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FECUNDITY AND EGG-LAYING PATTERNS OF CAPTIVE YEARLING BROWN-HEADED COWBIRDS[1]

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Abstract. Yearling Brown-headed Cowbirds (*Molothrus ater*) were monitored in captivity to determine individual annual fecundity, patterns of egg-laying, and clutch size. Twenty-five juvenile females were captured in the wild, placed in separate pens, and provided with nests containing eggs and/or mock eggs throughout the breeding season. These females produced a total of 361 eggs over a 68 day breeding period from 16 May to 22 July. Individual fecundity of productive females (n = 22) ranged from 1–40 eggs and averaged 16.4 eggs. Individual laying rates during the laying period ranged from 0.18–0.91 eggs/day and averaged 0.56 eggs/day. Laying patterns were highly variable; one female laid an egg each day for 32 consecutive days. Laying patterns of most females were not significantly different from random and gave no indication that eggs were produced in clutches or sets. The results indicate that Brown-headed Cowbirds are indeterminant layers capable of daily egg production over extended periods and that individual females are capable of producing over 30 eggs in their first breeding season. Given an adequate supply of suitable host nests in the wild, these reproductive traits have clear adaptive significance for an obligate brood parasite.

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

INTRODUCTION

Fecundity and egg-laying patterns of the Brown-headed Cowbird (*Molothrus ater*), an obligate brood parasite, have been the subject of considerable study on free-ranging birds (Payne 1965, 1973, 1976; Scott and Ankney 1979, 1980, 1983; Rothstein et al. 1986; Fleischer et al. 1987). Recent estimates of average annual fecundity range from 30–50 eggs/year (Scott and Ankney 1980, Fleischer et al. 1987), and were calculated from the product of average laying period and the proportion of females with an oviductal egg during the laying period. However, data on the fecundity of individual free-ranging cowbirds have been elusive because of the difficulty in continuously monitoring egg production throughout the breeding season. The pattern of egg-laying in individual females has similarly been difficult to infer from either field observations or examination of reproductive tracts.

Friedmann (1929:182) concluded that about five eggs constitutes a clutch in this species, but that cowbirds may be in transition (in an evolutionary sense) from determinate to indeterminate layers. He cited a letter by F. L. Rand indicating that a captive female cowbird laid 13 eggs in 14 days (Friedmann 1929:184). Several other investigators have referred to cowbirds laying in clutches or "sets" (Nice 1937; Payne 1965, 1976; Scott 1978; Ankney and Scott 1980); but the evidence appears to be equivocal, partly because of a lack of consensus among these authors as to what constitutes a clutch. Scott and Ankney (1983) discovered that the ovaries and oviducts of cowbirds do not regress between clutches, that the average period between clutches is only two days, and that some birds miss only a day between clutches. They suggested that the laying pattern of cowbirds is unlike other passerines and more like chickens that are not allowed to complete their clutches.

Our intent in studying captive cowbirds is to investigate potential limiting factors for egg production. Our objective in this paper is solely to present fecundity and laying patterns of individual captive females that were monitored throughout the breeding season. This information provides additional insight into previously published data from wild populations. The difficulties inherent in directly determining fecundity and laying patterns of free-ranging individuals makes observations on captive birds a valuable contribution toward understanding cowbird breeding biology.

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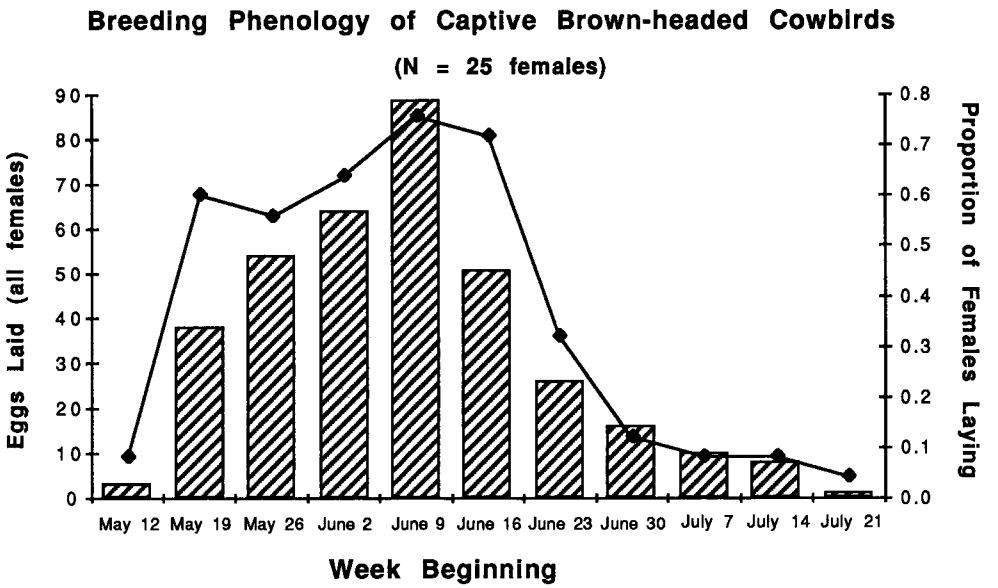

FIGURE 1. Phenology of egg production in 25 captive yearling female Brown-headed Cowbirds during the 1991 breeding season. Solid bars indicate the total number of eggs produced each week by all females and the line indicates the proportion of captive females that laid at least one egg.

METHODS AND MATERIALS

We captured cowbirds in baited traps at the Southern Illinois University Farms in August and September 1990. Only juvenile birds (as determined by plumage) were placed in captivity, because wild-caught adults are known to acclimate poorly (M. J. West, pers. comm.). Captive cowbirds were housed over winter in outdoor pens (5.1 m × 1.3 m × 1.3 m) in mixed-sex flocks of 10 individuals. In mid-March 1991, two weeks before the earliest recorded egg date (Bent 1958: 450), we moved 25 captive females to separate outdoor breeding pens (2.5 m × 1.3 m × 1.3 m). Twenty-one of those females were housed with males, while four were housed alone due to a shortage of males. Lone females could see and hear other captive males and were frequently displayed to by wild males. A specially formulated diet for cowbirds (M. J. West and A. P. King, pers. comm.) and white Proso millet seed were offered *ad libitum*. Crushed oyster-shell was provided as a dietary calcium supplement. Mealworms, wax worms, and fresh water with a vitamin supplement were also offered daily. We provided each female with five nests containing a varying (1–3) and rotating number of real host eggs (House Sparrow [*Passer domesticus*], House Finch [*Carpodacus mexicanus*], Red-winged Blackbird [*Agelaius phoeniceus*], or Barn Swallow [*Hirundo rustica*]) and/or jelly beans as mock eggs. All pens were checked daily within a half hour of sunrise to minimize egg-eating (M. J. West, pers. comm.), and all cowbird eggs were collected. The pen area also was checked daily for signs of predator activity. We followed this protocol from 26 April until two weeks after each female last laid.

RESULTS

The first egg was laid on 16 May and the last on 22 July, for a breeding season of 68 days (Fig. 1). Twenty-two females (88%) laid a total of 361 eggs; three females did not lay. The median laying date was 10 June; the modal laying date was 11 June. Seventy-six percent of all eggs laid were produced during the first half of the breeding season (16 May–18 June). Fecundity of productive females ranged from 1 to 40 eggs, with a median of 15 and a mean of 16.4 eggs (SD = 11.07, n = 22) (Fig. 2). The distribution of individual fecundity was not significantly different from normal (P = 0.321), so parametric statistical analyses were used. The average fecundity of females housed alone (14.8 eggs, SD = 9.95, range = 1–23, n = 4) was not significantly different from those housed with males (14.4 eggs,

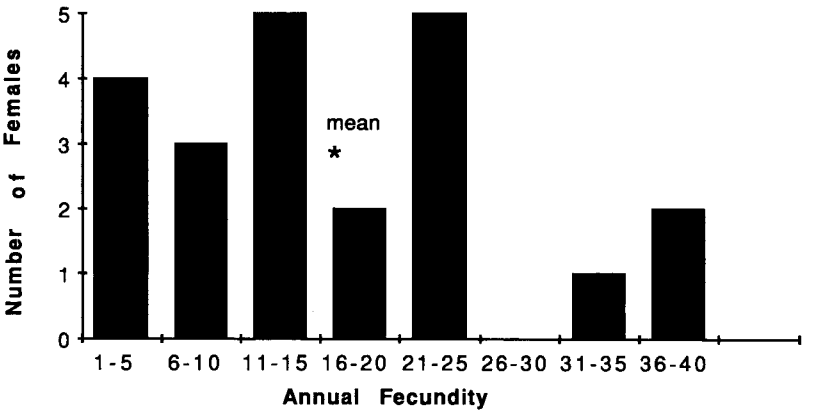

FIGURE 2. Frequency histogram of individual fecundity in 22 wild-caught, yearling female Brown-headed Cowbirds that laid eggs in captivity during the 1991 breeding season.

SD = 12.23, range = 0–40, $n = 21$, $t = 0.07$, $P > 0.05$), and data from the two groups were combined for further analyses. Laying rate during each female's laying period (from first egg to last egg inclusive) averaged 0.56 eggs/day (SD = 0.213, $n = 21$ females) with a range of 0.18–0.91 eggs/day. The longest laying period for an individual female was 56 days.

Variation in individual fecundity of productive females ($n = 22$) was significantly related to both laying rate ($r^2 = 0.690$, $F_{1,19} = 43.79$, $P < 0.0005$) and length of laying period ($r^2 = 0.761$, $F_{1,20} = 63.78$, $P < 0.0005$). Thus the most fecund females tended to have relatively high laying rates and long laying periods. Laying termination date was not significantly correlated with laying initiation date ($r = -0.034$, $P = 0.875$ and $r = -0.177$, $P = 0.552$, respectively), indicating that females that initiated laying early did not terminate early.

Laying patterns of individual females varied considerably (Fig. 3). The most fecund female (R) laid 40 eggs in 44 days, for a laying rate of 0.91 eggs/day, and included a run of 32 eggs in 32 consecutive days. For females laying more than five eggs ($n = 18$), the maximum laying run (period of uninterrupted laying) averaged 9.0 days (SD = 8.07). Six females had laying runs greater than 10 days, while one female (0) never laid consecutively. The maximum nonlaying run averaged 5.0 days (SD = 3.61, range = 2–17 days, $n = 18$ females). Average nonlaying run for the 18 females depicted in Figure 3 was 2.2 days ($n = 99$); many nonlaying runs lasted for only a single day. If clutch size is defined as the number of eggs laid without interruption, the average clutch size for these 18 females was 3.0 eggs ($n = 118$ clutches).

We used runs analysis to test for randomness of laying over each female's laying period (Sokal and Rohlf 1981:782). If captive females laid eggs in sets or clutches, the number of runs of laying and nonlaying days would be significantly less than expected by chance. Only 19 captive females laid a sufficient number of eggs to apply runs tests. Of these 19 females, 15 (79%) had laying patterns that were not significantly different from random ($P > 0.05$). Of the four females whose laying patterns were significantly different from random (females B, J, L, R; Fig. 3), all had significantly fewer runs than predicted by chance. However, none of the four laid in clutches; three of the four had long runs of uninterrupted laying, and one had a long run of nonlaying.

DISCUSSION

Fleischer et al. (1987) estimated average annual fecundity for wild yearling females at 30.5 eggs, nearly twice the average fecundity of captive yearling females in the present study. Several factors may account for the lower average fecundity of captive females: (1) subjects were wild-caught and experienced daily human disturbance throughout the breeding season, (2) there was evidence that predators periodically visited pens during the breeding season, and (3) captive females were deprived of stimuli from host nesting activity. These factors may have caused laying interruptions or early cessation of laying in some birds, contributing to the large variation of in-

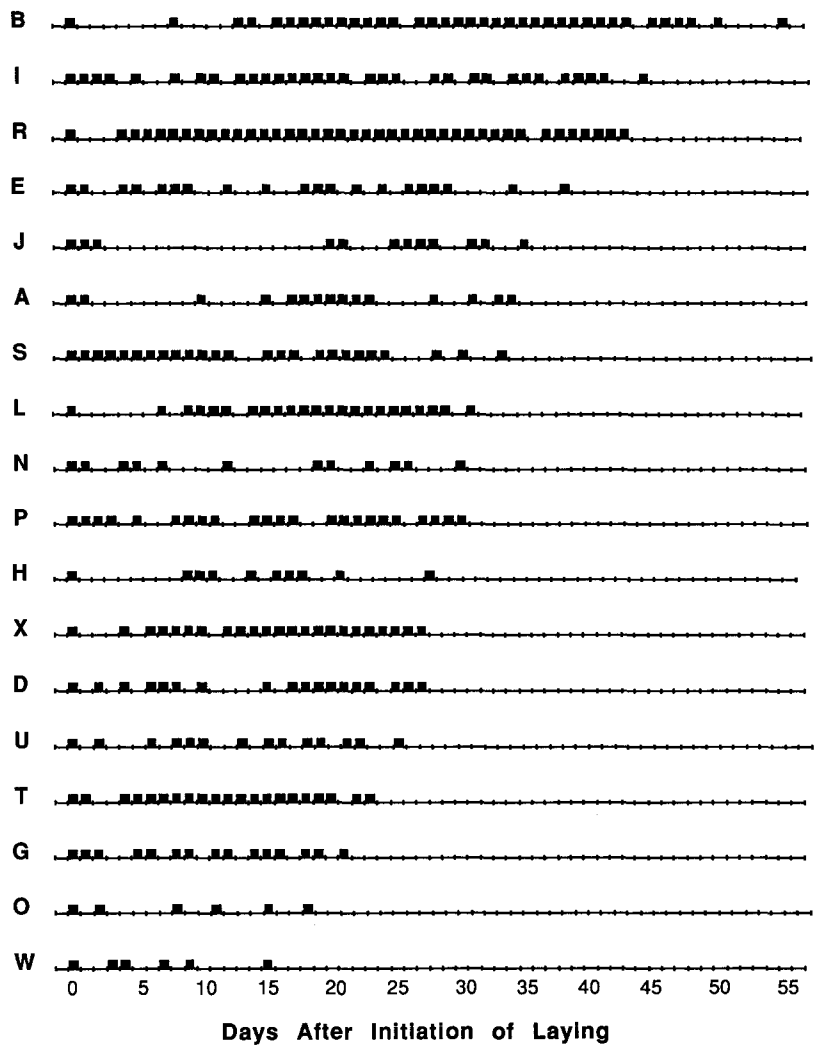

FIGURE 3. Egg-laying patterns of 18 captive yearling female cowbirds (identified by upper case letters) during the 1991 breeding season. Each bar represents a day when a single egg was produced.

dividual fecundity. In the absence of information on the factors affecting fecundity and laying patterns of captive and free-ranging cowbirds, the results from studies of captive birds must be interpreted with caution.

Wild cowbirds lay as early as 17 April in southern Illinois (D. D. Roby, unpubl. data). The last egg laid by a captive female in the present study was on 22 July, similar to the latest recorded laying date for wild cowbirds in southern Illinois (S. K. Robinson, unpubl. data). Therefore, captive yearling cowbirds initiated laying about one month later than wild birds, but terminated laying at about the same time. Fleischer et al. (1987) confirmed that the onset of laying in yearling females is delayed compared with adults in the wild, and laying rates of yearling females may be lower as well.

The results of this study support Fleischer et al.'s (1987) estimate of average annual fecundity, demonstrating that yearling female cowbirds are capable of producing over 30 eggs/year. If captive females had initiated laying a month earlier, when wild cowbirds did, individual fecundity would have been greater. The absence of a correlation between laying initiation date and ter-

mination date indicates that females that initiate earlier do not terminate earlier. Because of the late onset of laying in captive yearlings and the potential inhibition of laying caused by captivity, we believe 40 eggs/year (Scott and Ankney 1980) is closer to the norm for wild females than our observed mean (16.4 eggs). Even during the peak of laying (week of 9 June; Fig. 1), the average laying rate of captive females was only 0.51 eggs/day, considerably less than the rate of 0.80 eggs/day reported by Scott and Ankney (1979) for wild birds in late May/early June. However, we cannot be sure that the low mean and high variance in laying rate of captive females was solely an artifact of captivity. Payne (1965) and Scott and Ankney (1980) concluded from their examination of cowbird reproductive tracts that some wild females produced few, if any, eggs.

We conclude from the laying patterns of captive females that Brown-headed Cowbirds are indeterminate layers capable of daily egg production over an extended period. Our observations corroborate Scott and Ankney's (1983) comparison of Brown-headed Cowbirds to chickens prior to the onset of broodiness. There was no indication that captive female cowbirds laid in clutches or sets. If wild cowbirds produce eggs in clutches, then such a laying pattern must be the result of exogenous factors, not endogenous constraints. Payne (1965) and Scott and Ankney (1983) suggested that clutch size and frequency might be limited by either the availability of host nests or nutritional constraints. Captive females in the present study were not limited by the first factor, and the diet provided to all captive females was adequate to support extended and uninterrupted laying in at least some females.

It is apparent from the fecundity and laying patterns of some captive cowbirds that the potential effect of a single female cowbird on host reproductive success may be greater than previously thought. If laying commenced on 17 April (D. D. Roby, unpubl. data) and terminated 22 July (this study), laying at the rate of 0.91 eggs/day (maximum observed in this study) would result in annual fecundity of 88 eggs. This must be close to the upper limit for cowbird annual fecundity. Further research into Brown-headed Cowbird breeding biology is important for a better understanding of factors limiting egg production, as well as relationships between this brood parasite and host populations.

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