THE REPRODUCTIVE CYCLE OF THE MALE RED-WINGED BLACKBIRD

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Most North American passerine birds come into adult plumage in their first year of life so that yearling and older birds are indistinguishable during the breeding season. In several species, among them the Red-winged Blackbird (*Agelaius phoeniceus*), the adult male plumage is not acquired until after the breeding season in the second year, when the birds are 13 to 15 months of age. McIlhenny (1940) states that the year-old male Red-wings in Louisiana do not breed. Most authors, if they mention the plumage of the yearling male at all, designate it as an immature plumage (Bailey, 1917; Chapman, 1934; Peterson, 1939 and 1941), although at least two (Dwight, 1900; Forbush, 1927) call it the first nuptial plumage. In his extensive study of the ecology of the Eastern Red-wing (*Agelaius p. phoeniceus*), Allen (1914) briefly describes the gross changes in the testes of Red-wings taken in the spring months. His collections apparently were not extensive, and he makes no statement concerning the final state of the testes of the yearling males, which he calls "immature." He does state, however (p. 95), that "the resident immature males" migrate later in the spring and breed later than do the adults. Smith (1943) states that in the region of Chicago "males with duller brownish feather tips on the body and the wing coverts" establish territories though they do so later than the adult males. There seems to be no doubt but that the yearling females of *Agelaius phoeniceus* breed. In the closely related Tri-colored Red-wing (*Agelaius tricolor*), Lack and Emlen (1939) report that the males with the dull epaulets (year-olds?) usually are not restricted to territories, yet these birds showed some evidence of mating behavior. They chased females, and one copulated with a taxidermic mount of a female.

The present investigation has been made to determine what differences exist between the testis cycles of the adult and yearling Red-wings and to obtain additional data on the status of the yearlings as breeders.

MATERIALS

Red-wings are abundant breeders in the irrigated Flathead and Bitterroot valleys of western Montana. A total of two hundred and fifteen males was collected in western Montana. Some were taken in every month of the year except December. In addition, twenty-five males were taken in southern Wisconsin during July, 1941, and August, 1940, and eleven were taken in Montana east of the continental divide during June and July, 1942. Birds from Wisconsin and eastern Montana are excluded from all calculations unless specific reference to them is made. Dr. H. C. Oberholser examined some of the birds from western Montana and wrote that they were Thick-billed Red-wings (*Agelaius p. fortis*).

The spring migration begins in western Montana in early March and continues into April. Since western Montana does not lie along an important flyway, it is doubtful if there are large numbers of spring migrants which do not remain to breed. The earliest migrants are largely males and the latest largely females, although adult and year-old males and females may be found in the same flocks throughout the spring migration. The first nests are built in early May, and the first juvenal birds are commonly seen in mid-June. By early July many of the adults have left their nesting territories, but a few are still feeding young as late as the fourth week in July. The young and some of the adults begin to form loose flocks by mid-July. Most of the birds migrate from the region before the first of November, although some birds may be found throughout the winter. We do not know whether the wintering birds are birds which breed locally and have lost the migratory habit or whether they represent birds which have come from

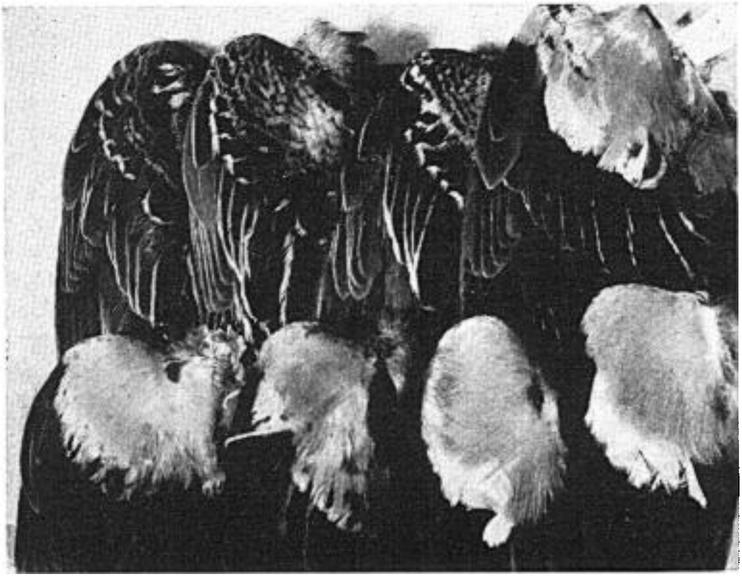

Fig. 8. Wings of year-old and adult male Red-wings taken in April and May. Four in upper row and two on left in lower row from year-olds, two on right in lower row from adults.

breeding grounds farther north. In one series taken in January the birds were definitely larger (10-20 gm.) than breeding birds, but other winter specimens were the same size.

Male Red-wings occur in three distinct plumages according to the age of the bird. These plumages and the associated molts are discussed by Dwight (1900), Forbush (1927), Ridgway (1902), and others; they will not be described in detail here. The juvenal plumage, which is somewhat like that of the adult female, is carried from the time the bird leaves the nest until the postjuvenal molt which may begin from late July until late August. The postjuvenal molt is complete and the immature bird then resembles somewhat the adult male, but the black contour feathers are more heavily edged with brown and the wing coverts instead of being the Scarlet Red (Ridgway, 1912) of the adult range through the less intense reds into orange and yellow with varying amounts of black. This plumage is worn until the following July when the molt into adult plumage begins. Adult males have a single, complete postnuptial molt beginning in July. Forbush (1927) states that some of the wing coverts of the yearling may be replaced in the spring. Ridgway (1902) writes that the wing coverts of the young males taken in the winter are less intensely colored than they are in the spring. We have seen no evidence of molting of these wing coverts except during the usual molting time as described above. Thus we feel that any late winter or early spring molting of wing coverts in the yearling males must be quite rare if it occurs at all. Ridgway also points out that great individual variation exists in the degree of "adultness" of the first-winter plumage. Allen (1914) also was impressed by the great variation in the plumage of the year-old birds and believed that the most adult-appearing birds were two-year-olds. Figure 8 shows marked plumage differences in spring-taken birds, especially in the coloration of the wing coverts.

In this work young birds taken during June, July, and August are called juveniles. From September through January they are called immatures, and from the beginning of March until the inception of the molt into second-winter plumage in July, when they become indistinguishable from adults, the birds are called year-olds. All other birds, those over 13 to 15 months of age and in adult plumage, are called adults. In order to be sure that the birds in the so-called first-winter plumage were actually young birds and did not represent adults in another color phase, many of the birds obtained during late summer and fall were examined for the presence of the bursa of Fabricius which is known to be a reliable age character since it is present in the young birds and absent in adults (Gower, 1939). Birds in juvenal and first-winter plumage were found to have the bursa well developed while it was absent in all birds in adult plumage in which search was made. The bursa was last seen as a scarcely discernible vestige in immatures taken in January, but it could not be found in birds taken in March. Several birds taken during the molt in July and August showed only these combinations: (1) first-winter plumage replacing juvenal plumage, (2) adult replacing first-winter plumage, and (3) adult replacing adult. We are convinced, then, that the birds obtained during the spring which are in the so-called first-winter plumage actually are yearling birds. That none of the birds in adult plumage are actually year-olds we are also reasonably certain. The employment of the bursa technique further makes it quite certain that birds which Allen (1914) suggested might be two-year-olds are actually year-olds. Packard (1936) in describing the plumages of the Eastern Red-wing as an aid to bird-banders in properly sexing and aging trapped birds mentions difficulty in distinguishing the immature and adult male plumages in museum specimens. In most instances we had no difficulty in distinguishing between these plumages even when the birds were at a considerable distance in the field. The plumages of almost all of the 115 birds taken in this study which were classed as immatures and year-olds were so distinct that there could be no doubt as to their age. Only two or three specimens had plumages very nearly like those of adults (see fig. 8, second from left in lower row). The only one of these which was taken in the fall possessed a well-developed bursa of Fabricius typical of immature birds.

Most of the birds for March, April, and May were taken in 1940; the summer birds were taken in 1942 and 1943; and the fall and winter birds were taken in 1941 and 1942. We saw no evidence of any pronounced annual variation in the testis cycle.

All birds were shot with a rifle or shotgun and the testes were removed immediately and placed in Bouin's fluid. Large testes were bisected with a razor blade after they had been in the fixative for a few minutes. Upon return to the laboratory the extraneous material was removed from the testes and they were weighed on a precision balance. In most studies of the sexual cycles of birds the gonads have been measured with calipers or the volume calculated. We think that weighing the testes on a fine balance gives more accurate indication of their size than the other methods. Usually the combined weight of both testes was recorded, although when one testis was punctured by the bullet or shot, the weight of the intact testis was doubled. This involved some error but since either testis may be the larger it was not possible to make a correction. If both testes were destroyed, the bird was discarded. After fixation, one testis was sectioned at 7 or 8 μ and stained in Heidenhain's or Erlich's hematoxylin.

The carcasses of all birds were weighed upon return to the laboratory. In many cases desiccation materially reduced the recorded weights. From specimens in which drying was not excessive, it was found that the normal weight of both adult and year-old males was close to 72 gm. The body weights of the young and adult birds were not found to differ markedly.

Acknowledgment.—We are indebted to B. W. Brink, who helped materially in collecting birds in the spring of 1940; to Dr. R. K. Meyer, who made helpful criticisms; and to Professor M. S. Morris, who made suggestions on the statistical work.

RESULTS

Changes in testis size.—The data on testis weights are summarized in table 1. When the young birds leave the nest at 10 to 12 days of age, their testes weigh under 2 mg. During the few weeks following the nestling stage a slight increase in testis weight was found so that the July specimens showed average testis weights of 3 mg. By August the testes have decreased in size slightly and they remain at this minimum (average 1.5 mg.) until after mid-January. Birds taken in early March (now called year-olds) showed slight increases in testis weight, and the growth continued slowly through March and early April. A period of most rapid growth occurred in late April so that in early May all birds taken (29) had testes weighing over 300 mg. Maximum testis weights in year-olds were obtained from birds taken the second and third weeks of May (9 birds,

Table 1

Type of bird	Month	No. in sample	Mean testis weight in mg.	Standard deviation	Minimum	Maximum	Coefficient of variation
Juvenile	June	2	1.9	0.71	1.4	2.4	37.4
	July	7	3.0	0.43	1.6	4.2	14.4
	August	5	1.4	0.26	1.2	1.8	18.6
Immature	September	1	1.6	......	....	....	......
	October	5	1.5	0.33	1.2	2.0	22.0
	November	5	1.5	0.51	0.8	1.9	34.0
	December	0	....	......	....	....	......
	January	3	1.3	0.31	1.0	1.6	23.8
	February	0	....	......	....	....	......
Year-old	March 1-15	5	4.6	0.83	3.8	5.0	18.0
	March 16-31	6	17.1	12.13	7.6	34.0	71.0
	April 1-15	6	103.6	122.90	18.6	302.2	118.6
	April 16-30	13	435.4	205.01	92.8	732.0	47.1
	May 1-15	29	575.5	110.65	339.0	767.0	19.2
	May 16-31	3	637.9	69.35	589.4	717.4	10.9
	June 1-15	4	476.3	176.74	372.0	614.8	37.1
	June 16-30	5	388.1	207.76	162.6	515.0	53.5
	July 1-15	2	14.1	11.45	6.0	22.2	81.2
	July 16-31	1	3.2	......	....	....	......
Adult	August	8	3.1	1.35	1.6	6.0	43.4
	September	3	2.0	0.57	1.4	2.5	28.5
	October	4	3.4	0.91	2.0	5.2	26.8
	November	5	3.9	1.61	2.2	6.4	41.3
	December	0	....	......	....	....	......
	January	9	3.3	1.09	2.0	5.3	33.0
	February	6	12.9	4.01	8.5	17.8	31.1
	March 1-15	16	25.1	8.17	8.8	41.2	32.5
	March 16-31	17	100.8	84.51	20.0	366.0	83.8
	April 1-15	6	646.4	295.31	358.6	1089.0	45.7
	April 16-30	8	748.9	250.82	230.0	1061.4	33.6
	May 1-15	11	862.5	193.52	571.4	1212.8	22.4
	May 16-31	3	857.2	43.86	809.6	896.0	5.1
	June 1-15	4	888.7	214.47	806.4	1068.6	24.2
	June 16-30	4	954.2	145.15	841.6	1166.2	15.2
	July 1-15	7	120.2	193.57	14.6	551.6	161.0
	July 16-31	2	4.7	0.02	4.6	4.8	0.4

average 647 mg.). By the first of June the testes of some of the year-olds have already begun regressing and in the few July specimens available the testes were approaching the minimum. The molt which begins in July makes these year-olds indistinguishable from the adults.

The testes of the adults were at the minimum (average 3.2 mg.) from mid-August until late January, but during this time they were larger than those of the juveniles and immatures for the corresponding period. Growth was found to begin in late January and the period of most active increase was in early April. The maximum weights were reached in most instances by late April (average weight of testes at the maximum 925 mg.) and no important changes in weight occurred until late June. At this time the testes of some of the birds had begun to regress while those of others remained active until early July. It may be seen from table 1 that regression proceeds at a considerably faster rate than does recrudescence.

The testes of the adults are consistently larger than those of the year-olds and immatures throughout the year. The period of most active growth in the adult testes precedes that in the year-olds by three weeks, and the average maximum testis weight of the adults is nearly 300 mg. larger than the same figure for the year-olds.

With data of the sort here available it is impossible to state exactly how long the testes of any one bird might be expected to remain at maximum size. Testes of maximum size were taken from adult birds first on April 13 and last on June 17, but some of the birds taken on July 5 showed testes just beginning regression. Testes from adults which were not at the maximum were taken on May 3 and again on July 5. Judging from the small size of some of the testes taken on this latter date, regression must have started by the beginning of the fourth week of June. From these data it can be seen that the testes of any single adult could remain at the maximum from 50 to 75 days. Analysis of similar data from year-olds shows that the period during which the testes could be at the maximum varies from 30 to 55 days, the month of May being the only period during which the testes of all year-olds seem to be at the maximum.

The standard deviations and coefficients of variation supplied in table 1 are calculated from rather small samples and for that reason are not to be regarded as precise values. They are supplied only to show that variation in testis weights is greater when the testes are increasing or decreasing than when they are at the maximum or the minimum. The testis weights of adults taken in early July showed the greatest variation (coefficient of variation was highest), when regression in some was almost complete and in others just beginning.

Histology of the testes.—A detailed description of spermatogenesis for the Red-wing is deemed unnecessary, because there have been so many studies made of spermatogenesis in various species of passerine birds (for example, Rowan, 1928; Bissonnette and Chapnick, 1930; Bissonnette, 1930; Kirschbaum and Ringoen, 1936; Blanchard, 1941; Wolfson, 1942; Bullough, 1942). Blanchard has delimited seven stages in the progress of spermatogenesis in the White-crowned Sparrow which are useful in this study. These stages which are described in some detail by her will only be named here: stage 1, the inactive condition; stage 2, the first change from the inactive condition; stage 3, marked increase in germinal elements and interstitial cells; stage 4, appearance of primary spermatocytes in synapsis; stage 5, predominance of primary spermatocytes in synapsis; stage 6, spermatids present; and stage 7, breeding condition. The Red-wing material conforms to Blanchard's descriptions except that spermatozoa were commonly found free in the lumens of the tubules of the testes of the White-crowned Sparrow, but seldom found in the Red-wing. However, the seminal vesicles of Red-wings in breeding condition were packed with sperm, so there would need be no release of sperm from the testis at the time of copulation as Rowan (1928) has suggested might occur in the Slate-colored Junco (*Junco hyemalis*).

We were unable to find Blanchard's stage 2 represented in our material, but this stage probably occurs in late January in the adult birds and in February for the year-olds, and we have no material taken at these times. Table 2 summarizes the data on the dates the various stages were first seen and also the time when the majority of specimens had reached each stage. The delay in the development of the testes of the year-olds by approximately three weeks is brought out clearly by the figures in this table.

Table 2

Blanchard's stages	Year-olds: Date stage first seen	Year-olds: Weight of testes showing stage	Year-olds: Date stage shown by majority of birds	Year-olds: Av. wt. of testes showing stage	Adults: Date stage first seen	Adults: Weight of testes showing stage	Adults: Date stage shown by majority of birds	Adults: Av. wt. of testes showing stage
Stage 3	March 2	3.8	March 2	4.2	Feb. 9	8.5	Feb. 9	9.1
Stage 4	March 22	9.6	March 30	21.1	Feb. 16	14.4	Feb. 16	14.1
Stage 5	March 24	34.0	April 13	115.8	March 2	35.4	March 9	40.6
Stage 6	April 13	211.0	April 20	328.5	March 24	140.6	March 30	184.1
Stage 7	April 13	302.2	April 20	328.5	March 30	366.0	April 6	498.8

It is important to emphasize that all of the 29 year-old birds taken during the first half of May showed testes in active spermatogenesis. Spermatogenesis continues until late June in the adults, but only until mid-June in the year-olds.

Tubule diameters.—Average diameters of the seminiferous tubules were calculated for most testes. The slides were projected on to the ground glass of a photomicrographic camera at varying magnifications depending on the size of the testis. The diameters of the tubules were obtained by calculation from measurements of the projected image. Fifty measurements of the diameters of tubules chosen at random were made from each testis and in each case the smallest diameter was measured to avoid unduly large measurements due to the coiling of the tubules. Even for specimens exhibiting the most variation this size of sample was large enough to insure that the calculated mean was within 5 per cent of the true mean on the basis of a probability of 95 per cent. Many

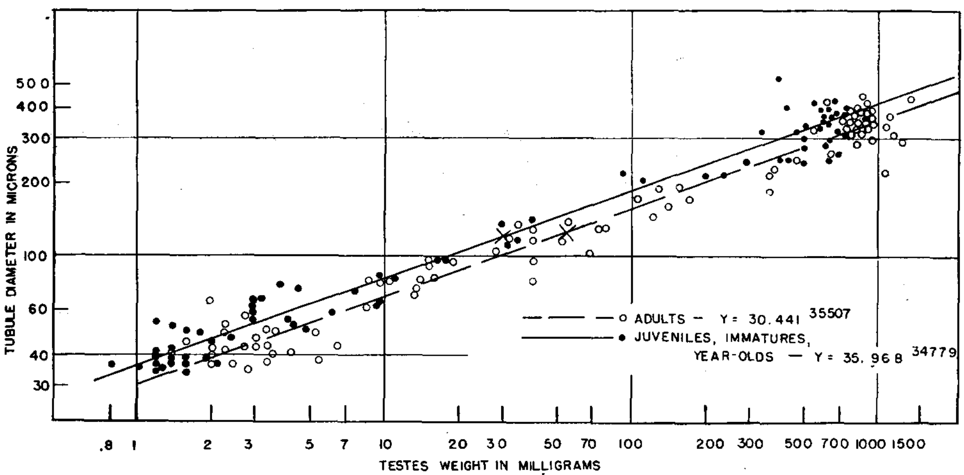

Fig. 9. Double logarithmic plotting of the relation of tubule diameters to testis weights.

specimens, the smaller testes in particular, exhibited means within the 5 per cent limits for a probability of 99.5 per cent. All of the figures obtained in this fashion except those of testes in regression were plotted on double logarithmic paper (fig. 9) which was necessary to rectify the values. Equations were calculated to show the relationship during growth between testis weights and tubule diameters by the method of least squares as described by Simpson and Roe (1939:364). The equations show that as the testis weights increase, the tubules increase in diameter but at a slower rate. The calculated values in the equations express the precise nature of this relation. The equations obtained for the growth of the adult testes from the minimum to the maximum differed from the equation for the growth of the juvenal, immature, and year-old testes. The equations where X is the testis weight and Y the tubule diameter follow:

$$Y = 30.441X^{.35507} \text{ (for adults)}$$
$$Y = 35.968X^{.34779} \text{ (for juveniles, immatures, and year-olds)}$$

It is readily seen from figure 9 that the tubules of the small testes of the juveniles, immatures, and year-olds have greater diameters in proportion to the testis weights than those of the adults. This is due to a difference in the amount of the intertubular material in these small testes, a situation which will be discussed later. It is not to be inferred that the tubules of testes of the adults are smaller than those of the juveniles, immatures, and year-olds when compared by month, for such is the reverse of the actual situation, as is pointed out beyond.

Difference between adult and juvenal and immature testes during the quiescent period.—Studies were made to determine what monthly changes occurred in the testes and what differences there were between the testes of adults and juveniles and immatures during the quiescent period. Fisher's method of analysis of variance allows the analysis of a series of data for two criteria with a single set of calculations. Accordingly this method, as described by Snedecor (1940), was employed to test the validity of suspected differences. The data on testis weights as analyzed are summarized as follows:

	Adult		Juvenile and immature	
Month	No. in sample	Mean value of testis weight	No. in sample	Mean value of testis weight
August	8	3.1	5	1.4
September	3	2.0	1	1.6
October	4	3.4	5	1.5
November	5	3.9	5	1.5
January	9	3.3	3	1.3

It appears that the testes of the adults are consistently larger than those of the juveniles and immatures and that there is no significant difference within each group by months. The results of the analysis of variance test follow:

	Calculated F	F for probability of 1 per cent
Difference in testis weights between ages	38.63	7.35
Difference in testis weights between months	0.77	3.86

The very high calculated value of F for the difference in testis weights between ages in contrast to the significant value of F taken from the table in Snedecor shows that the difference in testis weights by ages is significant. In other words, the observed differences in testis weights could have occurred by chance, where no real difference exists, less than once in a hundred cases. The value of F for the difference between months being smaller than the significant value of F shows that the variation in testis weights by month is not significant.

The data obtained on tubule diameters for use in the previous section on the relation of tubule diameters to the weight of the testes are considered again here to determine what differences exist in tubule diameters when the specimens are compared by month and by ages. The data are summarized as follows:

	Adult		Juvenile and immature	
Month	No. in sample	Mean value for tubule diameter in μ	No. in sample	Mean value for tubule diameter in μ
August	8	49.3	4	45.2
September	3	40.7	1	33.9
October	4	46.0	8	39.3
November	5	40.3	5	37.3
January	8	41.4	3	36.2

The indications are that the tubules of the adult testes are significantly larger than those of the juveniles and immatures and that there is a decrease in tubule size from August to January in both groups. The very high calculated values for F below, in contrast to the significant value of F, show that this is undoubtedly true.

	Calculated F	F for probability of 1 per cent
Difference in tubule diameter between months	7.56	3.84
Difference in tubule diameter between ages	13.53	7.33

Intertubular tissue.—The cells of the testes which are commonly thought to produce male hormone are the Leydig cells of the intertubular spaces. As pointed out by Pfeiffer and Kirschbaum (1943), most of the evidence for this view has been obtained from mammalian material, and these authors state that while many workers have described Leydig cells from avian testes, others have been unable to find them. Apparently Leydig cells occur in the testes of the Red-wing only during the early stages of active growth. They are not as abundant then as in mammalian testes, but they are by no means rare (fig. 10). Leydig cells appear to be absent when the testes are at the maximum, during regression and during the inactive period. As has been found in other avian studies, when testes are at the minimum, the intertubular tissue is relatively most abundant. As they undergo growth in the spring, the tubular tissue increases at a rapid rate; yet there is only slight growth in the intertubular tissue so that by the time the tubules have reached maximum size the intertubular tissue appears to be almost entirely absent because it has become such a relatively small proportion of the total testis. The very small amount of intertubular tissue in active testes makes quantitative studies of it impractical at this time.

Since the first analysis-of-variance test shows that there was no change in the testis weights by month during the quiescent period, and the second test shows that the tubule diameters decreased during the period, it is apparent that either the tubules are increasing in length as they decrease in diameter or else there is an increase in the intertubular tissue. The former suggestion is unreasonable. Examination of the slides suggests that the intertubular tissue is increasing and that the adult testes have relatively more intertubular tissue during this quiescent period than juvenal and immature testes.

In order to study these apparent differences, the method of Bascom (1925) was employed. Representative sections of each testis from all birds obtained between August and mid-January were projected with a photomicrographic camera on papers of uniform thickness and the outlines of the tubules traced in with pencil. The pieces of paper with the areas representing the tubules were cut apart from the intertubular areas with scissors and the two sets of paper fragments weighed separately and the percentage of each

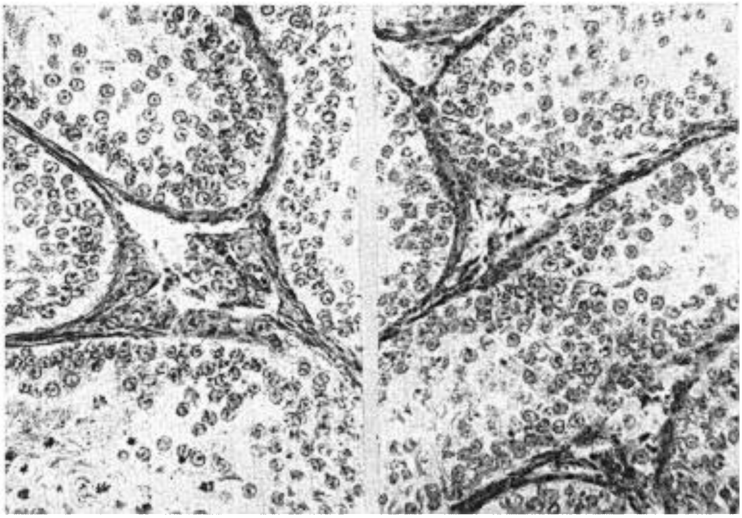

Fig. 10. Photomicrographs of Red-wing testes to show Leydig cells, ×300. At left, section of adult testis weighing 23.2 mg. taken on March 2. At right, year-old testis weighing 10.6 mg. taken on March 30. Both testes exhibit stage 4 of Blanchard, where there are a few primary spermatocytes in synapsis in the centers of the tubules. It is at this stage that Leydig cells are most conspicuous in the Red-wing. These large interstitial cells lie in groups in the spaces between the tubules. The nuclei which are as large as those of the spermatogonia within the tubules are much larger than those of the connective tissue cells lying along the outer edge of the tubules. Note the characteristic distinct nucleolus in the nucleus of each Leydig cell.

calculated. Five representative sections were taken from each testis and the values averaged. The results were then subjected to the analysis of variance method to calculate their significance. The data as analyzed are summarized as follows:

	Adults		Juvenile and immature	
	No. of specimens	Mean value for percentage of tubules	No. of specimens	Mean value for percentage of tubules
August	8	48.4	4	55.2
September	3	45.5	1	46.0
October	4	46.4	6	48.5
November	5	45.2	5	49.4
January	9	42.8	3	45.1

The figures appear to indicate that the relative amount of tubular tissue decreases from August to January, and that the percentage of tubular tissue is less in testes of adults than those of juveniles and immatures. The results of the analysis-of-variance test are:

	Calculated F	F for probability of 1 per cent
Difference in percentage of tubular tissue between months	4.42	3.86
Difference in percentage of tubular tissue between ages	9.54	7.35

The calculated values for F, higher in both cases than the table values for a probability of 1 per cent, clearly indicate that the observed differences are real. Whether or not these differences are indicative of a differential rate of hormone production between the ages is doubtful. In this connection it is to be noted that Pfeiffer and Kirschbaum (1943) conclude that the intertubular areas in birds normally seem not to be the site of male hormone production. Typical Leydig cells were not found in the testes of either adult or juvenal and immature Red-wings taken during the quiescent period. It is likely that androgen production in both age groups during this time is negligible.

Testis regression in relation to the molt.—The presence or absence of molting and the degree to which it had proceeded were recorded in all birds obtained in the course of the molting period. Since many of the birds obtained in Wisconsin were taken in the molting period and since the molting time differs by some two or three weeks from the corresponding time in Montana, data from the Wisconsin birds are discussed in this section. The 26 adult males obtained from July to September seemed to show a correlation between the degree of completion of the molt and the size of the testes. When the presence or absence, or the extent of the molt were assigned to five classes and the testis weights assigned to 8 classes (2.4 mg. intervals), a correlation coefficient was calculated. The value obtained, $r = 0.76$ with P less than one, indicates highly significant correlation. The molt begins when the testes have regressed to a weight of about 20 mg. and decrease in testis size continues so that by the time the molt is complete the testes are at the minimum size. Molting in adult males was first detected in Montana specimens on July 10, although corresponding stages in the molt were not obtained in Wisconsin until August 1. In spite of the differences in time of the beginning of the molt in the two localities the testes were of the same size when the molt started. That the physiological factors which bring about the regression of the testes may also bring about the molt is strongly suggested by the above data.

Observations made on two collecting trips suggest that those males which take part in the rearing of second broods remain in breeding condition longer than those which raise only one brood. On July 5, 1941, four adult males were obtained in Wisconsin. The testes of three were still near the maximum, whereas the fourth bird's testes had regressed considerably (56.0 mg.). On July 10, 1943, in western Montana three adults were obtained. Two had left the region of their territories and had started the molt, whereas the third was still defending its territory, was engaged in feeding young, and had not begun the molt. Although the differences in testis weights were not striking, the last bird had somewhat larger testes (25.0 mg.) than the other two (17.5 mg.).

Even though the year-old's testes regressed sooner than those of the adults, from the eleven specimens available during July and early August it does not appear that the molt starts any earlier than in the early molting adults.

DISCUSSION

It is well known that adult male Red-wings establish territories on the breeding grounds which they defend against other male Red-wings (Allen, 1914, and Smith, 1943). These authors point out that the territories are established by the males some time before nesting begins. Our observations, which were confined to the time spent in collecting the birds, indicate that very few year-old males establish territories. When they are approached during the breeding season, they often fly distances of several hundred yards and are consequently more difficult to collect than the adults which remain in the vicinity of their territories. When nests with young are present, the adult males are often as active in flying at the intruder as are the females. This type of behavior was rarely seen among the year-old males. We did observe four of the latter which were definitely defending territories. One in particular in Toole County, Montana, east of the divide, on July 1, 1942, had two females in attendance and young just able to fly were found close by. Since there were no other male Red-wings seen in the vicinity, it can hardly be doubted that this bird was breeding. Three other year-olds defending territories were found in the vicinity of other nesting birds, but we are unable to state definitely that the females in the vicinities of their territories were mates of these year-olds rather than of the adult males in the same area. All four of the above-mentioned year-olds were collected. Although two of them had testes which were larger than the average for year-olds taken at that time, the other two did not.

The observation that year-old males are in active spermatogenesis during the breeding season, but that very few individuals appear to breed, leads one to suspect that the failure to mate is a psychological phenomenon that purely anatomical studies can not explain. If the psychological behavior associated with the whole breeding process is conditioned by the physiological state of the reproductive system, it is indeed possible that the year-old males, coming into sexual activity at a later date than the adults, may find the females already mated with the adult males and be left out of the breeding activity. Perhaps the smaller testes of the year-old bird are producing less male hormone which in turn would render the bird less aggressive and less able successfully to compete with adult males in maintaining a territory. That the aggressive nature of birds may be due to the amount of male hormone present is suggested by Allee (1942). He found that in female fowls injections of male hormone enables a bird, which is socially at the bottom of the series of birds it is caged with, gradually to ascend through the ranks until it dominates all the birds which formerly dominated it.

Noble and Vogt (1935) observed that a year-old Red-wing attempted copulation with a taxidermic mount of a female and then hastily retreated. Our observations indicate that the year-old males often chase females about the nesting area, but they in turn are chased away by the adult males. Perhaps the year-old males are deliberately avoided by the females as mates because of their less spectacular plumage.

Bullough (1942) in an extensive study of the sexual cycle of the Starling (*Sturnus vulgaris*) on the British Isles found that the year-old male does not breed and that it does not come into active spermatogenesis until two years old. He found some increase in the size of the testes of the year-olds in the spring so that they reached a stage in April with primary spermatocytes in synizesis stages, although none was found in which spermatozoa had been produced. Whether or not the yearling males of the same species of starling in this country exhibit only partial development of the testes without spermatozoa being produced is not answered by study of the papers of Bissonnette and Chapnick (1930) and Bissonnette (1930). Steinbacher (1936) states that Starlings regularly breed at the age of one year in Hungary, but they do so only rarely in Latvia.

Male English Sparrows (*Passer domesticus*) undoubtedly go into active spermatogenesis and probably breed at one year of age since Kirschbaum and Ringoen (1936) found that the juvenal male can not be distinguished from the adult after the latter part of January, and they describe no birds with testes in the inactive state in the spring season. In the White-crowned Sparrow (*Zonotrichia leucophrys*) the year-old birds are distinguishable from the adults by plumage differences and young birds come into active spermatogenesis and breed (Blanchard, 1941). Wolfson (1942) states that in the Oregon Junco (*Junco oreganus*), where the ages are distinguishable in the fall but not in the spring, the testes of experimental birds of both ages responded alike to experimental light conditions and reached the breeding condition.

It is of interest that the testes of adult Red-wings may remain in the fully developed condition for more than two months and according to Bullough (1942) those of the Starling are at the maximum only during April, yet both species produce spermatozoa over a sufficiently long period so that two broods of young may be produced. Bullough also found that the testes of juvenal Starlings were larger during June than they were later during the year, thus the Red-wing and the Starling are similar in showing slight increase in the testes just after the young have left the nest. Both Bissonnette and Chapnick (1930) and Bullough (1942) find that the testes of adult Starlings begin to grow slightly during the fall months and continue the growth to the next spring. The testes of the English Sparrow according to Kirschbaum and Ringoen (1936) undergo no growth until late January, the same condition as found in the Red-wing.

Among passerine birds in which the males do not commonly breed in the first year several are icterids: Tri-colored Red-wing, *Agelaius tricolor* (Lack and Emlen, 1939), Boat-tailed Grackle, *Cassidix mexicanus* (McIlhenny, 1937), Yellow-headed Blackbird, *Xanthocephalus xanthocephalus* (Fautin, 1940) and the species under discussion. It is perhaps no coincidence that these are all species in which plumage differences readily distinguish the adult male from the year-old. It is generally assumed that birds do not reach sexual maturity until they are in adult plumage, although there are exceptions, for example, several species of gulls, hawks, and herons (Mayaud, 1941), the White-crowned Sparrow (Blanchard, 1941), and the Orchard Oriole, *Icterus spurius* (Ridgway, 1902). With species which acquire their breeding plumage during a partial spring molt it is clear that the state of the reproductive system may determine the nature of the plumage acquired when it is under hormonal control. Thus, the male Indigo Bunting (*Passerina cyanea*) and the African Orange Weaver Finch (*Pyromelana franciscana*), which acquire the nuptial plumage in the spring, are believed to develop those plumages as a result of stimulation by gonadotropic hormones (Witschi, 1935 and 1936). The nuptial plumage of the male Ruff (*Philomachus pugnax*) develops as a result of stimulation from testis hormone (Van Oordt and Junge, 1934 and 1936). In the Red-wing, and we assume the other blackbirds as well, the adult and year-old plumages develop in July and August at a time when the size of the testes is close to the minimum and when it is likely that both testis hormone and gonadotropic hormones are at the minimum. Therefore, it is difficult to believe that male hormone in differential rates of production in the adult and juveniles could produce the two types of plumage. Whether or not the plumages of the male Red-wing are under hormonal control can not be ascertained without experiments performed in the laboratory.

As mentioned previously the variation in the first-winter plumage is considerably greater than that in the adult plumage. Ridgway (1902) believes that the plumage differences in the immature are correlated with age differences. Since young birds are hatching from late May until early July in western Montana, there may be considerable difference in age at the postjuvenal molt. That birds which hatch earliest come into the most adult-like plumage, whereas the late hatched birds molt into the immature-like plumage is suggested, but not proved, by our data. It was also thought that there might be some correlation between the nature of the plumage and the size of the testes in year-old birds taken in the spring, the more adult-like year-olds having larger testes than the immature-like ones. A series of 16 year-olds taken on May 4, 1941, to test this supposition, however, indicated no significant correlation.

The occasional appearance of a female Red-wing with red or orange wing coverts similar to those of the yearling males is of interest. Baird (1858) has described one such bird which he stated was "barren." We took two females with bright wing patches, in both cases mistaking them for year-old males before they were shot. One was taken in May and was in breeding condition, and the other taken in July apparently was normal sexually as its reproductive tract was similar to those of other females taken on the same date, and it possessed a brood patch.

SUMMARY

A study of the testis cycle of the Red-wing based on 215 birds taken in western Montana and 36 taken in eastern Montana and in southern Wisconsin leads to the following conclusions:

1. The year-old birds as well as the adults come into active spermatogenesis in the spring. The testes of the year-olds grow to a maximum of two-thirds that reached by the adults.

2. The testes of the year-olds reach the maximum in May three weeks later than those of the adults.

3. Most of the year-olds do not develop territories and thus do not breed. A few do breed, however.

4. The testes of the adults are maintained at the maximum from 50 to 75 days, but in the year-olds the period is from 30 to 55 days.

5. Equations showing the relation of tubule diameters to testis weights were calculated for both age groups.

6. During the quiescent period, August to January, the testes of the adults are larger, have larger tubules and more intertubular tissue than those of the juveniles and immatures. In both groups there is a progressive decrease in tubule diameters from August to January.

7. The state of regression of the testes in the adult is significantly correlated with the progression of the postnuptial molt.

8. Great variation in the plumage of the year-olds was noted, but no correlation between this variation and the testes was discovered.

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