THE HATCHING MUSCLE IN NORTH AMERICAN GREBES

By HARVEY I. FISHER

The "hatching muscle," M. complexus, extends from the dorsal lateral part of the anterior cervical vertebrae to the posterior dorsal surface of the skull. Its function is to raise the head. During the later embryological development in the chick the muscle increases rapidly in bulk, reaching its maximum size the day before hatching and diminishing in weight very rapidly thereafter. The pattern of elaboration of the egg tooth is chronologically similar. This concurrence of events has led to the theory that the muscle furnishes the power to bring the egg tooth sharply against the inner surface of the shell, and thus pip the shell, as the chick breaks its way out of the egg.

The developmental history, and even the presence or absence, of this muscle is unknown except in the chicken (Keibel, Anat. Anz., 41, 1912:381–382; Pohlman, Anat. Rec., 17, 1919:89–104; Fisher, Auk, 75, 1958:391–399). Therefore, it seems worthwhile to record any information on its occurrence in other species, even though the data are not definitive.

The purpose here is to report the gross morphological features of the muscle in the Pied-billed Grebe (*Podilymbus podiceps podiceps*), Horned Grebe (*Podiceps auritus cornutus*), Eared Grebe (*Podiceps caspicus californicus*), Western Grebe (*Aechmophorus occidentalis*), and in a few specimens of the Red-necked Grebe (*Podiceps grisegena holböllii*).

MATERIALS AND METHODS

Four kinds of grebes nest in the vicinity of the Delta Waterfowl Research Station at Delta, Manitoba, Canada. The Horned Grebe nests in numbers not far away in the "Pothole Country" near Minnedosa, Manitoba. Since there is great similarity between the eggs of the Pied-billed, Horned and Eared grebes, and between those of the Western and Red-necked grebes, no clutches of eggs were taken in the above-mentioned localities unless the incubating bird was identified as it left the nest.

Eggs collected for this investigation included: Western Grebe, 28; Red-necked Grebe, 4; Eared Grebe, 36; Pied-billed Grebe, 24; and Horned Grebe, 14. The eggs were numbered by clutches and incubated in the duck hatchery at Delta at 99.5°F. and approximately 60 to 70 per cent relative humidity. Samples from each clutch were taken when the eggs were first collected, to determine the stage of incubation since the eggs could not be candled.

It was not possible to determine the number of days an egg had been incubated, even upon examination. Further, the eggs in a grebe clutch may be several days apart in their relative development. Therefore, in all instances body weight has been used as the basis for defining the stage of development.

When the embryos were taken from the eggs, all the extra-embryonic membranes were removed, and in embryos "nearly ready to pip" and "pipping" the yolk was drawn from the body. Removal of yolk already intruded was done to insure uniformity and consistency; in earlier embryos the yolk was impossible to weigh accurately, and in any event it is not truly a part of the body. However, in comparing weights of embryos near hatching and after hatching one must recognize that the apparent increase in weight may not be real. Sample weights of intruded yolk, not included in the body weights before hatching, ranged from one to two grams in the small-bodied species and up to four grams in Western Grebes. Before it was weighed to the nearest tenth of a gram, the embryo was blotted on newspaper to remove surface moisture.

Hatching muscles were excised with iridectomy scissors and weighed in milligrams

on a Roller-Smith Precision Balance. Muscles from embryos weighing as little as three grams could be cleanly removed. All muscles were weighed within 30 seconds of removal, to prevent undue desiccation. It is also important to mention that removal took no more than a minute or two after the skin was slit above the muscle.

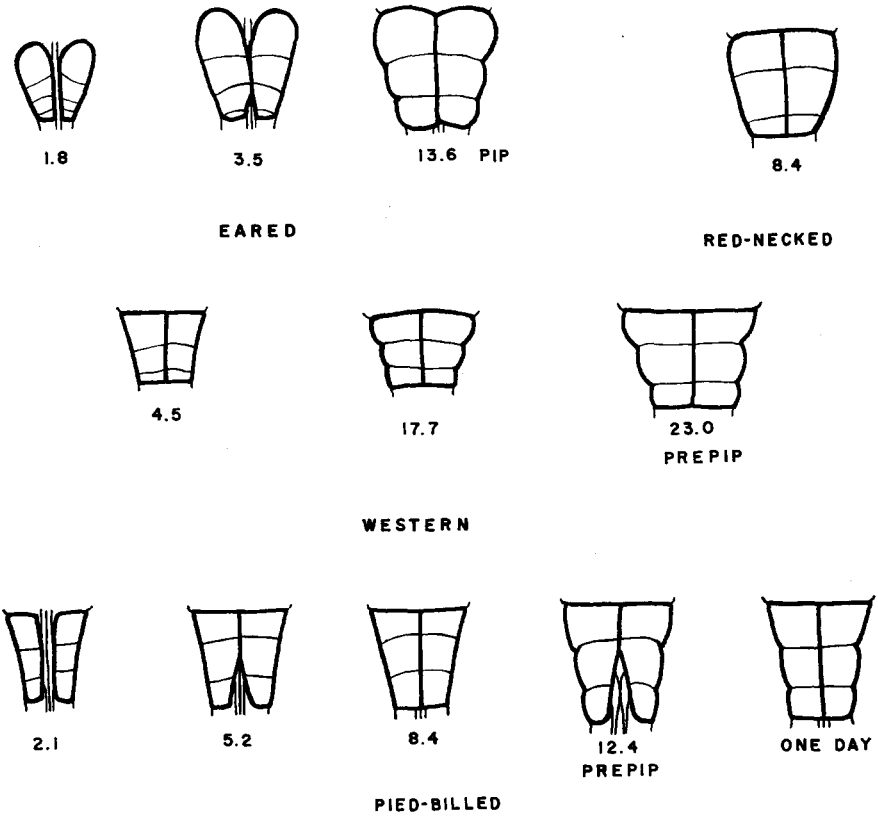

Fig. 1. Diagrams of dorsal views of the hatching muscles of grebes, twice natural size. Numerals below each drawing represent the body weight in grams.

After the muscles were taken out, the embryos were preserved in formalin for later study of the egg tooth and other features.

RESULTS

Description of the muscle.—In all species examined the hatching muscle is a paired structure lying on the dorsal and lateral aspects of the anterior cervical region. Usually the left and right members of the pair of muscles have some degree of medial contact as will be discussed later. Each member arises primarily from the lateral ends of the transverse processes of the third and fourth cervical vertebrae, with some fibrous connection medially to the tips of the neural spines of these vertebrae. Its posterior tip may have fascial attachment to the deeper musculature. Insertion is superficial on the posterior crest of the skull; it extends laterally into the origin of M. depressor mandibularis on either side, and its anterolateral corner is overlapped by the posterodorsal tip of the hyoid apparatus.

Basically, M. complexus consists of three segments easily visible from early in incu-

bation until after hatching (fig. 1) except that just before pipping the segments may be obscured. In the Pied-billed Grebe one-third of the specimens possessed four segments, and two Eared Grebes showed this condition. The figures show that in grebes the segments are wider than long; they extend ventrally halfway around the neck. It is also evident that there is a gradient, anterior to posterior, of decreasing size of the segments. When a fourth segment is present, it is always smaller than the third segment. The anterior margin of the first pair of segments demonstrates some interspecific variation; in the Pied-bill the edge is straight, as is usually the case in the Western and Red-necked grebes. In the Eared and Horned grebes this border is convex anteriorly and frequently is notched in the middle of its length where the muscles of the two sides are in juxtaposition.

Development of the muscle.—Figure 1 delineates the qualitative features, and figures 2 and 3 the quantitative development, but some significant aspects should be mentioned. The Pied-billed Grebe will be used as the example and other species compared to it.

Specimens as small as 2.1 grams exhibited the muscle upon gross dissection. Segmentation visible to the naked eye first appears, faintly at this time, in the three small grebes, and at four grams of body weight in the Western Grebe. The segments become more and more distinct, until just before pipping when the dividing septa are obscured by the swollen condition of the muscle.

At the two-gram stage there is usually no medial contact between the muscles of the two sides (fig. 1); at three grams the medial contact begins anteriorly and proceeds posteriorly. Some three-gram specimens show complete medial contact, but this stage is not reached in most specimens until they weigh six or seven grams. Just before pipping, in the Pied-billed Grebe, a pair of narrow, band-like muscles, Mm. biventer cervices, appears deep and medial to the two components of the hatching muscle (fig. 1). This development reduces the medial contact to the first and sometimes second pair of segments. Some Eared Grebes also have this secondary separation, but it was found in none of the embryos of Horned, Red-necked, or Western grebes. Continuous medial contact throughout the length of the muscle is evident in Horned Grebes after the six-gram stage and in Western Grebes after the 12-gram stage. By the time of hatching and for at least one day thereafter the muscles of the two sides are again in continuous contact in all species.

No major lymph glands were observed near M. complexus; in only two specimens (one Western Grebe just before pipping and a Horned Grebe that had just pipped) were there even a few lymph granules in the position of the lymph glands described for the chick by Fisher (*op. cit.*).

Despite the absence of nearby lymph glands, it is evident that there is lymph infiltration of the muscle in grebes. Beginning at seven grams in the Pied-billed Grebe, at eight to ten grams in the Western, and at five or six grams in the Eared and Horned grebes, the muscle assumes a faint straw color. Infiltration and the resulting turgidity reach their peak just before pipping. At this time the lymph color is present even in the lateral and ventral cervical muscles and in M. depressor mandibularis. In those specimens where there was secondary separation of the two sides of M. complexus, lymph was evident medially. No lymph was observed subdermally, superficial to the muscle. The muscle complex appears as a nearly solid, swollen block of tissue with the segments only faintly discernible. During pipping and hatching the lymph begins to disappear. In day-old Pied-billed Grebes the lymph color was receding, and in a Western Grebe two days old the muscle was pinkish red as were other cranial and cervical muscles.

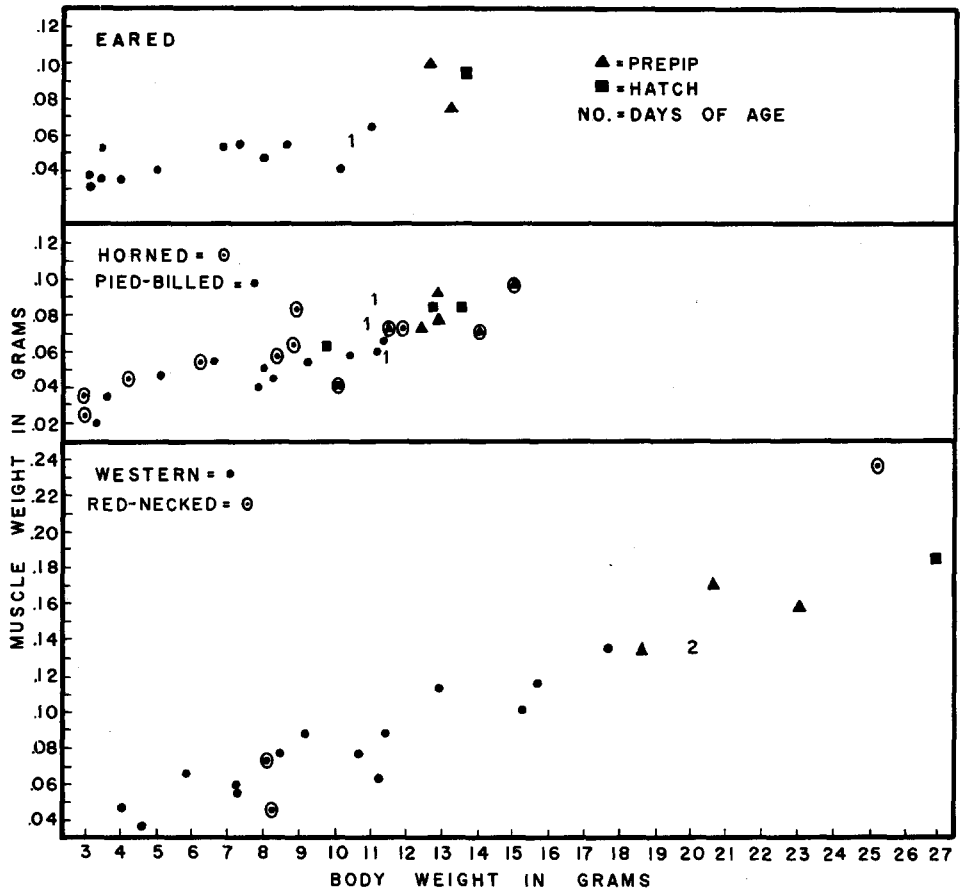

Fig. 2. Scattergram illustrating gradual increase in weight of the hatching muscle in grebes.

Comparison of the blood vessels serving the hatching muscle and those serving the rest of the neck revealed that the former were much larger and more obvious, particularly during the prepipping and pipping stages.

Figure 2 shows that in all the species there is a gradual, and straight-line, increase in the weight of the hatching muscle as the body weight increases. There is no major upsurge in the weight of the muscle prior to hatching and no observable decline during hatching or the first day, although the data are few in the latter instance.

In figure 3, where muscle weight is expressed as per cent of body weight, it may be observed that the relative weight of the muscle is greatest early in development (at 3 to 5 grams) in all grebes studied. Thereafter it declines in relative weight until shortly before the embryo starts to pip. The scattergram for the Pied-billed, Eared, and Western grebes illustrates the increase in the weight of the muscle before pipping. Note that the Red-necked and Western grebes have, in general, a relatively larger muscle throughout development than do the smaller Pied-billed, Horned, and Eared grebes. Particularly is this true at the "ready to pip" stage. There is close similarity in relative muscle weight among the small grebes at this stage. In the three species (Western, Eared, and Pied-billed) for which "just-hatched" specimens were available the relative muscle weights are essentially the same.

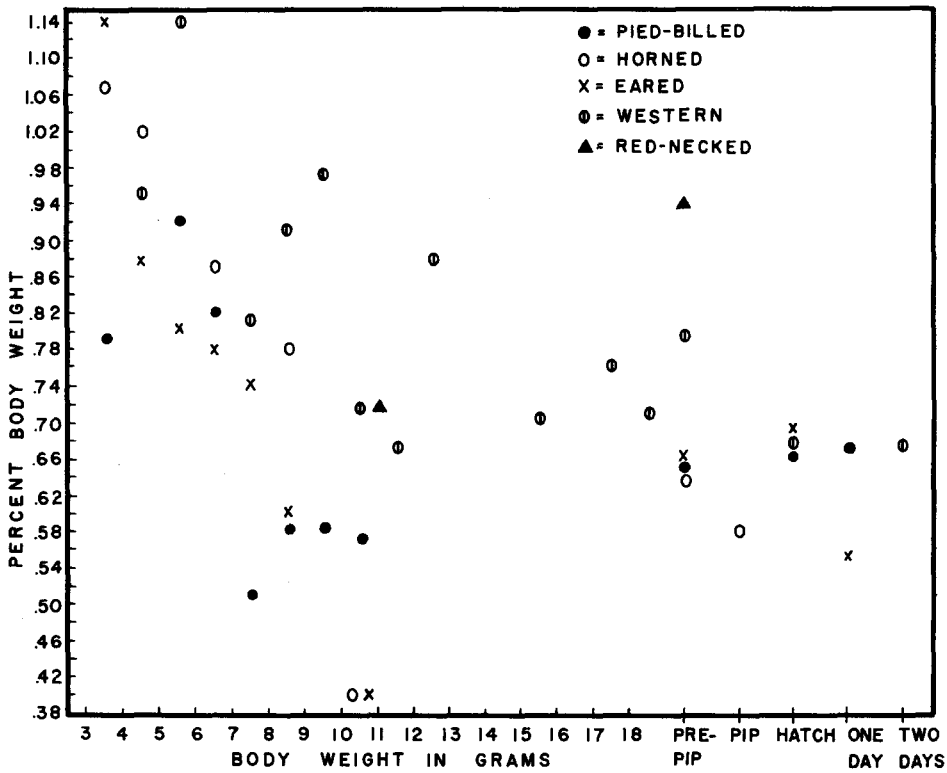

Fig. 3. Scattergram showing average size of hatching muscle relative to body weight of grebes. Number of specimens may be obtained from figure 2.

The few data indicate that Pied-billed Grebes hatch at 10 to 14 grams in body weight, Horned Grebes between 13 and 14 grams, and Western Grebes at about 28 grams.

The egg tooth.—In Eared Grebes at 0.63 grams of body weight, the egg tooth is not formed, but there may be a slight elevation at the future site of the tooth on the culmen. At 0.80 grams the tooth is present and is a contrasting white in color (fig. 4). By the time the embryo is one gram in weight an obvious tooth, 0.5 mm. in diameter, is present. Gradual increase in height and diameter continues until hatching. Note in the figures that the egg tooth is not so much a projection upward or dorsal as it is a forward extension parallel to the long axis of the bill. During the first and second days after hatching the tooth begins to disappear (fig. 4).

The only exception to the above in grebes is that in the Western Grebe the egg tooth was not found until the one-gram stage of body weight.

DISCUSSION AND SUMMARY

The hatching muscle in grebes is grossly similar in its morphology to the muscle in the chicken (Fisher, *op. cit.*). However, in grebes the segments are much wider than long, and they extend farther laterally. This lateral extension is least evident in the Pied-billed Grebe.

Virtual absence of the lymph glands on the dorsolateral surface of the neck, coupled with massive lymph infiltration of cervical muscles, leads to the conclusion that lymph

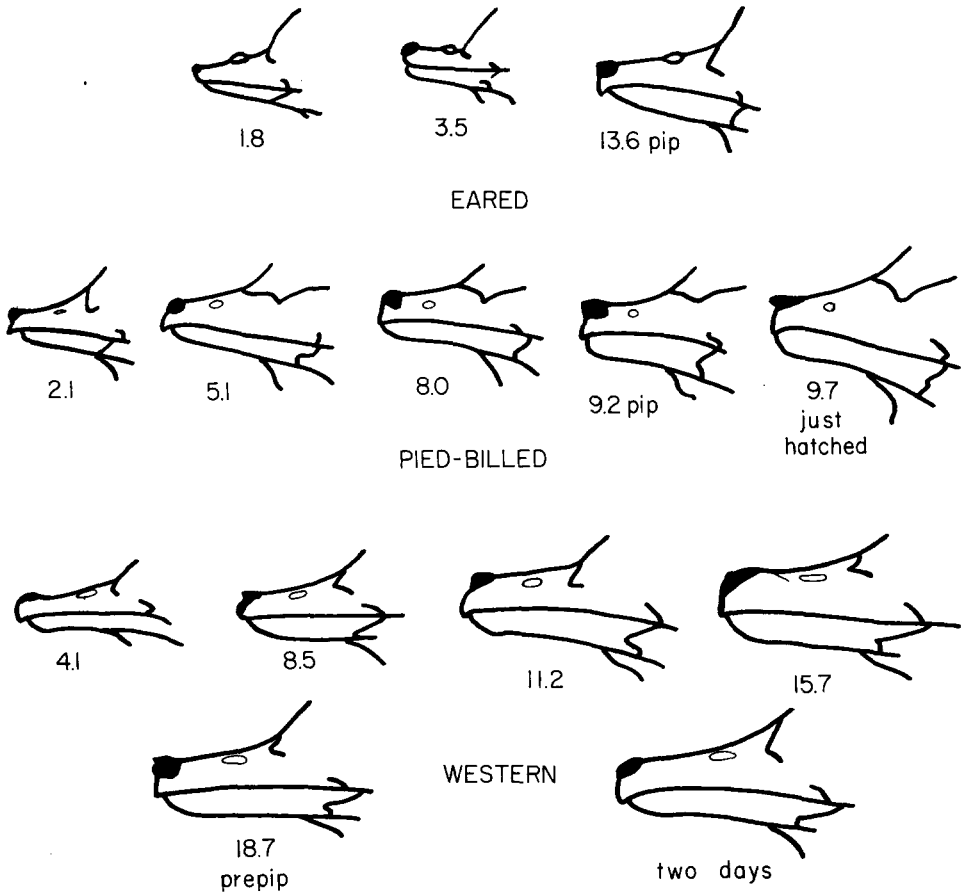

Fig. 4. Sketches of the development of the egg tooth in grebes, twice natural size.

moves in from some more distant glands. Much of the increase in weight of the hatching muscle results from increases in lymph content.

Although Pohlman (*op. cit.*) believed that the lymph hindered the activity of the muscle, it is my thought that the lymph may be the carrier for large sources of energy —glycogen and even fat. The relatively larger blood vessels serving the hatching muscle in the grebes also indicate that lymph infiltration is not a "biological accident," as one could perhaps theorize when the glands overlie the muscle as in the chick. There is no question that the lymph disappears rapidly during the pipping and hatching process. This depletion might result from use of the materials for energy during this critical time or it might simply be regression from the muscle due to increased pressures during active contraction. Some evidence for the first hypothesis lies in the frequent observation that in chicks and in ducks (Fisher, MS) eggs which are pipped and do not hatch within 24 hours usually do not hatch successfully. It seems plausible to believe that the energy resources were depleted before hatching could be accomplished. Fisher (Auk, 75, 1958: 394) found that the hatching muscle in chicks that pipped but could not emerge was significantly smaller than in "normally pipped chicks."

Although the absolute weight of the muscle increases gradually throughout the

period of development, it is relatively greatest early in incubation. This phenomenon is a result of the initial, more rapid, development of the cephalic portion of the embryo. My study of the chick (Fisher, *op. cit.*) did not include material prior to 15 days of incubation and thus this early development was not observed. It is not until shortly before pipping that the muscle shows its phenomenal increase relative to body weight.

The relative weight of the muscle is greater in the larger Western and Red-necked grebes, and there is close agreement in relative size between the Pied-billed, Horned, and Eared grebes. Note, however, that after hatching the relative size of the muscle in the Western Grebe is the same as in the Eared and Pied-billed grebes. This leads to the supposition that size of the egg and composition of the shell may be factors in determining muscle size. All grebe eggs observed during this study were soft to the touch, chalky, and rather easily broken, but eggs of the Western and Red-necked grebes had harder shells. Further, although grebe eggs are normally moist as a result of proximity to the water and the habit the incubating bird has of covering the eggs with wet vegetation, eggs of the two larger species never seemed as wet and frequently there was only a "token" covering of vegetation. Non-attended eggs of the smaller grebes were rather uniformly covered. It is realized that extent of covering of the eggs depends in part on the manner in which the incubating bird is flushed from the nest, but there seems to be an interspecific difference in the grebes.

Comparison of relative muscle weights in the chick and in the grebes, at the pre-pipping and hatching stages, further enforces the view that muscle size is related to egg size and to composition of the shell. Relative muscle sizes in the grebes are only one-third to one-half as great as in the chick (Fisher, *op. cit.*:394). Studies of the structure and composition of the shell are sorely needed; virtually all of the data in the literature pertain to the chick.

The massive development of the muscle is transitory, the muscle is not; this point was not clear in my paper of 1958.

These further studies of M. complexus lead me to believe that the muscle represents all or part of the caput portion of M. cucullaris.

The egg tooth first appears, upon gross examination, when embryos of Eared, Pied-billed, and Horned grebes are between 0.70 and 0.80 grams in body weight. It is present in Western Grebes only after the one-gram stage. Once hatching has occurred the tooth begins to regress rapidly.

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