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REJECTION OF ARTIFICIAL PARASITE EGGS BY GRAY KINGBIRDS IN THE BAHAMAS¹

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Abstract. We added artificial Shiny Cowbird (*Molothrus bonariensis*) eggs to Gray Kingbird (*Tyrannus dominicensis*) nests in the Bahamas, where Shiny Cowbirds were first recorded in 1993. Gray Kingbirds ejected 85% of artificial eggs within 48 hr of addition. Based upon the short time of contact between the two species, we suggest that egg ejection by Gray Kingbirds in the Bahamas is retention of ejection behavior from ancestral populations.

Key words: brood parasitism, egg ejection, Gray Kingbird, *Molothrus bonariensis*, Shiny Cowbird, *Tyrannus dominicensis*.

The Shiny Cowbird (*Molothrus bonariensis*) is a generalist brood parasite that has invaded the West Indies from South America during this century, recently arriving in North America (Post and Wiley 1977b, Post et al. 1993, Baltz 1995). The Shiny Cowbird parasitizes several host species in the West Indies region (Cruz et al. 1995), and some of these have been documented rejecting experimentally added cowbird eggs in Puerto Rico and St. Lucia (Cruz et al. 1985, Post et al. 1990). In many areas in the West Indies, Shiny Cowbirds have been in contact with host species for

over 90 years, enough time to have evolved egg ejection behavior (Rothstein 1975b). However, Shiny Cowbirds have only recently arrived in the Bahamas (Baltz 1995). Because Shiny Cowbirds have not been in prolonged contact with potential host species in the Bahamas, egg rejection behavior should not have had time to evolve in response to interspecific parasitism. We predicted that the Gray Kingbird (*Tyrannus dominicensis*), a known rejector of parasite eggs in Puerto Rico and St. Lucia (Cruz et al. 1985, Post et al. 1990), would not reject Shiny Cowbird eggs in the Bahamas. We tested this prediction by documenting the response of Gray Kingbirds in the Bahamas to artificial cowbird eggs added to their nests.

METHODS

The experiment was conducted from 3–14 July 1996, in the vicinity of Staniard Creek, North Andros Island, Bahamas. We generally followed Rothstein's (1975a) method of experimentally parasitizing nests. Artificial eggs were shaped by hand from Sculpey Modeling Clay (Polyform Products Inc., Elk Grove Village, Illinois), baked to harden, and painted with waterproof acrylic and enamel paints to resemble real Shiny Cowbird eggs: white ground color with "burnt umber" maculation. Real Shiny Cowbird eggs average 20.3 × 16.7 mm (Post and Wiley 1977a) and the artificial eggs averaged 20.8 × 16.4 mm ($n = 24$). Single artificial Shiny Cowbird eggs were added to 20 Gray Kingbird

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nests. None of the manipulated Gray Kingbird nests contained real Shiny Cowbird eggs. Attempts were made to add artificial eggs during egg laying to simulate actual cowbird parasitism, but most eggs (16 of 20) were added after incubation had begun. A single Gray Kingbird egg was removed from each nest immediately before adding artificial eggs to further simulate natural parasitism. Ten host clutches were changed to one host eggs and one artificial egg. Another 10 host clutches were changed to one host and one artificial egg. Clutches were manipulated between 07:30 and 18:00 and checked approximately 24 hr after manipulation. Nests in which artificial eggs were not ejected after 24 hr were checked again at 48 hr post-manipulation. If artificial eggs were present after 48 hr, they were assumed to have been accepted. Whereas most egg addition experiments continue to monitor manipulated nests for up to 5 days after adding eggs (Rothstein 1975a), logistical considerations made this impossible for our study. Our results are thus a conservative measure of rejection frequency because additional monitoring could only have revealed more ejections.

RESULTS

Gray Kingbirds ejected artificial eggs in 16 of the 20 (80%) manipulated nests within 24 hr. An artificial egg was ejected in another nest after 48 hr, raising the ejection rate to 85.0%. The one nest checked on the same day of the manipulation was missing the artificial egg within 2 hr. Ejected artificial eggs were found under two nests, but were not checked for the presence/absence of bill marks. Nests with two kingbird eggs and one artificial egg ($n = 10$) and nests with a single kingbird and artificial egg ($n = 10$) had identical ejection rates after 24 hr (80.0%). The single ejection after 48 hr was from a nest with a single kingbird and artificial egg. The ejection rate in nests manipulated during egg laying was 75.0% (3 of 4) after 48 hr.

DISCUSSION

Gray Kingbirds in the Bahamas are rejectors of artificial Shiny Cowbird eggs. The egg ejection rates were 85.0% overall and 75.0% in nests manipulated during egg laying. These ejection rates are similar to that recorded for Gray Kingbirds in Puerto Rico (87.5%, Cruz et al. 1985). Cruz et al. (1985) did not believe that the egg ejection behavior they observed in Gray Kingbirds and other species had evolved since the Shiny Cowbird arrived on the island. However, Shiny Cowbirds have been in Puerto Rico since the 1950s (Post and Wiley 1977b), long enough for a host to have developed the observed levels of ejection based upon calculations in Rothstein (1975b). In the Bahamas, Shiny Cowbirds were first detected in 1993 (Baltz 1995), and thus, the observed level of egg rejection in Gray Kingbirds is not a response to recent interspecific brood parasitism.

One possible explanation for egg ejection behavior observed in this study is that egg recognition and ejection evolved as a defense against intraspecific brood parasitism. We did not test for recognition of foreign conspecific eggs by Gray Kingbirds in this study. However, studies of a Gray Kingbird congener, the Eastern Kingbird (*T. tyrannus*) have shown that fe-

males accepted virtually all foreign kingbird eggs (Bischoff and Murphy 1993, Sealy and Bazin 1995) despite the fact that frequencies of intraspecific parasitism can be high in at least some populations of Eastern Kingbirds (McKittrick 1990). This is consistent with the fact that there is little evidence for ejection of intraspecific parasite eggs in general (Petrie and Møller 1991). These lines of evidence suggest that the levels of egg rejection we observed in the Bahamas are likely not a response to intraspecific brood parasitism.

Egg ejection behavior by Gray Kingbirds in the Bahamas also could be explained by gene flow from other populations that have putatively evolved this behavior. This is an unlikely scenario for two reasons. First, Gray Kingbirds in the Bahamas are part of the migratory subspecies (*T. d. fugax*), wintering in northern South America, whereas Gray Kingbirds from Hispaniola eastward in the West Indies and small populations breeding in South America are nonmigratory (*T. d. dominicensis*; Haberman et al. 1991). Thus, there would be no exchange of genetic information between Bahamian kingbirds and other Gray Kingbird populations that have been in contact with Shiny Cowbirds for relatively long periods of time. Second, in the event that there was some immigration from ejector populations, the trait would not be expected to become common in Bahamian kingbird populations in the absence of any selective advantage to egg ejection (Rothstein 1975b).

We suggest that the egg ejection behavior observed in this population of Gray Kingbirds from the Bahamas is a retained trait that evolved in an ancestral population or species in response to interspecific brood parasitism. This conclusion is supported by the fact that all *Tyrannus* kingbirds that have been tested exhibit this trait, including Scissor-tailed Flycatcher (*T. forficatus*), Western Kingbird (*T. verticalis*), Couch's Kingbird (*T. couchii*), Eastern Kingbird, Fork-tailed Flycatcher (*T. savana*; Carter 1986, Mason 1986, Regosin 1994), and Cassin's Kingbird (*T. vociferans*; Rothstein cited in Rohwer and Spaw 1988). It appears that ejection of parasite eggs and egg recognition (sensu Rothstein 1975c) are traits that once they appear may not be lost, even through speciation events, because they have virtually no costs (Rothstein 1990, Sealy and Bazin 1995). This would be especially true if the traits were determined by nonpleiotropic genes (Rothstein 1975b). We suspect that rejection behavior may be common to all *Tyrannus* and suggest that researchers test other species.

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SKELETAL DEVELOPMENT AT THE TIME OF FLEDGING IN HOUSE WRENS¹

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Abstract. We examined skeletal development at the time of first flight in House Wrens (*Troglodytes aedon*) as one step in assessing whether calcium availability limits nestling growth in this species. Young wrens begin flying with about 49 mg of calcium in their skeletons, 30% less calcium than is found in adult skeletons. Degree of calcification varies greatly from bone to bone at first flight which suggests that, during development, growing nestlings selectively allocate more calcium to certain skeletal components than to others. The coracoids, which directly resist contrac-

tions of the large flight muscles, are the most calcified bones in the fledgling body. Unexpectedly, long bones of the wing are not highly calcified at nest-leaving and are less calcified than leg bones. Strong leg bones may reflect the fact that young use legs extensively when competing for food within nests, and that legs probably bear the brunt of hard, awkward landings which young birds experience before flight is perfected.

Key words: calcium, growth, House Wren, skeleton, *Troglodytes aedon*.

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In many bird species, selection should favor individuals who, as young, most rapidly develop the ability to fly because flight usually provides young with several survival advantages including increased access to food and an increased ability to escape predators (Sul-