

REPRODUCTIVE SUCCESS OF THE NORTHERN CARDINAL, A LARGE HOST OF BROWN-HEADED COWBIRDS¹

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Abstract. We investigated the effects of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) on Northern Cardinal (*Cardinalis cardinalis*) reproductive success to test the hypothesis that cowbird hosts of similar size and incubation period to cowbirds are able to raise their own offspring when parasitized. During the breeding seasons of 1993-1995, we collected data on the frequency and intensity of cowbird parasitism, the effect of cowbird parasitism on cardinal reproductive success, and the defensive response of cardinals to parasitism. Of the 115 cardinal nests, 48% were parasitized, and the mean number of cowbird eggs per parasitized nest was 1.3. Nest survival, as calculated by the Mayfield analysis, was higher in parasitized than unparasitized nests across all stages of the nesting cycle. Although female cowbirds removed significantly more cardinal eggs per parasitized than unparasitized nest, parasitized cardinals did not suffer losses attributable to reduced hatching success or nestling competition. The growth rates of cardinals in parasitized and unparasitized nests did not differ, nor did that of cardinals and cowbirds in the same nest. We detected cardinal defensive response at only three (5%) parasitized nests. These data suggest that this population of cardinals pays only a slight cost in being parasitized by cowbirds, which may explain the lack of defensive response.

Key words: Northern Cardinal, Brown-headed Cowbird, nesting success, reproductive success, Mayfield analysis, anti-parasite behavior, brood parasitism.

INTRODUCTION

Because of a recent decline in North American songbird populations, much attention has been paid to the effects of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) on songbird host reproductive success (Mayfield 1977, Brittingham and Temple 1983, Robinson 1992, Robinson et al. 1995). Cowbirds are generalists, known to parasitize over 200 avian species (Friedmann 1971), and as obligate interspecific parasites, they rely completely on their hosts for the care of their offspring. As a result, hosts of cowbirds can incur significant reproductive losses through removal of host eggs by female cowbirds, decreased hatchability of host eggs remaining in parasitized nests, and increased nestling competition (Friedmann 1963, Payne 1977, Rothstein 1990, Robinson et al. 1995).

The degree of harm to hosts caused by cowbirds varies relative to host and cowbird size,

host and parasite incubation periods, and host and parasite nestling growth rates (Friedmann 1963, Rothstein 1975a). Losses are most severe for hosts smaller than cowbirds and hosts whose incubation period is longer than that of cowbirds. Smaller host nestlings frequently starve as a result of competition with their larger cowbird nest mates (Friedmann 1963, Nolan 1978, Marvel and Cruz 1989, Weatherhead 1989), and the earlier hatching of cowbird nestlings can reduce host incubation behavior, decreasing the hatchability of host eggs (Mayfield 1977). However, when hosts are of similar or larger size than cowbirds and have a similar incubation period, they are usually able to raise both their own offspring and the nestling cowbirds to nest-leaving (Smith 1981, Ortega and Cruz 1988, 1991, Weatherhead 1989).

Although the degree of harm caused by Brown-headed Cowbirds varies among hosts, there is no evidence that parasitism by cowbirds ever benefits hosts (Rothstein 1975a). Therefore, selection should favor host defenses against brood parasitism (Rothstein 1975a, Robertson and Norman 1976, Briskie et al. 1992). Some hosts actively defend nests against cowbirds, desert parasitized nests, bury cowbird eggs under a new nest

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floor, or eject cowbird eggs from parasitized nests (Rothstein 1990). However, the majority of cowbird hosts accept the parasitic eggs with no defensive response (Rothstein 1975a, 1975b).

In this study we explored the patterns of cowbird parasitism in a frequently parasitized population of Northern Cardinals (*Cardinalis cardinalis*) (R. Breitwisch, pers. observ.) and determined the effects of cowbird parasitism on cardinal reproductive success. Cardinals are similar to cowbirds in size and mass (Ricklefs 1968), as well as incubation period (Nice 1953, Bent 1958, 1968, Breitwisch pers. observ.). Therefore, we tested the hypothesis that cowbird hosts of similar size and incubation period to cowbirds are able to raise their own offspring when parasitized (Smith 1981, Ortega and Cruz 1988, 1991, Weatherhead 1989). This hypothesis predicts that the only reproductive loss suffered by parasitized cardinals would be through the removal of host eggs by female cowbirds, and not reduced hatching success or nestling competition. We also described the defensive behavior displayed by cardinals against cowbirds. Although Rothstein (1975b) characterized cardinals as accepters of parasitism (they accept all, or nearly all, nonmimetic eggs), cardinals are known to desert parasitized nests (Berger 1951, Friedmann 1963, Graham 1988), and at least one instance of a cardinal ejecting a cowbird egg has been documented (Rothstein 1975a).

METHODS

STUDY SITE

We conducted this study on the Aullwood Audubon Center and Farm property (39°52'N, 84°16'W), located near Dayton, Ohio, from April to August 1993–1995. The property consists of approximately 80 ha of primarily reclaimed farmland with a variety of habitats present (for a more detailed description, see Filliater et al. 1994). Approximately 30 to 40 pairs of Northern Cardinals reside year-round on the property (R. Breitwisch et al., unpubl. data), and cowbirds are common in all habitats. Most observations in 1993 and all observations in 1994 and 1995 were made on the southern half of the property where about 25 breeding pairs of cardinals on adjacent territories were studied.

NEST LOCATION AND OBSERVATION

We located nests by actively searching appropriate habitats and by using behavioral cues of parental birds attending nests. We visited and recorded the number of eggs or nestlings in each active nest on average every other day between 07:30 and 12:00 EST. We monitored nest progress until either the nest was successful (at least one nestling survived to leave the nest) or failed.

During egg laying, we uniquely marked newly discovered eggs on the more pointed end with black, indelible ink to determine the egg-laying sequence and to detect any changes in nest contents between visits. We checked eggs to determine if marked eggs had disappeared on day six or seven of incubation and on the day before hatching was expected. We carefully counted and identified nestlings as to species six days post-hatching. Nestlings were assumed to have survived to leave the nest only if they were seen or heard on the breeding territory at the appropriate age (ca. 10 days after hatching).

We determined seasonal patterns in parasitic frequency (proportion of nests parasitized) and intensity (the number of cowbird eggs per parasitized nest) by dividing the breeding season into 10-day periods beginning on 19 April (the day the first cardinal egg was found) and determining the date of clutch initiation for each nest. When we discovered nests after incubation had begun, we back-dated them (using 3 days for the egg laying period, 12 days for the incubation period, and 10 days for the nestling period [Breitwisch, pers. observ.]) to determine when clutches were initiated.

We discovered nests at all stages of the nesting cycle, and many were already at the complete clutch or nestling stage. Therefore, we calculated total nest days of observation for the nest building and egg laying, egg incubation, and nestling periods, and used Mayfield's (1975) calculation to avoid biasing estimates of nest success. We included the last two days of nest building because cowbird eggs were found in cardinal nests prior to the first cardinal egg and these nests were subsequently abandoned, indicating that cardinal nests can fail prior to the laying of the first cardinal egg.

NESTLING GROWTH

During 1995 we documented nestling growth to determine (1) if a cowbird was a better com-

petitor than a cardinal for food delivered, and (2) whether cardinal growth was slowed in a parasitized nest relative to an unparasitized nest of equal brood size. If a nest was discovered before eggs hatched, we began to measure nestlings on the day of hatching (day 0) or the next day (day 1). If a nest was discovered with nestlings, we measured the nestlings on the day of discovery. In both cases, we attempted to obtain measurements on successive days until day 8 (a day prior to fledging), although predation on nestlings produced many incomplete sets of measurements.

We weighed each nestling with a Pesola spring scale (10 g or 50 g) to the nearest 0.1 g, and measured the length of the tarsometatarsus (= tarsus) to the nearest 0.1 mm with calipers. Nestling cowbirds are distinguishable from nestling cardinals no later than the day after hatching. Nestlings were marked with black nail polish on a claw for identification, and cardinals were banded 6 or 7 days after hatching.

STATISTICAL ANALYSIS

We used non-parametric analyses because of the small to moderate sample sizes (Siegel and Castellan 1988). The Kolmogorov-Smirnov two-sample test (D_{max} value reported) was used to test for differences in the shapes of frequency distributions. We tested for seasonal trends in parasitic frequency and intensity with Spearman rank correlations (r_s value reported). Tests of independence (G_{adj} value reported) were used to determine if associations existed between pairs of variables; all were corrected for small sample sizes using Williams' correction (Sokal and Rohlf 1995). We used a Multiway test of independence (χ^2 value reported) (PROC CATMOD [SAS Institute 1988]) using a maximum likelihood model to test the results of the Mayfield analysis. Comparisons of growth among different brood sizes of cardinals were by Kruskal-Wallis one-way ANOVAs (H value reported). The Wilcoxon two-sample test (U value reported) was used to test for differences between two sample medians. All tests were two-tailed; results are reported as significant if $P \leq 0.05$. Means \pm SD are reported for all descriptive statistics.

Similar descriptive data were collected in 1993 and 1994. Yearly data were compared, and if no differences were found, the data were

TABLE 1. Frequency of parasitism in Northern Cardinal nests.

	Year		Combined years total
	1993	1994	
Unparasitized nests	27	33	60
Parasitized nests	24	31	55
Parasitism (%) ^a	47.1	48.4	47.8

^a Frequency of parasitism in cardinal nests was independent of year ($G_{adj} = 0.02$, $P > 0.50$).

combined to increase sample size. Except where noted, no yearly differences were found.

RESULTS

NESTING PHENOLOGY

Nesting data were collected from 115 cardinal nests during 1993–1994. Parasitism occurred in 48% of these nests (Table 1). Fourteen (25%) of these parasitized nests were multiply parasitized (11 nests with two cowbird eggs, and three nests with three cowbird eggs), for an overall mean of 1.31 ± 0.57 ($n = 55$) cowbird eggs per parasitized nest.

We tested for correlations between the time at which a clutch was initiated and both parasitic frequency and intensity to determine seasonal patterns of cowbird parasitism in 103 cardinal nests. Dates of clutch initiation could not be determined for 12 nests because they were discovered in, and failed prior to the completion of, a particular nesting stage.

There were no yearly differences in the temporal distribution for the initiation of cardinal nests ($D_{max} = 0.25$, $P > 0.05$) nor in the laying of cowbird eggs in cardinal nests ($D_{max} = 0.15$, $P > 0.05$), so we combined data from both years. Cardinals and cowbirds in southwestern Ohio began breeding in mid-late April and cowbird eggs were discovered in cardinal nests from 24 April to 15 July (Eckerle 1994). The frequency of parasitism in cardinal nests increased from 24 April to 4 May, but declined thereafter, and was negatively correlated with the period in the cardinal breeding season ($r_s = -0.75$, $n = 9$, $P < 0.05$; Fig. 1). Similarly, the intensity of parasitism was highest in late April, but there was no correlation between the intensity of parasitism and the period in the breeding season ($r_s = -0.32$, $n = 9$, $P > 0.20$; Fig. 2).

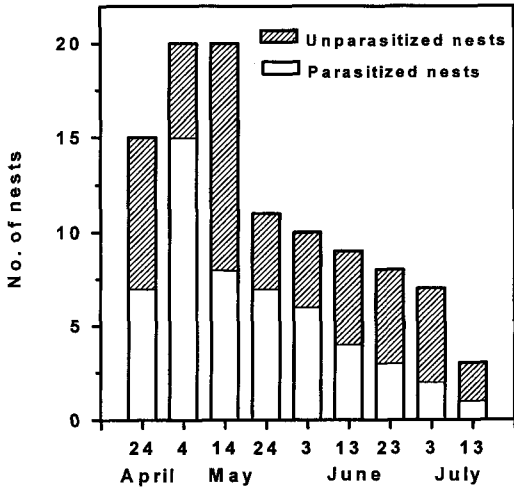


FIGURE 1. Seasonal trends in the frequency of cowbird brood parasitism in 103 cardinal nests during 1993–1994. Bars represent the number of cardinal nests initiated in each ten-day period of the breeding season (beginning 19 April) that remained unparasitized or were subsequently parasitized.

NEST SUCCESS

Because we were interested in the reproductive success of cardinals, we considered nests successful only if at least one cardinal survived to leave the nest. Data on the success of two nests were excluded from this analysis because the identity of the nestlings that survived to leave

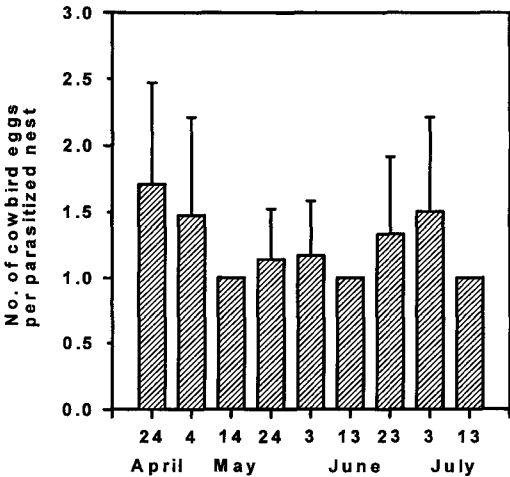


FIGURE 2. Seasonal trends in the intensity of cowbird brood parasitism in 53 cardinal nests during 1993–1994. Bars represent the mean number (\pm SD) of cowbird eggs per parasitized nest initiated in each ten-day period of the breeding season beginning 19 April.

the nest could not be determined (i.e., in two parasitized nests there were partial losses of nestlings between day 6 and the day of nest leaving, and the identity of the surviving nestlings was not determined prior to nest leaving). The overall success for the remaining cardinal nests was 30.1% (34/113). There was no significant difference in the success of multiply parasitized nests (23% [3/13]) and nests with a single cowbird egg (40% [16/40]) ($G_{adj} = 1.23$, $df = 1$, $P > 0.10$), so all parasitized nests were combined. The success of a nest was independent of its status as parasitized (36% [19/53]) or unparasitized (25% [15/60]) ($G_{adj} = 1.55$, $df = 1$, $P > 0.10$).

Because not all nests were found during egg laying, we calculated and compared the per stage survival of parasitized and unparasitized nests at each stage of the nesting cycle using the Mayfield (1975) analysis (Table 2). Three nests (one from 1993 and two from 1994) were excluded from this analysis (in one nest the stage of nesting could not be determined because it was found with a single egg and on the next visit the female was sitting on an empty nest, a second nest was depredated prior to the subsequent nest visit, and the third nest was found with only a single cowbird nestling). Using the frequency data from the Mayfield analysis, we tested for the effects of parasitism, year, nesting stage, and all possible interactions on nest survival. The first test showed no significant interactions, so all interaction terms were eliminated and the analysis was redone. The results of this test showed a significant effect of parasitism on nest survival and no significant effects of either year or nesting stage (Table 3). Thus, nest survival was consistently higher in parasitized than unparasitized nests across all stages of the nesting cycle and in both years of study. We used the likelihood ratio as a goodness-of-fit test for the main effects of parasitism, year and nesting stage, and found that the results were not significant, indicating that the data are consistent with this model.

EGG AND NESTLING SUCCESS

We analyzed the effect of cowbird parasitism on cardinal reproductive success in parasitized and unparasitized nests by comparing the number of cardinal eggs and nestlings present in each nest at the beginning of each stage in the nesting cycle, and by comparing the number of cardi-

TABLE 2. Survival of parasitized and unparasitized nests at different stages of the nesting cycle as calculated by the Mayfield analysis (sample sizes in parentheses).

Nesting stage	1993		1994	
	Parasitized	Unparasitized	Parasitized	Unparasitized
Egg laying	0.92 (15)	0.60 (18)	0.85 (17)	0.58 (15)
Incubation	0.74 (22)	0.51 (19)	0.47 (26)	0.35 (22)
Nestling	0.63 (14)	0.35 (11)	0.68 (16)	0.68 (15)
Overall	0.43 (24)	0.11 (26)	0.27 (30)	0.14 (32)

nal eggs and nestlings lost in each surviving nest during each stage of the nesting cycle. All parasitized nests were combined for these analyses because we found no significant differences in the number of cardinal eggs or nestlings present at any stage of the nesting cycle or in the number of cardinal eggs or nestlings lost during any nesting stage between multiply parasitized nests and nests with a single cowbird egg (Eckerle, unpubl. data).

There were no significant differences between parasitized and unparasitized nests in the number of cardinal eggs or nestlings present in each nest at any stage of the nesting cycle (Table 4). However, significantly more cardinal eggs were removed per parasitized than unparasitized nest during egg laying ($U = 264.5$, $P = 0.05$; Fig. 3). During incubation and at hatching, losses in parasitized and unparasitized nests did not differ significantly (during incubation: $U = 74$, $P > 0.10$; at hatching: $U = 285.5$, $P > 0.50$; Fig. 3). After hatching, there were no nestling losses in either parasitized or unparasitized nests, other than complete loss of nest contents to predators.

NESTLING GROWTH

We collected nestling measurements for 13 unparasitized and 4 parasitized nests in 1995. Brood sizes in unparasitized nests were one ($n = 4$), two ($n = 7$), and three ($n = 2$). Brood sizes in parasitized nests (including cowbirds) were three ($n = 3$) and four ($n = 1$). The single

TABLE 3. Effects of parasitism, year, and nesting stage on nest survival. Results are from a Multiway test of independence using a maximum likelihood model (see Methods).

Source	df	χ^2	P
Parasitism	1	7.19	0.007
Year	1	0.49	0.48
Nesting stage	2	1.57	0.46
Likelihood ratio	7	9.04	0.25

nest with a brood size of four had five nestlings initially (three cardinals and two cowbirds), but one cowbird nestling grew very slowly and eventually died several days after hatching. All other nestlings (both cardinal and cowbird) that were not taken by predators, survived to leave the nest.

The variability in brood size first required testing for brood-size effects within a nest class. Only the sample of unparasitized nests ($n = 13$) was large enough to test for such an effect. Because of the limited number of days with data for different nests and different ages, we compared both weights and tarsus lengths for nestlings at day 6 of age. This was the oldest nestling age for which we retained adequate sample sizes, although sample sizes were small. We found no brood size effect on nestling mass ($H = 3.16$, $df = 2$, $P > 0.05$) or tarsus length ($H = 1.30$, $df = 2$, $P > 0.05$). Therefore, we

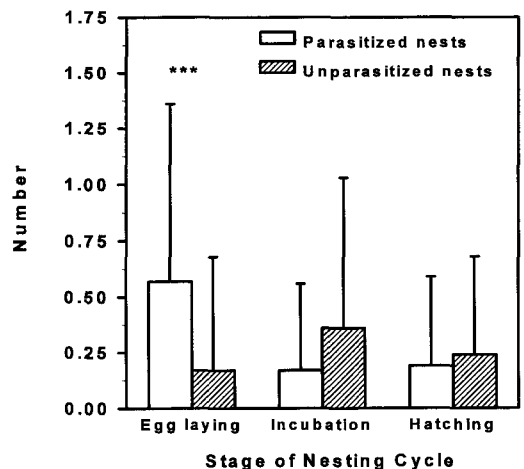


FIGURE 3. The mean number (\pm SD) of cardinal eggs lost during egg laying and incubation, and the number not hatching in parasitized and unparasitized nests. Values are from 23, 12, and 26 parasitized nests, and from 18, 11, and 21 unparasitized nests, respectively. (***) $P = 0.05$; all other statistical tests were nonsignificant, $P > 0.05$.)

TABLE 4. The number of cardinal eggs and nestlings (mean \pm SD) in parasitized and unparasitized nests at each stage of the nesting cycle (sample sizes in parentheses).

Stage	Parasitized	Unparasitized	U^a	P
At incubation	2.39 \pm 0.66 (23)	2.67 \pm 0.59 (18)	256.5	ns ^b
At hatching	2.14 \pm 0.65 (28)	2.24 \pm 0.83 (21)	322.0	ns
Nestling	1.92 \pm 0.69 (26)	2.00 \pm 0.77 (21)	288.0	ns
At nest leaving	2.06 \pm 0.68 (16)	1.93 \pm 0.80 (15)	131.5	ns

^a Wilcoxon two-sample test.^b nonsignificant, $P > 0.05$.

pooled data across brood sizes for comparisons between parasitized and unparasitized broods.

Cardinals in parasitized broods grew as rapidly as those in unparasitized broods. Comparisons of both mass (Fig. 4) and tarsus length (Fig. 5) for cardinal nestlings in parasitized and unparasitized nests showed no significant differences (weights: $U = 15.5$, $P > 0.05$; tarsus: $U = 24.5$, $P > 0.05$, $n_1 = 13$, $n_2 = 4$ for both). On day six, cowbird nestlings were very similar in size and mass to cardinals in both parasitized and unparasitized broods (overall mean of mean weight for cardinals in unparasitized broods = 23.4 g [$n = 13$ broods], parasitized broods = 22.3 g [$n = 4$ broods], cowbirds = 24.0 g [$n = 4$ broods]; mean tarsus length for cardinals in unparasitized broods = 22.0 mm, parasitized broods = 22.1 mm, cowbirds = 22.5 mm).

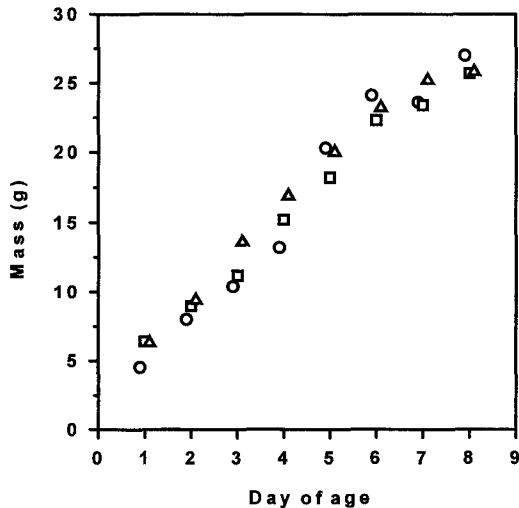


FIGURE 4. Growth of nestling cowbirds (open circles; $n = 4$ broods), cardinals in parasitized nests (open squares; $n = 4$ broods), and cardinals in unparasitized nests (open triangles; $n = 13$ broods), as measured by body mass. Symbols represent means of brood means at each day of age for cardinals and means at each day of age for cowbirds.

We also estimated the growth constant (K) for cardinal nestlings in unparasitized nests, using the methods of Ricklefs (1967), and yielded $K = 0.650$. The cowbirds included in our sample are too few for estimating their growth constant, but Lowther (1993) states that $K = 0.660$ for male and $K = 0.619$ for female cowbird nestlings, with no significant variation among host species. This comparison supports our finding that cardinals and cowbirds grow at similar rates.

DEFENSIVE BEHAVIOR

We documented only three instances of cardinal defensive behavior in parasitized nests. In two nests known to be under construction, a cowbird egg was the first to be laid, and the nests were abandoned without a cardinal egg added. In the remaining nest, a cowbird egg and

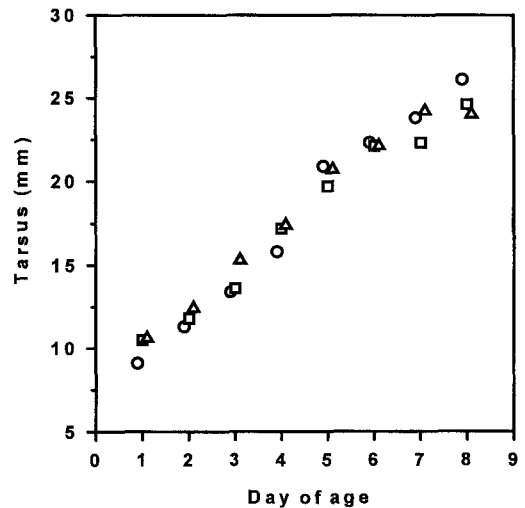


FIGURE 5. Growth of nestling cowbirds (open circles; $n = 4$ broods), cardinals in parasitized nests (open squares; $n = 4$ broods), and cardinals in unparasitized nests (open triangles; $n = 13$ broods), as measured by tarsus length. Symbols represent means of brood means at each day of age for cardinals and means at each day of age for cowbirds.

a cardinal egg were found buried underneath new nesting material. No similar type of behavior occurred in undisturbed, unparasitized nests.

DISCUSSION

NESTING PHENOLOGY

Cardinals in southwestern Ohio are frequent hosts to cowbirds. The frequency and intensity of cowbird parasitism in this population were similar to those reported in other studies of cardinals (Norris 1947, Berger 1951, Scott 1963, Graham 1988, Robinson 1992). Although the number of nests investigated in these studies varied from eight to 187, all data are consistent with Friedmann's (1963) classification of cardinals as common and frequent hosts to cowbirds.

Laskey (1950) and Scott (1963) suggested that cardinals suffer a higher frequency and intensity of parasitism early in the breeding season because of the sudden onset of cowbird breeding and the lack of other available hosts in early spring. In this study, both parasitic frequency and intensity were highest early in the season (late April to early May). Although no seasonal change in parasitic intensity occurred, parasitic frequency did decline over the season. It is unlikely that this decline is due to a seasonal decrease in female cowbird activity because female cowbirds may produce eggs almost continuously throughout their breeding season (Scott and Ankney 1980, 1983, Holford and Roby 1993). Thus, no seasonal change in the parasitism of cardinal nests would be expected.

The seasonal decrease in cowbird parasitism of cardinal nests may be due to the seasonal increase in available hosts. In addition to cardinals, 25 species classified by Friedmann (1963) as frequent hosts to cowbirds breed on our study site (J. Ritzenthaler, pers. comm.), and the majority of these species do not breed until after mid-May. Thus, the decrease in parasitism of cardinal nests may be due to female cowbirds taking advantage of the other available hosts later in the cowbird breeding season. Further studies in the seasonal patterns of nest usage by female cowbirds should be conducted to test this hypothesis.

NEST SUCCESS

Although the proportions of successful parasitized and unparasitized nests were not signifi-

cantly different, results of the Mayfield analysis indicate that parasitized nests had higher survival across all stages of the nesting cycle. This difference in success may result from female cowbirds selecting relatively "safe" cardinal nests (Kittleman and Cruz 1986, Weatherhead 1989). However, there were no differences in the nest site characteristics (location and cover) of parasitized and unparasitized nests (Eckerle 1994). Therefore, female cowbirds were not discriminating among cardinal nests based on the nest site characteristics we measured.

It also has been suggested that the differential survival of parasitized nests may be due to cowbirds depredating unparasitized nests to enhance their future laying opportunities (Smith and Arcese 1994, Arcese et al. 1996). We did not directly test the cowbird predation hypothesis. However, the fact that parasitized nests survived better than unparasitized nests is consistent with this hypothesis. Further analyses are necessary to test directly the cowbird predation hypothesis and to determine the cause of differential survival of parasitized and unparasitized cardinal nests.

EGG AND NESTLING SUCCESS

Cardinals in this population do suffer reproductive losses when parasitized by cowbirds although the degree of harm caused by parasitism seems to be unrelated to the number of cowbird eggs laid in a single nest. Approximately 40% of the parasitized nests had cardinal eggs removed, and parasitized nests lost an average of 0.40 more cardinal eggs per nest than unparasitized nests. These higher losses in parasitized nests are almost certainly caused by removal of cardinal eggs by female cowbirds.

This estimate for host-egg removal may be conservative for this population because these data were collected from only 36% (41/115) of the nests in this study. Estimates from other populations are much higher, suggesting that for every cowbird egg laid at least 0.80 eggs are apparently removed by cowbirds (reviewed in Scott et al. 1992). There is, however, much variability. Smith and Arcese (1994) report that 0.67 host eggs were removed per parasitized Song Sparrow (*Melospiza melodia*) nest. Clark and Robertson (1981) report that ca. 50% of parasitized Yellow Warbler (*Dendroica petechia*) nests had host eggs removed, whereas Burgham and Picman (1989) report that fewer than 15%

of parasitized Yellow Warbler nests had host eggs removed. Thus, other published estimates for host-egg removal are similar to or lower than those in this study. Nevertheless, our data indicate that cardinals in southwestern Ohio pay an "egg cost" when parasitized by cowbirds.

Parasitized cardinals did not suffer reproductive losses attributable to reduced hatching success or nestling competition. Although sample sizes were small, there were no differences in the growth of cardinal nestlings in parasitized and unparasitized nests, nor in cardinal and cowbird nestlings in parasitized nests. Similarly, no cardinal nestlings were lost in successful parasitized nests. Therefore, it appears that cowbird nestlings did not outcompete cardinal nestlings in parasitized broods but are as competitive as typical cardinal nestlings. Thus, the only cost of parasitism for a pair of cardinals was that caused by removal of an egg by a female cowbird. These results are consistent with the hypothesis that large hosts, such as cardinals, are usually able to raise their own offspring to nest leaving when parasitized by cowbirds (Smith 1981, Ortega and Cruz 1988, 1991, Weatherhead 1989).

DEFENSIVE BEHAVIOR

Data from this study are consistent with Rothstein's (1975a, 1975b) conclusion that cardinals are accepters of cowbird parasitism. Nevertheless, because cardinals were frequently parasitized and suffered reproductive losses when parasitized, selection should favor the evolution of rejection behavior in this population.

The lack of rejection behavior in this population cannot be explained by the inability of cardinals to eject cowbird eggs. Rothstein (1975a) indicated that all accepters should be capable of ejecting cowbird eggs and documents one instance of a cardinal ejecting a cowbird egg. Similarly, the absence of rejection cannot be explained by the cardinals' lack of experience with cowbirds. An Ontario population of cardinals exposed to cowbird parasitism for a similar length of time to the Dayton population (Mayfield 1965, Bent 1968) frequently rejected cowbird eggs (Graham 1988), whereas cardinals in this study showed little rejection behavior. Thus, it is likely that cardinals in our study population have been exposed to cowbird parasitism sufficiently long to develop rejection behavior.

The absence of rejection behavior may be attributable to the small costs resulting from cowbird parasitism, the costs of anti-cowbird defenses, or both. Ortega and Cruz (1988) and Smith and Arcese (1994) suggested that the lack of rejection in their host populations (Red-winged Blackbirds [*Agelaius phoeniceus*] and Song Sparrows, respectively) was due to the ability of parasitized individuals to produce their own young. In this study, although parasitized cardinals suffered losses from female cowbirds removing cardinal eggs, the overall production of cardinal young was not significantly different in parasitized and unparasitized nests. The absence of a significant cost of parasitism however, may not fully explain the lack of rejection, because most birds considered rejecters of parasitism are larger than cowbirds, and would likely be able to raise their own offspring when parasitized (Rothstein 1975a).

The lack of defensive behavior also could be explained if cardinals incur a significant ejection or recognition cost (Rothstein 1975a, Davies and Brooke 1988) by rejecting cowbird eggs. Cardinal and cowbird eggs are similar in coloration, which may make adaptations based on egg recognition difficult to evolve (Rothstein 1975a). Thus, the potential costs associated with evolving rejection may be too high, and the losses resulting from being parasitized may be too small for rejection to become common in this population.

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LITERATURE CITED

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

- BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211.
- BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237.
- BERGER, A. J. 1951. The cowbird and certain host species in Michigan. *Wilson Bull.* 63:26–34.
- BRISKIE, J. V., S. G. SEALY, AND K. A. HOBSON. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. *Evolution* 46:334–340.
- BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31–35.
- BURGHAM, M. C. J., AND J. PICMAN. 1989. Effect of Brown-headed Cowbirds on the evolution of Yellow Warbler anti-parasite strategies. *Anim. Behav.* 38:298–308.
- CLARK, K. L., AND R. J. ROBERTSON. 1981. Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler. *Wilson Bull.* 93:249–258.
- DAVIES, N. B., AND M. DE L. BROOKE. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Anim. Behav.* 36:262–284.
- ECKERLE, K. P. 1994. Northern Cardinal response to brood parasitism by Brown-headed Cowbirds. M.Sc. thesis, Univ. Dayton, OH.
- FILLIATER, T. S., R. BREITWISCH, AND P. M. NEALEN. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? *Condor* 96:761–768.
- FRIEDMANN, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.
- FRIEDMANN, H. 1971. Further information on the host relations of the parasitic cowbirds. *Auk* 88:239–255.
- GRAHAM, D. S. 1988. Responses of five host species to cowbird parasitism. *Condor* 90:588–591.
- HOLFORD, K. C., AND D. D. ROBY. 1993. Factors limiting fecundity of captive Brown-headed Cowbirds. *Condor* 95:536–545.
- KITTLEMAN, C. P., AND A. CRUZ. 1986. Selection of blackbird nests by cowbirds: a prudent strategy? Cooper Ornithological Society Annual Meeting, Univ. California, Davis (abstract).
- LASKEY, A. 1950. Cowbird behavior. *Wilson Bull.* 62:157–174.
- LOWTHER, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). In A. Poole and F. Gill [eds.], *The birds of North America*, No. 47. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.
- 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.
- MAYFIELD, H. 1965. The Brown-headed Cowbird with old and new hosts. *Living Bird* 4:13–28.
- MAYFIELD, H. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456–466.
- MAYFIELD, H. 1977. Brown-headed Cowbird: agent of extermination. *Am. Birds* 31:107–113.
- NICE, M. M. 1953. The question of ten-day incubation periods. *Wilson Bull.* 65:81–93.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* 26.
- NORRIS, R. T. 1947. The cowbirds of Preston Frith. *Wilson Bull.* 59:83–103.
- ORTEGA, C. P., AND A. CRUZ. 1988. Mechanisms of egg acceptance by marsh dwelling blackbirds. *Condor* 90:349–358.
- ORTEGA, C. P., AND A. CRUZ. 1991. A comparative study of cowbird parasitism in Yellow-headed Blackbirds and Red-winged Blackbirds. *Auk* 108:16–24.
- PAYNE, R. B. 1977. The ecology of brood parasitism in birds. *Annu. Rev. Ecol. Syst.* 8:1–28.
- RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48:978–983.
- RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419–451.
- ROBERTSON, R. J., AND R. F. NORMAN. 1976. Behavioral defenses to brood parasitism by potential hosts of the Brown-headed Cowbird. *Condor* 78:166–173.
- ROBINSON, S. K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape, p. 408–418. In J. M. Hagan III and D. W. Johnston [eds.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Inst. Press, Washington, DC.
- ROBINSON, S. K., S. I. ROTHSTEIN, M. C. BRITTINGHAM, L. J. PETIT, AND J. A. GRZYBOWSKI. 1995. Ecology and behavior of cowbirds and their impact on host populations, p. 428–460. In T. E. Martin and D. M. Finch [eds.], *Ecology and management of Neotropical migratory birds*. Oxford Univ. Press, Oxford.
- ROTHSTEIN, S. I. 1975a. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77:250–271.
- ROTHSTEIN, S. I. 1975b. Evolutionary rates and host defenses against avian brood parasitism. *Am. Nat.* 109:161–176.
- ROTHSTEIN, S. I. 1990. A model system for coevolution: avian brood parasitism. *Annu. Rev. Ecol. Syst.* 21:481–508.
- SAS INSTITUTE, INC. 1988. SAS user's guide: statistics, version 6.03. SAS Institute, Inc., Cary, NC.
- SCOTT, D. M. 1963. Changes in the reproductive activity of the Brown-headed Cowbird within the breeding season. *Wilson Bull.* 75:123–129.
- SCOTT, D. M., AND C. D. ANKNEY. 1980. Fecundity of the Brown-headed Cowbird in southern Ontario. *Auk* 97:677–683.
- SCOTT, D. M., AND C. D. ANKNEY. 1983. The laying cycle of Brown-headed Cowbirds: passerine chickens? *Auk* 100:583–592.
- SCOTT, D. M., P. J. WEATHERHEAD, AND C. D. ANKNEY. 1992. Egg-eating by female Brown-headed Cowbirds. *Condor* 94:579–584.
- SIEGEL, S., AND N. J. CASTELLAN, JR. 1988. *Nonparametric statistics for the behavioral sciences*, 2nd ed. McGraw-Hill, New York.

- SMITH, J. N. M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island Song Sparrow population. *Condor* 83:152-161.
- SMITH, J. N. M., AND P. ARCESE. 1994. Brown-headed Cowbirds and an island population of Song Sparrows: a 16-year study. *Condor* 96:916-934.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*, 3rd ed. W. H. Freeman, New York.
- WEATHERHEAD, P. J. 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. *Auk* 106:358-366.