THE CLUTCH SIZE AND NUMBERS OF EGGS OF BROWN-HEADED COWBIRDS: EFFECTS OF LATITUDE AND BREEDING SEASON

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Geographic variation in reproduction in certain bird species has been explained in several ways. The larger clutch size at higher latitudes in several species of passerines in the northern regions of the Old World and New World (Lack 1947–48, 1968, Klomp 1970, Hussell 1972) has sometimes been accounted for by the extra hours of daylight for feeding activity by the parents at the higher latitudes (Lack 1947–48) and by the extra hazards faced by adult birds in more northern populations or by higher mortality of eggs and nestlings in the tropics (Skutch 1967). The short breeding season available to birds of the higher latitudes also may help explain the large clutch size of birds in those areas. With time for rearing no more than one brood, one adult may be likely to leave more offspring than another if it lays a large clutch. In more tropical areas the long nesting season, with repeated opportunities for rearing young e.g., Willis 1974) may provide an ecological setting where the long-term breeding success of a pair of birds is higher if little parental investment goes into a single nesting effort (Williams 1966).

The numbers of eggs laid in a season and the number in each set or clutch within a season may vary in parasitic birds as well as in birds that rear their own young. Such variation may help provide a general explanation for the trends in the nesting passerines. Parasitic birds such as the cowbirds provide a natural experiment to test the generality of some of the explanations of variation in clutch size, particularly those explanations that are based on the concept that family size in birds has a selective history shaped mainly by the amount of food the parents can provide to their young. The brood parasites lay eggs in the nests of other species that rear their young. As they do not feed their own young, they may be expected to lay more eggs than their nesting relatives, and so to show a different pattern of geographic variation in breeding effort.

To test the effectiveness of these general explanations in forecasting the reproductive variation of a parasitic bird, I sampled populations of Brown-headed Cowbirds (*Molothrus ater*) in Oklahoma, California, and Michigan. These areas differ in (a) latitude, (b) length of the breeding season, and (c) number of years the population has existed. The predictions were as follows: (1) if clutch is limited in birds by the amount of food the parents can find for their brood, then the northern (Michigan) cowbirds should not have larger clutches than cowbirds in Oklahoma or California. (2) If clutch size is smaller than the number of young that parents usually can feed because long-term seasonal reproductive success is adversely affected by a big early reproductive effort (Williams 1966), then the northern (Michigan) cowbirds should have larger clutches because they have a shorter breeding season, and hence should be less restrained in their initial reproductive effort. (3) If recent population histories of different growth patterns or size are associated with evolutionary or phenotypic changes in reproductive effort (i.e., if recently expanded or dispersed populations are *r*-selected in the terminology of MacArthur and Wilson 1967), and if any changes in reproductive effort show up within a few decades, then cowbirds that have invaded an area most recently should lay more eggs. The prediction here is that the largest clutches or egg numbers will be in California and the smallest in Oklahoma because cowbirds have been present in large numbers longer in Oklahoma. As nothing has been reported on differences in dispersal of birds in the three areas, it cannot be predicted that the most dispersive population will have the largest clutch size, and, though dispersal was examined in the work, data were found for only one of the three areas. The predictions are not all mutually exclusive nor do they include all possible results nor all possible explanations of why birds lay the number of eggs they do.

METHODS

Brown-headed Cowbirds were collected during the breeding season and dissected within a few minutes; their gonads were preserved in 10% neutral buffered formalin. The ovaries later were examined under a dissecting microscope. The number of eggs and timing of laying (in days before collection) within the preceding 10 days was determined by counting and measuring the post-ovulatory follicles visible in the gross dissected ovary (fig. 1). In icter-

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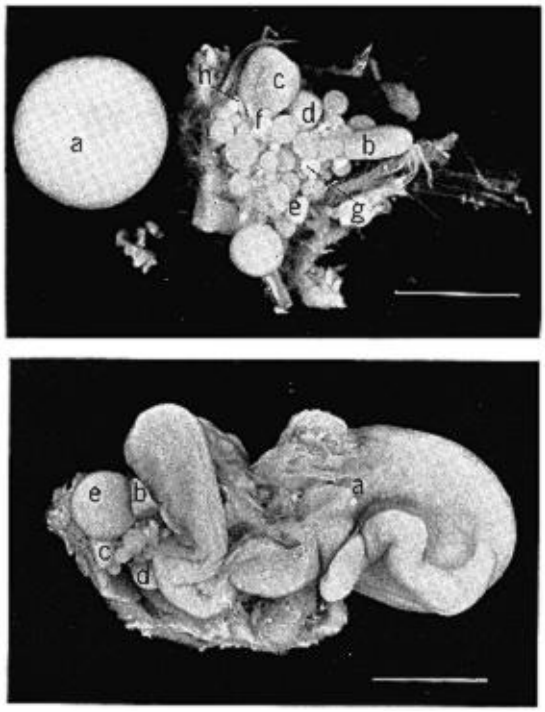

FIGURE 1. Ovaries of Brown-headed Cowbirds from Marshall County, Oklahoma. Above: bird taken 27 June 1968. Note one old completed clutch indicated by a set of 4 small, old post-ovulatory follicles (e, f, g, h), and another clutch of 4 indicated by three large postovulatory follicles (b, c, d, with the largest one corresponding to an egg in the oviduct), and one large, yolked follicle "a" that would have ovulated the following day. The ovary has no other large yolky follicles, so the clutch will be complete when the fourth egg is ovulated. Both clutches are considered to be "completed." Below: bird taken 9 June 1968. The large bulge in the oviduct "a" is a hard shelled egg in the oviduct. The ovary has three large post-ovulatory follicles (two visible, b, c) and two yolky follicles of 6.7 (d) and 3.7 (e) mm. It is possible that the next largest, unyolked follicle would have developed and ovulated or that the 3.7 mm follicle would have been resorbed before it was laid. The ovary illustrates the problem of determining clutch size from an incompleted or "current" clutch. Scale line = 1 cm.

ids the post-ovulatory follicles are recognizably distinct from regressing, atretic follicles for about 10 days after ovulation (Payne 1966, 1973b).

Cowbirds lay eggs in sets, one egg on each consecutive day, separated by a few days of non-laying. Evidence of laying in discrete series comes from (a) the size graduation of growing follicles (Payne 1965, 1973a), (b) the size and histology of ovulated follicles (Payne 1965, 1973a), and (c) field observations (Walkinshaw 1949). I refer to these series as "clutches." Clutch sizes were determined in two ways. First, "completed clutches" were determined by counting all post-ovulatory follicles that fell within a single clutch by size and appearance. This was the clutch size value determined from the older ovulated follicles and from any recent sets in ovaries which showed a size break in the follicles, with no more continuing yolking large yellow follicles. Also counted as "completed clutches" were sets of eggs where a bird had one yolky follicle large enough (8 mm or more) to ovulate the following day but with no other yolky follicles larger than 3 mm. Second, "current clutches" were determined from the sets of ovulated follicles in ovaries that also had two or three (there were never more) large yolky follicles of at least 3.0 mm. These values were derived from a study of the growth rate of cowbird ovarian follicles (Payne 1965). The "current clutches" thus estimated the minimum clutch size in the clutches that were currently being laid. The values are minimal insofar as more follicles may have grown and been ovulated in the series, but on average they probably overestimate the number of eggs actually ovulating because some yolky follicles (mainly the last one of a clutch) regress without ovulating. All of the Michigan ovaries and a few of the California ovaries for which I was unsure whether certain follicles had ovulated were serially sectioned to match up the follicles seen in the dissected material with that histological material. In nearly all cases intact ovaries yielded the same information on the laying histories of the individual cowbirds as did the serial sections. I used the microscope count when the counts differed.

I estimated the number of eggs laid in a season by (1) determining the length of the breeding season of local cowbirds, (2) sampling ovaries through the laying season and determining the proportion of laying birds with recently ovulated follicles in each 10-day period, and (3) determining the number of eggs each collected bird had laid during the preceding 10 days. This appears to give a more accurate estimate of the number of eggs laid by a typical female during a season than does determining the proportion of females at any time with an egg actually in the oviduct (as in Payne 1973a), because females with formed eggs in the duct seemed less shy and less reluctant to fly than other cowbirds as I approached to collect them. The estimated number of eggs laid in a season is therefore somewhat less than in an earlier study (Payne 1973a).

STUDY AREAS

In Oklahoma, cowbirds were collected mainly in a grazed Blackjack Oak-Post Oak (*Quercus marilandica-Q. stellata*) woodland with large patches of flooded willows. The birds were taken on a peninsula at Lake Texoma, near Willis, Marshall County, at 33°51′N, in June and July in 1968, 1969, and 1970. A few birds also were taken near Norman, Cleveland County, at 35°14′N. Cowbirds in Oklahoma are known to lay from 13 April to 4 July (Sutton 1967). Two dates in late July also have been reported (Sutton 1967), but I found no evidence of laying in birds taken after July 3 (three birds were taken 10–17 July), nor in one taken on 14 April. The laying season appears to be concentrated from the last week of April to the first week of July, or in 10 weeks as in central California (Sutton 1967, pers. obs.). Host species that are common and are parasitized frequently in southern Oklahoma (Wiens 1963, Sutton

1967) are Bell's Vireo (*Vireo bellii*), Orchard Oriole (*Icterus spurius*), Cardinal (*Cardinalis cardinalis*), Blue Grosbeak (*Guiraca caerulea*), Painted Bunting (*Passerina ciris*), Dickcissel (*Spiza americana*), Lark Sparrow (*Chondestes grammacus*), and Field Sparrow (*Spizella pusilla*). Lark Sparrows were particularly numerous in the study area, and three of seven nests with eggs had cowbird eggs. Newman (1970) found 15 of 33 Lark Sparrow nests to be parasitized from early June through the first week of July. Cowbirds have long been common breeding birds in Oklahoma, and the species probably evolved in the Great Plains (Friedmann 1929) along with the buffalo, with which the birds there still feed.

Cowbirds in central California were sampled mainly in the inner coast range in Colusa and Glenn counties between 39°20′N and 39°34′N latitude. The habitat was mainly open Blue Oak (*Quercus douglasii*) woodland with patches of sclerophyllous shrubs on hillsides and willows along streams and ponds. California birds were collected in each year from 1961 to 1965. Several host species nested in the study area. Probably the most commonly parasitized species were the Blue-gray Gnatcatcher (*Polioptila caerulea*), Hutton's Vireo (*Vireo huttoni*), Warbling Vireo (*V. gilvus*), Orange-crowned Warbler (*Vermivora celata*), Yellow Warbler (*Dendroica petechia*), Black-headed Grosbeak (*Pheucticus melanocephalus*), Lark Sparrow, and Song Sparrow (*Melospiza melodia*) as these were the more common small passerines in the area also known to be hosts. The study area and its passerine species and the details of the breeding season of local cowbirds (mainly early May to late June, but extending from the last week of April to the first week of July in some years) are described in more detail elsewhere (Payne 1973a). Cowbirds first appeared in central California as common breeding birds only as late as the 1920's, though they did occur earlier (Grinnell and Miller 1944).

Birds were collected in northern Michigan from 15 June to 15 July in 1963 in Emmet and Cheboygan counties between 45°25′N and 45°35′N. Birds were taken mainly in grazed pastures near the edge of the mixed northern hardwoods-coniferous forests. The breeding season of cowbirds lasts about six weeks from late May to early July. The season starts later than in the other two areas because the trees do not leaf out and the returning insectivorous passerine migrants do not start to nest until about the last week of May (Payne 1965). Only one bird (11 July) of 23 taken from 8 to 15 July was laying. Cowbird eggs or young have been found with 32 species of hosts in the area, including 11 species of mainly forest warblers and nine fringillid species generally of more open habitat (Nelson 1956, Pettingill 1974). Other commonly parasitized local species include the forest or forest-edge Eastern Wood Pewee (*Contopus virens*), Least Flycatcher (*Empidonax minimus*), and Red-eyed Vireo (*Vireo olivaceus*).

Cowbirds are thought to have evolved in the prairies and later to have become more numerous in the eastern United States with the opening of the forests by European settlers (Friedmann 1929: 150). Mayfield (1960) argued that Brown-headed Cowbirds did not occur in Michigan until the late 1800's after extensive logging and fires cleared much of the area and opened northern Michigan to birds of more open county. However, two of the four references cited by Mayfield state that cowbirds were present in Michigan and Ohio by the 1800's. Cowbirds were known nearby in northern Michigan by 1892 (Cook 1893). Certainly cowbirds were common through much of the northeastern part of the United States by the early 1800's (Wilson 1831, Baird et al. 1858). Natural open areas from burning and clearing of the land by Indian residents were found in Michigan centuries earlier, lightning fires were common in north-central Michigan (Mayfield 1960), and local soil conditions such as the Grayling sands most likely have long been associated with open vegetation. Systematic observations of birds in northern Michigan started with the establishment of the University of Michigan Biological Station in 1909 before the forest had regrown. At least by 1910 the cowbirds had invaded the area and parasitized vireos (Pettingill 1974). Cowbirds have been common in pasturelands in the area during the last 15 years. I suspect that cowbirds are more common now than they were 150 years ago, but the area has probably had cowbirds breeding for a much longer period.

SEASONAL VARIATION IN CLUTCH SIZE

The seasonal variation in clutch size is summarized in table 1 for the cowbirds in California, the largest and most seasonally complete of the three population samples. No tendency is evident for clutch size to change through the season. The "current clutches"

TABLE 1. Seasonal variation in clutch size of cowbirds in California.

	Completed clutch		Current clutch	
	N	$\bar{x}$	N	$\bar{x}$
April 16–30	—	—	1	4
May 1–15	4	4.0	12	4.3
May 16–31	6	4.0	20	4.8
June 1–15	7	4.1	16	5.0
June 16–30	2	4.5	3	5.7
July 1–15	1	3	1	6

tend to give larger values for progressively later dates through the season but the "completed clutches" show no increase in the number of eggs that are ovulated. The apparent increase in clutch size with date in the "current clutches" results from a larger number of large, yolking follicles later in the season; some of these follicles are not ovulated. Perhaps the birds later in the season find more food available for producing eggs but are then unable to locate proportionally more suitable host nests in which to lay late in the season. Or perhaps the increase indicates restraint earlier in the season. With small early clutches a female may avoid exhaustion late in the season, but with larger potential clutches developing later, she may have a final spurt of laying if she finds nests. The large non-ovulating yolky follicles near the end of a clutch generally appear to burst through the tissue layers of the theca (but not the ovarian epithelium), and the yolk is resorbed by macrophages (Payne 1965, 1966).

GEOGRAPHIC VARIATION IN CLUTCH SIZE

No tendency was found for clutch size in Brown-headed Cowbirds to vary among central California, southern Oklahoma, and northern Michigan (table 2). Average values for clutch size in the three areas all fell within a small range of 3.91 to 4.05 eggs. The slight differences in mean clutch size between populations are not statistically significant ($P > .70$ for all three pairs, t-test), nor do populations differ significantly when comparison of mean completed clutch size or current clutch size is restricted to any half-month period ($P > .60$ for all comparisons, t-test of two means).

TABLE 2. Clutch size in Brown-headed Cowbirds.

	Completed clutch			Current clutch		
	N[a]	$\bar{x}$[b]	$t_{.95}\,s_{\bar{x}}$[c]	N	$\bar{x}$	$t_{.95}\,s_{\bar{x}}$
Oklahoma	12	3.92	.69	19	4.24	.43
California	20	4.05	.39	53	4.82	.31
Michigan	11	3.91	.28	18	4.61	.64

[a] N = number of clutches determined.
[b] $\bar{x}$ = mean clutch size.
[c] $t_{.95}s_{\bar{x}}$ = t-statistic of the mean at .95 probability level.

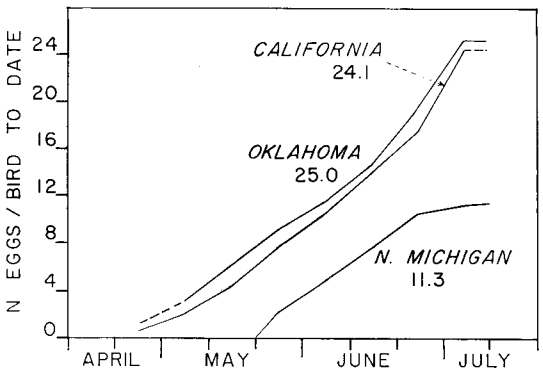

FIGURE 2. Cumulative number of eggs laid by a female cowbird during the breeding season. Figures by each line estimate seasonal totals of an average female in each population. Dotted lines are rough estimates based on literature descriptions of the start or end of the breeding season rather than on birds collected in this study.

NUMBER OF EGGS LAID IN A SEASON

The number of eggs ovulated during the 10 days before the female was collected was determined for each bird. The results (table 3) indicate that nearly all individual females lay throughout the population season, except during the first and last weeks. The mean number of eggs ovulated during the preceding 10 days appears to be very nearly the same throughout the main part of the breeding season. Figure 2 summarizes the cumulative mean number of eggs laid by the females (summing the values of the laying rates from table 3). Laying rates appear to be consistent within each population; there is no evidence of bimodal peaks such as Wiens (1963) reported for eggs found in nests in southern Oklahoma. Laying rates also appear to be the same in the three populations of cowbirds (note the similar slopes of all three cumulative curves in figure 2).

The number of eggs laid in a breeding season differs between Michigan and the other two localities (fig. 2). The laying season of cowbirds, which matches that of most of the local host species, is about 5–6 weeks in northern Michigan and about 8–10 weeks in Oklahoma and California. The lower reproductive output of female cowbirds in northern Michigan seems due to the shorter nesting period of their hosts in that area.

TABLE 3. Mean number of eggs ovulated during the 10 days preceding collection.

Date	Oklahoma			California			Michigan		
	No. birds	No. birds not laying	x̄ No. eggs ovulated	No. birds	No. birds not laying	x̄ No. eggs ovulated	No. birds	No. birds not laying	x̄ No. eggs ovulated
April 1–20	1	1		0			0		
21–30	0			4	3	0.50	0		
May 1–15	0			24	11	1.42	0		
16–31	12	0	3.00	25	1	3.28	2	2	
June 1–15	7	0	2.29	21	0	2.76	1	0	3.00
16–30	7	0	4.57	4	0	4.25	20	2	2.70
July 1–10	3	0	5.66	1	0	7.00	12	3	1.97
11–15	0			0			19	18	0.16

The estimate of 24.1 eggs per female in California is somewhat lower than that (30 eggs) based on the proportion of females in the sample with an egg in the oviduct (Payne 1973a). The estimate of 11.3 eggs per female in northern Michigan is very nearly the same as that ("10 to 12 eggs") based on a larger sample in which an attempt was made to age the ovulated follicles over a longer postovulatory period (Payne 1965).

DISCUSSION

The lack of geographic variation in clutch size in the cowbird populations limits the usefulness of the results in selecting among different general theories of the evolutionary history of clutch size differences among birds. The absence of a difference in clutch size between the northern Michigan birds and the two southern populations might be expected from Lack's explanation of the tendency of some other bird species to have larger clutches at higher latitudes, due to the extra hours of daylight in which they may get food for their young. Cowbirds do not feed their young, so they may be expected to have no such restraint at the lower latitudes. Nevertheless, the clutch size of cowbirds in southern Oklahoma and central California is not remarkably greater than that of sympatric icterid species that rear their own young. On the other hand, the results do not provide unequivocal support for the daylight hours hypothesis. Although cowbirds at higher latitudes have more daylight hours in which to feed, and hence, more food to use in forming eggs, they do not have larger clutches.

Recovery data of banded cowbirds through 1965, made available by the Bird Banding Laboratory, were checked to compare populations from the three areas for posible differences in genetically effective dispersal distances. However, few cowbirds banded as young were recovered in a later breeding season. Of 15 young cowbirds banded in Michigan during May through August and recovered or recaptured in a subsequent breeding season, 12 were recovered in the same locality (or same 10-minute block). The other three were recovered within 40 km of their hatching site. The pattern is similar to that of young birds banded at their hatching site in Massachusetts, Connecticut, and New Jersey, where 210 of the 234 recoveries were local. There were no recovery data for birds banded as young in the southern Great Plains or in California. Banding data for the other states do not indicate any regional differences in dispersal pattern. Perhaps there are no geographic differences in dispersal patterns that would be associated with different egg laying strategies. The banding data indicate that cowbirds are not very dispersive.

If the cowbirds in more recently populated areas had larger clutch sizes or faster laying rates, it might be argued that the invading or expanding population was either genetically *r*-selected (MacArthur and Wilson 1967) or had had a long history of individual female response to invasion conditions by laying more eggs. The lack of greater reproductive output in central California, where cowbirds were common no earlier than 40 years before the field study, may mean simply that population densities of cowbirds at the time of the study were near the long-term ones in areas where the cowbirds had lived for much longer times.

The adaptive significance of parasitic cowbirds laying eggs in series or "clutches" is not obvious. Cowbirds usually lay only one or two eggs in a host nest, and the hosts can generally rear no more than one or two young cowbirds (Friedmann 1963). Clutch size of a cowbird hence is larger than the number of eggs that are laid in a single host nest. The behavior of marked female cowbirds has not been studied in detail, and it is not known

whether a female keeps track of several host nests at once or whether she finds active nests one at a time. Perhaps the clutch size is limited by the amount of protein or fat that a female can store at one time in the breast muscle and convert into eggs, as Jones and Ward (unpubl. data) have described for other birds. But, if this is so, then it is not obvious why the physiological limits have evolved as they have, nor why a female cowbird that lays eggs in distinct sets or clutches would be more successful in leaving offspring than one that has evolved a finer tuning to the erratic availability of suitable host nests.

SUMMARY

A comparative study of populations of parasitic cowbirds in central California, southern Oklahoma, and northern Michigan showed a mean clutch size of 3.91 to 4.05 in all three areas. Estimates of the mean number of eggs laid in a season were 25.0 for Oklahoma, 24.1 for California, and 11.3 for northern Michigan. Laying rates (mean number of eggs ovulated during the previous ten days) were the same in all three populations. The smaller number of eggs laid by females in northern Michigan is due to the shorter breeding season of the local passerine hosts. Recoveries of banded cowbirds in the northeast show that most return to their hatching site in later breeding seasons, and genetically effective dispersal is limited to a few kilometers. No differences in clutch size were found that could be attributed to latitude, to total number of clutches laid in a season, or to the history of the populations.

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