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An Investigation of the Host Specificity of the Brown-headed Cowbird

(TITLE)

BY

BRIAN D. PEER

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

M.Sc. Zoology

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
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ABSTRACT

We attempted to determine the factors associated with the lack of parasitism of the Common Grackle (Quiscalus quiscula) by the Brown-headed Cowbird (Molothrus ater). We investigated the breeding phenology of the two species, the responses of colonial- and noncolonial-nesting grackles to female cowbird models, the frequency of artificial egg rejection by grackles, incubation success of cowbird eggs transferred into grackle nests, and the survival rates of cowbirds cross-fostered into grackle nests.

By the time cowbirds began egg-laying at our study sites, 88.5 % of all grackle nests were beyond the point of successful parasitism. Grackles responded much more aggressively toward female cowbird models than to Fox Sparrow (Passerella iliaca) models. Grackles rejected artificial cowbirds eggs more frequently during the prelay stage of the nesting cycle (13 rejections at 32 nests) compared to later stages. However, the rejection frequency during the later stages of nesting (lay and incubation) was virtually the same as in Rothstein's original study (1975) (12.4 % vs. 11.3 %).

A total of 14 cowbird eggs and nestlings were cross-fostered into grackle nests. Data were collected

on six cowbird nestlings, none of which survived to fledging. Five of the nestlings died after two days, and the sixth nestling survived five days despite having two grackle nestmates that were each a day older. Grackle nestlings weighed more than twice as much as cowbird nestlings at hatching (5.4 ± 0.91 g vs. 2.5 ± 0.72 g), and had significantly greater gape widths and culmen lengths for the first two days after hatching. The lack of survival of cowbird nestlings in grackle nests may be partially due to this size asymmetry. However, one cowbird nestling died after two days despite having no grackle nestmates to compete with, thus suggesting the possibility of some behavioral incompatibility. This was unexpected as it is generally believed that nestling passerines have similar dietary requirements, with the exception of those species that feed their young primarily seeds or fruit.

Of the eight eggs that did not hatch, four appeared to be the result of ineffective incubation. These clutches contained between four and six eggs total, whereas the clutches in which cowbird eggs hatched contained a total of three eggs or fewer. These data support the host incubation hypothesis for egg removal by female cowbirds. If Brown-headed

Cowbirds preferred larger hosts in the past (as indicated by the fact that all but one of the species that regularly eject cowbird eggs are larger than the cowbird), then it may have been advantageous for a female cowbird to remove at least one host egg to ensure more effective incubation of her own smaller egg.

Mourning Doves (Zenaida macroura) like Common Grackles exhibit a high rate of parasitic egg rejection behavior (31.2 %) for an accepter species. Despite Rothstein's (1975a) conclusion that no geographic variation in egg rejection behavior exists, we found Mourning Doves in central Illinois rejected artificial cowbird eggs at nearly twice the rate (58.6 %, $x^2 = 3.7$, df = 1, $P < 0.06$) of those in Rothstein's trials. The reason for the lack of geographic variation in Rothstein's trials may be the result of small sample sizes.

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TABLE OF CONTENTS

CHAPTER I: EXPLANATIONS FOR THE LACK OF PARASITISM OF THE COMMON GRACKLE (QUISCALUS QUISCULA) BY THE BROWN-HEADED COWBIRD (MOLOTHRUS ATER)

INTRODUCTION

Avian brood parasitism is a rare reproductive strategy in which the female lays her eggs in the nests of other birds thereby relinquishing further parental care to the host species. In order to maximize its reproductive effort, a brood parasite must locate a compatible host with life history traits similar to its own. Thus, a parasite must select a host whose breeding season overlaps with its own (Hamilton and Orians 1965, Briskie et al. 1990, DeGeus 1991, Ortega and Cruz 1991) and one without significant antiparasitic adaptations (e.g., rejection of the parasitic egg, burying the parasitic egg) (Rothstein 1975a).

Once a parasite's egg is in a host's nest it must be incubated effectively to ensure hatching (Hofslund 1957, Mayfield 1960, Friedmann 1929, Rothstein 1975a, Wiley 1982). The host's incubation period must be long enough and the egg must come into contact with the host's brood patch. If the host's eggs are considerably larger than the parasite's (Payne 1977) or if the clutch size is excessively large (Sealy 1992), the chances of the parasitic egg hatching will decrease.

After the parasitic egg hatches, the nestling requires an adequate diet (Friedmann 1929, Rothstein 1976, Middleton 1977, 1991, Payne 1977) and parental care (Friedmann 1929, Payne 1977, Eastzer 1980, Mills 1988). Finally, the host nestlings must have growth rates similar to the parasite's, for if they grow too quickly the parasitic nestling will be at a disadvantage (Friedmann 1963, Ortega and Cruz 1991, 1992).

The Brown-headed Cowbird (Molothrus ater) is the only obligate brood parasite that is widespread throughout North America. It is a host generalist, having parasitized at least 220 species of birds, 144 of which have successfully reared cowbird young (Friedmann and Kiff 1985). The Common Grackle (Quiscalus quiscula) is an infrequent host of the cowbird. There have been only 16 documented cases of parasitism (Friedmann and Kiff 1985, Lowther 1991), and Common Grackles have never been known to successfully fledge cowbird offspring. This is unusual because the Common Grackle is a widespread and abundant species, and both grackles and cowbirds have had overlapping ranges and habitat requirements throughout their evolutionary histories (Mayfield 1965). Furthermore, Common Grackles have large and conspicuous nests and are known to usually accept cowbird eggs (Rothstein 1975a). Therefore, it seems that they should be a much more common host of cowbirds.

Friedmann et al. (1977:39) commented on this ironic relationship:

> The reason for the lack of parasitism (of grackles) is not clearly known. The cowbird may avoid parasitizing species as large as the grackle, but the American Robin and the Brown Thrasher are nearly as large and have been found to be parasitized many more times than the grackle, even though they are rejecter species. Perhaps the grackle's colonial nesting may be a factor. It may be difficult for cowbirds to escape detection when entering grackle colonies. But many grackles do not nest in colonies, in which case other factors may be responsible for the low incidence of parasitism.

In this study we attempted to determine those factors responsible for the lack of parasitism of the Common Grackle by the Brown-headed Cowbird by

(1) placing artificial cowbird eggs into grackle nests to determine whether or not there has been a change in grackles' egg rejection frequency since Rothstein's original study (1975a), (2) determining if coloniality is an effective deterrent against brood parasitism by comparing the responses of colonial- and noncolonial-nesting grackles to female cowbird models, (3) observing if noncolonial-nesting grackles are parasitized more frequently than colonial-nesting grackles, (4) cross-fostering cowbird eggs into grackle nests to determine if nestling cowbirds could survive in grackle nests, and (5) determining the synchrony of grackle and cowbird breeding seasons.

METHODS

Study site - From 23 March to 4 July 1992 we monitored grackle nests located at ten sites throughout Coles County, Illinois. The majority of the data were collected at four sites, including two cemeteries and two Christmas tree farms. The cemeteries contained scattered rows of Northern White Cedar (*Thuja occidentalis*) 2-3 m in height, with other deciduous species interspersed. The Christmas tree farms had evenly distributed rows of Scotch Pine (*Pinus sylvestris*), 2-2.5 m in height. The remaining sites consisted of several roadside thickets, a small nature preserve, a lake edge, and a residential park. All of the sites were bordered on at least one side by agricultural fields.

Egg manipulations - Artificial cowbird eggs were made of wood and painted with waterbased acrylic paints and coated with a clear acrylic sealer. Their dimensions were 21.91 x 16.67 mm and they weighed 2.5 g. Real cowbird eggs average 21.45 x 16.42 mm (Bent 1958) and weigh 3.17 g (Ankney and Johnson 1985). Thus, we feel that our eggs were an effective mimic of real cowbird eggs (e.g. see Rothstein 1975a and below).

At each nest we attempted to simulate natural parasitism by replacing a single grackle egg with an artificial cowbird egg. Although there is variation in the frequency of host egg removal by cowbirds (Sealy 1992), we followed the same procedure used by Rothstein (1975a) to maintain consistency.

Each nest was categorized into one of three stages of the nesting period: (1) Prelay - nest construction was complete or near completion but no eggs had been laid; (2) Lay - eggs were actively being laid; and (3) Incubation - the clutch was complete and being incubated. Although grackles often begin incubation prior to clutch completion (Eyer 1954, Maxwell and

Putnam 1972), we did not classify nests as being in the incubation stage until laying was completed. Nests were also categorized as colonial or noncolonial based on the distance between nearby nests. Colonies consisted of at least three nests that were all within 10 m of each other. Colonial nesting grackles at our sites formed very cohesive groups and responded to the alarm calls of conspecifics from distances of at least 10 m.

Only one artificial cowbird egg was added per nest and no clutches were manipulated more than once. All manipulations were conducted between 0600 and 1300 (CST), since cowbirds confine egg-laying (Scott 1991) and host searching activities to the morning hours (Rothstein et al. 1984).

Nests were checked every 1-2 days for host response. Responses were considered "rejections" if the artificial egg was ejected from the nest, pecked, buried in the nest lining, or if the nest was deserted. A nest was considered a desertion only if the nest was abandoned within five days of egg replacement (Rothstein 1975a).

Response to Cowbird Model - The aggressive responses of grackles to cowbirds were evaluated using mounted models of female Brown-headed Cowbirds. Mounted Fox

Sparrows (<u>Passerella iliaca</u>) were used as controls. Although Fox Sparrows do not breed in Coles County, they are a common spring migrant throughout our study area during the early portion of the grackle breeding season.

Models were placed approximately 0.5 m from a grackle nest and at the same level as the nest. The Fox Sparrow model was presented first in one half of the trials, whereas the cowbird model was presented first in the other half of the trials. Each model was presented for five minutes with a ten minute interval before the presentation of the second model. Following the presentation of each cowbird model a grackle egg was replaced with an artificial cowbird egg. No nests were subjected to a model more than once, however, individual pairs of grackles may have been because we tested for differences in aggression between first and second clutches, and the grackles were not color-banded.

Responses were recorded by the same individual (BDP) in all trials and were scored using the following scale, modified from Robertson and Norman (1976): (0) absent during the trial, (1) distant and silent observation, (2) close and silent observation, (3) distant alarm calling, (4) close alarm calling, (5) fly-by investigation, (6) nest attentive (bird situated between the model and the nest, or sitting on the eggs before the incubation period), (7) hovering near the model, (8) single attack, (9) mob by $\geq$ 2 individuals, or (10) physically striking the model.

Each rating was multiplied by the duration of each action to determine the composite score (.2 = 1 minute, .4 = 2 minutes, .6 = 3 minutes, .8 = 4 minutes, and 1.0 = 5 minutes). For example, if a grackle was nest attentive for 3 minutes (.6 x 6 = 3.6) and hovering near the model for 2 minutes (.4 x 7 = 2.8) it would receive a score of 6.4. Once a model was physically struck the trial ended to preserve the model.

Cross-fostering cowbird eggs and nestlings - Cowbird eggs and nestlings were collected from the nests of Song Sparrows (<u>Melospiza melodia</u>), Red-winged Blackbirds (<u>Agelaius phoeniceus</u>), and Northern Cardinals (<u>Cardinalis cardinalis</u>). We replaced single grackle eggs with one and in some cases two cowbird eggs to ensure that at least one cowbird egg would hatch. In no instance did two cowbirds hatch within a single nest. All transferred cowbird eggs had been laid within 1-2 days of when the grackle eggs had been laid.

In some cases we cross-fostered cowbird nestlings into nests with grackle nestlings. In all of these cases the nestlings were the same age, with the only exception being a cowbird nestling that was one day younger than its two grackle nestmates.

Nestling and egg measurements - Nestling measurements were taken daily. We measured weight to the nearest gram using 50 g and 100 g Pesola scales, gape (width of bill at loral feathering) and exposed culmen to the nearest 0.01 mm with calipers according to Baldwin et al. (1931). Grackle and cowbird egg dimensions were measured to the nearest 0.01 mm using calipers.

Breeding season analysis - The breeding season analysis was performed by recording the dates of initiation of grackle clutches and the laying dates of cowbird eggs found at our study areas. Only eggs whose initiation dates could be determined were used in the analysis.

RESULTS

Breeding season phenology - The first grackle egg was laid on 23 March and clutch initiation peaked during the two week period between 12 - 25 April, when 54.3 % of all nests were initiated (113 of 208 nests) (Figure 1). The first female cowbird was sighted 15 May and the first egg was found on 16 May. Cowbird egg-laying peaked during the week of 31 May to 6 June, encompassing 52.0 % of all eggs detected (13 of 25 eggs) (Fig. 1). This is similar to the results of Jackson and Roby (1992) who found that captive cowbirds in southern Illinois began laying on 16 May and peaked on 10 June (but see Robinson unpubl. data, cited in Jackson and Roby 1992). By the time the first cowbird egg was laid in our study area (16 May) 88.5 % (184 of 208 nests) of all grackle nests were beyond the point of successful parasitism (i.e. nests that were in the incubation stage or later). We documented no cases of natural cowbird parasitism in the 208 grackle nests we monitored.

Artificial egg rejection - The artificial cowbird eggs were rejected in 17.0 % of the nests in which they were placed (Table 1). Rothstein (1975a) recorded eight rejections out of 70 nests (11.4 % rejection rate). However, since Rothstein performed no manipulations in the prelay stage, a direct comparison of our data without prelay numbers yields a remarkably similar rejection rate of 12.3 % (19 of 154 nests) ($x^2 = 0.024$, df = 1, $P > 0.75$). The most frequent method of rejection in our study was egg ejection, comprising 59.4 % of all rejections (Table 2).

Prelay rejections occurred significantly more often than rejections later in the nesting cycle (x^2 = 13.91, df = 2, $P < 0.001$). Noncolonial nesters were more likely to reject artificial eggs than their colonial-nesting counterparts (x^2 = 5.70, df = 1, $P < 0.025$). However, there were no significant differences between egg rejections at nests presented with models compared to those without models (x^2 = 1.54, df = 1, $P > 0.10$). There were also no significant differences in the rejection rates of first clutches compared to second clutches (x^2 = 1.23, df = 1, $P > 0.25$). Finally, natural cowbird eggs were rejected at similar rates to artificial cowbird eggs (21.0 %, 3 out of 14 nests, x^2 = 0.18, $P > 0.50$).

Response to cowbird model - Grackles responded more aggressively toward the cowbird models than to the Fox Sparrow models (Wilcoxon signed-rank test, T = 3697.5, $p < 0.0001$, n = 94). However, there were no significant differences in aggressive response to cowbird models between solitary and colonial-nesters (Mann-Whitney test, W = 1273.5, $p > 0.75$), between first and second clutches (Mann Whitney test, W = 605, $p > 0.50$), or among the three stages of the nesting cycle (Kruskal Wallis test, F = 1.56, $p > 0.10$).

Cross-fostering experiments - A total of 14 transfers of cowbird eggs and nestlings were made into grackle nests. Data were collected on six nestlings, of which two were egg transfers and four were nestling transfers. None of the cowbird nestlings fledged. Five of the six nestlings lived for only two days, and the remaining nestling lived for five days despite having two grackle nestmates that were both a day older.

Grackle nestlings were significantly larger than cowbird nestlings, weighing more than twice as much as the cowbird nestlings at hatching (2 sample t-test, $P = 0.001$) (Fig. 2). This difference was maintained at least through the second day (2 sample t-test, $P = 0.001$). The differences between grackle and cowbird gapes and culmen length were also significantly different for days one and two (2 sample t-tests, $P < 0.01$) (Fig. 3, 4).

Egg size - The average size of grackle eggs was 28.76 x 21.36 mm ($n = 131$), whereas cowbird eggs averaged 20.4 x 16.7 mm ($n = 19$). Of the eight cowbird eggs that did not hatch, four appeared to be the result of ineffective incubation. These clutches contained 4-6 eggs, whereas the two clutches in which cowbird eggs hatched contained three eggs at the most.

DISCUSSION

Breeding season phenology - Hamilton and Orians (1965) suggested that the optimal strategy for a brood parasite is to match its breeding season with the reproductive events of a specific host. Asynchronous breeding seasons with cowbirds have been suggested to contribute to the lack of parasitism of other species, including Least Flycatchers (*Epidonax minimus*) (Briskie et al. 1990), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) (Ortega and Cruz 1991), and Loggerhead Shrikes (*Lanius ludovicianus*) (DeGeus 1991). It is evident that cowbirds in east-central Illinois time their reproductive events to coincide with hosts other than the grackle. There were 24 grackle nests potentially available for parasitism once cowbirds began laying. Instead of parasitizing grackles, cowbirds parasitized individual nests of other species repeatedly. Song sparrows, the most common host throughout our study sites, received up to six cowbird eggs per nest on two separate occassions.

All grackle nests that were available for cowbirds to parasitize were second clutches, but the frequency with which grackles are double-brooded is debated. It was previously believed that the only time grackles produced a second clutch was after the first had been destroyed (Bent 1958, Howe 1976, 1978). However, at four of our sites (six colonies) grackles had two clutches despite little evidence of nest loss. Both Brown Thrashers (Toxoma rufum) and American Robins (Turdus migratorius) who are parasitized much more frequently than grackles (Friedmann et al. 1977) begin breeding at approximately the same time as grackles (pers. observ.). However, they consistently produce two clutches in a breeding season and sometimes three (Howell 1942, Young 1955, Murphy and Fleischer 1986). Thus, a greater proportion of robin and thrasher nests are exposed to cowbirds compared to grackle nests.

The unpredictable nature of grackle breeding behavior is compounded by their tendency to abandon nests, similar to Tricolored Blackbirds (Agelaius tricolor) (Orians 1960, 1961) and Yellow-headed Blackbirds (Ortega and Cruz 1991). Three colonies of grackles disappeared during the middle of May, abandoning their nests in the process. Since cowbirds began laying at our study sites on 16 May they would be better served by parasitizing more predictable hosts.

Response to cowbird models - Rothstein (1970) suggested that the best antiparasitic defense is to avoid being parasitized. Grackles in east-central

Illinois appear to use aggressive behavior quite effectively in deterring brood parasitism. The few grackle nests that are available for cowbirds to parasitize may not be worth the risk of injury due to the overt aggression displayed by grackles toward cowbirds.

This is similar to the prediction of Robertson and Norman (1976) that aggression is the best defense for accepters. However, our data do not agree with their hypothesis that the level of aggression displayed is correlated with the degree of parasitism. Grackles were not parasitized in our study areas and rarely are parasitized anywhere, yet they still behaved aggressively toward cowbirds. However, unlike the geographic uniformity of egg rejection (Rothstein 1975b), Robertson and Norman (1977) found geographic variation in grackle aggressive response to cowbirds. Nevertheless, our results indicate that grackles do recognize cowbirds as a threat to which they respond aggressively.

The vigilance associated with coloniality has been shown to benefit marsh-nesting Red-winged Blackbirds who are parasitized less frequently than those nesting in dispersed upland areas (Friedmann 1963, Robertson and Norman 1976, 1977, Freeman et al. 1990). However, neither noncolonial-nesting nor colonial-nesting grackles were parasitized. It has also been suggested that cowbirds cue in on the aggressive behavior of some host species to locate their nests (Robertson and Norman 1976, 1977, Smith et al. 1984, McLean 1987, Hobson and Sealy 1989, Freeman et al. 1990). Therefore, we would expect dispersed individuals to be parasitized more frequently because they are aggressive but lack the effective defense of the colony. However this was not the case. A possible explanation is that the large size of an adult grackle (113.3 g, Howe 1977) threatens the moderately sized cowbird (43.9 g, Weatherhead 1989), even when only one grackle is present. During our trials grackles often destroyed our models, so it is likely that cowbirds would be at great risk when approaching grackle nests.

Nevertheless, aggression is not a foolproof strategy because there were trials when all grackles were absent. The opportunity does exist for parasitism especially for solitary nesters since they lack the benefits of increased vigilance derived from a colony. However, colonial nesters were just as likely to be absent during the trials as were solitary nesters, and the majority of nest absences tended to occur later in the morning. Scott (1991) has shown that cowbirds lay before sunrise so absences later in the morning may be of little consequence. The only time that grackles were at risk of being parasitized was during their second clutches, but the level of aggression was maintained equally throughout the breeding season.

Egg rejection - Rothstein (1975b) classified grackles as Type 1 accepters (ie. accepters that are rarely parasitized), along with the Mourning Dove (*Zenaida macroura*), Black-billed Cuckoo (*Coccyzus erythropthalmus*), and Barn Swallow (*Hirundo rustica*). Since very few grackle nests were available to be parasitized and those that were available were aggressively protected, there appears to be little if any current selection pressure on grackles to reject parasitic eggs. This is supported by the fact that there has been virtually no change in the rejection frequency of grackles since Rothstein's original study (1975a). The potential costs of accepting a parasitic egg to grackles are the removal of one of their own eggs by a female cowbird and the diversion of food to the cowbird nestling instead of their own nestlings. The significance of these costs is questionable since cowbirds do not consistently remove host eggs (Sealy 1992) and cowbird nestlings may not survive well in grackle nests.

Grackles, like other species, were more likely to reject parasitic eggs deposited in their nest before they had begun laying (Briskie and Sealy 1987, Davies and Brooke 1988, Burgman and Picman 1989). However, rejections in the prelay stage, especially the egg burials, are probably a continuation of the nest building process rather than true recognition of a foreign egg (Rothstein 1986, Hobson and Sealy 1987).

Nevertheless, grackles do exhibit low levels of "true" rejection behavior (e.g., ejection and egg pecking), which may indicate that they were parasitized by cowbirds more often in the past. Grackles possess several characteristics which would make them good hosts, including their long history of sympatry with cowbirds, their large population size and range, their large and conspicuous nests, and their large body size. Large species may be better hosts, since they are able to raise larger broods and provide more effective defense against nest predators (Fretwell cited in Rothstein 1975a, Gottfried 1979, Carter 1986, Mason 1986a, Wiley 1988).

All of the rejecter species in North America are larger than the Brown-headed Cowbird, with the exception of the Cedar Waxwing (Bombycilla cedrorum), which is approximately the same size as the cowbird. Mason (1980) speculated that cowbirds may have been forced to parasitize smaller species after the heavily parasitized larger species began rejecting parasitic eggs. Both the Bronzed Cowbird (*Molothrus aeneus*) and Shiny Cowbird (*Molothrus bonariensis*) prefer larger hosts (Post and Wiley 1977, Mason 1980, 1986a, 1986b, Carter 1986). Carter (1986) has demonstrated that the Great-tailed Grackle (*Quiscalus mexicanus*) is a rejecter of Bronzed Cowbird eggs. The Great-tailed Grackle weighs an average of 152.3 g (Selander and Giller 1961), and the Bronzed Cowbird approximately 62.9 g (Carter 1986). Thus, the relative size difference between these two species is essentially the same as that between the Brown-headed Cowbird and the Common Grackle. Although the Great-tailed Grackle has not been reported to be parasitized by the Bronzed Cowbird this is likely the result of its status as a rejecter, and the paucity of information on the Bronzed Cowbird. Nevertheless, we feel that this example indicates the possibility that the Common Grackle was once a rejecter species as a result of Brown-headed Cowbird parasitism.

However, it is unknown whether or not egg removal by female cowbirds and the diversion of food to cowbird nestlings is significant enough to generate the egg rejection adaptation in grackles. Wiley (1986) has shown that growth rates of Greater Antillean Grackle

(Quiscalus niger) nestlings were significantly less in nests parasitized by Shiny Cowbirds despite the fact that adult Greater Antillean Grackles are 48 % larger than Shiny Cowbirds. However, this cost has not led to egg rejection in this species.

If the above scenario is correct, cowbirds eventually stopped parasitizing grackles because of rejection of their eggs combined with the lack of success suffered by cowbird nestlings in grackle nests (see below). Today grackles remain aggressive, but only low levels of true egg rejection are present within the population (see Cruz and Wiley 1989, Davies and Brooke 1989).

An alternative explanation for the maintenance of the low levels of egg rejection is that it is an adaptation to intraspecific nest parasitism (see Briskie et al. 1992). Grackles are a colonial-breeding species and there exists ample opportunity for conspecific nest parasitism. However, recent studies have shown that despite the coloniality of many species of Icterines very little intraspecific parasitism occurs within this group (Harms et al. 1991, Lyon et al. 1992, Rothstein in press). In this study, we recorded two cases of intraspecific parasitism (see Chapter III), and only two other cases have been documented in Common Grackles (H. Howe unpubl. data cited in Rohwer and Freeman 1989, S. Sealy, unpubl. data). Therefore, it seems unlikely that rejection behavior in grackles is maintained as a response to intraspecific parasitism.

Egg size, incubation, and nestling survival - Ortega and Cruz (1991) found that Yellow-headed Blackbirds effectively incubated cowbird eggs despite the larger size of Yellow-head eggs (26.33 ± 1.16 x 18.1 ± 0.57 mm vs. 20.9 ± 1.06 x 16.3 ± 0.62 mm). Our data suggest that the size and number of grackle eggs were correlated with the effectiveness of incubation. It may be necessary for a female cowbird to remove at least one grackle egg to ensure adequate incubation of her own eggs. If cowbirds did prefer larger hosts initially, then the explanation for the origin of egg removal by female cowbirds becomes clearer. Females that consistently parasitize larger hosts would benefit by removing a host egg both to increase incubation efficiency and decrease competition from the host's larger nestlings. Indeed, cowbirds almost always remove an egg from Red-winged Blackbird nests (Blankespoor et al. 1982, Roskaft et al. 1990), whereas they remove only one egg in every two to three nests in the smaller Yellow Warbler (Dendroica petechia) (Clark

Bronzed Cowbirds preferentially parasitize larger species, however effective incubation and reduced nestling competition are more likely for these cowbirds because tropical species tend to have smaller clutch sizes than temperate species (Ricklefs 1980).

The high mortality rate of cowbird nestlings in the nests of grackles is likely the result of both size asymmetry and some unknown behavioral incompatibility. Cowbirds nestlings typically gain an advantage over their nestmates by hatching earlier. The average cowbird incubation period is 11-12 days (Rothstein 1975a), whereas the grackle's is 13.2 days (Maxwell and Putnam 1972). Thus, cowbirds would require a three-day "head start" to equal the size of the average, recently-hatched grackle nestling. If a cowbird does not hatch considerably earlier than its grackle nestmates it probably has little chance of survival, since grackles selectively starve their smallest nestlings (i.e. brood reduction) (Howe 1976, 1978) and the cowbird nestling would inevitably be the smallest.

A behavioral incompatibility may help explain why cowbirds fail to fledge from grackle nests. This is unusual since grackles and cowbirds are closely related species, and grackles are similar to other passerines in that they primarily feed their nestlings insects (Hamilton 1951, Bent 1958). Cowbird nestlings averaged a 33.0 % weight gain between days one and two, so they were receiving some nourishment. However, what exactly the problem is remains to be seen and provides an opportunity for further investigation.

CONCLUSIONS

There appears to be many factors involved in the lack of parasitism of Common Grackles. The asynchrony of the two species' breeding seasons creates relatively few opportunities for parasitism. Those nests that are available are well protected by grackles and may not be worth the risk of injury when other, less formidable hosts are available to cowbirds. If a female cowbird successfully parasitizes a grackle nest her egg will be accepted in most cases. However, for her nestling to survive the conditions have to be perfect and even this may not be good enough. The clutch size may have to be smaller than normal and the nestling would probably need to hatch at least two days earlier to compete with the larger grackle nestlings. It is now clearer why very few cases of parasitism of the Common Grackle occur and why there are no records of grackles successfully raising cowbirds.

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TABLE 1. Results of artificial cowbird parasitism of Common Grackle nests. One artificial cowbird egg was placed in each nest. If grackle eggs were present one was removed when the artificial egg was added.

OVERALL REJECTION RATE	32/188	nests	17.0 %	
SOLITARY REJECTIONS	15/55	nests	27.3 %	*
COLONY REJECTIONS	17/133	nests	12.8 %	
MODEL REJECTIONS	13/95	nests	13.7 %	
NO MODEL REJECTIONS	19/93	nests	20.4 %	
PRELAY REJECTIONS	13/34	nests	38.2 %	+
LAY REJECTIONS	11/84	nests	13.1 %	
INCUBATION REJECTIONS	8/70	nests	11.4 %	
FIRST CLUTCH REJECTIONS	24/154	nests	15.6 %	
SECOND CLUTCH REJECTIONS	8/34	nests	23.5 %	

* Difference between solitary and colony rejections was significant ($x^2 = 5.70$, df = 1, $P < 0.05$).

\+ Differences between prelay rejections and rejections later in the nesting cycle were significant ($x^2 = 13.91$, df = 1, $P < 0.001$).

Table 2. Method of parasitic egg rejection by Common Grackles.

Method	#		%
Ejection	19	=	59.4 %
Peck	4	=	12.5 %
Bury	2	=	6.2 %
Abandon	7	=	21.9 %

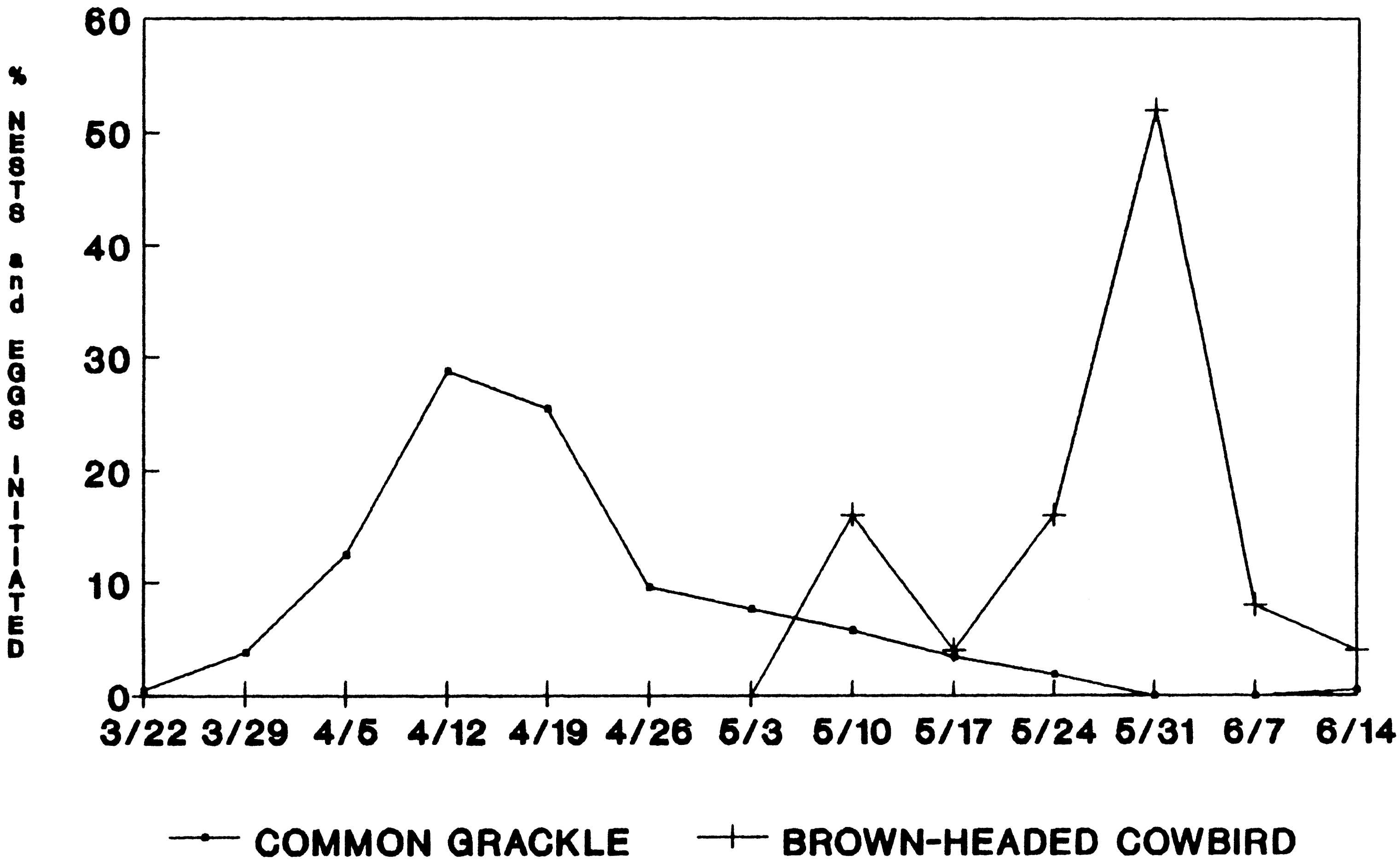

Figure 1. Percentages of nests initiated by Common Grackles and eggs laid by Brown-headed Cowbirds in Coles County, Illinois for the 1992 breeding season.

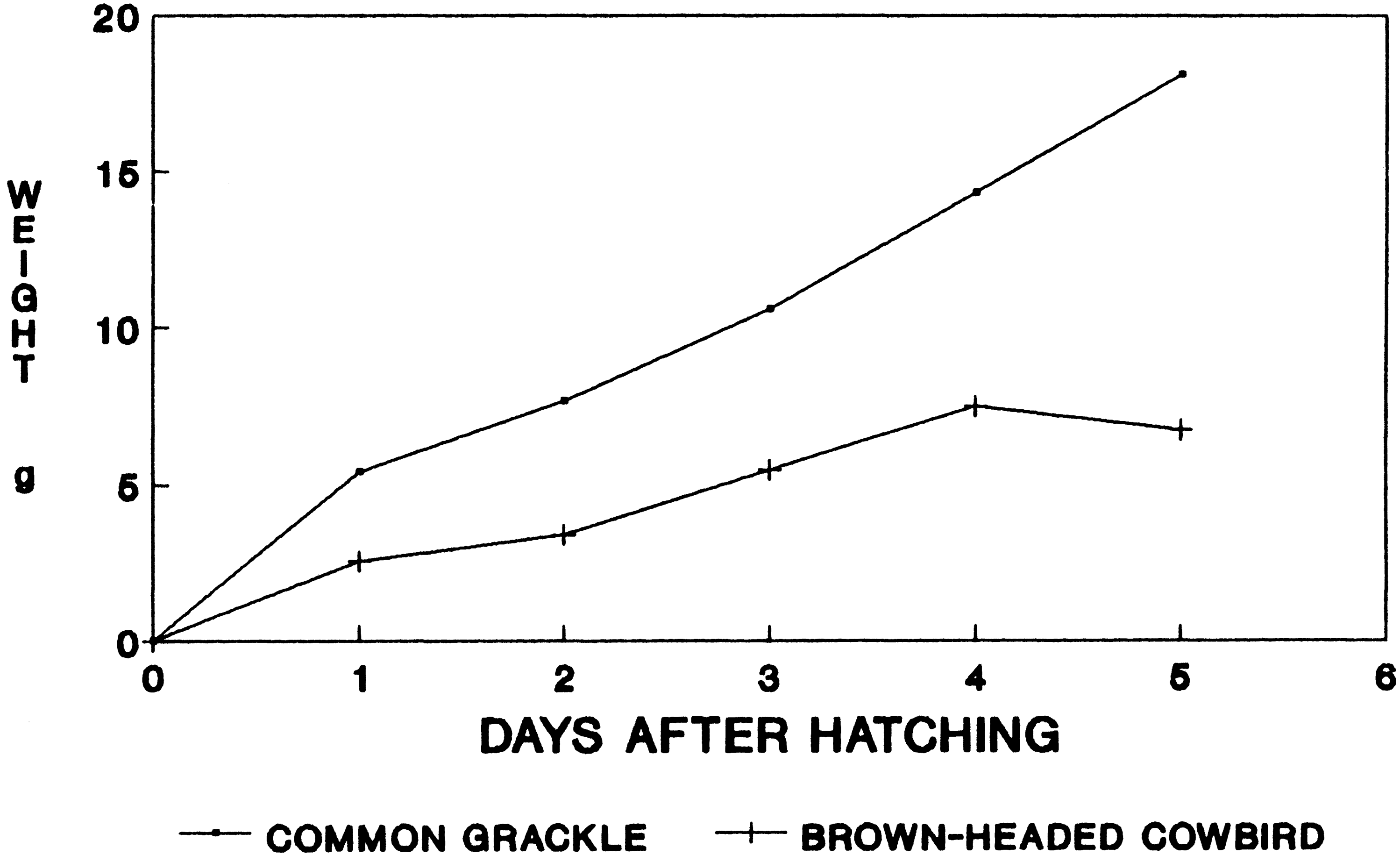

Figure 2. Relationship between age and weight (g) for nestling Common Grackles and Brown-headed Cowbirds.

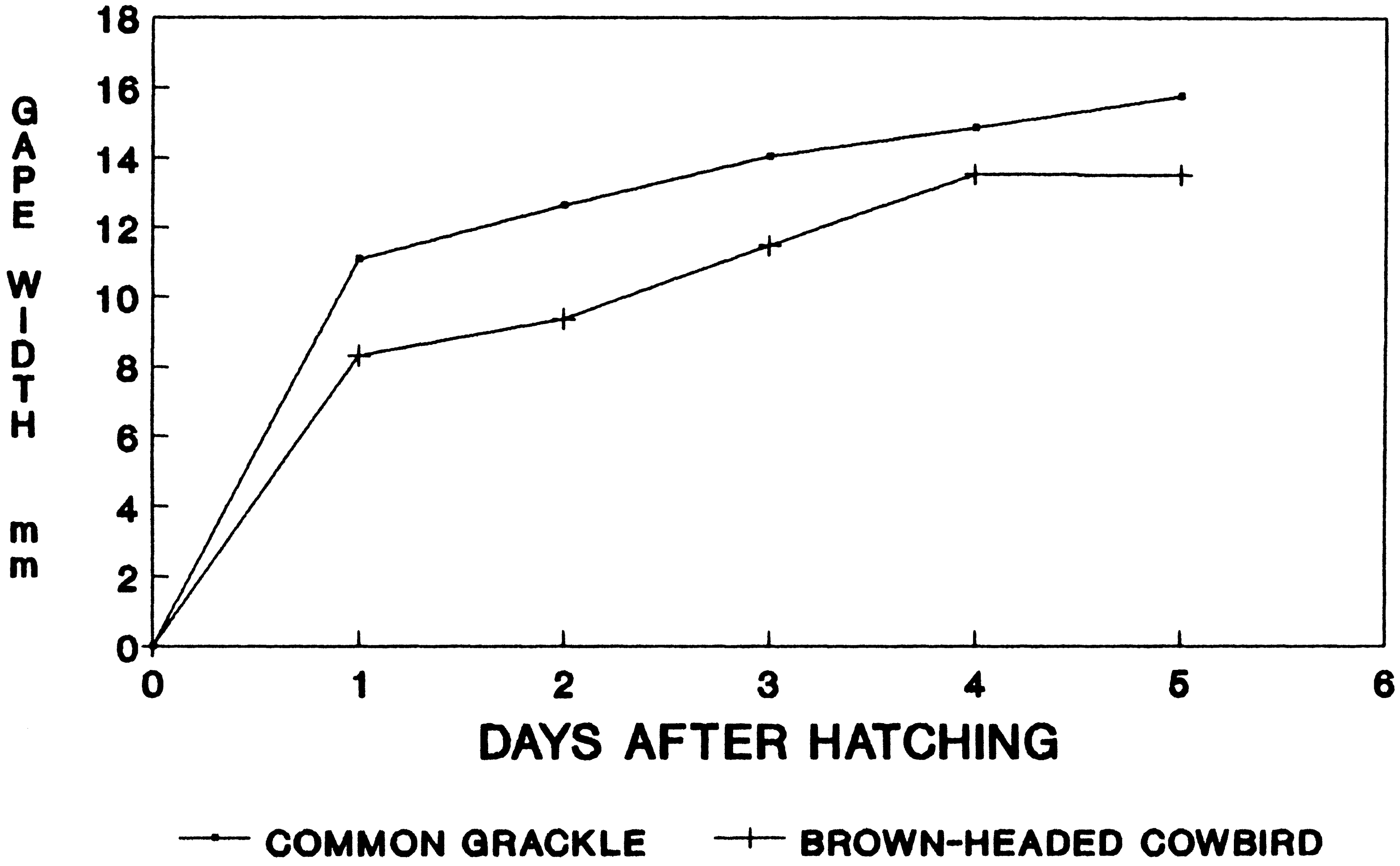

Figure 3. Relationship between age and gape width (mm) for nestling Common Grackles and Brown-headed Cowbirds.

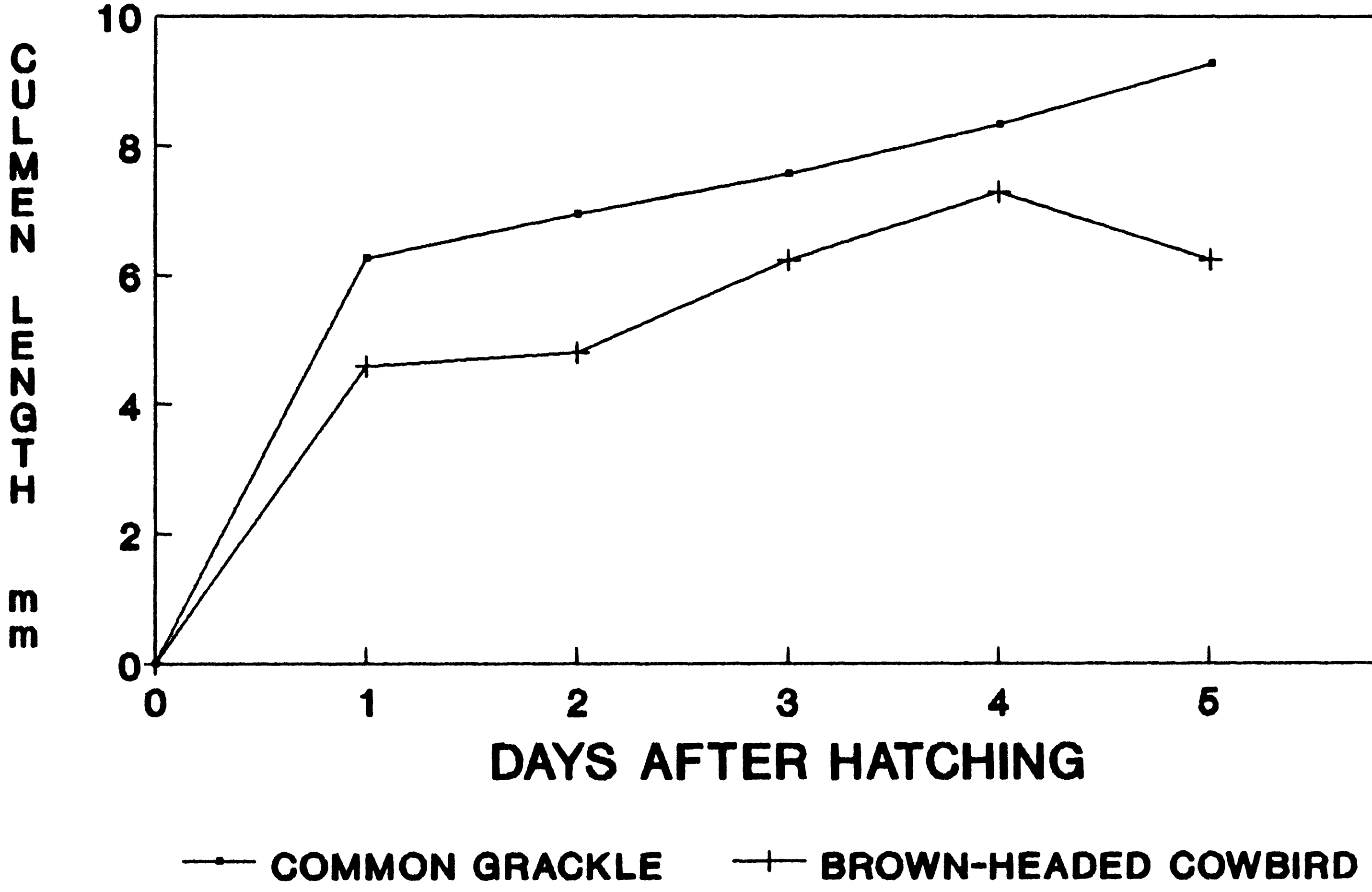

Figure 4. Relationship between age and culmen length (mm) for nestling Common Grackles and Brown-headed Cowbirds.

CHAPTER II: EVIDENCE OF GEOGRAPHIC VARIATION IN THE PARASITIC EGG REJECTION BEHAVIOR OF THE MOURNING DOVE (ZENAIDA MACROURA).

INTRODUCTION

The Brown-headed Cowbird (Molothrus ater) is the only obligate brood parasite widespread throughout North America. This species is known to have parasitized over 220 species of birds (Friedmann and Kiff 1985). The Mourning Dove (Zenaida macroura) is an infrequent host of the Brown-headed Cowbird, having been documented as being parasitized only eight times (Friedmann 1971, Friedmann et al. 1977). Rothstein (1975a) classified the Mourning Dove as a species that accepts parasitic eggs but is rarely parasitized, yet he documented a high rate of rejection (31.2 %) for an "accepter" species.

Rothstein conducted his studies throughout the United States and Canada and found no evidence of geographic variation in rejection behavior. The objectives of this study were twofold: (1) to determine if there had been a change in the parasitic egg rejection frequency by Mourning Doves since Rothstein's (1975a) original study conducted nearly 25 years ago, and (2) to determine if Mourning Doves exhibit geographic variation in parasitic egg rejection behavior.

METHODS

This study was conducted in Coles County, Illinois, from 23 March to 4 July 1992. Most of the data were collected at four sites, including two cemeteries, a Christmas tree farm, and a nature preserve. The majority of the nests were located in Northern White-Cedars (*Thuja occidentalis*), Scotch Pine (*Pinus sylvestris*), and Eastern Redcedars (*Juniperus virginiana*). At each Mourning Dove nest a single egg was removed and replaced with an artificial cowbird egg. Artificial cowbird eggs were made of wood and painted with waterbased acrylic paints and coated with a clear acrylic sealer. Their dimensions were 21.91 x 16.67 mm and they weighed 2.5 g. Real cowbird eggs average 21.45 x 16.42 mm (Bent 1958) and weigh 3.17 g. (Ankney and Johnson 1985).

I also replaced Mourning Dove eggs with artificial Mourning Dove eggs, made in the same manner as the artificial cowbird eggs, to serve as controls. These eggs averaged 30.2 mm x 21.9 mm, whereas real Mourning Dove eggs had dimensions of 28.1 x 21.1 mm (n = 18).

Nests were checked approximately every other day for signs of rejection. Eggs were considered rejected if they were pecked, absent from the nest (ejection), or if the nest was abandoned within five days (Rothstein 1975a).

RESULTS

There were a total of 34 rejections in 58 nests (58.6 %), nearly double the rejection rate recorded by Rothstein (5 of 16 nests, 31.2 %, $x^2 = 3.7$, df = 1, $P < 0.06$). Rothstein recorded one rejection in six nests in Connecticut, three rejections in seven nests in Michigan, and one rejection in three nests in Nebraska. A comparison of my data and that from Connecticut suggest that there is geographic variation in this behavior (Fisher's Exact Test, $P = 0.055$).

The most frequent method of rejection was abandonment (16 of 34 rejections). However, there were three cases of the parasitic egg being pecked (in addition to one case in which the parasitic egg was pecked and the nest was abandoned) and eight cases of the egg being ejected (in addition to six cases where the egg was ejected and the nest was also abandoned). There was also one case in which the egg was pecked, ejected, and abandoned. Rothstein (1975a) recorded no cases of egg pecking, one ejection, and four abandonments.

In this study, Mourning Doves were significantly more likely to reject the parasitic egg in one egg clutches (i.e., after egg replacement there remained only the artificial cowbird egg) compared to two egg clutches (15 rejections in 17 nests, $x^2 = 8.58$, df = 1, $P < 0.01$). Whereas in clutches of more than one, egg rejections and acceptances were nearly equal (22 acceptances vs. 19 rejections). All of the control eggs were accepted ($n = 11$).

DISCUSSION

Contrary to Rothstein's earlier conclusion (1975a), there appears to exist geographic variation in egg rejection behavior. Rothstein's lack of evidence for geographic variation may have been the result of small sample sizes (seven from Michigan, six from Connecticut, and three from Nebraska). The increased rejection frequency documented here is likely due to geographic variation and not the result of recent selection pressure, since Mourning Doves experience virtually no parasitism, and rejection has no adaptive value in a species unless it is parasitized (Rothstein 1975b, 1983). Geographic variation may be the result of a longer period of sympatry between cowbirds and

Mourning Doves in Illinois, compared to that experienced by doves in Connecticut. Brown-headed Cowbirds were originally restricted to the open areas of the Great Plains and progressed eastward as the forests were cleared (Mayfield 1965). Therefore, the doves in the central portion of North America would have experienced more cowbird parasitism than those in eastern North America, and the doves with the longer history of sympatry (e.g. those in Illinois) would be more likely to express rejection behavior.

Thus, Mourning Doves may have been parasitized earlier in their evolutionary history, similar to what has been proposed for Common Grackles (*Quiscalus quiscula*) (see Chapter 1). All of the North American species that reject cowbird eggs are larger than the cowbird (with the exception of the Cedar Waxwing, *Bombycilla cedrorum*, which is approximately the same size as the cowbird). Cowbirds may have resorted to parasitizing smaller species after the frequently parasitized larger species began rejecting parasitic eggs (Mason 1980). If this is true, Mourning Doves may have also been parasitized due to their large size and sympatry with cowbirds. Egg removal by female cowbirds would have a significant impact on the reproductive success of Mourning Doves due to their small clutch size of two eggs (Cowan 1952, Westmoreland et al.

1986). This might explain the relatively high rate of rejections that still exists in Mourning Doves.

Eventually, cowbirds would stop parasitizing the doves due to their inability to successfully raise cowbirds (see Friedmann 1963), as parasitism of poor hosts would be selected against (Finch 1982). The feeding process in Mourning Doves is reversed from the typical passerine system in which the adult forces food into the throat of the nestling. The nestling Mourning Dove forces its mouth into the throat of the adult to initiate feeding (Friedmann 1963). Furthermore, it is unlikely that a cowbird could survive on a diet of crop milk and seeds (see Middleton 1977).

It could be argued that Mourning Doves are responding to partial clutch reduction or PCR (Rothstein 1982, 1986), rather than cowbird parasitism per se. This may be particularly true in the case of single egg clutches because the exchange of an artificial cowbird egg for a Mourning Dove egg represents a substantial decrease in total egg volume. However, removal of an egg by a female cowbird represents the equivalent of PCR. Furthermore, the total number of "true" egg rejections (i.e. ejections and pecking) by doves was greater than abandonments. Nest abandonment is considered the typical response to

PCR (Rothstein 1982, 1986). Pecking of an egg is not likely a response to PCR, because there is no need to destroy the eggs as there would be in the case of parasitism. When a clutch is reduced beyond a certain point it will become beneficial to renest with a new clutch, but it is not necessary to also destroy a reduced clutch.

Although seven rejections also involved abandonment, this was likely a result of the compartmentalization of animal behavior (see Rothstein 1982). After a parasitic egg was rejected the clutch size became reduced enough to initiate desertion.

Considering the frequency of true egg rejections displayed by Mourning Doves suggests that there is evidence of egg recognition in Mourning Doves. However, further manipulations are required to be absolutely certain.

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CHAPTER III: INTRASPECIFIC NEST PARASITISM IN THE COMMON GRACKLE (QUISCALUS QUISCULA)

Intraspecific nest parasitism is considered to be a rare reproductive phenomenon having been documented in $\leq 2\%$ of all avian species (Yom-Tov 1980, MacWhirter 1989, Rohwer and Freeman 1989). Hamilton and Orians (1965) suggested that intraspecific parasitism may have originated in species that experienced frequent nest loss. A gravid female that lost her nest during the laying cycle would benefit from laying her eggs in the nest of a nearby conspecific. This would be especially convenient in colonial-nesting species. Eventually the species might begin laying eggs in the nests of other species, hence the development of interspecific parasitism. Recent studies with Icterines have documented little evidence of intraspecific parasitism as a result of nest loss despite the colonial-nesting habits of several species (Harms et al. 1991, Lyon et al. 1992, Rothstein, in press). Here I report two cases of intraspecific parasitism in the colonial-nesting Common Grackle (Quiscalus quiscula) that were likely induced by nest abandonment following artificial nest parasitism.

From 23 March to 4 July, I monitored 208 grackle nests at 10 sites located throughout Coles County, Illinois. This was part of a study of the response of grackles to experimental Brown-headed Cowbird (Molothrus ater) parasitism. At each nest a single grackle egg was removed and replaced with either an artificial or real cowbird egg. I recorded two instances of an additional egg being added to the nest following the onset of incubation. This is a reliable indicator of intraspecific parasitism because there is a regression in the size of the ovary and associated reproductive organs following clutch completion (Bullough 1942, Hutchison et al. 1968, Lewis 1975). Intraspecific nest parasitism in Common Grackles has been documented only once previously (H. Howe unpubl. data, cited in Rohwer and Freeman 1989), and it also occurred after incubation had begun. However, it is not known whether or not this case was a result of nest disturbance.

The first instance occurred at a cemetery, in a nest located in a Northern White-Cedar (Thuja occidentalis). The first egg was laid on 12 April and replaced on the same day with an artificial cowbird egg. Laying stopped after the fifth egg was laid on 16 April (the nest contained four grackle eggs and one artificial cowbird egg). The nest was checked on 18

April and there was no change. On 26 April the nest contained five grackle eggs and the single artificial cowbird egg. The parasitic egg could have come from a female grackle who had abandoned her nest on 23 April in response to artificial parasitism. Her nest was only 6 m away from the parasitized nest, and she was in the middle of the laying cycle. Grackles do not exhibit aggression toward conspecifics, and I often witnessed grackles visiting the nests of conspecifics without consequence.

The second instance occurred in a nest found in a small roadside stand of hawthorns (Crataegus sp.). On 5 June I replaced one of three grackle eggs in the nest with a real cowbird egg, and on the next day the nest had been abandoned. On 6 June I located a second grackle nest approximately 1.5 m from the first nest, in which four grackle eggs were being incubated. I replaced one grackle egg with a real cowbird egg, resulting in three grackle eggs and one cowbird egg. The nest contents were the same on 7 June, but on 8 June an additional egg was present, bringing the total to four grackle eggs and one cowbird egg. Two grackle nestlings were present on 18 June and a third had hatched by 19 June. Neither the fourth grackle egg nor the cowbird egg hatched. The grackle egg that did not hatch was probably the parasitic egg, but the eggs were not marked. The earliest likely hatching date for the parasitic egg would have been 21 June as the average incubation period for the Common Grackle is 13.2 days (Maxwell and Putnam 1972).

The extra egg in this case could have come from the female that had abandoned her nest on 6 June. Like the first suspected parasitic female, she was in the laying stage, and the nests were in very close proximity to each other (1.5 m). Thus, it is reasonable to conclude that both instances of intraspecific parasitism were by females that had abandoned their own nests as a result of my artificial parasitism.

There is convincing evidence that nest loss is correlated with intraspecific nest parasitism in two species, the White-fronted Bee-Eater (<u>Merops bullockoides</u>) (Emlen and Wrege 1986), and the European Starling (<u>Sturnus vulgaris</u>) (Feare 1991, Stouffer and Power 1991). Very low levels of nest loss associated with intraspecific nest parasitism have been documented in Brewer's Blackbirds (<u>Euphagus cyanocephalus</u>) (Harms et al. 1991), Red-winged Blackbirds (<u>Agelaius phoeniceus</u>) (Harms et al. 1991, Rothstein in press), and Yellow-headed Blackbirds (<u>Xanthocephalus xanthocephalus</u>) (Harms et al. 1991, Lyon et al. 1992).

Overall, nest loss is a common occurrence in passerines (Ricklefs 1969, Clark and Wilson 1981), yet, intraspecific parasitism appears to be relatively rare (MacWhirter 1989). However, it can not be concluded that the Hamilton-Orians hypothesis is incorrect because interspecific parasitism is also rare. Interspecific parasitism may have originated with a single unique individual (Rothstein in press), and since there is evidence that nest loss is sometimes associated with intraspecific parasitism the hypothesis may very well be accurate.

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