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Rejection of Cowbird Eggs by Mourning Doves: A Manifestation of Nest Usurpation?

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Three conditions are known to select for rejection of foreign eggs by birds: (1) nesting in dense colonies in which individuals risk confusing their eggs with

those of nearby conspecifics (Tschanz 1959); (2) conspecific brood parasitism (Jackson 1990); and, most frequently, (3) interspecific brood parasitism (Rothstein 1975b, 1990). The Mourning Dove (*Zenaidura macroura*) is an inappropriate host for parasitic Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbird"), and as a consequence, it is rarely parasitized (<10 records; Friedmann 1971, Friedmann et al.

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1977). The reason for this is that the nestling Mourning Dove initiates feeding by forcing its mouth into the throat of the adult (Friedmann 1963). This is the reverse of the typical passerine method in which the adult forces food into the throat of the nestling. It is unlikely that the cowbird could adapt to this mode of feeding and even more unlikely that they could survive on a diet of crop milk and seeds (see Middleton 1991). Mourning Doves also do not nest in colonies, and conspecific brood parasitism is rare (Weeks 1980, Mirarchi and Baskett 1994).

Despite this, Rothstein (1975b) found that Mourning Doves rejected 31.2% of cowbird eggs from experimentally parasitized nests. It is possible that these doves simply responded to partial clutch reduction, because Rothstein (1975b) replaced the dove eggs with smaller artificial cowbird eggs. Birds often desert their nests after some eggs have been lost, which decreases the overall clutch volume below some critical threshold. The replacement of a Mourning Dove egg with a smaller cowbird egg would reduce the clutch volume such that Mourning Doves may have responded to the reduced volume rather than to the presence of the cowbird egg per se (see Rothstein 1982, 1986; Hill and Sealy 1994). The objective of our study was to further test the egg-rejection ability of Mourning Doves in an attempt to determine the selective pressures responsible for this behavior.

Methods.—We conducted the study in Coles County, Illinois, from late March through mid-June in 1992 and 1993. Nests were located in eastern redcedars (*Juniperus virginiana*), northern white cedars (*Thuja occidentalis*), and Scotch pines (*Pinus sylvestris*). Each dove nest was subjected to one of four treatments.

In treatment I, we followed the protocol of Rothstein (1975b) and attempted to simulate cowbird parasitism by replacing a single Mourning Dove egg with an artificial cowbird egg in clutches of one or two dove eggs. Artificial cowbird eggs were made of wood, painted with water-based acrylic paints (i.e. white background with brown and gray spots), and coated with a clear acrylic sealer. Artificial eggs measured 23.9×16.7 mm and weighed 2.5 g (see Peer and Bollinger 1997b); real cowbird eggs average 21.4×16.4 mm (Bent 1958) and weigh 3.2 g (Ankney and Johnson 1985).

In treatment II, a single Mourning Dove egg was switched with an artificial Mourning Dove egg (from clutches of one or two eggs) that was constructed in the same fashion as the artificial cowbird eggs except that it was white and immaculate. These eggs measured 30.2×21.9 mm, whereas real Mourning Dove eggs averaged 28.1×21.1 mm ($n = 18$). This treatment served as a control to determine whether doves responded to artificial cowbird eggs because they were "parasitic," or simply because they were artificial (see Rothstein 1975b). This treatment also test-

ed whether Mourning Doves can recognize and reject conspecific eggs.

Treatment III tested whether doves deserted their nests in response to the presence of the parasitic eggs rather than to the reduction in clutch volume that occurred in treatment I after a larger Mourning Dove egg was replaced by the smaller artificial cowbird egg (see Rothstein 1982, 1986). A single dove egg was replaced with an oversized artificial cowbird egg (from clutches of one or two eggs). These were the same eggs used for treatment II, except they were painted to mimic cowbird eggs (i.e. brown and gray spots were painted on the white eggs). Treatment IV was a control that further allowed us to ascertain if Mourning Doves deserted their nests in response to partial clutch reduction. We experimentally created partial clutch reduction by removing single Mourning Dove eggs from two-egg clutches.

All manipulations were conducted during laying or early incubation. However, most were conducted during incubation because Mourning Doves usually lay only two eggs per clutch (Mirarchi and Baskett 1994), which made finding nests during laying difficult. The stage at which a nest is parasitized has no effect on the response of most rejecter species (Rothstein 1975b, Sealy 1996; but see Rothstein 1976) as long as the eggs are added after the host has begun laying (Peer and Bollinger 1997b).

We checked nests every one to three days for evidence of rejection. Eggs were considered rejected if they were absent from the nest (ejection), pecked, the nest was deserted within five days (Rothstein 1975b, Peer and Bollinger 1997b), or some combination of these responses. Eggs pecked by doves had relatively shallow indentations. Although we did not witness doves pecking cowbird eggs, we are confident that this damage was indeed caused by the doves. Eggs damaged by mammalian predators were severely damaged with deep indentations and marks consistent with chewing. Common Grackles (*Quiscalus quiscula*), which are egg predators (Peer and Bollinger 1997a), were abundant at our study sites. However, grackles have much stouter bills than doves, and artificial cowbird eggs pecked by grackles in other experiments had much deeper indentations (Peer and Bollinger 1997b). Moreover, only cowbird eggs received these shallow indentations. None of the control eggs was damaged in this manner (see below). Nests were considered deserted if the eggs were cold and the adults were absent on at least two consecutive visits. We considered eggs accepted if they remained in a nest attended by adults for at least five days (Rothstein 1975b, Peer and Bollinger 1997b).

Results.—We found no evidence of cowbird parasitism on Mourning Doves ($n = 102$ nests; Peer and Bollinger 1997b). One nest that contained three dove eggs was eliminated from analysis because it was probably parasitized by a conspecific (see Weeks

TABLE 1. Response of Mourning Doves to experimental egg replacement and removal, and method of rejection of experimental eggs.

| | Treatment ^a | | | |
|----------------------------|------------------------|----|-----|----|
| | I | II | III | IV |
| Response | | | | |
| Accepted | 34 | 14 | 3 | 3 |
| Rejected | 39 | 0 | 6 | 3 |
| Method of rejection | | | | |
| Desertion | 18 | — | 3 | 3 |
| Ejection | 8 | — | — | — |
| Ejection/desertion | 8 | — | — | — |
| Pecked | 2 | — | 1 | — |
| Pecked/ejection | — | — | 2 | — |
| Pecked/ejection/desertion | 2 | — | — | — |
| Pecked/desertion | 1 | — | — | — |

^aI: One dove egg replaced with artificial cowbird egg from clutches of one or two dove eggs. II: One dove egg replaced with artificial dove egg from clutches of one or two dove eggs. III: One dove egg replaced with oversized cowbird egg from clutches of one or two dove eggs. IV: One dove egg removed from clutches of two dove eggs.

1980). In treatment I, there were 39 rejections from 73 nests (53.4%; Table 1). This frequency of rejection was not significantly different from that recorded by Rothstein (1975b; 5 of 16 nests; $\chi^2 = 2.58$, $df = 1$, $P > 0.05$). Twenty-one of the rejections involved ejection or pecking of the cowbird egg (53.8%); 11 of these 21 rejections also involved nest desertion (Table 1).

Mourning Doves rejected cowbird eggs more frequently from one-egg clutches (i.e. after egg replacement only the artificial cowbird egg remained; 18 rejections in 20 nests) than from two-egg clutches (21 rejections in 53 nests; $\chi^2 = 14.81$, $df = 1$, $P < 0.001$). Eight rejections from one-egg clutches and 10 from two-egg clutches were by desertion. All of the control artificial dove eggs in treatment II were accepted (Table 1). In treatment III, oversized cowbird eggs were rejected in six of nine nests (66.7%; Table 1). This rejection frequency was significantly higher than that recorded for the artificial Mourning Dove eggs (Fisher exact test, $P = 0.0008$) but was not significantly different from that for the normal-sized cowbird eggs in treatment I (Fisher exact test, $P = 0.50$). Mourning Doves responded to experimental partial clutch reduction in treatment IV by deserting three of six nests (50%; Table 1).

Discussion.—Ejection and pecking of parasitic eggs occur in direct response to the eggs and are considered to be true rejections (Rothstein 1975b, Peer and Bollinger 1997b). Desertion of parasitized nests is a more nebulous response because birds may desert a nest for a variety of reasons (Rothstein 1975b, Hill and Sealy 1994). Most rejections by Mourning Doves in treatment I involved either ejection or pecking of

the artificial cowbird egg (53.8%). Although 11 of these rejections also involved desertion of the nests, this was likely a result of the compartmentalization of animal behavior (Rothstein 1982, Hill and Sealy 1994). After the parasitic egg was ejected, the clutch size may have become reduced enough to promote desertion. Doves also rejected 67% of the oversized cowbird eggs, and half of these rejections were accomplished through pecking and/or ejection. All of the artificial dove eggs were accepted, indicating that doves did not respond to the artificiality of the eggs. Therefore, our results demonstrate that some Mourning Doves recognize cowbird eggs for being different from their own eggs and reject them.

Mourning Doves deserted their nests in half of the trials in which we experimentally created partial clutch reduction. The removal of one dove egg reduced clutch volume by 50%, apparently reducing the volume below some critical level that caused doves to desert. Because our experiments were conducted in the first half of the nesting season (see Mirarchi and Baskett 1994), the probability of desertion could have been slightly higher given that there was ample time to renest. However, given the Mourning Dove's proclivity for multiple brooding (Mirarchi and Baskett 1994), it is unlikely that this significantly affected our results.

That Mourning Doves also responded to a reduction in clutch volume in treatment I after the larger dove eggs were replaced by smaller cowbird eggs (see Holcomb 1970, Rothstein 1982, 1986) seems doubtful. The typical response to partial clutch reduction is nest desertion (Rothstein 1982, 1986; Hill and Sealy 1994) and, as mentioned, at least half of the rejections in treatments I and III were by ejection or pecking. These behaviors do not occur in response to partial clutch reduction. Moreover, doves rejected more of the oversized cowbird eggs from treatment III than the normal-sized cowbird eggs in treatment I (66.7 vs. 53.4%, respectively), suggesting that the reduction in clutch volume in treatment I was not a factor.

In addition to Rothstein (1975b), others have directly or indirectly tested the egg-recognition ability of Mourning Doves. McClure (1945) recorded no rejection of Mourning Dove eggs from nine nests in which the eggs were dyed different colors or painted with stripes, whereas Westmoreland and Best (1986) found 20% of nests were deserted in which Mourning Dove eggs were "spattered" with brown paint. Others (Holcomb 1968, McNicholl 1968, Rothstein 1970) have also recorded ejections of parasitic eggs from Mourning Dove nests. However, each researcher suggested that the eggs were not ejected by the doves, but instead were knocked out of the frail platform nest following the rapid departure of the birds. Indeed, we witnessed such an act. Thus, it is possible that some ejections we recorded were instances where eggs were accidentally knocked out of the

nest. However, this cannot account for eggs that were pecked (13% in treatment I, 50% in treatment III). Furthermore, none of our control eggs was accidentally knocked out of the nest.

Our results are supported by Nice's (1922) observation of an American Robin (*Turdus migratorius*) nest (containing one robin egg) that was taken over by a Mourning Dove. The dove laid two eggs in the nest, and the robin's egg was later found on the ground below. Nice noted that the robin egg could not have fallen from the nest, presumably because of the deep nest cup, and must have been removed by the Mourning Dove. Nice's (1922) study also provides a possible explanation for rejection behavior in Mourning Doves, namely nest usurpation. Fifteen percent of the Mourning Dove nests studied by Nice ($n = 246$) were located in the nests of other species. After a dove takes over an active nest, it sometimes removes the eggs of the original nest owner, but apparently not until it has laid its own eggs (see Nice 1922). This produces a mixed clutch of eggs, a situation analogous to brood parasitism. Doves could avoid misdirecting parental care toward young of the original nest owner by rejecting foreign eggs.

Similar to Nice's (1922) findings, Harris et al. (1963) found that 22.8% of Mourning Dove nests ($n = 272$) were located in nests of American Robins and Common Grackles (see also Snyder 1923, Roads 1931, Holcomb 1967, Weeks 1980, Mirarchi and Bassett 1994). However, no study has quantified how often active nests are successfully usurped. It is likely that some of these "old" nests actually were active nests that were usurped by doves (see below). Moreover, with the exception of Nice (1922), the only reported cases have been mixed clutches in which doves did not reject the eggs of the owner species (see Nice 1922, Holcomb 1967, Skutch 1976). Oftentimes, usurpation and rejection of a former nest owner's eggs probably go undetected because the eggs may be ejected by the dove before the nests are observed. This is similar to the underestimation of cowbird parasitism rates in rejecter species in cases where the parasite's eggs are rejected before nests are visited by researchers (Scott 1977).

Single Mourning Dove eggs have been found in nests of other species numerous times (Holcomb 1967, Weeks 1980, Peer unpubl. data). Rather than being cases of "parasitism" (e.g. Weeks 1980), these may have been failed attempts at nest usurpation. For example, Holcomb (1967) reported two cases of doves laying eggs in and tending nests of other species, only to find the doves replaced by the original nest owners on subsequent visits (see also Neff 1945). In two cases, doves have shared nests with the original nest owner (Skutch 1976). Thus, this aspect of dove behavior appears to have been underappreciated and deserves further study.

If nest usurpation is the selective pressure responsible for egg rejection in Mourning Doves, then other

usurper species should exhibit this behavior. To our knowledge, information exists on the rejection behavior of only four facultative or obligate nest usurpers: Troupials (*Icterus icterus*), European Starlings (*Sturnus vulgaris*), Bay-winged Cowbirds (*Molothrus badius*), and House Wrens (*Troglodytes aedon*; Hudson 1920, Pribil and Picman 1991, Lindell 1996). Three of these species appear to accept parasitic eggs (Cruz et al. 1985, Mason 1986, Pribil and Picman 1997). Starlings remove the eggs of conspecifics prior to laying their own eggs (Stouffer et al. 1987, Pinxten et al. 1991); however, they are parasitized by conspecifics (Yom-Tov et al. 1974), which complicates the relationship between nest usurpation and egg rejection.

Acceptance of parasitic eggs by these nest usurpers is expected, however, because they remove foreign eggs or nestlings immediately after taking over a nest rather than waiting until they have laid their own eggs (Hudson 1920; Skutch 1960, 1996; Robinson 1985; Pribil and Picman 1991). Nest usurpers that immediately remove foreign eggs presumably should not exhibit rejection behavior because they are not exposed to a mixed-clutch situation unless they are also parasitized by a brood parasite. Immediate removal of foreign eggs seems to be the optimal behavior, because usurpers that wait to reject foreign eggs risk ejecting their own eggs by mistake. These examples cannot explain the relationship between nest usurpation and egg rejection in other species. To confirm this relationship, nest usurpers that wait to remove eggs until after they have laid their own, and those that are not exposed to the other three circumstances that select for rejection, need to be tested for rejection behavior.

Because of the extreme unsuitability of doves as hosts, egg rejection by Mourning Doves has not resulted from cowbird parasitism. Unsuitable hosts are usually avoided by parasites (Friedmann et al. 1977, Friedmann and Kiff 1985; but see Rothstein 1976, Kozlovic et al. 1996), which is evident given the few cases of parasitism that have been recorded for Mourning Doves (Friedmann 1971, Friedmann et al. 1977). Presumably, rejection behavior can evolve only if parasitism is costly to the host's reproductive success (Rothstein 1975a, b). Cowbird nestlings cannot survive on the food normally given to nestling Mourning Doves. Also, the addition of a cowbird egg should not decrease the incubation efficiency of dove eggs because the smaller cowbird egg would be negatively affected rather than the larger dove eggs (see Peer and Bollinger 1997b, 1999). The most significant potential cost to a Mourning Dove would be egg removal by the cowbird, which would decrease the dove's reproductive success by 50% in a typical nesting attempt. Egg rejection, however, would not eliminate the costs of egg removal.

Less frequently, conspecific brood parasitism may select for egg rejection (Jackson 1990). Mourning Doves occasionally dump their eggs in the nests of

conspecifics (Weeks 1980, this study). However, it does not appear that egg rejection is a response to conspecific egg dumping because the Mourning Doves that we studied did not reject artificial dove eggs. Recognition of conspecific eggs probably is difficult because dove eggs are immaculate. The only other known selective pressure favoring rejection behavior is dense colonial nesting (Tschanz 1959, Frederickson and Weller 1972, Schaffner 1990). Because Mourning Doves are solitary nesters, coloniality cannot account for egg rejection. Nest usurpation appears to be the most reasonable explanation for egg rejection in Mourning Doves. Therefore, usurpation should be considered an additional selective pressure responsible for egg-rejection behavior.

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