

## PAIR BONDS AND FACTORS INFLUENCING THE DIVERSITY OF MATING SYSTEMS IN BROWN-HEADED COWBIRDS<sup>1</sup>

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**Abstract.** Observations of radio-tagged Brown-headed Cowbirds (*Molothrus ater*) indicated that individual males and females engage in extended associations through the breeding season. Persistent courtship by males directed at particular females and extended time spent together by certain males and females suggests that cowbirds form pair bonds. When individuals of the pair are together, females are more likely to initiate departures than males, and males are more likely to follow their mates after they depart. These observations suggest that pair bonds are being maintained by males.

There were four cases of monogamy, as well as two bigamous and at least one trigamous relationship in the local population. Radio-tracking data showed that the range of a male encompassed most or all of that of his mate(s). The mating system of this population is compared with those of other populations in an attempt to assess factors influencing the diversity of cowbird mating systems. We suggest that cowbird mating systems may be influenced by both the sex ratio of the population as well as the habitat in which populations are found.

**Key words:** Brown-headed Cowbirds; mating systems; polygamy; pair bonds; spacing patterns.

### INTRODUCTION

Monogamy is thought to be the prevalent mating pattern in birds because in most species the number of offspring per individual is greater for pairs than for polygamous individuals or groups (Lack 1968). Although natural selection has favored breeding strategies that increase individual male and female reproductive success, common interests such as egg and nestling survival result in many similarities in the breeding activities of the two sexes. Brood parasites, in which males and females are both emancipated from duties associated with care of eggs and nestlings, offer a unique opportunity to examine mating systems when the breeding individuals are not constrained by the mutual requirements of parental care (Payne 1977).

Early studies on the social organization of the brood parasitic Brown-headed Cowbird (*Molothrus ater*) relied on periodic sightings of a few marked or unmarked birds and must be interpreted with caution. Friedmann (1929) suggested that cowbirds are generally monogamous (or in some cases polyandrous), while Nice (1937) suggested that cowbirds do not form pair bonds and are promiscuous. Laskey (1950) found no evidence of either polygamy or promiscuity and concluded that cowbirds are monogamous. More recent studies have added to the confusion. While Payne (1973) suggested that cowbirds are polygynous, Darley (1982) found them to be both monogamous and polygynous, and Elliott (1980) concluded

that they are promiscuous. Most recently, Dufty (1982a) found all birds in his study area to be mated monogamously.

These conflicting observations can be resolved in one of two ways. On the one hand, all cowbird populations might exhibit a similar mating system, and reported differences are simply the result of observer bias (Ankney and Scott 1982). Alternatively, the mating system of cowbirds might be flexible, and observed differences between populations are real. If this is true, it should be possible to identify and assess factors that may be influencing this diversity in mating systems.

We here provide information on the extent and maintenance of pair bonding of cowbirds in eastern Ontario, in an effort to understand their mating system and to evaluate the alternative explanations posed above.

### METHODS

This study was conducted on a 20-ha study site at the Queen's University Biological Station near Chaffey's Locks, Ontario, which is described in Teather and Robertson (1985). The study site was divided into 30 × 30 m quadrats and observations were plotted relative to this grid.

Trapping was conducted in 1981 and 1982 every day or every other day from the third week in April to the end of May and periodically thereafter until the end of the breeding season. Birds were attracted to areas baited with cracked corn and were captured in mist nets or Potter traps. Individuals were banded with Canadian Wildlife Service aluminum bands and a unique combination of colored leg bands. Since leg bands were not readily discernible if birds were walking in grass, wings were marked with one or two spots of acrylic

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paint corresponding to leg band sequence. This enabled individual identification of birds at distances up to 75 m using binoculars (7×) or up to 150 m using a spotting scope (20×).

We recorded initial observations while either systematically walking through the study area at various periods during the day or while remaining stationary (up to 3 hr) at locations known to be visited by cowbirds. We noted the location of all identifiable birds as well as courtship, aggressive, and feeding behaviors. Courtship involved males bowing to, and often closely following, females. The bow display was described in detail by Friedmann (1929). Aggressive interactions nearly always involved only females and consisted of chattering (a female aggressive vocalization [Dufty 1981]), bill pointing, and chasing, or a combination of these behaviors.

Upon establishing which birds were residents, we recaptured and attached radio transmitters to six males and seven females (see Teather and Robertson 1985). Birds were tracked continuously for periods ranging from one-half to three hours. The total time tracked for individuals ranged from 3.3 to 34.5 hr (average =  $16.41 \pm 10.14$  hr).

Home ranges were estimated using confidence ellipses (Koepl et al. 1975) based on coordinates obtained during radio-tracking and visual-observation periods. We omitted sightings of individuals at artificial feeding stations because the large number of observations at these sights would bias range calculations. Observations made while individuals were feeding in cattle pastures were also omitted, since pastures were not considered to be part of the breeding habitat. We feel that confidence ellipses are more indicative of range use than are convex polygons, which often contain large unused areas.

## RESULTS

### POPULATION STRUCTURE

Seventy-two males and 55 females were captured in 1981 (sex ratio = 1.31:1); in 1982, 64 males and 51 females were caught (sex ratio = 1.25:1). The observed sex ratio did not differ significantly from unity in either year nor when data from both years were combined ( $G = 1.86$ ,  $P > 0.1$ ).

In 1981, 20.8% (15) of all males initially captured were subsequently recaptured while only 12.7% (7) of all females were recaptured. A similar trend was apparent in 1982 with 26.6% of all males being recaptured compared to a recapture rate of 15.7% for females. Although the differences were not significant ( $G = 2.34$ ,  $P > 0.1$ ), these data might be in-

terpreted as indicative of a trapping bias in favor of males. This would contradict earlier investigations by Darley (1968) and by Burt and Giltz (1976), who found a recapture bias in favor of females and suggested that estimates of sex ratios based on capture data were minimum values. It is possible that although females may be trapped more readily than males, males are more likely to remain in the area after initial banding or to suffer lower mortality than females (Searcy and Yasukawa 1981). Either of these would result in a higher incidence of male recaptures.

### BREEDING STATUS OF RESIDENT BIRDS

Figure 1 outlines the relationships between all males and females in 1981 and 1982 that were considered to be residents. Two individuals were said to be paired if (i) they spent at least 10% of their time together (as determined by radiotelemetry) and (ii) if, during this time, they engaged in courtship activity (cf. Tables 1 and 3 discussed below). Using these criteria, breeding status could be determined accurately for 29 of the 33 residents. Pair relationships for the other individuals were postulated, but insufficient observations on these birds render these relationships inconclusive.

There were four clear cases of monogamy and three clear polygynous matings, two of which were bigamous and at least one of which was trigamous. There were two possible cases of polyandry, although data were insufficient to confirm this. In both years nearly 50% of all resident males remained unmated (1981—5/11, 1982—4/9). These males were observed either courting many different females or, alternatively, courting infrequently.

We consider some male cowbirds to have exhibited simultaneous polygyny because they were observed to associate with more than one female during a given period of the breeding season. This association usually took the form of the male being seen with one of the females one day, another female later that day, and again with the first female the next day. However, no temporal sequence was detected such that he always consorted with a particular female in the morning, for example. Occasionally we observed a polygynous male in the company of both (or all three) of his mates at the same time.

In 1982, Female YDY left the area immediately after being equipped with a transmitter on 28 May. She had previously been courted by both RRD and RGD males and probably would have paired, or was paired, with one or both of these birds. Male RGD was subsequently radio-tagged and was found to be un-

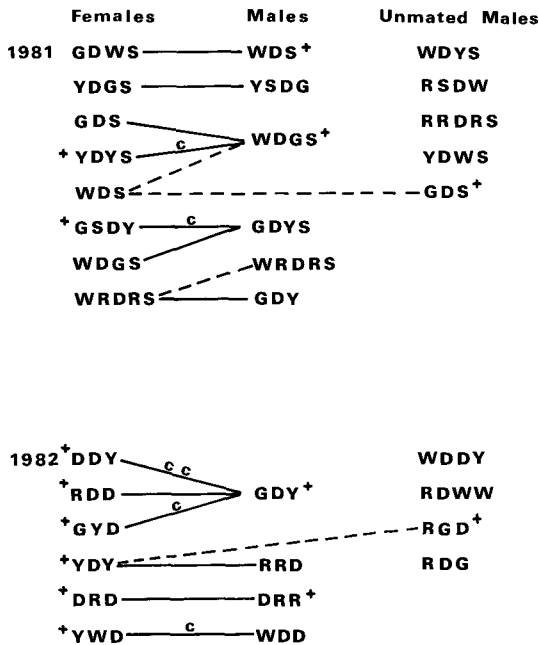


FIGURE 1. The mated status of resident male and female Brown-headed Cowbirds in 1981 and 1982. Solid lines join individuals known to have formed pair bonds. Dashed lines join individuals seen courting infrequently. WDD was also seen copulating with a marked nonresident female, and with an unmarked female. RGD copulated with DDY after her mate was removed. WDD copulated with an unidentified female.  
 + indicates a radio-tagged bird.  
 c indicates a copulation observed.

mated during the rest of the breeding season. Male GDS (1981), although unmated for most of the season, was seen frequently courting Female WDS in late June. It is unclear whether they were paired.

RANGE OVERLAP

As a preliminary indicator of the degree of pair bonding, we examined the degree of home range overlap between mated individuals. The

range locations of both members of a monogamous pair (Male DRR and Female DRD) were nearly identical, although the male's range was larger than that of the female (5.45 vs. 3.48 ha) (Fig. 2a). Similarly, the range of bigamous Male WDGS was larger (4.69 ha) and encompassed most of both female ranges (2.52 and 3.18 ha; Fig. 2b). Female GDS did not carry a radio transmitter and her range was calculated from general observations only. The range of trigamous Male GDY (4.94 ha) overlapped all three female ranges (1.95, 2.55, and 3.06 ha) although to a lesser extent than those of the monogamous and bigamous males (Fig. 2c). Note that this male was mated monogamously in 1981.

The three male ranges presented here were significantly larger than the six female ranges (Mann-Whitney *U*-test,  $U = 0$ ,  $P = 0.001$ ). The ranges of two unmated males (GDS, 1981; RGD, 1982) could not be determined accurately, as these males frequently left or were absent from the study area during radio-tracking. Mated males were nearly always present in the study area.

MATE ATTENDANCE

The percentage time that mated individuals were together was estimated from a subset of radiotelemetry data in which we were reasonably certain whether or not the birds were together (Table 1). The percentage of time both members of a pair spent together was estimated from the sum of the amount of time the female was observed with the male (while tracking the male) and the amount of time the male was observed with the female (while tracking the female), as a proportion of the total observation time. This represents the minimum time spent together by paired individuals, since in some cases mates may have been present but not visible to us.

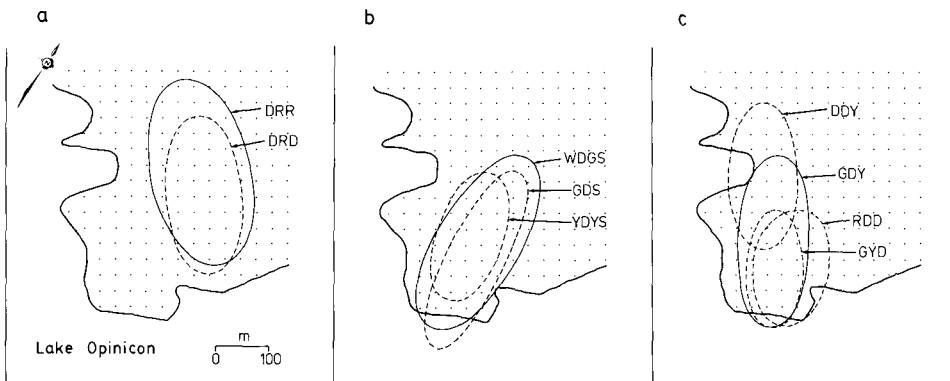


FIGURE 2. Fifty percent confidence ellipses showing the amount of range overlap between mated males and females. Solid lines indicate male ranges; dashed lines indicate female ranges. (a) a monogamous pair. (b) male mated bigamously. (c) male mated trigamously.

TABLE 1. Percentage of time spent together by cowbird pairs.

Male	Female	Percent time together	Total time tracked (min)
DRR	DRD	29.9	2,281
WDGS <sup>a</sup>	YDYS	48.6	473 <sup>b</sup>
WDGS <sup>a</sup>	GDS		
GDY	DDY	10.5	2,624
GDY	RDD	24.6	1,479
GDY	GYD	30.3	1,691
WDS <sup>a</sup>	GDS	32.0	359
WDD <sup>a</sup>	YWD	11.9	1,424
GDYS <sup>c</sup>	GSDY	40.5	690

<sup>a</sup> Only one member of the pair was radio-tagged.

<sup>b</sup> Data combined for both females. Since the two females mated to male WDGS were not radio-tagged, it was often difficult to determine which he was with at any one time. We estimated he was with at least one of these females, and sometimes both, approximately 49% of the time he was radio-tracked.

<sup>c</sup> This male was also mated to another female (cf. Fig. 2).

#### DEPARTURE INITIATION AND FOLLOWING

If males accompany females, then one would predict that females would more frequently initiate departures and that they would often be followed by males. If females accompany males, the reverse would be expected. If males and females are mutually responsible for mate attendance, or there is no mate attendance, no differences in either departure initiation or following should be apparent.

Females initiated significantly more (120) of the 155 observed departures than did males (35) ( $G = 26.47$ ,  $P < 0.001$ ; Table 2). In addition, males were significantly more likely to follow females within 10 sec (85%) than females were to follow males (17%) ( $G = 18.32$ ,  $P < 0.001$ ).

When they were seen together, females were followed by their mates 83% of the time and followed by males other than their mates 80% of the time ( $G = 0.009$ ,  $P > 0.9$ ). Females followed their mates 13.8% of the time and were not observed to follow other males.

#### COURTSHIP OF RESIDENT FEMALES

In 30% of the cases in which females were observed being courted by identifiable males, males other than their mates were involved (Table 3). To further examine the relative success of mate guarding, a male (GDY), which was mated to three females (DDY, RDD, GYD) was removed from the population on 23 June 1982. Courtship by other males directed at Female DDY increased from 9.4% of all observations before removal (omitting radio-tracking data) to 46.1% of all observations after removal ( $G = 7.93$ ,  $P < 0.01$ ). Similarly, Female RDD was courted more frequently by other males after removal of her mate (57.1%) than before (15.5%) ( $G = 6.65$ ,

TABLE 2. Following behavior in relation to which member of a pair initiates departure, for seven marked females.

Female	(a) When the male departs first, the female:		Follows other male	
	Follows mate	Follows other male	Yes	No
	Yes	No	Yes	No
DDY	2	13	0	1
DRD	1	6	0	3
RDD	1	3	0	1
GYD	0	2	0	0
YWD	0	1	0	1
GSDY	0	0	0	0
YDYS	0	0	0	0
Total	4	25	0	6

(b) When the female departs first, she is:

Female	Followed by mate		Followed by other male	
	Yes	No	Yes	No
DDY	19	5	4 (8)*	0
DRD	8	3	2	1
RDD	11	0	6 (10)*	2
GYD	14	0	0	0
YWD	1	1	4	1
GSDY	2	0	0	0
YDYS	13	5	0	0
Total	68	14	16 (18)*	4

\* Numbers in parentheses are the number of times the female was followed by another male after her mate had been removed.

$P < 0.01$ ). Female GYD was not observed in the study area after 9 June 1982 and could not be used in this analysis.

## DISCUSSION

#### EXTENT OF THE PAIR BOND

Since male and female cowbirds do not exhibit parental care, there is the potential for a highly promiscuous mating system. Indeed, since in some cases cowbirds appear to form very weak pair bonds or no pair bonds (Nice 1937, Elliott 1980) this potential may be realized under certain circumstances. Other studies, however, suggest that there is a strong tendency for individuals to form pair bonds.

Friedmann (1929) found that male and female cowbirds spent considerable time together in mutual territories. Recently, Darley (1982) showed that ranges of monogamous males encompassed most or all of the ranges of their mates. Similarly, Dufty (1982a) found the ranges of both members of a pair to be identical. The one monogamous pair for which we could accurately determine home ranges supports these studies. Darley also found that bigamous males have ranges which overlap most or all of the ranges of both females. These results are again consistent with our own. Although neither Dufty nor Darley found any males having three mates, one might expect such a male to have a range largely overlapping all three female ranges. Our results indicate this to be the case, although to a lesser extent

than for either the monogamous or bigamous male.

The amount of time spent together by cowbirds should be an indicator of the requirements of pair bonding and mate guarding, without the constraints of a mutual interest such as a nest site, as occurs in most other species (Leffelaar and Robertson 1985). Our results indicate that males and females spent an average of 23.5% of their time together. Dufty (1982a) also found a close association between pair members, as males accompanied females throughout much of the day. He noted that individuals of one pair were together for about 67% of the time in the morning, even though it was known that birds were often separated for extended periods during this time. Dufty's estimate was based on data where birds were being radio-tracked simultaneously, and he assumed that two birds were together if their signals came from the same area. Since males may not always be aware of the presence of their mates, even when close by, Dufty's value may be slightly inflated. Our estimates are minimum values since they are based on visual observations and it was sometimes difficult to ascertain if the mates of individuals being radio-tracked were present. However, the difference between 23.5% and 67% remains large, and it is quite likely that individuals in the New York population indeed showed a higher degree of mate attendance than in this area. The significance of this is discussed below.

#### MAINTENANCE OF THE PAIR BOND

Nice (1937) noted that inter-male aggression occurred only during communal courting parties which Laskey (1950) interpreted as resulting from males defending females from other males. Since then, mate guarding in cowbirds has been documented by both Darley (1982) and Dufty (1981, 1982b). Our data, which show that females are more likely to initiate movements than males, and that males are more likely to follow females than females are to follow males, further suggest that males are guarding females and are responsible for the high degree of mate attendance.

Mate guarding is generally considered to be a strategy employed by males to reduce the chances of being cuckolded. It has been well documented in a number of species (see references in Dufty 1982b). In each case, guarding behavior by males decreases rapidly after females become sexually unreceptive. However, as the breeding season of cowbirds is extended over a period of approximately eight weeks (Scott 1963) and individual females are reproductively active throughout this period (Scott and Ankney 1980), it is not surprising that a

TABLE 3. Courtship of resident females by their mates and other identified males.

Female	Number of times courted by:	
	Mate	Other male
DDY	23	7 (12)*
DRD	11	11
RDD	10	11 (12)*
GYD	21	1
YWD	5	3
GSDY	2	0
YDYS	5	1
Total	77	34 (24)*

\* Numbers in parentheses are the number of times females were courted by other males after their mates had been removed.

high level of mate guarding occurs throughout the season.

Copulations between cowbirds were seen infrequently, so it is difficult to assess the success of mate guarding. Of the ten copulations observed, six occurred between mated individuals (Fig. 1). The others occurred between an unmated resident male and an unidentified female, between a mated male and two different females (one nonresident and one unmarked) and between an unmated male and a mated female whose mate had been removed three days earlier. Therefore, there is the potential for unmated males to obtain copulations and for mated males to obtain extra-pair copulations. Darley (1968) reported that three of seven copulations in his study area involved non-mated birds. Elliott (1980) witnessed twenty-five copulations in which the identity of at least one participant was known and found that six individuals (five females and one male) had more than one sexual partner. Dufty (1981, 1982a) saw no copulations in the New York population.

If the percentage of times a female is courted by males other than her mate is an indication of the success of mate guarding, one might conclude that males were relatively unsuccessful. In 30% of all cases in which a female was courted, the courting male was a bird other than her mate. Thus, there would appear to be ample opportunity for unmated males to steal copulations. On the other hand, when Male GDY was removed, the number of times his mates were courted by other males increased significantly, suggesting mate guarding was quite effective.

The female's role in establishing and maintaining pair bonds is open to speculation. Laskey (1950) observed that a female would accept the dominant male in the area as a mate, suggesting a somewhat passive female role in mate selection. Ankney and Scott (1982) suggested that from the female's standpoint, cowbirds do not form pair bonds as there was little

reason for a female to remain faithful to her mate after egg-laying. However, West et al. (1981) found that females mated with the highest status male presented to them while rejecting subordinate males. As females would have the opportunity to evaluate a number of males under natural conditions, it is reasonable to assume that female preferences may be important. They also suggest that females play an active role in controlling when and how frequently copulations occur.

#### FACTORS INFLUENCING DIVERSITY IN COWBIRD MATING SYSTEMS

Although results of early investigations must be interpreted with caution because they often relied on anecdotal observations of unmarked birds, four recent studies can be accepted as reasonably accurate descriptions of cowbird mating systems. These show cowbirds as being highly promiscuous (Elliott 1980), monogamous or polygynous (this study), primarily monogamous with a few cases of polygyny (Darley 1968), and strictly monogamous (Dufty 1981). It is apparent that the diversity of reported mating systems for cowbirds is real and not simply a function of observer bias as suggested by Ankney and Scott (1982). In light of this, it is important to examine selection pressures which may be responsible for this diversity.

Habitat type and quality has an important effect on host nest density which may be related to female territoriality (Elliott 1980, Teather and Robertson 1985). Elliott postulated that in prairie habitats, where host nest density is low while density of cowbirds is high, available nests would be spread out over such a large area that territorial defense would be uneconomical. If the birds are not localized on territories, a close association between male and female may not be easily maintained and promiscuity may result. This appears to be the case in the Sierra Nevada where females range over large areas and do not form close associations with males (Rothstein et al. 1984). In contrast, in areas where host nests are abundant, and female cowbirds are found on restricted territories, males might profit from defending one or more females and monopolizing copulations with them (Dufty 1981).

The sex ratio of a population may influence the mating system of cowbirds by weighting the advantage of mate guarding. Wittenberger and Tilson (1980) stated that monogamy could be the result of males defending access to specific females. Evidence presented here indicates that males defend females from other males and that guarding behavior reduces access of females to other males. Wittenberger

and Tilson further suggested that a situation such as this would be especially advantageous when the sex ratio of a population is skewed in favor of males, and males might fare less well by "taking their chances in a promiscuous 'lottery' system" (p. 200).

Skewed sex ratios in cowbird populations are common. Friedmann (1929) suggested that males in his study area outnumbered females approximately three to two, and that this might vary in different parts of the country. This has been verified with reported sex ratios of 1.6:1 (Dufty 1981), 1.5:1 (Darley 1968), 1.3:1 (this study) and 1.1:1 (Elliott 1980).

Ankney and Scott (1982) proposed a mating system for cowbirds based on Wittenberger and Tilson's third hypothesis. They suggested that cowbirds express a system of both monogamy and promiscuity because males use two different tactics to obtain copulations. Males could obtain a mate and vigorously guard her from other males or, if, unable to obtain mates, could adopt a sneaker strategy. The result would be a system in which some males would be observed to be monogamous while others would appear to be promiscuous.

Given this, it is unclear why Ankney and Scott reject observations of different mating systems for different populations as "observer bias." Given that sex ratios vary between populations, mating systems should be variable. As the sex ratio approaches unity, the pressure on males to guard females from floating males is reduced, and subsequently a male would be free to seek (and possibly defend) additional mates. If, on the other hand, there are substantially more males than females, it would be in the male's best interest to monopolize one female.

Unfortunately, because of the few studies on cowbird mating systems, few data exist to accurately test this hypothesis. Those data that are available, however, appear to fit the prediction. Dufty (1981), investigating a population having the highest male to female sex ratio (1.6:1), found all the birds in his area were monogamous. Elliott (1980) at the other extreme, found a highly promiscuous population having a sex ratio of approximately 1.1:1. Between these extremes, Darley (1968) noted that while most of the birds in his area were monogamous, polygynous relationships did exist (sex ratio 1.5:1) and despite a small sample, it appears that monogamy and polygyny both occur relatively frequently in our population (sex ratio 1.3:1).

In conclusion, existing evidence indicates that both the spatial distribution of host nests and the sex ratio of the local population influence the mating system exhibited by Brown-

headed Cowbirds. Much of this influence is likely mediated through costs and benefits of mate guarding by males under different conditions. If the density of host nests is high, females may defend predictable areas; mate guarding by males would result in monogamous or polygynous associations, with the relative incidence of each being influenced by the size of the female's range and by the sex ratio. If the distribution of host nests is such that it precludes females from maintaining fixed home ranges, the effectiveness of mate guarding is reduced and promiscuity results. Pair bonds will also break down as the sex ratio approaches unity and the advantage to males of guarding individual females is reduced. We encourage future studies of cowbird mating systems to focus on these factors.

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