CHANGES IN THE REPRODUCTIVE ACTIVITY OF THE BROWN-HEADED COWBIRD WITHIN THE BREEDING SEASON

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The Brown-headed Cowbird (*Molothrus ater*) commonly parasitizes the nests of the Cardinal (*Richmondena cardinalis*) at London, Ontario, Canada. This behavior results locally in a reduction of 15–20 per cent in the annual production of the Cardinal (Scott and Lemon, unpublished data). To understand more fully the relationship between parasite and host, I began a study of the reproductive cycle of the cowbird.

Seasonal variation in the incidence of parasitism is immediately obvious in Table 1. This should depend upon changes in the reproductive activity of the cowbird and in the relative availability of nests of different hosts. Lacking detailed knowledge of the latter, I will deal mainly in this paper with the former. Evidence will be adduced from three sources: 1) data on parasitism on the Cardinal, 2) examination of reproductive organs of adult cowbirds, and 3) observations on post-nuptial flocks of adult cowbirds.

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PARASITISM ON THE CARDINAL

Table 1 shows that by the end of April, about two weeks after the first Cardinal clutch, the incidence of parasitized nests had reached 100 per cent. Afterwards, the incidence remained high until 2 July, fluctuating between 71 per cent and 100 per cent. It then declined rapidly, reaching zero before August. Changes in the intensity of parasitism (number of cowbird eggs per

Table 1

Parasitism by the Brown-headed Cowbird on 187 Cardinal Nests at London, Ontario, 1955 to 1961*

Week ending	April			May				June				July					August			
	16	23	30	7	14	21	28	4	11	18	25	2	9	16	23	30	6	13	20	27
No. of nests	1	8	8	11	9	18	17	18	15	7	10	2	15	13	8	5	10	6	4	2
Per cent parasitized	0	50	100	82	78	78	71	83	87	100	80	100	53	15	25	20	0	0	0	0
Mean no. of cowbird eggs per parasitized nest	–	1.3	3.3	3.0	2.4	1.5	2.1	2.1	1.8	1.7	1.9	1.0	1.5	1.0	1.0	1.0	–	–	–	–

* Data are based entirely on nests in which Cardinal laying had been completed. Nests containing young are excluded.

parasitized nest) did not always parallel changes in incidence. Intensity of parasitism rose rapidly to a maximum of 3.3 eggs by 30 April, then declined, more rapidly in May than in June, to the absolute minimum of one egg by 16 July.

Some of the observed variation in the incidence and intensity of parasitism seems definitely attributable to seasonal changes in the reproductive activity of the cowbird. Since the Cardinal is the first of the common local hosts to begin breeding, the observed rise in late April in incidence and intensity must result from increasing numbers of cowbirds laying at that time. The decreased parasitism on the Cardinal in July can be ascribed to waning reproductive activity of the cowbird. All hosts have begun nesting by early June, and a marked increase in July in the availability or use of their nests seems unlikely. But the causes of the decline in intensity in May and June, while the incidence remained high, are less obvious. I was unable, from the data in Table 1, to distinguish the effect of changes in the availability of nests of all hosts from that of reduced reproductive activity of the cowbird. To elucidate the relative importance of these factors, I examined the reproductive organs of adult cowbirds collected in 1959 and 1962.

REPRODUCTIVE ORGANS

To avoid disturbing the local cowbirds at the height of the breeding season, specimens were usually collected outside the study area but within a 25-mile radius of London. Late in June and after (see beyond), I was forced to collect wherever cowbirds could be found. Changes in the sampling areas possibly introduced some bias, since late samples may have contained a disproportionately large number of birds which had finished breeding.

The extent of cranial ossification was examined in all specimens, and only those in which it appeared complete are subsequently considered. This precaution was probably unnecessary since it is unlikely that any juvenile could have completed its post-juvenal molt (normally completed in August and September) in time to be confused with an adult in the late samples.

Gonads and oviducts were removed within 10 minutes of death, and fixed in Bouin's solution. Following paraffin-embedding, each right testis was sectioned at 7 μ and stained with Ehrlich's hematoxylin and eosin. The left testes were weighed on a Becker "Chainomatic" balance. I unfortunately neglected to weigh the right testes. As the disparity in size between the left and right testes was not extreme, however, the histology of the right testis was assumed to be reasonably similar to its left counterpart. Hence, it was not thought necessary to prepare sections of the left testes.

Testes.—Each right testis was assigned to one of two groups. Testes showing tubules with regularly aligned bundles of sperm and no degenerative

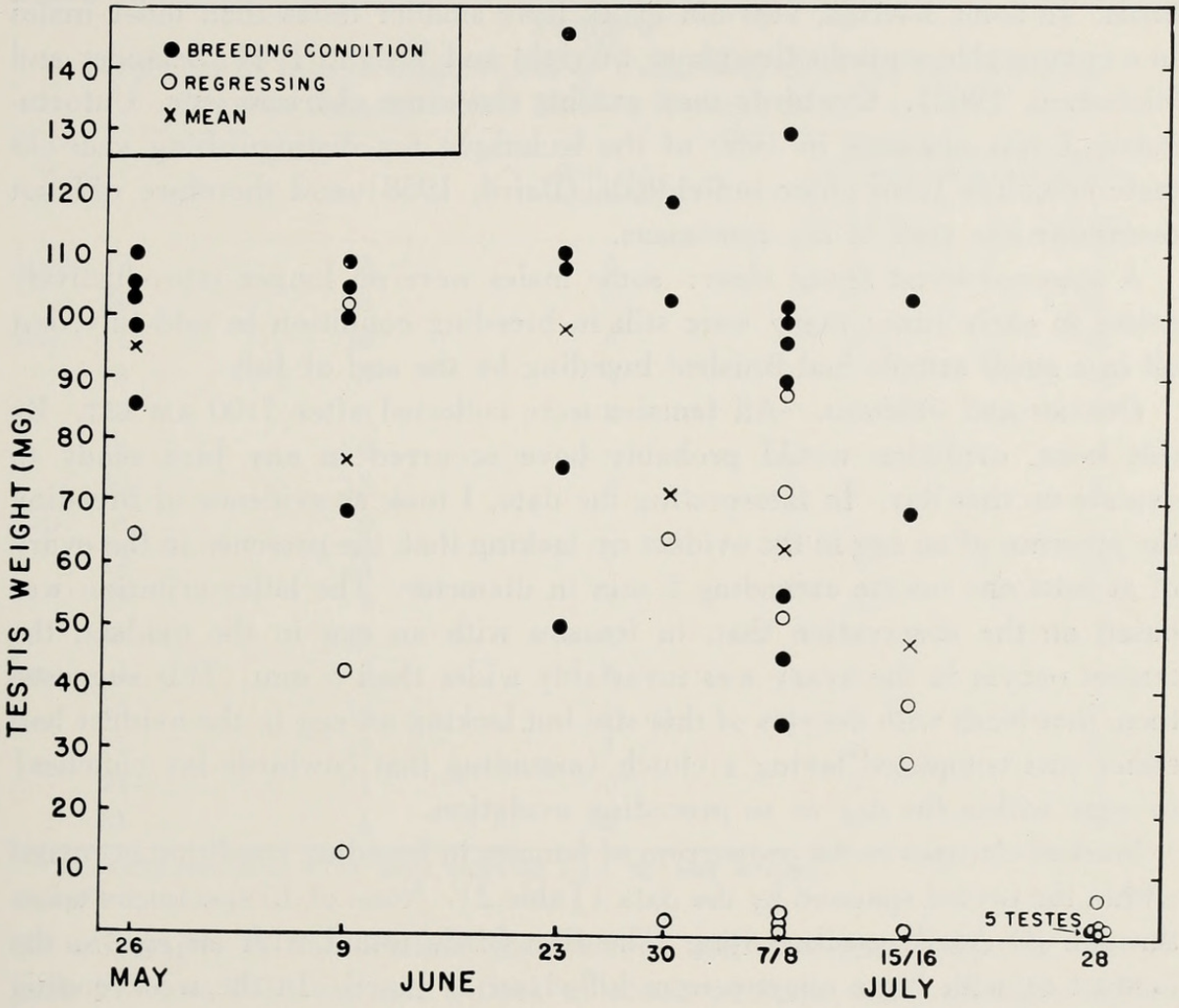

FIG. 1. Changes in the weight of the left testis of 47 Brown-headed Cowbirds collected in 1959 near London, Ontario. The histological condition of the right counterpart of each left testis is shown.

changes were considered to be in breeding condition. The remainder were classified as regressing.

Figure 1 shows the changes in weight and internal condition of 47 testes collected from 26 May to 28 July 1959. The average weight changed little until late June. Noteworthy, however, were pronounced degenerative changes in one testis on 26 May, and in three on 9 June. Later, mean weights dropped from 97.6 mg on 23 June to 2.3 mg on 28 July. Concurrently, spermatogenesis had clearly ceased in an increasing proportion of testes, until by 28 July a sample contained no testis in a breeding condition.

The significance of the low weights of a testis (50.0 mg) on 23 June and of three testes (34.2, 45.0, and 55.0 mg) on 7–8 July is not clear. These testes, despite their small size, were apparently still in breeding condition. Possibly, some testes decrease in size before post-nuptial regressive changes become obvious. Alternatively, these testes may have been taken from one-year-old

birds. In some icterids, year-old males have smaller testes than older males in a comparable reproductive phase (Wright and Wright, 1944; Selander and Nicholson, 1962). Cowbirds may exhibit the same characteristic. Unfortunately I was unaware in 1959 of the technique for distinguishing year-old male cowbirds from older individuals (Baird, 1958) and therefore did not determine the ages of my specimens.

A seasonal trend seems clear: some males were no longer reproductively active in early June; many were still in breeding condition in mid-July, but all in a small sample had finished breeding by the end of July.

Ovaries and oviducts.—All females were collected after 7:00 AM EST. By this hour, ovulation would probably have occurred in any bird ready to ovulate on that day. In interpreting the data, I took as evidence of breeding the presence of an egg in the oviduct or, lacking that, the presence in the ovary of at least one oocyte exceeding 5 mm in diameter. The latter criterion was based on the observation that, in females with an egg in the oviduct, the largest oocyte in the ovary was invariably wider than 5 mm. This suggests, then, that birds with oocytes of this size but lacking an egg in the oviduct had either just completed laying a clutch (assuming that cowbirds lay clutches) or were within the day or so preceding ovulation.

Marked changes in the proportion of females in breeding condition occurred within the period spanned by the data (Table 2). None of 13 specimens taken through 24 April was breeding. The first birds found with an egg in the oviduct or with large oocytes were killed on 27 April. In the week ending 1 May, eight of 16 birds had not attained breeding condition. But, in the following week, all five females were breeding. Afterwards, in the seven-week period ending 26 June, 23 (65.7%) of 35 birds had an egg in the oviduct. All but three of the remainder had enlarged oocytes. Two exceptions (15 and 24 May) had enlarged oviducts but small oocytes; their breeding status was uncertain. The third (23 June) had certainly finished breeding: its oviduct was shrunken and its oocytes were minute. Appreciable numbers of birds, lacking either an egg in the oviduct or enlarged oocytes first appeared in the samples for the week ending 3 July. The proportion of such females increased successively in each of the two subsequent weeks. Of 12 birds collected in the week ending 17 July, only one, with an egg in the oviduct on 16 July, was still breeding. Two individuals taken later in July were not breeding.

POST-NUPTIAL FLOCKS

A noticeable change in the behavior of adult cowbirds occurred about the third week of June. At this time cowbirds became difficult to find in their customary haunts and, simultaneously, flocks composed preponderantly of adult males appeared in grain fields, in pastures with cattle, and on lawns of

TABLE 2

FREQUENCY OF EGGS IN OVIDUCTS AND OF LARGE OOCYTES IN 104 BROWN-HEADED COWBIRDS COLLECTED NEAR LONDON, ONTARIO, IN 1959 AND 1962*

Week ending	N	With egg in oviduct	Without egg in oviduct Diameter of largest oocyte	
			> 5 mm	< 5 mm
April 17	3	0	0	3
24	10	0	0	10
May 1	16	4	4	8
8	5	4	1	0
15	4	2	1	1
22	0	–	–	–
29	12	7	4	1
June 5	0	–	–	–
12	11	7	4	0
19	3	1	2	0
26	5	4	0	1
July 3	7	4	0	3
10	14	5	2	7
17	12	1	0	11
24	1	0	0	1
31	1	0	0	1

* All 1959 specimens (15) were collected from 26 May onwards.

the university. A few detailed observations will illustrate this point. On 26 June 1959, at 7:30 PM EST, a flock of about 40 adult male cowbirds settled momentarily in a large maple tree outside my home in the city. By 29 June 1961, flocks containing more than 100 birds, predominantly adult males, were present on the campus. On 25 June 1962, I counted about 100 adult males and one adult female feeding together on university grounds. Larger numbers appeared in the following three weeks in 1962, and there was an increase in the proportion of adult females. The numbers of adult males and females trapped at this time were: 27–30 June, 29 males and 7 females; 4–6 July, 19 males and 9 females; and on 12, 14, 20, 21 July, a total of 21 males and 8 females. At no time did the numbers of adult females exceed or even closely approach those of adult males. The flocks of adult cowbirds disappeared from the campus after the third week in July.

Overt sexual behavior was rarely observed in July. Small groups of two or three males courting a female were seen sporadically, but courtship behavior was no longer the common sight so characteristic of May and June. The latest date on which I saw such behavior in four years of observations was 24 July 1962. Hence, the general absence of sexual activity in the large mixed flocks indicates that most of these birds were indeed in a post-nuptial condition.

DISCUSSION

The information on nest parasitism agrees closely with that on the female reproductive organs in showing, first, that few females begin laying before the final week in April and, secondly, that the onset of breeding is sudden.

The condition of the ovaries and oviducts in May and June indicates that maximum reproductive activity is maintained from the first week of May to the penultimate week of June, a period of about eight weeks. This conclusion differs from that of Norris (1947) who stated that near Butler, Pa., "the crest of the laying season comes late in May." His Fig. 2 shows a gradual increase in the number of cowbird eggs, found in 1944 and 1945, from 15 April to a maximum on about 30 May preceding a gradual decline terminating on 12 July. I think his conclusion is questionable because it is apparently based on the erroneous assumption that the number of cowbird eggs found is necessarily an index to the laying activity of the species. This will be true only when all, or at least a constant proportion, of the nests of each species of host are found throughout the entire breeding season of the cowbird. Norris' data indicate that this requirement was not met, his activities being evidently restricted largely to May in 1944, but expanded in 1945 to include the period from April to July. Since no allowance seems to have been made for this bias in sampling, it is not surprising that his data showed a laying peak in May. In contrast, Mayfield's data (1960:151) on cowbird parasitism on the Kirtland's Warbler support the idea that cowbird laying is maintained at a high level over several weeks and that there is not a clearly defined peak of laying activity.

Breeding wanes towards the end of June; all my observations agree on this point. Cessation of breeding appears earlier in males, perhaps by as much as a week. The significance of this difference is not clear. If, as Friedmann (1929) stated, males outnumber females, the first post-nuptial flocks may be formed by the surplus males. This suggestion is, however, unimportant in the present context. The critical point is that most females are still breeding by the end of June. The observed decrease, at this time, in the proportion of females still laying is apparently real, not merely a vagary of sampling, since it coincides with an abrupt decline in the intensity of parasitism on the Cardinal.

Several conclusions relating the reproductive cycle of the cowbird to parasitism on the Cardinal seem warranted. First, the rapid increase in the incidence and intensity of parasitism in late April is caused by the sudden onset of laying by the cowbird. Secondly, the intensity of parasitism declines rapidly in early May and then slowly until the end of June, in the absence of a corresponding decline in laying activity. The decline in parasitism during

this period must therefore depend on increased use of other hosts by the cowbird. Finally, the decrease in the incidence and the intensity of parasitism beginning in early July results from a contemporaneous and continuing reduction in the reproductive activity of the cowbird.

SUMMARY

The breeding season of the cowbird extends from late April to late July. Within this period maximum reproductive activity of female cowbirds is maintained over approximately an eight-week period in May and June. Parasitism on the Cardinal is discussed relative to changes in the laying activity of the cowbird.

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