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FACTORS LIMITING FECUNDITY OF CAPTIVE BROWN-HEADED COWBIRDS[1]

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Abstract. We conducted two controlled experiments with captive Brown-headed Cowbirds (*Molothrus ater*) to test potential limiting factors for egg production in this obligate brood parasite. Twenty-four wild-caught females were placed in separate pens during the breeding season and provided with crushed oyster shell and nests containing mock eggs. To test the calcium limitation hypothesis, we removed oyster shell from the diet of females and compared their fecundity to that of controls. The fecundity of females on the restricted calcium diet declined significantly and averaged 61% fewer eggs than the controls. To test the host nest availability hypothesis, we removed all nests from the pens of females and compared fecundity to that of controls. Fecundity of females deprived of host nests was not significantly different from controls. Results of these experiments suggest that fecundity of Brown-headed Cowbirds can be limited by dietary calcium, but not by availability of host nests.

The 12 control females produced a total of 316 eggs over a 89-day breeding period from 25 April to 22 July. Individual fecundity of control females averaged 26.3 eggs, significantly greater than that of the same females as yearlings. Three females laid more than 40 eggs during the breeding season and one female laid 77 eggs, including an egg each day for 67 consecutive days, surpassing the previous record for number of eggs produced in a single breeding season by a wild bird. Brown-headed Cowbirds appear to be under intense selection pressure to produce eggs at a high rate, but the ability of wild females to acquire sufficient dietary calcium to form egg shells may pose a constraint on fecundity.

Key words: Brown-headed Cowbird; Molothrus ater; *fecundity; egg production; calcium; laying rate.*

INTRODUCTION

The fecundity and egg-laying patterns of the Brown-headed Cowbird (*Molothrus ater*) are unusual among passerines in that annual egg production of individuals is high (Scott and Ankney 1980, Fleischer et al. 1987) and females can produce eggs daily for extended periods, rather than in clutches or sets (Scott and Ankney 1983, Jackson and Roby 1992). Scott and Ankney (1980) estimated the average fecundity of wild females at 40 eggs/year by multiplying the length in days of the laying season of an average female by the average laying rate. Working with captive yearling cowbirds, Jackson and Roby (1992) documented that individual females can produce eggs daily for up to 32 days. These reproductive traits have clear adaptive significance for an obligate brood parasite that is a generalist.

Several estimates of annual fecundity in wild cowbirds have been published, but there is little information on factors that affect fecundity (Payne 1973, 1976). Fleischer et al. (1987) found that the onset of laying in wild yearling females is delayed compared with adults, and laying rates of yearlings may be lower as well. Payne (1965) proposed that the laying of a limited number of eggs in sequence may be the "result of limited numbers of available nests in an area large enough to be scouted by a laying female." Ankney and Scott (1980) found that the laying rate of wild females approached one egg per day during late May and early June, when the availability of host nests was presumed at a peak. However, Payne (1965) also hypothesized that "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." Although Payne (1976) proposed that cowbird clutch size might be limited by the amount of protein or fat that a female can store, female cowbirds can presumably acquire the energy for egg production with little difficulty because the total energetic cost of producing an egg represents only 13–16% of normal daily energy requirements (Ricklefs 1974, Ankney and Scott 1980). Ankney and Scott

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(1980) found no indication that female cowbirds rely on fat or protein reserves for egg production, and concluded that energy and protein do not limit laying rate. However, they did find that leg bone masses of females completing a sequence of eggs were significantly less than those starting a sequence, suggesting that females deplete endogenous calcium reserves (medullary bone) during a laying sequence. They also reported that nearly all females with oviductal eggs had mollusc shell in their gizzards, indicating that laying females rely on dietary calcium supplements to meet requirements for egg shell production. Despite this evidence, Ankney and Scott (1980) proposed that nutrition does not constrain fecundity in wild cowbirds but that a female's laying rate "is directly related to the availability of host nests."

The main objective of our study was to investigate two hypothesized factors limiting egg production in Brown-headed Cowbirds: availability of host nests and availability of supplemental dietary calcium. We employed controlled experiments with captive cowbirds to test these hypotheses. This paper also compares fecundity and egg-laying patterns of individual two-year-old females with their performance as yearlings.

METHODS AND MATERIALS

Cowbirds used in this study were captured as juveniles in baited traps at Southern Illinois University Farms during August and September 1990. Captive cowbirds were housed during the nonbreeding season in outdoor pens (5.1 m × 1.3 m × 1.3 m) in mixed sex flocks of 7–10 individuals. Individual fecundity and egg-laying patterns of 25 captive yearling females during the 1991 breeding season were reported previously (Jackson and Roby 1992).

In early March 1992, 24 captive two-year-old females were moved to separate outdoor breeding pens (2.5 m × 1.3 m × 1.3 m) that were raised about 60 cm off the ground. Nineteen of the females were housed with males, but due to a shortage of males that were acclimated to captivity, five females had to be housed alone. Females housed without males during the 1991 breeding season did not lay significantly fewer eggs than females housed with males (Jackson and Roby 1992). Nevertheless, we kept males in most breeding pens to insure that females were not deprived of stimuli associated with courtship, in case this was critical for ovulation. Breeding pens were spaced at three meter intervals and females caged without males could see and hear other captive males through the wire walls of their pens. Also, wild male cowbirds frequently visited the pens and were often observed courting captive females.

Captive cowbirds were fed white millet ad libitum and a specially formulated mix for cowbirds (West and King, pers. comm.) consisting of Purina Gamebird Startena (Purina Mills, St. Louis, MO), Purina Hi-Pro Dog Food, hard-boiled eggs, ground carrots, molasses, and brewer's yeast. We modified this recipe slightly by not including the shells from the hard-boiled eggs, a calcium source that cowbirds could selectively consume. Mealworms and fresh water containing a soluble multi-vitamin for birds (Avi-con, Vet-a-Mix, Shenandoah, IA) were offered daily. Crushed oyster shell was provided ad libitum in a separate container as a dietary calcium supplement. Each breeding pen was also provided with three host nests (mostly Red-winged Blackbird [*Agelaius phoeniceus*] nests) containing egg-shaped candy (jelly beans) of assorted colors as mock host eggs. Captive females provided with mock eggs during the 1991 breeding season did not lay significantly fewer eggs than females provided with real host eggs (Jackson and Roby, unpubl. data). Each host nest contained one to three mock eggs on a rotating basis.

All breeding pens were carefully searched each day throughout the laying season for cowbird eggs, and notes were kept on the location and condition of all eggs found in pens. To minimize the destruction or consumption of their own eggs, each pen was searched within a half hour of sunrise. Despite this precaution, some cowbird eggs were punctured and removed from the host nest or partially eaten prior to collection. Black roofing felt was spread on the ground under each pen to minimize the possibility that remains of partially eaten eggs could fall through the wire floor of the pen to the ground and go undetected.

Calcium restriction experiment. We tested the hypothesis that cowbird fecundity is limited by the availability of dietary calcium supplements by removing the oyster shell containers from the pens of half the females. On 26 May, after most females had commenced egg-laying, 12 females were randomly selected as an experimental group and the remaining 12 females served as a control. (Of the five females that were caged without a male, three were in the control group and the other two were in the experimental group.) We removed the oyster shell container from the pens of experimental females late in the morning, after all cowbird eggs had been collected (and presumably after all ovulation for that day had occurred), and returned them to the pens 11 days later on 6 June.

Eggs from experimental and control females were collected daily as before and records of egg production were maintained for each female. Average fecundity of experimental females was compared statistically with that of controls for the 11-day pre-treatment period, the 11-day treatment period, and the 11-day post-treatment period.

Nest removal experiment. We tested the hypothesis that availability of host nests limits cowbird fecundity by removing all host nests and mock eggs from the pens of some females. Four days after termination of the calcium restriction experiment, the 24 captive females were again divided into experimental and control groups. Stratified random sampling was used to insure that half of the experimental females from the previous calcium restriction experiment were included in each of the new groups. Host nests and mock eggs were removed from the pens of experimental females in late morning of 10 June, after all cowbird eggs had been removed. We deprived the 12 experimental females of host nests and mock eggs for 20 days to observe any potential adjustments in laying behavior resulting from prolonged deprivation. Late on the morning of 30 June, three host nests containing mock eggs were returned to the pens of each experimental female.

Eggs from experimental and control females were collected daily as before and records were maintained for each female. Average fecundity of experimental females was compared statistically with that of controls for both the 20-day pre-treatment period and the 20-day treatment period using t-tests.

All data were checked for significant departure from normality prior to analysis using parametric statistical analysis procedures. All statistical analyses were performed with Statworks 1.0.

RESULTS

The first egg was laid by a captive female on 25 April 1992 and the last on 22 July, for an 89-day laying season. All 24 females laid at least one egg; mean fecundity of individual females was 24.0 eggs (SD = 16.93, range = 1–77 eggs, $n = 24$) and the distribution of individual fecundity did not differ significantly from normal ($P > 0.05$). The median initiation date for laying was 16 May (range: 25 April–9 June) and the median termination date was 4 July (range: 9 June–22 July). The average laying period of individual females was 47 days (SD = 19.6, range = 1–89 days, $n = 24$).

The average fecundity of females that were caged without a male (females J, Q, T, W, and X) was 21.8 eggs (SD = 12.13, range = 7–35 eggs, $n = 5$) and was not significantly different from average fecundity of females caged with a male (24.5 eggs, SD = 18.22, $n = 19$, $t = 0.314$, $P = 0.756$).

A total of 578 eggs were recovered from the pens during the breeding season. Of these, 337 (58.3%) were recovered intact from host nests, 131 (22.7%) were found punctured or broken outside of nests, 55 (9.5%) were found intact but not in a nest, 28 (4.8%) were found punctured or broken in a host nest, and 27 (4.7%) had been partially consumed prior to recovery. Of the 55 eggs found intact but not in a nest, 32 had been laid on the floor of the pen, 13 were laid in a food cup, and 10 were laid in a water container.

Calcium restriction experiment. The mean fecundity of control females during the 11-day pre-treatment period was 3.3 eggs (SD = 3.60, range = 0–10, $n = 12$) and did not differ significantly from the mean of 3.6 eggs (SD = 2.75, range = 0–9, $n = 12$) laid by experimental females during the same period ($t = 0.191$, df = 22, $P = 0.850$). During the 11-day treatment period, the mean fecundity of control females was 6.1 eggs (SD = 3.29, range = 1–11, $n = 12$), significantly greater than the average of 2.7 eggs (SD = 1.97, range = 0–5, $n = 12$) laid by experimental females ($t = 3.09$, df = 22, $P = 0.005$, Fig. 1). The mean fecundity of control females increased significantly from the 11-day pre-treatment period to the 11-day treatment period (paired $t = 7.40$, df = 11, $P < 0.0005$), indicating that the pre-treatment period was prior to the peak of egg-laying (Fig. 1). However, the mean fecundity of experimental females did not differ significantly between the pre-treatment and treatment periods (paired $t = 1.42$, df = 11, $P = 0.183$).

The effect of removing oyster shell from the pens of experimental females was not apparent the first day after removal: seven experimental females (58%) laid and only three control females

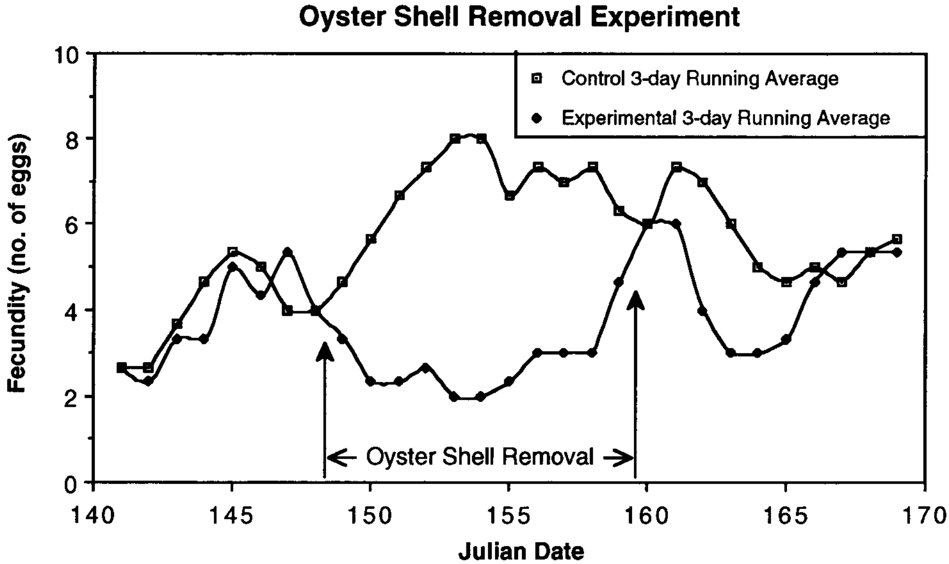

FIGURE 1. Total daily fecundity of 12 control and 12 experimental female Brown-headed Cowbirds before, during, and after an 11-day calcium restriction experiment. Plotted values are three-day running averages of daily fecundity.

(25%) laid. Removal of oyster shell had no effect on fecundity of experimental females the following morning presumably because experimental females that were to lay already had an oviductal egg. Similarly, the return of oyster shell to the pens 11 days later would not be expected to influence ovulation until the following morning. Because of this expected one day lag in the effect of oyster shell removal (and replacement), the average fecundities of control and experimental females were compared for the 11-day treatment period excluding the first day after oyster shell removal and including the first day after oyster shell was returned to the pens. Also, the 11-day pre-treatment period was shifted to include the first day after oyster shell removal. The mean fecundity of control females during the shifted pre-treatment period still did not differ significantly from that of experimental females (t = 0.487, df = 22, P = 0.631). Also, the mean fecundity of control females during the shifted treatment period (6.2 eggs) was significantly greater than that of experimental females (2.4 eggs, t = 3.40, df = 22, P = 0.003). However, the mean fecundity of experimental females during the shifted treatment period (2.4 eggs, SD = 2.07, range = 0–6, n = 12) was significantly less than during the shifted pre-treatment period (4.1 eggs, SD = 2.84, range = 0–9, n = 12; paired t = 2.74, df = 11, P = 0.019). This indicates that fecundity of experimental females declined significantly as a result of the calcium restriction experiment, and that average fecundity of females without access to oyster shell was 61% lower than that of control females.

The average fecundity of experimental females nearly doubled from the treatment period (2.4 eggs) to the post-treatment period (4.6 eggs). However, the fecundity of experimental females appeared to be lower than that of controls for about a week after the termination of the experiment (Fig. 1). Nevertheless, the average fecundity of experimental females during the 11-day post-treatment period (4.6 eggs) was not significantly different from that of control females during the same period (5.4 eggs, t = 0.744, df = 22, P = 0.465). This indicates that the experimental females rapidly recovered from calcium restriction and resumed higher egg production rates (Fig. 1).

The shells of their own eggs were one potential source of calcium for females in the calcium restriction experiment. However, of the 33 eggs produced by experimental females, only one (3%) was partially eaten. Of the 72 eggs laid by control females, three (4.2%) were partially eaten. Fifty-two percent of eggs laid by experimental females were found intact in a host nest, while 72% of eggs laid by control females were found intact in a host nest.

Nest removal experiment. The mean fecundity of experimental females during the 20 days prior to the nest removal experiment was 7.6 eggs (SD = 4.85, range = 2–17, n = 12) and did not differ significantly from that of control females (8.8 eggs, SD = 6.03, range = 1–20, n = 12; t = 0.522, df = 22, P = 0.607). During the 20-day treatment period when experimental females were deprived of nests, the mean fecundity of experimental females was 8.1 eggs (SD = 5.62, range = 0–17 eggs, n = 12) and did not differ significantly from that of control females (9.1 eggs, SD = 5.84, range = 0–20 eggs, n = 12; t = 0.428, df = 22, P = 0.673, Fig. 2). The fecundity of experimental females did not differ significantly between the pre-treatment and treatment periods (paired t = 0.295, df = 11, P = 0.773) and the fecundity of control females also did not differ significantly between the two periods (paired t = 0.287, df = 11, P = 0.780).

Because of the expected one day lag in the effect of nest removal and replacement (see above), we also statistically compared the average fecundity of experimental and control females during the treatment period minus the first day after nest removal and plus the first day after nest replacement. When the one day shift was incorporated into the treatment period, the average fecundity of control females (8.9 eggs) still did not differ significantly from that of experimental females (7.4 eggs, t = 0.643, df = 22, P = 0.527). No other comparison using the shifted pre-treatment and treatment periods was significantly different.

Most of the 94 eggs laid by experimental females deprived of host nests were found on the floor of the pen, but 13 eggs (13.8%) were laid in food cups and 6 eggs (6.4%) were laid in water containers. Of the 108 eggs produced by the control females during the same period, none were found in food cups and only one was found in a water container. Most of the eggs laid by experimental females were recovered in a punctured/broken condition (56.4%) or had been partially eaten (14.9%), whereas most eggs laid by control females were found intact and in a host nest (76.9%). For control females, 18 eggs (16.7%) were found on the floor of the pen in a punctured/broken condition, 5 eggs (4.6%) were found punctured/broken in a host nest, one egg was found intact on the floor of the pen, and none were found partially eaten. These results indicate that female cowbirds were more prone to manipulate or consume their own eggs when they were not laid in a host nest.

The return of host nests and mock eggs to the pens at the end of the experiment appeared to produce a small increase in average fecundity of experimental females (Fig. 2). However, the mean fecundity of experimental females during the seven days post-treatment (2.7 eggs) was not significantly greater than that of controls during the same period (2.3 eggs, t = 0.443, df = 22, P = 0.662).

Fecundity and egg-laying patterns of control females. Calcium restriction significantly reduced fecundity of experimental females, whereas the nest removal had no significant effect on the fecundity of experimental females. Consequently, the fecundity and egg-laying patterns of only the 12 control females in the calcium restriction experiment were statistically compared with those of the same individuals as yearlings.

The mean fecundity of two-year-old control females was 26.3 eggs (SD = 20.07, n = 12) and ranged from 8–77 eggs. The fecundity of these same 12 females as yearlings (15.4 eggs) was significantly less (paired t = 2.77, df = 11, P = 0.018). Fecundity of individuals as two-year-olds was highly correlated with fecundity as yearlings (r^2 = 0.571, $F_{1,10}$ = 13.33, P = 0.004), indicating that much of the variation in fecundity was a function of individual differences.

The mean laying rate during the individual's laying period was 0.53 eggs/day (SD = 0.206, range = 0.24–0.88, n = 12). The mean laying rate of the same females as yearlings was not significantly different (paired t = 0.356, df = 9, P = 0.730). However, average duration of individual laying periods was significantly greater in 1992 compared with 1991 (paired t = 3.193, df = 9, P = 0.011). This indicates that the higher average fecundity of two-year-olds in 1992 was a function of longer laying periods, not higher laying rates.

Average initiation dates in the two years were not significantly different (paired t = 1.708, df = 9, P = 0.122), but average termination date in 1992 (two-year-olds) was significantly later than that in 1991 (yearlings; paired t = 2.488, df = 9, P = 0.035). The median laying date of control females in 1992 was 11 June, compared with 10 June the previous year (Fig. 3). The peak of egg production occurred about a week earlier in 1992,

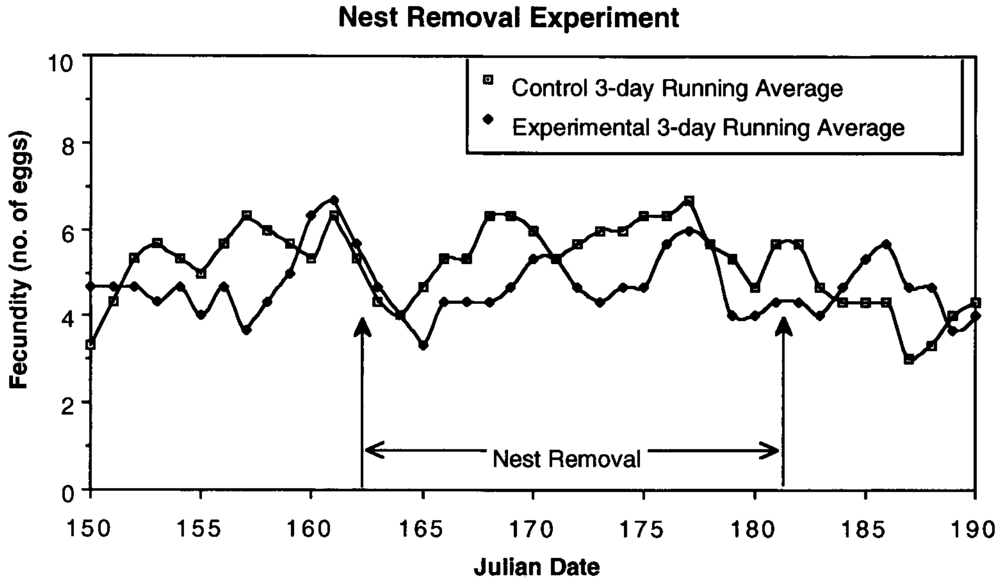

FIGURE 2. Total daily fecundity of 12 control and 12 experimental female Brown-headed Cowbirds before, during, and after a 20-day host nest removal experiment. Plotted values are three-day running averages of daily fecundity.

when the females were two-year-olds, compared with 1991 when the females were yearlings. But higher laying rates in late June and early July of 1992 (Fig. 3) resulted in similar median laying dates in the two years.

The laying patterns of control females are presented in Figure 4. Runs tests were used to test for randomness of laying over each female's laying period (Sokal and Rohlf 1981:782). If control females laid eggs in clutches or sets, the number

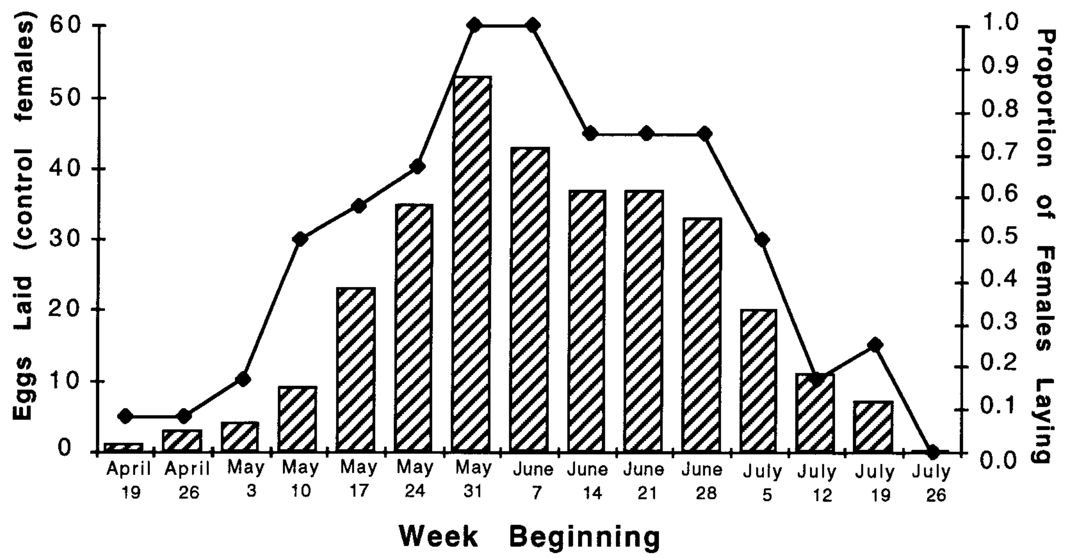

FIGURE 3. Chronology of egg production in captive two-year-old female Brown-headed Cowbirds during the 1992 breeding season. Only the egg production data of the 12 females that served as a control in the calcium restriction experiment are included. Solid bars indicate the total number of eggs produced each week by all 12 females and the line indicates the proportion of females that laid at least one egg.

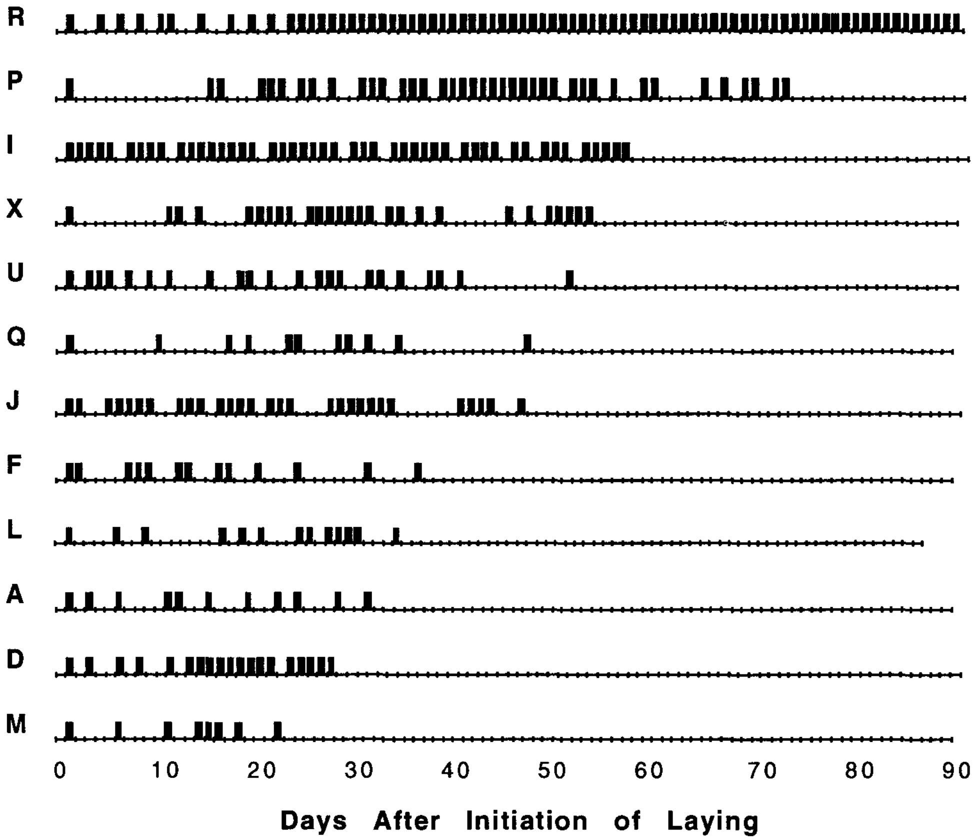

FIGURE 4. Egg-laying patterns of 12 control female cowbirds (identified by upper case letters) during the 1992 breeding season. Each bar represents a day when a single egg was produced.

of runs of laying and non-laying days would be significantly less than expected by chance. The laying pattern of only one female (J) was significantly different from random ($P = 0.03$), and this female was also the only one that appeared to be laying eggs in clutches or sets (Fig. 4). Female J laid a total of 29 eggs in eight sequences that varied from one to seven eggs.

DISCUSSION

Calcium restriction experiment. The results of this experiment demonstrate that availability of supplemental dietary calcium can significantly constrain egg production rates in Brown-headed Cowbirds. The average number of eggs produced by experimental females during the 11-day treatment period was less than 40% that of control females. Whereas the laying rates of females deprived of oyster shell were considerably lower than that of controls, experimental females were still able to produce some eggs. The source of calcium to produce egg shells in experimental females was presumably the cowbird mix that was offered ad libitum to all females throughout the breeding season. Gamebird Startena and Hi-Pro Dog Food together made up about 60% by volume of the cowbird mix, and both these feeds contain about 1.4% elemental calcium (Purina Mills, pers. comm.). Experimental females were able to obtain sufficient calcium to support limited egg production by consuming the cowbird mix.

The results of this experiment suggest that adequate supplies of supplemental dietary calcium are crucial for high fecundity in wild cowbirds. Most of the diet of free-ranging female cowbirds during the breeding season consists of insects (Ankney and Scott 1980), a poor source of dietary calcium (Allen 1989, Studier and Sevick 1992). The remainder of the diet of wild female cowbirds consists primarily of seeds (Ankney and Scott 1980, White et al. 1985), another calciumdeficient food (Robbins 1983). Consequently, wild female cowbirds may be more dependent on calcium supplements, such as mollusc shells (Ankney and Scott 1980) and shells of host eggs, than captive females to meet the calcium requirements for egg shell formation. The consumption of supplemental calcium by captive female cowbirds that were producing eggs at a high rate was considerable. For example, female R consumed an average of 1.0 g (SD = 0.52) of oyster shell per day over the 89-day laying period (Holford and Roby, unpubl. data). This high rate of oyster shell consumption was observed despite the offering of ad libitum cowbird mix with a calcium content of about 1%.

The calcium restriction experiment resulted in significantly lower average fecundity of experimental females compared with controls. However, the considerable variation in fecundity of both control and experimental females during the experimental period suggests that factors other than calcium constraints were limiting fecundity in some females. This factor(s) apparently affected individual captive females to varying degrees but consistently among years, because fecundity of individual females in 1992 was highly correlated with fecundity in 1991. In our opinion, the high variance in individual fecundity of captive female cowbirds was a function of individual differences in acclimation to captivity. The most fecund females tended to react less to our activity around their pens and exhibited fewer panic responses, and these differences in temperament were consistent over the two years of the study. The lower average fecundity of control females (26.3 eggs) compared with estimates of fecundity for wild females (40 eggs; Scott and Ankney 1980) suggests that captivity generally inhibited egg production in control females, but the high variance indicates that fecundity was not depressed for all females. Availability of dietary calcium would, presumably, have little bearing on fecundity in females that are already laying at a low rate due to other factors.

The results of the calcium restriction experiment do not prove that the fecundity of wild female cowbirds is calcium-limited. We think that in some breeding habitats calcium supplements may be readily available and female cowbirds may be calcium replete during the laying period. We suspect that other habitats with calcium-poor soils may lead to chronic calcium insufficiency in laying females, which would result in lower laying rates and lower annual fecundity. Availability of calcium supplements is one potential explanation for regional differences in cowbird parasitism rates on host nests. Even in habitats where female cowbirds are calcium replete throughout the laying period, the high calcium requirements associated with high laying rates may require significant expenditure of time and energy to obtain supplemental calcium.

Behavioral observations of experimental females in the calcium restriction experiment indicate that laying cowbirds have a strong calcium appetite and specifically seek out and consume material with high calcium content. At the end of the calcium restriction experiment, when oyster shell containers were returned to the pens of experimental females, several females were observed to immediately fly to the oyster shell container and rapidly consume the contents.

The shells of host eggs are one potential source of calcium supplements for wild female cowbirds. Host eggs are frequently eaten by wild female cowbirds, but Scott et al. (1992) found that as many as 40% of eggs removed from Northern Cardinal (*Cardinalis cardinalis*) nests were not eaten. If dietary calcium limits fecundity in wild females, it is difficult to explain these observations. Either wild females have some aversion to utilizing host eggs as a major source of calcium or mollusc shells and host eggs were so readily available that females could meet the calcium requirement for egg production without consuming the shells of all eggs removed from host nests.

Nest removal experiment. The results of the nest removal experiment indicate that, once egg-laying has commenced, the stimulus of host nests containing mock eggs is not necessary for continued egg production in captive female cowbirds. We conclude that availability of host nests does not limit fecundity of captive females and may not limit laying rates of wild females. We propose that female cowbirds are under strong selection pressure to produce eggs at the maximum rate, within the physiological and nutritional constraints imposed by feeding conditions. If sufficient suitable host nests are not available, this would necessitate depositing eggs in inappropriate sites. There are numerous reports of host nests containing several cowbird eggs, as well as cowbird eggs found in nests of species that rarely or never raise cowbird young, in nests of species that reject cowbird eggs, in host nests with hatched host young, in empty nests, or even on the ground (Friedmann 1929, 1963; Rothstein 1976; Friedmann et al. 1977; Friedmann and Kiff 1985).

Fecundity and egg-laying patterns of two-year-old cowbirds. The fecundity of two-year-old cowbirds averaged 11 eggs (70%) more than the same females as yearlings, in agreement with Fleischer et al.'s (1987) finding that wild yearling cowbirds are considerably less fecund than older females. The higher fecundity of captive two-year-olds was not a function of higher laying rates or earlier initiation of laying, as Fleischer et al. (1987) reported for wild females. Instead, captive two-year-olds had significantly longer laying periods than the previous year and maintained high laying rates into July. This discrepancy between the results of Fleischer et al. (1987) and our results with captive females is at least partly explained by the fact that our data were collected from the same individuals in different years; cooler, wetter weather during the 1992 laying season apparently delayed the onset of laying in some females and permitted laying well into the summer. Fleischer et al. (1987) also found major between-year differences in laying chronology of wild females.

The laying patterns of captive two-year-old females (Fig. 4), like those of captive yearlings (Jackson and Roby 1992), gave little indication of producing eggs in clutches or sets. Only one of 12 control females (J) had a laying pattern that was significantly different from random, with eggs produced in sequences interrupted by pauses. That this pattern was the exception rather than the rule provides further support for the conclusion that female Brown-headed Cowbirds are indeterminate layers capable of daily egg production for extended periods (Scott and Ankney 1983). The most fecund female (R) laid 77 eggs in 89 days, including a sequence of 67 eggs in 67 days (Fig. 4), the longest recorded laying run for any of the captive females. Female R also had the highest average laying rate (0.88 eggs/day), the longest laying period, and was the first to initiate laying and the last to terminate. Female R set a new record for number of eggs laid by a non-gallinaceous bird in a single breeding season, eclipsing the previous record of 71 eggs held by a Common Flicker (*Colaptes auratus*) that has stood for over 100 years (Phillips 1887). Female R nearly doubled her fecundity from the previous year, when as a yearling she was also the most fecund female, laying 40 eggs at an average rate of 0.91 eggs/day (Jackson and Roby 1992).

CONCLUSIONS

Our results provide no support for the hypothesis that fecundity of free-ranging Brown-headed Cowbirds is limited by the availability of host nests. We agree with Rothstein et al. (1986) that "selection has produced a generalized reproductive strategy that is relatively insensitive to host availability." Instead, our results support the hypothesis that fecundity can be constrained by the ability of females to acquire sufficient resources, specifically dietary calcium supplements, to support high egg production rates. We propose that wild female Brown-headed Cowbirds produce eggs at the maximum rate permitted by calcium availability within their home range and, in environments where calcium is not limiting, individual two-year-old females can produce an egg daily for over two months.

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