CLUTCH SIZE AND NUMBERS OF EGGS LAID BY BROWN-HEADED COWBIRDS

By Robert B. Payne

The evolution of reproductive rates in birds has often been explained on the basis of either one of two somewhat contrasting theories. Lack (1954), on the one hand, has maintained that the numbers of eggs laid by each species of birds has been established by natural selection to correspond with the largest number of young for which the parents can, on the average, find and provide sufficient food. Darwin (1859), on the other hand, pointed out that animal species with a high mortality rate have a high birth rate, and some Darwinian evolutionists have held recently that high mortality rates through selective action cause high birth rates. The concept that parental provision of food sets the upper limit for reproductive activity has been adopted by many ecologists who work with birds. Observational evidence in support of it is rather substantial (Lack, 1954; Lack, Gibb, and Owen, 1957; Kluyver, 1963; Perrins, 1963, 1964).

The numbers of eggs laid by brood parasites provide a source of information useful in evaluating theories of the evolution of reproductive rates. One might expect brood parasites to lay more eggs than birds which have to feed their own young, if food with which the parents nourish the young is the main determinant of the numbers of eggs laid by birds. Larger clutches, more clutches, or the abandonment of laying eggs in distinct clutches are possible adaptations in the brood parasites.

The present study is a report on the clutch sizes and the numbers of eggs laid by Brown-headed Cowbirds (*Molothrus ater*) during two breeding seasons in Michigan.

ACKNOWLEDGMENTS

I am grateful to Alfred H. Stockard, Director of the University of Michigan Biological Station, for aiding this study with a National Science Foundation summer research grant in 1963. Russell B. Payne, my father, and also Larry L. Wolf collected some of the birds, and I am thankful for their help. Alden H. Miller and Oliver P. Pearson read the manuscript and offered helpful suggestions.

BREEDING SEASONS OF COWBIRDS IN MICHIGAN

Brown-headed Cowbirds were collected in the southern peninsula of Michigan during their breeding seasons in 1960 and in 1963. The two study areas were located, respectively, in the extreme southern counties and in the extreme northern counties, areas which are about 200 miles apart. Cowbirds were taken near Ann Arbor in Washtenaw County from April through June 14 in 1960 and near Niles in Berrien County from June 15 to June 18 in 1963. These southern localities lie in a vegetation zone which was originally covered with mature beech-maple-oak forest. The prairies of the midwest, which Mayfield (1960) considered to be the prehistorical eastern limit of the range of the Brown-headed Cowbird, extended into Berrien County. Southern Michigan is now heavily farmed for fruit and grain, and many square miles are used for pasturing cattle. The northern Michigan study area was centered around the University of Michigan Biological Station in Cheboygan County, and some cowbirds were collected in adjacent Emmet and Presque Isle counties. Northern Michigan lies in a broad ecotone between deciduous forest and northern coniferous forest. The vegetation has been reviewed by Kendeigh (1948). A small per cent of northern Michigan is now used for cattle pastures and for growing alfalfa.

The breeding season for cowbirds in southern Michigan starts in late April, about a month after the arrival of the first migrants. Laying continues through May and June and ceases in July (Wood, 1951; Berger, 1951). Cowbirds arrive in northern lower Michigan about a month later than in the southern counties (Wood, 1951). Nelson (1956) reports that cowbirds have been seen near the Biological Station as early as April 14. However, all available evidence indicates that egg laying does not begin there until late May or early June. The main feature of the habitat which limits earlier breeding is probably the absence of suitable nests in which to lay. Two of the major habitats which are frequented by cowbirds and which make up most of the acreage between Douglas Lake and Burt Lake, where most cowbirds were collected, are not suitable for early nesting of most songbirds. The aspen woodlands, dominated by *Populus grandidentata*, do not begin to leaf out until the middle of May, and leafing out is completed in late May (Barnes, MS). Similarly, sugar maple (*Acer saccharum*) woods do not leaf out until late May (Southern, 1958). These two habitats and their edges are the main breeding sites (Kendeigh, 1948) of most of the important hosts of cowbirds in the area—Ovenbirds (*Seiurus aurocapillus*), Red-eyed Vireos (*Vireo olivaceus*), Wood Pewees (*Contopus virens*), and American Redstarts (*Setophaga ruticilla*). Nesting records from the Biological Station indicate no fledglings of these birds or other flycatchers, vireos, warblers, and sparrows before the last days of June, and only one record of nesting in May (an Ovenbird nest with eggs on May 24) has been recorded (Nelson, 1956). Life-history studies on birds of the area also indicate that nesting does not start generally until June (MacQueen, 1950; Southern, 1958). In the Kirtland Warbler (*Dendroica kirtlandii*) breeding colonies 40 to 80 miles south of the Biological Station, the first nestings start in the last week of May or in early June (Mayfield, 1960). Few nests are available for cowbirds before June.

Cowbirds in northern Michigan therefore lay their first eggs of the season at the time when the first nests of their hosts become available. Although study began there on June 20, it was possible to determine the relative numbers of eggs laid during each of the earliest weeks of the breeding season. Counts were made of juveniles feeding independently in pastures throughout the summer. (Independent young were not seen in other habitats.) The first juvenile was seen on July 11 feeding alone; several ventral feathers of the bird were still ensheathed. Censuses made on at least two days per week were continued through August 18. Numbers of independent young cowbirds increased gradually to August 1, when about 400 juveniles fed in a pasture near Brutus. The numbers of juveniles are recorded in figure 1.

The date of the first appearance of juveniles provides information about the time that the breeding season of cowbirds began. The incubation of cowbird eggs requires about 12 days (Nice, 1953; Southern, 1958). From one to four days pass between the laying of the cowbird egg to the start of incubation of the host. Development of the young from hatching to independent feeding requires about 30 days. Nice (1943) hand-reared a young cowbird to the age of 25 days and found the rate of development of behavior to be similar to that of a hand-reared Redwinged Blackbird (*Agelaius phoeniceus*) that fed well by itself at the age of 30 days. Mayfield (1960) observed one young cowbird 29 days old being fed by an adult Kirtland Warbler. In figure 1 are plotted the probable laying dates of the eggs that developed into the juveniles counted in the pasture. These dates were calculated by predating the census data by the 45 days required for development. The earliest successful eggs

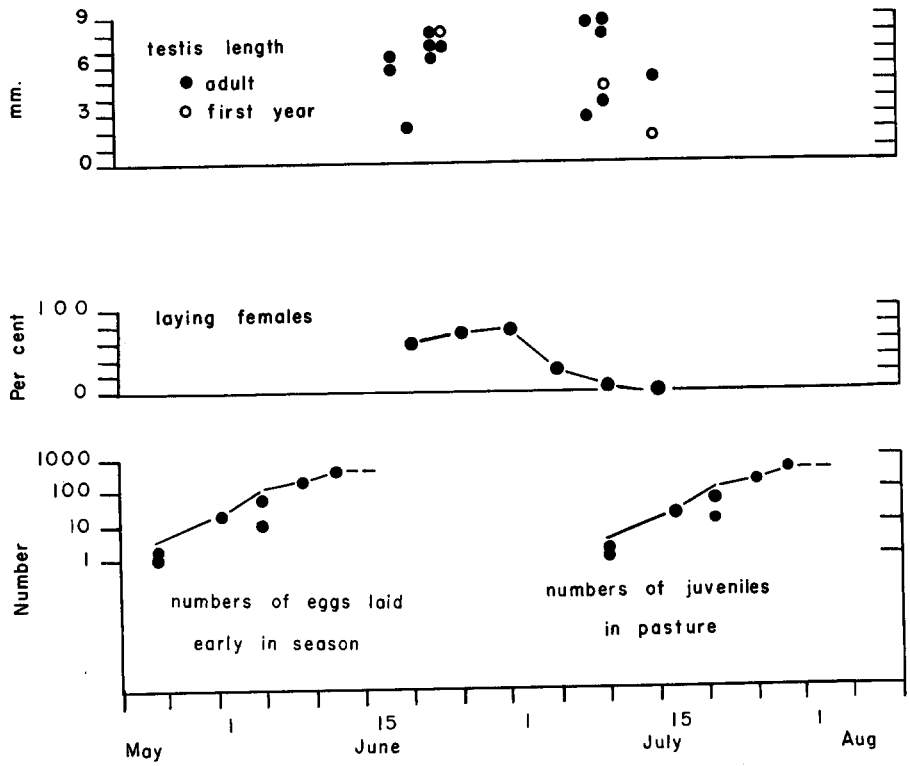

Fig. 1. Breeding season of Brown-headed Cowbirds in northern lower Michigan in 1963, as shown by testis size, per cent of females laying, and production of eggs and young.

of cowbirds were laid in the last week of May, but about 100 times that many eggs were laid in the second week of June.

The period in which many cowbird eggs were laid extended from about June 10 to about July 5. The proportion of laying females collected is recorded in figure 1. More than half of all females (19 of 29) collected from June 20 through July 5 had an egg in the oviduct. Less than half (2 of 6) were laying between July 6 and July 10. By July 15 egg laying had ceased (0 of 11 on July 15 were laying). Few suitable hosts breed later than the middle of July in northern Michigan (Nelson, 1956). The breeding season in southern Michigan also ends in July; a few cowbird eggs have been found in late July (Wood, 1951; Berger, 1951).

Males remained in breeding condition in northern Michigan through the first week of July. Testis length of all adult and first-year males is plotted in figure 1. First-year males were aged by the presence of retained, gray juvenal under-wing coverts in an otherwise adult plumage (Baird, 1958). Testis regression occurred early in some adults. On June 21 an adult male was collected with laying and inactive females; its testis was small, 2.0 mm. long, and gray. On July 11 about half of the males collected had regressed testes. Testis size of first-year males overlapped that of adults both in June and in July. The gonads of male and female juvenal cowbirds that were collected remained small throughout the summer.

Behavioral observations also showed a decrease in breeding in the middle of July.

Up to July 14, males were heard singing before 7 a.m. each day at the Biological Station, but no songs were heard there on July 15 or later. A flock of 40 cowbirds, mostly adults, was seen along the east shore of Burt Lake on July 19. Further observations two or more times each week turned up no more adults until August 3, when an adult male was heard singing once in a tree in an aspen savannah. Observations through August 18 indicated that the adult cowbirds had migrated from the breeding grounds. Sixteen adults taken in July had not started the postnuptial molt on the breeding grounds. Large flocks of juveniles remained through August 18. No postjuvenal molt occurred in any of the 64 juveniles taken in July and August.

The end of the breeding season was associated not only with the end of the breeding seasons of cowbird hosts but also with a change in diet of the cowbirds. Stomach analyses showed that the food of cowbirds collected in pastures consisted mainly of grasshoppers, leafhoppers, beetles, caterpillars, and small seeds. The relative amount of insect food found in the stomachs of both juveniles and adults dropped from 59 per cent volume (26 birds) before July 15 to 38 per cent (53 birds, all juveniles) after July 16.

FLOCKS AND TERRITORIES

Cowbirds in northern Michigan flocked throughout the summer. As early as June 23 a flock of about 100 adult cowbirds was seen feeding in a mowed alfalfa field. Five of seven females shot from this flock each had an egg in the oviduct and were breeding birds. Males in the flock likewise were in breeding condition, as four of five males taken had firm, white testes longer than 7.0 mm. Throughout the breeding season females with eggs in the oviduct and males with large testes were collected not only alone but also in flocks of from four to 200 adults. Laying females were also taken in flocks 20 minutes after sunset from communal roosts in trees at the edge of woods. The statements of Friedmann (1929) and of Scott (1963) that the flocks of cowbirds seen during and after the breeding season are composed of nonbreeding birds were not based on collections. Clearly, Brown-headed Cowbirds in breeding condition occurred in flocks during the breeding season.

The occurrence of many breeding cowbirds in flocks raises a question about the territorial behavior of the Brown-headed Cowbird. No significant turnover of the birds was apparent in flocks watched for several hours. Apparently many individual cowbirds spend most of their daylight hours in flocks feeding in alfalfa fields and in pastures; they were not defending territories and excluding other breeding cowbirds from available host nests. Songs of dispersed males and chatters of dispersed females were heard mainly in the early morning around the Biological Station. Females perched high in maples, about 200 feet apart, and chattered alternately with each other on several mornings. The songs of dispersed males and the chatter of dispersed females may be territorial advertisements. In fact, the chatter of female cowbirds sounds similar to the chatters of some other female icterids such as those of Red-winged Blackbirds and Tricolored Blackbirds (*Agelaius tricolor*) which are given in situations where the females defend their nests, and they may be homologous in territorial advertisement or defense.

Cowbirds lay in each other's areas and even in the same nests. Dump nests, containing the eggs of several individual cowbirds, have been reported by Bent (1958), Byers (1950), Millikan (*in* Friedmann, 1963), Roberts (1936), and Southern (1958). One nest of a Red-eyed Vireo at the Biological Station in 1963 con-

tained six cowbird eggs on July 6. The six eggs apparently came from four different females, as they were of four distinct colors, pigmentation patterns, and sizes.

Color-banded cowbirds remain on the same areas throughout much of the breeding season, according to Nice (1937) and Laskey (1950). The banded cowbirds watched by Nice were active on areas of 18 to 20 acres. The average numbers of breeding pairs of hosts (sparrows, warblers, vireos, and cup-nesting flycatchers) in northern Michigan range from 6 to 25 per 20 acres in aspen and maple habitats (Kendeigh, 1948). However, not all these pairs provide nests at the right time for successful parasitism by cowbirds. In rainy weeks few birds lay, and in sunny weeks overlap in breeding schedules of hosts occurs. Also, some breeding "pairs" may not represent nests at all, as the figures on density were determined from counts of singing males. Perhaps at some times during the breeding season suitable nests are not available to cowbirds on their areas.

Brown-headed Cowbirds have been considered to be territorial by Friedmann (1929) and by Laskey (1950). Friedmann found pairs remaining in areas during the breeding season and reasoned that they might defend these areas against other cowbirds. The spacing of singing males is reminiscent of territorial songbirds. The color-banded cowbirds watched by Laskey showed dominance over other cowbirds at a feeder, but they tolerated other cowbirds in their domain. The cowbirds in northern Michigan similarly do not maintain exclusive territories. The absence of singing males dispersed over woodlots throughout the day in the middle of the breeding season, the occurrence of eggs laid by more than one female in a host nest, the occurrence of breeding adults in large flocks, and the communal roosting habit of breeding birds all suggest that cowbirds do not exclude other cowbirds from the resource in short supply—the available nests in which to lay.

FOLLICLE GROWTH

Brown-headed Cowbirds were dissected in the field, usually within a few minutes after they were collected. Ovaries were removed and fixed in Bouin's and later stored in 70 per cent ethanol. Diameters of growing follicles and lengths of post-ovulatory follicles were measured with dial calipers. Ovaries were then embedded in paraffin, serially sectioned at 8 to 10 microns, and stained in Delafield's hematoxylin and eosin Y.

During the breeding season the ovaries of cowbirds each contain about 20 follicles ranging between 1.5 and 2.5 mm. in diameter. From one to four larger follicles also occur in laying cowbirds (birds with an egg in the oviduct). The large follicles show a gradation in size, and the rate of growth in the days before ovulation is indicated by the differences in size. Sizes of the four largest follicles in each of the ovaries of 10 laying cowbirds with a size gradation are given in table 1. These data show that the follicles four days before ovulation average 3.0 mm. Yolk is deposited at an increasing rate in the next three days, and the final deposits are made during the 18 hours before ovulation. Mature yolks that had ovulated and passed down the oviduct ranged from 10.5 mm. to 12.5 mm. Histological examination of these four largest follicles of each ovary showed that all were healthy and growing. The series of four growing follicles in the three birds which had ovulated four eggs in the current clutch suggests that some cowbirds may sometimes lay as many as eight eggs in a clutch.

The ovaries of the 12 other laying cowbirds did not show this progression in the size of the largest follicles. Some laying cowbirds had no follicles larger than 8 mm. and these birds had evidently completed the current clutch. One of these had ovu-

TABLE 1

FOLLICLE GROWTH OF LAYING COWBIRDS

Catalog number	Number of eggs ovulated	Follicle size (mm.) Largest (a) follicle	(b) follicle	(c) follicle	(d) follicle
2115	2	8.6	6.7	3.6	2.6
2102	2	8.5	6.8	3.7	2.9
2121	2	8.2	6.0	3.1	2.3
2138	2	9.7	7.0	4.4	2.7
2140	2	8.9	7.4	5.0	2.8
2147	2	9.6	7.8	6.7	4.3
2166	3	9.2	6.9	4.0	2.9
2106	4	8.4	6.0	4.1	2.8
2120	4	9.2	6.8	4.6	3.2
2124	4	9.9	8.2	6.1	3.5
Mean		9.02	6.94	4.53	3.00

lated only one egg, and the largest remaining follicle was 6.8 mm. Six cowbirds that had each ovulated two eggs had largest follicles of 2.6, 2.9, 3.0, 3.6, 4.6, and 7.7 mm. Another cowbird that had ovulated two eggs had another growing follicle 10.3 mm., but the next largest follicle was only 3.6 mm. In four birds that had ovulated three eggs each the largest remaining follicles measured 7.2, 6.6, 5.2, and 3.2 mm. The largest follicles in some of these 13 laying birds were degenerating, and in others the largest follicles were still growing. The growing follicles might start off a new clutch in four days or less and thus make possible a decrease in time between clutches. On the other hand, the degenerating follicles represent energy lost when opportunities for laying in anticipated suitable nests are not realized.

Old clutches of 1 and 2 post-ovulatory follicles as well as current small clutches were often ended by burst atretic follicles. Apparently after ovulation of the first egg, environmental conditions were poor for the probable success of subsequent eggs, and the energy stored in the yolk was reabsorbed by the female by bursting of the large follicle and phagocytosis in the lymph spaces of the ovary. Burst atretic follicles also terminated some large clutches. At the end of the breeding season in July, several cowbirds had mass bursting of many follicles. Fibroblastic atresia and oocytic amitoses also occurred in cowbird ovaries.

NUMBER OF EGGS LAID IN A DAY

It has been suggested that cowbirds sometimes lay two eggs in a single day (Southern, 1958). The evidence for this was the appearance of two eggs in a day in single host nests. Probably the eggs were laid by different cowbirds.

The rate of oviposition in Brown-headed Cowbirds is limited to one egg per day. Laying cowbirds collected before 9 a.m. each had one egg about halfway down the oviduct, and no shell had yet formed. Laying occurs early in the morning, before sunrise (Hann, 1941), and ovulation evidently follows within a few hours. Laying cowbirds taken by 1 p.m. had single ova in the shell gland, albumen around the yolk, and a thin, soft shell around the albumen. Birds taken after 7 p.m. had unspotted, leathery shells around the eggs. No birds were collected with more than one egg in the oviduct. Dissections showed that cowbirds are like other songbirds in having a

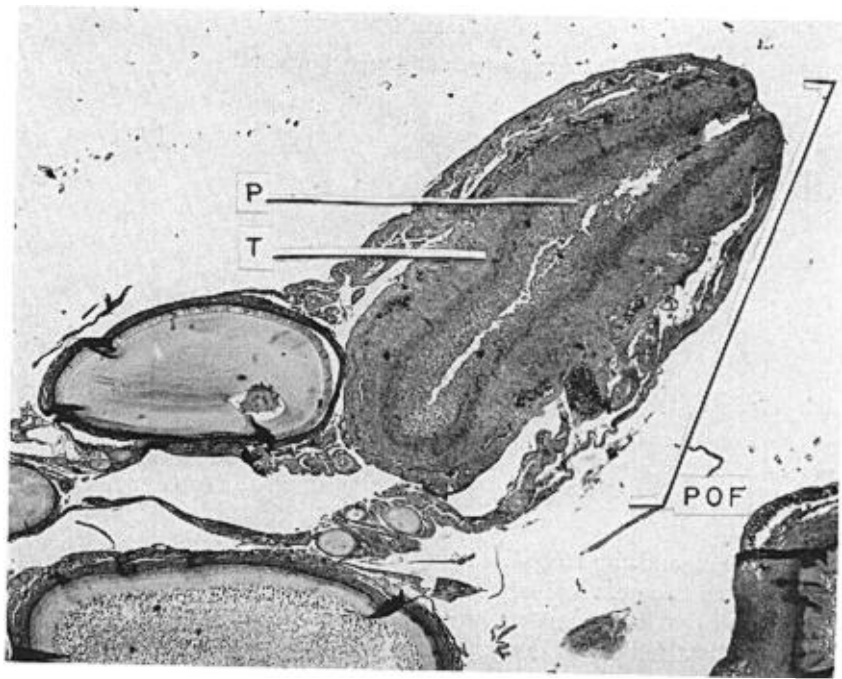

Fig. 2. Post-ovulatory follicle (POF) of Brown-headed Cowbird; ×40. Note absence of yolk, presence of phagocytes (P) in lumen, and dense layers of theca (T). About five days earlier the egg was ovulated through opening at upper right.

single, left ovary, a single oviduct, and no accessory pouches for holding extra eggs. Cowbirds then normally lay only a single egg in one day.

NUMBERS OF EGGS LAID BY COWBIRDS

Numbers of eggs which Brown-headed Cowbirds laid were determined by examining the ovaries of 74 adult females collected during the breeding season. Serial sections were made of 52 ovaries from cowbirds collected during and at the end of their breeding season in northern Michigan in 1963. In addition, serial sections were made of 14 ovaries from southern Michigan in 1960 and 1963 and of eight ovaries from northern Michigan in 1960. About 70,000 sections were made and examined.

The numbers of eggs which cowbirds had ovulated up to the day of collection were determined by counting the post-ovulatory follicles in the ovaries. The histology of this structure has been described by Davis (1942*a*) for other species of songbirds. The post-ovulatory follicles of Brown-headed Cowbirds are similar in appearance to those of the birds described by Davis. These follicles, from which mature primary oocytes had been ovulated, were characterized by an elongate shape, a lumen filled with granulosa cells and phagocytes, and a thickened, eosinophilic theca interna and externa. The outer layers became basophilic about two weeks after ovulation. The end of the follicle from which the oocyte had been ovulated remained open but occluded by a plug of phagocytes. A post-ovulatory follicle from a Brown-headed Cowbird is pictured in figure 2.

Serial sections were required in order to locate small post-ovulatory follicles which

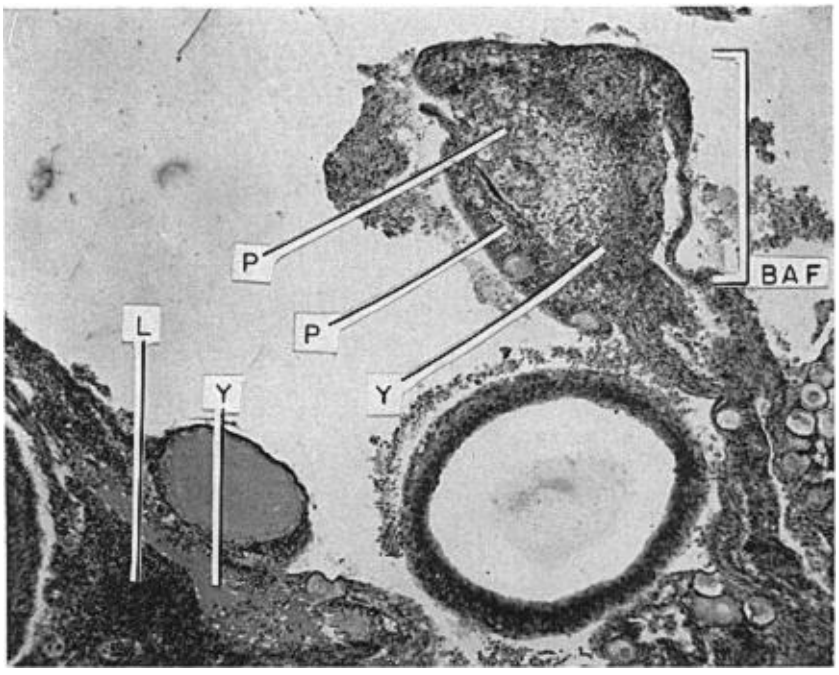

Fig. 3. Burst atretic follicle (BAF) after regression; ×107. Note yolk (Y) in lumen and neighboring connective tissue and also yolk from a larger burst atretic follicle below. Phagocytes (P) lie in lumen and between layers of thecae. Lymphocyte infiltration (L) present in neighboring burst follicles.

had regressed beyond recognition in whole ovaries. Serial sections were also required in order to distinguish between regressed post-ovulatory follicles and burst atretic follicles. Large ova (2–6 mm.) which were not ovulated often burst through the thecae. Yolk was extruded into the connective tissue of the ovary, into its lymph spaces, and sometimes through the ovarian epithelium onto the surface of the ovary. The remaining burst atretic follicles after regression were characterized by the presence of some reabsorbed yolk in the lumen of the follicle, the presence of yolk and/or masses of phagocytes between the layers of connective tissue surrounding the follicle, and the more spherical form. A regressed burst atretic follicle which shows yolk in the lumen and yolk and phagocytes in the connective tissue as well as the remains of an opening to the coelom out of which some yolk was forced is pictured in figure 3.

Comparative material was examined to age the post-ovulatory follicles and the growing oocytes of cowbird ovaries. A series of 38 adult female Tricolored Blackbirds was taken, each of which was laying eggs, incubating eggs with aged embryos, or feeding aged nestlings or fledglings. Post-ovulatory follicles were macroscopically recognizable only for 12 days after ovulation. Serial sections of some of these ovaries showed recognizable post-ovulatory follicles up to 25 days after ovulation. Follicles could be aged by size, thickness of thecal layers, and staining reactions to within about four days throughout this period. Histological details will be presented elsewhere.

Numbers of eggs laid by Brown-headed Cowbirds are recorded in figure 4.

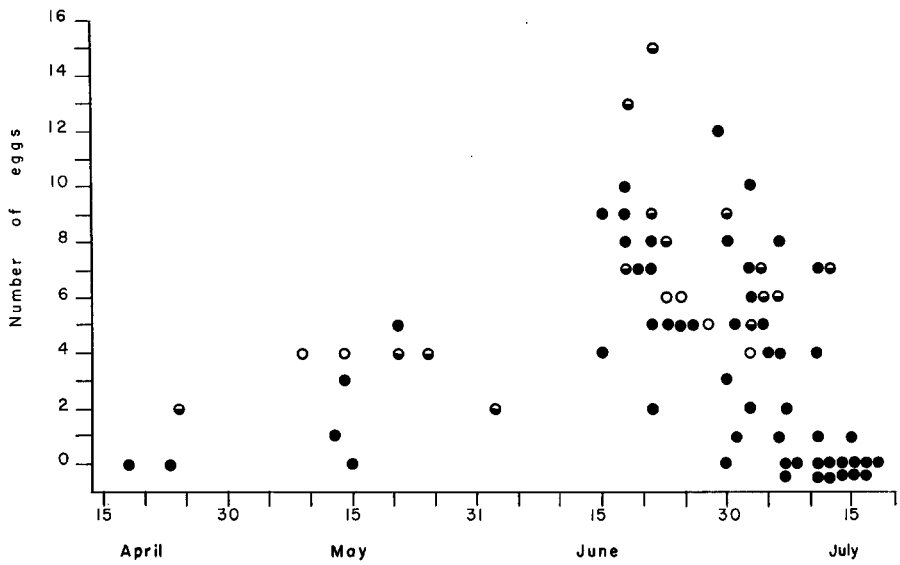

Fig. 4. Numbers of eggs laid by Brown-headed Cowbirds in Michigan in 1960 and 1963. Solid dots indicate total numbers of eggs laid as indicated by counts of post-ovulatory follicles. Half-open circles indicate total post-ovulatory follicles plus one growing follicle larger than 7.0 mm., and open circles indicate total post-ovulatory follicles plus two growing follicles larger than 7.0 mm.

Females all had similar plumage and could not be divided into first-year and older birds. No females collected early in spring showed remains of post-ovulatory follicles from previous years. The 33 females collected during the main part of the breeding season in northern Michigan in both years (June 15 through July 4) had laid, by the date of collection, an average of 6.0 eggs. However, since the median bird of this group was collected on June 29, eggs laid during the first week of June left no trace of a post-ovulatory follicle, and eggs that might have been laid in early July were not accounted for. The breeding season extended over a six-week period, but the technique of examining serial sections showed post-ovulatory follicles over a 25-day period. The mean number of eggs laid by cowbirds over the entire breeding season would be about double that number indicated by the post-ovulatory follicles after the midpoint of the breeding season. I estimate that the average number of eggs laid by female cowbirds in northern Michigan is 10 to 12 eggs.

Different females showed much variation in the numbers of eggs laid. Some birds collected late in the breeding season showed no evidence of having laid eggs that season. Other birds had laid, or would have laid by the next two days, as many as 15 eggs, and these fecund females may have laid more eggs later in the season. Evidently the first-year females as well as older females breed, as post-ovulatory follicles occurred in almost all females.

Several estimates based on indirect observations of the numbers of eggs laid by individual Brown-headed Cowbirds have been made. Walkinshaw (1949) carefully searched for nests in one study area in southern Michigan and found that 25 cowbird eggs had been laid on different days. He believed that a single female laid all these eggs, as the eggs were similar in size and in coloration. McGeen and McGeen (1962)

TABLE 2

NUMBERS OF EGGS LAID BY BROOD PARASITES

Species	Numbers of eggs	Reference
Molothrus badius	6	Davis, 1942
	5	Friedmann, 1929
	1–5, mode 4	Hoy and Ottow, 1964
Molothrus rufo-axillaris	6	Davis, 1942
	5?	Friedmann, 1929
Molothrus bonariensis	6–10?	Friedmann, 1929
	60–100?	Hudson (*in* Friedmann, 1929)
	1,2,3,3,4,4,4,5,7,7,7	Davis, 1942
	3,4,5	Miller, 1947, 1963
Molothrus ater	4,4,5; 3,3,4	Friedmann, 1929
	8?	Hann, 1937
	16?	Hicks (*in* Hann, 1937)
	8	Jones (*in* Friedmann, 1963)
	12–15?	Nice, 1937
	18,19,25	McGeen and McGeen, 1962
	0–15 plus, mean 10–12	Payne, present paper
	13	Rand (*in* Friedmann, 1929)
	25	Walkinshaw, 1949
Cuculus canorus	1–18 (lower range was not quantified)	Baker, 1942
	1–25, mean 11	Chance, 1940
	4,6,6,6,7	Diesselhorst, 1955
	1,1,1,2,3	Groebbels, 1957
	4–6 most, to 10	Harbø (*in* Makatsch, 1955)
	8,15,19	Kruger-Velthusen (*in* Makatsch, 1955)
	1,1,1,1,1,2,2,3,3,5,6	Labitte, 1948, 1954, 1958
	5	Owen, 1921
	5,6,6,8	Paulussen, 1957
	1–29, mean 4	Rey, 1892
	9,10,10	Moebert (*in* Groebbels, 1957)
	7,9	Ruthke (*in* Groebbels, 1957)
	4–8	Schiermann (*in* Groebbels, 1957)
	7,8,19	Scholey, 1921
	1–3 most, to 6	Warncke and Wittenberg, 1958

made a similar study and found 56 cowbird eggs which they attributed to five female cowbirds. One of these cowbirds laid 25 eggs in one season, they thought, as 25 eggs of similar color were found. These high estimates for some individual birds correspond well with results of the present study if variations of the breeding seasons and of different individuals are considered. Three of 33 females in northern Michigan laid 10 eggs or more by the date of collection and may have laid twice that number by the end of the season. However, such a high number is apparently not typical. It might also be noted that the breeding season is a month longer in southern Michigan than in northern Michigan (Wood, 1951; Berger, 1951; Mayfield, 1960; the present study). Cowbirds may lay more eggs in areas with longer breeding seasons of their hosts.

Evidence based on more casual observations of field ornithologists in various areas all indicate that cowbirds lay from 8 to 15 eggs in a breeding season (Hann, 1937; Nice, 1937; Norris, 1947). Friedmann (1929) found that six cowbirds each laid from three to five eggs in a season, but he found no evidence of breeding in June. Probably in most years cowbirds in New York, where his study was made, continue laying through June. Estimates of numbers of eggs laid by Brown-headed Cowbirds and other brood parasites are summarized in table 2.

CLUTCH SIZE

Cowbirds lay eggs on consecutive days and have periods of no laying between these volleys of laying, according to the histological material examined in this study. The series of eggs laid on consecutive days is termed a clutch and is considered to be

TABLE 3

CLUTCH SIZE OF BROWN-HEADED COWBIRDS

Date of ovulation of first egg	Clutch size* 1	2	3	4	5	6	Mean
NORTHERN MICHIGAN							
May 26–31			1				3.0
June 1– 5	1	3		3			2.7
6–10	1	1	2	2	3		3.6
11–15	1	1	2	1	1	1	3.4
16–20	2	2	2	3	1(3)	(1)	2.9(3.5)
21–25	2	1	2(3)	2			2.6(2.6)
26–30	1	1	3(4)				2.2(2.5)
July 1– 5	2	3	(1)	(4)	1		2.4(2.9)
6–10	1				(1)		1.0(3.0)
Total	11	12	12(15)	11(15)	6(9)	1(2)	2.9(3.1)
SOUTHERN MICHIGAN							
May–June	2		3	3	3(4)	1	3.7(3.8)

* Figures in parentheses are based on the number of post-ovulatory follicles plus the number of growing oocytes larger than 7.0 mm.

homologous with the series of eggs laid in a single nest on consecutive days by songbirds which raise their own young. Comparison with records from Tricolored Blackbirds permitted dating of the clutches laid by the cowbirds. Table 3 records the clutch sizes found by examining the ovaries of cowbirds from northern Michigan in 1963. Clutch size ranged widely from one to six. Individual females laid from one to four clutches (table 4). An analysis of Walkinshaw's (1949) data for one cowbird likewise indicated the laying of eggs in clutches (Nice, 1949).

TABLE 4

NUMBERS OF CLUTCHES LAID IN PREVIOUS 25 DAYS, NORTHERN MICHIGAN, 1963

Date collected	Numbers of clutches 0	1	2	3	4
June 21–25		3	8		1
26–30	1		3	8	
July 1– 5		2	6	1	
6–10	3	1	1	1	
11–15	13	3	2		

The average clutch size of Brown-headed Cowbirds in northern Michigan was 3.1. This average is based on 63 clutches from 52 ovaries. The average clutch size of 13 clutches from southern Michigan was slightly larger (3.8), but this difference was not statistically significant. Clutch size decreased in the last half of the breeding season in northern Michigan. Excluding the first two weeks of the breeding season, when few eggs were laid, the mean clutch size of the early clutches was significantly greater than the mean clutch size of the late clutches. The probability that mean clutch size from June 6 to June 20 was equal to mean clutch size from June 21 to July 10 (3.48 vs. 2.74) was less than 0.05 (t test).

Laying in clutches rather than in long series or other patterns in time in this brood parasite may be accounted for by one of several possible factors. First, physiological output of many eggs in quick succession may be limited by food availability and by the ability of cowbirds to convert food into eggs. Second, laying on successive days alternating with nonlaying intervals may be a hereditary tradition retained from ancestral icterids which reared their own limited number of young. Selection for retention of a clutch size of a limited number of eggs may have been the result of limited numbers of available nests in an area large enough to be scouted by a laying female.

The high degree of variance in clutch size and in numbers of eggs laid in a season suggests that the egg-laying response of cowbirds to their environment is plastic. Probably birds that laid few eggs and few clutches were birds that found only a small number of nests available for parasitism. Selection in these brood parasites may favor an ability to regulate the numbers of eggs laid in response to environmental conditions rather than a fixation of limited clutch size. A similar regulating mechanism has been reported to occur in Great Tits, *Parus major* (Kluyver, 1963).

Clutch size is to some extent positively correlated with the density of nesting hosts. Average clutch size in southern Michigan was slightly higher than in northern Michigan (table 3). This trend parallels the higher density of breeding birds in southern Michigan (Batts, 1961) and in deciduous forest biomes in general (Kendeigh, 1946), contrasted with the situation in northern Michigan near the Biological Station (Kendeigh, 1948). On the other hand, many species of songbirds which raise their own young have larger clutches at higher latitudes. This trend is associated with the longer summer photoperiod and period of daylight during which birds can feed their young in the north (Lack, 1954).

DISCUSSION

The term "brood parasitism" is used to describe the laying of eggs by a species into the nests of other species and the subsequent feeding of the young guests by the adult hosts. The classical interpretation of the high reproductive rates of many parasitic invertebrates is that it results from selection evoked by the high mortality of early stages of the life cycles. It has been reasoned, therefore, that birds which share the label "parasite" have similar high rates, and that these high reproductive rates are caused by high mortality rates. Evidence for Brown-headed Cowbirds indicates that this brood parasite does lay many eggs. However, the evidence that other species of brood parasites lay many eggs is contradictory, and the reasoning that high mortality rates are evolutionary causes of high reproductive rates requires much qualification.

Although the reproductive output of other species of cowbirds has not been studied over the entire breeding season, some data are available on clutch size and

on the minimal numbers of eggs laid. The Bay-winged Cowbird (*Molothrus badius*) rears its own young, but it often nests in the old nests of other species rather than building its own. This nest parasite in the highlands of Argentina usually lays clutches of four (Hoy and Ottow, 1964), about the same number as do cowbirds which are brood parasites. Friedmann (1929) reported clutches of five to be more common in other parts of the range of this species. The Shiny Cowbird (*Molothrus bonariensis*) was studied by Davis (1942*b*). Serial sections of ovaries from 11 breeding females showed a small number (less than 10) of eggs laid. However, the breeding season of Shiny Cowbirds in his study area spanned a few months, and the serial sections may not have shown traces of eggs laid early or evidence of eggs to be laid later. Study of the ovaries of this species indicates clutches of from three to five (Davis, 1942*b*; Miller, 1947, 1963). Evidently, no increase in clutch size has accompanied the evolution of other specializations for brood parasitism in the *Molothrus badius-M. rufo-axillaris-M. bonariensis-M. ater* series, which Friedmann (1929) considers to be the phylogenetic sequence of these parasitic cowbirds.

Evidence on numbers of eggs laid in a breeding season by the European Cuckoo (*Cuculus canorus*) does not support the generalization that brood parasites lay many eggs. Studies of numbers of eggs laid by this brood parasite have been based entirely on finding eggs of similar color and size inside an area small enough to accommodate only one cuckoo with eggs of these characteristics and in theory large enough to supply all the nests parasitized by that female. Observations that cuckoos lay, on the average, over 10 eggs has come mainly from observers who removed cuckoo eggs as they were laid or who manipulated nest availability further by using dummy nests (Scholey, 1921; Chance, 1940). These numbers should not be taken as representative of the numbers of eggs laid in natural habitats, where the numbers of eggs may well be determined by the availability of host nests. Demonstration that the density of breeding hosts is a limiting factor in numbers of eggs laid is suggested not only by Chance's observations that cuckoos lay many eggs when many nests are available but also by the observation of Moebert (*in* Makatsch, 1955) that the population density of breeding birds was directly correlated with and probably determined cuckoo density. Most studies on the European continent show that cuckoos generally do not lay over 10 eggs in a breeding season (table 2). The method of study of looking for characteristic eggs may easily miss eggs laid by parasites and ejected by discriminating hosts, may miss nests hidden in vegetation, and may involve many questions about the parentage of apparently similar eggs. Further study of numbers of eggs laid by different species of brood parasites should be made by observing individual birds or by examining the ovaries of breeding birds.

The role of mortality rate as a selective factor in the evolution of reproductive rates in birds may be examined by comparing numbers of eggs laid and the mortality of eggs and young both of brood parasites and of birds which feed their own young. The survival data for eggs and nestlings of Brown-headed Cowbirds have recently been compiled by Young (1963*a*). Analysis of his data and also of the recent data of Wiens (1963) and of Nolan (1963) of a total of 907 cowbird eggs and their fate shows that 22 per cent were successful and produced fledglings. This survival rate is no lower than that of many other songbirds. Nolan (1963) found in Indiana that less than 20 per cent of the eggs of several species of songbirds survived through hatching and fledging. Icterids other than cowbirds also have low egg-to-fledging survival. Young (1963*b*) found that only 23 per cent of 1632 eggs of Redwinged Blackbirds produced fledglings. Although mortality of eggs of cowbirds was higher

than that of eggs of Redwinged Blackbirds, mortality of nestlings was lower. Total cowbird survival in the nest is not lower than that of comparable birds. Furthermore, although the mortality rate in the nest is similar for these two species, the Redwinged Blackbirds in the Great Lakes region lay on the average only four or five eggs in a clutch (Nelson, 1956; Bent, 1958) and are single brooded (Beer and Tibbitts, 1950; Nero, 1956). Brown-headed Cowbirds lay, on the average, two or three times the number of eggs that their relatives do. It must be concluded that the reproductive rates of these female icterids is not correlated with the mortality of the eggs and nestlings.

A mechanism by which mortality rate might regulate reproductive rate through selection of genetic factors controlling the numbers of eggs laid by songbirds in general has yet to be described. While Ashmole (1963) has presented evidence that the breeding rates of many seabirds is determined in part by their great longevity, the mechanism of deferred maturation and the subsequent learning and increased efficiency in pelagic foraging is not present in cowbirds. Apparently both male and female cowbirds breed in their first year. The reduction in time between consecutive clutches and the increased numbers of eggs laid in a breeding season may have been a necessary preadaptation for the evolutionary establishment of cowbirds in the niche of brood parasitism. The mortality rate alone seems not to be a sufficient condition for a change in selective pressure favoring the observed increased numbers of eggs. The correlation which was pointed out by Darwin (1859:63–66) between birth rate and mortality rate was used by him to illustrate the occurrence of a geometric rate of increase of all animals, regardless of the time involved between successive generations. This property of populations was discussed by both Darwin and Malthus, and together with observations that most young of animals that have many young do not themselves reproduce and that hereditary variations between individuals occur, formed the basis for Darwin's deduction of natural selection. However, the correlation between birth rate and mortality rate has been interpreted by some as indicating a direct causal relationship. Allee, Emerson, Park, Park, and Schmidt (1949:272) and Mayr (1963:194) maintain this tradition by holding that high mortality rate is an evolutionary cause of high birth rate. It is probable that genotypes producing the greatest numbers of healthy young have been selected in all species whatever their mortality rates. Both observational and theoretical considerations indicate that the large number of eggs laid by Brown-headed Cowbirds is related to the removal of the upper limit of young to be fed by the parents, rather than to increased mortality of young of cowbirds.

SUMMARY

Brown-headed Cowbirds in northern lower Michigan breed from late May to early July. Throughout the breeding season laying females flocked with other breeding cowbirds. Communal roosting of breeding birds, flocking, and the occurrence of eggs laid by several females in a single host nest indicate that cowbirds do not maintain exclusive territories.

Serial sections of the ovaries of 60 adults were examined for post-ovulatory follicles. Numbers of eggs laid and the timing of laying were determined by comparing the size and histology of cowbird follicles to those of blackbirds of known breeding history. Female cowbirds lay an average of 10 to 12 eggs during the breeding season. Variation between birds is great, as some lay no eggs while others lay at least 15.

Cowbirds lay in clutches of one to six eggs. Mean clutch size is 3.1 eggs. Mean clutch size late in the breeding season is significantly lower than early in the breeding season. Both follicular growth rate and atresia limit clutch size by regulating the numbers of oocytes that mature in the ovary. Variation in clutch size suggests a high degree of environmental control of clutch size.

Most cowbirds lay several clutches in a season. Times between clutches range from a few days to a few weeks.

Mean clutch size has not increased in the evolution of the cowbirds. However, the numbers of clutches and the numbers of eggs laid in a season are greater in Brown-headed Cowbirds than in nonparasitic icterids. The large number of eggs laid by this brood parasite is associated with an evolutionary removal of an upper limit of young to be fed by the parents, rather than with a high mortality of the young.

LITERATURE CITED

Allee, W. C., Emerson, A. E., Park, O., Park, T., and Schmidt, K. P.
1949. Principles of animal ecology (W. B. Saunders Co., Philadelphia).

Ashmole, N. P.
1963. The regulation of numbers of tropical oceanic birds. Ibis, 103b:458–473.

Baird, J.
1958. The postjuvenal molt of the male brown-headed cowbird (*Molothrus ater*). Bird-Banding, 29:224–228.

Baker, E. C. S.
1942. Cuckoo problems (Witherby, London).

Batts, H. L., Jr.
1961. Nesting success of birds on a farm in southern Michigan. Jack-Pine Warbler, 39:72–83.

Beer, J. R., and Tibbitts, D.
1950. Nesting behavior of the red-wing blackbird. Flicker, 22:61–77.

Bent, A. C.
1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U. S. Nat. Mus. Bull. No. 211.

Berger, A. J.
1951. The cowbird and certain host species in Michigan. Wilson Bull., 63:26–34.

Byers, G. W.
1950. A black and white warbler's nest with eight cowbird eggs. Wilson Bull., 62:136–138.

Chance, E. P.
1940. The truth about the cuckoo (Country Life, Ltd., London).

Darwin, C.
1859. On the origin of species. A facsimile of the first edition (1964, Harvard).

Davis, D. E.
1942*a*. The regression of the avian post-ovulatory follicle. Anat. Rec., 82:297–307.
1942*b*. The number of eggs laid by cowbirds. Condor, 44:10–12.

Diesselhorst, G.
1955. Eizahl des Kuckucks. Vogelwelt, 76:53–58.

Friedmann, H.
1929. The cowbirds: a study in the biology of social parasitism (Charles C. Thomas, Springfield, Ill.).
1963. Host relations of the parasitic cowbirds. U. S. Nat. Mus. Bull. No. 223.

Groebbels, F.
1957. Rufe, Revier, und Eizahl beim Kuckuck. Vogelwelt, 78:89–94.

Hann, H. W.
1937. Life history of the oven-bird in southern Michigan. Wilson Bull., 49:145–237.
1941. The cowbird at the nest. Wilson Bull., 53:211–221.

Hoy, G., and Ottow, J.
1964. Biological and oological studies of the molothrine cowbirds (Icteridae) of Argentina. Auk, 81:186–203.
Kendeigh, S. C.
1946. Breeding birds of the beech-maple-hemlock community. Ecology, 27:226–245.
1948. Bird populations and biotic communities in northern lower Michigan. Ecology, 29: 101–114.
Kluyver, H. N.
1963. The determination of reproductive rates in Paridae. Proc. 13th Int. Ornith. Congr. (Ithaca), 2:706–716.
Labitte, A.
1948. Quelques notes sur le coucou *Cuculus canorus* L. en pays drouais. Oiseau, 18:78–93.
1954. Questions posées au sujet de la réproduction de *Cuculus canorus* L. Oiseau, 24:267–278.
1958. Observations sur le coucou. Oiseau, 28:153–163.
Lack, D.
1954. The natural regulation of animal numbers (Clarendon Press, Oxford).
Lack, D., Gibb, J., and Owen, D. F.
1957. Survival in relation to brood-size in tits. Proc. Zool. Soc. London, 128:313–326.
Laskey, A. R.
1950. Cowbird behavior. Wilson Bull., 62:157–174.
MacQueen, P. M.
1950. Territory and song in the least flycatcher. Wilson Bull., 62:194–205.
Makatsch, W.
1955. Der Brutparasitismus in der Vogelwelt (Neumann Verlag, Radebeul).
Mayfield, H.
1960. The Kirtland's warbler (Cranbrook Inst. Sci., Bloomfield Hills).
Mayr, E.
1963. Animal species and evolution (Harvard Univ. Press, Cambridge).
McGeen, D. S., and McGeen, J.
1962. Cowbird field studies in Michigan. Abstr. 13th Int. Ornith. Congr. (Ithaca), p. 45.
Miller, A. H.
1947. The tropical avifauna of the upper Magdalena Valley, Colombia. Auk, 64:351–381.
1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. Univ. Calif. Publ. Zool., 66:1–78.
Nelson, T.
1956. The history of ornithology at the University of Michigan Biological Station (Burgess, Minneapolis).
Nero, R. W.
1956. A behavior study of the red-winged blackbird. II. Territoriality. Wilson Bull., 68: 129–150.
Nice, M. M.
1937. Studies in the life history of the song sparrow. I. A population study of the song sparrow. Trans. Linn. Soc. N. Y., 4:vi + 1–239.
1943. Studies in the life history of the song sparrow. II. The behavior of the song sparrow and other passerines. Trans. Linn. Soc. N. Y., 6:viii + 1–328.
1949. The laying rhythm of cowbirds. Wilson Bull., 61:231–234.
1953. The question of ten-day incubation periods. Wilson Bull., 65:81–93.
Nolan, V., Jr.
1963. Reproductive success of birds in a deciduous scrub habitat. Ecology, 44:305–313.
Norris, R. T.
1947. The cowbirds of Preston Firth. Wilson Bull., 59:83–103.
Paulussen, W.
1957. Nieuwe gegevens over de eieren, de waarden en de biologie van de koekoek, *Cuculus canorus* L. Gerfaut, 47:241–258 (summary in French).

Perrins, C.
1963. Survival in the great tit, *Parus major*. Proc. 13th Int. Ornith. Congr. (Ithaca), 2: 717–728.
1964. Survival of young swifts in relation to brood-size. Nature, 201:1147–1149.
Rey, E.
1892. Altes und Neues aus dem Haushalte des Kuckucks (R. Freese, Leipzig).
Roberts, T. S.
1932. The birds of Minnesota. Vol. II (Univ. Minnesota, Minneapolis).
Scholey, G. J.
1921. Another cuckoo record. Brit. Birds, 15:180–186.
Scott, D. M.
1963. Changes in the reproductive activity of the brown-headed cowbird within the breeding season. Wilson Bull., 75:123–129.
Southern, W. E.
1958. Nesting of the red-eyed vireo in the Douglas Lake region, Michigan. Jack-Pine Warbler, 36:105–130, 185–207.
Walkinshaw, L. H.
1949. Twenty-five eggs apparently laid by a cowbird. Wilson Bull., 61:82–85.
Warncke, K., and Wittenberg, J.
1958. Eizahl des Kuckucks. Vogelwelt, 79:20–22.
Wiens, J. A.
1963. Aspects of cowbird parasitism in southern Oklahoma. Wilson Bull., 75:130–139.
Wood, N. A.
1951. The birds of Michigan. Misc. Publ. Mus. Zool. Univ. Michigan No. 75:1–559.
Young, H.
1963*a*. Breeding success of the cowbird. Wilson Bull., 75:115–122.
1963*b*. Age-specific mortality in the eggs and nestlings of blackbirds. Auk, 80:145–155.

University of Michigan Biological Station, Pellston, Michigan, and *Museum of Vertebrate Zoology, Berkeley, California, May 18, 1964.*