Short Communications and Commentaries

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Partial Rejection of Immaculate Foreign Eggs by Yellow-breasted Chats

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Egg ejection has been documented in numerous songbirds in response to natural or artificial brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; Rothstein 1975a, Finch 1982, Rich and Rothstein 1985, Regosin 1994). Ejection of foreign eggs is thought to occur because birds learn to recognize their own eggs through an imprinting-like process and remove eggs that differ substantially from their own (Rothstein 1974, 1978; Lotem et al. 1992, 1995). Selection pressure from brood parasitism appears to maintain egg recognition and response to foreign eggs (Davies and Brooke 1989, Soler and Møller 1990, Briskie et al. 1992, Dufty 1994, Soler et al. 1994).

The Yellow-breasted Chat (*Icteria virens*) is a common host of the Brown-headed Cowbird (Friedmann 1929, 1963; Berger 1951, Nolan 1963, Young 1963) and is considered an accepter of parasitism (Rohwer and Spaw 1988). However, varation in parasitism frequencies among populations has been noted, and Friedmann (1963) speculated that "parasitism intolerant" chat populations explained locally low parasitism frequencies. Moderate to high frequencies of parasitism should exert pressure on chats to evolve responses to parasitism, but responses to cowbird eggs may not evolve rapidly in chats because of close resemblance between the two species' eggs (Rothstein 1975a). In 1992, we noted a parasitized chat nest where a cowbird egg apparently was ejected and remained beneath the nest. We proposed that chats are capable of ejecting cowbird eggs, but generally fail to do so because cowbird and chat eggs are difficult to distinguish from one another. We predicted that chats would eject dissimilar eggs frequently, but would reject normal, maculated cowbird eggs, if at all, in proportion to their divergence from their own clutch. We tested these predictions by evaluating the response of Yellow-breasted Chats to white-painted cowbird eggs and normal cowbird eggs added to their nests.

Methods.—We searched for Yellow-breasted Chat nests at Thomas S. Baskett Wildlife Research and Education center in Boone County, Missouri (38°45′N, 92°12′W) from April through July 1994. Nests were flagged from at least 3 m distance. Brown-headed Cowbird eggs were salvaged from abandoned nests or nests of other species at the study site. We randomly assigned cowbird eggs to control treatments (henceforth "control eggs") or a painted treatment (henceforth "white eggs"). We also noted the presence of cowbird eggs that we did not add to chat nests (henceforth "natural eggs") and Yellow-breasted Chat eggs ("chat eggs"). White eggs were marked with a fine coat of interior/exterior almond spray paint (Krylon) because this color best approximates the ground color of cowbird eggs. All eggs were refrigerated when not in use.

We attempted to add eggs during the chat laying period because this is when natural parasitism occurs, but both egg types were added during incubation if nests were found after laying. We determined day of addition or ejection by backdating from the hatching date, using 11 days as the duration of incubation (Thompson and Nolan 1973, Ehrlich et al. 1988, pers. obs.). Each chat nest received a control egg and a white egg on consecutive days. We switched the order of first addition between white and control eggs with each new nest and left any natural cowbird eggs in nests. We checked nests daily for possible ejection of eggs and inspected each chat egg daily for damage. White and control cowbird eggs were removed after they were in nests for three days. Although we could have missed ejections if they occurred later than three days, most rejecter species eject eggs within three days, in most cases within one day (Rothstein 1975b, 1976, 1982a,b; Finch 1982; Rich and Rothstein 1985; Sealy 1996). If eggs were ejected, we searched below nests for eggs or egg remains while trying to minimize disturbance to the nest plant. We classified any missing eggs as "ejected," although partial nest predation or egg stealing by cowbirds could have accounted for some missing eggs (see below). Cases where a majority of eggs were missing and chats were subsequently absent from the nest were considered depredations rather than ejections and eliminated from the analysis.

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Color photographs of all chat, control, and natural cowbird eggs were taken against a neutral background with a 90-mm macro lens using Kodachrome 64 slide film on the day of egg addition. Photos were taken of new chat or natural cowbird eggs as they were laid. Distance of the camera from the eggs was maintained at 0.32 m with a tripod. We measured maximum length and width (± 0.1 mm) of all eggs with a dial calipers.

We scanned the Kodachrome slides of eggs with a Silverscan II (LaCie) flatbed using Photoshop (Adobe) at a resolution of 1,600 pixels per inch. These images were transferred to Image-1 analysis software (Universal Imaging Corp.), which measured only the dark (maculated) region within a defined rectangle. We anchored the corners of this rectangle on the egg images to encompass as much of the egg as possible. A ratio of dark (maculated) to white area was established for each egg. This percentage of dark to white was our measurement for "percent maculation" (± 0.001%). Because areas of rectangles varied slightly depending on where the corners were anchored, we measured percent maculation three times each for 11 randomly selected chat eggs and 11 randomly selected cowbird eggs. We performed arcsine square-root transformation to normalize the data and then calculated repeatability (Lessels and Boag 1987, Krebs 1989) on transformed measurements to see if variation between repeated measures of the same egg exceeded variation among eggs within species. Repeatability ranges from 0 to 1.0, where 1.0 indicates perfect repeatability on measures of the same item. We calculated 95% confidence intervals (95% C.I.) for repeatability, which are asymmetrical about the repeatability measure (Krebs 1989). Other eggs were measured for percent maculation only once.

We tested for differences in rejection frequency between egg types with Fisher exact tests and compared chat and cowbird eggs in the same nest using Wilcoxon signed-ranks tests, comparing the mean measurements of each chat clutch against the mean of combined control and natural cowbird eggs (if any) in the same nest. We compared ejected versus non-ejected eggs with Wilcoxon two-sample tests (Siegel and Castellan 1988). We also performed power analyses using t-tests with nonparametric adjustment assuming double-exponential distribution of the statistics (Al-Sunduqchi 1990). We used Bonferroni corrections for joint testing for simultaneously comparing multiple egg measurements (Neter et al. 1990).

Results.—Cowbird eggs of both types were added to four chat nests during laying and seven nests during incubation. White cowbird eggs were ejected from six nests, whereas a control cowbird egg was ejected from one nest (Fisher exact test, $P = 0.03$, $n = 11$). Two of these nests were naturally parasitized, including one nest where a white egg was missing. Of the nine nests that were not naturally parasitized by cowbirds, five white eggs were ejected compared with one control egg (Fisher exact test, $P = 0.06$, $n = 9$). All ejections of white eggs occurred within one day of addition, except for one incubation-stage nest where the white egg was ejected two days after addition. Two ejections were from from laying-stage nests; the other four ejections occurred at nests where white eggs were added during incubation. Ejections from unparasitized nests during the incubation stage occurred on days 2 and 9 of incubation. We could not backdate to day of ejection for the remaining incubation-stage nest because it was depredated before hatching. The one case of ejection at a parasitized nest occurred on day 3 of incubation.

In one nest where the white egg was ejected within a day, both the control egg, which had been placed in the nest two days previously, and one chat egg were missing. This nest remained active after the ejections and only the white egg was found beneath the nest. At another nest the white egg was added the day after the first-laid chat egg and was ejected the following day. Apparently, this female stopped laying for three days after ejecting the white egg, and then laid three more eggs for a total clutch size of four.

We found ejected white eggs under two nests, including the one mentioned above. Paint had been chipped from both of these eggs, which also were cracked. We were not able to find other missing eggs of any type. We did not detect any damage to chat eggs that remained in nests, although one chat egg from a nest where ejection occurred failed to hatch.

Repeatabilities of percent maculation measures of the same eggs were 0.981 (95% C.I. +0.012, −0.031) for 11 cowbird eggs and 0.987 (95% C.I. +0.008, −0.022) for 11 chat eggs. One naturally parasitized nest contained one natural cowbird egg in addition to the control egg that we added; the other contained three natural eggs plus a control egg for a total of four cowbird eggs. Means of control cowbird and chat egg measurements from the same nests differed significantly for percent maculation ($n = 11$ for each egg type in all comparisons; Bonferroni correction for joint testing, $\alpha = 0.017$). Maculation for control cowbird eggs averaged 27.68 ± SE of 1.38%, whereas chat eggs averaged 18.18 ± 1.61% (Wilcoxon signed-ranks test, $z = -2.93$, $P = 0.003$). Cowbird and chat eggs from the same nest did not differ significantly in length (control eggs, 21.4 ± 0.22 mm; chat eggs, 21.9 ± 0.23 mm; $z = -1.51$, $P = 0.13$) or width (control eggs, 16.3 ± 0.13 mm; chat eggs, 16.6 ± 0.16 mm; $z = -1.27$, $P = 0.20$).

Control eggs and white eggs from the same nest did not differ statistically in length ($z = -0.31$, $P = 0.76$) or width ($z = -0.09$, $P = 0.93$; $n = 11$ each for control and white eggs; Bonferroni correction for joint testing $\alpha = 0.025$). Average length and width of ejected white eggs (excluding those from naturally parasitized nests) did not differ from non-ejected eggs, although power to detect a difference was very low ($n = 5$ eggs of each type in both comparisons; length, $z = -0.42$, $P = 0.68$, power = 0.06; width, z

$= -0.84$, $P = 0.40$, power $= 0.07$). As stated previously, a control cowbird egg was missing from only one nest. The missing cowbird egg was 21.9 × 15.9 mm with 20.05% maculation. The chat eggs ($n = 4$) in this nest averaged 21.3 ± 0.11 mm in length, 16.8 ± 0.16 mm in width, and 13.65 ± 0.77% maculation.

Discussion.—Yellow-breasted Chats tested in this study ejected about half of the dissimilar eggs added to their nests and appeared to possess a coarse level of egg recognition. Recognition seemed to be based upon maculation rather than egg size. Although sample sizes for comparison are small, differences between length and width of white and control eggs from the same nests were not significant. However, Rothstein (1978, 1982a) noted that more than one egg parameter was important for ejection to occur in rejecter species (see Ortega and Cruz 1988).

Brown-headed Cowbird and Yellow-breasted Chat eggs generally are easy for humans to tell apart, although some chat and cowbird eggs resemble one another closely (Friedmann 1963), and inexperienced field assistants sometimes make errors in distinguishing the two (pers. obs.). In some parts of their range, Yellow-breasted Chats also are parasitized by Bronzed Cowbirds (*Molothrus aeneus*), which lay immaculate eggs (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985). Friedmann et al. (1977) reported that Yellow-breasted Chats were parasitized less frequently by Bronzed Cowbirds than by Brown-headed Cowbirds. Preferential ejection of Bronzed Cowbird eggs certainly could account for this observation.

In a manner similar to chats, and Brown-and-yellow Marshbirds (*Pseudoleistes virescens*) and Chalk-browed Mockingbirds (*Mimus saturninus*) ejected a white egg morph of the Shiny Cowbird (*Molothrus bonariensis*) while accepting a maculated morph that more closely resembled the host's egg (Fraga 1985, Mason 1986, Mermoz and Reboreda 1994). Ejection by hosts may thus select for one egg morph over another, because spotted Shiny Cowbird eggs seem to be more common than immaculate eggs (Hoy and Ottow 1964, King 1973, Fraga 1985). However, Fraga (1985) reported that Yellow-winged Blackbirds (*Agelaius thilius*) preferentially accept immaculate eggs (see also Orians *in* Friedmann et al. 1977).

Chats are small for a rejecter species (Rothstein 1975a, Rohwer and Spaw 1988; but see Sealy 1996), and they appeared to have some difficulty ejecting eggs. They may have accidentally ejected one of their own eggs in the process of ejecting a white egg, or perhaps accidentally damaged their egg and subsequently ejected it. Both white eggs that we found under nests were chipped and cracked, but not fully punctured.

Maintenance of ejection behavior in chats remains puzzling considering the rarity of rejection of natural cowbird eggs, because selection pressure from brood parasites generally is thought to maintain egg recognition and response to foreign eggs (Davies and Brooke 1989, Soler and Møller 1990, Briskie et al. 1992, Soler et al. 1994). One possibility is that chats mistook white eggs for fecal sacs, particularly for ejections that occurred later in incubation. However, even infrequent ejection of naturally laid cowbird eggs by chats may be advantageous enough to maintain rejection behavior. Experiments have shown that some accepter species are unresponsive even to extremely divergent egg types (Friedmann 1929, Rothstein 1986, Ortega and Cruz 1988), whereas others having eggs similar to cowbirds may show moderate levels of ejection of divergent eggs, as apparently demonstrated by Yellow-breasted Chats and Northern Cardinals (*Cardinalis cardinalis*) in another study (Burhans unpubl. data). Rarity of rejection in such species may explain why Brown-headed Cowbirds lay eggs in a maculated pattern common to many important hosts. Future studies of other common accepter species with cowbird-like eggs should examine host tolerance of foreign eggs over a range of egg appearances, and also should perform large-scale clutch manipulations in the manner of Rothstein (1975b, 1982b) to explore the possibility that these hosts show true egg recognition.

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