MOVEMENTS AND ACTIVITIES OF
RADIO-TRACKED BROWN-HEADED COWBIRDS

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Abstract.—The social organization of a color-marked Brown-headed Cowbird (*Molothrus ater*) population was investigated during the 1978–1980 breeding seasons. Several members of the population were radio tracked, some in more than one season. Monogamous associations were established between males and females, and each pair maintained a large nonfeeding range. Females appeared to defend their nonfeeding ranges from other females, and males guarded females from other males. Most cowbird pairs that returned in successive years exhibited mate fidelity and site fidelity, although some evidence indicates that the former is a coincidental result of the latter. I propose that variations in the mating system of this species are primarily due to habitat differences and differences in the relative abundance of the cowbird and its hosts. *Received 8 May 1981, accepted 2 September 1981.*

The Brown-headed Cowbird (*Molothrus ater*) is the most abundant cowbird in the United States and the best-studied member of its genus. Most investigations of this species have dealt with rates of brood parasitism and effects of parasitism on the reproductive success of hosts (e.g. Norris 1947; Walkinshaw 1949, 1961; Berger 1951; Wiens 1963; Rothstein 1976; Elliott 1978). In contrast, much less is known about the social relationships of cowbirds. The reasons for this relative dearth of information are twofold. First, cowbirds do not construct nests, so a convenient focal point for the observation of social activity is absent. Second, cowbirds range over large areas (Friedmann 1929, Nice 1937, Darley 1968), making continuous observation of individual birds quite difficult. Nice (1937), Laskey (1950), and Darley (1968) observed color-marked individuals, but only Darley followed a large number of birds over a broad area. Color-marking alleviates the problem of individual recognition but does not reduce the difficulties associated with locating and following cowbirds. This problem is especially acute with female cowbirds, which are more secretive than males.

These difficulties may have contributed to contrasting descriptions of social organization for this species, ranging from monogamy to promiscuity (Friedmann 1929, Nice 1937, Laskey 1950, Darley 1968, Rothstein 1972, Elliott 1980). Confounding the problem further is the likelihood that the mating system varies between geographic areas (Friedmann 1929, Elliott 1980).

This paper reports on a study of the movements and behavior of cowbirds, using color-marking and radiotelemetry. Radio tracking has been successfully employed in a number of investigations of passerines (e.g. Cochran et al. 1967; Bray et al. 1975a, 1979), and it is particularly suitable for use with a species as wide-ranging as the Brown-headed Cowbird.

Methods

Capture and banding.—Most cowbirds were captured in mist nets or Potter traps placed around each of two artificial feeders. The feeders were 0.16 km apart and were located approximately 0.8 km from the Binghamton campus of the State University of New York. In 1978, trapping began on 22 April and continued through the end of June. In 1979, trapping started on 30 March and continued almost daily until 29 May. In 1980, trapping was conducted from 20 March through 16 June. Trapping was less intense in 1979 and 1980 than in 1978. All captured birds were individually marked with colored leg bands and were fitted with colored leg streamers 2.54 cm in length. Yearling and adult male cowbirds were distinguished on the basis of retention of juvenal underwing coverts in the former group (Baird 1958, Selander and Giller 1960). Yearling and adult females were not differentiated.

Radio tracking.—Field observations of the color-marked population revealed that birds that were lo-

cal residents and appeared to be paired. If these were recaptured, they were fitted with transmitters (model SM1, AVM Instrument Co., Champaign, Illinois) with a Mallory Duracell RM-312T2 mercury battery power source. The birds were then released.

The radio transmitters were attached to the cowbirds by glueing them to the interscapular region of the spinal tract, just anterior to the points of articulation of the humeri. The birds were held in one hand in the manner illustrated by Raim (1978, Fig. 2). All the feathers in an area the size of the transmitter unit were cut to within 1–2 mm of the skin. The feathers were cut rather than pulled out, as the latter method reduces the retention time of the transmitter. Epoxy glue (Devcon 5 Minute Epoxy) was applied to the ventral surface of the transmitter, which was carefully placed onto the exposed area and held firmly for five minutes (longer if excess glue was applied). A few uncut feathers, just anterior and lateral to the transmitter, were glued to it to secure the unit further. Each transmitter-battery unit weighed approximately 2.5–3.0 g.

All of the cowbirds pulled at the transmitters initially, but most ignored them after a few hours. A few birds never accepted the transmitters and continued to peck at them until they became detached. Raim (1978) reports similar behavior. Many of the cowbirds had deeper wingbeats following attachment of the transmitters, but reaction time and flight speed did not appear to be affected. Transmitters remained on those birds that accepted them for 3–21 days, at which time they either fell off or were removed by me.

Most tracking was done in the morning and late afternoon when the birds were most active. Transmitter signals were received by a hand-held AVM Yagi antenna coupled to an AVM model LA 12 portable receiver. Tracking and behavioral observations were tape recorded in the field and later transcribed. Tracking locations were plotted on an aerial photograph of the study area. Only the nonfeeding locations of the birds were considered when plotting ranges. Movements to midday resting areas, where cowbirds from several ranges congregated, were excluded from consideration. One such resting area was located near my primary trapping site (Fig. 1). In 1979 birds from areas 1, 2, 4, 5, and 6 were known to rest there, as did several unidentified cowbirds. Likewise excluded were the locations of aggressive encounters in which birds were driven from the range of another pair. On occasion the signal of a tracked bird would disappear, reappearing a few minutes later. Most instances of this nature could be attributed to the signal being blocked by vegetation, the bird flying to the ground (thereby reducing the effective range of the transmitter), interference from citizens' band radios, and solar interference (especially near midday). I cannot eliminate the possibility, however, that some of these disappearances re-

sulted from birds leaving their ranges for short periods of time, and such movements (if they occurred) are not plotted. Each nonfeeding range was determined by connecting the remaining outermost locations of a bird. The area of each range was calculated using a polar planimeter.

Birds from a particular range were assigned the letter M or F, which designated them as male or female, and a number corresponding to their range. Birds radio-tracked in more than one year retained the same number. Primed (') numbers represent replacement birds.

Both resident and nonresident females were present in the study area. Resident females maintained nonfeeding ranges that overlapped those of neighboring females only slightly. These females were observed frequently. Nonresident females were rarely observed and never exhibited aggressive behavior in the study area. They were seen primarily at feeding areas. There was no evidence of nonterritorial resident females in my population, although Darley (1968) noted such females in his. Male cowbirds were designated as mated or unmated according to their relationships with the resident females. No attempt was made to catalog systematically all the resident unmated males, and a number of males remained unbanded throughout the study period.

RESULTS

Banding and sex ratio.—In 1978, 50 males and 38 females were banded, a male : female ratio of 1.32:1. In 1979, 38 males and 27 females were captured, a ratio of 1.41:1. These values are not significantly different from unity for the two years ($\chi^2 = 1.65$ and 1.88, respectively; $P > 0.05$ for both). In 1980, 45 males and 21 females were trapped. This male : female ratio of 2.14:1 is significantly different from unity ($\chi^2 = 8.74$, $P < 0.005$), as is the combined data for the three years ($\chi^2 = 10.09$, $P < 0.005$), which give an overall male : female ratio of 1.55:1. Thirteen yearling and 36 adult males were captured in 1978 (one male was not aged). In 1979 and 1980 these age classes had 11 yearlings and 27 adults and 13 yearlings and 32 adults, respectively, for a total of 37 yearling and 95 adult cowbirds.

Radio tracking.—Seven cowbirds were radio tracked in 1978, four females and three males. The nonfeeding ranges of these birds are shown in Fig. 1. Areas 1, 2, and 4 of Fig. 1 represent ranges that were identical for both a male and a female cowbird. These birds were considered to be paired. The fourth female also appeared to be paired, but, because her mate was unbanded, her status could not be determined with certainty.
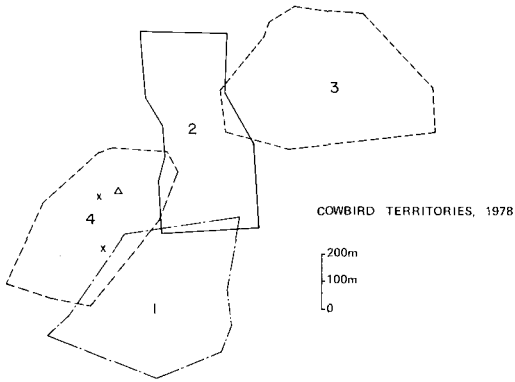
because few data were obtained at these locations.

Three birds are known to have been killed in 1979. F5 was taken by a predator on 21 April. Her mate was seen with a replacement female on 23 April, and this female (F5′) was subsequently captured and radio tracked. Her range appeared to be the same as that of F5. M6 and M9 were found dead on 11 May and 22 May, respectively. Each had been shot with a pellet gun. A second male (M6′) paired with F6; he was radio tracked and maintained a nonfeeding range identical to that of M6. Female F9 was subsequently guarded by an unbanded male whose range was not determined.

M8 was tracked for 71 min over 2 days before his transmitter malfunctioned. Observational data were used to supplement the tracking data in determining his range.

Two pairs of cowbirds tracked in 1979 had also been tracked in 1978. These birds settled in much the same areas as in 1978 and once again had identical ranges (Figs. 3 and 4). The male from the remaining pair (M1) returned and mated with a different female. His 1978 mate was not seen in the study area in 1979. The 1979 pair established themselves near the male's 1978 area (Fig. 5).

Eleven birds were radio tracked in 1979 (Fig. 2). Pairs of birds were tracked in areas 2, 4, 5, and 6. Male members of pairs were followed in areas 8 and 9. A mated female was tracked in area 7. The male in area 1 was not radio tracked in 1979. Area 1 had few large trees to obstruct my vision, and I was able to follow his movements over most of his range. The areas where observations of this male were difficult are labeled as "proposed boundary,"
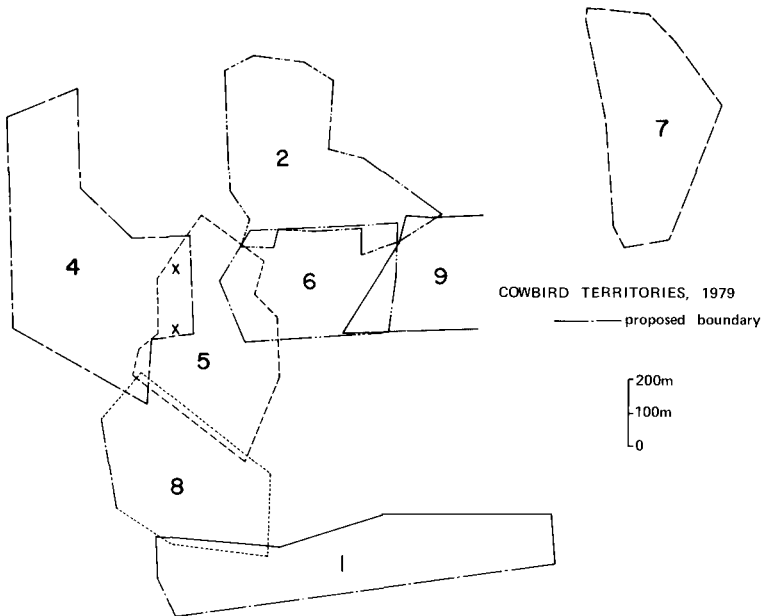

Fig. 2. Nonfeeding ranges of Brown-headed Cowbirds in 1979. "Proposed boundary" refers to areas in ranges 1 and 8 where data were sparse.
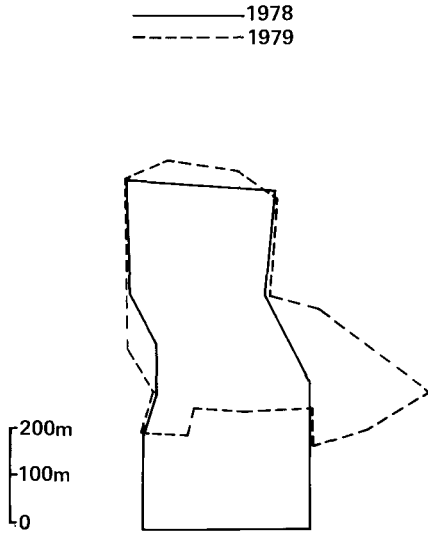
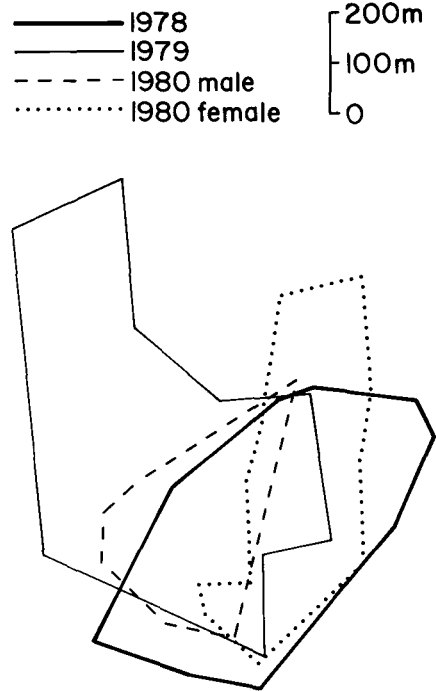Fig. 3. Superimposed nonfeeding ranges of a cowbird pair (number 2 in Figs. 1 and 2) in 1978 and 1979.

Fig. 4. Superimposed nonfeeding ranges of a cowbird pair (number 4 in Figs. 1, 2, and 6) in 1978–1980. In 1980 the male and female paired with different mates.

Tracking data for 1980 are shown in Fig. 6. Females were followed in areas 4 and 11. Both birds in areas 6 and 10 were tracked, but the data for M10 were lost due to equipment failure. Nonetheless, his range coincided with that of F10.

Two males and two females tracked in 1979 returned in 1980. One pair (M4-F4) returned for the third consecutive year. Instead of pairing and assuming identical home ranges, as they had done in 1978 and 1979, F4 settled with a new male in an area adjacent to the one in which M4 was located with a new female. Each of their 1980 ranges partially overlapped their 1979 ranges (Fig. 4). The range sizes for all birds, 1978–1980, are presented in Table 1.

Of the 12 males that were tracked during the course of this investigation, five were yearling birds and the rest were adults.

Pairing.—The evidence suggests monogamous associations between male and female cowbirds. Figures 1, 2, and 6 show that cowbirds limited their nonfeeding activities to large yet well-defined areas. The fact that certain males and females exhibited identical ranges implies that these birds were paired. On nine occasions both members of presumptive pairs had simultaneously active transmitters. Both signals were often found together and moved together throughout the ranges.

The close association between pair members, resulting primarily from males assiduously following females (Darley 1968, Dufty 1981; see also below), accounts for the uniformity of range boundaries for males and females of pairs. Males accompainied females throughout much of the day, although there were extended periods in the mornings when females were stationary and alone, presumably searching for nests. For example, F4 was tracked for 1,371 min during the mornings of 13–18 June 1978, a time when both members of pair 4 had active transmitters. She was alone and relatively inactive on 25 occasions, for a total of 457 min ($\bar{x}$ = 18.28 ± 10.18 min, range = 7–48 min) or 33.3% of the time she was tracked.

The coincidental movement of the signals of a male and female does not preclude the possibility that birds without transmitters also accompanied them, but when both members of a tracked pair were visible there was no evidence of additional cowbirds of either sex in regular attendance. When a pair was not visible, I could usually detect the presence of other

—————1978
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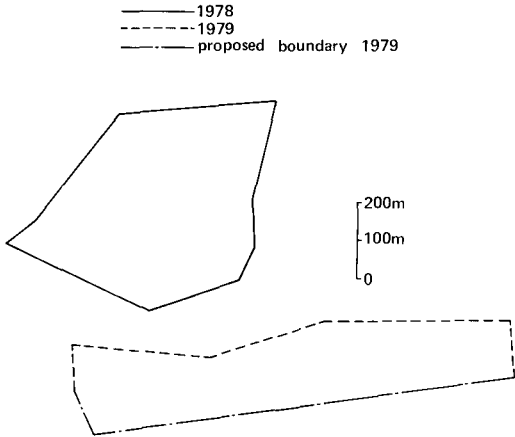—— · —— proposed boundary 1979

Fig. 5. Superimposed nonfeeding ranges of a cowbird pair (number 1 in Figs. 1 and 2) in 1978 and 1979. In 1979 the male paired with a different (untracked) female. He was tracked visually in 1979. "Proposed boundary" refers to areas where data were sparse.

TABLE 1. Sizes of the nonfeeding ranges of Brown-headed Cowbirds, 1978–1980.

Range number[a]	Size (ha)		
	1978	1979	1980
1	25.5	22.7	
2	22.8	21.1	
3	29.3		
4	20.5	29.7	
4a			9.9
4b			14.1
5		19.3	
6		15.6	33.2
7		18.1	
8		17.5	
10			11.0
11			15.3

[a] Range numbers correspond to those found in Figs. 1, 2, and 6.

cowbirds by differences in their vocalizations. These instances also occurred irregularly.

Further evidence that males and females were paired is presented in Tables 2 and 3. Table 2 shows the amount of time each female was seen with her presumptive mate only, with her mate and other males, and with other males only, in 1978 and 1979. Instances are considered only if the identities of both members of a pair were known. Some male mates

had active transmitters, which could have made them easier to locate than unmarked males, thereby biasing the data. To avoid this bias, data are included only if the birds were visible, thus obviating the need for radio tracking in locating birds. Each female cowbird was seen more often with her mate only than with other males [Wilcoxon matched pairs signed-rank test (Siegel 1956), $T = 0$, $P < 0.01$]. Data for 1980 show a similar trend but are not presented, because many of the tracked birds' mates were not banded at the time of tracking, so sample sizes are small.
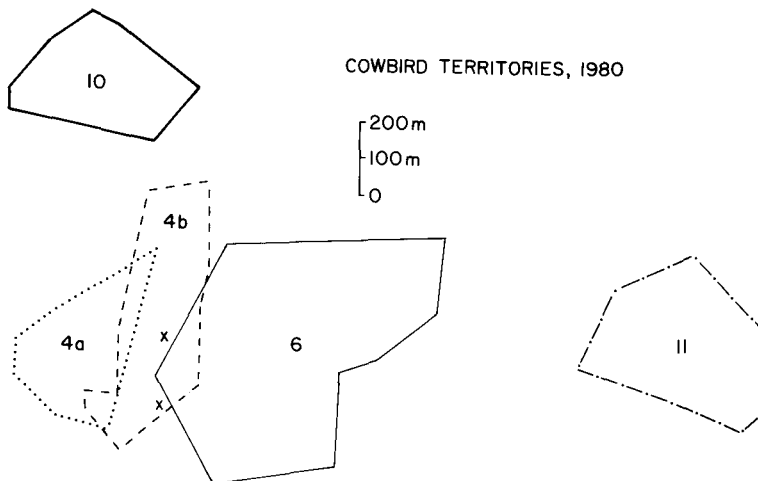

Fig. 6. Nonfeeding ranges of Brown-headed Cowbirds in 1980. The male (a) and female (b) from area 4 returned to their range of the previous 2 yr but had different mates.

TABLE 2. Time (min) that each female cowbird was seen in the presence of her mate, her mate and other males, and other males.

Year	Cowbird $(n)^a$	Mate $(n)^b$	Mate and other males $(n)^b$	Other males $(n)^b$
1978	F1 (7)	53 (11)	7 (3)	20 (5)
	F2 (7)	530 (66)	295 (36)	15 (4)
	F4 (13)	163 (33)	53 (12)	1 (1)
1979	F2 (10)	125 (23)	147 (24)	8 (4)
	F4 (3)	25 (6)	11 (3)	24 (4)
	F5 (1)	29 (3)	1 (1)	0
	F5' (2)	28 (4)	5 (1)	0
	F6 (2)	15 (4)	2 (2)	3 (1)

^{a} Number of days of observation.
^{b} Number of observation sessions.

TABLE 3. Time (min) that each male cowbird was seen in the presence of his mate, his mate and other females, and other females.

Year	Cowbird $(n)^a$	Mate $(n)^b$	Mate and other females $(n)^b$	Other females $(n)^b$
1978	M1 (7)	54 (14)	6 (1)	0
	M2 (6)	545 (71)	280 (27)	2 (1)
	M4 (14)	174 (39)	42 (6)	8 (3)
1979	M2 (9)	151 (27)	71 (14)	3 (1)
	M4 (3)	25 (6)	11 (2)	0
	M5 (8)	134 (13)	41 (3)	0
	M6 (4)	19 (6)	18 (3)	15 (3)
	M6' (8)	28 (6)	15 (1)	7 (1)

^{a} Number of days of observation.
^{b} Number of observation sessions.

The analagous data for males are presented in Table 3. As with females, each male was seen more often with his mate only than with all other females combined ($T = 0$, $P < 0.01$). A male accompanied his mate and other females on feeding grounds and during territorial interactions between the females. If the mate of the other female was also present, the males would sing and display to each other. If the other female's mate was not present, the male would sing to the females or sit quietly nearby while the females interacted. When a paired male was with a female other than his mate, he would sing to her (if she was alone) or engage in a display bout with her mate.

"Following" behavior of males.—I have indicated above that mated males attempt to stay near their females. If such is the case, then males should follow their females when the latter take flight, while the converse should not necessarily occur. In testing this prediction, flights of pairs were recorded. When one member of a pair flew, the other member was watched to determine if he or she followed the first member within 10 s. Of 314 such flights, females flew first 239 times. Males followed females in 206 (86%) of these flights. Several instances in which male cowbirds did not follow females occurred when females made short flights into vegetation, possibly to begin nest searching. Males flew first 75 times, with females following on only 12 (16%) occasions. The difference between the tendency of males to follow females and females to follow males is significant ($\chi^2 = 129.22$, $P < 0.005$).

Aggressive behavior.—To determine whether or not male cowbirds defend their mates from other males, I observed the outcome of display bouts between guarding and intruding males in the presence of resident females. The departure of a male in advance of the female was scored as a defeat for that male. I scored 74 instances, involving 9 guarding males ($\bar{x} = 8.2 \pm 7.1$ instances/male, range = 1–22) and 101 intruders. The guarding males won 64/74 bouts (86%); thus, mated males were significantly more likely to win such bouts than were intruders ($\chi^2 = 39.42$, $P < 0.005$). Of the 10 cases in which guarding males flew off, four occurred early in the season, when guarding ability may not have been completely established. Two others occurred the day after a male (M4) had been fitted with a transmitter, perhaps while he was still adjusting to its presence.

Aggressive behavior between females was less regularly observed. I never saw a female guard her mate from other females. In the mornings, most female-female encounters were at territorial boundaries ($n = 51$), with fewer (16) occurring deep within a female's territory. In the afternoons cowbirds fed communally, either on lawns or elsewhere (e.g. horse pastures). Feeding sites were not defended, even those lying entirely within a female's range, and little aggressive behavior was recorded at these locations.

As might be expected in encounters between neighboring territorial females, there was often no clearly observable victor. The females

would chatter and give aggressive bill-up displays to each other as they hopped from branch to branch. Eventually they would become separated, each toward her own territory, and the interaction would end. At other times the females would take flight in opposite directions or would fly together out of sight. Raim (1979) reports similar activities. Whereas the social relationships between males were readily discernable, such relationships between females were less obvious and may have operated at a more subtle level.

Removal of females.—Females from seven pairs were temporarily removed from the population in May 1979 and May 1980, in addition to the permanent removal of F5 by a predator in April 1979. These females were kept in isolation for 3–8 days. The male member of each pair confined his movements to the established nonfeeding range, and none was seen in association with a lone female up to the time their females were returned. On those infrequent occasions when a male was seen with a female, she was a neighbor in the company of her mate, and the encounters occurred at the boundary of the nonfeeding range or on communal feeding grounds. The females all returned to their respective territories upon release, and their mates resumed guarding behavior.

DISCUSSION

The skewed sex ratio of the captured cowbirds (1.55:1) is similar to the 1.5:1 ratio observed by Friedmann (1929) and Darley (1971). The imbalance in the sex ratio may be an artifact, because the male : female ratio of immature cowbirds is 1:1 (Hill 1976) and females are more secretive in their movements than males. Fankhauser (1971) and Searcy and Yasukawa (1981), however, have found that male cowbirds have a higher survival rate than do females. Furthermore, Darley (1971) and Burtt and Giltz (1976) have shown that female cowbirds are retrapped significantly more often than are males, suggesting that the proportion of males in the population may actually be underestimated.

Despite my bias of deliberately selecting males that had been tracked in previous years, almost half ($^5/_{12}$) of the paired radio-tracked males were yearling birds, breeding for the first time. This is not significantly different from their representation in the population as a whole ($\chi^2 = 0.44$, $P < 0.05$). Payne (1965) and Darley (1968) also reported that yearling males breed successfully. This contrasts with yearling males of polygynous icterid species, such as the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) and the Red-winged Blackbird (*Agelaius phoeniceus*), where juvenile males either do not breed or have reduced reproductive success (Willson 1966, Searcy 1979).

The cowbirds that were radio tracked showed nonfeeding ranges that averaged 20.4 ha in size. These ranges were identical for both members of a pair. Darley (1968) mapped the nonfeeding ranges of color-marked cowbirds and found that the male member of a pair usually had a larger range, which overlapped that of the female. The nonfeeding ranges averaged 4.5 ha for his females and 6.6 ha for his mated males, considerably smaller than the ranges in my population. It is possible that Darley was not able to track his birds visually over all parts of their ranges, resulting in smaller apparent ranges than would have been found by radio tracking. Alternatively, the smaller ranges of the cowbirds studied by Darley may have reflected a higher population density in his study area. This would increase the cost of defense of the ranges (Brown 1964) and reduce the size of each range. Changes in territory size in populations with different densities have been found in several species, such as the Song Sparrow (*Melospiza melodia*), Dickcissel (*Spiza americana*), and Great Tit (*Parus major*) (Tompa 1962, Zimmerman 1971, Krebs 1971).

In addition to having identical nonfeeding ranges, paired cowbirds spent significantly more time in the presence of their mates than in the presence of other cowbirds of the opposite sex. This was effected primarily by the male, who attended the female diligently, following her as she moved through her territory and defending her from the approach of other males. Guarding behavior may reduce the risk that a female will engage in extra-pair copulations, for solitary male cowbirds presented with a model of a female and tape-recorded female vocalizations rapidly approach the model and occasionally attempt to copulate with it (Dufty 1981). Energetically, it may be more feasible for a male to guard his mate than to attempt to patrol her entire nonfeeding range (Conder 1949, Brown 1964), especially because the skewed sex ratio of breeding cowbirds suggests that males must compete for access to females (cf. Emlen and Oring 1977). The

severity of the intermale competition for fe-
males is demonstrated by the results of the fe-
male removal experiment. None of the males
whose mate had been removed was able to se-
cure a second female within the time con-
straints of the experiment. A male whose mate
was taken by a predator did obtain a second
female, although this occurred early in the sea-
son when some females may still have been
searching for territories.

Females, in contrast to males, do appear to
defend their nonfeeding ranges from other
same-sexed conspecifics, resulting in minimal
overlap of territories of neighboring females.
Spacing-out of adjacent females is not simply
due to mutual avoidance, for female-female
encounters were characterized by aggressive
rather than avoidance behavior. The aggres-
sive response of these females to simulated fe-
male intruders further supports this hypothe-
sis (Dufty 1981). Darley (1968) has suggested
that female cowbirds defend access to host
nests. Such territorial behavior may increase
the reproductive success of individual female
cowbirds by reducing the amount of multiple
parasitism, thereby reducing competition be-
tween their nestlings and those of other fe-
males.

The integrity of the pair bond between cow-
birds was maintained in successive breeding
seasons, with pairs exhibiting site fidelity.
Friedmann (1929) felt that his birds returned
to the same territories each spring, although
he worked with unmarked birds. Nice (1937)
reported faithfulness to breeding sites in her
color-banded cowbirds. Darley (1968) also not-
ed that pairs occupy the same (or overlapping)
nonfeeding areas in successive years. Addi-
tional reports of site fidelity can be found in
Laskey (1950), Hunt (1977), and Kennard
(1978).

The significance of a durable pair bond in
cowbirds is unclear. In long-lived species,
birds that have paired in previous years have
higher reproductive success than newly formed
pairs. Coulson (1966) found that Black-legged
Kittiwakes (*Rissa tridactyla*) are able to raise
more young if they have bred together previ-
ously. Likewise, both members of Song Spar-
row, Skylark (*Alauda arvensis*), and Great Tit
pairs will return to their previous nesting area
if they successfully fledged young (Nice 1937,
Delius 1965, Harvey et al. 1979). It is unlikely
that cowbirds are afforded a similar advantage,

because cowbirds perform no parental care.
Fledging success in cowbirds is determined by
the timing of egg deposition, the reaction of
the host to the cowbird egg, and any subse-
quent nestling-foster parent interactions, fac-
tors that would appear to be little affected by
the presence or absence of a lasting pair bond.

Breeding-site fidelity may play a more prom-
inent role in the determination of reproductive
success in individual cowbirds. Males form
hierarchies, with the dominant male pairing
with the female of that particular area (Laskey
1950, Darley 1968). Copulation with a female
may be largely restricted to the dominant male
(West et al. 1981), although early in the season,
when the hierarchy may not be firmly estab-
lished, other males may copulate with her
(Darley 1968). Therefore, dominance in an area
probably translates into high reproductive suc-
cess relative to subordinate male cowbirds.

Fidelity to an area where a male has suc-
cessfully bred in previous years may facilitate
acquisition of a dominant position in succeed-
ing seasons. In the Red-winged Blackbird,
males who have had prior reproductive expe-
rience in a territory return to that territory the
following year and readily establish them-
selves therein (Nero 1956, Searcy 1979). Simi-
larly, site fidelity in male cowbirds may have
evolved as a result of intrasexual selection
pressure, and a male's faithfulness may be to
his breeding area and not to his female. Three
observations are consistent with this hypoth-
esis. Male M1, whose mate did not return in
1979, paired with a new female, yet he main-
tained a nonfeeding range juxtaposed to his
1979 range. Furthermore, when females were
temporarily removed from the population,
none of the males abandoned their ranges. Fi-
nally, the members of a pair (M4-F4) that had
bred together for two consecutive years on the
same territory consorted with different mates
the third year, each on a different part of the
old territory, indicating that site fidelity may
take precedence over mate fidelity.

Data from Darley (1968) also support the
view that successful breeding facilitates site
fidelity. Ten of 12 of his paired males returned
to the study area in the second year; only 2 of
9 unmated resident males did so.

The apparent mate fidelity results from co-
incidental site fidelity on the part of the fe-
males. Females defend their territories, as
shown by the results of playbacks of cowbird

vocalizations to resident females (Dufty 1981). They do not desert their territories if their mates are killed; females F6 and F9 both remained in their territories and paired again after their mates died. This is consistent with Darley's (1968) data. As with males, prior breeding experience in an area may ease a female's subsequent establishment in that area. Additionally, because females spend much time searching for nests (Friedmann 1929), familiarity with territories could enhance the efficiency of their nest-searching activities, allowing them to find more nests or to spend more time in other activities such as territorial defense or feeding. Therefore, intrasexual pressure on males to obtain mates and on females to obtain breeding territories probably results in site fidelity in both sexes and, secondarily, in mate fidelity. Nolan (1978) similarly concluded that mate fidelity in Prairie Warblers (*Dendroica discolor*) occurs coincidentally, a result of site fidelity on the part of both members of a pair.

While the data strongly suggest a monogamous relationship between male and female Brown-headed Cowbirds in my population, the supposition of monogamy must be tempered by the fact that no copulations were observed during this study, so the actual mating pattern is unknown. Because other species thought to be monogamous or polygynous have been shown to be more promiscuous than previously suspected (Bray et al. 1975b, Burns et al. 1980), a final conclusion regarding monogamy in these cowbirds must await information regarding mating patterns in the wild.

MATING SYSTEMS IN THE BROWN-HEADED COWBIRD

Territoriality is thought to have evolved through competition for a limiting resource (Brown 1964). If the resource is economically defensible, then territorial behavior may develop, that is, the cost to the bird of securing the resource must not outweigh the benefits. Competition for resources varies directly with the density of the population and inversely with the abundance of the defended resource. Emlen and Oring (1977) have applied Brown's ideas to the evolution of mating systems. They feel (p. 222) that "considerable lability in mating systems is . . . expected between different populations of a given species in different environmental or density situations."

The mating system of the Brown-headed Cowbird is not identical throughout its range. The system I have described is similar to that reported by Friedmann (1929) in New York and by Darley (1968) in Ontario, yet Elliott (1980) has shown that cowbirds are promiscuous in prairie habitats. Differences in population size and habitat may be crucial factors in explaining these contrasting breeding systems.

Cowbirds apparently entered the United States through Texas and the Prairie States (Friedmann 1929) and extended their range eastward with the removal of large tracts of woodland that had served as a barrier to dispersal (Mayfield 1965). The Prairie States still have the highest densities of cowbirds. Surveys show that the population densities of cowbirds in Oklahoma, Kansas, and Nebraska are 2–3.5 times higher than those in New York, and the difference is increasing (Van Velzen 1972, Dolbeer and Stehn 1979). In contrast, Wiens (1973) has shown that overall species diversity and population density in the open grasslands of the Prairie States is significantly lower than in the shrub/forest ecosystems of the Northeast. Thus, there is a higher density of breeding cowbirds competing for relatively fewer host species in the grasslands of the Prairie States than in the shrub/forests of New York. Competition in the grasslands would be further increased by the fact that many of the parasitized nests are located on the edge of the grasslands in shrubs or thickets, while those in the open expanse of the grasslands are relatively free from parasitism (Wiens 1963). Similar occurrences have been noted in open fields of other localities (Berger 1951; Best 1978, Fig. 4; Gates and Gysel 1978; Gochfeld 1979).

The relatively low cowbird population in the Northeast, coupled with the more abundant supply of host nests, could make defense of these nests profitable for female cowbirds in terms of reproductive success. McGeen (1972) and Elliott (1978) have shown that high levels of multiple parasitism reduce cowbird fledging success, so territoriality in female cowbirds could act to reduce competition between nestling cowbirds. In prairies, where competition from other females may be keener and the supply of nests available for parasitism lower, females may undergo a kind of "scramble" competition. That is, they may not be able to defend successfully an area from all other females and still locate enough nests in which to

lay eggs. Under these circumstances they would be expected to abandon territoriality and simply lay in whatever nests they find. A similar situation occurs in other species, in which territorial behavior is reduced or abandoned when resources are not economically defensible, yet exclusive territories are maintained when the cost of such maintenance is low (Ewald and Carpenter 1978, Myers et al. 1979, Ewald et al. 1980).

Females in the Northeast are able to confine their nonfeeding activities to areas that are small enough that a single male cowbird is dominant in each. This results in monogamous associations between the birds. In contrast, Elliott (1980) reports that males in the prairies do not guard females and do copulate with more than one female. As argued above, females in prairie habitats may travel more widely than those in the Northeast, and a male cowbird may not be dominant in all parts of any given female's range. Because males may not be able to defend females from other males under these circumstances, males may maximize their reproductive output by adopting the alternate behavior of copulating with those females that enter the area where they are dominant. According to this interpretation, male cowbirds in the Prairie States should have smaller ranges than females.

As a consequence of these presumed differences in cowbird spatial patterns, certain predictions can be made regarding the deposition of cowbird eggs in the Northeast and Prairie States: (1) If females exclude same-sexed conspecifics from breeding areas in the Northeast, then the cowbird eggs found in any one territory should be similar to each other (indicating that they were laid by the same female), yet different from eggs found in adjacent territories. Remarks by Friedmann (1929:176) support this prediction, although no data are presented. Exceptions should occur at areas of territorial overlap, where eggs from neighboring birds may be found. In contrast, (2) local, parasitized nests in the Prairie States should contain dissimilar cowbird eggs, reflecting a lack of territorial behavior in females. Finally, (3) if territoriality functions to increase a female's reproductive success by limiting multiple parasitism, there should be relatively fewer cases of multiple parasitism involving two or more females in the Northeast than in the Prairie States.

Multiform mating systems have been reported in a number of avian species (Armstrong 1955, Case and Hewitt 1963, Verner 1964, Carey and Nolan 1975, Balfour and Cadbury 1979). Such variability may promote the efficient use of limited resources, such as mates (for male cowbirds) and host nests (for female cowbirds), and it provides these organisms with a certain amount of flexibility in their responses to differing demographic and/or environmental circumstances.

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