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IMPACT OF BROOD PARASITISM BY BROWN-HEADED COWBIRDS ON RED-WINGED BLACKBIRD REPRODUCTIVE SUCCESS[1]

ETHAN D. CLOTFELTER
Department of Zoology, University of Wisconsin, Madison, WI 53706,
e-mail: ecltfltr@macc.wisc.edu

KEN YASUKAWA
Department of Biology, Beloit College, Beloit, WI 53511

Abstract. We examined brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) on a prairie-nesting population of Red-winged Blackbirds (*Agelaius phoeniceus*) from 1984 to 1997 and the extent to which parasitism affected host reproductive success. During this 14-year period, 2–32% of redwing nests were parasitized per year. Two measures of cowbird parasitism, the proportion of nests parasitized and the number of cowbird eggs laid per year, significantly increased over time. Increases in these estimates of the intensity of parasitism were independent of annual changes in nesting density of Red-winged Blackbirds. Clutch size was reduced in parasitized nests, most likely as a result of host egg removal by cowbirds, but hatching success was similar between parasitized and unparasitized nests. Red-winged Blackbirds abandoned more than one-third of all parasitized nests. We estimated the cost of abandonment in terms of increased failure rate and decreased fledgling production of re-nesting attempts. When we excluded abandoned nests from the analysis, there was no difference in the probability of success between parasitized and unparasitized nests. Nestlings from parasitized nests were similar in mass and tarsus length to nestlings from unparasitized nests, but parasitized nests produced fewer redwing fledglings per successful nest. The success of unparasitized nests was negatively related to the intensity of cowbird parasitism, suggesting that cowbirds are predators as well as brood parasites of redwing clutches.

Key words: Agelaius phoeniceus, *brood parasitism, clutch size, fledgling production,* Molothrus ater, *nest abandonment, nest success.*

INTRODUCTION

Nearly 100 species of birds are obligate brood parasites. Instead of constructing nests, these birds deposit their eggs in the nests of one or more host species. The host then provides all parental care for the parasitic egg and nestling. As a consequence of parasitism, hosts suffer decreased clutch size, hatching success, nest success, and/or fledgling production (Lack 1968, Payne 1977, Rothstein 1990). Brood parasitism has attracted considerable attention recently because of its probable role in the decline of many host populations and because of the adaptations and counter-adaptations characteristic of many host-parasite systems (Davies and Brooke 1988, Rothstein 1990).

Here we examine patterns and impact of parasitism by Brown-headed Cowbirds (*Molothrus ater*) on a prairie-nesting population of Red-winged Blackbirds (*Agelaius phoeniceus*) over a 14-year period. Throughout most of their range, Red-winged Blackbirds are a common host of Brown-headed Cowbirds, although parasitism frequencies vary considerably among sites (Freeman et al. 1990). Redwings accept cowbird eggs despite their physical ability to eject them, and they often abandon nests parasitized early in the egg-laying period (Rothstein 1975, Ortega and Cruz 1988). In the current study, we evaluate the reduction in Red-winged Blackbird reproductive success as a result of cowbird parasitism and differentiate among the mechanisms responsible for this reduction. The data presented here complement previous studies of cowbird parasitism of redwings (Ortega and Cruz 1988, Weatherhead 1989, Røskaft et al. 1990).

METHODS

We studied Brown-headed Cowbirds and Red-winged Blackbirds on two grass and sedge meadows in southern Wisconsin (42°32′N, 89°08′W). Newark Road Prairie (hereafter NRP) is a 13-ha wet-mesic prairie that supports 25–30

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territorial male redwings each year. Diehls Prairie (hereafter DP) is a 12-ha oldfield/prairie that supports 30–35 males each year. Territories typically supported 0–5 nesting females; in most years the mean number of females per territorial male was 2–3. The two study areas are contiguous, and redwings regularly moved between sites. Because of the way in which we treated parasitized nests (see below), however, we discuss the two sites separately throughout this paper. Descriptions of the Red-winged Blackbird population in this area can be found in Yasukawa et al. (1990) and Searcy and Yasukawa (1995). We studied the redwings of NRP and DP from 1984–1997 and 1995–1997, respectively.

We located redwing nests by searching the vegetation and by observing female behavior. We found the majority of nests during construction or egg-laying (Yasukawa et al. 1990), and revisited them daily to determine their final outcomes. Cowbird eggs laid in redwing nests on DP were allowed to hatch, but we removed cowbird eggs found in redwing nests on NRP. Beginning in 1995, we salvaged cowbird eggs from redwing nests on NRP and placed them in redwing nests on DP, 2–24 hr after laying. The recipient nest was selected at random from among those at approximately the same stage in egg laying as the nest from which the egg was removed. These nests are referred to as experimentally parasitized nests, and are excluded from the comparisons of naturally parasitized and unparasitized nests. In 1995, we removed a single redwing egg from each experimentally parasitized nest to simulate egg removal by cowbirds (Weatherhead 1989, Røskaft et al. 1990). Redwing eggs were removed concurrent with the addition of the cowbird egg. In 1996 and 1997, no redwing eggs were removed from experimentally parasitized nests.

In this study, we defined clutch size as the number of redwing eggs present at the end of the egg-laying period. Nests that were abandoned or depredated during egg laying were excluded from calculations of clutch size. We defined hatching success as the proportion of eggs that hatched, not including eggs lost to cowbirds or predators during the incubation period. In other words, hatching success was the proportion of eggs that hatched of those present at the end of incubation. We considered a nest successful if at least one nestling (including a cowbird nestling) survived for at least 10 days after hatching. Fledgling production was the number of redwing fledglings produced per successful nest. We measured the mass and tarsus (tarsometatarsus) length of redwing nestlings 7–8 days after hatching using a Pesola spring balance (± 0.5 g) and dial calipers (± 0.1 mm), respectively.

When a female redwing abandoned her nest, we estimated the re-nesting interval as the number of days between the first egg of the abandoned nest and the first egg of the re-nesting attempt. To determine the impact of this delay on nest success, we calculated the relationship between nest initiation date and the probability of success using all nests for 1984–1997. First, we calculated the proportion of nests succeeding for each day in the nesting season, then combined Julian dates into 10-day intervals (120–129, 130–139, . . . 190–200) after Langston et al. (1990). We performed a linear regression of the 10-day nesting date interval on the proportion of nests succeeding. We performed a similar analysis to determine the relationship between nest initiation date and fledgling production.

We performed statistical analyses using SYSTAT 6.0 (Wilkinson 1996). Regression results show adjusted r^2 values, and t-test results are for independent samples. A $\log_{10}$ transformation of the independent variable was used for the regression of the study year on the number of redwing nests. All tests were two-tailed, and means are presented ± SE. Differences were considered significant if $P < 0.05$.

RESULTS

PATTERNS OF COWBIRD PARASITISM

We monitored a total of 1,320 Red-winged Blackbird nests on NRP and DP over the period 1984–1997. The number of redwing nests found per year on NRP and DP ranged from 34 to 126 and from 86 to 123, respectively. The number of nests constructed on NRP increased during the period 1984–1991 and decreased during 1992–1997, but the overall change in number of nests was not significant ($r^2 = 0.14$, $n = 17$, $P = 0.08$).

Of these 1,320 nests, 222 (16.8%) were parasitized by cowbirds. Forty-seven of 222 parasitized nests (21.2%) contained more than one cowbird egg. The frequency of parasitism was higher on DP, where 79 of 319 (24.8%) nests received cowbird eggs, than on NRP, where 143 of 1,001 (14.3%) nests were parasitized. The re-

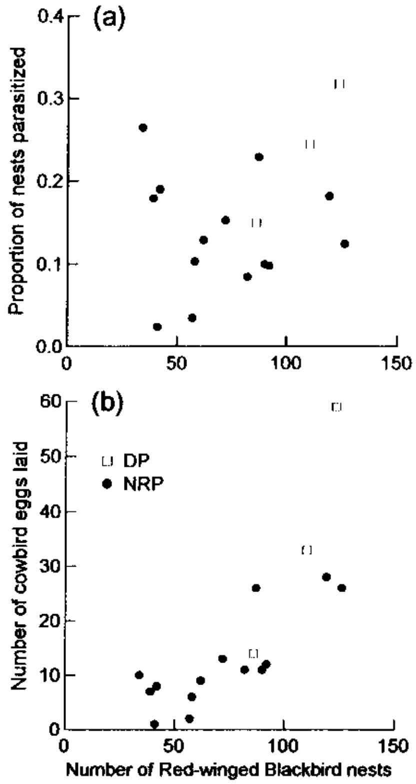

FIGURE 1. The relationship between the number of Red-winged Blackbird nests per year and (a) the proportion of them that were parasitized by Brown-headed Cowbirds and (b) the number of Brown-headed Cowbird eggs laid in them on NRP (1984–1997) and DP (1995–1997).

lationship between the number of redwing nests per year and the proportion of nests parasitized was not significant ($r^2 = 0.01$, $n = 17$, $P > 0.2$; Fig. 1a), but the number of cowbird eggs laid and the number of redwing nests were positively related ($r^2 = 0.59$, $n = 17$, $P < 0.001$; Fig. 1b). Thirty-four of the 319 nests (10.7%) on DP were experimentally parasitized with cowbird eggs taken from nests on NRP during the period 1995–1997. None of the experimentally parasitized nests were subsequently parasitized by cowbirds.

The proportion of nests parasitized increased significantly during the 1984–1997 study period ($r^2 = 0.49$, $n = 17$, $P = 0.001$; Fig. 2a). The number of cowbird eggs laid per year also increased over time ($r^2 = 0.27$, $n = 17$, $P = 0.02$; Fig. 2b). These increases were significant even when the number of redwing nests was included in the respective regression models (proportion of nests parasitized: partial $t_1 = 3.61$, $P = 0.003$; number of cowbird eggs laid: partial $t_1 = 2.19$, $P < 0.05$).

CLUTCH SIZE

On NRP, clutches in parasitized nests contained 0.42 fewer redwing eggs than clutches in unparasitized nests (parasitized $\bar{x} = 2.96 \pm 0.09$ eggs, $n = 116$ nests; unparasitized: $\bar{x} = 3.38 \pm 0.03$ eggs, $n = 774$ nests; $t_{888} = 5.78$, $P < 0.001$; Table 1). On DP there was a difference of 0.97 redwing eggs (parasitized: $\bar{x} = 2.62 \pm 0.13$ eggs, $n = 60$ nests; unparasitized: $\bar{x} = 3.59 \pm 0.05$ eggs, $n = 193$ nests; $t_{251} = 8.62$, $P < 0.001$). The difference in clutch size between parasitized and unparasitized nests on DP was similar to the difference resulting from investigator removal of eggs from experimentally parasitized nests (1995: $\bar{x} = 2.71 \pm 0.11$ eggs, $n = 17$ nests; 1996–1997: $\bar{x} = 3.88 \pm 0.15$ eggs, $n = 17$ nests; Mann-Whitney $U = 265$, $P < 0.001$). Therefore,

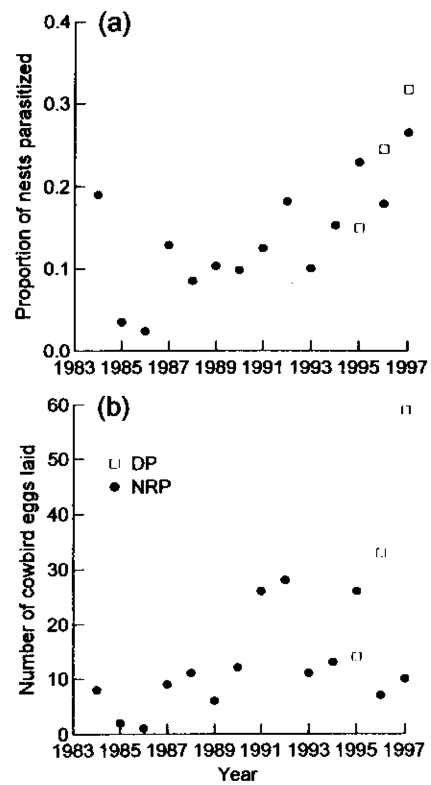

FIGURE 2. Change in (a) the proportion of Red-winged Blackbird nests parasitized by Brown-headed Cowbirds and (b) the number of Brown-headed Cowbird eggs laid in Red-winged Blackbird nests per year over the period 1984–1997.

TABLE 1. Clutch sizes and hatching success in parasitized and unparasitized Red-winged Blackbird nests on Newark Road Prairie (NRP; 1984–1997) and Diehls Prairie (DP; 1995–1997). Hatching success is the proportion of redwing eggs surviving the incubation period that hatched. Sample sizes (n) represent numbers of nests.

	NRP			DP		
	Unparasitized (n = 858)		Parasitized (n = 143)	Unparasitized (n = 206)[a]		Parasitized (n = 79)[a]
Mean clutch size ± SE (n)	3.38 ± 0.03 (773)	***[b]	2.96 ± 0.09 (116)	3.59 ± 0.05 (193)	***[b]	2.62 ± 0.13 (60)
Hatching success (n)	0.91 (471)		0.88 (53)	0.91 (108)		0.89 (31)

[a] Excludes 34 experimentally parasitized nests (Table 3).
[b] Comparison of unparasitized versus parasitized nests, two-tailed t-test, *** $P < 0.001$.

the observed difference in clutch size between naturally parasitized nests and unparasitized nests is consistent with egg removal by Brown-headed Cowbirds.

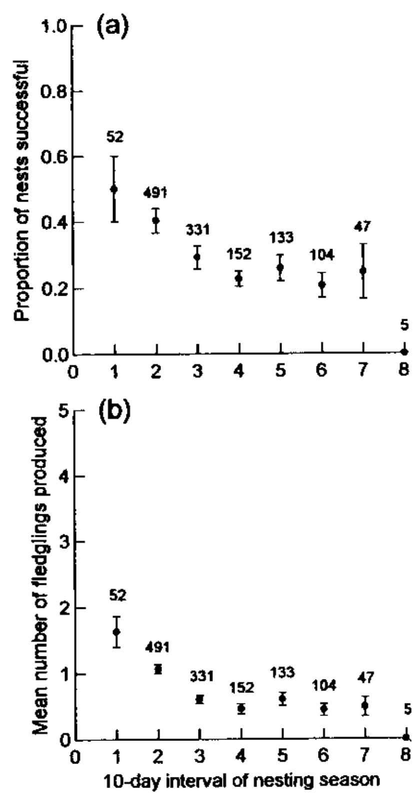

FIGURE 3. Seasonal decline in Red-winged Blackbird reproductive success. (a) mean (± SE) proportion of nests initiated within each 10-day interval of the nesting season that were successful and (b) the mean (± SE) number of fledglings produced by nests initiated within each 10-day interval. Interval 1 = Julian date 120–129, 2 = 130–139, . . . 8 = 190–200, where Julian date 120 = 30 April. Data taken from NRP 1984–1997 and DP 1995–1997 (number of nests listed for each nesting interval).

NEST ABANDONMENT

Of the 143 parasitized nests on NRP, female redwings abandoned 56 (39.2%). On DP, females abandoned 25 of 79 (31.6%) parasitized nests. We found no evidence of females abandoning nests that were parasitized after their own clutches were complete. The frequency of abandonment of unparasitized nests was much lower: 17 of 203 (8.4%) on DP and 43 of 858 (5%) on NRP.

We followed re-nesting attempts of 13 banded females on NRP that abandoned their nests following parasitism or another disturbance during egg laying (excluding predation). The mean re-nesting interval for these females was 10.92 ± 1.72 days. Data from NRP (1984–1997) and DP (1995–1997) showed that nests were initiated on a total of 71 days between 30 April (Julian date = 120) and 10 July (Julian date = 191). We found a significant, negative relationship between nest success and nesting date interval (r^2 = 0.24, n = 71 days, $P < 0.001$; Fig. 3a) described by the equation:

proportion of nests successful
= 0.481 − 0.045(10-day nesting-date interval).

This equation shows that with each 10-day interval, there was a 0.045 decrease in the probability of nest success. Because the mean re-nesting interval for female redwings on NRP and DP was approximately 11 days, these females suffered a 5% increase in their probability of nest failure. Thus, of the 81 females from NRP and DP that abandoned their nests due to cowbird parasitism, 4 of them failed in their subsequent nesting attempt as a result of the delay (4 more than would have failed otherwise).

In addition to reducing the probability of nest success, delays associated with nest abandonment also reduced the number of fledglings pro-

TABLE 2. Nest success and fledgling production in parasitized and unparasitized Red-winged Blackbird nests on Newark Road Prairie (NRP; 1984–1997) and Diehls Prairie (DP; 1995–1997). Nest success is the proportion of nests that succeeded in producing at least one fledgling. Adjusted nest success excludes abandoned nests. Fledgling production is the number of redwing fledglings produced per successful nest. Sample sizes (n) represent numbers of nests.

	NRP			DP		
	Unparasitized (n = 858)		Parasitized (n = 116)	Unparasitized (n = 206)[a]		Parasitized (n = 79)[a]
Nest success (n)	0.33 (858)	***	0.22 (143)	0.33 (203)		0.23 (78)
Adjusted nest success (n)	0.34 (815)		0.35 (87)	0.37 (186)		0.34 (53)
Mean fledgling production ± SE (n)	2.48 ± 0.05 (286)		2.53 ± 0.19 (30)	2.66 ± 0.13 (68)	***	1.83 ± 0.26 (18)

[a] Total includes 4 nests (3 unparasitized, 1 parasitized) whose fates were unknown, and excludes 34 experimentally parasitized nests (Table 3).
*** $P < 0.005$.

duced in re-nesting attempts. We found a significant negative relationship between the mean number of fledglings produced per nest and the nesting date interval ($r^2 = 0.04$, $n = 1{,}316$ nests, $P < 0.001$; Fig. 3b) described by the equation:

$$\text{mean number of fledglings produced} = 1.31 - 0.16(\text{10-day nesting-date interval}).$$

This equation shows that with each 10-day interval, 0.16 fewer fledglings were produced per nest. In other words, the 81 female Red-winged Blackbirds that abandoned their parasitized nests and re-nested 11 days later produced a total of 14 fewer fledglings in their re-nesting attempts than they would have if they had incubated their original clutches.

HATCHING SUCCESS

There was no evidence that hatching success differed between parasitized and unparasitized nests on either NRP or DP (Table 1). There also was no difference in hatching success between the two sites. Eggs in experimentally parasitized clutches from 1995 had a higher probability of hatching than their 1996–1997 counterparts, but this trend was not significant (1995: 96% of eggs hatched, $n = 8$ nests; 1996–1997: 78% of eggs hatched, $n = 9$ nests; $\chi^2_1 = 3.22$, $P < 0.1$).

NEST SUCCESS

Nest success rates of parasitized and unparasitized nests are summarized in Table 2. Parasitized nests on NRP were significantly less successful than unparasitized nests ($\chi^2_1 = 8.66$, $P < 0.005$). However, when nest success was adjusted by removing abandoned nests from the analysis, the success rates of parasitized and unparasitized nests were nearly identical ($\chi^2_1 = 0.01$). The proportions of parasitized and unparasitized nests that succeeded on DP were similar when all nests were considered ($\chi^2_1 = 2.91$, $P < 0.10$) and nearly identical when abandoned nests were excluded from the analysis ($\chi^2_1 = 0.12$). Experimentally parasitized nests were similar in nest success (0.42, $n = 33$ nests) to their naturally parasitized counterparts on DP (0.34, $n = 53$ nests) when nest success was adjusted to exclude cases of abandonment ($\chi^2_1 = 0.61$).

FLEDGLING PRODUCTION AND SIZE

Among successful nests on NRP, there was no difference in redwing fledgling production between parasitized ($\bar{x} = 2.53 \pm 0.19$ fledglings, $n = 30$ nests) and unparasitized nests ($\bar{x} = 2.48 \pm 0.05$ fledglings, $n = 286$ nests; $t_{314} = -0.31$; Table 2). The significant reduction in fledgling production between parasitized and unparasitized nests on DP (parasitized: $\bar{x} = 1.83 \pm 0.26$ fledglings, $n = 18$ nests; unparasitized: $\bar{x} = 2.66 \pm 0.13$ fledglings, $n = 68$ nests; $t_{84} = 2.96$, $P = 0.004$; Table 2) was roughly equivalent to the reduction in clutch size in these nests. However, fledgling production did not differ between experimentally parasitized nests from which an egg was removed (1995: $\bar{x} = 2.57 \pm 0.20$ fledglings, $n = 7$ nests) and experimentally parasitized nests from which no eggs were removed (1996–1997: $\bar{x} = 2.29 \pm 0.42$ fledglings, $n = 7$ nests; $t_{12} = -0.61$). Experimentally parasitized nests produced more redwing fledglings than naturally parasitized nests on DP, but this difference was not significant (1995–1997 experimentally parasitized nests: 2.43 ± 0.19 fledglings, $n = 14$ nests; $t_{30} = -1.67$, $P = 0.1$).

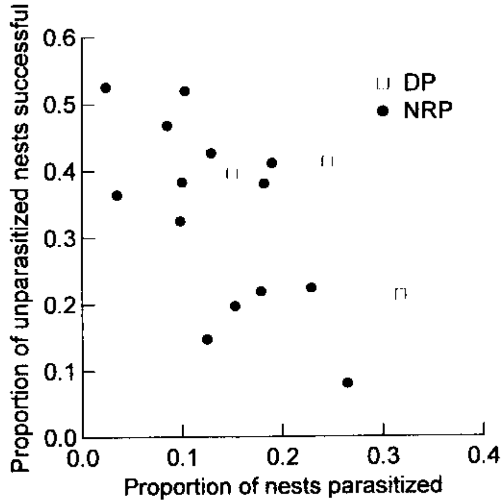

FIGURE 4. Decline in the success rate of unparasitized Red-winged Blackbird nests with increasing proportion of nests parasitized by Brown-headed Cowbirds.

We measured mass and tarsus length of 240 Red-winged Blackbird nestlings from 92 broods from DP, of which 21 broods were parasitized. Redwing nestlings from parasitized broods had lower masses (parasitized: $\bar{x}$ = 32.75 ± 0.74 g, n = 50 nestlings; unparasitized: $\bar{x}$ = 34.37 ± 0.38 g, n = 190 nestlings) and slightly longer tarsus lengths (parasitized: $\bar{x}$ = 25.29 ± 0.29 mm, n = 50 nestlings; unparasitized: $\bar{x}$ = 24.88 ± 0.19 mm, n = 190 nestlings) than nestlings from unparasitized nests. These differences were not significant when total brood size (including cowbird nestlings) was included as a covariate in an ANCOVA (mass: $F_{1,237} = 1.11$, $P > 0.2$; tarsus length: $F_{1,237} = 1.08$, $P = 0.3$). Because sexual dimorphism in Red-winged Blackbirds manifests itself during the nestling stage (Holcomb and Tweist 1971), we had to assume similar sex ratios among parasitized and unparasitized broods.

COWBIRD PARASITISM AND NEST FAILURE

To evaluate the potential importance of adult cowbirds as nest predators, we correlated two measures of cowbird parasitism pressure (the proportion of nests parasitized per year and the number of cowbird eggs laid per year) with the proportion of nests succeeding that year. We found that the proportion of nests parasitized was significantly negatively correlated with the proportion of unparasitized nests that succeeded ($r_S = -0.46$, $n = 17$, $P < 0.05$; Fig. 4), but was unrelated to the success of parasitized nests ($r_S = 0.08$, $n = 17$). There was a similar but nonsignificant trend for the number of cowbird eggs laid to vary inversely with the success of unparasitized nests ($r_S = -0.39$, $n = 17$, $P < 0.1$), but not with the success of parasitized nests ($r_S = -0.04$, $n = 17$). These results indicate that when cowbird parasitism pressure increased, unparasitized nests were more likely to fail.

COWBIRD REPRODUCTIVE SUCCESS

The reproductive success of Brown-headed Cowbirds on DP is summarized in Table 3. There were 114 cowbird eggs laid in Red-winged Blackbird nests on DP. Of these, 42 survived the incubation period (i.e., were not abandoned or depredated) and 31 hatched. Thirty-four eggs were salvaged from NRP nests and used to parasitize DP nests experimentally. Of these, 19 survived incubation and 17 hatched. Therefore, when we removed abandoned and depredated nests from the analysis, the hatching success of cowbird eggs in natural and experimentally parasitized nests did not differ ($\chi^2_1 = 1.83$, $P > 0.10$). There was no difference in the hatching success of cowbird eggs between 1995 experimentally parasitized nests, from which a redwing egg was removed (8 of 8 hatched; 1.0 eggs nest^{-1}), and 1996–1997 experimentally parasitized nests from which no redwing eggs were removed (9 of 11 hatched; 0.82 eggs nest^{-1}). Of

TABLE 3. Reproductive success of Brown-headed Cowbirds in Red-winged Blackbird nests on Diehls Prairie (1995–1997). Hatching success is the proportion of cowbird eggs surviving the incubation period that hatched. Sample sizes (n) represent number of nests.

	Naturally parasitized nests 1995–1997	Experimentally parasitized nests 1995	Experimentally parasitized nests 1996–1997
Total number of cowbird eggs laid	114 (79)	17 (17)	17 (17)
Hatching success (number of eggs hatched)	0.74 (31)	1.0 (8)	0.82 (9)
Cowbird fledglings per egg (number fledged)	0.096 (11)	0.35 (6)	0.12 (2)

the 48 total cowbird eggs that hatched on DP from 1995–1997, 19 successfully produced fledglings. Therefore, 0.13 cowbirds fledged from each egg on DP and 0.36 cowbirds fledged from each egg that hatched. If only hatched eggs are considered, fledgling production was no different in experimentally parasitized nests (8 of 17 eggs, 0.47 fledglings egg^{-1}) than in naturally parasitized nests (11 of 31 eggs, 0.36 fledglings egg^{-1}; $\chi^2_1 = 0.64$).

DISCUSSION

PATTERNS OF PARASITISM

Both the proportion of Red-winged Blackbird nests parasitized and the total number of Brown-headed Cowbird eggs laid in redwing nests increased over the 14-year period 1984–1997. Whether this was the result of a functional (proportion of nests parasitized) or a numerical (number of cowbird eggs laid) response by female cowbirds is unclear; these values increased even when the number of redwing nests was controlled statistically. These results suggest a significant increase in cowbird abundance or in the extent to which redwings were parasitized. This change may be a result of increased fragmentation of nearby habitats or a decline of other host species (Robinson et al. 1995). The increase in parasitism occurred despite a decrease in Brown-headed Cowbird abundance along the nearest Breeding Bird Survey route to our sites during the period 1984–1996 (National Biological Survey 1998).

CLUTCH SIZE AND EGG REMOVAL

Clutch sizes were significantly smaller in parasitized nests than in unparasitized nests. We believe that this difference in clutch size was a result of egg removal by cowbirds and not of variation in host clutch size with nest initiation date or with host age (Smith and Arcese 1994). First, the disappearance of redwing eggs usually occurred on the same day as the appearance of the cowbird egg. Second, parasitism on this population of Red-winged Blackbirds was most common early in the season, and clutch size in redwings usually decreases with increasing laying date (Caccamise 1978). Therefore, it is more likely that we underestimated the frequency of egg removal by cowbirds rather than overestimated it.

Parasitized nests on DP suffered a greater reduction in clutch size than did parasitized nests on NRP (0.97 and 0.42 fewer eggs, respectively). This difference may be the result of damage caused by thick-shelled cowbird eggs (Spaw and Rohwer 1987, Rahn et al. 1988); cowbird eggs were removed from NRP nests soon after laying and therefore would not have affected subsequent eggs laid in those clutches. There was no difference in hatching success between parasitized and unparasitized nests, suggesting that parasitism did not cause additional egg loss in redwing nests beyond initial egg removal by cowbirds. Egg loss in nests parasitized by cowbirds was no greater than in experimentally parasitized nests, implying that cowbirds were no more or less skilled than we were at placing their eggs in nests without damaging host eggs. Weatherhead (1991) found similar results in his study of egg loss and hatching success in parasitized redwing nests.

Experimentally parasitized nests from which no redwing eggs were removed had the lowest hatching success of all nests. Reduced hatching success in these enlarged clutches might have resulted from inefficient incubation by redwing females. One of the putative functions of host egg removal by brood parasites is to reduce the total clutch size so the host can effectively incubate it (Wood and Bollinger 1997, McMaster and Sealy 1998). We found that egg removal by cowbirds slightly improved the hatching success of remaining host eggs compared with eggs in parasitized nests from which no eggs were removed. However, this does not provide an evolutionary explanation for host egg removal by cowbirds.

Another explanation for decreased clutch size in parasitized nests on DP compared with nests on NRP is the frequency of multiple parasitism. Parasitized DP nests received approximately 0.12 more cowbird eggs than parasitized nests on NRP. If cowbirds remove a host egg with each parasitic event (Elliott 1978, Wolf 1987), multiple parasitism could account for some of the difference in clutch size of parasitized nests on DP and NRP. Although the function of egg removal is unclear, several hypotheses predict that a host egg should be removed for each parasitic egg added (Scott et al. 1991, Sealy 1992).

NEST ABANDONMENT

More than one-third of all parasitized redwing nests were abandoned. Red-winged Blackbirds abandon parasitized nests rather than eject cowbird eggs despite the fact that they are physically able to remove eggs and egg-shaped objects from their nests (Kemal and Rothstein 1988, Ortega and Cruz 1988). The lack of true rejection behavior in this species has been attributed to evolutionary lag (Rothstein 1975, Ward et al. 1996), bill-size constraints (Rohwer and Spaw 1988), and the costs of ejection (Rohwer et al. 1989). What remains to be assessed are the costs of abandonment. Potential nest sites for female redwings are virtually unlimited, especially in upland habitats. Therefore, the primary cost of re-nesting is in terms of time lost (Pease and Grzybowski 1995). Hill and Sealy (1994) studied nest abandonment by Clay-colored Sparrows (*Spizella pallida*) in response to cowbird parasitism, but this host does not suffer a decrease in nest success with advancing date. Red-winged Blackbirds, like many other passerines, show seasonal declines in both nest success and post-fledging offspring survival (Lack 1968, Caccamise 1978, Price et al. 1988). We evaluated the decrease in nesting success and fledgling production over the season and the re-nesting interval for females that abandoned their nests during egg laying. From this information we determined the number of additional nests that failed and the number of additional fledglings that died as a result of the re-nesting delay, providing one of the first estimates of the cost of nest abandonment by a host in response to cowbird parasitism. This estimate of the cost of re-nesting is probably conservative, as the seasonal decline in nest success in our study area was less steep than in other populations of Red-winged Blackbirds (Langston et al. 1990).

NEST SUCCESS AND FLEDGLING PRODUCTION

When abandoned nests were excluded from the analysis, there was no difference in nest success between parasitized and unparasitized nests on DP or NRP. This result gives no support for the predation facilitation hypothesis, which predicts that predation should be greater at parasitized nests (Arcese et al. 1992, 1996, Payne and Payne 1998). We also found no difference in adjusted nest success between parasitized nests on DP (with cowbird nestlings present) and parasitized nests on NRP (with no cowbirds present), suggesting that highly vocal cowbird nestlings did not increase the risk of predation at parasitized nests (Massoni and Reboreda 1998).

Parasitized nests on DP fledged significantly fewer offspring than their unparasitized counterparts, although there was no comparable difference on NRP. The magnitude of the difference in fledgling production on DP (0.83 fledglings) was similar to the difference in clutch size (0.97 eggs). Such a decrease in fledgling production is consistent with a previous study of Red-winged Blackbirds (Røskaft et al. 1990), but not with others (Ortega and Cruz 1988, Weatherhead 1989). Redwing nestlings approaching fledging age in parasitized nests were similar in mass and tarsus length to nestlings in unparasitized nests, as was reported by Weatherhead (1989). In general, host nestlings similar in body size to cowbird nestlings fare better than do nestlings of smaller hosts (Marvil and Cruz 1989, Weatherhead 1989, Goguen and Mathews 1996).

COWBIRDS AS NEST PREDATORS

Studies of several host-parasite systems have suggested that, in addition to laying their eggs in host nests, adult brood parasites also are predators of host clutches (Davies and Brooke 1988, Soler et al. 1995, Arcese et al. 1996). One function of predation by parasites could be to increase future opportunities for parasitism by forcing hosts to re-nest. In our study, we found evidence to support the hypothesis that Brown-headed Cowbirds depredate Red-winged Blackbird nests. The intensity of cowbird parasitism (measured by the number of cowbird eggs laid and the proportion of nests parasitized) was negatively correlated with the success of unparasitized nests but not with the success of parasitized nests. Increased rates of predation on unparasitized nests, in which cowbirds have invested nothing, compared to parasitized nests is a central prediction of this hypothesis (Arcese et al. 1996). Our results suggest that the role of cowbirds as nest predators on Red-winged Blackbirds (as well as other hosts) deserves further attention.

Another way in which cowbirds might facilitate nest failure is to induce nest abandonment by reducing the clutch below a desertion threshold (Rothstein 1982). From an evolutionary standpoint, however, this has the same effect as deliberate predation. The vast majority of nest failures in our study area were the result of whole clutch or brood loss rather than clutch reduction (Yasukawa et al. 1990).

COWBIRD REPRODUCTIVE SUCCESS

As a consequence of poor host selection (Rothstein 1976, Middleton 1977), poor synchronization with host egg-laying (Nolan 1978, Freeman et al. 1990), or host rejection (Hill and Sealy 1994, Goguen and Mathews 1996), the probability of a Brown-headed Cowbird egg producing a fledgling is small. For example, cowbird eggs in nests of several small-bodied hosts produced only 0.03–0.05 fledglings egg^{-1} (Nolan 1978, Weatherhead 1989). In our study, we found that cowbird eggs in redwing nests produced 0.13 cowbird fledglings egg^{-1}, which is lower than the 0.27 cowbird fledglings egg^{-1} reported for Red-winged Blackbirds by Weatherhead (1989). Elliott (1978) found high rates of cowbird fledgling production in nests of several grassland host species, but this was partly a consequence of frequent multiple parasitism. Cowbird eggs laid in Song Sparrow (*Melospiza melodia*) nests showed remarkably high survival to fledging age (0.65 fledglings egg^{-1}), although their post-fledging survival was thought to be low (Smith 1981). Therefore, Brown-headed Cowbirds in our study achieved greater reproductive success in Red-winged Blackbirds nests than they would have in the nests of most small-bodied hosts, but not as high as has been reported for other populations of redwings.

In summary, brood parasitism by Brown-headed Cowbirds reduced the reproductive success of Red-winged Blackbirds as a consequence of (1) host egg removal by cowbirds (and an associated decrease in fledgling production) and (2) reduced nest success and fledgling production of re-nesting attempts following abandonment of parasitized nests. We found no negative effect of cowbird parasitism on Red-winged Blackbirds after the cowbird egg was laid. These findings suggest that there is little selective pressure on redwings to identify and eject cowbird eggs, but rather to evolve defenses that prevent parasitism from occurring (Robertson and Norman 1977, Røskaft et al. 1990, Ward et al. 1996). These defenses are particularly important in light of the evidence we present that cowbirds are nest predators as well as brood parasites.

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LITERATURE CITED

ARCESE, P., J. M. N. SMITH, W. M. HOCHACHKA, C. M. ROGERS, AND D. LUDWIG. 1992. Stability, regulation, and the determination of abundance in an insular Song Sparrow population. Ecology 73: 805–822.

ARCESE, P., J. M. N. SMITH, AND M. I. HATCH. 1996. Nest predation by cowbirds and its consequences for passerine demography. Proc. Natl. Acad. Sci. 93:4608–4611.

BLANKENSPOOR, G. W., J. OOLMAN, AND C. UTHE. 1982. Eggshell strength and cowbird parasitism of Red-winged Blackbirds. Auk 99:363–365.

CACCAMISE, D. F. 1978. Seasonal patterns of nesting mortality in the Red-winged Blackbird. Condor 80:290–294.

DAVIES, N. B., AND M. DE L. BROOKE. 1988. Cuckoos versus Reed Warblers: adaptations and counter-adaptations. Anim. Behav. 36:262–284.

ELLIOTT, P. F. 1978. Cowbird parasitism in the Kansas tallgrass prairie. Auk 95:161–167.

FREEMAN, S., D. F. GORI, AND S. ROHWER. 1990. Red-winged Blackbirds and Brown-headed Cowbirds: some aspects of a host-parasite relationship. Condor 92:336–340.

GOGUEN, C. B., AND N. E. MATHEWS. 1996. Nest desertion by Blue-gray Gnatcatchers in association with Brown-headed Cowbird parasitism. Anim. Behav. 52:613–619.

HILL, D. P., AND S. G. SEALY. 1994. Desertion of nests parasitized by cowbirds: have Clay-coloured Sparrows evolved an anti-parasite defence? Anim. Behav. 48:1063–1070.

HOLCOMB, L. C., AND G. TWEIST. 1971. Growth and calculation of age for Red-winged Blackbird nestlings. Bird Banding 42:1–17.

KEMAL, R. E., AND S. I. ROTHSTEIN. 1988. Mechanisms of avian egg recognition: adaptive responses to eggs with broken shells. Anim. Behav. 36:175–183.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LANGSTON, N. E., S. FREEMAN, S. ROHWER, AND D. GORI. 1990. The evolution of female body size in Red-winged Blackbirds: the effects of timing of breeding, social competition, and reproductive energetics. Evolution 44:1764–1779.

MARVIL, R. E., AND A. CRUZ. 1989. Impact of Brown-headed Cowbird parasitism on the reproductive success of the Solitary Vireo. Auk 106:476–480.

MASSONI, V., AND J. C. REBOREDA. 1998. Costs of brood parasitism and the lack of defenses on the Yellow-winged Blackbird–Shiny Cowbird system. Behav. Ecol. Sociobiol. 42:273–280.

MCMASTER, D. G., AND S. G. SEALY. 1998. Host-egg removal by Brown-headed Cowbirds: a test of the host incubation limit hypothesis. Auk 114:212–220.

MIDDLETON, A. L. A. 1977. Effect of cowbird parasitism on American Goldfinch nesting. Auk 94:304–307.

NATIONAL BIOLOGICAL SURVEY. 1998. Website—http://www.mbr.nbs.gov

NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithol. Monogr. 26.

ORTEGA, C. P., AND A. CRUZ. 1988. Mechanisms of egg acceptance by marsh-dwelling blackbirds. Condor 90:349–358.

PAYNE, R. B. 1977. The ecology of brood parasitism in birds. Annu. Rev. Ecol. Syst. 8:1–28.

PAYNE, R. B., AND L. L. PAYNE. 1998. Brood parasitism by cowbirds: risks and effects on reproductive success and survival in Indigo Buntings. Behav. Ecol. 9:64–73.

PEASE, C. M., AND J. A. GRZYBOWSKI. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. Auk 112:343–363.

PRICE, T., M. KIRKPATRICK, AND S. J. ARNOLD. 1988. Directional selection and the evolution of breeding date in birds. Science 240:798–799.

RAHN, H., L. CURRAN-EVERETT, AND D. T. BOOTH. 1988. Eggshell differences between parasitic and nonparasitic Icteridae. Condor 90:962–964.

ROBERTSON, R. J., AND R. F. NORMAN. 1977. The function and evolution of aggressive host behavior towards the Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 55:508–518.

ROBINSON, S. K., F. R. THOMPSON III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

ROHWER, S., AND C. D. SPAW. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. Evol. Ecol. 2:27–36.

ROHWER, S., C. D. SPAW, AND E. RØSKAFT. 1989. Costs to Northern Orioles of puncture-ejecting parasitic cowbird eggs from their nests. Auk 106:734–738.

RØSKAFT, E., G. H. ORIANS, AND L. D. BELETSKY. 1990. Why do Red-winged Blackbirds accept eggs of Brown-headed Cowbirds? Evol. Ecol. 4:35–42.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

ROTHSTEIN, S. I. 1976. Cowbird parasitism of the Cedar Waxwing and its evolutionary implications. Auk 93:498–509.

ROTHSTEIN, S. I. 1982. Successes and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. Am. Zool. 22: 547–560.

ROTHSTEIN, S. I. 1990. A model system for coevolution: avian brood parasitism. Annu. Rev. Ecol. Syst. 21:481–508.

SCOTT, D. M., P. J. WEATHERHEAD, AND C. D. ANKNEY. 1992. Egg-eating by female Brown-headed Cowbirds. Condor 94:579–584.

SEALY, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor 94:40–54.

SEARCY, W. A., AND K. YASUKAWA. 1995. Polygyny and sexual selection in Red-winged Blackbirds. Princeton Univ. Press, Princeton, NJ.

SMITH, J. M. N. 1981. Cowbird parasitism, host fitness, and age of the host female in an island Song Sparrow population. Condor 83:152–161.

SMITH, J. M. N., AND P. ARCESE. 1994. Brown-headed Cowbirds and an island population of Song Sparrows: a 16-year study. Condor 96:916–934.

SOLER, M., J. J. SOLER, J. G. MARTINEZ, AND A. P. MØLLER. 1995. Magpie host manipulation by Great Spotted Cuckoos: evidence for an avian mafia? Evolution 49:770–775.

SPAW, C. D., AND S. ROHWER. 1987. A comparative study of eggshell thickness in cowbirds and other passerines. Condor 89:307–318.

WARD, D., A. K. LINDHOLM, AND J. M. N. SMITH. 1996. Multiple parasitism of the Red-winged Blackbird: further experimental evidence of evolutionary lag in a common host of the Brown-headed Cowbird. Auk 113:408–413.

WEATHERHEAD, P. J. 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. Auk 106:358–366.

WEATHERHEAD, P. J. 1991. The adaptive value of thick-shelled eggs for Brown-headed Cowbirds. Auk 108:196–198.

WILKINSON, L. 1996. SYSTAT: the system for statistics. SYSTAT, Evanston, IL.

WOLF, L. 1987. Host-parasite interactions of Brown-headed Cowbirds and Dark-eyed Juncos in Virginia. Wilson Bull. 99:338–350.

WOOD, D. R., AND E. K. BOLLINGER. 1997. Egg removal by Brown-headed Cowbirds: a field test of the host incubation efficiency hypothesis. Condor 99:851–857.

YASUKAWA, K., J. L. MCCLURE, R. A. BOLEY, AND J. ZANOCCO. 1990. Provisioning of nestlings by male and female Red-winged Blackbirds, *Agelaius phoeniceus*. Anim. Behav. 40:153–166.