HOST-PARASITE RELATIONSHIPS OF THE BROWN-HEADED COWBIRD IN A PRAIRIE HABITAT OF WEST-CENTRAL KANSAS

RICHARD A. HILL

The parasitic nature of the Brown-headed Cowbird (*Molothrus ater*) is believed to have developed as a result of its association with the bison (*Bison bison*). Cowbirds subsisted on insects flushed by herds of bison, however, the nomadic nature of the bison made it impossible for cowbirds to remain with the herd and simultaneously perform nesting activities. Theoretically the evolution of parasitic habits allowed the cowbird to achieve reproductive success and concurrently maintain the established feeding relationship with the bison. Thus the distribution of the cowbird was similar to that of the bison or as Friedmann (1929) states, "the home of the cowbird was the open grasslands of the midcontinent." Therefore the reproductive success of the cowbird was determined by the establishment of a functional equilibrium of a host-parasite relationship in a prairie habitat.

In this regard, Sutton (1967) states that possible ground-nesting hosts in open grassland in Oklahoma are not heavily parasitized. Mayfield (1965) states that host species of the cowbird in western grassland have had long ancestral experience with parasitism and are much less receptive than host species of the eastern forest which have little experience with the social parasite.

Data from breeding bird surveys, Van Velzen (1972) show that the center of abundance of the cowbird is still within the central plains of the United States. This suggests that species nesting in these predominantly grassland states are receptive hosts. The purpose of this paper is to present data on the extent of cowbird parasitism and to discuss adaptations to parasitism of hosts nesting in a predominantly prairie habitat.

MATERIALS AND METHODS

The study was conducted in Ellis County, in west-central Kansas in 1973 and 1974. The county is composed of 62% cropland, 38% pastureland, and 0.4% woodland (U.S.D.C. 1969). In 1973 efforts were made to study nests of all passerine species nesting in Ellis County, and in 1974 efforts were concentrated on finding nests of likely host species of the cowbird. Data from all available Ellis County nesting records were used to determine the frequency of parasitism of each species (Tables 1 and 2).

The term "grassland species" refers to the following 6 species listed by Shelford (1963) as characteristic of a grassland habitat: Horned Lark, Western Meadowlark, Dickcissel, Lark Bunting, Grasshopper Sparrow, and Lark Sparrow. The young of grassland species are prone to leave the nest at an early age. The young of Horned Larks,

TABLE 1

FREQUENCY OF PARASITISM OF HOST SPECIES IN ELLIS COUNTY, KANSAS

Species	Nests Investigated	Number Parasitized	Percent Parasitized
Cardinal (*Cardinalis cardinalis*)	3	3	100.0
Lark Sparrow (*Chondestes grammacus*)	11	9	81.8
Pine Siskin (*Spinus pinus*)	51	28	54.9
Orchard Oriole (*Icterus spurius*)	15	8	53.3
Dickcissel (*Spiza americana*)	28	14	50.0
Bell's Vireo (*Vireo belli*)	2	1	50.0
Horned Lark (*Eremophila alpestris*)	31	14	45.2
Grasshopper Sparrow (*Ammodramus savannarum*)	18	4	22.2
Red-winged Blackbird (*Agelaius phoeniceus*)	228	50	21.9
Lark Bunting (*Calamospiza melanocorys*)	142	22	15.5
Eastern Phoebe (*Sayornis phoebe*)	68	7	10.1
Western Meadowlark (*Sturnella neglecta*)	29	2	6.9
Brown Thrasher (*Toxostoma rufum*)	49	3	6.1
Say's Phoebe (*Sayornis saya*)	37	1	2.7

Brown-headed Cowbirds, Dickcissels, and Grasshopper Sparrows were each observed to leave the nest at an estimated age of 6 to 7 days. Nests of grassland species were approached from different directions each time the nest was checked in an attempt to reduce predation, but still 44% were destroyed by predators. Consequently a category of "presumed fledged" was established to aid in the interpretation of fledging success due to the high rate of predation and the tendency of the young to leave the nest early. It is obvious that the "presumed fledged" category cannot be accurate, but it is probably nearer to the actual rate of fledging success than is the number actually known to fledge. Thus references here to fledging success of grassland species refer to the number presumed to have fledged. Young birds surviving at least 4 days would probably fledge, barring predation; thus the young of grassland species which were at least 4 days old were presumed to have fledged.

TABLE 2

NUMBER OF NESTS OF NON-PARASITIZED SPECIES INVESTIGATED IN ELLIS COUNTY

Species	Nests Investigated
Mourning Dove (*Zenaida macroura*)	1023
Barn Swallow (*Hirundo rustica*)	284
Common Grackle (*Quiscalus quiscula*)	79
Western Kingbird (*Tyrannus verticalis*)	51
American Robin (*Turdus migratorius*)	32
House Sparrow (*Passer domesticus*)	26
Eastern Kingbird (*Tyrannus tyrannus*)	16
Common Nighthawk (*Chordeiles minor*)	14
Mockingbird (*Mimus polyglottos*)	12
Loggerhead Shrike (*Lanius ludovicianus*)	9
Scissor-tailed Flycatcher (*Muscivora forficata*)	7
Black-billed Magpie (*Pica pica*)	6
Northern Oriole (*Icterus galbula*)	6
Killdeer (*Charadrius vociferus*)	5
Yellow-billed Cuckoo (*Coccyzus americanus*)	4
Blue Jay (*Cyanocitta cristata*)	3
Catbird (*Dumatella carolinensis*)	1

The predation rate appeared to increase with the frequency of nest visits by researchers so visits were reduced to 5-day intervals until the young reached an age of 4 or 5 days. After this time nests were checked at 3-day intervals when possible.

Species described as common, or uncommon to common summer residents in Ellis County (Ely 1971) are collectively referred to as common species while those described as uncommon or low-density are referred to as uncommon species.

I have used the criteria established by Mayfield (1965) for evaluating frequency of parasitism—less than 10% light; 10–30% moderate; over 30% heavy.

RESULTS AND DISCUSSION

Cowbird parasitism occurred from 21 April until 16 July with the greatest intensity of egg-laying occurring between 25 April and 1 July (Fig. 1). Six of the 14 species parasitized are grassland species. The overall frequency of parasitism ranged from 100% for the Cardinal to 2.7% for Say's Phoebe. The range for the grassland species was 81.8% (Lark Sparrow) to 6.9% (Western Meadowlark).

The small number of nests investigated for each species, the high rate of nest predation among grassland species, and the tendency of grassland species to leave the nest early have made the interpretation of the effect of cowbird parasitism difficult. Although the relatively small number of parasitized

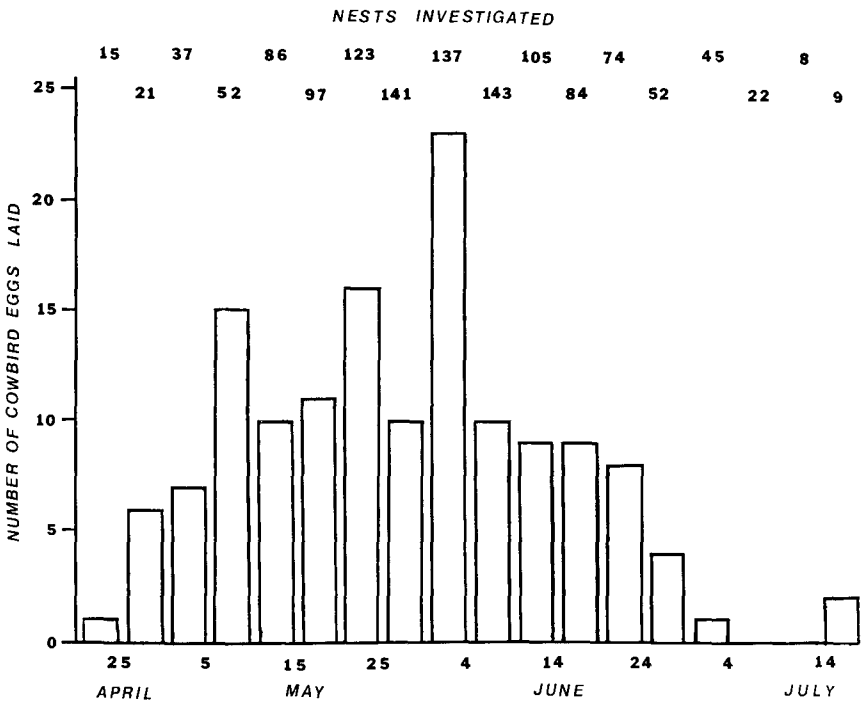

FIG. 1. Number of cowbird eggs laid per 5 day interval in Ellis County, Kansas, 1973–1974.

nests investigated may be inconclusive evidence of the role played by each host species, a substantial amount of parasitism seems to occur among grassland species.

The measure of the success of cowbird parasitism is determined by the number of cowbirds raised by each host species. Mayfield (1965) has defined "tolerance" to cowbird parasitism as the ratio of cowbirds fledged to the number of cowbird eggs laid in the nest of the host. He regarded a fledging rate from cowbird eggs of more than 20% as an indication of a tolerant host. By this measure, 3 of the 6 grassland species are tolerant hosts: Lark Sparrow, Grasshopper Sparrow, and Horned Lark. The situation for the Dickcissel and Lark Bunting is uncertain. Nine of 13 parasitized Dickcissel nests (69%) were destroyed by predators or human activities and 5 of 13 parasitized Lark Bunting nests were destroyed by predators. Consequently, very few eggs laid by the cowbird in nests of these species had an opportunity to fledge. Since I observed Dickcissels to rear 2 cowbirds to at

TABLE 3

COWBIRD NESTING SUCCESS IN ELLIS COUNTY, KANSAS 1973–1974

Species	Parasitized Nests	Cowbird Eggs	Number Fledged	Percent of Success
Lark Sparrow	9	16	11	69
Grasshopper Sparrow	4	5	3	60
Eastern Phoebe	7	10	4	40
Orchard Oriole	2	3	1	33
Horned Lark	14	24	7	25
Dickcissel	13	14	2	14
Red-winged Blackbird	18	19	2	11
Lark Bunting	13	15	1	7
Pine Siskin	16	20	1	5
Say's Phoebe	1	1	0	0
Brown Thrasher	1	3	0	0
Bell's Vireo	1	1	0	0
Western Meadowlark	1	1	0	0

least 6 days of age and a pair of Lark Buntings raised a cowbird for at least 5 days, it is possible that only the Western Meadowlark, among the grassland species, is intolerant to cowbird parasitism (Table 3).

All of the species in which no cowbird parasitism was observed are among

TABLE 4

NUMBER OF COWBIRD EGGS LAID PER NEST FOR EACH OF 13 SPECIES IN ELLIS COUNTY, KANSAS

Host Species	Nests Investigated	1 Egg	2 Eggs	3 Eggs	Number of Eggs per Parasitized Nest	Number of Eggs for all Nests
Lark Sparrow	9	4	3	2	1.78	1.78
Pine Siskin	23	12	4	0	1.25	.87
Horned Lark	30	6	6	2	1.71	.80
Orchard Oriole	5	1	1	0	1.50	.60
Dickcissel	26	12	1	0	1.08	.54
Bell's Vireo	2	1	0	0	1.00	.50
Grasshopper Sparrow	15	3	1	0	1.25	.33
Red-winged Blackbird	90	17	1	0	1.05	.21
Lark Bunting	135	19	3	0	1.32	.19
Brown Thrasher	20	0	0	1	3.00	.15
Eastern Phoebe	68	5	1	1	1.43	.14
Western Meadowlark	22	1	0	0	1.00	.05
Say's Phoebe	37	1	0	0	1.00	.03
Total	520	84	21	6	1.41	.48

TABLE 5

FLEDGING SUCCESS OF 13 COWBIRD HOST SPECIES AT NON-PARASITIZED NESTS, ELLIS COUNTY, KANSAS

Species	Number of Nests	Number Fledged	Number Fledged per Nest	Presumed Fledged	Number Presumed Fledged per Nest
Eastern Phoebe	61	137	2.3		
Say's Phoebe	36	51	1.4		
Horned Lark	16	4	0.3	22	1.4
Brown Thrasher	14	7	0.5		
Bell's Vireo	1	0	0.0		
Western Meadowlark	16	11	0.7	34	2.1
Red-winged Blackbird	63	6	0.1		
Orchard Oriole	3	9	3.0		
Dickcissel	12	5	0.4	18	1.5
Pine Siskin	7	14	2.0		
Lark Bunting	49	19	0.4	71	1.5
Grasshopper Sparrow	8	4	0.5	20	2.5
Lark Sparrow	0	0	0.0		

those regarded by Friedmann (1963) as uncommon, rare, or accidental victims of cowbird parasitism.

The number of cowbird eggs found in each parasitized nest varied from 1 to 3 eggs. Twenty-five percent of 110 parasitized nests contained more than 1 cowbird egg per nest, yet the percentage of multiple parasitism was lower than the 40% reported by Friedmann (1963). He also stated that in more recent and more carefully made studies, nests with multiple eggs slightly outnumber nests with single cowbird eggs.

The frequency of parasitism and the number of cowbird eggs laid per nest of each host species should reflect the use of each host by the cowbird. The host species with the greatest frequency of parasitism and the highest number of cowbird eggs per nest should be an indication of a preferred host. On this assumption 4 of the 7 most "preferred" hosts are grassland species (Table 4).

Cowbird parasitism decreased the number of host fledglings, as an average of 1.54 young fledged from each non-parasitized nest while only 0.53 young of the host species fledged from each parasitized nest. Cowbirds were less successful than their nest-mates as only 0.32 cowbirds fledged per parasitized nest (Tables 5 and 6).

The relatively greater abundance of Brown-headed Cowbirds in Kansas (Van Velzen 1972) is also indicated by the high frequency of cowbird parasitism found in several species nesting in Ellis County. Breeding-bird surveys

TABLE 6

FLEDGING SUCCESS OF 13 COWBIRD HOST SPECIES AT PARASITIZED NESTS, ELLIS COUNTY, KANSAS

	Host Species					Cowbird			
Species	Number of Nests	Number Fledged	Fledged per Nest	Presumed Fledged	Presumed Fledged per Nest	Number Fledged	Fledged per Nest	Presumed Fledged	Presumed Fledged per Nest
Eastern Phoebe	7	1	0.1			4	0.6		
Say's Phoebe	1	0	0.0			0	0.0		
Horned Lark	14	0	0.0	10	0.7	7	0.5	7	0.5
Brown Thrasher	1	0	0.0			0	0.0		
Bell's Vireo	1	0	0.0			0	0.0		
Western Meadowlark	1	0	0.0	0	0.0	0	0.0	0	0.0
Red-winged Blackbird	17	6	0.4			2	0.1		
Orchard Oriole	2	3	1.5			1	0.5		
Dickcissel	13	0	0.0	9	0.7	0	0.0	2	0.2
Pine Siskin	16	3	0.2			1	0.1		
Lark Bunting	13	0	0.0	7	0.5	0	0.0	1	0.1
Grasshopper Sparrow	4	2	0.5	8	2.0	2	0.5	3	0.8
Lark Sparrow	9	2	0.2	5	0.6	8	0.9	11	1.2

show the greatest abundance of cowbirds to be in the north-central part of Kansas (Fig. 2) and it is possible that an even greater intensity of parasitic activity may occur there.

The high relative abundance of cowbirds in the plains states and my findings of relatively heavy parasitic activities among most grassland species suggests that grassland species do contribute greatly to the success of the cowbird.

SPECIES ACCOUNTS

Eastern Phoebe.—Friedmann (1963) reports that the Eastern Phoebe is a very common victim of cowbird parasitism, but the degree to which the phoebe is affected varies locally. In this study 7 of 68 nests investigated were parasitized and the phoebe was a tolerant host: 40% of the cowbird eggs laid, fledged young. Five of 7 instances of parasitism occurred in the first half of the breeding season. The phoebe is an uncommon summer resident of Ellis County, and considering the relatively low frequency of parasitism, the Eastern Phoebe does not play a major role as a host.

Say's Phoebe.—Only 6 instances of cowbird parasitism of Say's Phoebe were reported by Friedmann (1963), 5 of them from Kansas. The only parasitized nest I found held 4 phoebe eggs and 1 cowbird egg, but 3 days later held only 5 phoebe eggs. Fried-

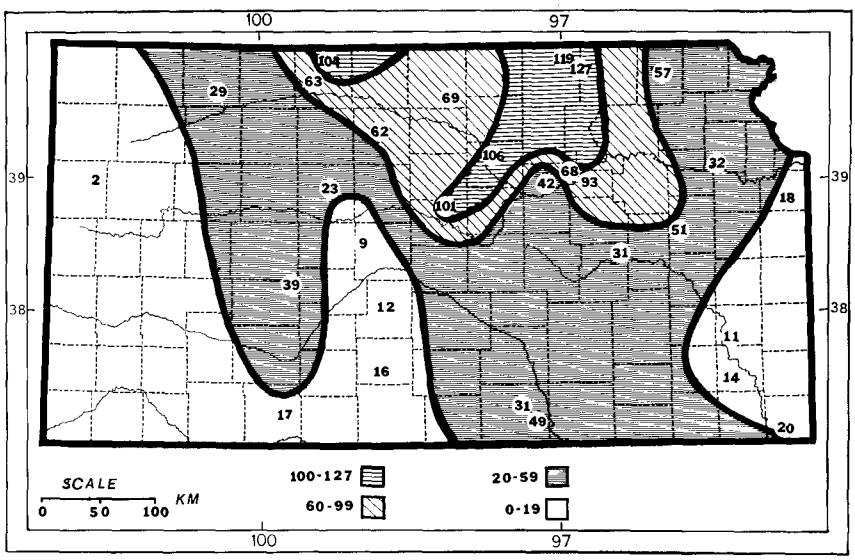

FIG. 2. Relative abundance of the Brown-headed Cowbird in Kansas during the breeding season.

mann suggests that Say's Phoebe is not of much importance to the cowbird and the latter in turn is not an important factor in the economy of the phoebe. My finding of only 1 parasitized nest out of 37 studied supports Friedmann's belief.

Horned Lark.—Horned Larks characteristically laid 2 clutches, the first between 20 March and 14 April, the second between 15 May and 15 June. I observed no parasitism in the first clutch (8 nests) but 14 of 22 (63.3%) of second clutches were parasitized. Three nests fledged 2 cowbirds each and 2 other Horned Lark nests each contained two 9-day-old cowbirds. Friedmann (1963) regards the Horned Lark as a generally infrequent victim of the cowbird, although in some places it is a fairly frequent host. If the frequency of parasitism of the second clutch (63.3%) is considered, it seems to be more than just a fairly frequent host in Ellis County. The Horned Lark is a common summer resident, is heavily parasitized, and is a tolerant host. Consequently it appears to play a major part in the reproductive success of the cowbird. It is also possible that the Horned Lark has adapted to a heavy frequency of parasitism by laying its first clutch of eggs prior to the breeding season of the cowbird.

Brown Thrasher.—Friedmann (1963) states that the Brown Thrasher is occasionally parasitized. This is supported by a 6.1% parasitism rate of the nests I investigated. The low frequency of parasitism appears to exclude the Brown Thrasher as a host of any major importance.

Bell's Vireo.—Friedmann (1963) lists Bell's Vireo as a frequent victim of the cowbird within an area that includes Kansas. The single parasitized nest of only 2 investigated is insufficient evidence for speculation on the role of Bell's Vireo as a host. Barlow's work in Kansas (1962) revealed that 24 of 35 occupied nests (68%) were para-

sitized. Since Bell's Vireo is a fairly common summer resident of Ellis County and since a high rate of parasitism was observed by Barlow it is possible that Bell's Vireo is an important host of the cowbird in Ellis County.

Western Meadowlark.—Friedmann (1963) states that the Western Meadowlark like the Eastern Meadowlark is an uncommon host and is parasitized even less. The Western Meadowlark was the only grassland species in which a low frequency of parasitism was observed (6.9%). Hergenrader (1962) noted several instances of cowbird eggs near meadowlark nests in Nebraska which suggested to him that the meadowlark is sometimes successful in expelling the eggs from the nest. I recorded no instances of cowbird eggs that had been removed from meadowlark nests. No adaptations that would explain the low frequency of parasitism were evident.

Red-winged Blackbird.—Friedmann (1963) stated that the Red-winged Blackbird is a common victim in some areas but is almost unmolested by the cowbird in other localities. In Ellis County nests of Red-wings were moderately parasitized (21.9%). Fledging success was relatively low, apparently due in large part to predators following paths to nests checked too frequently at the beginning of this study. The extremely high proportion of Red-wing nests destroyed by predators makes the Red-wing appear as an intolerant host, but since 2 cowbirds were known to have fledged from Red-wing nests, it is possible that the Red-wing actually is a tolerant host. Since the Red-wing is a common summer resident, is moderately parasitized, and possibly is a tolerant host, it probably is of some importance to the reproductive success of the cowbird.

Orchard Oriole.—Friedmann (1963) regarded the Orchard Oriole as a fairly frequent host although actual records are few. Though an uncommon summer resident it was heavily parasitized (53.3%) in this study. Although fledging success could be assessed for only 2 parasitized nests, it appears that the Orchard Oriole is a tolerant host and produces a few cowbirds from the limited number of nests occurring in Ellis County.

Cardinal.—Friedmann (1963) states that the status of the Cardinal as a cowbird fosterer varies in different parts of its range. Cardinals are uncommon in Ellis County and although all 3 nests investigated were parasitized, the Cardinal probably plays an insignificant role as a host species.

Dickcissel.—Friedmann (1963) states that the Dickcissel is a common victim and it appears to be parasitized more often in Texas, Oklahoma, Nebraska, and Kansas than elsewhere. I found a 50% parasitism rate for the Dickcissel, though Zimmerman (1966) found a 78% rate of parasitism in eastern Kansas. A high rate of nest predation obscured a determination of tolerance, but since 2 cowbirds were raised by Dickcissels to an age of 6 days it is probable that the Dickcissel is a tolerant host. Since it is a fairly common summer resident, heavily parasitized, and possibly a tolerant host, it is probably one of the more important host species in Ellis County.

Pine Siskin.—The Pine Siskin is generally allopatric with the cowbird; however, wherever the 2 species do overlap, the Pine Siskin occasionally is imposed upon (Friedmann 1963). Nesting records of the Pine Siskin are rare, but in Ellis County it is subject to heavy cowbird parasitism (54.9%). Tolerance of parasitism is low (5%) and the effect of parasitism on the siskin is detrimental. Irregular nesting of the Pine Siskin in Ellis County and a low tolerance of parasitism eliminate it as a productive host species. The Pine Siskin appears to be an example of a receptive host that has had little exposure to nest parasitism (see Mayfield 1965).

Lark Bunting.—The Lark Bunting is a common local victim of northwestern cowbird populations but overall it is a rather infrequent victim (see Friedmann 1963). In

my study it was subject to moderate parasitism (15.5%). The most frequent nesting habitat appeared to be milo stubble. Consequently 52% of the nests were destroyed by farming activity and these are omitted from calculation of fledging success. The tolerance of the Lark Bunting is questionable because of a high rate of predation and nest desertion. Seven of the 13 parasitized nests were destroyed by predators and 5 were deserted. Since 1 cowbird was raised to an age of 5 days it is possible that the Lark Bunting is a tolerant host. Because of a relatively low frequency of parasitism and the high proportion of nests destroyed by farming practices, the Lark Bunting appears to be a species of little value to the cowbird as a host. One possible adaptation of the bunting to cowbird parasitism may be the removal of cowbird eggs from the nest. The color contrast of the blue bunting egg and the brown speckled egg of the cowbird is greater than that of all other grassland species except the Dickcissel. Thus, if any grassland species is capable of distinguishing between eggs of their own and those of the cowbird it would be the Lark Bunting. The recognition and subsequent removal of a foreign egg is suggested by 5 separate observations of cowbird eggs found outside of bunting nests. The removal of cowbird eggs would help explain the relatively low frequency of parasitism in comparison to other grassland species. Nest desertion may be another adaptation to parasitism as 5 out of 13 parasitized nests were deserted. However, at least one was a direct result of human interference. Only 3 of 49 non-parasitized nests were deserted.

Grasshopper Sparrow.—Instances of parasitism of the Grasshopper Sparrow are few, but Friedmann (1971) reports one case in which a young nestling cowbird was ready to leave the nest. Two 8-day-old and one 4-day-old cowbird I observed in separate nests of Grasshopper Sparrows further reinforce the evidence that the sparrow is a true host. Although the frequency of parasitism was relatively low (22.2%) I found the Grasshopper Sparrow to be a very tolerant host (60%). Considering that it is one of the most abundant summer residents in Ellis County, a significant portion of the cowbirds produced in Ellis County may fledge from Grasshopper Sparrow nests.

Lark Sparrow.—Friedmann (1963) lists the Lark Sparrow as a relatively uncommon host, but this was not the case in Ellis County where 81.8% of the nests investigated were parasitized. In my study the Lark Sparrow had the highest tolerance to parasitism of all host species (69%). Even though it is an uncommon summer resident in Ellis County, the high frequency of parasitism and the high level of tolerance to parasitism suggests that the Lark Sparrow is an important host of the cowbird.

SUMMARY

Of 520 nests of 14 host species, 111 (21%) were parasitized. The frequency of parasitism varied from 2.7% (Say's Phoebe) to 100% for 3 Cardinal nests. All but 1 grassland host species received moderate to heavy parasitism. Parasitized nests fledged 1 less host (0.5 per nest) than non-parasitized nests (1.5 per nest). Only 0.3 cowbirds fledged per nest.

Probable adaptations to parasitism were nesting prior to the cowbirds breeding season by Horned Larks and nest desertion and removal of cowbird eggs by Lark Buntings.

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DEPT. OF BIOLOGICAL SCIENCES, FORT HAYS KANSAS STATE COLLEGE, HAYS 67601.
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