THE LAYING CYCLE OF BROWN-HEADED COWBIRDS: PASSERINE CHICKENS?

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ABSTRACT—We collected 270 female Brown-headed Cowbirds (*Molothrus ater*) in southern Ontario in 1976 to determine ovarian and oviducal growth during the breeding season and 188 female cowbirds in 1977 to estimate clutch size and the interval between clutches. Ovaries and oviducts grew rapidly in April, reached breeding size in early May, and remained at this size, *without regression between clutches*, until the end of the breeding season in early July. Ovaries and oviducts then regressed rapidly and by the end of July weighed about the same as those in early April. The clutch size averaged about 4.0–4.6 eggs, similar to clutch sizes of nonparasitic icterids. It varied greatly from 1 egg, in about 10% of the birds, to about 7 eggs. Two days without laying usually separated consecutive clutches, but some birds appeared to miss laying for only 1 day. Although atresia of large yolky follicles was common in birds between clutches, it did not always precede the end of a clutch. The long reproductive period without regression and the short interval between clutches are atypical of passerine reproduction. Rather, the laying cycle of cowbirds is similar to that of domestic chickens (*Gallus gallus*). The laying cycle of cowbirds seems adapted to a continuous supply of host nests; atresia may be related to a shortage of nests. *Received 16 June 1982, accepted 18 January 1983.*

THE annual egg production of the brood parasite, the Brown-headed Cowbird (*Molothrus ater*), greatly exceeds that known for any other wild passerine. An average female cowbird lays about 40 eggs in an 8-week laying season in southern Ontario (Scott and Ankney 1980). This remarkably high laying rate depends, as we will document, upon two deviations from the laying cycle characteristic of nonparasitic passerines. First, the ovaries and oviducts of cowbirds do not regress between sets or clutches of eggs, as do those of normal passerines (Hutchison et al. 1968, Lewis 1975). Second, only 1 or 2 days without laying often separate consecutive clutches or sequences of eggs. In normal passerines at least 5 days without laying usually intervene between loss of a nest and the first egg in the replacement nest (Delius 1965, Dixon 1978). Thus, a cowbird lays for several consecutive days, then ceases briefly before resuming laying. This pattern of laying is similar to that of a domestic hen (*Gallus gallus*) when she is not allowed to incubate (Gilbert and Wood-Gush 1971, Sturkie and Mueller 1976). We chose the title of this paper to emphasize that similarity.

METHODS

Collections of 270 female cowbirds in 1976 and 188 in 1977 made near London, Ontario, supplemented by several smaller collections, provided the base for this paper. Ankney and Scott (1980) and Scott and Ankney (1979, 1980) give details about the collections, which were representative of the local cowbird populations.

Ovaries, and oviducts if collected, were removed in the field and fixed in 10% buffered formalin. In 1976, we weighed undamaged ovaries and oviducts (following removal of any oviducal egg) to the nearest 0.01 g, and, using vernier calipers, we measured to the nearest 0.1 mm the diameters of all ovarian follicles (oocytes) greater than 2.9 mm in diameter. We counted all recognizable postovulatory follicles (POFs). In so doing, we distinguished between Certain and Probable POFs. The former were similar to the structures designated and illustrated as POFs by Lewin (1963, Fig. 10e–g) and described by Parmelee and Payne (1973: 220). We designated as Certain POFs those in which we could insert the tip of a fine probe through the ruptured stigma. Some structures closely resembled Certain POFs but were smaller and lacked an open stigma; these we called Probable POFs. Thus, we recorded the numbers of POFs as, for example, 3/2 or 2/0, ratios which mean, in the first instance, 3 Certain and 2 Probable POFs and, in the second, 2

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Certain and 0 Probable POFs. Often there were still smaller structures, not normal oocytes, that we could not recognize as either Probable POFs or atretic follicles.

We excised the Certain and Probable POFs from each ovary and measured their lengths and maximum widths with an ocular micrometer. We estimated the area of each POF as the product of those dimensions. To determine the regression of POFs, we plotted the areas of the POFs of each laying bird against the hour of collection.

Some follicles, greater than 2 mm in diameter, were clearly atretic, as they were cream colored, unlike the orange-yellow (yolk) color of most large follicles. Moreover, unlike the latter, they appeared flaccid and wrinkled or irregular in outline. We estimated the irregular diameter of the atretic follicles to the nearest 1 mm.

A few large follicles about 8 mm in diameter appeared normal except for a small pimple-like protuberance, which may have indicated an early stage of bursting atresia (see Gilbert 1979: 296, Fig. 5.24a), but, as these follicles were found only in birds that had been shot, shot damage might have caused the abnormality.

We call birds with an egg in the oviduct laying birds, those with an enlarged oviduct (>1.0 g) but without an egg in the oviduct nonlaying birds.

Statistical tests follow Sokal and Rohlf (1969).

RESULTS

Ovarian and oviducal weights.—Seasonal variation in ovarian weights was great. The mean weight increased about 10-fold between early April and mid-May (Fig. 1) as a result of the development of large yolky ovarian follicles, of which the largest usually exceeded 8 or 9 mm in diameter (see Payne 1973: Fig. 2, Scott 1978). Throughout May and June, most birds had 3 follicles wider than 2.9 mm and virtually all had at least 1 follicle greater than 6 mm in diameter. Consequently, ovarian weights remained high in both laying and nonlaying birds at that time and did not decline until early July. Ovarian regression in weight continued throughout July and by 31 July the mean weight was 0.03 g, which must have been near the annual minimum for adult females.

The minimum weight of an oviduct that contained an oviducal egg was 1.06 g (Fig. 1). Hence, we assumed that any oviduct weighing greater than 1.05 g was in reproductive condition, i.e. was functionally capable of receiving an ovum.

Seasonal changes in oviducal weights paralleled those of ovaries. By late April, oviducts associated with ovaries containing large yolky follicles weighed greater than 1 g, and, notably, from 8 May to 26 June all but 2 birds (of 86 with oviducal eggs and 33 without) had oviducts weighing greater than 1 g (the weekly means greatly exceeded 1 g). The exceptions were a bird, collected 10 May, that had not begun to lay and one, collected 23 June, that had a minute oviduct (0.02 g) and apparently no ovary. Otherwise, oviducal weights less than 1 g were not recorded again until 3 July. To sum up, ovarian and oviducal weights were high throughout May and June, even in nonlaying birds that had laid a clutch.

Postovulatory follicles.—Most laying birds had 2 or 3 Certain POFs (Table 1), at least 1 Probable POF, and smaller structures that might have been POFs. The Certain and large Probable POFs in a particular bird often form a graded series in size (Fig. 2). Only the age of the largest POF in a laying bird is certain (the 1's in Fig. 2 are less than 1 day old). The POFs ranked 2, 3, 4, and 5 in a sequence are in their 2nd, 3rd, 4th, and 5th day after ovulation only if they represent ovulations on the consecutive days preceding the day of collection. This assumption is probably valid for large POFs, as the scatter distributions of 1's, 2's, and 3's are essentially discrete. The size of a POF ranked 2 in a sequence, however, occasionally is within the distribution for 3's or 4's (see 0700 h column in Fig. 2). Such a POF was probably older than its ranking suggested and belonged to an earlier series of eggs, separated from the current clutch by one or two days without ovulations. We think that those POFs, labelled as 2's in Fig. 2, that were smaller than 200 units in area were more than 1 day older than POFs indicated by 1's.

POFs regressed rapidly. Ovulation, as inferred from the position of the egg in the oviduct, occurred before 0700. Then, the most recently formed POF was large and conspicuous, about 5–6 mm long by 3–4 mm wide or about 800 ocular micrometer units in area. This area decreased by 50% in 12 h, a rate of regression that persisted for at least 2 or 3 days. The sizes of the largest Probable POFs suggest that the opening of the POF became occluded by the 3rd or 4th day following ovulation. The overlap in sizes between POFs ranking 3rd or 4th in a sequence was great; POFs at these stages

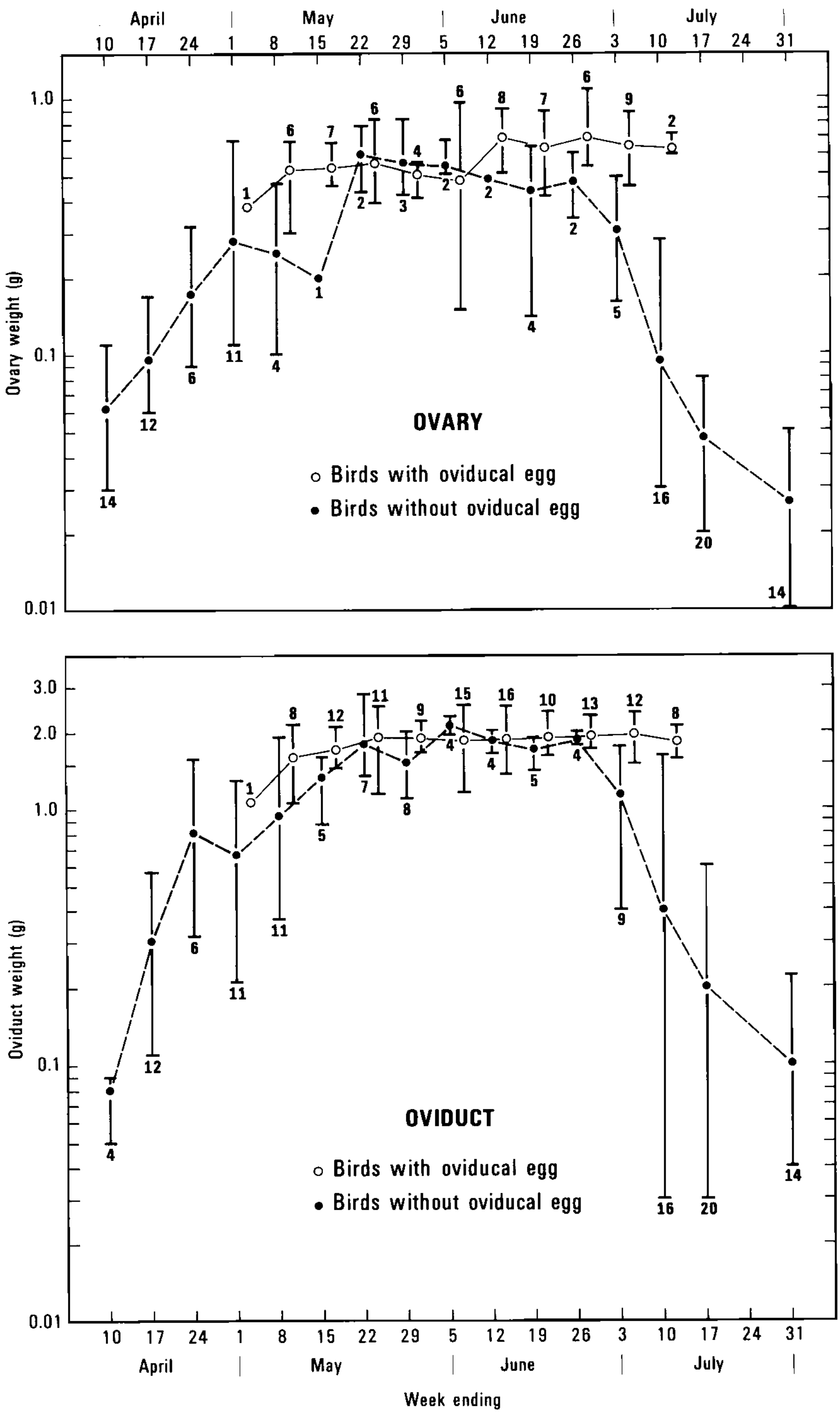

Fig. 1. Seasonal changes (1976) in the means and ranges of weights (g) of ovaries and oviducts of cowbirds. Weekly sample sizes are shown.

TABLE 1. Seasonal variation in frequency distributions of Certain POFs in combined samples of laying birds from 1976 and 1977 (R × C test: $G = 15.55$, df = 3, $P < 0.01$).

Frequency of Certain POFs	23 May to 5 June	20 June to 7 July	Total
1	14	7	21
2	48	27	75
3	75	15	90
4 and 5	34	3	37
Totals	171	52	223

were small, frequently being less than 2 mm long. Thus, age determination of POFs older than 2 or 3 days was uncertain.

Nonlaying period.—Our analysis was based on 33 nonlaying birds collected in 1977 (Table 2) and 37 in 1976 (details not shown). We excluded 5 nonlaying birds, because their reproductive organs were minute or missing. We used two methods to estimate the number of days of nonlaying between clutches.

First, the reciprocal of the proportion of birds on a given day in their nonlaying period estimates the length of the period (Scott 1978: 2232). That is, if the nonlaying period is 3 days, about ⅓ of the nonlaying birds should be in each of the 3 days. We identified birds from 2 different days of the nonlaying period, those that had completed laying a clutch on the day of collection (day 1 of the period, indicated by a POF large enough to be only 1 day old), and those that would have ovulated on the following day (penultimate day of period, indicated by an ovarian follicle >7.9 mm in diameter). Birds destined to skip ovulating on only one day fall into both the above categories.

Second, we estimated the day upon which a bird had last ovulated by comparing the area of her largest POF with the areas of POFs of estimated ages from laying birds (Fig. 2). Then, we predicted the day of her next ovulation from the size of her largest yolky follicle. The difference in days between these two ovulations was the nonlaying period for that bird. For example, bird 1 (Table 2) had a large POF, representing ovulation on the previous day, and a large yolky follicle (8.1 mm in diameter) indicating an ovulation to occur on the next day. Thus, this bird would have skipped ovulating on only one day.

Both methods indicated that the nonlaying period averaged about 2 days. In 1977, 22 of 32 nonlaying birds had at least one Certain POF (Table 2), and, as all also had at least one large yolky follicle, they were apparently between clutches. Birds 1–11 had apparently last ovulated on the day before collection and, thus, were in day 1 of the nonlaying period. Birds 12–17 were either in day 1 or day 2 of the interval; the sizes of their largest POFs suggest that some were in day 1 of the nonlaying period. We assume, for the sake of argument, that 3 of birds 12–17 were in nonlaying day 1, giving a total of 14 such birds in the sample of 32. The reciprocal of this proportion is 2.3; if any of birds 26–32 had not previously laid, the nonlaying period would be less than 2.3 days. Twenty birds were in their penultimate day of the nonlaying period, and, thus, the nonlaying period equals 33/20 or 1.65 days. In 1976, of 37 nonlaying birds, 20 were in day 1 and 18 in the penultimate day of the nonlaying period. Thus, a nonlaying period of about 2 days is again indicated. In 1977, 16 of 33 birds, if they had survived, would have skipped ovulating on 1 or 2 days only (Table 2, last column), and similarly, in 1976, the predicted nonlaying period for 22 of 37 birds was 1 or 2 days.

A brief nonlaying period could account for the unexpectedly low proportion of laying birds with only one Certain POF (Table 1). Some birds with 2 or 3 Certain POFs, despite appearances, might actually have been beginning a new clutch (represented by the largest POF), in which cases the smallest Certain POFs would represent the last eggs in the preceding clutch. Because Certain POFs remain recognizable for only about 3 or 4 days, the nonlaying period between the two clutches could not have been more than 2 days. Note (Fig. 2) the bird collected about 1700; she had 3 Certain and 1 Probable POFs. The great disparity in size between the 2 largest POFs suggests that the smaller POF represented an egg ovulated 2 or 3 days previously. This bird was apparently beginning a clutch and, thus, really belonged in the 1 Certain POF class.

We conclude that, on average, cowbirds skip laying for about 2 days between clutches.

Clutch size.—We could not devise a method, *with measurable biases,* for estimating the average clutch size. Although we could estimate the proportion of birds that lays 1-egg clutches, we could not estimate the maximum clutch size.

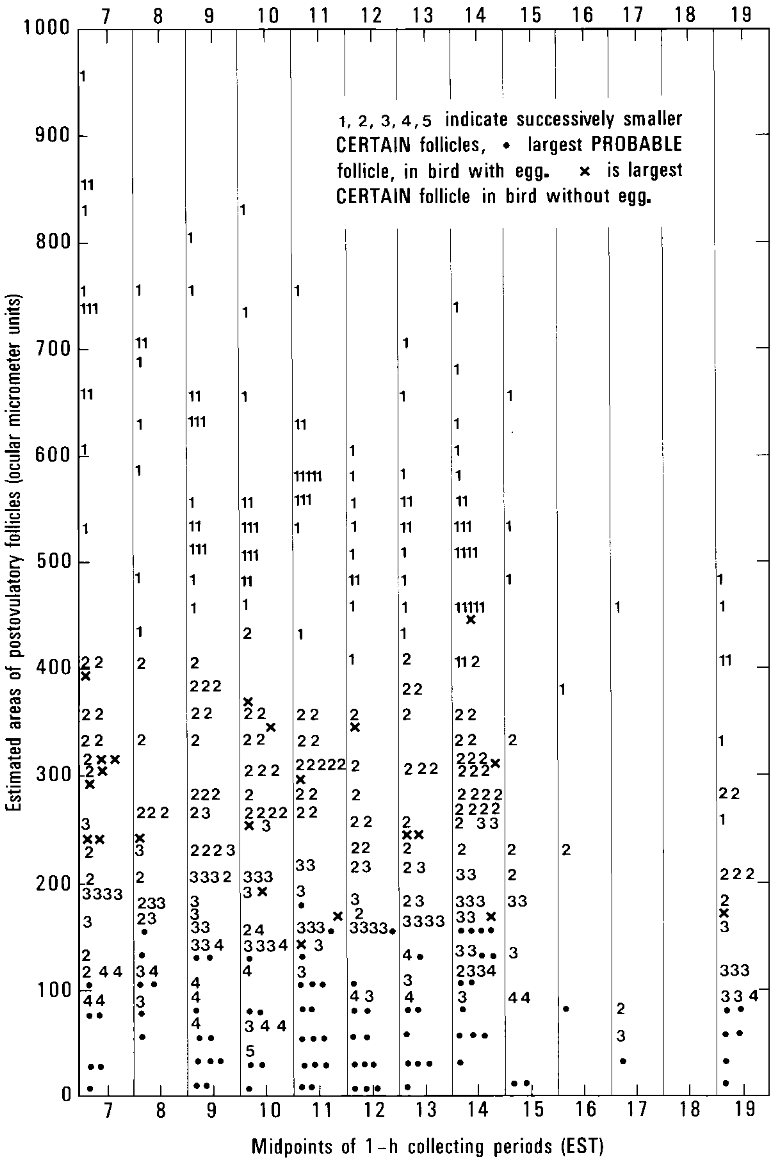

Fig. 2. Regression of postovulatory follicles (POFs). It is based on 114 laying birds, collected between about 0630 and 1930 EST in 1977. The area of each Certain POF in each bird is indicated by a number showing its position in a sequence of successively smaller POFs in that bird. In each sequence the largest POF, indicated by a 1, was assumed to be from the bird's oviducal egg. Successively smaller POFs in a bird are numbered 2, 3, 4, and 5, depending upon the number of POFs in that bird. Thus, a bird with only 2 POFs is represented by a 1 and a 2, but one with 4 POFs is represented by a 1, a 2, a 3, and a 4. The dots indicate Probable POFs. An X indicates the largest Certain POF in a nonlaying bird. Consider the right-most column: it contains the records for 6 laying birds and 1 nonlaying bird; 5 of these laying birds each had 3 Certain and 1 Probable POFs and 1 had 4 Certain and 1 Probable POFs.

TABLE 2. Estimate of number of days without ovulation between clutches, based on 33 nonlaying birds[a] collected 24 May to 4 June 1977.

Specimen number and hour of collection	Number of POFs (Cert./Prob.)	Area of largest POF	Estimated day of last ovulation	Diameter (mm) of largest follicle	Predicted day of next ovulation	Days without ovulation
1. 0630	2/1	396	D − 1[b]	8.1	D + 1	1
2. 0645	2/2	304	D − 1	>8[c]	D + 1	1
3. 0720	2/0	300	D − 1	<3[c]	?	?
4. 0720	2/0	285	D − 1	7.7	D + 2	2
5. 0730	2/1	315	D − 1	>8[c]	D + 1	1
6. 1000	1/0	336	D − 1	7.7	D + 2	2
7. 1005	1/0	360	D − 1	<3[c]	?	?
8. 1030	1/3	285	D − 1	9.3	D + 1	1
9. 1225	1/0	342	D − 1	>8[c]	D + 1	1
10. 1345	2/1	437	D − 1	9.0	D + 1	1
11. 1409	2/1	324	D − 1	9.4	D + 1	1
12. 0640	2/1	240	D − 1 or 2	>8[c]	D + 1	1 or 2
13. 0720	1/1	231	D − 1 or 2	>8[c]	D + 1	1 or 2
14. 0740	2/1	231	D − 1 or 2	>8[c]	D + 1	1 or 2
15. 0945	3/0	252	D − 1 or 2	8.4	D + 1	1 or 2
16. 1245	2/0	252	D − 1 or 2	>5[c]	D + 2	2 or 3
17. 1305	2/0	240	D − 1 or 2	>8[c]	D + 1	1 or 2
18. 0950	2/0	195	D − 2	>5[c]	D + 2	3
19. 1050	1/3	150	D − 2	6.1	D + 2	3
20. 1115	1/1	130	D − 2	>5[c]	D + 2	3
21. 1415	1/0	156	D − 2	9.6	D + 1	2
22. 1955	1/1	160	D − 2	>8[c]	D + 1	2
23. 1230	0/2	99	D − 3	6.2	D + 2	4
24. 0730	0/2	50	?	>5[c]	D + 2	>4?
25. 0910	0/1	50	?	9.3	D + 1	>4?
26. 0710	0/0	—	—	3.9	D + 3	—
27. 0745	0/0	—	—	5.6	D + 2	—
28. 1235	0/0	—	—	8.3	D + 1	—
29. 1300	0/0	—	—	8.0	D + 1	—
30. 1305	0/0	—	—	8.7	D + 1	—
31. 1310	0/0	—	—	9.6	D + 1	—
32. 1850	0/0	—	—	6.7	D + 2	—
33. 1920	?	—	—	>8[c]	D + 1	—

[a] Four nonbreeding adults were excluded.
[b] D was day of collection.
[c] At least one large follicle broken; diameter of largest was estimated.

Thus, we could not use the mid-point of the range of clutch sizes as an estimate of the average clutch size. The method proposed by Scott (1978) yielded unrealistically high estimates. Instead, we used the following method, which has two variants, based solely on the number and inferred ages of POFs. This method, unlike ones proposed earlier (Payne 1976, Scott 1978), does not rely at all upon interpretation of large, yolky follicles. To estimate the average clutch size, we had to estimate (1) the total number of eggs that would have been laid in the current clutches by laying birds and (2) the number of eggs laid in the most recent clutches by nonlaying birds. The average clutch size is then estimated by the sum of the two estimates of egg numbers divided by the sample size. To determine the potential number of eggs in the current clutches of laying birds, we propose the following. These birds will, on average, have reached the mid-point of their laying sequences. For example, 100 laying birds, each with a clutch of 5, would eventually lay 500 eggs and have 500 POFs. At the mid-point of their laying sequences, these 100 birds would have 300 POFs, because the mid-point POF of a sequence of 5 is the third. Note that *twice* the mid-point number of POFs minus the sample size equals the number of eggs that would have been laid upon completion of the current clutches [e.g. $(2 \times 300) - 100 = 500$].

We determined the mid-point number in two ways. First, we equated the mid-point value to the total number of Certain POFs only, assum-

TABLE 3. Two estimates of average clutch size in cowbirds collected 24 May to 4 June 1977.

Method 1

Laying birds			Nonlaying birds		
Number of Certain POFs per bird	Number of birds	Number of POFs	Estimated clutch size	Number of birds	Estimated number of POFs
1	12	12	?	11	18[a]
2	42	84	1	9	9
3	65	195	2	12	24
4	28	112	3	1	3
5	2	10	4	0	0
Totals	149	413		33	54

Average clutch size $\frac{[(413 \times 2) - 149] + 54}{149 + 33} = 4.02$ eggs

Method 2

Laying birds			Nonlaying birds		
Day in laying sequence	Number of birds	Number of POFs	Estimated clutch size	Number of birds	Estimated number of POFs
1	20	20	?	11	20[a]
2	29	58	1	7	7
3	32	96	2	12	24
4	52	208	3	3	9
5	16	80	4	0	0
Totals	149	462		33	60

Average clutch size $\frac{[(462 \times 2) - 149] + 60}{149 + 33} = 4.59$ eggs

[a] Number of POFs estimated to be one-half the number in the other 22 birds in the sample.

ing that all Certain POFs in a bird were part of the same clutch (Table 3, Method 1, midpoint number was 413). Because this assumption is almost certainly not true, the mid-point value will be overestimated. However, the exclusion of Probable POFs, some of which probably represented earlier ovulations in the sequence containing the Certain POFs, will underestimate the mid-point value. Second, we equated the mid-point value to the number of Certain and Probable POFs that belonged to the same clutch, judged from the relative sizes of the POFs (Table 3, Method 2, mid-point number was 462). For example, although a bird may have been scored as having 2/1 POFs, the sizes of the two Certain POFs differed so much that the smaller Certain POF apparently represented the last egg in the preceding clutch while the larger represented the first ovulation in a new clutch. Hence, we recorded such a bird as contributing only 1 POF to the total of current POFs for the sample. Sometimes, however, the relative sizes of POFs in a bird scored as 4/1 POFs indicated that the bird had ovulated on 5 consecutive days, so, in this case, 5 POFs contributed to the total of POFs for the sample.

It was difficult to estimate the clutch size of nonlaying birds because of uncertainty about the laying history of some birds. The POFs in birds that had recently finished a clutch were easily recognized, but there were no recognizable POFs in the ovaries of some birds. We assumed that these birds had laid much earlier and that their clutch sizes had the same frequency distribution as that inferred for nonlaying birds with recognizable POFs.

Average clutches, estimated by the two methods (Table 3), were 4.0 and 4.6 eggs for 182 birds in late May and early June 1977.

At that time, clutches varied from 1 to about 7 eggs. Many birds had clutches of only 1 or 2 eggs. About 8 and about 12 birds of the 22 nonlaying birds with at least 1 Certain POF had laid 1 and 2 eggs in their most recent clutches (Table 3). Of the 92 laying birds with undamaged ovarian follicles, 12 had the last egg of their clutches in their oviducts, judged from the absence in any of these 12 birds of an ovarian follicle large enough to be ovulated the next day (i.e. none >7.9 mm in diameter, see Scott 1978). As 3 of these 12 birds had no POF estimated to be 1 day old, their clutches consisted of only 1 egg. Five of the 12 birds had only 2 Certain POFs, both younger than 2 days of age, and no ovarian follicle large enough to be ovulated on the next day; their oviducts, therefore, contained the last or second egg of a 2-egg clutch. We inferred that there were another 5 birds in the sample of 92 that had the first egg of a 2-egg clutch in their oviducts, because the numbers of birds in each laying day of a particular size of clutch are theoretically equal. In total, then, 10 of 92 laying birds had 2-egg clutches. Extrapolating, we estimate that 12 and 18 of 33 nonlaying birds and 5 and 16 of the 149 laying birds had clutches of 1 or 2 eggs, respectively. Thus, about 51 (28%) of the entire sample of 182 birds had clutches of 1 or 2 eggs. If the average clutch size is between 4 and 5 and about 28% have clutches of 1 or 2 eggs, probably some birds lay as many as 7 eggs in a clutch. POFs regress too rapidly to permit certain identification of the POFs representing the first eggs of large clutches. Some birds with 4/1 or more POFs, however, also had large ovarian follicles that, barring atresia, represent an extension of the clutch. In 1977, 17 birds had 4/1 or more POFs, and the sizes of their POFs indicated that at least 9 birds had ovulated on 5 consecutive days. As each of these 9 birds had 2 large ovarian follicles greater than 6 mm in diameter, each bird appeared capable of laying at least 7 eggs in a clutch.

The frequency distributions of Certain POFs in laying birds differed significantly ($P < 0.01$) between a sample from late May and early June and one from late June and early July (Table 1). The average clutch size, estimated from the frequency distributions, declined from about 4.5 eggs in the earlier sample to about 3.5 eggs in the later sample.

Atresia.—Atresia was much more common in the yolky ovarian follicles of nonlaying birds than in those of laying birds. In both groups it occurred only rarely in follicles close to maximum size, i.e., greater than 6.9 mm in diameter, but atresia of smaller follicles was more common in nonlaying birds. Although about 40% of follicles between 3 and 7 mm in diameter were atretic in nonlaying birds, only about 5% were atretic in laying birds. Of 84 nonlaying birds, 54 (64%) had at least one large atretic follicle each. These were observed not only in birds that had laid but also in birds without any recognizable POFs. As some of these birds were collected at the beginning of laying in 1976 (April 29), clearly some atresia occurs before laying begins. Nonlaying birds without obviously atretic follicles had significantly more Certain POFs than nonlayers with atretic follicles ($P < 0.01$). Most of the former group had terminated a clutch on the day of collection. Thus, atresia of large follicles did not always precede the end of a clutch.

DISCUSSION

The ovaries and oviducts of Brown-headed Cowbirds remain near their maximum weights for about 8 weeks in May and June. Throughout this period, cowbirds lay series of eggs separated by days of nonlaying, often only 1 day. Birds in the nonlaying interval, like actively laying birds, have large yolky follicles that are within a day or so of ovulation. Also, their oviducts weigh almost as much as those containing an egg. Such a laying cycle has not been reported for any wild passerine. In contrast, the laying cycle of other passerines is marked by rapid regression of the ovary and oviduct following completion of a clutch (Petersen 1955, Hutchison et al. 1968, Lewis 1975). Typically, the largest follicle in small incubating passerines is about 2–3 mm in diameter (Payne 1969, Lewis 1975) and requires 4 or 5 days to grow to ovulable size (Petersen 1955, Delius 1965).

The special features of the cowbird laying cycle appear adapted to a more-or-less continuous supply of host nests, which is ensured by the interplay of three variables: (1) the number of host pairs per female cowbird, which has not been accurately determined, although at London, Ontario it is probably about 10 (Darley 1968, Scott MS), (2) the daily mortality rate of passerine nests, which is about 5% (Mayfield 1960, Nolan 1978, Zimmerman 1982), and (3) the occurrence of parasitism of a nest on any of several days while a host is laying (Nolan 1978). Hence, at least one host nest may often be available each day for parasitism. Although a female cowbird probably finds many nests by watching hosts building them (references in Scott 1977), she may not find some until they have been completed or laying has begun. Even then, she can still synchronize her laying with that of the host, because she usually has large follicles close to ovulation. Thus, the unusual aspects of cowbird reproduction underlie the exceptionally high fecundity recorded by Scott and Ankney (1980).

The laying cycle of cowbirds resembles more closely that of domestic hens when they are prevented from brooding than it does that of other passerines. In such circumstances, the ovary of a hen remains large (Sturkie and Mueller 1976), as does her oviduct (Aitken 1971). Laying hens vary in performance: some have clutches of 2 eggs, separated by 3 days of no eggs, while others have clutches of 3, 4, or many more eggs separated by a single day (Jull 1952, Fraps 1955). Similarly, clutch sizes vary greatly in cowbirds. We emphasize that we do not know whether or not some cowbirds habitually lay small clutches while others lay large ones. The common occurrence of 1- and 2-egg clutches, coupled with the estimated mean value of 4–5 implies a variance greater than that of other icterids (Payne 1969, Howe 1978).

We know neither why cowbirds lay in clutches nor the causes of failure to ovulate; more than one factor may inhibit ovulation. In laying cowbirds atresia of follicles large enough (i.e. >7.9 mm) to be ovulated the next day was virtually absent (0.6% of large follicles). Atretic follicles about 3–5 mm in diameter were more common and were seen twice in laying birds that lacked a large ovulable follicle. This suggests that atresia exerts its effect several days before the end of a clutch. In most cases, however, failure to ovulate was not associated with recent atresia.

We do not understand the significance of atresia. As it occurred much more commonly in nonlaying females, we suggest, as did Payne (1965), that atresia is a response to a shortage of suitable nests. Unfortunately, the variation in the number of suitable nests available to different cowbirds is unknown, but it could be determined. Female cowbirds and most of their hosts could be easily banded and the home ranges of a few female cowbirds could be determined (Darley 1968, Raim 1978, Dufty 1982), as could the daily nesting status of most of their hosts. Thus, it would be feasible to conduct a descriptive and an experimental study of the effect of the availability of host nests upon variations in laying rates and atresia in cowbirds. The density of hosts could not be increased, but the availability of host nests could be (Scott 1977). We predict that the incidence of atresia would be inversely related to the availability of hosts' nests.

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Note Added in Proof

One of us (CDA) trapped female cowbirds in 1983 to obtain eggs for analyses of egg-weight variation and composition. Each individually marked bird was held overnight in a separate cage so that CDA could determine which female(s) had laid. One female was trapped on 12 days between 2–15 June and had this laying pattern (where Y = an egg laid, N = no egg laid, and ? = no trapping done on these days): N, Y, Y, N, Y, Y, Y, Y, N, ?, ?, Y, Y, Y. This confirms our inference that cowbird clutches are sometimes separated by intervals as short as 1 day. This bird's laying rate (minimum = 9 eggs/14 days = 0.63, maximum = 11 eggs/14 days = 0.79) is consistent with the rate of 0.73 reported by Scott and Ankney (1980) from a sample of shot birds; its laying pattern is very similar to that shown by chickens.