COWBIRD PARASITISM IN THE KANSAS TALLGRASS PRAIRIE

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ABSTRACT.—During 1974 and 1975 brood parasitism by the Brown-headed Cowbird was studied in a tallgrass prairie community in northeastern Kansas. Hosts of primary interest were the Grasshopper Sparrow, Dickcissel, and Eastern Meadowlark, although ancillary data are recorded for the Cardinal, (*Cardinalis cardinalis*), Blue Grosbeak (*Guiraca caerulea*), Red-winged Blackbird (*Agelaius phoeniceus*), Robin (*Turdus migratorius*), Brown Thrasher (*Toxostoma rufum*), and Orchard Oriole (*Icterus spurius*).

A total of 77 nests of the three ground-nesting species were found, of which 54 (70.1%) were parasitized. Parasitized nests contained an average of 2.7 cowbird eggs per nest. In parasitized nests of 5 species, 13 (8.3%) of 157 cowbird eggs were successful, while 17 (12.4%) of 137 host eggs were successful. In the unparasitized nests, 23 (21.5%) of 107 eggs were successful.

A high intensity of brood parasitism is indicative of high relative densities of cowbirds. In this system nesting success was very low, suggesting that the high densities of cowbirds were due to high adult survival. The implications of this situation are discussed.—*Division of Biology, Kansas State University, Manhattan, Kansas 66506. Present address: Department of Biology, Eastern Connecticut State College, Willimantic, Connecticut 06226.* Accepted 7 May 1976.

BROOD parasitism by the Brown-headed Cowbird (*Molothrus ater*) has been reviewed extensively by Friedmann (1929, 1963), and several arguments have been proposed concerning the potential effect of cowbird parasitism on host populations (Friedmann 1929, 1963; Mayfield 1960; McGeen 1972). Most of the data on which these arguments are based have come from studies of forest-edge communities of the northern and northeastern United States (Nice 1937, Norris 1947, Berger 1951, Mayfield 1960, Nolan 1963, McGeen and McGeen 1968), a region only recently invaded by cowbirds (Mayfield 1965a). Conversely except for Wiens (1963), virtually no studies dealing specifically with cowbird parasitism have been conducted in the central regions of the United States. Excepting ancillary data provided from nesting success studies of potential host species (Overmire 1962, Hergenrader 1962), little information is available on parasitism of grassland species. This is significant as the midwestern prairie is part of the older breeding range of cowbirds (Mayfield 1965a). My purpose is to provide information on the incidence and intensity of cowbird parasitism of three prairie ground-nesting species common to northeastern Kansas, the Grasshopper Sparrow (*Ammodramus savannarum*), the Dickcissel (*Spiza americana*), and the Eastern Meadowlark (*Sturnella magna*). I also applied previously proposed models (Friedmann 1929, 1963; McGeen 1972) dealing with the stability of host and parasite populations to this system. While ancillary data on other host species are included, the emphasis of the study is on the three ground-nesting species, as they are the numerically dominant species in the community. The remaining species, restricted to nesting along fences and streams, are responsible for only a small fraction of the cowbird production in this community.

STUDY AREA AND METHODS

The study was conducted during 1974 and 1975 in the tallgrass prairie of the Flint Hills in Riley County, Kansas. The terrain is rolling to hilly with relatively smooth narrow divides bordered by rock outcrops and steep slopes. The dominant native grasses are big bluestem (*Andropogon gerardi*), Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), little bluestem (*Andropogon scoparius*), sideoats grama (*Bouteloua curtipendula*), and Kentucky bluegrass (*Poa pratensis*). Various species of trees and

TABLE 1
INCIDENCE OF COWBIRD PARASITISM

Species	Total nests	Parasitized nests
Grasshopper Sparrow	18	9 (50.0%)
Dickcissel	19	18 (94.7%)
Eastern Meadowlark	40	28 (70.0%)
Red-winged Blackbird	1	1
Orchard Oriole	1	1
Cardinal	1	1
Blue Grosbeak	1	1
Robin	5	2 (40.0%)
Brown Thrasher	8	3 (37.5%)

woody shrubs are present along the streams. The actual study site was part of the Range Research Pastures of Kansas State University and was being grazed by cattle during the course of the study (one steer/2.4 ha).

Nests of the ground-nesting species were located by cable-chain dragging (see Higgins, Kirsch, and Ball 1970), walking and searching for nests, and watching adult birds during nest-building activities. Nests were checked every 1 or 2 days until the young fledged or the nest was abandoned or destroyed.

RESULTS AND DISCUSSION

Table 1 shows that this host community suffers a relatively high degree of cowbird parasitism. In contrast to the 57.7% incidence of parasitism in this system, Wiens (1963) reported a 36.9% rate of parasitism of nine species in southern Oklahoma, and Berger (1951) recorded a 22.4% incidence of parasitism of 20 host species in Michigan. Likewise, Hergenrader (1962) reported a combined incidence of 30.8% of four passerine species nesting along roadsides in Nebraska. In addition to the high rates of parasitism recorded in my study, multiple parasitism, i.e. more than one cowbird egg per host nest, was the rule (see Table 2), rather than the exception. Data from studies by Friedmann (1929); Mayfield (1960, 1965b), and Norris (1947) indicate that in forest-edge systems multiple parasitism is comparatively rare.

Grasshopper Sparrow.—Cowbird parasitism of Grasshopper Sparrows has rarely been documented according to Friedmann (1963, 1971). In the only quantitative study, Price (1934) reported only 2 of 100 Grasshopper Sparrow nests parasitized in a study conducted in Ohio. The 50% incidence of parasitism recorded in my study is obviously much higher than would have been predicted from the data in the literature, and yet it should be pointed out that Grasshopper Sparrows were parasitized less frequently than meadowlarks or Dickcissels. This may be indicative of the increased difficulty experienced by cowbirds in locating the sparrow nests (Bent 1968, p. 741). Two of the 9 parasitized nests (22.2%) were successful, while 3 of 9 unparasitized nests successfully produced young. Ten of the 18 nests suffered predation (55.5%), while 3 nests (16.7%) were abandoned. A comparison of parasitized and unparasitized nests is illustrated in Table 3.

TABLE 2
MEAN NUMBER OF COWBIRD EGGS PER PARASITIZED NEST AND RESPECTIVE COWBIRD PRODUCTION

Species	Cowbird eggs/nest	Cowbird eggs/ successful nest	Cowbird fledglings per successful nest
Grasshopper Sparrow	2.0	1.0	0.50
Dickcissel	2.4	1.5	1.25
Eastern Meadowlark	3.1	2.0	0.83

TABLE 3
INCIDENCE OF PARASITISM, PREDATION, AND ABANDONMENT

	Grasshopper Sparrow			Dickcissel			Eastern Meadowlark		
	1974	1975	Total	1974	1975	Total	1974	1975	Total
No. nests	6	12	18	11	8	19	22	18	40
No. parasitized nests	3	6	9	11	7	18	15	13	28
% multiple parasitized nests	66.7	33.4	44.4	81.8	37.5	63.2	73.3	92.3	82.0
% nests abandoned	33.3	8.3	16.7	27.3	0.0	15.8	45.5	38.9	42.5
% nests preyed upon	33.3	66.7	55.5	63.6	50.0	57.9	22.7	27.7	25.0
% unparasitized nests preyed upon	33.3	66.7	55.6	—	50.0	50.0	20.0	40.0	30.0
% parasitized nests preyed upon	0.0	50.0	33.3	63.6	57.1	61.1	26.7	30.8	28.6
% unparasitized nests abandoned	0.0	33.3	22.2	—	0.0	0.0	50.0	40.0	45.5
% parasitized nests abandoned	50.0	0.0	22.2	27.3	0.0	16.7	46.7	46.2	46.4

Dickcissel.—Of 19 Dickcissel nests found on the study area, 18 (94.7%) were parasitized. This exceptionally high rate of parasitism is supported by a 1974 study by Hatch (MS) in which 90.8% of 65 nests were parasitized. Hatch's study was conducted in the same type of habitat, except that it was ungrazed. Likewise, Zimmerman (1966), also working in northeastern Kansas, recorded cowbird parasitism of 78% of 55 nests. In comparison, Wiens (1963) reported 33.3% of 15 Dickcissel nests parasitized in southern Oklahoma; Overmire (1962) reported 31% for northern Oklahoma, and Hergenrader (1962) recorded 52.9% of 17 nests parasitized in Nebraska. Of 18 parasitized nests in this study 4 were successful. Of the 19 nests, 11 suffered predation and 3 were abandoned. Table 3 summarizes the fates of the nests with respect to cowbird parasitism.

Eastern Meadowlark.—Of 40 meadowlark nests, 28 (70.0%) were parasitized, even though the literature suggests that the meadowlark is an infrequent host (Friedmann 1963). For example, Hergenrader (1962) reported that 16.1% of 31 nests were parasitized in Nebraska, and Lanyon (1957) reported 16.0% parasitism in Wisconsin. My results, however, corroborate previous work by Bowen (1976), who recorded cowbird parasitism in 14 or 15 nests found in the same general area in which this study was conducted. Of the 28 parasitized nests found, 5 (17.9%) were successful. Of all the nests found, 10 (25.0%) were destroyed by predators, and 17 nests (42.5%) were abandoned. The fates of parasitized and unparasitized nests are shown in Table 3.

Other species.—Parasitism of the remaining species listed in Table 1 is not discussed individually for each species because of the small amount of data for each

TABLE 4
SUCCESS OF PARASITIZED AND NONPARASITIZED NESTS

	Parasitized nests				Nonparasitized nests	
	Cowbird eggs	Cowbirds fledged	Host eggs	Hosts fledged	Host eggs	Hosts fledged
Grasshopper Sparrow	14	1 (7.1%)	17	1 (5.9%)	32	6 (18.8%)
Dickcissel	44	5 (11.4%)	47	5 (10.6%)	8	2 (25.0%)
Eastern Meadowlark	86	5 (5.8%)	58	7 (12.1%)	49	12 (24.5%)
Red-winged Blackbird	7	1 (14.3%)	9	2 (22.2%)	0	— —
Brown Thrasher	6	1 (16.7%)	6	2 (33.3%)	18	3 (16.7%)
Totals	157	13 (8.3%)	137	17 (12.4%)	107	23 (21.5%)

TABLE 5
HOST CLUTCH SIZE, PRODUCTION, AND EGG EJECTIONS BY COWBIRDS

Species	Mean clutch size	Unparasitized: Fledglings per successful nest	Parasitized: Host fledglings per successful nest	Mean host eggs ejected by cowbirds/nest
Grasshopper Sparrow	5.0	2.50	0.50	3.0
Dickcissel	4.0	2.00	1.25	3.0
Eastern Meadowlark	4.5	2.16	1.17	2.7

host. They are mentioned only as a point of information in describing the total host community. The cowbird parasitism of Brown Thrashers (*Toxostoma rufum*) does merit consideration as a possible example of geographic variation in host responses to cowbird parasitism. The Brown Thrasher, considered an occasional host by Friedmann (1963), was shown by Rothstein (1971) to be a regular ejector of foreign eggs. In my study 3 of 8 nests (37.5%) were parasitized, and no evidence was found in any of the nests that indicated cowbird eggs had been ejected. Of the 3 parasitized nests one was successful (33.3%), and a cowbird nestling was fledged. It should be emphasized that Rothstein's studies were conducted with artificial, non-mimetic eggs; thus, the two studies are not completely comparable.

Table 4 illustrates the nesting success of cowbirds and both parasitized and unparasitized hosts in terms of the percentage of the total number of eggs laid that produced fledglings. The 8.3% success rate of cowbirds and 12.4% production of host young suggest that the parasitized nests may be less successful in producing parasite and host young, but the difference is not statistically significant. The 21.5% production of host young in unparasitized nests illustrates the depressing effects of cowbird parasitism on host production.

The production estimates of cowbird and host young from parasitized nests are considerably lower than estimates reported by Wiens (1963), Berger (1951), and Norris (1947), suggesting that heavy cowbird parasitism affects both parasite and host young. The high incidence of parasitism and high frequency of multiple parasitism in this community apparently has a depressing effect on both cowbird and host nesting success, an observation consistent with the arguments of McGeen (1972). The production of host young from unparasitized nests (21.5%) is also considerably lower than Wiens' (1963) estimate of 36.2% for southern Oklahoma. This suggests that factors other than cowbird parasitism may be responsible for the low nesting success of this community of hosts.

In terms of the mean number of host fledglings produced per nest, cowbird parasitism costs Grasshopper Sparrows approximately two young per parasitized nest, while the cost to Dickcissels and meadowlarks is approximately one young per nest (Table 5). Similar estimates were made by Norris (1947), Nice (1937), and King (1973) concerning the cost of brood parasitism to host species.

Of particular interest in Table 5 is the low production of successful unparasitized nests in comparison to the mean clutch sizes of the respective hosts. The mean number of host egg ejections by cowbirds was estimated by subtracting the mean number of host hatchlings in parasitized nests from the mean number of hatchlings in unparasitized nests. It is interesting and perhaps coincidental that the mean number of eggs ejected by cowbirds approximates the differences between the hosts' clutch sizes and numbers of fledglings per successful unparasitized nest. This suggests some

type of brood reduction strategy, perhaps to offset losses to cowbird parasitism. This follows from the observation that the host species appear to be unable to raise young to fledging from all the eggs laid. Although the ejected host eggs are generally replaced with corresponding cowbird eggs, parasite eggs have a lower hatching rate than do the host eggs, as a result of being unfertilized and/or being laid too late to be adequately incubated. Thus, it is possible that hosts are laying large clutches to offset the loss of eggs due to cowbird ejections. Among the three host species listed in Table 4, only one nest in 2 years produced as many as 4 young.

The reactions of the host species to multiple parasitism in this study are also of interest. Wiens (1963) noted that only 6 of 31 parasitized nests contained as many as 2 cowbird eggs, and of these 6 nests, 4 were deserted. Norris (1947) reported that nests containing more than one cowbird egg were usually deserted. The data from my study indicate that different host species in a community may react differently to the deposition of more than one cowbird egg in the nest. As illustrated in Table 3, only in Dickcissels does nest abandonment appear to be related to cowbird parasitism, as no unparasitized nests were deserted. In both Grasshopper Sparrows and meadowlarks the likelihood of nest abandonment appears unrelated to cowbird parasitism. Furthermore, an examination of individual nests of these two host species indicates that nests with more than one cowbird egg are no more likely to be deserted than unparasitized or singly parasitized nests. In fact, the frequency of nest abandonment in meadowlarks, though higher than in Dickcissels and Grasshopper Sparrows, declined slightly in 1975 from 45.5% to 38.9%, even though the incidence of multiple parasitism increased from 73.3% to 92.3%. Thus, it appears that meadowlarks may tolerate more nest disturbance than do the other two species. The fact that meadowlarks exhibit a higher frequency of nest abandonment than either Grasshopper Sparrows or Dickcissels appears to be the result of factors other than multiple parasitism. My observations of meadowlark nests agree with this interpretation, as I have often visited active meadowlark nests within a meter of which were scattered several cowbird and meadowlark eggs and broken egg shells. Similar observations of meadowlark nests have been reported previously (Friedmann 1963). This tolerance of repeated parasitism accounts for the apparent paradox of the comparatively low success rate, relative to the other two host species, for cowbirds in meadowlark nests given in Table 4 and the higher estimate given in Table 2. Meadowlarks appear able to feed more than one cowbird per nest easier than do the two smaller host species. Indeed, the estimate of cowbird production by Dickcissels given in Table 2 is somewhat misleading, as it probably would not have been nearly so high, except for a very late breeding season by Dickcissels in 1975. The majority of their nesting was done after most female cowbirds had stopped laying; consequently, Dickcissels experienced a considerably lowered degree of multiple parasitism in 1975. The implication is that more than two cowbird eggs per nest yield fewer cowbirds, rather than more cowbirds.

Neither the frequency nor intensity of cowbird parasitism appears to affect the amount of nest predation experienced by the hosts (Table 3). At least, no obvious trends in predation rates result from changes in intensity of parasitism. A much lower predation rate is experienced by meadowlarks as compared to Dickcissels and Grasshopper Sparrows. This supports arguments by Bowen (1976) that smaller ground-nesting species should experience greater predation than larger species because of the larger array of predators that can accommodate the smaller eggs, while some predators are excluded from taking larger eggs because of size limitations. In addition,

larger ground-nesting species would drive certain small predators away from their nests.

The high intensity of cowbird parasitism in this prairie community causes an ominously lowered production of both host and parasite young. It appears that the high relative density of cowbirds (cowbirds per host), as evidenced by the high frequency of multiple parasitism (McGeen 1972), and high absolute density (Van Velzen 1972) in this region is not the result of high breeding success. Consequently, the current densities of cowbirds must be due to high juvenile and/or adult survival rates. The implications this has on the community stability, in terms of the relative numbers of cowbirds and hosts, are not completely clear. However, it is apparent that arguments and models dealing solely with the breeding season (Friedmann 1963, McGeen 1972) may not be applicable in predicting the potential effect of cowbird parasitism on host populations.

The interpretation of lower than average yearly mortality in cowbirds from this area is supported by banding data. Of 14 adults banded in 1974, 3 returns (2 males and 1 female) were obtained in 1975. Of only 13 nestlings banded in 1974, 2 returns (1 male and 1 female) were obtained in 1975. These return rates are extremely high in comparison to the usual cowbird return rate of 1 per 100 cowbird fledglings banded (Shepherd pers. comm.).

It is not yet clear whether or not increased winter survival of cowbirds could significantly affect host populations in this system, as host populations may be constantly bolstered by immigration from more productive areas. Species populations on the fringe of their breeding distribution or small isolated populations, i.e. Kirtland's Warbler (*Dendroica kirtlandi*), appear especially vulnerable in this type of situation, as cowbird populations in these systems will probably not decrease as much as host populations following a bad breeding year. Thus the following year the host species is faced with proportionally more cowbirds than were present the year before.

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