EVALUATION OF A METHOD FOR ESTIMATING THE LAYING RATE OF BROWN-HEADED COWBIRDS

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ABSTRACT.—The proportion of female Brown-headed Cowbirds (*Molothrus ater*) with an egg in the oviduct in a sample collected on a particular day can be used to estimate the daily laying rate of the population. To evaluate several potential biases in the use of this method of estimation, we collected about 400 female cowbirds in southern Ontario in the breeding seasons of 1976 and 1977. There was no evidence that birds with an egg in the oviduct were more wary than those without. The proportion of birds with an egg in the oviduct was independent of six variables: habitat (breeding or feeding), year, time of day, method of detection in breeding and feeding habitats (by sight or sound), sociality (alone, with a male only, with more than one male, and miscellaneous associations), and method of collecting (searching for birds, waiting for them at feedlots, or trapping). We conclude that the proportion of collected females with an oviducal egg can be a good estimate of the average daily laying rate. This was about 0.8 eggs per female in late May and early June. *Received 14 August 1978, accepted 5 March 1979.*

WE have been hampered in our studies of the fecundity and the energetics of reproduction of Brown-headed Cowbirds (*Molothrus ater*) by the difficulty of obtaining an unbiased estimate of their average daily laying rate during the breeding season. Payne (1973a) proposed and applied two methods for estimating the daily laying rate of birds, specifically parasitic cuckoos, based on (1) the proportion of birds with an egg in the oviduct, or (2) the average number and estimated ages of post-ovulatory follicles. These methods yielded widely disparate estimates when applied to a sample of cowbirds collected by Payne (1973b, 1976) in California. There, 49 of 57 females collected between 15 May and 30 June (Payne 1973b: 86) had an oviducal egg; he stated that "probably most females laid six to eight eggs in a 10-day period." His second method yielded an estimate of 0.31 eggs/day in the middle of the breeding season (Payne 1976: Table 3). He rejected the validity of his first method because he believed that birds with an egg in the oviduct were easier to collect than those without an egg (Payne 1976: 338).

The proportion of female cowbirds with an egg in the oviduct in samples collected by shooting during the breeding season varies between about 0.6 and 0.8 [Payne (1965) in Michigan and (1973b) in California; Scott (1963, 1978), and Ankney, referred to in Scott (1978), in southern Ontario]. This consistency of values suggests that the sampling biases of different collectors in different geographic areas are similar, if they exist. To reconcile these values with Payne's (1976) estimates of a daily laying rate of about 0.3 eggs for cowbirds in California, Michigan, and Oklahoma, one must postulate either that most females lacking an oviducal egg are invulnerable or inaccessible to hunters, or that cowbirds retain an egg in the oviduct for more than 1 day. Are birds without an oviducal egg more wary than those with an oviducal egg, as Payne (1976: 338) implied? Are they more difficult to find in habitats visited by collectors, or are they in habitats unvisited by collectors?

To answer these questions, we collected cowbirds in 1976 and 1977 to assess the following factors that might contribute to a biased representation of the two reproductive groups in collections: (1) differential wariness, (2) differential distribution among habitats, (3) differential conspicuousness, (4) differential activity during the day, and (5) differential effects of three methods of collecting.

We will show that differential wariness was unimportant and that the proportion of birds with an egg in the oviduct was independent of six collecting variables. Consequently, we will conclude that our samples were not excessively biased and were representative of the population. Thus, the proportion of birds with an egg in the oviduct can be used to estimate the average daily laying rate.

METHODS

In 1976 we collected, by shooting with .410 shotguns loaded with No. 9 shot, weekly samples totalling 210 female cowbirds between early April and early July. In 1977 we similarly collected 188 female cowbirds between 24 May and 4 June. Each weekly sample in 1976 and each daily one in 1977 was collected in a different area within a 75-km radius of London, Ontario. This general area is intensively farmed, and the main breeding habitat for cowbirds is found in second-growth in creek valleys, in drier upland areas where hawthorns (*Crataegus*) are dominant, along the edges of small woodlots, and along roadsides. We made no attempt to hunt in proportion to the amounts of different breeding habitats. We collected also in ploughed or planted fields where cowbirds feed. In collecting, we missed no major habitat except that we spent little time in mature woodlots, as we know from experience that cowbirds are uncommon there. No large marshes or swamps occur within our study area.

In 1977 we collected in two distinct ways: (1) we searched for female cowbirds, and (2) we waited, usually unconcealed, at livestock feedlots and shot females as they came in to feed, either on livestock food or on insects associated with the food or the manure. For comparison with these two collections we have a sample of birds trapped in Potter traps baited with grain on the campus of the University of Western Ontario between 17 May and 16 June 1965.

In 1976 and 1977 we recorded for each specimen the locality, date and hour of collection, habitat, sex and number of cowbirds associating with a particular specimen, and the presence or absence of an oviducal egg (determined by dissection immediately after death). We assumed that we did not kill any bird before ovulation on the day of collection. In 1977 we recorded additional information: how we detected birds (by sight or sound), the behavior of birds on being approached (did not fly, flew away from the collector once, or more than once, before being killed), and the distance in yards (determined by pacing) at which the bird was killed. Occasional failure to record some information accounts for numerical discrepancies between some later tabulations.

We used the *G*-test of independence, as described by Sokal and Rohlf (1969: 591, 599, and 601), to evaluate our observations.

RESULTS

Wariness.—We regarded as less wary (1) birds that did not fly when a collector first approached, and (2) those of the above that were shot at the shortest distances. The proportion of birds with an egg in the oviduct did not vary significantly ($P > 0.5$) among the birds that did not fly, flew once, or flew more than once (Table 1A-1).

Birds with an egg in the oviduct may be *more wary* than those without (Table 1A-2). The proportion of the former increased significantly with distance ($0.05 > P > 0.01$). Thus, differences in collecting skills may introduce some bias; shooting at short range overestimated the proportion of birds without an egg in the oviduct. As the proportion of birds shot at close range was small, however, the bias so introduced was not great. The effort required to collect cowbirds remained about the same in April and May, although the proportion of females with oviducal eggs increased greatly (Table 2). In June cowbirds were more difficult to collect, while the proportion of birds with an oviducal egg remained high. Thus, differential wariness did not result in a disproportionate excess of birds with an egg in the oviduct in samples collected by shooting.

Habitat and year.—The behavior of females conceivably may vary with their reproductive state, so that the time spent in a particular habitat may also vary. For

TABLE 1. Relationship between proportions of birds with an oviducal egg and several potential sources of sampling bias.

A. Wariness—1977

1. Behavior on approach by collector

	Did not fly	Flew once	Flew > once
Egg	54	35	8
No egg	16	7	3

2 × 3 test, $G = 0.8860 < \chi^2_{0.5\,[2]} = 1.386$, $P > 0.5$

2. Distance at which 'did not fly' birds shot

	<15 yards	15–19	20–24	25–29
Egg	4	8	22	18
No egg	4	6	4	2

2 × 4 test, $G = 8.660 > \chi^2_{0.05\,[3]} = 7.815$, $P < 0.05$

B. Habitat and year

	1976[a]		1977	
Habitat	Egg	No egg	Egg	No egg
Breeding	42	19	50	15
Feeding	23	15	38	8
Roadside	10	0	10	3

Multiway test, $G = 12.704 < \chi^2_{0.05\,[7]} = 14.067$, $P > 0.05$

C. Time of day[b]

	0530–0729	0730–0929	0930–1129	1130–1329	1330–1930
Egg	15	37	39	20	18
No egg	8	8	9	6	3

2 × 5 test, $G = 3.458 < \chi^2_{0.3\,[4]} = 4.878$, $P > 0.3$

D. Mode of detection—1977

	By sight	By sound
Egg	39	54
No egg	10	16

2 × 2 test, $G = 0.100 < \chi^2_{0.7\,[1]} = 0.148$, $P > 0.7$

E. Sociality and habitat—1976[a] and 1977

♀ collected was associating with

	Alone		1 ♂ only		No ♀ > 1 ♂		Other	
Habitat	Egg	No egg	Egg	No egg	Egg	No egg	Egg	No egg
Breeding	19	6	36	13	25	11	10	4
Feeding	8	7	23	10	15	2	13	4
Roadside	7	0	5	1	4	2	3	0

Multiway test (excluding roadside), $G = 9.904 < \chi^2_{0.3\,[10]} = 11.781$, $P > 0.3$

[a] 17 May to 24 June, when proportions of birds with egg in oviduct did not vary significantly ($P > 0.5$) in six weekly samples.
[b] Values from 1977 except for 40 birds collected 1 June to 9 June 1976, when proportion with an egg in the oviduct was similar to that in 1977 sample.

instance, a bird having completed a clutch might spend less time in breeding habitat and more in feeding habitat than one that has not. Perhaps birds about to begin a clutch spend more time in breeding habitat early in the day, searching for nests when hosts are building. Accordingly, biases might be introduced if collectors concentrate on a particular habitat or collect mostly at one time of day.

TABLE 2. Relationship between collecting effort and proportion of birds with an oviducal egg in 1976.

	April[a]	May	June[b]
Hours collecting	12.75	19.50	38.50
Birds collected per hour	2.35	2.21	1.51
Proportion with oviducal egg	0.03	0.65	0.78

[a] Last 2 weeks, when it was assumed that most birds had returned to breeding area.
[b] Until 24 June.

In 1977 the proportion of birds with an egg in the oviduct was 15/16 in birds from woodland edge, 13/18 in hawthorn uplands, and 22/31 in those collected in creek valleys. As this variation was not significant (2 × 3 test of independence, $G = 4.122 < \chi^2_{0.05[2]} = 5.991$), we pooled the values from different breeding habitats in 1977 for comparison with values from other habitats and from 1976 (Table 1B). The proportion of birds with an oviducal egg varied, but not significantly ($P > 0.05$), from a high of 10/10 in 1976 roadside habitat to a low of 23/38 in 1976 feeding habitat. Thus, the chance of collecting a bird in a particular reproductive state was independent of the habitats studied and of the 2 years when the collections were made.

Time of day.—The time at which collections were made did not influence the relative frequencies of the two reproductive groups ($P > 0.3$, Table 1C).

Mode of detection.—Although there was no sampling bias associated with collecting in different habitats, some behavioral difference between the two reproductive groups could result in a sampling bias that applies equally in all habitats. Also, the manner by which collectors detect or are attracted to cowbirds (by sight or by sound) might cause a sampling bias.

The mode of detection varied significantly among the different habitats. The proportions of birds detected first by sound rather than by sight were 51/63 in breeding habitat, 5/12 along roadsides, and 14/44 in feeding habitat (2 × 3 test of independence, $G = 28.550 > \chi^2_{0.005[2]} = 10.597$). However, the proportion of birds detected by sight that had an egg in the oviduct did not differ significantly ($P > 0.7$, Table 1D) from that of birds that were heard first. Therefore, differences in the method of detection did not bias the representation of birds with an oviducal egg in our samples.

Sociality.—Female cowbirds when first detected were usually associating with one or more males, were less often alone (Table 1E), and only very rarely (<5% of observations in 1977) were they only with other females. The proportion of birds with an oviducal egg was clearly independent of the social group ($P > 0.3$).

If the representation of different social groups in our samples were biased, solitary silent females in breeding habitats would likely be underrepresented, as they would be the most difficult to find. We collected only six such females, of which five had an egg in the oviduct. This proportion is such that, even if this group were greatly underrepresented, the overall proportion of birds with an oviducal egg would not be substantially altered.

We found no instance where different states of a variable in collecting (habitat, year, time of day, method of detection, and sociality), other than wariness, were related to significant differences in the proportion of birds with an egg in the oviduct. Thus, we conclude that our method provided a representative sample of the cowbird population during the middle of the breeding season. We now offer supporting evidence for this conclusion.

Methods of collecting.—If collecting cowbirds in the fashion just described results in substantial sampling error, then distinctively different collecting methods should not likely yield similar results. The proportions of birds with an oviducal egg in three samples collected in three different ways, however, were remarkably similar: 98/124 (0.79) by searching and shooting (as described), 52/63 (0.83) by waiting and shooting at feedlots, and 35/44 (0.80) by trapping. These proportions do not differ significantly (2 × 3 test of independence, $G = 0.340 < \chi^2_{0.8\,[2]} = 0.446$). These results suggest that collecting by searching for cowbirds was unbiased.

Proportion of non-laying birds in a local population.—Payne (1973b: 86) observed that about 80% of his sample of cowbirds had an oviducal egg, but he later estimated (Payne 1976) that the daily laying rate of the population was about 0.3 eggs. If the latter is accurate and assuming that an egg remains in the oviduct for only 1 day, then on a particular day about 70% of the females should lack an oviducal egg, i.e. they are non-laying birds. Conversion of an observed proportion of 80% with an oviducal egg to an expected proportion of 30% requires that, for every 80 birds with an oviducal egg and 20 without that are collected, there must be about 170 non-laying birds (those without an oviducal egg) that are essentially invulnerable to shooting or trapping. It follows, then, that if most of a local population could be collected in a brief period, one could determine if this large proportion of non-laying birds actually exists.

We probably collected most of a local population on 30 and 31 May 1977. On 30 May we saw several cowbirds feeding at food provided for some pigs lying in a bare unplanted field, in which we were permitted to shoot. We shot under ideal conditions and missed few birds. Upon a shot being fired, the survivors flew to nearby wooded slopes. Although we were usually in full view, cowbirds returned or arrived within minutes to feed, only to be shot at again. We collected 33 females between 1330 and 1515 and left at 1530, as no more female cowbirds were coming to the feedlot. In addition, five females were collected in nearby breeding habitat. Next day, under similar conditions, we collected 19 females between 0815 and 1415, including one that apparently had been wounded on 30 May. Only three females came to feed between noon and 1415; all were killed. Thus, in 2 days the number killed and the collecting rate dropped from 38 collected in about 2 h to 19 collected in about 6 h. We attributed this decline to our intensive collecting and not to wariness of the survivors. The rapidity with which birds returned to the feedlot after a shot, and the wounded bird that returned next day, suggest little wariness. Birds too wary to come to the feedlot should, nevertheless, have still been in the adjacent breeding habitat. On 31 May, however, while others were shooting at the feedlot, Scott walked about 2.5 km through and beyond the area of breeding habitat where he had killed three females and had seen several others on the previous afternoon. He detected only one female. There is thus no evidence to suggest that heightened wariness was responsible for the decline in numbers. Thus, the 57 females killed on 30 and 31 May apparently represented most of the females that habitually used this feedlot. Forty-two (75%) of 56 females had an oviducal egg (the remaining bird was lost before dissection).

Assuming that there is a large proportion of birds without an oviducal egg and that they are exceptionally difficult to collect while in this reproductive stage, one would expect that, eventually, these birds should become accessible to a collector when they begin to lay. One would predict that the number of birds coming to the feedlot should have increased in the days following 31 May, but an increase did not occur. At the feedlot on 4 June we saw no more than 7 females and collected 6 (5 with an oviducal egg) between 1210 and 1530. Therefore, we conclude that there was not a large number of birds relatively invulnerable to collecting because they lacked an oviducal egg. It follows that the true proportion of this population with an egg in the oviduct was about 75%.

DISCUSSION

We have shown that birds with an oviducal egg were not less wary than those without. This does not support Payne's (1976) contention that his estimate of the laying rate, deduced from the proportion of birds with an oviducal egg, was too high because laying birds were less wary than non-laying birds. We have also shown that the chance of collecting a female with an oviducal egg was independent of six other variables: habitat, year, time of day, method of detection, sociality, and method of collecting. As our samples seem representative of the population, the proportion of birds with an egg in the oviduct in our samples can be validly used to estimate the average daily laying rate. The absence of hard-shelled eggs in the oviduct in morning samples and of soft-shelled eggs in evening samples (Payne 1965, Ankney and Scott MS.) shows that a cowbird retains an egg in the oviduct for only 1 day. Hence, the daily proportion of birds with an egg in the oviduct must equal the average daily laying rate. This was about 0.8 eggs in late May and early June in 1977 and in 1976 (Scott 1978). Scott (1978), using a different method of estimation, found the average daily laying rate to be about 0.66 eggs in a heterogeneous group of samples collected between 15 May and 10 June in 1965 and 1976. At present we cannot reconcile our estimate of a high laying rate with the much lower laying rate reported by Payne (1976). Either there is an undetected bias in our three sampling methods or Payne's assumption (1976: 338) that all cowbird post-ovulatory follicles remain recognizable for 10 days is incorrect.

ACKNOWLEDGMENTS

We thank G. Bain, K. Hurrell, D. Seip, and S. Johnson for their assistance in collecting cowbirds. The co-operation of many landowners was greatly appreciated. This study was supported by grants from the National Research Council of Canada.

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