THE COWBIRDS OF OTTER LAKE¹

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 D^{URING} a study of the nesting birds on 55 acres just west of Pontiac, Michigan, data on the Brown-headed Cowbird (*Molothrus ater*) parasitism were collected. This paper is a report on findings and inferences as to number of female cowbirds present, size of clutches, number of eggs laid, length and peaks of egg laying seasons, hosts used, and area covered by the birds.

The study area consisted of unused, hilly pasture in the early successional stages of reforestation and low, wet thicket bordering a canal connecting Cass and Otter Lakes. The host species studied primarily was the Yellow Warbler (*Dendroica petechia*). Approximately 50 pairs and their nests were found in the area in 1950. Complete seasonal censuses of breeding species have already been reported. (O'Reilly et al., 1951a:71; 1951b:66; 1954:93).

Nice (pers. comm.) has confirmed our feeling that, though unproven, most investigators believe that different cowbird egg types indicate different females laying them.

Since we desired to know how many cowbirds were laying on the area we decided to use this generally accepted, though unproven, approach to cross-check on actual counts of females on the area. In 1950, therefore, a reference collection of unblown cowbird eggs were started as soon as possible so that accepted eggs could be compared at the nest without collecting them. (Blowing eggs changes color values for comparison with those left in nests when accepted by hosts.) Only deserted, covered, or broken eggs were collected from the warbler host, but five accepted eggs were taken, one at a time, from Song Sparrow (*Melospiza melodia*) nests to build up the collection. Broken eggs were repaired into usable specimens by means of plaster of Paris. This reference collection was carried on daily rounds and comparisons were made at nests containing accepted eggs. A Boley millimeter caliper was used to measure eggs when compared.

NUMBER AND IDENTIFICATION OF FEMALES ON AREA

We believe that five females were responsible for the 34 eggs collected and the 56 eggs recorded during this one season for the following reasons: First, repeated censuses counted five females on the area and never more. Second, ground color and marking comparisons divided these eggs into five types (Table 1). Third, only two of these types were not found deposited on the same day at least once (Table 3). These types, B and E, were widely dissimilar in coloration, markings, and measurements (Table 1). Since passerines lay but once a day, eggs found laid the same day are almost certainly from different females.

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TABLE 1	
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COWBIRD EGG CHARACTERISTICS-1950

Female	Mean size (mm)	Description
в	20.3 imes 15.8	Smallest; usually fine brown and light purple markings
D	21.3 imes16.5	Marbled type; chocolate brown and light purple markings
А	21.2×16.7	Light glossy brown and faint purple traces of markings
С	22×16.9	Dark brown, minute markings covering the whole egg densely
Е	22.2 imes16.7	Marbled type; light greenish hue to the base white, markings brown in bold splotches, much less purple

The most interesting series, Type E, showed a remarkable similarity in length measurements. A statistical analysis was made of these lengths on the 18 eggs and on a sampling of 24 unselected cowbird eggs, therefore, presumably from different females (Mayfield, 1960:167). The F and t tests proved the variances and means of the lengths of the E type to be significantly different from those of the Mayfield sample at the 5 per cent confidence level (Table 2). This supports the hypothesis of the single origin for the E type eggs.

The similarity in lengths of the smaller type D series of eggs was not great enough to support this hypothesis. Inadequate sampling prevents valid analysis in the other three types.

Walkinshaw (1949:82) had a remarkable series of 25 cowbird eggs found in Field Sparrow (*Spizella pusilla*) nests (with two exceptions) in a very restricted area, which from color, markings, and similarities of length measurements, also supported by statistical analysis, he believed to be the production of one female.

Both Friedmann (1929) and Nice (1937) believed different females to be responsible for their different egg types, but had smaller series to work with and statistical support was thus denied them.

Perhaps organic dyes or radioactive tracers (phosphorus or calcium salts for shell components) fed or injected into captured breeding female cowbirds prior to color banding and release would help answer some of these questions in the field since eggs and their source female could thus be indisputably matched.

The study of captive females would undoubtedly be of value if they could be induced to lay. This has apparently been done by F. L. Rand (Friedmann, 1929:184) with a hand-raised bird. He merely supplied this young bird of the previous year with nests containing candy eggs. It laid 13 eggs in 14 days and frequently removed the pseudo-host eggs as they were often found on the floor.

TABLE 2 Egg Lengths									
Туре	No. eggs	Extremes (mm)	Range	Median	Mode	Mean	Std. dev.		
D	11	20.7-21.8	1.1	21.1	21.0	21.2	0.336		
Е	18	21.4 - 23.2	1.8	22.1	22.1	22.2	0.417		
Walkinshaw (1949:82)	11	21.4 - 22.1	0.7			21.8	0.20		
Mayfield (1960:167)	24 unselected	20.0–23.6 1	3.6	20.65	20.6	20.9	0.859		

COWBIRD EGG LAYING SEASON

Table 3 is a condensation of laying data from three seasons. Since nests were checked daily in 1950, exact dates of laying were known in most instances or the date could be ascertained easily within a day or two by knowledge of the host's cycle. In these few cases eggs usually fitted into an empty day in a clutch like a piece into a jigsaw puzzle. As less time was spent in the field in 1948 and 1949, and as less attention was directed to this phase of the problem at that time, we may indicate those dates as probable ones for the depositions in those years. However, the actual date of laying for a reasonable number of them is known, with ample justification for dating the others as we have. The maximum error possible would be one or two days.

The peak for the 1949 season appears to be nine days earlier than the 1950 peak. This correlates with the lateness of the latter season as a whole, and with the beginning of the Yellow Warbler cycle for both years. In 1950 at least four female cowbirds were laying at the time when the warblers were finishing nest construction.

SUMMARY OF LAYINGS

Female A laid six eggs in two clutches of five and one, with a four-day nonlaying period between. The total observed laying period was 11 days. Female B also had six eggs in two clutches of four and two, with a four-day interval noted and a known laying period of 10 days. Female C had seven eggs in two clutches of four and three with an interval of 20 days and a 30-day laying period. Female D had 19 eggs in six clutches of six, five, one, two, four, and one, with intervals of three, five, six, four, and four days, with a known laying period of 41 days. Female E had 18 eggs in five clutches of three, seven, five, one, and two with intervals of five, two, thirteen, and two days, and a known laying period of 40 days. Perhaps the last three eggs belonged to one clutch instead of two, making a total of only four McGeen and McGeen

3 9 Different Tyd Ichigan	pe C	OWBII	id Egg	S AT	
June	5	D*	Е		
	6		Е		
2	7				
	8				
	9		Е		
	10	D^{+}	F		

			Тав	LE	3				
LAVING DATES,	Clutches,	AND	Hosts	ÓF	DIFFERENT	Туре	COWBIRD	Eccs	АТ
		Pe	ONTIAC,	MI	CHIGAN				

	x*	May 9								June	5	D^*	Е	
		10									6		Е	
2 (3)		11	D^*					z			7			
(2)		12	D^*								8			
		13	D^*								9		Ε	
		14	D^*								10	D‡	Е	
s		15									11	D‡	Е	
		16									12	D^*	Ε	
5		17									13	D	Ε	
		18	D			Α	В				14			С
		19	D				В				15			
		20	D		С	Α	В		х		16			
		21	D^*		С	Α	в				17			C*
2	х	22	D			Α					18	D^*		C*
5		23		Е	С	A^*					19			
2		24		Е	С						20			
2		25		Е							21			
		26					в				22			
	х	27					В				23			
		28	D			Α					24			
5		29									25			
		30									26			
	x	31		Е							27		Е	
		June 1		Е							28			
		2		Е							29			
z		3		Е							30		\mathbf{E}	
		4	\mathbf{D}^*	Е						July	1		Е	
						x =	- 194	8 Sea	son E	ggs	5 T	otal		
									son E		15 T			
			A, B, C	C, D,	E Tyj						56 T			
				•		Т	hree	Year	Tota	l ==	76 E	ggs		

* = Song Sparrow host; ‡ = Traill's Flycatcher host; All others = Yellow Warbler host.

clutches. This would eliminate the last two-day interval, but the other one is between two full-sized clutches of seven and five eggs, respectively.

DISCUSSION OF INDIVIDUAL CLUTCHES

Judging from known egg depositions, Females A, B, and C apparently laid only two clutches apiece, although this is uncertain for it will be noted later that they may have covered some territory not under observation.

The incompleteness of known second clutches for Females A and B seems

apparent. Probably the gaps in the first clutches of Females A and C and in the second of C did not actually exist. Also, another clutch may have been missed entirely in the 20-day interval between the two known clutches of Female C.

Female D had the earliest cycle of all the females, being synchronized with the earliest known Song Sparrow nestings on the area. In one instance, its nonlaying interval appeared to be only three days with 11 eggs apparently deposited in 14 days.

Female E had the latest start for her cycle, or possibly we missed finding evidence of an entire previous clutch. It is more likely that we only missed the first few eggs of its first clutch, however, since from a glance at the hosts (Table 3) we suspect this female was a "specialist" on Yellow Warblers. If it did have an earlier first clutch, like Female D, it would have had to impose upon the Song Sparrows, since the first warbler nests were not available until 17 and 18 May that year. The first four eggs we attributed to this female showed a progressive increase in width which would seem to be more indicative of a first clutch than a later one. The first known egg of this bird was found 23 May. We had located only the nests of 32 pairs of warblers, up to that time, out of the complete population of 50 pairs. The possibility exists that a few earlier eggs were missed, therefore.

This female, like Female D, presents a very interesting picture, in that 12 eggs apparently are laid in 14 days with only a two-day nonlaying interval between the two clutches. This is reminiscent, too, of Rand's captive female.

In the case of Female D, the short three-day interval was following the first clutch on the Song Sparrows when the majority of the warbler population started nesting practically simultaneously on the area, which apparently was covered most thoroughly by this female. Female E's short interval was between the second and third clutches, however, when only warbler pairs engaged in second or third nesting attempts (due to cowbird or predator interference) were available to her.

LENGTH OF EGG LAYING SEASONS

Table 4 summarizes material on length of laying for apparent individual birds, as well as for the species in single seasons. It will be noted that Walkinshaw's (1949) female had a season one month longer than either of the two Pontiac birds. Its season was only 24 days less than the longest cycle (94 days) noted for a group of females in one season.

About two-thirds of the depositions in this study were found in May (47 eggs) and one-third in June (27 eggs). Only one was found in July. Berger (1951) found two in August. If several or more seasons are counted the

		TA	ble 4	,	
		COWBIRD ECC	LAYIN	IC SEASONS	
Individuals	Source				
Female D	19	9 May–18 June	41	6	This work
Female E	18	23 May–1 July	40	4 or 5	This work
Female Battle Creek	25	15 May–20 July	70	71	Walkinshaw (1949:82)
1932 A	9 ²	27 April–24 May	29	3	Nice (1937:156)
		The	speci	es	
Location	Eggs	Dates	Days	Area	Source
Butler, Penna.	81	10 April-12 July	94	90 Acres	Norris (1947:86)
Ann Arbor, Mich.	67	25 April–26 July	92	Washtenaw County	Berger (1951:27)
Cleveland, Ohio		13 May–26 July	75	Cleveland area	Williams (1950:153)
Buckeye Lake, Ohio		19 April–30 June	72	44 Sq. Mi.	Trautman (1940)
Pontiac, Mich.	56	9 May–1 July	53	55 Acres	This work
Madison, Wis.		20 May–3 July	44	5 Acres	Young (1949) and pers. comm.

¹ Nice's analysis-Nice 1949:232.

 2 Assuming gaps in clutches were off area depositions, not skipped days in laying, the eggs would total 17.

length of total egg laying cycle can be extended, but this is misleading since no single seasonal cycle would approach in size such a compound overall cycle.

HOSTS

Examination of Table 3 reveals that Females A and C parasitized both the warblers and the Song Sparrows. Female D included the Traill's Flycatcher (*Empidonax traillii*) in its host group as well as the above two species. But Females B and E were only known to parasitize the warblers. The small number of eggs in the case of Female B makes the classification of it as a specialist highly problematical. (It had the smallest eggs and these most closely resembled the warbler's in coloration and markings.) Female E is the second example of a female cowbird that has been identified circumstantially to be host specific on the basis of a fair-sized series of eggs. In the case of Female E no variation from choice of the warblers as host for 18 eggs was uncovered, while Walkinshaw (1949) found that only the first two eggs of the 25 he attributed to one female were laid in the nest of a host other than the Field Sparrows he was studying. Since no Field Sparrow nests were yet available, the cowbird used an earlier nesting towhee for these first two depositions. Friedmann (1929) cited several records wherein there was a suggestion of specialization involving as host species the Lark Bunting (*Calamospiza melanocorys*), the Red-winged Blackbird (*Agelaius phoeniceus*), and the Prothonotary Warbler (*Protonotaria citrea*). He also believed a seasonal type specialization to be evident due to lack of other hosts, as in the case of the parasitized early nesting Eastern Phoebes (*Sayornis phoebe*) in the Ithaca, New York region. (This may also be inferred from the manner in which Female D, the "opportunist" of this Pontiac group of females, switched to using the Yellow Warblers when this host's cycle began.) The three females Friedmann studied at Ithaca were not specialists, however, since his Females A and C used three host species, and Female B, two, for the 14 eggs noted for all three females (1929:183).

Several interesting questions are brought up by these results. If a female does specialize, what is the determining factor in her host choice? Would she choose the host which reared her, due to imprinting? Obviously a great deal of work remains to be done before we can hope to answer these questions satisfactorily.

AREA USED

Eggs of Females A, B, and C were found only in a narrow strip along the western edge of the area involving about 15 acres or less. Female D covered nearly the whole area (40 acres of 55) judging from actual egg locations, and may have covered more. Female E covered slightly less (35 acres) according to egg finds, but again may have covered more.

The three females for whom the lesser numbers of eggs were found were confined to the smaller areas as might be expected on a numerical basis. They may have ranged beyond the bounds of our study area, to the north. However at least 20 acres of cultivated field just across the road from the western boundary cut down the number of nests available to them in that direction. This would not prevent such ranging, of course.

Since cowbirds apparently do not defend an area (Laskey, 1950), the home acreage covered by a single cowbird female may best be called her range. There can be an extensive overlapping where cowbirds are abundant. For instance three of four nesting attempts of one pair of Yellow Warblers on the Pontiac area were parasitized with all five cowbirds participating. Any acreage-per-female figure derived by dividing total acreage by number of females present must be a minimum figure because of this overlapping.

Walkinshaw's (1949) female confined herself to a small range of 12.5 acres according to his egg finds. Nice (1937:154) believed 18-20 acres to be the ordinary range with occasional birds covering 30 acres.

From the above we may deduce that cowbird females may regularly cover

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ranges of 12-40 acres depending upon, presumably, choice of host, host density or spacing, and perhaps fecundity of the cowbird. The mean figure would be 26 acres derived from these two extremes, close to the 24-acre mean observed for the five Pontiac females.

It would seem likely that the density of hosts on an area is the controlling factor in range size rather than area *per se* and cowbird range ought to be reckoned in units of host-pairs as well as units of area measurement.

The number of hosts available per female on the Pontiac area was 20 pairs (99 pairs per five cowbirds), counting only the three species actually noted to be parasitized on the area in the 1950 season. If we consider other commonly used hosts as available even though we observed no parasitism on them we could extend the list to over 25 pairs of hosts per female.

Nice's (1937) figures varied from 14–15 pairs available per female to only eight pairs of hosts per parasite female during the later years of her study when adverse conditions, mostly caused by man, had decimated the Song Sparrow population especially. The average figure on that area was 11.5 pairs per female, making it close to another Ohio report (Hicks, 1934) of 12.5 pairs per female. The female studied by Walkinshaw (1949) had about 19 pairs of Field Sparrows to utilize, but chose only 15. A study of the Ovenbird (*Seiurus aurocapillus*) (Hann, 1937) indicates about four pairs of Ovenbirds per female, but no figures are given on other hosts, so the picture is obviously incomplete.

DISCUSSION

The tendency toward indeterminate laying as exhibited by Females D and E with 11 and 12 eggs in 14 days, respectively, with intervals of 3 and 2 days between the clutches may corroborate Rand's observation cited above. Friedmann (1929) mentioned L. J. Cole's theory that the cowbird could be in a transitional state from a determinate layer to an indeterminate layer where laying may continue daily for longer periods of time. This obviously would be advantageous for a parasite.

Both Cole and Hamerstrom found a tendency towards indeterminate laying in the House Wren (*Troglodytes aedon*) (Kendeigh et al., 1956:50). Cole's wren laid 30 eggs in 43 days with the first group having 13 eggs in 13 days, then a 4-day interval. Apparently 13 eggs in a series is about the limit for passerines. Hamerstrom's banded female laid 14 eggs in 17 days and 12 eggs in 15 days at the beginning and end of its season.

Davis (1942:12) believed that the Brown-headed Cowbird lays no more than 5 eggs in a clutch. From our records they may lay 6 or 7 in a clutch. Nice (1949:234) assumed intervals of at least 5 days, while our two birds seemed to have intervals of 4, 4, 4, 4, 3, and 2 days. Davis (1942:11) believed from histological evidence that a female Shiny Cowbird (M. bon-ariensis) had only a two- to three-day interval between clutches.

Payne reports (1965:57) an average of 10 to 12 eggs, with 15 a maximum per season for the Brown-headed Cowbird on histological evidence; clutches of one to six with 3.1 eggs average, and time between clutches to vary from a few days to a few weeks. These were northern Michigan birds, with a breeding season a month shorter than in lower Michigan. He also reported three of 33 females laid 10 eggs or more by the date of collection and might have laid twice that number by the end of the season.

SUMMARY

Brown-headed Cowbird parasitism observations were made at Otter Lake, Pontiac, Michigan while working on a colony of 50 pairs of Yellow Warblers on a 55-acre area.

It is believed on the basis of the appearance and size of eggs plus dates of laying and female censuses that in 1950 five females deposited the 56 parasite eggs found on the area.

The laying cycle varied from year to year with host cycles. Probable single female cycles of 18, 19, and 25 eggs in four or five, six, and seven clutches, covering 40, 41, and 70 days, respectively, are suggested from the Otter Lake E and D types and Walkinshaw's data. Single year egg laying seasons of 75, 92, and 94 days have been reported in the literature for the species. Possible non-laying intervals between clutches of only two or three days are reported. The number of eggs laid on and off the area was undoubtedly greater than observed.

If our inferences are correct, some cowbird females appear to specialize on certain hosts. Others do not. We believe one female laid 18 eggs all in Yellow Warbler nests in a 35-acre area. Statistical analysis on the 18 egg lengths supports this conclusion. The 19 eggs of another presumed single female, by contrast, were found in the nests of three hosts.

From 12 to 40 acres may be covered by a single female with about 25 acres being a likely mean. A great amount of overlapping of ranges occurred. The number of hosts available per female is important in determining the density of parasites.

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