

EVOLUTION OF PROMISCUITY IN THE BROWN-HEADED COWBIRD

PHILLIP F. ELLIOTT

ABSTRACT.—A study of the social behavior of Brown-headed Cowbirds (*Molothrus ater*) in 1974 and 1975 suggests that in prairie communities the predominant mating behavior is promiscuous. Individually marked cowbirds of both sexes were observed copulating with more than one individual, suggesting that long-term pair bonds were non-existent. On the study area cowbirds parasitized three ground-nesting species and foraged among grazing cattle. Thus, cowbirds bred and fed in the same area. Since the cowbirds foraged with grazing cattle, the latter became a "moving resource." It is hypothesized that this situation selects against the evolution of territorial behavior, and for the evolution of promiscuity.

Promiscuity is generally considered to be mating behavior in which there is no lasting pair bond, and males and females are both likely to copulate with more than one individual of the opposite sex (Verner and Willson 1966, Lack 1968). Promiscuous mating behavior in passerine birds should be rare because promiscuity implies almost complete freedom of males from parental care (Selander 1972) and, possibly, territorial responsibilities, if a female's choice of a male is unaffected by his territory. However, promiscuity may be more prevalent than has generally been thought, as is suggested by the results of Bray, Kenelly, and Guarino's (1975) study of vasectomized male Red-winged Blackbirds (*Agelaius phoeniceus*). In their study, females of vasectomized males regularly laid fertile eggs if there were fertile territorial males nearby. Promiscuous behavior of females suggests that differences among males may not be critical; this would be more probable if the parental care contributions of the males were minimal.

In brood parasites, such as the Brown-headed Cowbird (*Molothrus ater*), both males and females are relieved of responsibilities for parental care. Thus it might be expected that cowbirds would be promiscuous. However, cowbirds have generally been considered to be monogamous, as well as confined to a breeding territory (Friedmann 1929, Bent 1958, Dufty unpubl. data). In situations where cowbirds are abundant, territorial boundaries are less well defined, and mating systems other than monogamy have been reported (Nice 1937, Bent 1958). Bigamy has been described for cowbirds by Darley (1971); Payne (1973) also suggested the likelihood of polygamy in cowbirds, based upon evidence that first-year males

may not breed, thus creating a skewed sex ratio among breeding adults. Most data that have been reported on cowbird breeding systems have been from studies conducted in either urban or woodland habitats in the northeastern United States. Breeding Bird Surveys indicate that midwestern prairie habitats have higher densities of cowbirds and lower densities and diversities of potential hosts, relative to northeastern habitats. I believe this is an important determinant of cowbird mating systems, and my purpose here is to discuss several ecological aspects of prairie communities that may favor a promiscuous mating system in cowbirds.

METHODS

This study was conducted in 1974 and 1975 on the Range Research Pastures of Kansas State University. Host species were heavily parasitized (Elliott 1978), suggesting relatively high densities of cowbirds with respect to host numbers (McGeen 1972). The pastures consisted of native prairie grasses and were grazed by cattle throughout the summer. The cowbirds foraged among the cattle as they moved about the pastures and also concentrated their parasitic activities on the three ground-nesting species that used the pastures. These primary hosts were the Eastern Meadowlark (*Sturnella magna*), the Dickcissel (*Spiza americana*) and the Grasshopper Sparrow (*Ammodramus saviannarum*). Cowbirds on the study area were censused weekly during May, June, and July at varying times of the day, though no effort was made to randomize census times.

Adult cowbirds were captured in 1975 using decoy traps similar to those used by the U.S. Fish and Wildlife Service in their cowbird trapping program involving the Kirtland's Warbler (*Dendroica kirtlandii*; Shake and Mattson 1975). Twenty-four cowbirds were individually marked by dyeing certain feathers with a weak hair dye, and by color banding. The use of the dye enabled individual identification up to 200 m.

RESULTS

Thirty-eight male and six female cowbirds were trapped; these numbers are consistent

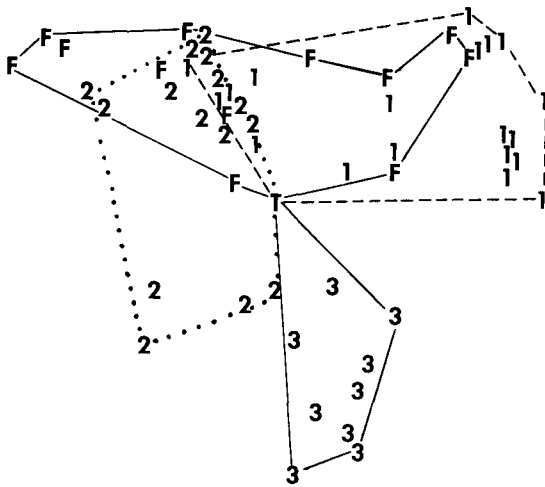


FIGURE 1. Home ranges of one female and three male cowbirds. Each number represents the location of an observation of that particular male cowbird. Each "F" represents the location of an observation of the female. The "T" represents the location of the trap where the four birds were captured and individually marked. The lines connecting the respective observations indicate the spatial relationship of the home ranges and do not denote specific boundaries.

TABLE 1. The dates of observed copulations of Brown-headed Cowbirds and the identities of one or both participants when known.

Date	Male	Female
21 May 1975	Unmarked	Unmarked
23 May	Unmarked	C
23 May	A	C
24 May	B	Unmarked
24 May	C	D
28 May	Unmarked	Unmarked
29 May	Unmarked	D
1 June	A	Unmarked
1 June	A	Unmarked
1 June	A	C
3 June	Unmarked	C
4 June	Unmarked	Unmarked
5 June	Unmarked	E
5 June	B	E
6 June	B	Unmarked
10 June	A	Unmarked
11 June	A	Unmarked
12 June	Unmarked	Unmarked
14 June	A	D
17 June	Unmarked	D
18 June	Unmarked	Unmarked
19 June	Unmarked	E
19 June	Unmarked	E
22 June	Unmarked	Unmarked
3 July	Unmarked	C

with other reports of skewed sex ratios in adult cowbirds (Friedmann 1929, Darley 1971, Payne 1973). However, weekly census results totaled 262 males and 244 females. The census data suggest that the sex ratio of cowbirds in this habitat was not significantly different from unity and also indicate that males may be more easily trapped than females. The capture data provide an indication of the movements and degree of "range overlap" among males, in that 38 different males were captured within two weeks at the same place.

Figure 1 shows the areas of activity of four individually marked cowbirds (3 males and 1 female). Several other cowbirds of both sexes also were active in this area, but are not included because either they were not individually identifiable or the numbers of observations/individual were too few to demonstrate an area of activity. The location of the trap in Figure 1 was the capture site of all 44 captured cowbirds. Although Figure 1 suggests relatively exclusive male ranges, no territorial defense behavior was observed. Thus, I believe home range is a more accurate description of the spacing system. Male 3 was never seen again in the area where he was trapped, indicating the occasional movements of male cowbirds in this area. I often saw males fly considerable distances from their usual ranges, only to return within a few minutes. The function

of these trips is not known; they may be a means of finding females or the grazing herd of cattle, and/or assessing the density or location of other males (Schartz and Zimmerman 1971).

Bent (1958) and Friedmann (1929), reported accounts of individual males using specific "singing trees" from which they sing and display. I observed a similar phenomenon, except that the "singing trees" were used by several males simultaneously, and appeared to be used as temporary sites for displays between males. Of 103 observations of courtship behavior, 63% involved two or more males/female. The use of these display areas peaked during the last two weeks of May, decreased markedly throughout June, and virtually ceased during July and August. Trapping of adult cowbirds also was most successful during late May and early June. The trend toward lower trapping success as summer progressed may have been due partly to the reluctance of once-captured birds to return to the trap.

Data pertaining to the mating behavior of cowbirds in this area are summarized in Table 1, which lists the dates of observed copulations and the identities of one or both participants when the identity was known.

DISCUSSION

The data concerned with the mating system of the cowbirds in this study consist of ob-

servations of three types of behaviors. First, I observed courtship and copulation by the same male with different females. The courtship and pursuit by the same male of different females was practically a daily event, but copulation of a marked male with different females was seen only twice (Table 1). Second, I recorded courtship and copulation of a female with different males. The courtship and pursuit of a single female by different males was noted repeatedly; copulations of a marked female with different males was witnessed only five times. The copulations just described were out of a total of 25 which were observed. The other copulations may have been of the same types, but the birds were not individually recognizable. Finally, I observed courtship and pursuit of individual females by several males while nearby females were ignored. Males directed their attentions toward different females on different days. Payne's (1965) demonstration that cowbirds seemingly lay eggs in clutches of 4 or 5 eggs with 5- or 6-day intervals between clutches may explain this behavior, since it would be maladaptive for both males and females to spend time and energy in courtship when the female was not ovulating, unless a permanent pair bond was sought. Females may use the intervals between clutches for seeking nests and increased feeding for egg production, while males should be soliciting copulations from other females, who are ovulating.

The habit of female cowbirds laying eggs in clutches may be an important causal, or at least permissive, factor in the evolution of promiscuity in this system.

The mating behavior of cowbirds in this area may be the result of ecological factors inherent in a prairie habitat. The cowbirds' habit of feeding in flocks among grazing ungulates causes them to feed and breed in the same area (Hamilton and Orians 1965). Thus, the grazing herd actually becomes a "moving resource," and the cowbirds could not defend potential feeding and/or breeding territories. Results from a study by Duffy (unpubl. data) indicate that 1) females may be territorial in order to prevent other females from parasitizing potential host nests in the defended area, and 2) male cowbirds attempt to defend females from other males. In prairie communities, hosts are less numerous than in deciduous woodlands, and females may have to extend their nest-searching activities over such a large area that territorial defense is uneconomical. Also, the large female ranges may pre-

clude the ability of an individual male to defend his "mate" from other males (Fig. 1).

If territoriality does not exist and males are free of territorial and parental responsibilities, there should be few, if any, selection pressures against males who attempt to court and copulate with as many different females as possible. Repeated observations of marked males engaged in courting different females supports this reasoning. Likewise, the effort expended by female cowbirds in searching for host nests in a stage suitable for parasitizing should require much of their available energy, thus limiting the amount of energy available for courtship. If so, this would favor a promiscuous mating system, as time and energy need not be expended for the development and maintenance of a pair bond. Observations of a marked female successively copulating with different males within the span of one hour support this logic. In addition, numerous observations of different males involved in courting the same female were made repeatedly, supporting the idea that long-term pair bonds were not the rule. Although the adaptive basis for this behavior of females is obscure, it is apparent that in this system female cowbirds frequently, if not regularly, bred with different males.

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Department of Biology, Eastern Connecticut State College, Willimantic, Connecticut 06226. Accepted for publication 17 September 1979.

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RECENT PUBLICATIONS

Handbook of the Birds of Europe, the Middle East, and North Africa/The Birds of the Western Palearctic. Volume II. Hawks to Bustards.—Edited by Stanley Cramp, with K. E. L. Simmons, Robert Gillmor, P. A. D. Hollom, Robert Hudson, E. M. Nicholson, M. A. Ogilvie, P. J. S. Olney, C. S. Roselaar, K. H. Voous, D. I. M. Wallace, and Jan Wattel. 1980. Oxford University Press, Oxford, London, and New York. 695 p. £30.00. This is the second volume in a projected series (first noted in *Condor* 80:253). The basic plan is the same as before, yet certain improvements and modifications have been made, as pointed out in the Introduction. Orders and families are each introduced with a description of their general characteristics. Species accounts treat field characters, habitat, distribution, population, movements, food, social pattern and behavior, breeding, plumages and external morphology, weights, and geographic variation. These are illustrated with a great many drawings, color plates, diagrams of the annual cycle, maps, sonograms, and life-size color photographs of eggs. In sum, this is an exceedingly rich storehouse of information on the birds within its scope, unsurpassed by any other regional handbook. References; corrections to Volume I, and indexes.

The Complete Birds of the World.—Michael Walters. 1980. David & Charles, North Pomfret, Vermont. 340 p. \$35.50. "This book attempts to list every bird species known to exist or to have existed in . . . post-Pleistocene times. This includes species known only from skeletal remains (but not fossil birds), and a number whose status remains doubtful for a variety of reasons." The sequence of families follows that of Peters' *Check-List of Birds of the World*; treatment within families follows that work or later revisions by other taxonomists. Walters consulted many ornithological references until 1977, when he completed his manuscript, but he overlooked numerous others that would have been pertinent. Each species entry gives the scientific name, the authority for that name, and an English name, i.e., the conventional stuff. What distinguishes this list from others of its kind is that it also provides basic data on distribution, habitat, food, nest site, clutch size, incubation, and fledging period. A brief account of general characteristics is given at the beginning of each family, and details are given, where known, for every species. By using abbreviations, an amazing amount of information is presented in an ordinary-sized book. Specialists will doubtless question certain taxonomic treatments or know of gaps in information that could have been filled. Nevertheless, many

ornithologists should find this book to be a most useful reference. Compare it with those by Edwards (1974. The author, Sweetbriar, Virginia); Gruson (1976. Noted in *Condor* 78:279); Morony, Bock and Farrand (1975. Noted in *Condor* 77:521); and Wolters (1975-. Noted in *Condor* 78:149, 79:138, 80:456, and 81:416). References; indexes.

Conservation Biology/An Evolutionary-Ecological Perspective.—Edited by Michael E. Soulé and Bruce A. Wilcox. 1980. Sinauer Associates, Inc., Sunderland, MA. 395 p. Paper cover. \$14.95. Growing awareness of the urgency of halting the loss of species and habitats has given impetus to the study and teaching of biological conservation during the past decade. The field has gained breadth and intellectual rigor, and thereby acquired academic responsibility and more students. This textbook for advanced undergraduates reflects those trends. Each of its four parts addresses a particular problem or theme: ecological principles of conservation, the consequences of insularization, captive propagation, and exploitation and preservation. Birds are mentioned in several chapters but they are explicitly the subject of only one, by Jared M. Diamond. The book merits consideration not only for conservation courses as such, but also other biology courses which include this subject—or should. Illustrations, bibliography, index.

The Imperative Call/A Naturalist's Quest in Temperate and Tropical America.—Alexander F. Skutch. 1979. University Presses of Florida, Gainesville. 331 p. \$20.00. This is the first part of Skutch's autobiography, although its publication follows that of its companion volumes, *A Naturalist in Costa Rica* (1971. U. Florida Press, Gainesville) and *A Bird Watcher's Adventures in Tropical America* (noted in *Condor* 80:118). The story begins with early years in Maryland and New England, concentrates on travels in Central America, and ends at the author's arrival in Costa Rica. Since his career has been dominated by the study of natural history, abundant observations of plants, birds, and other animals, are woven into the personal narrative. Unfettered by the strictures of scientific journals, Skutch writes in a fascinating and colorful style. He joins company with other explorer-naturalist-writers of the neotropics, such as Thomas Barbour, William Beebe, Archie Carr, and George M. Sutton. Photographs; end-paper maps; index.