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RED-WINGED BLACKBIRDS AND BROWN-HEADED COWBIRDS: SOME ASPECTS OF A HOST-PARASITE RELATIONSHIP[1]

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Abstract. We studied the interaction between brood-parasitic Brown-headed Cowbirds (*Molothrus ater*) and Red-winged Blackbirds (*Agelaius phoeniceus*) in eastern Washington, and report four results. First, the overall rate of cowbird parasitism in our redwing nests was 7.7%. Second, the density of breeding redwings strongly affected parasitism rates among marshes within our study area, probably because of the importance of group defense. Third, over 20% of cowbird eggs laid in redwing nests at our study site appeared in inactive nests. We show that the frequency of this "inappropriate laying" by cowbirds is a function of the number of trees available in redwing nesting areas, possibly because perch sites allow female cowbirds to gain better information on the status of prospective host nests. Finally, the percentage of redwing nests parasitized increases dramatically as the breeding season progresses. We suggest that the late-season decline in rate of chick starvation found in our redwing population may increase cowbird reproductive success, even though late redwing nests are more likely to be lost to predation than early redwing nests.

Key words: Red-winged Blackbirds; Brown-headed Cowbirds; brood parasitism.

INTRODUCTION

Although it is well-known that Red-winged Blackbirds (*Agelaius phoeniceus*) are parasitized by Brown-headed Cowbirds (*Molothrus ater*), less is known about the dynamics of this host-parasite relationship. In this paper we address four questions about redwing-cowbird interactions. First, are redwings in eastern Washington heavily parasitized by cowbirds relative to redwing populations in other localities? If so, why? Second, is there evidence that group defense by redwings is important in deterring cowbird females as Friedmann (1963) and Robertson and Norman (1977) suggest? Third, Berger (1951) and Furrer (in Friedmann et al. 1977) have reported that cowbirds sometimes lay in abandoned or otherwise inappropriate host nests. How frequent is this behavior when cowbirds parasitize redwings, and what factors influence the ability of cowbirds to lay in host nests at an appropriate time and avoid "dumping" eggs? And finally, in eastern Washington late-nesting Brewer's Blackbirds (*Euphagus cyanocephalus*) are much more heavily parasitized by cowbirds than early-nesting Brewer's Blackbirds (Friedmann et al. 1977). Does the same pattern hold for Red-winged Blackbirds in the same area? If so, why don't cowbirds parasitize earlier redwing nests?

METHODS

We studied records from 1,325 redwing nests observed during the breeding seasons of 1978, 1986, 1987, and 1988. The nest records we used came from 14 marshes near the Winchester Wasteway in Grant County, Washington, where we conducted nest checks every 6 days on average throughout the 1978 breeding season and every 3 to 4 days throughout the 1986–1988 breeding seasons. During nest checks we recorded the location and contents of each nest. In 1978 and 1986 we continued nest checks until the end of the breeding season; in 1987 and 1988 we stopped doing nest checks before nest initiation had ended.

RESULTS

OVERALL RATE OF PARASITISM

Of the 1,325 blackbird nests we studied, 102, or 7.7%, were parasitized by cowbirds while the nests were active. This estimate of the overall rate of cowbird parasitism may be slightly conservative for two reasons: we may have missed cowbird eggs that were destroyed in predation events before we were able to record them (approximately 17% of the redwing nests in our sample were destroyed by predators during or immediately after the laying period), and we are missing data

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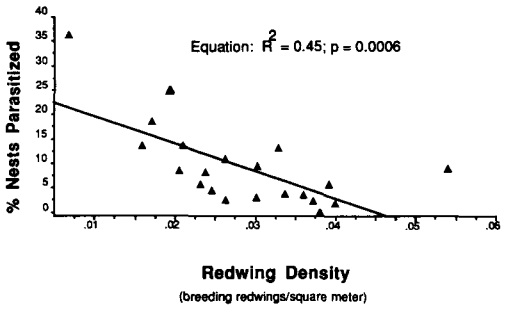

FIGURE 1. The percentage of Red-winged Blackbird nests parasitized by Brown-headed Cowbirds as a function of redwing density. Redwing density is calculated as the number of males that bred on a marsh during a year plus the sum of the largest number of females simultaneously nesting on each of the males' territories in that year, divided by the area of each marsh in square meters.

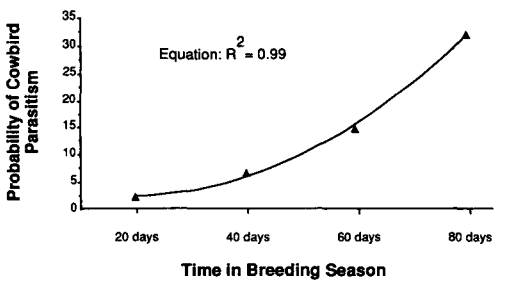

FIGURE 2. Seasonal increase in incidence of Brown-headed Cowbird parasitism in Red-winged Blackbird nests. The breeding season is divided into 20-day intervals beginning when the first redwing egg was laid in a marsh in that year. Probability of cowbird parasitism is calculated as the number of parasitized nests divided by the total number of nests initiated during that interval in the season.

for short intervals in the 1987 and 1988 seasons (since our nest checks ended early in those years) when cowbird activity was typically high.

GROUP DEFENSE AND RATE OF PARASITISM

Although we were not able to quantify the effects of group defense on cowbird success directly, the density of redwings defending active nests had a strong influence on rate of parasitism among marshes: dense redwing colonies had lower rates of cowbird parasitism (Fig. 1). This result suggests that group defense against cowbirds is indeed important.

INAPPROPRIATE LAYING BY FEMALE COWBIRDS

In addition to the 102 parasitized nests analyzed above, we observed 28 previously unparasitized redwing nests where cowbird eggs appeared after the redwing clutch had been destroyed by predators or had fledged. In other words, 21.5% of the 130 total parasitism events that we observed occurred in inactive nests, where cowbird young had no probability of fledging. Since several of these inactive redwing nests received more than one cowbird egg, substantially greater than one in five of all cowbird eggs laid was "dumped" into a redwing nest where there was no chance of fledging young.

To examine this phenomenon further we divided our study marshes into three groups: those that contained (1) no trees, (2) one to four trees within 4 m of the marsh perimeter, or (3) greater than four trees on the perimeter or within the marsh itself. We then calculated the percentage of parasitized nests in each marsh that were parasitized after the nest had become inactive.

TABLE 1. Overall rates of Brown-headed Cowbird parasitism in Red-winged Blackbird marshes with contrasting densities of trees. Tree density does not affect overall rate of parasitism (Kruskal-Wallis H = 3.8, P = 0.15), but tree density does affect the percentage of redwing nests parasitized by cowbirds after they have become inactive (Kruskal-Wallis H = 6.8, $P < 0.05$).

Marsh name	Tree density	No. parasitized	Overall % parasitized	% parasitized when inactive
86	None	16	6.9	18.8
Reprieve	None	2	1.7	100
Rest Area	None	25	9.4	16.0
Peter's	None	7	9.1	14.3
Skeleton	1–2 <4 m from marsh	21	6.7	23.8
Dead Cow	1–2 <4 m from marsh	13	7.1	38.5
1–10	1–2 <4 m from marsh	11	12.4	45.5
Beda's Satellite	>4 within marsh	7	8.3	0
Mars	>4 within marsh	20	12.3	5.0
Folly	>4 within marsh	4	36.4	0

TABLE 2. Parasitism rates of Red-winged Blackbirds by Brown-headed Cowbirds.

Locality	Range[1]	No. nests	% parasitized	Nest check dates; habitat	Reference
Texas	Traditional	71	23.9	no data (museum collections)	Friedmann et al. 1977
Oklahoma	Traditional	106	1.9	June–August; floodplain forest	Wiens 1963
Kansas	Traditional	29	31.0	"summer"; marshes	Facemire 1980
Kansas	Traditional	228	21.9	April–July; uplands	Hill 1976
Nebraska	Traditional	59	54.2	June–July; roadside ditches	Hergenrader 1962
Illinois	Traditional	653	2.1	no data; marshes	Smith in Friedmann 1963
North Dakota	Traditional	258	42.0	May–June; roadside marshes	Linz and Bolin 1982
Ontario	Traditional	363	0.0	no data; marshes	Robertson and Norman 1976
Ontario	Traditional	3,336	2.5	no data (nest records)	Friedmann et al. 1977
Ontario	Traditional	35	22.8	no data; uplands	Robertson and Norman 1976
Manitoba	Traditional	707	8.7	no data (nest records)	Friedmann et al. 1977
Maryland	Recent	367	1.3	no data	Meaney in Friedmann 1963
Michigan	Recent	1,300	0.5	no data; marshes	Nickell 1955
Michigan	Recent	99	5.0	April–September; no data	Berger 1951
Rocky Mountains	Recent	50	6.0	no data (museum collections)	Friedmann et al. 1977
Washington	Recent	1,325	7.7	April–June; marshes	This study
California	?	779	0.6	no data (museum collections)	Friedmann et al. 1977

[1] Following Mayfield (1965), "Traditional" indicates localities dominated by grassland ecosystems prior to settlement by Europeans where cowbirds have probably parasitized redwings for many centuries; "Recent" indicates localities that were dominated by woodland ecosystems prior to European settlement but were subsequently cleared for agriculture, and where cowbirds have probably only parasitized redwings for a century or less; "?" indicates localities with mixed grassland-woodland ecosystems prior to European settlement.

Marshes with more trees had a lower percentage of cowbird eggs that were laid in inactive redwing nests, although the number of trees did not affect the overall rate of parasitism among marshes (Table 1). Apparently cowbird females are able to perch in or near the marsh when trees are available, and gain better information on when to parasitize by watching nesting activity (Berger 1951, Payne 1973, Norman and Robertson 1975).

SEASONAL INCREASE IN RATE OF COWBIRD PARASITISM

The rate of cowbird parasitism increases strongly as the redwing nesting season advances: early nests are almost never parasitized while late nests are frequently parasitized (Fig. 2).

DISCUSSION

Following Mayfield (1965), we would classify redwings as a lightly parasitized host species in our study area. Although it is tempting to suggest that lightly parasitized species are minor or less-preferred hosts for cowbirds (Friedmann 1963), overall rates of parasitism are also a function of relative host and parasite abundance and availability of alternative hosts. Comparing overall rates of parasitism between species may therefore say little about actual host preferences.

Comparing overall rates of parasitism within species, however, may be more informative. For example, parasitism rates vary enormously among redwing populations (Table 2), suggesting that there is geographic and/or habitat-specific heterogeneity in parasite pressure on redwings (Wiens 1963, Friedmann et al. 1977). There are at least three compatible hypotheses to explain why the rate of cowbird parasitism varies among redwing populations. The first follows from the view that redwings are not a preferred host (Friedmann 1963, Friedmann et al. 1977), and suggests that parasite pressure on redwings depends on the availability of other, more-preferred hosts. Overall rates of cowbird parasitism do seem to be somewhat lower in localities where cowbirds are recent arrivals—that is, where cowbird populations are probably expanding (Table 2, Mann-Whitney U-test, $U = 45$, one-tailed $P < 0.05$). If the host preference hypothesis is true, parasitism rates in these localities may be low because cowbirds have not yet "saturated" their preferred hosts.

A second hypothesis regarding heterogeneity in parasite pressure is that overall rates of parasitism may vary because some localities have perch sites that cowbirds use in surveying for prospective host nests (Gates and Gysel 1978, Gochfeld 1979). The fact that marshes with trees do not have a higher percentage of redwing nests

parasitized by cowbirds in our study area argues against this hypothesis, however.

Finally, group defense (mobbing of cowbird females) in dense redwing colonies might keep overall parasitism rates low in marshy habitats while individual defense of widely scattered nests located in upland areas might allow higher overall rates of parasitism (Friedmann 1963, Robertson and Norman 1977). Overall rates of parasitism are, however, no higher for redwings nesting in upland vs. marsh habitats (Table 2, Mann-Whitney U-test, $U = 16$, $P > 0.20$). Yet within our study site the density of redwings defending active nests had a strong influence on rate of parasitism. Clearly, geographic variation in rate of cowbird parasitism on redwings warrants further study.

Poor host-nest selection by cowbirds, as reported here, is not limited to redwings. Berger (1951) observed the same inappropriate laying phenomenon in a Michigan Song Sparrow (*Melospiza melodia*) population, and Furrer reported it in nests of Brewer's Blackbirds (Friedmann et al. 1977). In Berger's (1951) study area 1.35% ($n = 37$) of parasitized nests had been deserted before the cowbird egg appeared. Whether rate of inappropriate laying between species or populations varies as a function of perch availability, nest location, and/or degree of host defense remains to be seen.

The strong increase that we observed in rate of parasitism as the nesting season advanced also occurs in Brewer's Blackbirds that nest in eastern Washington (Friedmann et al. 1977). Why cowbirds do not parasitize Red-winged Blackbirds earlier in the season, when total nest loss due to predation is dramatically lower (Langston et al., unpubl.), is not clear. In our sample, less than 30% of unparasitized, late-season redwing nests are successful while up to 60% of unparasitized, early-season redwing nests fledge young.

One hypothesis for the seasonality of cowbird parasitism is that redwings are simply not a preferred host in our study area, and that cowbirds time their breeding season to overlap later-nesting, more-preferred hosts. Data from central California, however, show that cowbirds are capable of advancing their breeding season, at least in some localities, so that it overlaps the peak nesting periods of a large number of hosts including redwings (Payne 1973). Also, Meanley (pers. comm. cited in Friedmann 1963) reported that the only cowbird eggs he found in nests of a

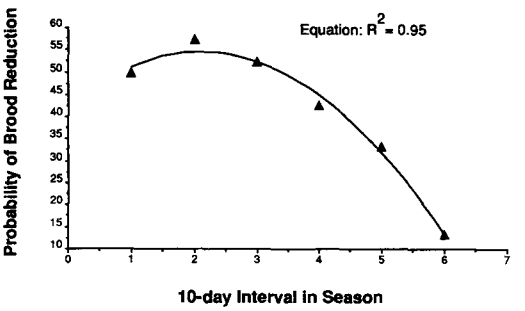

FIGURE 3. Probability of at least one chick starving in a Red-winged Blackbird nest as the breeding season advances. The 10-day interval in the season is counted from the first redwing egg laid in a marsh in our study area in that year.

Maryland population of redwings appeared in the earliest nests in the season.

Second, cowbird parasitism could increase late in the redwing breeding season simply because fewer redwing females are present to participate in group defense of active nests. If avoiding group defense was solely responsible for the timing of cowbird breeding, however, we would expect that cowbirds would prefer to parasitize the very earliest nests initiated in the season, when few are lost to predators.

A new observation regarding redwing nesting biology suggests a third explanation for the seasonality of cowbird parasitism. In our study population, the probability of chicks dying in the nest decreases dramatically after the first month of the redwing breeding season (Fig. 3). Since their offspring are less likely to starve to death late in the season, cowbird females may do better by parasitizing late redwing nests, even though their probability of avoiding predation is lower. Since redwings are about 50% larger than cowbirds, cowbird young may do poorly when competing with nestling redwings during the early, food-limited weeks of the breeding season. If this logic is correct, we predict that cowbird breeding will be strongly seasonal relative to the hosts' breeding season only when the host species is substantially larger than the parasite and the brood reduction pattern illustrated in Figure 3 occurs. We also predict that in localities where cowbirds breed early they may parasitize small hosts early in the season and switch to large hosts later in the season, if the large hosts show a late-season decline in partial loss of chicks due to starvation.

In conclusion, our results suggest that cowbirds face formidable obstacles when parasitizing redwings. First, since redwings are larger than cowbirds their young may out-compete cowbird chicks when food is scarce. This risk of starvation may force female cowbirds to delay parasitizing redwings until late in the redwing nesting season when food is more abundant, even though risk of predation is sharply higher. Second, although female redwings do not eject cowbird eggs, probably because their beaks are too small to allow grasp ejection (Rohwer and Spaw 1988), both males and females show marked aggressiveness toward adult cowbirds (Robertson and Norman 1976, 1977). Our data show a strong negative relationship between rate of parasitism and density of redwings. Furthermore, variation in colony density may be at least partially responsible for the variation observed in rate of overall cowbird parasitism among redwing populations. Finally, the importance of perch sites to the timing of laying by cowbirds suggests that, in treeless habitats, cowbirds may frequently be unable to gather enough information on the status of redwing nests to lay at an appropriate time.

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