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INTRASEXUAL AGGRESSION AND THE MATING BEHAVIOR OF BROWN-HEADED COWBIRDS: THEIR RELATION TO POPULATION DENSITIES AND SEX RATIOS[1]

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Abstract. I describe population densities, sex ratios, and the social behavior of Brown-headed Cowbirds (*Molothrus ater*) at two sites in eastern California. Sex ratios are similar here, but differ from those observed elsewhere. Population densities vary between the two study areas and elsewhere. Although the level of intrasexual aggression among females differs between my study areas, female territoriality is absent. Most mated males at both study areas are monogamous, but a few are bigamists. Males differ in their attendance of females here and elsewhere. Local variation in cowbird social behavior may be correlated with population density, rather than sex ratio. In low density populations, selection may favor aggression among females, monogamy, and more frequent mate attendance by males.

Key words: Brown-headed Cowbird; intrasexual aggression; mate attendance; mating system; Molothrus ater; *population density; sex ratio; social behavior; territoriality.*

INTRODUCTION

The Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite. Females lay in nests of other species, abandoning their eggs and nestlings to the care of the hosts. Parental investment is a critical variable in models of avian mating systems (Orians 1969, Emlen and Oring 1977, Wittenberger and Tilson 1980). The absence of parental behavior among brood parasites may allow their social systems to be flexible enough to respond to local environmental conditions (Emlen and Oring 1977; Elliott 1980; Dufty 1982a; Rothstein et al. 1984, 1986; Teather and Robertson 1986; Yokel 1986b).

The mating system of free-ranging cowbirds has been characterized as monogamous with and without female territoriality (Friedmann 1929; Nice 1937; Laskey 1950; Darley 1982, 1983; Dufty 1982a, 1982b; Yokel 1986a, 1986b), polygynous (Payne 1973, Teather and Robertson 1986), promiscuous (Nice 1937, Elliott 1980), and polyandrous (Friedmann 1929). Ankney and Scott (1982) suggested that these apparent differences are due to observer bias. However, the only studies which were based on observations of copulations among marked birds showed conclusively that cowbirds were monogamous in eastern California (Yokel 1986a) but promiscuous in northeastern Kansas (Elliott 1980).

I studied the social behavior of cowbirds in two separate areas with different environments. I report population densities and sex ratios for these sites. Cowbird density may affect the spacing system. Territoriality may be unnecessary at very low densities, adaptive at some intermediate density, and too expensive to maintain at very high densities (Davies 1978). Both density and sex ratio might influence the mating system. High density may increase the number of individuals of both sexes with which any one bird interacts. It may likewise decrease the degree of organization within any dominance hierarchies (Balph 1977). Thus, higher density may be associated with a greater degree of promiscuity. A male-biased sex ratio may have the opposite effect, leading to monogamy, if it favors the guarding of a single female by each mated male (Wittenberger and Tilson 1980).

I describe the cowbird's mating system in each area. I also examine differences in aggression among individuals, and the tendency of males to attend females throughout their home ranges. Sex ratios are similar and monogamy is prevalent in both areas. However, aggression among females is greater in the area of higher density, and males attend females less consistently in that area also.

STUDY AREAS AND METHODS

The first study site was in the Owens Valley near Bishop, Inyo County, California. Observations

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were made along 4.2 km of the Owens River and Bishop Creek in 1983, but concentrated along a shorter section (2.9 km) of the river in 1984. This study area is hereafter referred to as OR. The vegetation in this riparian habitat consisted of dense stands of willow (*Salix*) 2–3 m high with occasional trees (*Populus* and *Salix*) projecting up to 15 m above the low willows. The riparian corridor was bordered on both sides by broad expanses of desert scrub, a habitat type rarely used by cowbirds (Rothstein and Fleischer 1987).

The second study site was 65 km to the northwest and 1,200 m higher in elevation, where Mammoth Creek (Mono County, California) flows down the eastern slope of the Sierra Nevada. The vegetation along its banks consists of a much greater proportion of trees (*Pinus* and *Populus*) and fewer willow shrubs than in OR. The surrounding area is sagebrush (*Artemisia*) and open coniferous woodlands. Study sites in 1983 were widely scattered along 8.1 km of Mammoth Creek, at nearby Laurel and Sherwin creeks, and also included one at Deadman Creek, 10–13 km N of the other sites. As for the Owens Valley, work in the Mammoth Creek vicinity was concentrated in a smaller area during 1984. This involved a 3.3 km section of Mammoth Creek only. The Mammoth Creek study area is hereafter referred to as MC.

Cowbirds of both sexes are very mobile. They are dispersed from dawn to late morning in areas of high host density (breeding habitat) where they conduct courtship, agonistic, and egg-laying activities (Dufty 1982a; Rothstein et al. 1984, 1986; Yokel 1986b). The remainder of the day is primarily spent communally at sites used for feeding, such as concentrations of livestock or feeders established by humans.

The concentration on a single subpopulation in each area during 1984 allowed observation of mating relationships for most birds and the estimation of cowbird density. These estimates describe density in breeding habitat, but not necessarily over larger areas. The areas of riparian habitat (breeding habitat) for both study locations in 1984 were calculated using aerial photos and a digital planimeter.

The two study areas were visited sequentially in each year, OR before MC. The higher elevation at MC results in a later start to the breeding season, and females there maintain peak laying rates through mid-July (Fleischer et al. 1987).

Cowbirds were captured at feeding sites in Potter traps baited with millet. Each bird was individually marked with colored leg bands. Sex ratios for each local breeding population were estimated from the numbers of trapped birds, excluding juveniles (birds fledged that breeding season). Migrant cowbirds may be present in either study area before 15 May and after 14 July (Rothstein et al. 1980, Yokel 1986a). Cowbirds trapped between these dates are local birds.

Observations were made on breeding ranges from fixed sites along the streams. Individuals seen for ≥2 days (at least 2 days of observation were conducted at each site) were designated as residents. This description was necessary since cowbirds were very mobile, as noted above. A second estimate of population sex ratio was determined using the numbers of resident birds observed on breeding range, again excluding juveniles.

Playback experiments measured levels of intrasexual aggression. For females, a recording of the *chatter* vocalization (Dufty 1982b) from an OR female was used during 1983 and from a female recorded near MC for 1984. Recordings were made with a Marantz PMD 340 cassette recorder and a Sennheiser 803-V directional microphone. Playbacks were run with the same recorder, an Ampli-Vox S702 amplifier, and a Realistic power horn on a 2.5-m tall pole. The playback emitted two *chatters* every 20 sec. A freeze-dried mount of a female, in a nonaggressive perching posture, was placed 20 cm from the speaker. Playbacks involving males were conducted in 1984 only, using a recording made near Morro Bay, San Luis Obispo County, California, approximately 320 km SW of both study areas. The playback tape emitted three "perched songs" and one "single-syllable flight call" (Rothstein et al. 1988) every 60 sec. A freeze-dried male cowbird (same posture) was presented with the speaker. Distances from the speaker to prominent trees were measured at each site with a rangefinder; intermediate distances were estimated. For either sex, the playback began when the targeted bird was observed within 100 m of the speaker, a distance at which the recording could be heard readily with the human ear. All aggressive displays (Nero 1963) were noted, including *chatters* for females, song-spreads for males, and bill-wipe and head-up displays for both sexes. An "approach" occurred if the bird flew toward the speaker and perched closer than it had been. If it attacked the mount, the playback

TABLE 1. Sex ratio estimates of breeding populations. Each estimate is subjected to a two-tailed binomial test to determine if it represents a significant departure from a 1:1 ratio.

Method	Year	Area	Number of males	Number of females	Sex ratio (M:F)	*P*
Trapped at feeding site	1983	OR	43	25	1.7:1	0.040
		MC	168	74	2.3:1	<0.001
	1984	OR	134	76	1.8:1	<0.001
		MC	115	81	1.4:1	0.018
Observed on breeding range	1983	OR	55	24	2.3:1	<0.001
		MC	30	13	2.3:1	0.015
	1984	OR	59	30	2.0:1	0.003
		MC	15	9	1.7:1	0.310

was terminated early to protect the freeze-dried specimen.

At OR, nonmanipulative observations were conducted for 81 hr on 24 days during 1983 and for 192 hr on 29 days in 1984. At MC, 137 hr of observation were spent on 35 days during 1983 and 193 hr on 21 days in 1984. The greater hours/day in 1984 were due to the addition of a field assistant. He and I each worked at every site.

An intersexual interaction involving courtship behavior was defined as a consort event. If more than one male and/or female were present, consorting pairs were defined by proximity. A consort event ended when one participant flew and left the other, or both flew, but in different directions. The number of consort events for each unique pair was tallied. Analysis of consort events and copulations (Yokel 1986a) showed that the mating status of individuals could be determined from consort event data alone if copulation data were lacking. In the absence of observed copulations, my criterion for designating a male and female as mated was that $\geq 50\%$ of each individual's consort events had to be with the other individual.

When one member of a pair flew away during a consort event, its sex, and whether or not the other individual followed, were noted. Thus four "following response" types were possible: (1) female flies, male follows; (2) female flies, male does not follow; (3) male flies, female follows; (4) male flies, female does not follow. If the first type of response occurred, it could be said that the male maintained his attendance of the female. The remaining three types represented the actual or potential abandonment of the female by the male, especially since the third type was very rare (1.8% of all events). A fifth type of occurrence was not included. Rarely, a male flew off, the female did not follow, and the male circled and returned. This immediate return to the perch did not constitute leaving the area or the female. For analysis, types 2–4 were lumped so that a male either maintained attendance or he did not. To prevent an inflated sample size and the bias of the sample by certain pairs for which a disproportionate number of data points were obtained, only the first following response event observed for each unique male-female dyad was used in the analysis of all pairs.

RESULTS

SEX RATIO AND DENSITY

A significantly higher proportion of males than females occurred in both study areas (Table 1). There was no difference between years for the two methods of estimation for OR or for the breeding range estimate for MC (two-tailed *G*-tests of independence; *P*s > 0.50 to 0.90). However, the two estimates for feeding sites near MC (2.3:1 in 1983 and 1.4:1 in 1984) differed significantly ($P = 0.02$). None of the four comparisons between the two study populations revealed a significant difference in sex ratio (two-tailed *G*-test of independence; *P*s > 0.20 to 0.98).

The calculated areas of riparian habitat were 0.575 km^2 and 0.504 km^2 for the 1984 OR and MC study areas, respectively. The resulting density of cowbirds using the numbers observed in those breeding areas (Table 1) were 103 males and 52 females per km^2 for OR, but only 30 males and 18 females per km^2 for MC.

PLAYBACK EXPERIMENTS

The greater density at OR corresponded to a higher level of female aggression. Ten females

TABLE 2. Distribution of each female's consort events and copulations among males at MC. When two males were involved in a single female's consort events, a binomial test was used to determine the significance of the distribution of consort events across males. When three males were involved, a χ^2 value was determined based on a 1 × 3 table. All tests were two-tailed.

Female identity	Total of female's consort events	Male identity	Number of copulations	Percent of female's consort events	P
A	13	E	1	100.0	—
B	11	F	3	90.9	<0.010
		H	0	9.1	
C	23	B	3	87.0	<0.001
		F	0	13.0	
D	37	C	1	86.5	<0.001
		D	0	10.8	
		J	0	2.7	
E	6	A	0	83.3	0.220
		G	0	16.7	
F	29	F	0	75.9	<0.001
		E	0	17.2	
		I	0	6.9	
G	16	D	0	75.0	<0.050
		C	0	25.0	

were subjected to playbacks at OR (12–31 May) and nine at MC (19 June–17 July) in 1983, and 11 (OR: 18 May–12 June) and seven (MC: 17 June–11 July) respectively in 1984. In 1983, all OR females approached the speaker, but only four did so at MC (two-tailed Fisher exact $P = 0.02$). Two OR females attacked the mount, but none did at MC. In 1984, eight of 11 approached at OR and two of seven at MC ($P = 0.08$). Three attacked the mount at OR in 1984, but none at MC. Three females at OR and one at MC were tested in both years. Before combining samples, the 1984 data for these four were deleted. Over both years, 16 of 18 OR females approached and six of 15 at MC ($P < 0.005$). Five of the 16 at OR attacked the mount, whereas none did so at MC ($P = 0.07$).

In 1984, when vocalization and display data were recorded, OR females responded more than MC females. No MC female gave bill-wipe or head-up displays, but six of 11 OR females each gave one to 17 displays. Eight of 11 OR females, but only four of seven MC females, responded with *chatters*. Overall, OR females gave a mean of 9.1 displays and vocalizations ($n = 11$, range = 1–38) vs. 1.4 at MC ($n = 7$, range = 0–4; Mann-Whitney U-test, two-tailed $P < 0.05$).

TABLE 3. Distribution of each male's consort events and copulations among females at MC. Analysis as described for Table 2.

Male identity	Total of male's consort events	Female identity	Number of copulations	Percent of male's consort events	P
A	5	E	0	100.0	—
B	21	C	3	100.0	—
C	36	D	1	88.9	<0.001
		G	0	11.1	
D	18	G	0	66.7	<0.010
		D	0	27.8	
		H	0	5.5	
E	20	A	1	65.0	<0.010
		F	0	25.0	
		H	0	10.0	
F	39	F	0	56.4	<0.001
		B	3	25.6	
		H	0	10.3	
		C	0	7.7	

Females displayed more aggression at OR than at MC in both years. The distance of females from the speaker at the beginning of each trial was greater at MC, but not significantly so ($\bar{x}$ = 28.4 m at OR, range = 0.5–80.0; $\bar{x}$ = 38.7 m at MC, range = 5.0–100.0; Mann-Whitney U-test, two-tailed $P > 0.20$). There was no significant difference in initial distance between females that approached the mount and those that did not at OR (approach: $\bar{x}$ = 28.5 m, range = 0.4–80; no approach: $\bar{x}$ = 27.5 m, range = 25–30; two-tailed Mann-Whitney U-test, $P > 0.50$), at MC (approach: $\bar{x}$ = 43.3 m, range = 10–100; no approach: $\bar{x}$ = 35.6 m, range = 5–70; $P > 0.50$), or at both areas combined (approach: $\bar{x}$ = 32.5 m, range = 0.4–100; no approach: $\bar{x}$ = 34.1 m, range = 5–70; $P > 0.50$).

Similar parameters were tested for the responses to the male playback experiment by 12 OR males and seven MC males. Only two OR males approached the mount. One was the only unmated male tested. No male approached the mount at MC. None of the parameters displayed a significant difference between study areas.

MATING SYSTEMS

The analysis of 1,280 consort events and 73 copulations for the OR population in 1984 showed that nearly all copulations were between a female and the male that most often consorted with her. All females and most mated males were monogamous, though two males were bigamous (Yokel 1986a).

TABLE 4. Distribution of following response types among groups and between study area.

				Percent occurrence of each following response type[a]				
Male–female dyad type	Area	Year	No. dyads	Type 1	Type 2	Type 3	Type 4	Types 2 + 3 + 4
Unmated yearling with any female	OR	1984	17	17.6	35.3	0.0	47.1	82.4
Unmated adult with any female	OR	1984	21	23.8	19.1	0.0	57.1	76.2
Mated male with nonmate female	OR	1983	7	0.0	14.3	0.0	85.7	100.0
	OR	1984	54	13.0	38.9	1.8	46.3	87.0
	MC	1983	1	100.0	0.0	0.0	0.0	0.0
	MC	1984	7	42.8	28.6	0.0	28.6	57.2
Mated male with his mate	OR	1983	10	20.0	60.0	0.0	20.0	80.0
	OR	1984	29	20.7	41.4	3.4	34.5	79.3
	MC	1983	3	66.7	33.3	0.0	0.0	33.3
	MC	1984	8	50.0	0.0	0.0	50.0	50.0
All unique pairs	OR	1983	51	13.7	29.4	3.9	53.0	86.3
	OR	1984	136	18.4	33.8	1.5	46.3	81.6
	MC	1983	19	52.6	10.5	0.0	36.9	47.4
	MC	1984	17	47.0	11.8	0.0	41.2	53.0

[a] Type 1: female flies, male follows; Type 2: female flies, male does not follow; Type 3: male flies, female follows; Type 4: male flies, female does not follow.

With fewer birds and denser tree stands at MC, fewer consort events (145) and copulations (8) were observed. However, the results were strongly similar to those of OR. Seven pairs were recognized, involving six males and seven females (Tables 2 and 3), and four of the pairs were supported by observed copulations. Among the three pairs for which observed copulations were lacking, a mean of 78.1% (range = 75.0–83.3%) of each female's consort events were with the male identified as her mate. The corresponding mean for males was 74.4% (range = 56.4–100.0%).

A significant majority of the consort events of most females was with a single male (Table 2). The six consort events of female E were too few to reach significance. Observed copulations occurred with the male that accounted for the majority of the female's consort events. A similar distribution of consort events and copulations occurred for males, with the exception of male F (Table 3). This male was observed to consort most with one female, but to copulate with another. He was possibly mated to both. Thus all females for which mating relationships could be determined were monogamous, as were all mated males except for one possible bigamist.

ATTENDANCE OF FEMALES

Table 4 presents following response data broken down by the mating relationships of the male-female dyads involved. All females are probably mated as Fleischer et al. (1987) found that all lay eggs. Since only copulation, and not consort event, data were collected in 1983, no males could be defined as unmated. Furthermore, no consort events were observed for the few males defined as unmated at MC for 1984. The category of all unique pairs involves more than the sum of the prior categories because it includes males of unknown status and nonresidents.

Within a study area the proportions of the two basic following responses of males (Type 1 vs. 2–4 combined) were independent of the year and the male and female involved in the dyad. For each dyad category and study area, there were no differences between years in the proportions of response types (two-tailed G-tests of independence; Ps > 0.20 to 0.95). Furthermore, there was no difference among unmated males (adult vs. yearling; $P > 0.60$), between mated males with their own mates vs. with other females (Ps > 0.30 to 0.70), or between all unmated males and all mated males regardless of the female ($P > 0.40$).

The proportions of response types were not, however, independent of study area. Males maintained their attendance of females more frequently at MC than at OR. This was so for dyads including only mated males ($P < 0.025$, 1983; $P < 0.02$, 1984) and for those including all unique pairs ($P < 0.005$, 1983; $P < 0.02$, 1984). Males maintained their attendance of females during about 50% of following response events at MC, but only during about 17% at OR.

TABLE 5. Cowbird population densities, sex ratios, and social behavior at different North American study sites.

Study area	Density (males and females per km^2)	Sex ratio	Attendance of females (see text)	Mating system	References
New York	8 and 5	1.5:1.0	65.6%	Monogamy	Dufty 1982a, 1982b
MC	30 and 18	1.9:1.0	50.0%	Monogamy (some bigamy)	(This paper)
Ontario	48 and 35	1.3:1.0	65.8%	Monogamy (some polygyny)	Teather and Robertson 1985, 1986
OR	103 and 52	1.9:1.0	17.1%	Monogamy (some bigamy)	(This paper)
Ontario	104 and 61	1.5:1.0	—	Monogamy (some bigamy)	Darley 1971, 1982, 1983
Kansas	Very high	1.1:1.0	—	Promiscuity	Elliott 1978, 1980; Dolbeer and Stehn 1979

DISCUSSION

FEMALE AGGRESSION AND TERRITORIALITY

At OR, females do not have exclusive use of breeding ranges (Yokel 1986b), one of the key characteristics of territoriality (Brown 1975). No female was observed to attack or chase another female. Similar observations were made at MC. Using radiotelemetry, Rothstein et al. (1984) found the breeding range of an MC female to be 0.40 km^2, yet this study found 18 females per km^2 of MC breeding habitat. Thus female breeding ranges overlap at both MC and OR. The playbacks suggest greater aggression among females at OR than MC, which is correlated with greater cowbird density. Female territoriality is apparently absent at both OR and MC, so the difference in levels of aggression may be influenced by cowbird density rather than the presence vs. absence of territoriality.

Several investigators (Friedmann 1929, Nice 1937, McGeen and McGeen 1968, Nolan 1978, Fleischer 1985) have found host nests that contained eggs of more than one female cowbird, clearly demonstrating that females in various parts of North America do not have exclusive access to the nests of a particular area. An investigation of marked cowbirds in Ontario determined that females had breeding ranges of 0.09 km^2 and were not territorial (Teather and Robertson 1985). Two others concluded that females did defend breeding ranges of about 0.05 km^2 (Ontario, Darley 1983) and 0.20 km^2 (New York; Dufty 1982a, 1982b). Darley's maps of females' breeding ranges exhibited considerable overlap, as was the case in the other Ontario study and at OR and MC. Dufty's figures show less overlap, but he excluded "the locations of aggressive encounters in which birds were driven from the range of another pair."

Using the data in these previously published reports, I calculated the densities of cowbirds in those other study areas (Table 5). The results were 104 males and 61 females per km^2 for one area of Ontario (Darley 1982, 1983), similar to my OR area, but only 48 males and 35 females per km^2 for the other Ontario site (Teather and Robertson 1986). The estimated densities at my MC area were 30 males and 18 females per km^2. Dufty (1982a) did not catalog unmated resident males, but he stated that no resident, nonterritorial females were present. Taking his mean territory size for females, and adjusting for males according to the reported sex ratio, gave densities of only eight males and five females per km^2. These are remarkably lower than any of the other four study areas above.

Since a female cowbird lays at least 30–40 eggs during the 2- to 3-month breeding season (Scott and Ankney 1980, 1983; Fleischer et al. 1987), the availability of suitable host nests in which to place them is certainly an important factor in her reproductive success. The exclusive use of a set of host nests would obviously be beneficial if they were economically defendable (Brown 1964). Different populations of cowbirds may lie along a continuum between no expression of territoriality and complete expression of defense and exclusive use of a fixed area. Dufty's (1982a) maps of female breeding ranges show the least overlap. Low cowbird density in his area might result from territoriality. Alternatively, an appearance of territoriality may be explained by low density.

Conclusions of territoriality do not correlate with the associated cowbird densities or estimates of breeding range size. The two reports of territoriality (Dufty 1982a, 1982b; Darley 1983) come from the areas with the least and greatest cowbird densities, respectively. Where northeastern cowbirds are described as territorial they have breeding ranges of 0.05 km^2 (Darley 1983) and 0.20 km^2 (Dufty 1982a, 1982b), but range size is intermediate (0.09 km^2; Teather and Robertson 1985) where they are not territorial. However, female aggression at OR and MC is positively correlated with cowbird density.

MATING SYSTEM AND MATE ATTENDANCE

The cowbird mating system is similar at OR and MC. All females are monogamous, as are the majority of mated males. Only a small proportion of males in each area maintained two mates simultaneously.

However, MC males attend females more continuously than do OR males (50% of following response events vs. 17%). Similar data from two other studies (Table 5) place these values at 65.6% in New York (Dufty 1982a) and 65.8% in Ontario (Teather and Robertson 1986). These workers, in addition to Darley (1982), interpret this behavior by males as mate guarding. They and Wittenberger and Tilson (1980) suggest that monogamy via mate guarding becomes increasingly adaptive to males as the male bias in sex ratios increases. The greater competition among males may increase the adaptiveness of being the sole mate of a single female.

Sex ratios differ among the above areas (Table 5). The least male-biased are 1.1:1 (Kansas, Elliott 1980) and 1.3:1 (Teather and Robertson 1986) and neither is significantly different from unity. Others are significantly different from unity for 1 year, and for combined years of study, and average 1.5:1 (Darley 1971, Dufty 1982a). My estimates average 1.9:1 (OR and MC; 2 years and two methods combined for each area). Teather and Robertson (1986) suggest that promiscuity in Kansas (Elliott 1980) correlates with reduced mate guarding by males, due to a sex ratio of unity. However, promiscuity there should provide a selective pressure for increased mate guarding. Furthermore, following response data and sex ratios of four different areas do not support their hypothesis. Males attend females most closely in Ontario and New York where the ratio of males to females is only 1.3:1 and 1.5:1. Attendance is reduced at OR and MC (see also Rothstein et al. 1984) where the ratio is 1.9:1, and following responses are significantly different for these two areas although sex ratios are not.

The explanation for female monogamy via mate guarding by males primarily addresses selection to maximize the reproductive success of males. It connotes no adaptive value for females. If a monogamous situation was not adaptive for females, males would have to guard their mates constantly to enforce fidelity. Otherwise, cuckoldry by females could readily occur and the benefit from mate guarding could be greatly reduced. Male attendance of females is not constant even where it is the most predominant in New York and Ontario (only 66% of departure events). Females have ample opportunity to copulate with males other than a single mate, as shown by consort event data for OR (Yokel 1986a, 1987), MC (above), and Ontario (Teather and Robertson 1986). Even at OR, where a large number of copulations has been observed, there is evidence that females refuse to mate with other males when given the opportunity. The influence of female choice on the mating system is suggested (Yokel 1987). Male attendance of females may not be a result of mate guarding. Both Darley (1982) and Teather and Robertson (1986) state that "mate" guarding also occurs between nonmated males and females. Dufty (1982a) does not mention whether or not males follow nonmate females, but he states that such pairs occur in the absence of the mated male. An alternative hypothesis for attendance is that males need to demonstrate their qualities to females, especially as regards social dominance, as indicated by studies of captive cowbirds (West et al. 1981).

Although the trend in following responses does not correspond to sex ratios, it is related negatively to cowbird density. Another role for density in the cowbird mating system, involving site-based dominance among males, has been previously suggested (Elliott 1980, Dufty 1982a, Teather and Robertson 1986, but see Yokel 1986a). Cowbird densities cannot be calculated from Elliott's (1980) data, but his study area is in a region with densities much higher than areas of other cowbird studies (Dolbeer and Stehn 1979). Variation in attendance by males may be a result of density, and not of mate guarding due to male-biased sex ratios. With higher densities, each male comes in contact with more females, so he spends less time demonstrating his dominance to any particular one. Mated males attempt bigamy, although few are successful. Alternatively, a male may require the presence of additional males to demonstrate his dominance to a female. With low cowbird density, a male may have to attend his female more regularly in order to be with her on the fewer occasions when he interacts with other males.

The cowbird mating system is similar in all studied areas except Kansas. Pair bonds and monogamy prevail, though a slight degree of polygyny is possible. In Kansas, where cowbird density is exceptionally high (Elliott 1978, Dolbeer and Stehn 1979), pair bonds are absent and a promiscuous system exists. Density may be so high that a single male cannot attend a particular female adequately to demonstrate dominance qualities. Alternatively, high density may preclude the development of sufficiently well-defined dominance patterns.

CONCLUSIONS

Sufficient evidence to demonstrate that female cowbirds defend areas of exclusive use has not been presented by any investigator, but levels of female aggression vary among areas. Males attend females more consistently in some areas than in others, and attendance may be negatively correlated with cowbird density. The mating system of the cowbird is predominantly monogamous.

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