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Brood Parasitism of Eastern Kingbirds by Brown-headed Cowbirds

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Understanding why brood parasites lay eggs in the nests of hosts that reject eggs is hampered by insufficient data on the frequency with which parasites lay in rejecter nests, and by ignorance of which individuals practice this seemingly inappropriate behavior. Parasitism rates of rejecters can be determined only when host nests are observed during egg laying because most parasite eggs are rejected rapidly (e.g. Scott 1977). Even then, however, a certain percentage of parasitized nests may go undetected. Determining the selective value of host defense mechanisms also depends on knowledge of the frequency of parasitism, and the amount of reproductive loss caused by parasitism when it occurs (Rothstein 1976a).

Experimental investigations of brood parasite relations between Brown-headed Cowbirds (Molothrus ater) and Eastern Kingbirds (Tyrannus tyrannus) have demonstrated unequivocally that kingbirds are rejecters of cowbird eggs (Rothstein 1975, 1976b). Existing

data suggest that kingbirds are rarely parasitized: the percentage of kingbird nests containing cowbird eggs ranges from 0% to 0.8% (Robertson and Norman 1976, Goertz 1977, Lowther 1977). Friedmann (1963) also reported Eastern Kingbirds to be infrequent cowbird hosts. My purpose is to present estimates of actual rates of brood parasitism on Eastern Kingbirds by Brown-headed Cowbirds, including annual variation in parasitism; to describe the consequences of, and responses to, naturally occurring cowbird parasitism on kingbirds; and to test whether female cowbirds select kingbird nests on the basis of host egg size. For the last objective, I assumed that cowbird nestlings are disadvantaged when competing for food with equal-aged nestling kingbirds because of their smaller size. Because egg and hatchling size are correlated positively in both species (Nolan and Thompson 1979, Murphy 1981), I predicted that one mechanism cowbirds may use to reduce the kingbirds' advantage is to lay large eggs in nests containing large kingbird eggs.

I studied kingbirds in Erie Co., western New York, in 1979 and in Douglas Co., eastern Kansas, in 1980-

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1983 (see Murphy 1983 for descriptions of the study sites and field methods). I attempted to locate kingbird nests before egg laying and then to monitor egg laying within nests on a daily basis. I weighed, measured, and numbered all eggs in a clutch, and therefore was able to document the appearance and disappearance of cowbird eggs and to examine kingbird eggs for evidence of cowbird damage (i.e. punctures; see below). Eggs were weighed to the nearest 0.1 g using a 50-g Pesola spring scale, and maximum egg length and breadth were measured to the nearest 0.05 mm with dial calipers. I used egg dimensions to determine whether cases of multiple parasitisms involved one or more females and to test whether cowbirds attempted to match host nests for egg size. Nestlings also were weighed and tarsi measured during nest visits (made daily in 1980, but every 2-3 days in other years). I can merely estimate the effects of my visits on kingbird nest success and on behavior toward parasites and their eggs. I suspect that my presence reduced nest success by attracting the attention of several abundant avian nest predators (Greattailed Grackle, Quiscalus mexicanus; American Crow, Corvus brachyrhynchos). On the other hand, I doubt that my visits influenced parasitism rates because cowbirds discover most host nests during nest building (Gochfeld 1979), and I purposely minimized nest visits prior to egg laying.

I calculated two estimates of the frequency of parasitism to determine if the stage at which nests were located influenced my estimated frequency of parasitism. The first was a conservative estimate and included only nests observed during egg laying (= the restricted sample). The second estimate included all nests that contained kingbird eggs, and included as a parasitized nest any nest with a cowbird egg or with small punctures in a kingbird egg (= the total sample). I assumed that two small, triangular punctures indicated an attempt by a cowbird to eject a host egg, and that parasitism had occurred at that nest. For both samples, I divided the number parasitized by the total number of nests to estimate the frequency of parasitism. Because my primary purpose was not the documentation of cowbird parasitism, I did not check nests at the normal time for cowbird egg laying (0500-0600, Scott 1977). Hence, the ratios are minimum estimates of the actual frequency of parasitism because cowbirds do not always leave evidence of their activity (i.e. a cowbird egg, or punctured or missing host eggs).

Cowbird eggs were found from 30 May to 22 June in 19 kingbird nests. In 79% of parasitized nests (15 of 19), only one cowbird egg was found in a nest. There were 3 cases of two eggs per nest, and 1 of three eggs per nest. I measured more than one cowbird egg in 2 of the 4 multiply parasitized nests. Assuming that individual females laid eggs of characteristic sizes and shapes (Walkinshaw 1949, Ojanen et al. 1979), the ratio of the length divided by the width gives an indication of whether one or more

Table 1. The frequency of Brown-headed Cowbird parasitism of Eastern Kingbirds in New York (1979) and Kansas (1980–1983), and the mean egg-laying date for kingbirds in each year.

| | | Early nests ^a | | Total nests ^b | |
|-------|-----------------------------|--------------------------|-----------------------------------|--------------------------|-----------------------------------|
| Year | Mean egg- laying date | n | Number (%) para- sitized | n | Number (%) para- sitized |
| 1979 | 11 June | 26 | 2 (8) | 42 | 2 (5) |
| 1980 | 7 June | 27 | 2 (7) | 47 | 4 (9) |
| 1981 | 2 June | 47 | 2(4) | 55 | 3 (7) |
| 1982 | 7 June | 39 | 4 (10) | 54 | 5 (9) |
| 1983 | 16 June | 56 | 7 (13) | 64 | 9 (14) |
| Total | | 195 | 17 (9) | 262 | 23 (9) |

- ^a Nests found before or during egg laying.
- b Nests found at all stages of the nestling cycle.

females laid in a nest. In one of the multiply parasitized nests, the eggs were of distinctly different sizes (3.4 vs. 2.7 g) and shapes (length/width: 1.20 vs. 1.30). I concluded that two females were responsible for the eggs. In the second nest there were no differences (3.2 vs. 3.1 g, and 1.24 vs. 1.25). I did not weigh or measure the third egg in this nest because it was severely punctured and broke when I handled it.

Mean cowbird egg mass was 3.1 g (SD = 0.264, n = 14) in Kansas. The mean maximum length was 21.08 mm (SD = 0.818, n = 14) and mean breadth was 16.21 mm (SD = 0.553, n = 14). These values are smaller but not significantly different from egg dimensions in Indiana (Nolan and Thompson 1979; t-test for the comparison of length, t = 1.18; t-test for breadth, t = 1.38; df = 53 and P > 0.20 for both). Female cowbirds did not select host nests on the basis of egg size, as the correlation between parasite and host egg mass was not significant (r = -0.263, df = 11, $P \gg 0.05$; data from Kansas only).

The frequency of parasitism of kingbird nests observed during egg laying ranged from 4% to 13% over the 5-yr period, and averaged about 9% (Table 1). Inclusion of all nests had no influence on either the range or frequency of parasitism over years or on the total mean values (Table 1). Annual frequency of parasitism varied 2–3-fold in Kansas. A direct relationship appeared to exist between mean annual egg-laying date for kingbirds (in Kansas) and the frequency of parasitism (Table 1), suggesting that a delay in breeding may have increased the probability of being parasitized.

Estimated rates of Brown-headed Cowbird parasitism on other rejecters vary from 0% to nearly 50% (Finch 1982, Rothstein 1976a, Elliott 1978, Scott 1977). The estimate for Eastern Kingbirds (8–10%) appears to be relatively low, especially in comparison with other species that breed in the Great Plains (Elliott 1978). I make this statement cautiously, however, because I probably underestimated the actual frequen-

cy of parasitism (Scott 1977). Nevertheless, the rate of parasitism I detected was much higher than would be expected from 24 known instances (Friedmann et al. 1977).

I recorded the kingbird's response to foreign eggs in only 7 of 19 cases. Using the persistence of the parasite egg in the nest for 5 or more days as the criterion for acceptance (Rothstein 1975), 3 of 7 (42.9%) kingbirds accepted cowbird eggs. Assuming that cowbird eggs were ejected from three nests with evidence of cowbird activity but no cowbird egg (i.e. small, triangular punctures in kingbird eggs), 3 of 10 (30.0%) females accepted eggs. These estimates contrast sharply with Rothstein's (1975) results in which all 33 females ejected cowbird eggs, 70% within one day of the appearance of the foreign egg (Rothstein 1976a). Indeed, a cowbird egg was successfully hatched and the nestling fledged from one nest in 1983, as were all three kingbird eggs and nestlings. The cowbird fledged at 11 days of age, when the kingbirds were only 5-6 days old. Parasitism did not appear to influence negatively the growth of the kingbird nestlings because the mean rate of weight gain and asymptotic weight for the kingbird brood were above average (K = 0.457, A = 34.9 g; cf. Murphy 1983).

Two explanations may account for the high acceptance rate compared with Rothstein's (1975) findings of total rejection. First, accepters and slow rejecters were more likely to be detected than rapid rejecters. Unlike Rothstein's experimental work, I could not document how many kingbird females actually received cowbird eggs. Although unlikely, it is possible that many more female kingbirds were parasitized than I recorded, and that the acceptance rate was in fact very low. Second, both cowbird and kingbird eggs are spotted, yet both are extremely variable for this character and occasionally overlap. Rothstein used a single, unkingbird-like pattern for the artificial eggs in his experiments (Rothstein pers. comm.). It is possible, therefore, that some of the parasitized kingbirds in my study laid lightly spotted eggs and could not clearly distinguish the cowbird egg from their own (Rothstein pers. comm.).

In 11 of 16 cases (68.7%) a kingbird egg was either ejected from the nest (6 times) or damaged such that the embryo died (5 times). Cowbird parasitism therefore had a potentially strong negative impact on kingbird reproductive success, mainly through loss of eggs. Because of my interference I could not determine accurately what percentage of cowbird eggs yield fledglings in kingbird nests. Given the extreme rarity of observations of kingbirds successfully fledging cowbird young, however, kingbirds are poor hosts for cowbird eggs.

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