DAWSON, W. R., AND J. W. HUDSON. 1970. Birds. *In* G. Causey Whittow [ed.] Comparative physiology of thermoregulation. Academic Press, London.

FRYER, T. B., G. J. DEBOO AND C. M. WINGETT. 1966. Miniature long-life temperature telemetry system. J. Appl. Physiol. 21:295–298.

GATEHOUSE, S. N., AND B. J. MARKHAM. 1970. Respiratory metabolism of three species of raptors. Auk 87:738–741.

GESSAMAN, J. A. 1972. Bioenergetics of the snowy owl (*Nyctea scandiaca*). Arct. Alp. Res. 4:223–238.

GRABER, R. R. 1962. Food and oxygen consumption in three species of owl (Strigidae). Condor 64:473–487.

MCNAB, B. K. 1966. An analysis of the body temperatures of birds. Condor 68:47–55.

NICHOLLS, T. H. 1968. Minnesota's 1966–67 snowy owl invasion. Loon 40:90–92.

NICHOLLS, T. H., AND D. W. WARNER. 1968. A harness for attaching radio transmitters to large owls. Bird-Banding 39:209–214.

WATSON, A. L. 1957. The behaviour, breeding, and food-ecology of the snowy owl (*Nyctea scandiaca*). Ibis 99:419–462.

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INCUBATION PATCH FLUCTUATIONS IN RED-WINGED BLACKBIRDS

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Most incubating passerine birds develop an incubation patch in the region of the ventral apterium. The patch loses feathers and becomes thicker and more vascular to serve as an area for better heat transfer to the incubated eggs.

Jones (1969, 1971) reviewed the literature on incubation patch development in birds. Selander and Kuich (1963) reported changes in incubation patch tissues of wild Red-winged Blackbirds (*Agelaius phoeniceus*) in some stages of nonbreeding and breeding. They experimentally induced feather loss and incubation patch development with hormone injections.

In my investigations of the incubation and parental behavior of Red-wings, I sought a detailed description of changes occurring in the incubation patch throughout the entire reproductive cycle. By separating the cycle into portions of nest building, egg laying, normal incubation, extended incubation, nestling care and fledgling care, I intended to determine the quantitative changes occurring in the stratum germinativum, dermis, blood vessels and fat cells in a sample size adequate to justify discussion of anatomical changes that occur. Observations of changes could then aid in interpreting the theories and observations that have been made with regard to hormonal, tissue and behavioral interactions (Jones 1971, Holcomb 1974).

I began studying Red-wings in 1963 but most data on tissues were collected in 1967 at Wooster, Ohio, and in 1968 and 1969 near Omaha, Nebraska. Birds were breeding in a variety of habitats including alfalfa and clover field, old weed fields, hedgerows, ditch banks, and marshes. Investigators visited nesting areas nearly every day beginning in March and ending in August. Males generally arrived back from migration in early March and females soon afterward. Pairing began in late March and continued through April and early May. Nero (1956a, b) described details of territory establishment and pairing.

When nesting occurred, from late April until mid-August, I attempted to discover nests during nest-building and then to visit these nests each day.

The normal incubation period of Red-wings is 11 days (Allen 1914). To prolong incubation, four artificial eggs of the same size and coloration as normal eggs were placed in nests.

Female Red-wings were collected in pre-breeding, breeding, and post-breeding seasons. The pre-breeding birds were designated as unpaired and were females flying about in flocks in March and April before pairing with a mate. Breeding females were designated as (1) paired with the male (collected in April and early May); (2) nest-building; (3) nest completed before egg-laying; (4) egg-laying, day 1–2; (5) egg-laying, day 3–4; and (6) incubation, day 1–3, 4–6, 7–9, 10–12, 13–15, 16–18, and 19–21. Most of the breeding females were collected in late April, May, or June, including those caring for nestlings or fledglings. Post-breeding females were all collected in August. When a female was collected, the ventral side of the body where incubation patch should develop was carefully examined to determine (1) extent of feather loss in all regions and (2) degree of apparent edema of tissues.

Four pieces (approx. 5 mm^2) of incubation patch were taken from each female; one piece each from the right and left anterior and right and left posterior portions of the incubation patch.

Approximately 2 mm of tissue in each square represented the abdominal feather tract area along the edge of the incubation patch. This served as a reference point for beginning observations when analyzing the histology of the incubation patch. Both front and rear sections were taken to determine if development of the patch was different in these regions. It was assumed that right and left portions would be the same and these two samples would insure having at least one good sample for analysis from both front and rear. Pieces of incubation patch were laid on dry paper towelling to which they adhered when placed in 10% formaldehyde. This prevented the tissue from rolling into a ball. After a few days, they were placed in 70% alcohol for storage, and any feathers present were carefully removed from the tissue with forceps.

The patch was sectioned at 5–7 μ and stained with haematoxylin and eosin. A mean of 30 serial sections of tissue was taken from each sample; three of these were selected at random for detailed examination. Starting at the edge of the incubation patch tissue in a section, at least 3 mm of tissue were available for study. From each of the three selected sections, the first, second, or third millimeter of tissue was chosen at random and used for the examination. In each bird, 3 mm of tissues were analyzed from both the front and rear portions of the incubation patch.

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I made microscopic examinations of each millimeter of selected tissue, at between 100× and 500×, using a graduated eyepiece and a 20 × 20 square grid for measurements of (1) stratum germinativum thickness to nearest micron, (2) dermal thickness to nearest micron, and (3) size of blood vessels 10 μ or larger in diameter. Size of blood vessels was determined by counting the squares and portions of squares in the grid represented by the total area of the blood vessel shown in the cross section. In addition, the cell layers in the stratum germinativum were counted, as were fat cells and number of blood vessels per millimeter. The relative abundance of smooth muscle was classified as follows: (1) normal abundance (as determined by viewing many sections of tissues from pre-breeding females), (2) small quantity, (3) very small quantity and (4) not present. A subjective rating of edema was given (0–5) depending on the overall appearance of the tissue including thickness of the dermis, blood vessels, and organization of the connective tissue elements in the dermal layer (see Jones 1971, for review).

Since one of the purposes of development of the incubation patch is to provide warmth for incubation, both the number and size of blood vessels are important, for a bird could have a few larger blood vessels that would not necessarily give off as much heat as several smaller vessels. Thus, I calculated a rough approximation of total surface area of blood vessels shown in cross-section by taking the approximate mean size of blood vessels multiplied by the number of blood vessels per millimeter.

Statistical analyses were done by means of a Students' *t*-test with significance considered at the 0.05 level.

When females arrive back from the south in spring, the ventral apterium is completely feathered. All of the seven paired females had no feather loss before nest-building. During building of the first nest, 8 of 12 females had no feather loss; the remaining 4 had loss ranging from a few feathers to two-thirds of the patch.

In general, there is little to no feather loss while building the first nest. Birds with a complete nest usually have lost at least one-third of their feathers on the patch and may have lost all of them. While egg-laying, most females complete feather loss. Up to the end of egg-laying, the tissues are beginning to appear slightly edematous when viewed grossly.

Only 2 of 14 females had any feathers remaining in the incubation patch on days 1–3 of incubation. The skin of all females at this breeding stage appeared somewhat edematous. From day 4 through 21, or during care of young, no females were observed with feather follicles in the incubation patch. External appearance showed edema through day 15, with some decrease in watery appearance in the very late stages. The tissues became thin and nearly transparent in birds caring for fledglings. Feathers did not appear in any female until the post-nuptial molt began in mid-August.

The external surface of the incubation patch became slightly scaly in some birds by day 10–12 of incubation but this condition was more likely to occur in the later portions of prolonged incubation. At the same time the stratum germinativum cells appeared a little more flattened than during egg-laying and early days of incubation. This may be due to the physical abrasion of nest and eggs against the patch and of pressure of eggs against the cells.

All of the properties of incubation patch changes were analyzed for the front and rear sections of tissues. These two regions did not differ significantly in the developmental or regressive stages of the incubation patch; therefore, all of the data were combined for the final analysis (table 1).

Table 1 shows that cell layers of the stratum germinativum increased from the time birds were unpaired through day 9 of incubation. This stratum then decreased in number of cell layers. Thickness of the stratum germinativum increased from the time females were unpaired until the time of egg-laying and then declined through incubation, prolonged incubation, and care of young. Dermal thickness, edema rating, numbers of blood vessels, and size of blood vessels followed a similar pattern. The relative surface area of blood vessels per millimeter (last column of table 1) shows a stepwise pattern of development and regression that matches incubation and nestling-care behavior. Blood vessels probably do not change in number and morphology as quickly as other tissues. Nevertheless, there is a peak of development in day 4–9 of incubation and a decline in prolonged incubation. If nestlings hatch at day 11, the surface area of blood vessels present remains high enough to provide warmth for brooding the altricial young.

Some fat is present in the tissues of the ventral apterium in paired and unpaired birds. This gradually disappears as incubation approaches and then reappears in some birds after nestlings hatch.

Smooth muscle tissue which interconnects follicles is present in most female dermal tissues but becomes less abundant as the incubation patch develops and becomes normally abundant in the post-breeding females.

Since it was impossible to cut through exactly homologous sections in tissues representing different birds, the presence of smooth muscle in the sections could vary depending on the plane of the section. However, since sections for observation were chosen at random in several different females for each interval of reproduction, the qualitative observation of a general reduction of smooth muscle should be valid. Since feathers are absent at this time it appears reasonable to expect a decrease in the volume of muscle functional in interconnecting these follicles. I am not aware of literature revealing changes of this nature but certainly any further studies should be carefully planned to quantitatively evaluate smooth muscle.

In post-breeding females all of the values for incubation patch tissues decrease to nearly the same as that shown in unpaired females before reproduction began.

The role of hormones in incubation patch development has been reviewed by Jones (1971). Selander and Kuich (1963) reported the degree of feather loss, stratum germinativum, dermis thickness, and blood vessels per millimeter in stages of pre-laying, laying and incubation of wild Red-winged Blackbird females. Their groups of birds were small (total of 17), but there is evidence that dermal thickness and blood vessels per mm were greater in their birds than in mine. This is probably because they took tissue samples from the center of the incubation patch, whereas I took them from the edge. The center of the patch does appear to be thicker.

Selander and Kuich showed that thickening of the stratum germinativum and the dermis, and increase in the number of blood vessels take place before loss of feathers. My data show similar changes as well as an increase in blood vessel size at this time.

Selander and Kuich reported that defeathering was usually complete before egg-laying began. Although

TABLE 1. Incubation patch tissue changes in female Red-winged Blackbirds throughout reproduction, from pre-breeding until post-breeding times.

Status of bird	No	Stratum germinativum cell layers	Stratum germinativum thickness (μ)	Dermis thickness (μ)	Edema rating	Fat cells/mm	No. of blood vessels/mm	Size of blood vessels in μ^2	Relative surface area of blood vessels $\sqrt{\text{Value in Col. 9}} \times \text{Value in Col. 8}$
Unpaired	5	1.0 ± 0.0	4.7 ± 0.4		0.0	60.6 ± 36.1	0.8 ± 0.2	450 ± 80	67.8
Paired	7	1.6 ± 0.2	5.8 ± 0.5	74.6 ± 9.9	0.9 ± 0.3	8.9 ± 6.3	1.1 ± 0.3	990 ± 200	138.8
Nest building	12	1.8 ± 0.2	7.6 ± 0.9	93.8 ± 21.3	1.3 ± 0.5	0.3 ± 0.3	1.8 ± 0.6	990 ± 280	226.8
Nest building Complete to day 1–2 Egg-laying	12	3.1 ± 0.3	15.5 ± 1.6	117.3 ± 11.5	2.7 ± 0.2	—	3.7 ± 0.5	1420 ± 310	558.0
Day 3 or 4 Egg-laying to Day 1–3 Incubation	14	2.7 ± 0.3	11.9 ± 1.0	118.1 ± 10.5	2.4 ± 0.3	—	3.7 ± 0.5	1080 ± 130	467.7
Day 4–9 Incubation	18	2.8 ± 0.2	11.4 ± 0.8	125.4 ± 12.0	3.2 ± 0.3	—	5.7 ± 0.7	1160 ± 170	777.5
Day 10–15 Incubation	16	2.5 ± 0.1	9.1 ± 0.6	106.5 ± 8.0	2.7 ± 0.2	—	4.4 ± 0.5	1650 ± 230	714.6
Day 16–21 Incubation	16	2.2 ± 0.1	8.7 ± 0.6	104.4 ± 7.3	2.3 ± 0.2	0.2 ± 0.2	4.7 ± 0.6	1100 ± 190	584.3
Nestling care	10	1.8 ± 0.1	6.9 ± 0.5	104.3 ± 9.2	1.6 ± 0.3	1.9 ± 1.7	4.1 ± 0.8	1590 ± 310	654.4
Fledgling care	3	1.6 ± 0.2	5.9 ± 0.4	70.7 ± 6.9	0.9 ± 0.0	1.4 ± 0.9	2.3 ± 0.6	1210 ± 290	320.2
Post-breeding	20	1.7 ± 0.1	6.5 ± 0.3	58.2 ± 4.3	0.3 ± 0.1	—	1.9 ± 0.2	600 ± 60	186.2

I found much variation among females, most birds had some feathers left before beginning to lay eggs in first nests, but most had lost all feathers by the third or fourth day of egg-laying. Some had a few feathers on the second and third days of incubation but none thereafter.

Very few feather follicles remained evident during the incubation period although they were present in non-breeding females.

Selander and Kuich (1963) reported feather loss in Red-wings after injection with a combination of estrogen and prolactin. Their results suggest that in Red-wings, prolactin may be secreted even before egg-laying and would influence defeathering. My results show that defeathering begins before egg-laying but in some females may not be complete until day 3 of incubation. This indicates individual differences either in (1) the quantity or timing of hormone release or (2) the responsiveness of the incubation patch tissues to the hormones.

The incubation patch actually diminishes in thickness before normal incubation ceases in Bank Swallows (*Riparia riparia*) (Petersen 1955) and in the Red-wings reported on here. Incubation constancy in the Red-wings also declines during the final days of normal incubation (Holcomb 1974) suggesting that secretion of prolactin may be declining before the end of incubation.

SUMMARY

Incubation patch tissues were collected from female Red-winged Blackbirds (*Agelaius phoeniceus*) throughout pre-breeding, breeding, prolonged incubation and post-breeding seasons to discover some of the morphological changes that may affect reproductive behavior.

Changes in stratum germinativum cell layers and thickness, dermis thickness, edema, fat cells, smooth muscle, number and size of blood vessels and relative surface area of blood vessels occurred between the time females arrived at the breeding areas in spring until egg-laying. Feather loss began before egg-laying in most females and was usually complete by day one of incubation. During normal incubation, the stratum germinativum and the dermis of the incubation patch thicken, while the blood vessels increase in size and number. Throughout prolonged incubation, the incubation patch tissues decline only after the time when they would function in brooding.

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LITERATURE CITED

ALLEN, A. A. 1914. The Red-winged Blackbird: a study in the ecology of a cat-tail marsh. Proc. Linnaean Soc. New York, Nos. 24–25:43–128.

HOLCOMB, L. C. 1968. Problems in the use of an embryocide to control passerine bird populations. Trans. 33rd North Amer. Wildl. Nat. Resour. Conf., p. 307–316.

HOLCOMB, L. C. 1974. Incubation constancy of Red-winged Blackbirds. Wilson Bull. 86:450–460.

JONES, R. E. 1969. Hormonal control of incubation patch development in the California Quail, *Lophortyx californicus*. Gen. Comp. Endocrinol. 13:1–13.

JONES, R. E. 1971. The incubation patch of birds. Biol. Rev. 46:315–339.

NERO, R. W. 1956a. A behavior study of the Red-winged Blackbird. I. Mating and nesting activities. Wilson Bull. 68:5–37.

NERO, R. W. 1956b. A behavior study of the Red-winged Blackbird. II. Territoriality. Wilson Bull. 68:129–150.

PETERSEN, A. J. 1955. The breeding cycle in the Bank Swallow. Wilson Bull. 67:235–286.

SELANDER, R. K., AND L. L. KUICH. 1963. Hormonal control and development of the incubation patch in icterids with notes on behavior of cowbirds. Condor 65:73–90.

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INDIGO BUNTINGS IN UTAH WITH SPECIAL REFERENCE TO INTERSPECIFIC COMPETITION WITH LAZULI BUNTINGS

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The Indigo Bunting (*Passerina cyanea*) appears to be expanding its range into many parts of southern and central Utah. Hardy (1939) listed one male in the collection of Dixie College taken in St. George, Washington County, Utah on 11 July 1937, which is the first Utah record. Cottam (1941), Behle (1943), and Woodbury et al. (1949) listed it as a rare or sparse breeder in streamside or irrigated vegetation in the Virgin River Basin of the extreme southwestern corner of Utah, based on one skin and two sight records. Wells (1958) cited a case of interspecific competition between the Indigo Bunting and its congener the Lazuli Bunting (*P. amoena*) along the Virgin River drainage at Leeds Creek 10–15 km from St. George, in the Pine Valley Mountains at an elevation of approximately 1,524 m. Wauer (1969) listed the Indigo Bunting as a common breeder in streamside vegetation below 915 m in southwestern Utah.

During the summer of 1973 I found Indigo Buntings to be common in the Virgin River Valley. I secured data for 16 territorial male Lazuli Buntings and 21 Indigo Buntings. It is quite probable that these individuals were "pure" types since examination of skins collected between 1937 and 1968 revealed no evidence of hybridization; all Lazuli Buntings had values of 16 on the Short and Sibley (1959) hybrid index. However, two vagrant hybrids have been recorded in the northern part of the state, one of which is in the University of Utah collection. I subjected the above data to multivariate analysis of variance and discriminant function analysis and found that the habitats utilized by the two species were significantly different at alpha = 0.01 ($F = 6.1425$

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