

ON THE MATING SYSTEM OF BROWN-HEADED COWBIRDS

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The mating system of Brown-headed Cowbirds (*Molothrus ater*; hereafter called cowbirds) is poorly understood. Cowbirds have been reported to be monogamous (Laskey 1950, Darley 1968, Rothstein 1972), monogamous and polyandrous (Friedmann 1929), polygynous (Payne 1973), and promiscuous (Nice 1937, Elliot 1980). There is also disagreement about whether or not yearling males obtain mates (or copulations) (Payne 1973, Darley 1978). These uncertainties have prompted the suggestion that different geographic populations may have different mating systems (Elliot 1980, West et al. 1981a). We think it is more likely that these differences are more apparent than real and have resulted from observer bias.

Several aspects of the social and reproductive biology of cowbirds are reasonably well known: (1) the sex ratio of breeding birds is 1.5 (or more) males to 1 female (Friedmann 1929, Darley 1971, Payne 1973, Rothstein et al. 1980); (2) adult and yearling males court females and guard them from other males (Darley 1968, Rothstein 1972); (3) yearling males produce sperm (Scott and Middleton 1968, Darley 1968) and are as likely as adults to obtain mates in a laboratory situation (Darley 1978); (4) some males copulate with more than one female and some females copulate with more than one male (Elliot 1980); (5) dominant males pair (Darley 1978) and copulate (West et al. 1981b) more often than subordinates under controlled conditions; and (6) females defend territories but males do not (Darley 1968).

Wittenberger and Tilson (1980:Hypothesis 3) proposed that monogamy should evolve in any nonterritorial species if males can reproduce most successfully by defending access to a single female; they suggested that this was particularly true when sex ratios are male biased as in the case of cowbirds. They realized, from reviewing the literature, that the cowbird mating system was complex and proposed that it might involve both monogamy and promiscuity.

In this paper, we report new data about cowbird social groups and use these data, and those summarized above, to hypothesize about the mating system of cowbirds. Our hypothesis is similar to that proposed by Wittenberger and Tilson (1980), but is based largely on different assumptions, interpretations and data about cowbirds.

METHODS

During a study of the fecundity and nutrient-reserve dynamics of cowbirds, we collected 115 males in the breeding season in 1976. Breeding season is here defined as time from when the first laying female was collected (29 April) until before the date (7 July) that the first post-laying female was collected; on 7 July we began collecting at feedlots where social groupings could not be determined and many males and females were out of breeding condition. No laying females were collected after 7 July. Birds were collected within 50 km of London, Ontario; to avoid potential bias associated with repeated sampling of a local population, we collected in a different area each week (each collection area was >8 km from all other such areas). Details of collecting are in Scott and Ankney (1979) and Ankney and Scott (1980). Birds were weighed in the field (to nearest 1 g) and the social group from which each came was recorded. We distinguished four social groups: (1) 'alone'—no other cowbirds detected nearby; (2) 'paired'—with a female; (3) 'male group'—with one or more males; and (4) 'mixed party'—with one or more males and females. The overall proportions of males which we collected from each social category likely did not reflect the true proportion of all males in those categories. That is because we intentionally collected more females than males (20 vs 15 each week) for our research about fecundity and nutrient reserves. This meant that, for example, when a pair was encountered the female was the primary target and the male was collected only if it did not disappear at the first shot, and if the weekly quota of males had not been met. Males were probably most likely to be collected as singles or from male groups but this would not affect the probability of an adult or yearling being collected from a particular social group, i.e., if the true proportion of adults and yearlings did not differ between social groups, they would not differ in our sample. Males were classed as adult or yearling according to the criteria of Selander and Giller (1960). This method is not 100% accurate as some yearlings are indistinguishable from adults, but there is no evidence that a male classed as a yearling could be adult.

Total body fat was determined by ether extraction of aliquots of oven-dried (95°C) carcasses; lean dry body weight was calculated by subtracting total body fat from the dried carcass weight. Complete details of carcass analysis are given in Ankney and Scott (1980).

RESULTS

The ratio of adult to yearling males in our sample was 1.56:1, which is very similar to the ratio (1.65:1) reported by Darley (1968) from a sample trapped during the breeding season. Birds were collected in breeding habitat (71%) and feeding habitat (29%), but the proportion collected in breeding habitat was independent ($P > 0.5$, G-test) of social group: single—75%, paired—67%, male group—75%, mixed party—69%. Also, 71% of adults and 70% of yearlings were collected in breeding habitat. Thus, the proportions of adults and yearlings we collected from each social group were not biased by where we collected (see Scott and Ankney [1979] for details about habitats). The social group from which a male was collected was not independent ($P < 0.025$) of the male's age (Table 1). Yearlings were more likely to be paired or in male groups and adults were much more likely to be single.

Although there were no significant differences ($P > 0.1$) in mean body weights among social groups, the mean weights of paired males were the

TABLE 1
SOCIAL GROUP VS AGE OF MALE BROWN-HEADED COWBIRDS

	Social group				Total
	Single	Paired	Male group	Mixed party	
Adult	28 (40%)	10 (14%)	11 (16%)	21 (30%)	70
Yearling	7 (16%)	11 (24%)	15 (33%)	12 (27%)	45

$G = 11.164, P < 0.025$

heaviest and those of birds from male groups were the lightest (Table 2A). However, when the data for adults and yearlings were combined (they did not differ in body weight [Ankney and Scott 1980]), and paired males tested against all other males, we found that paired males were heavier ($P < 0.05$, Table 2B). This is especially striking as the 'all other male' category undoubtedly contained some paired males. For example, mixed parties frequently are formed when a pair of cowbirds is joined by one or more males and, thus, a male collected from a mixed party could have been the paired male.

There were no significant differences ($0.25 > P > 0.1$) in mean fat reserves or lean dry weights (an index of protein reserves) among males in the four social groups. However, in both cases the mean for paired males was the largest and that for males from male groups was smallest. This suggests that paired males were heaviest because they had slightly larger fat and protein reserves.

TABLE 2
BODY WEIGHT VS SOCIAL GROUP OF MALE BROWN-HEADED COWBIRDS^a

A. Adults and yearlings	Social group				P^b
	Single $\bar{x} \pm SE$	Paired $\bar{x} \pm SE$	Male group $\bar{x} \pm SE$	Mixed party $\bar{x} \pm SE$	
Adult weight (g)	51.7 \pm 0.5	52.3 \pm 1.0	50.4 \pm 0.8	50.8 \pm 0.7	0.25 > P > 0.1
Yearling weight (g)	50.9 \pm 1.4	52.6 \pm 0.9	50.3 \pm 0.8	51.2 \pm 0.8	0.25 > P > 0.1

B. Combined data	Social group		P
	Paired males $\bar{x} \pm SE$	All other males $\bar{x} \pm SE$	
Male weight (g)	52.5 \pm 0.6	51.0 \pm 0.3	0.05 > P > 0.01

^a Sample sizes as in Table 1.

^b Probability, from one-way ANOVA, that means in a row differ by chance.

DISCUSSION AND HYPOTHESIS

Possibly some single males were actually paired; Darley (1968) noted that although a female was normally alone when searching for nests, her mate was usually nearby on a prominent perch or "singing tree." However, such males eventually re-joined the female and if all single males were paired then the age ratio would have been similar in the single and paired categories, but it was not (10:11 vs 28:7 = $P < 0.025$, Table 1).

There is an anomaly in the social biology of male cowbirds: yearlings appear as likely as adults to participate in breeding. That is particularly puzzling because the sex ratio of breeding cowbirds is strongly skewed (1.5:1) in favor of males (Laskey 1950, Darley 1971, Payne 1973). Clearly, under such conditions and strict monogamy, one-third of all males would not obtain mates and it could be expected that yearlings would be excluded from breeding or participate much less than adults, especially as adult males return in spring almost 2 weeks, on average, before yearling males (Darley 1968). Yearling males in several other icterids participate little or not at all in breeding. For instance, adult male Red-winged Blackbirds (*Agelaius phoeniceus*) are much more likely to obtain territories, and thus mates, than are yearlings (Payne 1979), and adults are dominant over yearlings (Searcy 1979). However, all available evidence shows that yearling male cowbirds do breed. First, the yearling and adult testes cycles are very similar (Scott and Middleton 1968); Darley (1968) found that of 19 adult and 16 yearling males collected in late June, the testes of 16 adults and 15 yearlings contained mature sperm (testes of three adults and one yearling were regressed). Second, Darley (1968) showed that in 32 individually marked, mated pairs there were 21 adult and 11 yearling males, which was similar to the overall age ratio of males in that population. Third, Darley (1978) found that under laboratory conditions, yearlings were as equally likely as adults to obtain mates. Finally, and most important, Darley (1968) demonstrated that some adults do not obtain mates. When he removed 15 mated males from the population, 12 were replaced by eight adults and four yearlings; 9 of the 12 were previously unmated and the other three were already mated and became bigamists (Darley did not report the age of the bigamists).

We have developed an hypothesis to explain the foregoing anomaly which also rationalizes the contradictory reports about cowbird mating systems. We propose that the mating system of cowbirds is a combination of monogamy and promiscuity which occurs because males use two tactics to obtain copulations. The first is to obtain a mate, vigorously guard her from other males, and thus monopolize copulations with her (hereafter called 'paired' males). Apparently, larger, more dominant males, are most suc-

cessful at this (Table 2B). Darley (1968) observed that in 18 mated male–unmated male encounters, mated males were dominant in 16 ($P < 0.001$). The second tactic is either to not attempt to pair, or if unsuccessful at pairing, to steal copulations from ‘paired’ males. Possibly, the second tactic is not really a tactic, in an evolutionary sense, but simply a result of some males being unsuccessful at pairing, and thus having to be ‘sneaky’ males. In either case, given the skewed sex ratio, there are many males which can only obtain copulations by stealing them from ‘paired’ males. Darley’s (1968) data suggest that at least some ‘sneaky’ males are successful. He observed seven copulations and in three the male was not the one paired to the copulating female. Elliot (1980) observed copulation by the same male with different females and vice versa, but he did not know which, if any, were ‘paired’ males.

Do cowbirds actually form pairs? We suggest that from the female’s viewpoint they do not. This is logical because of the peculiar breeding biology of cowbirds. There is no parental care by cowbirds and it is the female which defends a territory (Darley 1968). All a female cowbird gets from a male is genetic material, and, through the guarding behavior of the ‘paired’ male (Laskey 1950, Darley 1968), some relief from harassment by other males, especially when she is feeding. However, the presence of a male may be a cost for the female when she is searching for host nests; a female normally drives away the ‘paired’ male before searching for nests (Darley 1968). Wittenberger and Tilson (1980:200, Hypothesis 3) noted that for monogamy to evolve it was not necessary for a female to benefit from being guarded by a male, but “the costs of resisting the male’s continual presence must exceed the cost of accepting his presence.” Apparently, a female cowbird accepts a male’s presence when it benefits her and not when there is a cost.

A female cowbird has little or no reason to be faithful to the ‘paired’ male and may increase her fitness by being receptive to other males. If the ‘paired’ male is adept at guarding and prevents other males from copulating with her, that is an excellent trait to pass on to her sons. But, if another male is sufficiently sneaky to circumvent the ‘paired’ male, that ability is also worth passing on. It is difficult to see how a female’s fitness could be lowered by mating with a ‘sneaky’ male; even if the cuckolded ‘paired’ male were to desert her he would quickly be replaced, as shown by Darley’s (1968) removal experiment.

The average female cowbird, in southern Ontario, lays about 40 eggs over 8 weeks (Scott and Ankney 1980) and the average interval between clutches is about 3 days (Scott 1978). During this interval, most females have large ovarian follicles ready to ovulate within a day or so (Scott and Ankney, unpubl.). Thus, most females are continuously susceptible to

fertilization for a long period, thereby greatly increasing the chances of 'sneaky' males to steal copulations. This contrasts markedly with the pattern of fertility in most other birds.

That male cowbirds establish dominance hierarchies and the dominant males become the 'paired' males (Rothstein 1972, Darley 1978) suggests that there is value in being a 'paired' male. Thus, there should be selection for increased body size in male cowbirds. Male cowbirds are about 25% heavier than females (Ankney and Scott 1980), but that is much less than the dimorphism in some other icterids, e.g., Red-winged Blackbirds—65% (Brenner 1968), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*)—80% (Searcy 1979), in which male dominance is important in mating success. Large adult male cowbirds apparently have higher mortality rates at winter roosts than do smaller adult males (Johnson et al. 1980). However, that cannot counter selection for increased size if only larger, dominant males copulate, especially as there was no relation between body size and mortality rate in juvenile males (Johnson et al. 1980), i.e., differential mortality does not occur until after males have had an opportunity to breed. We hypothesize that the selection for increased size in males is countered because smaller males are able to steal copulations.

Why are adult males single more frequently than are yearlings? This may result from the higher winter mortality of large adults (Johnson et al. 1980 (in winter, adult males include the yearling males from the previous breeding season). Thus, in the breeding season, the yearling cohort may contain as many large males as the adult group, resulting in more adults being unpaired. However, our data show that adults did not weigh less, on average, than yearlings. Possibly, some adults do not attempt to pair and employ a 'sneaky' strategy throughout the breeding season. We cannot explain why that should be a better tactic for adults than for yearlings.

A mating system such as we have proposed could easily lead researchers to conclude differently about the system. Only intensive observations of marked birds (e.g., Darley 1968) would reveal the monogamous aspects of the system, i.e., that a particular female is usually seen with a particular male. More casual observations of marked birds (e.g., Nice 1937, Elliot 1980) or of unmarked birds (Payne 1973) would miss that and thus lead to the conclusion that cowbirds are promiscuous or polygamous. Studies of captive cowbirds would suggest a monogamous system if several males are placed with one female (e.g., Rothstein 1972, Darley 1978) or a polygynous system if several males are placed with several females (West et al. 1981b). Under such conditions the males establish a clear dominance hierarchy and the dominant male can successfully guard the female(s) from subordinate males.

To summarize, we propose that male cowbirds try to pair with females,

but, due to the skewed sex ratio, not all are able to do so. The unpaired males are apparently quite successful at stealing copulations from 'paired' males. It seems likely that 'paired' males also attempt to steal copulations, i.e., they may have a "mixed reproductive strategy" (Trivers 1972), similar to that of Bank Swallows (*Riparia riparia*) (Beecher and Beecher 1979). Females may be quite passive in this system and are as promiscuous as the 'paired' male allows. Such a situation may not be that uncommon in other species (see Bray et al. 1975, Beecher and Beecher 1979, Fujioka and Yamagishi 1981) but is perhaps more pervasive in cowbirds because the greatly extended laying period of females gives 'sneaky' males many opportunities to steal copulations.

More data are needed to evaluate the mating system of cowbirds, e.g., When, where and how frequently do females copulate? Does the social status of a male change in subsequent breeding seasons? Are there differences in annual return rates of banded males from different social groups? Particularly valuable would be information about the frequency at which 'unpaired' males fertilize eggs. Vasectomizing paired males would determine whether or not unpaired males obtain copulations, but not how successful they normally are at obtaining fertilizations. An electrophoretic analysis of the paired male, his female and her offspring would accomplish that (see Sherman 1981).

SUMMARY

The mating system of Brown-headed Cowbirds (*Molothrus ater*) is poorly understood despite frequent comments in the literature. Cowbirds have been reported to be monogamous, polygynous, or promiscuous. We present an hypothesis that the mating system of cowbirds combines monogamy and promiscuity. It is based on our observations of social groupings and weights of wild adult and yearling males, and on published observations of social behavior of cowbirds. We propose that males use two tactics to obtain copulations. The first is to guard a female from other males, i.e., be a 'paired' male to monopolize her copulations. The second is to be a 'sneaky' male and to steal copulations from 'paired' males. 'Paired' males could also be 'sneaky' males. Females are probably as promiscuous as the 'paired' male allows. This system is likely because: (1) the sex ratio of 1.5 males to 1 female excludes many males from being 'paired'; (2) females have no apparent reason to be faithful to the 'paired' male and may increase their fitness by copulating with 'sneaky' males; (3) females are continuously fertile for 8 weeks, thus 'sneaky' males have many opportunities to steal copulations.

ACKNOWLEDGMENTS

We thank S. Johnson, R. Seguin and D. Seip for helping us collect cowbirds and the many landowners who gave us permission to collect cowbirds. P. Handford, J. Millar, S. Rothstein, P. Weatherhead and an anonymous reviewer made helpful suggestions on the manuscript. The research was supported by the National Sciences and Engineering Research Council of Canada.

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CANADA. ACCEPTED 10 MAR. 1982.