 hours (9.3-13.9). The two clutches of June 23 (19 eggs) took an average of 23.2 hours.

TABLE 5. Thickness of Egg Shell (Ten-thousandths of an Inch) at Hatching.

	N	M
Ducks		
Mallard	9	111±2
Pintail	11	78±2
Blue-winged Teal	45	75±1
Shoveler	13	83±1
Redhead	37	129±2
Ruddy	29	142±2
Franklin's Gull	18	72±4
American Coot	34	105±1
Grebes		
Horned	3	77±3
Eared	4	88±1
Pied-billed	8	91±2
Red-necked	2	97
Western	4	126

Shoveler: The one clutch of 11 eggs emerged in 11.5 hours, but the hatching time was 17 hours.

Pintail: Two clutches (11 and 8 eggs) emerged in 12.5 and 13.5 hours. Elapsed time between pipping of the first egg and hatching of the last egg was 16.5 (11.0-22.0) hours.

Franklin's Gull: Ten clutches of 2 eggs each showed mean emergence times of 24.3 hours (18.0-27.5), and 5 clutches of 3 eggs each had elapsed times of 46.0 hours (40.5-57.5). Hatching times for 2-egg clutches averaged 31.4 hours (26.5-36.5); for 3-egg clutches the times ranged from 58 to 72 hours (mean, 61).

American Coot: Because the number of eggs was so different in the various clutches, no numerical means for hatching and emergence times were calculated. Hatching times by clutches were: 8 eggs, 6 days; 10 eggs, 8 days; 11 eggs, 9 days; 14 eggs, 10 days; and 17 eggs, 12 days.

FERTILITY AND HATCHABILITY

Blue-winged Teal: No infertile eggs were found among the 123 incubated. Six eggs failed to hatch; one was from a partly incubated clutch of 8 collected June 3, 2 from a fresh clutch of 7 taken on June 21, and 3 from a clutch of 9 that had been incubated for perhaps 5 days before being collected on July 5.

Redhead: Of 117 eggs taken from 3 dump nests 61 were infertile. Thirty embryos died within seven days after being placed in the incubators; these deaths occurred in three different incubators and at body weights varying from 3.6 to 31.0 grams. Forty-one of 43 eggs from "clean, down-covered" nests hatched; one egg was infertile and one embryo died at 28.5 grams.

Ruddy Duck: All 69 eggs collected were fertile and produced viable embryos to the time of sampling.

Shoveler: Only two of the 57 eggs were infertile and the embryos in all others were viable to the time of sampling.

Pintail: One of 43 eggs was infertile and 2 eggs had dead embryos at the time of sampling (5.8 and 11.4 grams).

Gadwall: Three of 39 eggs were infertile and 5 died during incubation.

DISCUSSION AND SUMMARY

The hatching muscle: morphology and segmentation. - As in all birds thus far studied, M. complexus is made up of three segments in ducks; the fourth segment is small even in its occasional occurrence. The conformation, origin and insertion, in general, are the same in the species of ducks studied and closely similar to the hatching muscles in the chick (H. I. Fisher, 1958), in grebes (H. I. Fisher, 1961), the American Coot (J. R. Fisher, 1962), and Franklin's Gull, and the Common and Black terns (H. I. Fisher, 1962).

In all species the first evidence of segmentation is the fibrous line between segments 1 and 2, and it is a curious and thus far inexplicable fact that in all species the segmenta-

Table 6. Chronology of Pipping and Hatching Times for a Clutch of Ruddy Duck Eggs Collected June 23.

Egg	First pip	Hatch	Elapsed time (hours)
1.	8:00 a.m.—July 20	1:30 p.m —July 20	5.5
2.	7:30 a.m.— ” ”	11:00 p.m.— ” ”	15.5
3.	8:00 a.m.— ” ”	3:00 p.m.— ” ”	7.0
4.	5:00 p.m.— ” ”	8:00 a.m.— ” 21	15.0
5.	1:30 p.m. — ” ”	12:30 a.m.— ” ”	23.0
6.	2:00 p.m.— ” ”	6:00 a.m.— ” 22	40.0
7.	3:00 a.m.— ” 21	10:30 a.m. ” 21	7.5
8.	10:00 a.m.— ” 21	4:00 p.m.— ” 21	6.0
9.	1:00 a.m.— ” 21	2:00 p.m.— ” 21	13.0

Table 7. Chronology of Pipping and Hatching Times for a Clutch of Redhead Eggs Collected June 27.

Egg	First pip	Hatch	Elapsed time (hours)
1.	3 p.m.—July 23	10 p.m.—July 24	31
2.	3 p.m.— ” ”	10 p.m.— ” ”	31
3.	3 p.m.— ” ”	9 p.m.— ” ”	30
4.	7 a.m.— ” 24	11 p.m.— ” ”	16
5.	8 a.m.— ” ”	3 a.m.— ” 25	19
6.	8 a.m.— ” ”	8 a.m.— ” ”	24
7.	9 a.m.— ” ”	7 a.m.— ” ”	22
8.	8 a.m.— ” ”	11 p.m.— ” 24	15

TABLE 8. The Relationship Between the Length of the Incubation Period and the Weight of the Hatching Muscle when Segmentation first appears.

	Incubation (days)	Muscle wt. at seg. (gms.)
Franklin's Gull	18-20	.04 – .07
Coot	21	.05 – .08
Shoveler, Blue-winged Teal, Pintail	21-23	.03 – .05
Grebes	22–25	.02 – .05
Gadwall, Mallard, Redhead	25–28	.03 – .06
Ruddy	30	.07 – .09

tion first appears when the embryo weighs 5 to 9 grams, except in the grebes in which it is already present at 2 to 3 grams body weight. Uniformity of time of appearance of muscle segments in a species, within a range of 2 grams of body weight, might be expected, but not in a range of kinds of birds from terns to ducks which vary so greatly in weights at hatching time (Common Tern, 14 gms. versus Ruddy Duck, 45 gms.) and in weights of adults.

It is well known that different kinds of tissue tend to differentiate on topographical and time schedules or patterns. In the present instance the pattern may relate to functional "need" or mass of the structure. We can only speculate on the physiological or morphological basis for "need" at the time of the first segmentation, but we can consider the possibility that when the absolute mass of the muscle reaches a certain level the hatching muscle begins its segmentation in all species. However, segmentation shows first at the following absolute weights of the hatching muscle: —grebes, 0.020-0.050 grams; gull, 0.044-0.070; Gadwall, 0.026-0.049; American Coot, 0.045-0.076; Mallard, 0.031-0.059; and Ruddy Duck, 0.073-0.090, to cite a few examples. First segmentation of the muscle, then, does not occur at a uniform, interspecific biomass of the muscle, and there are the aforementioned facts suggesting that it takes place at a fairly uniform biomass of the embryo, except in grebes.

Nor is there any evidence that this event correlates in any way with attainment of a certain proportion of adult weight or of hatching weight.

It is also possible, even likely, that time of segmentation is related to total period of development, that is, the incubation period. If this be true, segmentation of the hatching muscle would follow the general pattern of functional development of vertebrates illustrated, for example, by the fact that the heart first begins to beat in such diverse organisms as the chick and the human when approximately one-tenth of the embryonic period for the organism has elapsed.

We may arrange the species by reported incubation periods (Table 8) to show that there is among the ducks a rough correlation between the weight of the hatching muscle at the time of first segmentation and the length of the incubation period. However, the grebes are still an exception, and the coot and gull relate more closely in size of muscle to the larger ducks with longer incubation periods than they do to the small ducks that have periods similar to those of the coot and gull.

Segmentation is completed relatively quickly, with an increase usually of only a gram or two in body weight, except for segment 4 which first appears to the unaided eye at the prepip stage.

The segments retain throughout their existence a cline of decreasing size from anterior to posterior, but in the pre-hatching period absolute size increases in all dimensions. Most marked are the mediad extensions which bring into midline contact the comparable segments of the two sides and hide from dorsal view the underlying biventer cervicis and spinalis muscles. The contact first occurs between the segments of pair 1, shortly after the first indications of segmentation, and progresses posteriorly until at the time of pipping or hatching the muscles of the two sides touch throughout the length of their medial edges in most duck embryos, as they do earlier in development. This is the pattern, with minor variations, in half of the ducks investigated; the Gadwall exhibits much less medial contact and is extremely variable in this regard.

Initial separation of the pair of muscles begins prior to or at the time the first muscle segments appear in the Blue-winged Teal, but in the other species that show this disjunction it takes place later. In the Redhead the muscles in only a few embryos are apart before hatching, and in the Mallard and Ruddy Duck there is no separation during embryonic development. It is believed the absence of initial separation is a correlate of the inherently larger muscle mass and the thicker egg shells in these species, as will be discussed later.

After hatching, regression of the muscle results in permanent loss of medial contact. The time this second separation occurs is highly variable interspecifically– at 4 or 5 days of age in the Blue-winged Teal, at 2 days in the Shoveler, before the end of the first day in the Redhead, and as long after hatching as 13 days in the Ruddy Duck and nearly a week in the Mallard. The possible significance of the variation will be discussed in connection with changes in total muscle mass.

The second most noticeable change in segment size during the embryonic phase is increased thickness due in large part to the infiltration of lymph although, as I indicated in 1958 for the chick, there is some increase in the number and size of the muscle fibers. So great are the turgidity and mass produced by lymph in the muscle that segmentation is only faintly visible or completely hidden in the prepip or pip stages.

After hatching and the depletion of the lymph through use as a nutrient for muscular activity (George and Iype, 1963) or perhaps as a result of its being forced out by powerful contributions of M. complexus, segmentation reappears temporarily and the segments are thin. By the end of a week only traces of segmentation are visible in such ducks as the Blue-winged Teal and Shoveler; traces persist for as long as 13 days in the Ruddy Duck, 22-30 days in the Mallard, and 14-19 days in the Redhead. It appears that the retention of segmentation, in these latter species, is still another correlate of larger muscle mass and thicker egg shell.

The infiltration of lymph. — The evidence for the filtration of lymph into the hatching muscle in ducks, as in coots, gulls, and chickens, is strong, though presumptive and unquantified. Even in the grebes in which I (1961) found no lymph areas comparable to those of ducks and in the American Coot where J. R. Fisher (1962) reported only scattered kernels or lobes of lymph glands, the muscle assumes a yellowish, lymph-color prior to hatching and is filled with a thin viscous fluid that pushes apart the muscle fibers (H. I. Fisher, 1958).

The changes in the sizes of the lymph glands and the hatching muscles in chicks are directly correlated, in almost a straight-line relationship during the first two-thirds of prehatching development (Fig. 6, Table 1). Increases in lymph area in this time are greater than those in muscle size and tend to precede the latter. In the phases just before prepip, muscle size increases more rapidly than lymph area, perhaps indicative of a more rapid movement of lymph from lymph area to muscle than from the body as a whole to lymph area. With the exigencies of hatching over, absolute muscle size and lymph area regress equally until approximately two weeks of age, at which time both increase; but muscle size increases more rapidly than lymph area (Fig. 6).

Mass of the hatching muscle. — Size of muscle relative to embryo weight follows in ducks the pattern established by previous studies for other species. After a period of early development in which the muscle is relatively very small because of

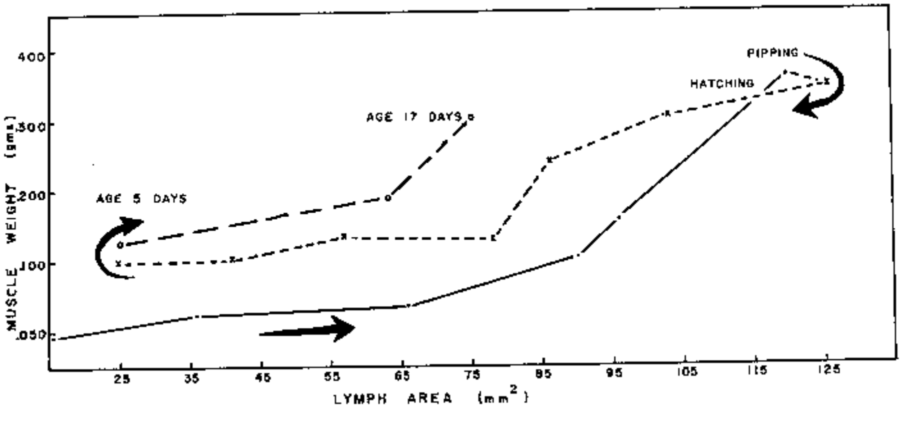

FIGURE 6.—The relationship between actual weight of the hatching muscle and area of lymph during three periods of change in the Redhead.

the greater size of the anterior part of the embryo, the muscle gains in relative size until the prepip or early pipping stage. The greatest relative size the muscle ever attains is variable interspecifically, ranging from 0.51% of body weight in the Gadwall (small sample) to more than 1.0% in the Pintail, Blue-winged Teal, Redhead, and Ruddy Duck (Table 3). In most of the species of ducks, however, the muscle may well constitute 1.0±% of body weight, which is considerably less than in the American Coot (1.20%, 1.12-1.64) or the chicken (1.93%, 0.70-3.41) but more than in grebes (0.65-0.90%) or gulls and terns (0.80-1.0%). In this same table are data showing that the pre-hatching gain in relative size from the prenatal low is also variable, from 46 to 276%.

It is difficult to explain these interspecific variations in relative mass. They do not correlate with differences in weight at hatching; the Ruddy has a muscle equal to 1.0% of body weight and hatches at 45 grams, while the Pintail's relative muscle weight is 1.24% and it hatches at 28 grams. Comparison of weight of adult birds and of hatching muscles indicates no correlation; the light-weight tern and gull have hatching muscles the relative size of those in the Teal and the Mallard, and the Mallard, despite an adult weight approximately the same as the Redhead's, has a muscle one-fifth to one-fourth smaller.

Although the muscle shows continuous gains in actual weights, it is just previous to pipping that it reaches its maximum. In the day or so previous to the first pip of the egg the muscle may double in weight, but once pipping starts the muscle usually fails to gain weight and, most often, begins to shrink. During hatching the loss in muscular weight increases; in the 24-hour period after emergence one-fourth to one-half the mass disappears, and in the next day a similar, proportional loss occurs.

All these rapid fluctuations are caused by the movement of lymph into or out of the hatching muscles. It is not until after the post-natal low that the muscle begins to add weight in normal fashion and to proceed to its adult function of extending the head.

Thickness of egg shell. — Thickness of egg shell might be judged to be a factor at least partly influencing the power of the mechanism designed to break the shell, although to demonstrate any certain relationship would require very large samples since it is known in chickens at least (Romanoff and Romanoff, 1949: 115, 116, 119), that there is great individual variation in the shells within a species and even in the shells of the eggs laid by the same individual. Further, there is increased fragility with incubation and changes in organic and inorganic constituents, the kind and extent of which are largely unknown in wild birds.

Study of the data in Tables 3 and 5 reveals no correlations in ducks between thickness of shell and relative size of the hatching muscle; the Blue-winged Teal, for example, has a relatively larger muscle but a thinner shell than the Shoveler, Mallard or Redhead. However, there is a rough correlation between shell thickness and actual weight of the hatching muscle. The Ruddy and Redhead have the heaviest shells and muscles weighing 0.35 and 0.36 grams, respectively. The Mallard has the next thickest shell and a muscle of 0.32 grams, and the Blue-winged Teal has the smallest muscle (0.11 gms.) and thinnest shell. The Shoveler has a shell heavier than the Blue-winged Teal's and a larger muscle (0.14 gms.). Only the Pintail, of the ducks whose shells were measured, does not conform; its shell is 0.0078 inches thick, intermediate to the Shoveler's and Teal's, but its muscle is nearly twice as heavy (0.22 gms.).

The Coot, however, has a shell 0.0105 inches thick and a muscle of only 0.19 grams or approximately half as large as the Mallard which has essentially the same thickness of shell; it does not fit into the duck series. Kortwright (1943:233) noted the exceptional hardness and toughness of the egg of the Redhead, and I suggested (1961:233) that eggs of grebes were, as compared to other species of water birds, soft and rather easily broken and that some of the difference in these features within the grebe group might relate to the differences in the amount of wet vegetation the various species used to cover the eggs when the incubating birds left the nest.

Subsequent measurement of shell thickness in the grebes (Table 5) showed by far the heaviest shell in the Western and the next thickest in the Red-necked, but the muscle was larger in the latter. However, both these grebes had muscles twice as large (0.16-0.24 gms.) as those in the smaller grebes (0.08-0.09 gms.), all of which had significantly thinner-shelled eggs. Thus, within the grebes as in the ducks there is a gross correlation between size of hatching muscle and thickness of egg shell.

Franklin's Gull has a muscle of 0.17 grams, and its shell is comparable in thickness (0.0072 inches) to that of the Blue-winged Teal which has a muscle of 0.11 grams. Moreover, the teal's egg is laid on land and might be presumed to be harder than the gull's egg which lies on a water-soaked mat of vegetation.

If one plots relative muscle size against presumed place in avian phylogeny, the factors determining muscle size are even less understandable. It is obvious that genetic and environmental factors, such as humidity in the nest, are interacting and that no one-line, simple correlation is present.

Body weight at hatching. — Absence of any increase in body weight between the pipping and hatching stages in the Mallard, Ruddy Duck, and perhaps in the Redhead, may be related to two factors: 1) There may be a greater utilization of energy in pipping and cracking the thicker shells in these species; or 2) there may be a difference in the time at which the yolk sac is intruded. If the yolk enters the body early in the pipping process in the Mallard and Ruddy and much later in the others, especially the Redhead, it could be the sole factor.

If the few data on weights of yolk sacs are truly significant, and if the differential comparison between these weights for the Redhead, Mallard and Ruddy Duck are valid, they suggest that ducklings weighing approximately 40 grams at hatching may expend the equivalent energy of 2 grams of body weight in freeing themselves from the egg.

Hatching weight equals: 2.8 to 3.0% of adult weight in the Mallard, Gadwall and Pintail; 3.4 and 3.7 in the Shoveler and Redhead, respectively; 4.3% in the Blue-winged Teal; and 7.3 in the Ruddy. Thus, there is no direct correlation between hatching weight and adult weight.

Hatching time: single eggs.—The fact that all eggs were artificially incubated may have influenced the actual time required for a duckling to emerge after the first pip of the egg, but since all eggs used in this part of the study were incubated under the same conditions the relative times are considered valid.

Eggs pipped first at any time of the day and ducklings emerged at random times; no diurnal rhythm was observed in either process.

Blue-winged Teals hatch most rapidly, in less than half the time required by their not-too-distant relatives—the Shoveler and the Pintail—whose eggs have comparable shells. Of the five species of ducks whose hatching times were studied, the Redhead had the longest period (26.4 hrs.), and the Ruddy Duck, which hatches at nearly the same body weight and has a somewhat thicker shell, emerges in 5.6 hours. Since the species of the "teal group" nest under similar conditions and the Redhead and Ruddy in nearly identical situations, the differences in hatching time do not appear to be the result of different environmental factors. Nor are they apparently related to shell thickness, egg size, body weight at hatching or adult weight.

There is some indication in the Ruddy Duck and in the Redhead that embryos from eggs laid late in the season may take longer in the emergence process, but the data are few. Until a greater series of species and of individuals are studied early and late in the season it is impossible to generalize.

Eggs in two-egg clutches of Franklin's Gull had a mean hatching time of 8.6 hours which is not significantly different from the 7.9 hours required by eggs in 3-egg clutches. Times for first and last eggs that pipped were not different.

In American Coots, the hatching time of individual eggs appears to vary with the number of eggs in the clutch; eggs in clutches of 8 to 11 eggs hatched in 11.6 hours and eggs in 14- to 17-egg clutches averaged only 7.9 hours. Further, within the clutches there was a cline of hatching times; the first eggs to pip had significantly longer hatching times than did the eggs that pipped later.

Hatching time: entire clutch.—Two aspects are of importance here. First is the total elapsed time between pipping of the first egg and emergence of the last one (hatching time). The second is the time between emergence of the first and last ducklings from a clutch (emergence time).

The Blue-winged Teal and Redhead had total hatching times of 31 hours, the Ruddy 18 hours, and the Shoveler and Pintail approximately 17 hours, in clutches laid throughout the month of June. However, late-June clutches of Redheads and Ruddies had significantly longer times. Whether this was a direct seasonal effect or the result of more than one female laying in a nest, a habit these species have, is not known.

The period in which the ducklings emerged was much more uniform, within and between species, and much shorter than total hatching time. Further, the chronologies of the hatching of individual clutches of duck eggs and of clutches of American Coot eggs showed that in most instances the first eggs to pip took the longest time to emerge. This was not true for clutches of Franklin's Gulls, however. Thus, the evidence, though scanty, indicates, as Vince (1964, 1966) has suggested, that in precocial species emergence of the young from late-pipping eggs is in some way speeded-up, perhaps by the activities of the early-pipping embryos. The evidence from five clutches of Coot eggs further suggested that the facilitation might be, in part at least, a function of clutch size.

Obviously, any shortening of the emergence period in precocial birds means greater survival. If it is generally true for ducks that emergence time increases with season (Redhead —10, 24, 46, and 60 hours), the decreased survival might be a major factor in limiting the length of the breeding season and in explaining why re-nestings in ducks are not too frequently undertaken.

Fertility and hatchability. — Of 374 eggs taken from normal nests only 7 eggs proved to be infertile (3 Gadwall, 2 Shoveler, 1 Pintail, and 1 Redhead). The overall infertility rate was 1.9%, but it varied interspecifically; it was zero in 123 eggs of Blue-winged Teals and in 69 of Ruddies, but approached 8% in Gadwall eggs.

Gadwalls also had the highest rate of deaths of embryos (13%). All fertile eggs of Ruddy Ducks hatched. Hatchability appears to decline with the season, if the series of eggs of Blue-winged Teals is typical.

However, these are but straws of evidence and until large-scale controlled experiments are undertaken we can draw no conclusions. We know little or nothing of the effects at different stages of incubation of humidity, intermittent cooling, agitation or movement of eggs as in moving them from field to laboratory, or indeed of the temperatures most suitable for each species.

General comments. — Although the study was not designed to bring out taxonomic differences and members of only three subfamilies were represented, some differences may be mentioned.

The Ruddy Duck (subfamily Oxyurinae) in its hatching mechanism varies markedly from the ducks representing the Anatinae and the Aythyinae. The muscle is always—prenatal, at hatching and post-hatching—significantly largest. The muscle shows the least relative losses in weight during the hatching process. No fourth segment is present. Lymph moves into the muscle much more rapidly and later, and there is greater infiltration of lymph into tissues surrounding the hatching muscles. Only in the Ruddy are the lateral lymph areas covered by yellow fat in the immediate post-hatching period. Regression of M. complexus is slowest; medial contact between the muscles of the two sides is maintained for at least 13 days, and the muscle loses less weight and more slowly. The shell of the egg is significantly thickest and, of course, the egg is the largest.

The Redhead, representative of the Aythyinae, demonstrated no constant differences from the five species of the Anatinae, and we may conclude that these two families are more closely related to each other than either is to the Oxyurinae, insofar as the hatching mechanism is concerned.

ACKNOWLEDGMENTS

The work was supported by the Graduate School of Southern Illinois University, the Wildlife Management Institute, and the Delta Waterfowl Research Station.

My sincere appreciation goes to my wife, Mildred, and my son, James, for unflagging aid in the field and laboratory parts of the investigation and to Mr. H. Albert Hochbaum, Director, Delta Waterfowl Research Station, for so kindly placing at my disposal the facilities of the Station.

LITERATURE CITED

DRIVER, PETER M. 1960. Field studies on the behaviour of sea-ducklings. Arctic, 13(3):201-204.

FISHER, HARVEY I. 1958. The "hatching muscle" in the chick. Auk, 75:391-399, 12 figs., 3 tables.

——————. 1961. The hatching muscle in North American grebes. Condor, 63(3):227-233, 4 figs.

——————. 1962. The hatching muscle in Franklin's Gull. Wilson Bull., 74(2):166-172, 1 fig., 1 table.

FISHER, JAMES R. 1962. The hatching muscle in the American Coot. Trans. Illinois Acad. Sci., 55(1):71-77, 2 figs.

FÜRBRINGER, M. 1888. Untersuchungen zur Morphologie und Systematik der Vögel zugleich ein Beitrag zur Anatomie der Stütz- und Bewegungsorgane. Amsterdam: van Holkema, 2 vols., xlix + 1751 pp., 30 pls.

GEORGE, J. C., and P. T. IYPE. 1963. The mechanism of hatching in the chick. Pavo. 1:52-56.

GEORGE, J. C., and A. J. BERGER. 1966. Avian Myology. New York: Academic Press, xii + 500 pp.

KEIBEL, FRANZ. 1912 Wie zerbricht der ausschlüpfende Vogel die Eischale? Anat. Anz., 41:381-382.

KORTWRIGHT, FRANCIS H. 1943. The ducks, geese and swans of North America. Wash., D.C.: Amer. Wildl. Inst., viii + 476 pp.

POHLMAN, A. C. 1919. Concerning the causal factor in the hatching of the chick, with particular reference to the musculus complexus. Anat. Rec., 17:89-104, 2 figs., 8 tables.

ROMANOFF, ALEXIS L. and ANASTASIA J. 1949. The Avian Egg. New York: John Wiley and Sons. xiii + 918 pp.

ROSENSTADT, B. 1912. Untersuchungen über die Histogenese des Eizahnes und des Schnabels beim Hühnchen. Arch. f. Mikro. Anat., 79:612-636, 1 pl.

VINCE, M. A. 1964. Social facilitation of hatching in the bobwhite quail. Animal Behav., 12:531-534, 2 figs., 2 tables.

——————. 1966. Potential stimulation produced by avian embryos. Animal Behav., 14:34-40, 1 pl., 3 figs., 1 table.

WETHERBEE, DAVID K., and L. M. BARTLETT. 1962. Egg teeth and shell rupture of the American Woodcock. Auk, 79(1):117.

Manuscript received July 20, 1966.