

AN EMBRYOLOGICAL COMPARISON OF THE DOMESTIC  
FOWL AND THE RED-WINGED BLACKBIRD

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THE extensive investigations that have been carried on in the field of avian embryology have largely concerned the chicken as a representative subject. There are, however, two different general types of development among birds, namely: the nidifugous type, which results in the precocial condition at hatching, and the nidicolous type, which gives rise to the altricial condition. Various degrees and gradations of the two types are exemplified among the birds, but most embryological research has not considered the possible differences. Sutter (1950) in examining this problem stated, "Field ornithology has done much work in the domain of . . . contrasting postembryonic development of birds . . . but the comparative morphology of different types of ontogenesis is still at the beginning."

The purpose of this investigation is to compare an example of ontogeny from a precocial order (*Galliformes*) with one of an altricial order (*Passeriformes*), noting especially morphological differences of large magnitude or time discrepancies, and attempting to throw some light on the problem of why one bird hatches in about 21 days while the other requires only twelve days. Much information was readily available on the chicken (*Gallus domesticus*), so it was the logical choice to represent the first order. Among the passerines, however, very little concentrated work on any one species has been done. Consequently, I selected the Thick-billed Red-wing (*Agelaius phoeniceus fortis*) to represent this group because of the accessibility of the nests and the large number of eggs available for collection and preparation.

Prepared material of the Red-wing was compared to corresponding information on the chick as recorded in numerous sources, but mainly in Hamilton (1952), Patten (1951), and Arey (1954). Chick embryo microscope slides were also used to supplement the published material. Discussion of postembryonic development is omitted except where needed for clarification.

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Over a three-year period 750 Red-wing eggs were collected from ten colonies located within a twenty-mile radius of Alamosa, Colorado. Of these, only about 300 proved useful. Sterility, breakage, dead embryos, preparation errors, and partial early incubation account for the rest.

All eggs were retained in an incubator at 37° C. and at high humidity for the length of time desired. Twenty minutes were allowed for the eggs to reach incubation temperatures.

Stages were selected for preparation at every six hours of incubation for the first four days, every twelve hours for the next two days, and every 24 hours for the days thereafter. As in the chick, Red-wing embryos of the same age may be notably different from each other, so enough specimens were prepared of each age to facilitate the establishment of a norm.

Artificial incubation seemed adequate for proper development of the embryo for the period preceding the seventh day, and again beyond the seventh day to hatching; but for reasons that are poorly understood it was extremely difficult to incubate and retain the embryo alive over the seventh day. Several authorities record and discuss similar observations of critical periods for other birds (see Kendeigh, 1940, and Romanoff, 1949). In order to complete the embryo series across the seventh day, nests were marked and one egg collected from them early each morning, thereby providing a series of eggs, each one day older than the preceding one. Other eggs were incubated by the parent birds beyond the seventh day and then removed to be artificially incubated, thereby further adding to the later desired stages. A few discrepancies resulted, but because of the large number collected, most of the embryos fell easily into 24-hour categories.

After removal from the yolk, the blastoderm was supported inside paper rings according to the method described by Roudabush (1942). Larger embryos (above 96 hours) were removed from the yolk and handled directly without use of the paper rings. Since the small size and delicacy of the yolk in an egg this small resulted in the destruction of a high proportion of the blastoderms, I devised a hot ring technique to simplify the removal process (Daniel, 1955).

Preparations of the whole mounts and sections were carried out according to standard techniques. Specimens were variously stained with hematein, Grenacher's borax carmine, and Delafield's hematoxylin. Rings cut from xylol-insoluble plastic tubing (Tygon-S-22) were used as mounting cells for embryos older than four days.

Whole embryos and serial transverse sections were made of all stages described up to eight days of development and sagittal sections were also made of a few stages where better understanding of the subject made them desirable (24, 96, and 144 hours). Sections were cut at fifteen microns. It was not practical to prepare serial sections of embryos above eight days of development. Embryos from this stage to hatching were studied by dissection, with some of the organs

sectioned for a more detailed observation. Blood smears were also made of these later stages.

Several special preparations were made of six- to twelve-day-old embryos, including a series for bone development stained with alizarin, a series for cartilage development using the Lundvall technique with methylene blue, and a series of circulatory injections with India ink.

#### RESULTS AND DISCUSSION

*Incubation Time.*—From observations made on partially incubated eggs, it can be concluded that natural incubation may start with any egg of the Red-wing clutch, but usually does so with the third one to be laid. The natural incubation time of the Red-wing is generally quoted as being eleven to twelve days (Nice, 1953). Under the artificial conditions employed in the present study, the Red-wing requires a twelve- to twelve-and-one-half-day incubation period. This slight discrepancy between natural and artificial incubation times has been observed, discussed, and satisfactorily accounted for by Graber (1955), Huggins (1941), and Kendeigh (1955).

The nine-day difference in incubation time between the Red-wing and the chicken is less easily accounted for. Differences in egg size, period of retention of the ova by the adult, optimum humidity, and individual metabolism have been used to account partially for this. The most significant contribution, however, is that of Kendeigh (1940), who presented a scale to measure the increase or decrease in the incubation time that changes in temperature can cause. Employing this scale to the 2.9° difference (Huggins, 1941) found between the incubation temperature of the chicken and that of the Red-wing, we may expect a three-and-one-half day incubation time difference on this basis alone. Morphological and physiological differences must account for the remainder.

*The Egg.*—Differences in the egg structure between the two birds reflect incubation time differences. In reference to data from Asmundson *et al.* (1943), it will be noted that the percentage of yolk is decidedly lower and that of albumen higher in the chicken than in the Red-wing. This is to be expected since the yolk is consumed more rapidly the larger the embryo becomes; hence proportionally less would be needed for a twelve-day growing period than for a 21-day growing period, if growth rate is roughly comparable. This can be illustrated in the Red-wing by noting that the average yolk weight at laying is 0.8 grams, at eight days of incubation 0.64 grams, at ten days 0.42 grams, and disappears by hatching time at twelve days. The difference in yolk size is partially due to the presence of fewer concentric layers of yellow

yolk in the Red-wing egg than in that of the chicken, but the diameters of these layers are also relatively smaller in the Red-wing.

*The Blastoderm.*—In the chicken the blastoderm, at laying, averages about 3.5 mm. in diameter, but in the Red-wing, only 2 mm. in diameter. Because of differences in the size of the yolk, the curvature of the Red-wing blastoderm (0.20) is four times greater than that of the chick blastoderm (0.05), even though the arcs described by them are almost equal ( $12^\circ$  and  $10^\circ$  respectively). The relative position of the blastoderm on the yolk appears to be the same, since the angles between the embryonic axis and the principal egg axis vary from  $45^\circ$  to  $125^\circ$  in passerines (sparrows) and about  $45^\circ$  to  $135^\circ$  in chick embryos (Bartelmez, 1918). Dehnel (1928), in observations of ten- to thirty-hour-old embryos of 32 species of birds, found that he could divide them into two distinct types (i.e., nidifugous and nidicolous) on the basis of their early blastoderm characteristics.

*Body Form.*—In general, the gross morphology of the chicken and Red-wing embryo is much alike in all stages up to the hatching date of twelve days for the Red-wing. A few minor differences may be noted: the eyes are relatively larger in the chick than in the Red-wing; the beak of the Red-wing is slightly larger near hatching than that of the chick; the Red-wing possesses the egg tooth anlage on the lower jaw as described by Ludicke (1933), whereas the chick does not; and the feathers of the eleven- to twelve-day Red-wing are better developed and larger than in the chick of the same age.

In addition to the minor superficial differences noted above, a consistent difference in size persists throughout, as would be expected because of the size difference both in the eggs and in the parent birds.

| <i>Age</i> | <i>Red-wing</i> | <i>Chick</i> |
|------------|-----------------|--------------|
| 0 hours    | 2 mm.           | 3.5 mm.      |
| 24 hours   | 3.5 mm.         | 5 mm.        |
| 48 hours   | 5.5 mm.         | 7 mm.        |
| 72 hours   | 5.5 mm.         | 7 mm.        |
| 96 hours   | 6 mm.           | 7.5 mm.      |
| 5 days     | 7 mm.           | 12 mm.       |
| 6 days     | 9 mm.           | 15 mm.       |
| 7 days     | 11 mm.          | 17 mm.       |
| 8 days     | 14 mm.          | 21 mm.       |
| 9 days     | 19 mm.          | 23 mm.       |
| 10 days    | 21 mm.          | 31 mm.       |
| 11 days    | 30 mm.          | 37 mm.       |
| 12 days    | 35 mm.          | 46 mm.       |

A listing of approximate maximum lengths of the two embryos for daily timed stages makes this difference apparent.

Plotting these measurements against the age of the embryo will give us rough relative growth curves (Figure 1). The growth curves are

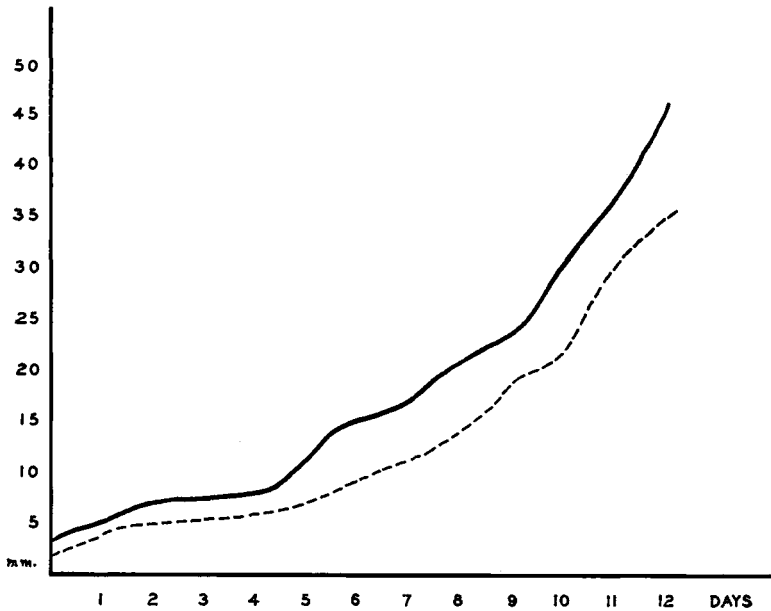


FIGURE 1. Growth curve of the chick (solid line) as compared to that of the redwing (broken line).

| <i>Age</i><br>(in hours) | <i>Number of Somites</i> |                 |
|--------------------------|--------------------------|-----------------|
|                          | <i>Chicken</i>           | <i>Red-wing</i> |
| 24                       | 1                        | 1               |
| 30                       | 7                        | 8               |
| 36                       | 10                       | 12              |
| 42                       | 13                       | 14              |
| 48                       | 17                       | 17              |
| 54                       | 27                       | 25              |
| 60                       | 30                       | 28              |
| 66                       | 33                       | 32              |
| 72                       | 36                       | 35              |
| 78                       | 41                       | 40              |
| 84                       | 44                       | 42              |
| 96                       | To tip of tail           |                 |

very similar and possibly would be parallel if body length would lend itself to more accurate measurement. The "plateau" in growth rate, present between the second and fourth day in both birds, is the result of extreme flexion increase of both head and tail. Therefore, body lengths are not comparable directly to other periods.

The average number of somites at any given age is very nearly equal in the two birds. A variation of one or two is observed in most cases but the normal range within a single species is usually as great.

The final number of somites in the chick may be about six more than in the Red-wing; this would account for the larger number of vertebrae in this bird. The observation on somite numbers corresponds closely to the data described earlier on relative growth.

*Embryonic Membranes.*—The general mode of development of the extraembryonic membranes is similar in the two birds, but a few minor differences occur. Trossarelli (1930) described a vitelline caecal diverticulum, which represents the remains of the vitelline canal, coming off the ileum of the chicken. In the chicken it may persist into adulthood, but in the passerines it is completely absorbed at the beginning of post-embryonic life. The yolk sac umbilicus, which closes in the chick about four days before hatching, appears not to close until after retraction in the redwing. Relatively speaking, the allantois develops more slowly and to a less definitive degree in the Red-wing than it does in the chick.

*Nervous System.*—Vaugien (1949) said, "The only important difference between the nidifugous and nidicolous birds is to be found in the relative growth of the brain and the optic lobes." Between the Red-wing and the chick many morphological differences appear, but without a doubt the nervous system is the seat of the greatest developmental discrepancies. The first such discrepancy appears with the closure of the neural groove. In the Red-wing the closing process starts in the anterior end and works mainly backward, whereas in the chick it starts farther back and works both ways. Holmdahl (1928), working with Starlings, made the same observation as noted for the Red-wing. He further noted that closure is complete at an early stage in the chick except for the temporary persistence of the anterior neuropore, and perhaps one other secondary neuropore, whereas in the Starling, it closes sporadically so that as many as seven neuropores may be observed along the length of the neural tube. Gogl (1930) describes three consistent neuropores in canaries. In the present study five such neuropores can be distinguished in the Red-wing by following serial sections and India ink injections.

Sutter (1950) has prepared some interesting charts on the relative

wet and dry weights ("dry weight is in close relation to myelinization") of the hemispheres, the corpora bigemina, the cerebellum and the stem remnant (i.e., the medulla oblongata and the basal parts of the mesencephalon and diencephalon) to show differences of development. He found that the galliform brain represents forty per cent of the adult weight at hatching while the passerine brain represents only ten per cent of the adult weight at hatching. In general, at any given age the brains of the two birds are approximately the same size. Since the chick embryo is larger than that of the Red-wing, the relative brain development is greater at any age in the nidicolous bird. In a series of studies, involving more than 219 species of birds, Portmann (1946, 1947a, 1947b) tried several possible indices of "cerebralization" with fair success. His work clearly indicates that the Passeriformes, as nidicolous birds, have relatively much better developed cerebral hemispheres and therefore more potential higher nervous control than the Galliformes, as nidifugous birds.

The optic chiasma, in the floor of the diencephalon, is a conspicuous fiber bundle after five and one half to six days of development in both birds, but one obvious difference presents itself. In the chick it is said to continue as a ridge in the lateral zones on each side up to the optic centers in the mesencephalon. In the Red-wing the optic tracts are buried immediately after decussation, in the floor and walls of the diencephalon. Here they pursue an internal course into the mesencephalon rather than a fairly superficial course as in the chick.

The epiphysial protuberance evaginates in the 72-hour chick and by seven days has elongated, branched, and shifted its point of attachment somewhat posteriorly. At 54 hours the Red-wing already exhibits this primordium, and it has reached the described point of development by six days of incubation.

The postotic ganglion in the chick completely splits into the superior ganglion of the ninth cranial nerve and the jugular ganglion of the tenth, presumably owing to the mechanical action of the formation of the third visceral cleft. In the Red-wing the two separate ganglia may be distinguished before the third cleft appears, and they do not entirely separate but remain joined by a slender connecting piece just at the point of entrance into the brain. In the chick, the hypoglossal nerve arises from two roots or bundles of axones that immediately fuse into the main nerve trunk. In the Red-wing, I find three original rootlets, the smaller two of which seem to join first before final fusion with the third.

In the chick eye, the inner and outer layers of the lenticular zone of the optic cup become actually fused together after about six days

of development. In the Red-wing, they do not fuse until at least the eighth day. Consequently the ciliary processes that begin to form in the eight-day chick do not do so until about one day later in the Red-wing. The lens epithelium, forming the annular pad that serves to transfer stress from the ciliary processes to the lens fiber, begins to thicken in the eight-day chick, but because the ciliary process is slow in forming in the Red-wing this pad does not develop until after the tenth day. The sphincter muscles of the iris arise by the eighth day in the chick, becoming more pronounced thereafter. I cannot distinguish these primordia by the time of hatching in the Red-wing, though Slonaker (1921) observed them first in the English Sparrow in the eleven-day embryo.

With the formation of the chick cornea, before and during the seventh day, the lens withdraws from the corneal surface to produce an anterior chamber that is continuous with the posterior chamber around the margins of the lens. This communicating canal is presumed to be closed in the living state of slightly older embryos. In the embryonic Red-wing, the corneal development parallels that of the chick, but the lens does not withdraw from the surface except at its periphery, because of its curvature in this zone, to produce a ring-shaped anterior chamber. This chamber is not continuous with the posterior chamber. In the English Sparrow the aqueous chamber does not separate the lens from the cornea until the thirteenth day (Slonaker, 1921).

The chick pecten develops the adult condition of seventeen to eighteen folds from the ninth to the seventeenth days of incubation, and pigment appears in it after the twelfth day. By the hatching time, the Red-wing pecten shows only a few slight folds and no pigmentation. Slonaker (1921), working with the English Sparrow, noted three folds at hatching and specified that twenty folds are present in the adult stage and that pigmentation appears after hatching, which he suspects might deposit as a result of light stimulus. In the Red-wing a thickened area of the chorioid coat that is to become the fovea appears just at hatching. In the English Sparrow it continues to thicken, accumulates a greater blood supply, and develops a pit in the thinner center (Slonaker, 1921). The postembryonic development of the Red-wing is outside the scope of this paper, but foveal development in this bird is presumed to parallel that in the English Sparrow. The chicken has no fovea.

The eyelids arise at about the same time in both birds, but the smaller eye of the Red-wing permits them to reach their definitive condition earlier than in the larger-eyed chick. In the nine-day



Red-wing the conjunctival papillae are almost entirely covered by the eyelids, a condition that is not reached until about eleven days in the chick.

Hamilton (1952) states that in the ear of the chick, "the paratympanic organ is a small ovoid vesicle . . . lined with a simple cuboidal epithelium except on the medial walls where there is a thickened ridge containing sensory cells." The paratympanic organ in the Red-wing is relatively larger than that of the chick, and thickened, interspersed, columnar cells, which might all be sensory, form an epithelium lining the entire vesicle. Since this organ is believed to be barethetic in function, it appears that the Red-wing might be more sensitive to altitude than the chick.

*Digestive System.*—In an attempt to show structural organogenesis in relation to total body weight, Portmann (1947b) concluded that the entire digestive tract and the liver, in respect to weight, are relatively much better developed in the passerine embryos than in the galliform embryos. Most of my observations support this conclusion, and it might be further noted that the anlage of the digestive tract appears in the Red-wing some six to twelve hours earlier than in the chick.

The mouth in general is alike in both birds except for the development of a slightly longer beak in the Red-wing. Tongue development is basically the same in all birds, as pointed out in the meticulously detailed account by Kallius (1905), but differences in shape do occur, usually reflecting differences in food habits.

In the chick four visceral pouches are known to form, and Hamilton (1952) cited several other references suggesting that five, six, and even seven pouches could possibly be accounted for, but that anything beyond four is questionable. Sections through a 72-hour Red-wing embryo show very clearly that five pouches do develop in this bird and that a sixth one makes a rudimentary appearance. This supports Kallius (1905) in his observation of a well-developed fifth visceral pouch in English Sparrows. The sixth pouch seems to be the same as the debatable postbranchial body in the chick.

In the chick the lumen of the esophagus becomes occluded at its cephalic end by proliferation of the lining cells. Fluid vesicles appear in it on the ninth and tenth days; and by fusion, they eventually restore the lumen by the eleventh day. The Red-wing shows the same occlusion, but it appears one day earlier and the lumen is re-opened by the ninth day. The esophageal glands appear in the chick at sixteen days of incubation and are fully formed by the nineteenth day. These same glands may be seen in their final condition by the time of hatching in the Red-wing.

The crop is well developed by the eighth day in the chick embryo, but a distinct crop never appears in the Red-wing. Stomach development is very similar in both birds, except possibly for a slight chronological difference in the appearance of the tubular glands of the gizzard. They form at about the thirteenth or fourteenth day in the chick, becoming functional at seventeen and one half days. The hatchling Red-wing shows these glands well formed and presumably functioning because the lining of the gizzard, which is the hardened secretion of these glands, is already present at this time.

The convolutions of the small intestine that lie in the umbilical cord are retracted into the abdominal cavity on the seventeenth to eighteenth day in the chick, three and one half to four days before hatching. In the Red-wing they are retracted on the eleventh day, immediately before hatching. In the chicken at hatching, the intestine is arranged in four longitudinal loops with the ileum exhibiting a few secondary coils. The Red-wing at hatching appears to have a relatively shorter intestinal tract and possesses only one major loop, with the others ill defined. The origin of the two intestinal caeca can be detected on about the seventh day in both birds. In the Red-wing they are vestigial and attain a total length of only four mm. by adulthood, while in the chicken they may become as long as 250 mm. by this time. The large intestine of the chick remains closed, up to as late as the seventeenth day, by a cellular plug which originated on the fifth or sixth day. The Red-wing also exhibits a cellular plug, but it disappears on the eleventh day.

The origin of the liver in the chick appears to be a controversial subject. Kingsbury *et al.* (1956), discuss liver development in the chick in great detail. The observations reported here parallel those made on the Red-wing, with one exception. Instead of two separate diverticula arising from the margin of the anterior intestinal portal as observed in the chick, only one diverticulum seems to appear in the Red-wing, but that one immediately (within six hours) forks into two branches. This single diverticulum might be interpreted as being the hepatic furrow and the two branches might represent the two separate diverticula noted in the chick. If this is so, the only difference would be in the relative depth of the hepatic furrow.

*Respiratory System.*—In the chick the parabronchi meet and fuse to form an intercommunicating network of tubes from the eleventh to the eighteenth day. It would seem necessary that this process be initiated earlier in the Red-wing so as to be completed by the twelfth day, but this appears not to be true. The Red-wing lung at hatching shows the same fusion of the parabronchi to be in progress

but not completed. We may therefore assume that the network is not completed until several days after usage has started and therefore that the early respiratory activities of the young Red-wing are relatively inefficient. The Red-wing lung seems to develop fewer primary branches of the mesobronchus than that of the chick. For example, the six-day chick exhibits ten branches, but in the six-day Red-wing only eight can be distinguished. One difference exists in the air sacs of the adults that probably originates postembryologically. The chicken exhibits two anterior thoracic air sacs, whereas the Red-wing has only one large one. Wetherbee (1951) observed the same condition in comparing the English Sparrow with the pigeon and assumed that a fusion had taken place.

*Circulatory System.*—Miller (1903) in investigating the development of the postcaval vein in the chick and the English Sparrow observed that the "mode of development of the two forms is found to be very similar, differing in only a few unessential points." This observation of Miller holds true for the entire circulatory system in a comparison of the Red-wing and the chick.

A few minor differences bear mentioning. The fifth aortic arch is very rudimentary in the chick and even absent in some embryos. When it is present, Hamilton (1952) describes it as "a slender vessel passing from near the base to near the summit of the sixth arch." In the Red-wing, the fifth arch is much better developed and passes unattended from the ventral aorta to the dorsal aorta without communicating with the sixth arch, except possibly just at the points of contact with the two aortae.

The ductus arteriosus and the foramina in the interatrial septum do not close in the chick until a short while after hatching. Red-wing specimens taken within two hours after hatching do not exhibit any foramina in the interatrial septum, and it is therefore assumed that they close just at or before hatching and that the ductus arteriosus has also closed in order to establish pulmonary circulation. The efficiency of the incompletely developed lungs would be improved somewhat by a well-formed pulmonary circulation at this time.

The omphalomesenteric vessels enter the embryonic Red-wing body farther cephalad than they do in the chick. Somite 22 marks the point of entrance in the chick, but in the Red-wing they enter at about the level of the nineteenth somite.

Witschi (1935) noted that the mesenteric arteries come off the dorsal aorta at the level of the twentieth somite in the Red-wing and the twenty-second one in the chick.

Sandreuter (1951) prepared an extensive comparative account

of blood components and blood-forming tissues on numerous birds. He found no major differences in the blood itself, but found striking differences in the hemopoiesis of the different species. He concluded that there is a more efficient type of erythrocyte in the species with the higher degree of cerebralization. Smaller birds, in general, have a higher erythrocyte number and smaller size than larger birds.

*Excretory System.*—The solid sprout that forms the pronephric tubule arises from the intermediate cell mass halfway between the somite and the lateral plate and projects dorso-laterally in the chick. Later, as the coelomic cavity enlarges to divide the definitive somatic layer from the splanchnic layer, the pronephric anlage becomes secondarily attached to the somatic layer. In the Red-wing this sprout seems to arise directly from the point of junction of the somatic mesoderm with the intermediate cell mass and is therefore primarily attached to the coelomic roof layer. From the point of attachment it projects dorsomedially. This slight difference in orientation of the pronephric anlage may account for the condition of the pronephric glomeruli somewhat later. In the chick, glomeruli develop transitionally in relation to the posterior pronephric tubules. They are well imbedded in the mesoderm of the area and are poorly suggested at best. The same glomeruli in the Red-wing appear as if contained within distinct bulbous bodies that project into the body cavity, and vascular connections may be traced to both the dorsal aorta and the post-cardinal veins. The projected position conveniently places the glomerulus closer to the nephrostome of the Red-wing's pronephric tubule.

Stampfli (1950), in his comparative investigations of mesonephric kidney growth in eleven different birds, was able to distinguish four distinct periods or quarters of development. His observations show that the mesonephros of the Passeriformes differs from that of the Galliformes in time of development but apparently not morphologically. In adult passerines the glomeruli of the metanephros number about 30,000 and in the adult chicken about 200,000 (Benoit, 1950).

*Reproductive System.*—Witschi (1933, 1935) has investigated the asymmetry in the avian reproductive system, comparing the chick, Red-wing, and English Sparrow, and in so doing has already noted the major differences between precocial and altricial birds. Other minor differences, especially in tubule formation, have been reported by Kummerlöwe (1930). The development of the reproductive system in the Red-wing essentially parallels that in the other passerines that were investigated by these authors.

*Endocrine System.*—Considering all of the endocrine glands as a

unit, no major points of difference in the Red-wing and the chick can be detected in their embryology. All the glands, except the interstitial cells of the gonads that do not mature until after hatching, are developed and functioning by the twelfth to the thirteenth day in both types of birds.

*Skeletal System.*—Most of the differences in the skeletal development of the Red-wing and that of the chick are chronological. The major ones may best be described by listing them as follows:

|   | <i>Chicken</i>               | <i>Red-wing</i>                    |
|---|------------------------------|------------------------------------|
| Scapula and coracoid begin ossification | 12th day                     | 9th day                            |
| Furcula forming from fusion of rods     | 12th–13th day                | 10th day                           |
| Ischium and ilium united by cartilage   | about 10th day               | after hatching<br>(post-embryonic) |
| Femur begins to ossify                  | 9th day                      | 7th day                            |
| Fibula begins to ossify                 | 13th day                     | 11th day                           |
| Patella begins to ossify                | 12th day                     | after hatching<br>(post-embryonic) |
| Notochord contacts hypophysis           | 52 hours<br>(Adelmann, 1926) | 36 hours                           |
| Presumptive sternal plates appear       | 4th day<br>(Fell, 1939)      | 6th day                            |

Other differences of a morphological nature exist. The preacetabular process is larger and better ossified in the Red-wing than it is in the chick. The first digit of the foot is quite short in the chick but in the Red-wing is larger than the other three. This condition is retained in the adult and is an adaptation to a perching habit. Skull development is very much the same in all birds as is the lower jaw development, since they differ only in relative size and proportion according to species.

The ossification of the vertebrae takes place in anteroposterior order in the chick. In the Red-wing the process is initiated in the region between the sixth and tenth cervical vertebrae and proceeds both anteriorly and posteriorly from this point. Cocchi (1944) noted that in the Starling, vertebral ossification may begin as far back as the pelvic girdle and continue in both directions, which suggests that there is no fixed point at which it must occur. Forty-four

vertebrae appear in the chicken, but I can distinguish only about 37 in the Red-wing, the differences being located in the lumbar, sacral, and caudal region. Extensive coalescence in these areas makes it difficult to pinpoint the differences. The cervical and thoracic vertebrae appear to be equal in number in both birds.

In the chick, Hamilton (1952) notes, "the sternum ossifies from five centers, a median anterior center and paired centers in the antero-lateral and abdominal processes." Dissection of seven- to eight-day nestling Red-wings suggests that only two such centers in the sternum are present, one in the anterior end of each original sternal plate. The ossification then spreads posteriorly, laterally, and into the keel. The thoracic ribs of the chick chondrify and ossify at two different centers, one vertebral and one sternal. In the Red-wing I find two such centers of chondrification, but can distinguish only a single (vertebral) center of ossification.

Cocchi (1944), in comparing the Starling and the hen, noted that only the femur, tibia, and fibula were completely ossified in the Starling by hatching time, whereas almost the entire skeleton of the chick was ossified by hatching time. The difference in incubation time, of course, accounts for these observations.

*Muscular System.*—By the time of hatching, the Red-wing muscles seem to be in about the same stage of development as those of the twelve-day chick embryo. The spinalis and biventer muscles, used to extend the head and neck, may be heavier in the Red-wing at this stage. This condition is possibly correlated with their use in breaking the shell. Young Red-wings also extend the head and neck when demanding food, so the heavier development of these muscles may further be accounted for by their immediate need in food-getting. It is known that the vocal membranes in the syrinx of oscine birds are controlled by five to seven pairs of muscles, while the suboscines exhibit less than five. This difference between the chick and Red-wing cannot be detected embryologically.

*Integumentary System.*—The skin and its derivatives show few major points of variation between the chick and the Red-wing. Scale outlines first appear on the leg in the eleven-day incubated chick. They may first be detected as early as the ninth day in the Red-wing. Down feathers cover the entire chick at hatching, having first appeared as early as the eighth day and being fairly well distributed over the body by twelve to thirteen days. Growth ceases abruptly on the thirteenth day and only cornification takes place thereafter. In the Red-wing feathers arise at the same time but remain sparse until a day or two after hatching. See Willier and Rawles (1940)

for a comparison of feather pigment development in the chick and the Robin. The primordium of the spur is discernible in the chick embryo at ten days of incubation. The Red-wing adult does not possess a spur and it does not appear in the embryo, except possibly as a slight dermal swelling. Similarly, the comb and wattles may be seen in chick embryos of about eleven days, with a dense vascular network in the underlying dermis providing the red color. Neither of these structures develops in the Red-wing. A somewhat denser vascular network is apparent in these areas in the Red-wing of eight to nine days of incubation, but it is not obvious thereafter.

Weber (1950), studying the skin in twenty different birds (including seven passerines), observed that the epidermis is divisible into distinct layers or "phases." The time of fusion and cornification of these layers differs between the nidicolous birds and the nidifugous ones.

The egg tooth (callosity) begins to form on the seventh day in both the Red-wing and the chick. In the chick it begins to cornify on the tenth day and is completely formed by the fourteenth day, at which time the gradual cornification of the jaws begins. The Red-wing initiates cornification of the tooth on the ninth day and has completed its formation at about eleven and one half days of incubation. The jaws begin to cornify on the tenth day of incubation and are relatively well cornified by the hatching date of the Red-wing, two days before they start the process in the chicken.

#### CONCLUSIONS

The subtle differences in developmental anatomy that have been described in the chicken embryo and the Red-wing embryo do not lend themselves to the drawing of clear-cut conclusions. Most of these differences are chronological, interpretive, or a function of general body size. As has been noted, the chicken requires 21 days of incubation and the Red-wing only twelve days. It is interesting, however, that most of the conditions (both morphological and physiological) that are present at the time of hatching in the Red-wing, and presumably necessary for that phenomenon to occur, are also present in the chick embryo of twelve to thirteen days of incubation. The reader may assume that conditions not described are very similar in the two species. Willier (1954), concerning himself with the physiological phases of embryonic development, concluded that most functional integration in the chick occurs between the tenth and thirteenth days, though functional maturation may continue even postembryonically.

The nidicolous birds, arising later in the avian evolutionary sequence,

could have evolved a twelve- to thirteen-day incubation period, because the ancestral nidifugous forms were in essentially hatchable condition at that age. There, the opportunity existed to select the shorter incubation time from the longer. If these birds were not in potentially hatchable condition, it would be difficult to infer a natural selection because a choice would not be present. This reasoning makes it unlikely that any bird could have an incubation period of *much* less than twelve days, without necessitating extensive embryological changes. Nice (1953), in discussing the question of presumed ten-day incubation periods, discounted their likelihood, and observed that eleven days is the shortest probable time and that even eleven days is quite rare. Friedmann (1927) attempted to show a ten-day period in cowbirds, but except for this he notes that "no case is known in nature where an adaptive acceleration of the rate of embryonic development seems to have accompanied the evolution of new species within a group."

Actually the Red-wing never undergoes a stage exactly comparable to that of the hatchling chick. It is interesting, however, that the young bird leaves the nest at ten days, able to hop and learn to hunt for its food (Nice, 1950). The twelve days of incubation plus the ten days as a nestling total 22 days, almost the exact time needed for incubation of the chick to a similar condition. The differences between the precocial and altricial birds seem to lie in the time of their retention within the protective shell and therefore may possibly be a function of yolk size.

The reader is referred to the work on the postembryonic brain by Sutter (1950) for other interesting conclusions that concern the same problem investigated in the present paper.

#### SUMMARY

Over 750 eggs of the Red-wing were collected during a three-year period and the embryos prepared in diverse ways for the study of particular structures. Observations on the Red-wing were then compared with those in the literature on the chicken.

Many differences are recorded in incubation practices, egg structure, blastoderm, general body form, embryonic membranes, and most body systems. Essentially both birds are equally well developed, both morphologically and physiologically, except possibly in the nervous and digestive systems, by twelve to thirteen days of incubation. Many of the observed differences are readily correlated with different life habits, feeding, and earlier hatching in the Red-wing. Some of these differences are at the species, or even individual, level, and are not as significant as order differences.



Nevertheless, the equality of development made possible the evolution of altricial birds from precocial ones, by giving the opportunity to select the short incubation type.

An incubation time of much less than twelve days appears to be unlikely.

It is noted that incubation may start with any egg of the Red-wing, but usually does so with the third egg. The seventh day seems to be a critical period in development and it is difficult to incubate artificially over this time.

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