# FECUNDITY OF THE BROWN-HEADED COWBIRD IN SOUTHERN ONTARIO

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ABSTRACT.—We collected about 850 female Brown-headed Cowbirds (*Molothrus ater*) in southern Ontario in six breeding seasons to determine the average number of eggs laid annually by a cowbird. We estimated this number by multiplying the length in days of the laying season of an average female by the average daily laying rate. In each of 1965 and 1976, two unexceptional years, the laying season was about 56 days and the average daily laying rate was 0.73 eggs (95% confidence limits of 0.65–0.80 eggs). Thus, an average female cowbird lays annually about 40 eggs. As she lives for about two breeding seasons, her lifetime fecundity is about 80 eggs. This estimate is consistent with estimates of cowbird survival: 0.15 from egg to fledging, 0.50 from fledging to independence, and 0.40 from independence to adulthood. *Received 5 December 1979, accepted 12 May 1980.*

DESPITE continuing interest in the Brown-headed Cowbird (*Molothrus ater*) (e.g. Payne 1977), surprisingly little is known about the two fundamentals of cowbird demography: fecundity and mortality. We believe that this has hindered a full understanding of many aspects of cowbird biology, e.g. the dramatic range expansion (Mayfield 1965), reproductive energetics (Payne 1973a), and the reproductive strategy of female cowbirds (Rothstein 1976).

Our present study arose from observations of the incidence of parasitism at London, Ontario (Scott 1963, 1977). This incidence was so high that it suggested that the fecundity of cowbirds was higher than the estimates then available (see Payne 1965: Table 2). We will show that the average female cowbird in southern Ontario lays about 40 eggs annually. We argue that this high fecundity is consistent with knowledge about cowbird mortality.

## COLLECTING METHODS

We collected about 850 female cowbirds throughout the complete breeding seasons of 1962, 1965, and 1976 and in limited periods of the breeding seasons of 1966, 1967, and 1977 from an area of about 2,000 km$^2$ centered on London, Ontario. Usually we collected by shooting, but in late June and early July, when flocks appear, we also netted birds.

In 1965 we had repeatedly sampled from three areas. The removal of some birds at the first sampling might have been followed by an abnormal influx of replacement birds or by changes in the reproductive activity of the survivors because of an increase in the ratio of hosts to cowbirds. In either event, subsequent samples from the same area might no longer have been representative of an undisturbed population. Accordingly, in 1976, to avoid this potential bias, we collected each weekly sample (except three in July from one cattle feedlot) from different areas at least 8 km apart.

Ovaries, and oviducts if collected, were fixed in Bouin's solution or in 10% buffered formalin. Oviducts were weighed to the nearest 0.01 g. The presence of postovulatory follicles was recorded in 1965, 1967, 1976, and 1977. Scott and Ankney (1979) give more details about collecting.

## ESTIMATION OF ANNUAL FECUNDITY

*Definitions.*—We wish to emphasize our usage of the following terms. **Laying bird**: One with an oviducal egg or, if not, with at least one postovulatory follicle, an enlarged oviduct (>1.05 g), and usually one or more ovarian follicles greater than 5 mm in diameter. The latter birds were probably between clutches. **Nonlaying bird**: One without an oviducal egg, without a postovulatory follicle or, if present, with a regressed oviduct (<1.06 g), and typically with all ovarian follicles less than 5 mm in diameter.

TABLE 1. Proportions of cowbirds with an oviducal egg in weekly samples in 1962, 1965, and 1976.

| In week ending | Year | | |
|---|---|---|---|
| | 1962 | 1965 | 1976 |
| 24 April | 0/10 | 0/4 (4)[a] | 0/5 (5)[a] |
| 1 May | 6/16 | 0/9 (9) | 1/12 (1) |
| 8 May | 4/5 | 13/21 (2) | 8/19 (8) |
| 15 May | 2/5 | 15/23 (4) | 12/17 (3) |
| 22 May | — | 18/23 (0) | 11/18 (1) |
| 29 May | 6/10 | 14/22 (1) | 10/18 (1) |
| 5 June | — | 14/22 (1) | 15/19 (0) |
| 12 June | 7/9 | 3/7 (0) | 16/21 (0) |
| 19 June | 2/3 | 11/12 (1) | 10/15 (0) |
| 26 June | 2/2 | 9/14 (2) | 13/17 (0) |
| 3 July | 1/7 | 3/12 (6) | 12/21 (4) |
| 10 July | 3/11 | 2/10 (6) | 8/24 (16) |
| 17 July | 0/8 | 1/9 (8) | 0/20 (20) |

[a] Numbers in brackets are nonlaying birds; they were not recorded in 1962; estimates of nonlayers in 1965 are minimal as reproductive organs of about 10 birds were not examined.

**Breeding season**: The period between the first and last records of a bird with an oviducal egg. **Laying season**: The period over which the *average* female lays. It was estimated to be the number of days from the first date when 50% of the birds had ovulated to the first date when 50% were no longer in laying condition. This is a good approximation of the true value, because virtually all females lay over a period of about 6 weeks, and, relative to this period, the onset and termination of laying are rapid (Table 1). **Average daily laying rate**: The proportion of birds in laying condition with an oviducal egg in any period of the laying season.

*Method.*—The annual fecundity is estimated by the product of the length in days of the laying season and the average daily laying rate. This method is a modification of those proposed by Payne (1973b: 415 and 421; 1976: 340). It is preferable because, unlike Payne's methods, it neither gives undue weight to small samples (see Payne 1976: Table 3) nor relies on data from late in the breeding season. Then, it is impracticable to obtain random samples, because some birds are in postbreeding flocks while others are not.

*Assumptions and their validation.*—We assume that (1) birds with an oviducal egg and those without were equally vulnerable to collecting during the laying season, as defined above; (2) all members of the local populations had returned to the breeding area by early May; and (3) no members of the local populations had left the breeding area, or otherwise changed in behavior, by late June.

Assumption 1 was valid in late May and early June 1977 (Scott and Ankney 1979), and we assume its validity for that period in other years. The following evidence shows that collections made in early May (assumption 2) and in late June (assumption 3) were also representative of the populations.

Cowbirds begin to return to local breeding areas in early April, and almost all have returned by the first week of May, as indicated by banding data. Banders of the Long Point Observatory banded 241 female cowbirds at Long Point, about 110 km southeast of London, between 22 March and 31 May over an 11-yr period (D. J. T. Hussell pers. comm.). Ninety-eight percent were banded before 6 May. The banders also made daily censuses of cowbirds (sexes combined) in a defined area at the tip of Long Point. The daily average for each of the 9 weeks beginning 1 April and ending 2 June was 130, 66, 24, 18, 8, 8, 4, 3, and 2. As some of the birds seen in May were probably residents, clearly cowbird migration had largely ceased by 1 May.

Conceivably, our samples in late June might be biased, because (1) some birds, although still in the area, might have become less accessible to collecting because of some behavioral change associated with the end of laying, and (2) some nonlaying birds might have left the area. In 1976, we first collected a bird that had finished laying on 1 July. Shortly thereafter, on 5 July, we first saw a flock containing female cowbirds (we define a flock as a group of 10 or more birds; this size excludes groups of courting birds commonly seen in May). Flocks form in late June and early July (Scott 1963) and signal the end of laying. We found that most females in flocks, unlike most single females, were nonlayers with regressed oviducts and small ovarian follicles. Hence, we infer that, if any birds had finished laying before 1 July, they had left the collecting area; otherwise flocks would have been seen earlier. Thus, our samples from late June were representative of the birds still in the area. It could be argued that birds, upon finishing laying, move out of the area. Lacking any information to the contrary, we think that those birds would

TABLE 2. Relationship between proportion (P) of birds with an oviducal egg and weekly mean temperatures (°C) at London.

| Date | 1962 | | 1965 | | 1966 | | 1976 | |
|---|---|---|---|---|---|---|---|---|
| | P | °C[a] | P | °C | P | °C | P | °C |
| 17–23 April (8.9°)[b] | 0/6 | 5.2 (19)[c] | 0/4 | 2.2 (20) | — | 9.1 (8) | 0/12 | 14.5 (1) |
| 24–30 April (8.3°) | 3/16 | 18.4 (1) | 0/9 | 7.3 (11) | 0/16 | 6.3 (14) | 1/17 | 4.4 (19) |
| 1–7 May (9.8°) | 7/12 | 11.3 (6) | 13/21 | 13.8 (2) | 3/25 | 5.1 (20) | 8/19 | 8.1 (14) |
| 8–14 May (10.9°) | 1/1 | 11.2 (10) | 15/20 | 15.6 (2) | 6/14 | 3.9 (20) | 12/17 | 10.1 (15) |
| Date of first sample with 50% laying | 3 May | | 4 May | | 13 May | | 3 May | |

[a] Mean of daily maxima and minima.
[b] Mean weekly temperature for 1958–1977.
[c] Mean temperature ranked from 1 to 20 for 1958–1977.

be replaced by nonlaying birds moving into the area. In that case, the numbers of nonlaying birds should have increased as June progressed, but they did not (Table 1). Thus, there is no evidence of movement by nonlaying birds in June. Therefore, we conclude that our samples in June were unbiased.

## RESULTS

*The laying season.*—In 1962, 1965, and 1976, 50% of the birds had ovulated by 3 or 4 May but not until 13 May in 1966 (Table 2). The first 2 weeks of May 1966 were the coldest recorded in the period 1958–1977. On the other hand, the earliest onset of laying, that in 1962, was associated with the highest temperatures recorded for the last week of April in 1958–1977. As the temperatures for the first week of May in 1962, 1965, and 1976 varied from well above normal in 1965 to slightly below normal in 1976 without obviously affecting the onset of laying, we believe that in most years the average female begins laying by 4 May.

Fifty percent of female cowbirds were still laying in the last week of June (Table 3). We considered that any bird without an oviducal egg and with no ovarian follicle greater than 5 mm in diameter at that time had finished laying for that year. The status of birds without an oviducal egg but with at least one follicle greater than 5 mm in diameter was uncertain; probably some would have laid again. Hence, we combined such birds with those with an oviducal egg to estimate the maximum proportion that could have been in laying condition. The exact date when less than 50% were laying lies between 26–27 June, when 60% of the birds had an oviducal egg, and 30 June–1 July, when the maximum proportion that could still have been in laying condition was 48%. This agrees well with Darley's observations (1968, pers. comm.) of a color-banded population of 24 female cowbirds resident on the campus of the University of Western Ontario. Nine of 14 resident birds trapped there in late June 1967 had an oviducal egg. Each of the remaining birds had an ovarian follicle greater than 8 mm in diameter, suggesting that ovulations would have occurred on the next day (Payne 1976, Scott 1978). Thus, more than half of the resident population was still in laying condition.

Hence, the laying season for an average female usually extends from about 4 May to 28 June, i.e. 56 days.

*Laying rate.*—We estimated the average laying rate during the laying season from the eight weekly samples ending 26 June (Table 1). All nonlaying birds were excluded from our calculations for 1976, most if not all for 1965, and none for 1962 when no record of postovulatory follicles was kept. The eight weekly laying rates did not

TABLE 3. Changes in proportion of birds in laying condition in late June (all years combined).

| Date | *n* | Proportion with oviducal egg | No oviducal eggs; proportion with largest ovarian follicle | | Maximum probable proportion in laying condition |
|---|---|---|---|---|---|
| | | | >5 mm | <5 mm | |
| 22–23 June | 11 | 0.82 | 0.18 | 0 | 1.0 |
| 24–25 June | 16 | 0.63 | 0.25 | 0.13 | 0.88 |
| 26–27 June | 42 | 0.60 | 0.31 | 0.09 | 0.91 |
| 28–29 June | 44 | 0.45 | 0.21 | 0.34 | 0.66 |
| 30 June–1 July | 21 | 0.32 | 0.14 | 0.52 | 0.48 |

vary significantly in 1976 ($P > 0.7$, $G$-test of independence, Sokal and Rohlf 1969). We did not test the 1962 or 1965 values because of uncertainty about the inclusion of nonlaying birds in the samples, but the variability in these years appears similar to that in 1976. Hence, we felt justified in pooling the weekly values for each year. Thus, the average daily laying rate is estimated by the proportion of birds with an oviducal egg in the pooled 8-week sample. It was 23/34 (0.68) in 1962, 97/133 (0.73) in 1965, and 95/131 (0.73) eggs in 1976. The 95% confidence limits for both the 1965 and 1976 estimates were 0.65–0.80 eggs (Rohlf and Sokal 1969: 208). These rates agree closely with that of 0.66 eggs calculated by Scott (1978) using another method.

*Annual fecundity.*—The average fecundity in 1962 was 56 days × 0.68 eggs/day = 38 eggs; in both 1965 and 1976, it was 56 × 0.73 = 41 eggs. We conclude that an average female cowbird in this area lays annually about 40 eggs. In years when the laying season would begin very late, such as 1966, (Table 3), the fecundity would probably be lower.

## DISCUSSION

Our estimate of an annual production of 40 eggs per female is higher than any previously recorded. Payne (1973a), studying cowbirds in California, where the breeding season is about as long as in southern Ontario, estimated that most females lay "several dozen" (p. 86) or "30 eggs" (p. 87) in a breeding season. Later Payne (1976) revised this estimate to 24 eggs. Regardless of the exact value for fecundity, clearly it is exceptionally high.

Our estimate is consistent with what is known about (1) the demography of the cowbird and (2) the nutrients required by passerines for egg production.

*Cowbird demography.*—The average lifetime fecundity of adult female cowbirds exceeds 40 eggs, because many reproduce more than once. Darley (1971) concluded that the annual mortality of adult female cowbirds at London was 54.5%, similar to the estimate of 59.6% derived differently by Fankhauser (1971). Using a mortality rate ($m$) of 57%, the mean of the preceding estimates, the life expectancy of a female at the beginning of a breeding season would be $(2 - m)/2m = 1.25$ yr or 15 months; that is, an average adult female lives long enough to breed twice and thus would lay about 80 eggs. If the population were stable, the survival rate from egg to recruitment to replace one adult female would be 0.025. Can this value be reasonably reconciled with what is known about survival of cowbirds?

Young (1963) estimated that the probability of a cowbird egg producing a fledgling was about 0.25. There were, however, biases in Young's data that, if considered, suggest that 0.25 is too high. One bias applies to estimates of nesting success in

TABLE 4. Recent estimates of survival rates of cowbird eggs to fledging.[a]

| Species | Cowbird eggs | Percent fledged | Authority |
|---|---|---|---|
| Eastern Phoebe (*Sayornis phoebe*) | 169 | 34 | Klaas 1975 |
| Yellow Warbler (*Dendroica petechia*) | 180 | 14 | McGeen 1972 |
| Yellow Warbler | 36 | 6 | Scott MS |
| Prairie Warbler (*Dendroica discolor*)[b] | 102 | 5 | Nolan 1978 |
| Eastern Meadowlark (*Sturnella magna*) | 86 | 6 | Elliott 1978 |
| Cardinal (*Cardinalis cardinalis*) | 126 | 8 | Scott MS |
| Dickcissel (*Spiza americana*) | 44 | 11 | Elliott 1978 |
| Dickcissel | 132 | 7 | Zimmerman 1966 |
| Field Sparrow (*Spizella pusilla*) | 234 | 12 | Walkinshaw 1968 |
| Several species | 34 | 12 | Gates and Gysel 1978 |
| TOTAL | 1,143 | 13 | |

[a] Based on samples greater than 30 cowbird eggs.
[b] Nolan (1978: 396) comments that his studies of several other hosts indicate that the success rate of parasites of the Prairie Warbler was typical.

general, while three are peculiar to parasitism. The first, as cogently argued by Mayfield (1960) and recently considered by Nolan (1978: 396) in the specific context of cowbird survival, results from the exclusion in many studies on nesting success of nests that failed before they could be found by an investigator. As some of Young's data were based on such studies, his estimate of survival from egg to fledging was probably too high. Most reports since Young's compilation show survival rates to be less than 0.15 (Table 4).

There are three other sources of bias in estimating the success of cowbird eggs. First, several species normally eject cowbird eggs (Rothstein 1971). This mortality is usually undetected by observers, and so its magnitude is unknown. Scott (1977) estimated that about 9% of all cowbird eggs laid in the nests of the five species that he studied were laid in nests of the Gray Catbird (*Dumetella carolinensis*). Second, a female cowbird may remove a cowbird egg rather than a host egg. This apparently occurs most commonly in cases of multiple parasitism or when the host egg is larger than the cowbird's (Berger 1948, Elliott 1977, Scott 1977). This mortality will not always be detected unless cowbird eggs are marked. Finally, cowbird eggs laid in abandoned nests will not usually be recorded; yet they probably occur quite commonly (Nice 1937: 162, Berger 1951, Nolan 1978: 373) and might account for as many as 5% of all cowbird eggs.

Hence, we believe that Young's estimate of 25% survival from egg to fledgling is much too high. In our subsequent argument we assume that the survival rate is 15%, which is slightly higher than that recorded in Table 4.

Little is known about the survival of a fledgling cowbird to the following year. Woodward and Woodward (1979) found that 10 of 21 banded fledgling cowbirds reached independence; Scott (MS) observed that not more than 5 of 10 cowbirds fledged by Cardinals (*Cardinalis cardinalis*) survived to independence. Nothing is known about survival of cowbirds between independence and breeding the following year. Nolan (1978: 470) estimated that about 39% of young Prairie Warblers (*Dendroica discolor*) survived this period, while Smith (1969) obtained the same rate for young Cardinals at London, Ontario. In the absence of information to the contrary, we assume that the survival rate of cowbirds for this period is about 40%. The product of the probabilities of survival from egg to fledging (0.15), from fledging to independence (0.50), and from independence to breeding (0.40) indicates that the

probability of a cowbird egg surviving to adulthood is about 0.03. When it is also considered that the cowbird is still increasing its range (Mayfield 1965), presumably because the total population is increasing, the estimated survival rate of 0.03 is reasonably consistent with the survival rate of 0.025 required in a stable population with an average lifetime fecundity of about 80 eggs per female.

*Nutrients and cowbird egg-production.*—There is no reason to suppose that female cowbirds are unable to obtain sufficient energy and other nutrients to lay 40 eggs annually. King (1973: 93) calculated that a passerine need only increase its daily energy intake by about 15% to acquire the energy needed for egg production. This requirement should be readily met by cowbirds at a time of year when other passerines can find sufficient food to rear young. Most north temperate-zone passerines lay about four eggs; on average, then, each parent must be able to find enough food to feed one or two young for up to about 30 days. The energy requirements of nestlings greatly exceed those of the adult female for egg production or for incubation (Ricklefs 1974: 269); yet this increased demand upon the mother does not obviously affect her ability to produce in a few days a replacement clutch if a brood is destroyed. The interval between destruction of a nest and the first egg in the replacement clutch (or the beginning of the new nest) varies little whether a nest is lost during incubation or when it contains young (Nice 1937, Verner 1963, Delius 1965, Nolan 1978, and Scott (MS) on Cardinals and Gray Catbirds). Apparently then, a female passerine can usually quickly obtain nutrients for egg production. Exceptionally high egg-production, under manipulated conditions, of wild birds such as the Common Flicker (*Colaptes auratus*) and the Wryneck (*Jynx torquilla*), as reported by Phillips (1887) and Klomp (1970), respectively, also indicates that nutrients were readily available. Collectively, the preceding observations support our contention that there are sufficient nutrients available in May and June to allow a female cowbird to produce 40 eggs (see Ankney and Scott 1980).

We emphasize that this value is an average. Some females probably lay few eggs, perhaps none, in a breeding season. About 2% of females in the middle of the breeding season (mid-May to mid-June) may be nonbreeders (Scott 1978 and our observations on the 1977 collection). The breeding season here averages 78 days (Scott MS). Walkinshaw (1949) provided evidence that a female laid over a 67-day period between 15 May and 20 July. Thus, any female laying early in the season and continuing until late in the season likely lays more than 50 eggs.

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