



INCREASED INVESTIGATION OF MANIPULATED CLUTCHES SUGGESTS EGG RECOGNITION WITHOUT REJECTION IN A BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*) HOST, THE YELLOW WARBLER (*SETOPHAGA PETECHIA*)

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ABSTRACT.—Egg discrimination underlies the evolution of a host's ability to reject a brood parasite's egg, but some hosts do not reject if it is too costly or if the parasitic egg mimics the host egg. We examined cues used by the Yellow Warbler (*Setophaga petechia*), a host of the Brown-headed Cowbird (*Molothrus ater*), in its decision to reject (bury or desert) experimentally parasitized clutches. Yellow Warblers that returned to nests after a model egg was added spent significantly more time peering at and probing their nest contents and shuffling than before eggs were added. Rejection probability increased with the proportion of time Yellow Warblers probed their nest contents after settling on their clutch. Acceptors and rejecters, however, peered at or shuffled their eggs the same amount of time and visited the nest and probed its contents (before settling) the same number of times. Burial occurred at 29 of 144 nests (20.1%) experimentally parasitized with model cowbird eggs, of which 14 nests survived long enough for replacement clutches to be parasitized. Only one of the 14 (7.1%) females that initially buried parasitized clutches buried again when the replacement clutch was parasitized, whereas the others accepted their parasitized replacement clutch. Repeated parasitism revealed that an individual's response to parasitic eggs is plastic and that it may reject or forgo rejection after recognizing a parasitism event. *Received 23 June 2011, accepted 21 November 2011.*

Key words: brood parasitism, Brown-headed Cowbird, clutch abandonment, egg discrimination, *Molothrus ater*, phenotypic plasticity, repeated parasitism, *Setophaga petechia*, Yellow Warbler.

El Incremento en la Investigación de Nidadas Manipuladas Sugiere Reconocimiento de los Huevos sin Rechazo de éstos en *Setophaga petechia*, un Hospedero de *Molothrus ater*

RESUMEN.—La capacidad de discriminación de huevos subyace a la evolución de la habilidad de los hospederos de rechazar los huevos de los parásitos de cría, pero algunos hospederos no los rechazan si es muy costoso o si los huevos parásitos imitan a los huevos del hospedero. Examinamos las pistas usadas por *Setophaga petechia*, un hospedero de *Molothrus ater*, en su decisión de rechazar (enterrar o abandonar) nidadas parasitadas experimentalmente. Las reinitas que volvieron al nido luego de que un huevo modelo fue añadido invirtieron significativamente más tiempo escrutando los contenidos de su nido y reordenando los huevos que antes de que los huevos fueran añadidos. La probabilidad de rechazo aumentó con la proporción del tiempo que las reinitas probaban los contenidos del nido luego de establecerse sobre la nidada. Sin embargo, tanto los que aceptaban como los que rechazaban los huevos, escrutaron o reordenaron sus huevos la misma cantidad de tiempo y visitaron el nido y probaron sus contenidos (antes de establecerse) el mismo número de veces. El entierro ocurrió en 29 de 144 nidos (20.1%) parasitados experimentalmente con huevos modelo de *Molothrus*, de los cuales 14 nidos sobrevivieron lo suficiente como para que las nidadas de reemplazo fueran parasitadas. Sólo una de las 14 (7.1%) hembras que inicialmente enterraron nidadas parasitadas, enterró de nuevo la nidada de reemplazo cuando ésta fue parasitada, mientras que las demás aceptaron que su nidada de reemplazo fuera parasitada. El parasitismo repetido reveló que la respuesta de un individuo a los huevos del parásito es plástica y que éste puede rechazar o renunciar al rechazo después de reconocer un evento de parasitismo.

EGG DISCRIMINATION IS the most common adaptation in hosts of avian brood parasites. Hosts normally learn to recognize their own eggs visually before they develop egg ejection, and then reduce their fitness costs (Rothstein 1974, Moskát et al. 2010). However, egg recognition may also be innate

(Honza et al. 2004, Moskát et al. 2010). Some hosts eject parasitic nestlings, likely in response to parasites laying eggs that are cryptic in dark nests (Lotem 1993, Langmore and Kilner 2010, Sato et al. 2010, Grim 2011). Egg discrimination is well developed in many Common Cuckoo (*Cuculus canorus*) hosts that have

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had a long coevolutionary history with the parasite (Davies and Brooke 1998, Stokke et al. 2005). More than 80% of known Common Cuckoo hosts eject nonmimetic eggs, compared with only 10% of Brown-headed Cowbird (*Molothrus ater*) hosts (Rothstein 1982, Davies and Brooke 1998, Peer and Sealy 2004). Ejection is generally cost-free unless hosts damage or mistakenly eject their own eggs in the process (Rothstein 1975, 1982; Underwood and Sealy 2006b, c). The cuckoo or cowbird may remove a host egg at or around the time of parasitism, which is an irrecoverable cost (Sealy 1992, Lorenzana and Sealy 2001, Stokke et al. 2008). Egg discrimination abilities of potential hosts and an increase in ejection frequency by the host population may be responses to rapid increases in parasitism frequency in as few as 10 to 20 years (Nakamura et al. 1998), probably reflecting adaptive phenotypic flexibility rather than genetic change (see Brooke et al. 1998).

Hosts that recognize a parasite's egg may not necessarily eject it (Spaw and Rohwer 1987, Antonov et al. 2009). The Eastern Olivaceous Warbler (*Hippolais pallida*), a small host of the Common Cuckoo, pecks cuckoo eggs, although most of the parasite's eggs are "accepted" because the warbler cannot penetrate the unusually strong shells (Antonov et al. 2009). The Baltimore Oriole (*Icterus galbula*), a host of the Brown-headed Cowbird that puncture-ejects real cowbird eggs (Sealy and Neudorf 1995), no longer attempts to eject impenetrable model eggs after numerous attempts (Rothstein 1977, Underwood and Sealy 2006a). "Forced" acceptance in orioles confronted with model eggs, however, did not realistically simulate real eggs. Egg recognition without rejection has not been documented in a species that, as its form of rejection, abandons clutches instead of ejecting eggs.

The Yellow Warbler (*Setophaga petechia*; hereafter "warbler"), a small host of the Brown-headed Cowbird (hereafter "cowbird"), is unique among cowbird hosts in that some females abandon parasitized clutches by burying cowbird eggs and their own eggs, then laying a new clutch above the buried eggs (Sealy 1995, Mico 1998). Their bills are apparently too small to grasp-eject a cowbird egg (Rohwer and Spaw 1988, Guigueno and Sealy 2010; also see Rasmussen et al. 2010). Burial is a specialized antiparasite defense because (1) warblers buried ~37% of naturally parasitized clutches but no control clutches in which host eggs were handled daily without egg addition (Sealy 1995); (2) burial usually occurred up to the midpoint of each individual female's laying cycle (after the appearance of a cowbird egg), but acceptance prevailed in incubation, by which time the probability of the nest being parasitized had declined (Clark and Robertson 1981, Sealy 1995, Guigueno and Sealy 2010); and (3) reproductive success of unparasitized nests and nests in which cowbird eggs were buried was similar (Clark and Robertson 1981). Another antiparasite defense, practiced by about one-third of females that reject parasitized clutches by abandonment, is to renest at a new nest site (Hosoi and Rothstein 2000, Guigueno and Sealy 2010).

If warblers' bills were long enough to grasp-eject cowbird eggs, rejection by burial and desertion would be more costly than grasp ejection because host eggs and time are lost with burial and desertion (Sealy 1992, 1995; Guigueno and Sealy 2010). Warblers naturally parasitized early in the breeding season were more likely to abandon parasitized clutches than those parasitized later, when limited time remained for renesting (Sealy 1995, Guigueno and Sealy 2010). However, it is unknown whether the individuals' response changed over the season because the same females

were not repeatedly parasitized. Thus, our objectives in the present study were to compare experimentally (1) the responses of acceptor and rejecter individuals and their behavior before and after experimental parasitism to determine whether some individuals recognize experimental parasitism but do not reject and (2) the consistency of response of individuals to experimental parasitism. By repeatedly parasitizing individuals, we determined whether an individual's response to parasitic eggs was plastic and whether an individual that rejects may forgo rejection after recognizing a parasitism event.

Recognition of experimental parasitism.—Results of experiments by Sealy and Lorenzana (1998) suggested that warblers do not visually recognize their own eggs. However, sample sizes in that study were small; therefore, we further investigated egg recognition by warblers by recording their response to model cowbird-like and nonmimetic (blue) eggs. Unlike ejection, females that bury must only recognize that parasitism has occurred, and other cues, such as interaction with an egg-removing cowbird, increase the probability of burial (Guigueno and Sealy 2011). Cowbird and warbler eggs are similar in color, but cowbird eggs are twice the size and mass (Guigueno and Sealy 2009). We hypothesized that warblers would bury or desert model blue eggs more frequently than model cowbird eggs because blue eggs diverge more in color from their own eggs and thus provide a stronger visual cue.

We also examined behaviors before the warblers settled on their clutch (peering time, number of visits to the nest, and probes of the eggs) and after the warblers settled (proportion of time shuffling and probing eggs), before and after we added a model egg or visited a control nest. We hypothesized that changes in behavior before versus after clutch manipulation predicted whether individuals with more pronounced changes in behavior in response to the addition of the model egg would be more likely to reject.

Individual responses over the breeding season.—We retested the response of female warblers that buried experimentally added eggs. Hosts of brood parasites that are intermediate rejecters (rejected 20–80% of naturally parasitized clutches), such as the warbler, are expected to face high rejection costs and be more plastic in their rejection behavior (Rothstein 1975, Stokke et al. 2005, Guigueno and Sealy 2010). We predicted that not all females that buried eggs during a first parasitism event would bury a second time. Male warblers do not incubate (Hébert and Sealy 1993) and apparently do not reject eggs (Guigueno and Sealy 2009).

METHODS

Study site and species.—We conducted our study at Delta Marsh, Manitoba, Canada (50°11'N, 98°19'W), in May and June 2009, on the properties of the Delta Marsh Field Station (University of Manitoba), Portage Country Club, Bell Estate, and Delta Waterfowl Station (MacKenzie 1982, Briskie et al. 1992). Warblers and cowbirds are common at Delta Marsh and have been recorded there since at least the 19th century (Thompson 1891). This has resulted in selection for the evolution of cowbird-specific alarm calls and other nest-defense behavior by warblers (Hobson and Sealy 1989, Gill and Sealy 2004). The frequency of cowbird parasitism on warblers at Delta Marsh has varied from year to year through the mid- to late 1990s (13.6–31.3%, Sealy 1995; 8–35%, Woolfenden et al. 2004).

Model eggs.—Models were made by shaping floral foam into the shape of an egg that was placed in a cowbird egg mold and covered with a thin layer of plaster of Paris so that warblers could peck through the plaster as they do with real eggs (similar to those employed by Lee et al. 2005). Dimensions and weights of model eggs (means \pm SE; cowbird [$n = 110$]: length = 22.80 ± 0.04 mm, width = 17.88 ± 0.03 mm, mass = 3.00 ± 0.02 g; blue [$n = 110$]: length = 22.85 ± 0.04 mm, width = 17.93 ± 0.02 mm, mass = 3.01 ± 0.03 g) were similar to those of real cowbird eggs (length = 21.07 ± 0.12 mm, width = 16.36 ± 0.09 mm, mass = 3.14 ± 0.04 g; $n = 77$; Sealy 1992). Also, the length (21.1–23.3 mm), width (17.1–18.3 mm), and mass (2.3–3.7 g) of model eggs were within the range of the length (18.1–23.3 mm), width (14.3–18.3 mm), and mass (2.1–3.9 g) of real cowbird eggs. Model eggs were sanded before being painted. Each model was heated in the hand for 10 s before being added to a nest, and each nest was used only once except in the case of reparasitism events, in which case nests were parasitized twice with the same type of model used during the first parasitism event. Warblers reject experimentally added real eggs of American Robins (*Turdus migratorius*; 37%, $n = 27$) as frequently as model eggs of Black-billed Cuckoos (*Coccyzus erythrophthalmus*; 37%, $n = 27$). The eggs of these two species are similar in color and size (Stewart et al. 2011). We thus have no reason to believe that female warblers treated our model eggs differently than they would have treated real eggs.

Our goal in this experiment was not to test the limits of the warblers' egg-discrimination ability. If that had been our purpose, we would have used model eggs that differed incrementally from the spotted eggs with grayish-white background of the cowbird. Instead, we sought to determine more generally whether warblers had any ability to discriminate. To that end, we painted nonmimetic model eggs blue with no spots so that they differed strongly in ground color and lacked the maculation of warbler eggs. This satisfied the need for the test eggs to differ in two parameters, which is important for egg discrimination by some hosts of brood parasites (Underwood and Sealy 2002). We also selected blue as the color of the nonmimetic egg because the Black-billed Cuckoo has occasionally been reported to lay its immaculate bluish eggs in warbler nests. Our nonmimetic model eggs thus also simulated a possible natural parasitism event (see Hughes 1997, Stewart et al. 2011). Blue eggs have been used as nonmimetic eggs in previous studies to identify discrimination (Bolen et al. 2000, Peer et al. 2000, Davis et al. 2002, Underwood et al. 2004, Klippenstine and Sealy 2008). White eggs (Burhans and Freeman 1997, Bolen et al. 2000) also have been used, although they may be mistaken for fecal sacs (see Guigueno and Sealy 2012).

Model eggs were painted with water-resistant, nontoxic acrylic paints (Folk Art Opaque Acrylic Paints by Plaid; Plaid Enterprises, Norcross, Georgia) to resemble cowbird eggs or nonmimetic blue eggs, similar to those used by Klippenstine and Sealy (2008). The background of cowbird eggs was grayish-white (Wicker White 1643 mixed with Licorice 1506) with brownish markings (Burnt Umber 1618 mixed with Wicker White) of variable size (Lowther 1993, Guigueno and Sealy 2009). We mixed the colors to resemble closely the coloration of real cowbird eggs (at the same time resembling warbler eggs; Fig. 1A). Nonmimetic eggs were painted with Cobalt Blue 1631 mixed with Wicker White 1643 (Fig. 1B).

Addition of model eggs to nests.—Model eggs were added to nests between 0415 and 1000 hours CDT on the morning the warblers laid their second egg (LD2), because cowbirds usually



FIG. 1. Parasitized clutches in our experiment. Each treatment nest contained one model egg (A = cowbird, B = blue) and real Yellow Warbler eggs. All eggs were experimentally added to nests the morning of the hosts' second laying day and during the first half of the breeding season.

parasitize nests before sunrise (Sealy et al. 1995, McMaster et al. 2004). Warblers are more likely to reject a clutch parasitized during the first 2 days of laying because the cost of rejection increases once the warbler has laid its entire clutch of 4 or 5 eggs (Clark and Robertson 1981, Goossen and Sealy 1982, Sealy 1995, Guigueno and Sealy 2009). Cowbirds at Delta Marsh also parasitize warbler nests most frequently up to the midpoint of the individual's laying cycle (i.e., laying day 2; Sealy 1995, Guigueno and Sealy 2010). We touched all eggs at control nests, whereas at treatment nests, eggs were touched and a model egg was added to the clutch. A host egg was not removed at the time of egg addition because cowbirds at our field site remove a warbler egg from only one in three nests that they parasitize, and the removal of host eggs does not influence rejection (Sealy 1992, Guigueno and Sealy 2011). We randomly parasitized, as part of another experiment, half of the nests before and after sunrise; however, the data were pooled because the rejection frequencies did not differ statistically in relation to time since sunrise (cowbird: before sunrise 7/32, after sunrise 8/38, continuity-adjusted $\chi^2 < 0.001$, $df = 1$, $P > 0.999$, blue: before sunrise 15/42, after sunrise 8/32, continuity-adjusted $\chi^2 = 0.54$, $df = 1$, $P = 0.46$). Treatments were randomly assigned by rolling a die the night before the

tests were to be conducted. We reparasitized on LD2 the replacement nests of all females that buried the experimentally parasitized clutch during the first parasitism event. Females were reparasitized with the same egg type (cowbird or blue model egg) and at the same time (before vs. after sunrise) as their first parasitism event. It was not possible to reparasitize females that accepted because the time of parasitism in relation to the laying cycle always had to be on LD2. Warblers are less likely to abandon parasitized clutches later in the breeding season because there may not be enough time to start again (Clark and Robertson 1981, Sealy 1995); therefore, to minimize this effect on abandonment frequencies, we conducted the first parasitism tests during the first half of the breeding season, between 5 and 20 June. Nests were parasitized again (reparasitism events) ~5 days after the first parasitism event, but no later than 21 June (see below). Warblers at our site attempt to rear only one brood per season in most years (Goossen and Sealy 1982); regardless, the clutch initiation period (laying of the first egg among all clutches) lasts about 35 days (Guigueno and Sealy 2009). Thus, all experimental parasitism events occurred during the first half of the clutch initiation period.

Acceptance and rejection criteria.—We checked each nest every 24 h after the addition of the model egg or after the initial disturbance (for controls) on LD2 for a total of 6 days (Sealy 1995). Experimental eggs were considered accepted if warblers completed their clutches and tended them for 6 days (Sealy 1995, Guigueno and Sealy 2009). During daily inspections, we looked into each nest to see whether the clutch was being buried and gently pressed the bottom of the nest cup if a new cup had been constructed to confirm that burial had taken the warblers only a day to complete. We recorded a nest as deserted when the eggs were cold and the parents were not observed near the nest for 3 consecutive days (Sealy 1992, 1995). If a clutch appeared to be abandoned, the nest was inspected for another 1 to 5 days to confirm the response because a nest may seem deserted one day, but the adults may be tending the eggs the next day, and burial may take more than a day to complete (Guigueno and Sealy 2010). Ejections were included in our analyses because a hole could be pecked through the models' thin layer of plaster (see below). Naturally parasitized experimental nests were omitted. Model eggs not buried were retrieved from experimental nests and examined for peck marks that would reveal attempts to puncture-eject them (Rothstein 1977).

Behavioral responses.—A subset of nests from each group was video-recorded to compare behavioral changes before versus after manipulation (addition of cowbird-colored or blue model egg or handling of the host eggs only) between experimental groups. Behavior was recorded approximately 30–45 min before each visit until approximately 30–45 min after the visit. A tripod and camera case were placed ~7.5 m from the nest by early evening the day before to ensure that the warblers habituated to the equipment. Attached to each tripod was a clear plastic container in which the camcorder was placed when recording began, to protect the camcorders from light rain. Each was partly covered with burlap, along with the tripod's legs, to conceal the equipment. Camcorders were equipped with 12-h batteries that were charged daily. M.F.G. viewed all the videos and was blind to the treatment groups. Five different behaviors were quantified (for similar comparisons, see Sealy and Lorenzana 1998): number of (1) seconds

that warblers perched on the nest rim and peered at their eggs, (2) visits to the nest before settling on the clutch, (3) times that warblers probed eggs before settling on the clutch, (4) times that females “shuffled” their bodies once they settled on the clutch divided by the length of time they were settled on the clutch (Höhn 1993), and (5) the proportion of time females spent probing the eggs after settling on the clutch. We defined “probing” as a behavior in which the female warbler, while settled on her clutch, lifted her body and turned or rotated eggs with her bill (Sealy and Lorenzana 1998, Deeming 2002).

Statistical analyses.—We used a 2×2 Fisher's exact test to compare the rejection frequency between control and experimental groups (burial and desertion occurred rarely without egg addition; see Sealy 1995) because one of the cells contained a frequency of zero (Zar 1999). We used a chi-square test with continuity correction to compare the rejection frequency between model cowbird and model blue eggs. The method of rejection (burial and desertion vs. ejection) between groups receiving model cowbird eggs and model blue eggs was analyzed using a Fisher's exact test because one of the cells contained a frequency of zero (Zar 1999). We also used a Fisher's exact test to compare the number of ejections against acceptances, as there would be no need for warblers to eject eggs from clutches that were abandoned via burial or desertion. We used these tests to determine the importance of visual cues by warblers; if visual cues are important and warblers recognized eggs, we would expect model blue eggs to be ejected more frequently than model cowbird eggs. Our data were not normally distributed, therefore, we conducted a Wilcoxon two-sample test to determine whether the time to rejection for blue eggs was different than that for cowbird-colored eggs.

Our video-recorded data were not normally distributed, even after a log transformation, so we compared behavior before and after manipulations among the three experimental groups (control, cowbird-colored egg, and blue egg) using a Kruskal-Wallis test; multiple Wilcoxon two-sample tests were then used to analyze behavioral changes between different pairs of groups (i.e., control vs. cowbird, control vs. blue, cowbird vs. blue). We did not perform Bonferroni corrections because most Kruskal-Wallis tests were significant and most of the Wilcoxon two-sample tests associated with significant Kruskal-Wallis tests were also significant. We also performed exact logistic regression in SAS, version 6 (SAS Institute, Cary, North Carolina), to determine whether egg rejection (reject = 1, accept = 0) was the response more likely expected by an individual that showed a more pronounced change in behavior after, as compared with before, experimental parasitism.

Nests at which burial was recorded were parasitized again on LD2 of the warbler's replacement clutch, and the second response was recorded to determine whether the individual's rejection behavior was flexible. This manipulation also allowed us to determine the frequency of rejection by individual rejecters (Peer and Rothstein 2010). We also reparasitized nests at which ejections were recorded, but, because the birds were not banded, we could not reparasitize the replacement clutches of females that deserted their experimentally parasitized clutch and moved to a new site. Statistics are reported as means \pm SE. All P values ≤ 0.05 were considered significant, and all tests were two-tailed.

TABLE 1. Responses of Yellow Warblers at Delta Marsh, Manitoba, in 2009 to experimental parasitism with model cowbird and model cowbird-sized blue eggs.

Group	Rejection			Acceptance	Total nests	Rejection (%)
	Burial	Desertion ^a	Ejection			
Control	0	0	0	72	72	0.0
Cowbird egg	13	2	0	55	70	21.4
Blue egg	16	1	6	51	74	31.1

^aSealy (1995) recorded desertion at one-third of rejections of naturally parasitized clutches. The discrepancy with the present study was likely due to yearly variation in rejection method.

RESULTS

A total of 216 experimental nests survived for 6 days (Table 1). The difference in rejection frequency between the control and experimental (cowbird and nonmimetic eggs) groups was significant (Fisher’s exact test, $P < 0.0001$); however, model blue eggs and model cowbird eggs were rejected at similar frequencies (chi-square test with continuity correction, $\chi^2 = 1.26, P = 0.26$; Table 1). The time to burial or desertion for blue eggs (1.76 ± 0.22 days) was similar to the time to burial or desertion for cowbird-colored eggs (2.13 ± 0.23 days; $z = 1.14, P = 0.27, n = 32$). The differences in rejection methods (burials or desertions vs. ejections) between nests that received a cowbird-colored egg and nests that received a blue egg approached significance because only blue eggs were ejected (Fisher’s exact test, $P = 0.06$; Table 1). When we compared the number of ejections in relation to acceptances, model blue eggs were ejected more frequently than model cowbird eggs (Fisher’s exact test, $P = 0.03$; Table 1).

Behavior was filmed at 18 control nests, 20 nests that received a model cowbird egg, and 19 nests with a model blue egg. Not all behaviors were recorded from each nest because some birds did

not settle on their clutch before the manipulation. The change in behavior during manipulation differed significantly between nests that received a model egg and those that did not (Table 2). Individuals that returned to their nests after a model egg had been added peered longer at their clutch, shuffled more frequently, and spent more time probing eggs once they settled on their clutch in comparison to controls (Table 2).

Twenty-eight treatment nests (25 acceptances and 3 burials) that were video-recorded survived long enough to record acceptance or rejection. Although behavior changed during experimental parasitism, most warblers accepted parasitized clutches (10.7% rejection frequency, $n = 28$). Individuals that rejected the “parasitized” nests did not behave differently from those that accepted, with one exception: they were more likely to probe their manipulated clutch longer than accepters (proportion of time probing for acceptances: $0.13 \pm 0.03, n = 22$, for burials: $0.38 \pm 0.15, n = 3$; exact conditional analysis, $\beta = 6.42 \pm 3.36, P = 0.047$).

No significant behavioral changes occurred after model egg addition for individuals that received a model blue egg versus a model cowbird egg (Table 2). However, the number of visits to the nest before settling on the clutch varied more among individuals that received a blue egg (mean = $0.84 \pm 0.03, n = 19$, variance: 0.0164 visits²) than in those that received a cowbird-colored egg (mean = $0.81 \pm 0.01, n = 20$, variance: 0.0027 visits²; Levene’s test, $F = 6.22, P = 0.02$).

Nests that were parasitized twice were parasitized for the first time, on average, 7.1 ± 0.67 days ($n = 14$) after the first female in the population began to lay, and reparasitism events occurred 12.4 days ± 0.72 ($n = 14$) after the first female’s laying date. All females that were experimentally parasitized twice buried during their first parasitism event, as required by the experiment, but only 1 of 14 (7.1%) also buried during the second parasitism event. The other 13 nests remained active.

Six nests were also reparasitized after model eggs were ejected, with one burial and one acceptance recorded; all other nests were depredated. Of seven ejections (including one at a

TABLE 2. Behavioral changes^a in Yellow Warblers at Delta Marsh, Manitoba, in 2009 in response to model egg addition. Averages are the actual data, although the data were log-transformed for the analyses. All significant comparisons are in bold.

Variable	Group	n	Average \pm SE	Kruskal-Wallis test		Wilcoxon rank-sum test (S statistic), P		
				χ^2	P	Control vs. Cowbird	Control vs. Blue	Blue vs. Cowbird
Peering time (s)	Control	14	0.75 ± 0.65	17.87	<0.001	224, 0.004	121, 0.001	134, 0.170
	Cowbird	12	11.77 ± 4.58					
	Blue	14	13.95 ± 2.31					
Number of visits to nest before settling	Control	14	-0.07 ± 0.13	5.56	0.062	184, 0.213	178, 0.052	192, 0.163
	Cowbird	14	0.14 ± 0.10					
	Blue	17	1.53 ± 0.63					
Number of times probing eggs before settling	Control	14	0.64 ± 0.51	3.98	0.137	196, 0.085	168.5, 0.114	156.5, 0.797
	Cowbird	12	1.83 ± 0.94					
	Blue	14	1.93 ± 0.68					
Proportion of time shuffling when on clutch	Control	14	0.0006 ± 0.0004	13.92	0.001	142, 0.006	135.5, 0.002	189, 0.375
	Cowbird	14	0.08 ± 0.07					
	Blue	15	0.05 ± 0.03					
Proportion of time probing eggs when on clutch	Control	14	-0.01 ± 0.02	7.01	0.030	155, 0.038	156, 0.027	208, 0.948
	Cowbird	14	0.09 ± 0.03					
	Blue	15	0.07 ± 0.02					

^aCalculated by subtracting the behavioral measurement before egg addition from the behavioral measurement after egg addition.

reparasitized nest), two host eggs at two nests and one host egg at two other nests went missing. The frequency of egg loss was greater at nests where ejection occurred (57%, $n = 7$) than at control nests (6%, $n = 72$; Fisher's exact test, $P = 0.001$). Cost of ejection averaged 0.86 ± 0.34 host eggs. After ejection, females continued to lay eggs or incubate and no eggs were damaged. Ejected nonmitotic eggs were recovered on the ground below three nests, approximately 0.3 m, 0.7 m, and 1.0 m from the base of the nest trees. One model egg had a single puncture mark ~ 2 mm in diameter.

DISCUSSION

Recognition of experimental parasitism without rejection.—Yellow Warblers that probed their eggs the most after settling on their clutches were most likely to reject manipulated clutches. However, most of the video-recorded warblers did not reject, despite altering their behavior significantly after experimental parasitism (Table 2). The increase in peering time by individuals that received an egg compared with those that did not, and the warblers' responses to model cowbird eggs compared with model blue eggs (i.e., increased number of nest visits before settling and higher proportion of ejections relative to acceptances for blue eggs), suggest some ability to recognize their own eggs. Warblers likely demonstrated a conditional acceptance with recognition of experimental parasitism (Antonov et al. 2009). To our knowledge, the present study is the first to demonstrate recognition of experimental parasitism without subsequent rejection in a cowbird host and one that usually abandons parasitized clutches rather than ejecting. Hence, egg recognition is not the only necessary condition for rejection to occur in a cowbird host that rejects by abandonment (Rothstein 1977, Underwood and Sealy 2006a, Antonov et al. 2009).

Whether a species that regularly accepts cowbird eggs, or one that is rarely parasitized, would respond similarly to what we have described in warblers is unknown. As Antonov et al. (2009) noted, this would be especially useful information because it would provide insight on how widespread similar egg-recognition behavior is in other species. A difference in behavior between birds tending a control nest and one that received a parasite's egg may emerge when a species that never rejects is tested. Individuals may investigate a change in their clutch but not recognize the foreign egg for what it is and not associate the change with an act of brood parasitism. Or they may associate the change with brood parasitism but still accept parasitism (see Antonov et al. 2009). Video-recording may reveal that most or all hosts detect a change in their clutches.

Mechanisms by which warblers recognized experimental parasitism.—Warblers visually recognized a change in their clutch by detecting the presence of an egg that differed from their own (see Hauser 2001, Moskát et al. 2010). The increase in time spent peering into the nest by treatment birds before settling on the clutch (Table 2) strongly suggests that warblers saw a change in their clutch. Warblers also responded more to blue eggs in that variation in the number of visits was statistically greater for blue eggs than for cowbird eggs. Indeed, we expected individuals to behave less consistently when presented with a less familiar stimulus (i.e., blue eggs). We also found that only blue eggs were ejected (Table 1), which is consistent with the view that some warblers visually discriminate between the parasite egg and their own eggs.

Sealy and Lorenzana (1998) concluded that warblers do not recognize their own eggs because (1) there was no change in peering time before settling on the clutch before versus after egg addition and (2) warblers did not reject clutches that contained either blue warbler-sized eggs or clutches with different proportions of cowbird and host eggs. One explanation for the discrepancy between Sealy and Lorenzana's (1998) results and those of the present study may be methodological. Behavior in Sealy and Lorenzana's (1998) study was quantified from a blind rather than by videotaping. Sample sizes were also smaller than ours. Equally likely is the possibility that the differences in our study are real and arose because female egg recognition ability is phenotypically plastic. Regardless, we are confident in our results because of our larger sample sizes, absence of a human near the nest during the testing period, and quantification of behavior by a single person.

Warblers may also use tactile cues to detect experimental parasitism. Individuals that probed their eggs longer after settling on their clutch were more likely to reject. Although they may see their clutch while probing their eggs, most of the "proportion of time spent probing" (Table 2) involved warblers lifting their bodies to initiate probing. Warblers also probed control clutches and their own eggs in experimental clutches. This behavior, therefore, was initiated by a tactile cue, and eggs were rearranged regardless of their type (host or parasite egg). In addition, once settled on an experimentally parasitized clutch, warblers shuffled more frequently than they did on control clutches, presumably bringing their developing brood patch in contact with the eggs (Deeming 2002; Table 2). Warblers likely felt the addition of a foreign egg in their clutch by comparing their clutch volume before versus after the manipulation (Rothstein 1982) or possibly even by detecting an increase in egg-size asymmetry (Mason and Rothstein 1986, Marchetti 2000). Rejection of large experimental eggs in a related study tended to occur at warbler nests with cups of smaller volumes, which suggests that egg crowding may alert the warbler that it has been parasitized (Stewart et al. 2011). Warblers may first visually recognize a difference in their clutch after parasitism, but tactile cues reinforced this stimulus before they decided to abandon the parasitized clutch.

Ejections.—Warblers ejected only blue eggs. An increase in the difference in color between the parasite and host eggs likely facilitated egg discrimination in warblers, as was reported in grassland hosts (Klippenstine and Sealy 2008). The propensity of warblers to grasp and remove objects from their nests was confirmed with video records by Guigueno and Sealy (2009); however, we did not clarify the method of ejection in the present study because ejection was never observed. Models that were retrieved from partially depredated nests in previous studies were damaged (Guigueno and Sealy 2009, 2011). All of the retrieved blue model eggs and nests in the present study were intact, and, therefore, warblers may have rolled the egg out of the nest (Marchetti 1992). Sealy (1995) recorded ejections of real cowbird eggs, but because none of the ejected eggs was found near the nest, he thought that the "ejected" eggs had been removed by predators. Warblers can lift a cowbird egg (Sealy and Lorenzana 1998); however, the cost of ejection incurred by the warblers was high (0.86 host eggs lost per model egg ejected), more than double the cost of puncture-ejection by small cowbird hosts that regularly eject (Sealy and Neudorf 1995, Sealy 1996).

Significantly more host eggs were lost from nests where ejection occurred than from control clutches, which strongly suggests that these eggs were lost during attempts to eject the model blue egg. The high cost to warblers for accepting a cowbird egg on our field site was 0.6 fledgling (Lorenzana and Sealy 1999), which may explain why ejections were rarely recorded. We assumed that our use of penetrable model cowbird eggs reflected the cost of ejecting real cowbird eggs.

Phenotypic plasticity in host response.—Egg rejection by Yellow Warblers is not fixed: burial is plastic, and only a small proportion of individuals that are rejecters express it at any given time. The Reed Warbler (*Acrocephalus scirpaceus*), a cuckoo host, similarly incurs costly rejection through burial, desertion, and ejection, which is flexible because it is affected by environmental cues, including interaction with the brood parasite (Davies and Brooke 1988, Moksnes et al. 2000, Stokke et al. 2005). Guigueno and Sealy (2011) found that a robotic egg-removing cowbird plus addition of a cowbird egg at nests increased the probability of clutch abandonment by Yellow Warblers, revealing this species' flexible and condition-dependent responses. Phenotypic plasticity in response is consistent with our other conclusion that many warblers likely recognized a change in their clutch but did not act on it, possibly because of other factors such as the cost of rejection. Multiple cues are likely necessary to elicit this costly behavior.

Abandoning clutches during a second attempt in the same breeding season may cost too much time and energy (Guigueno and Sealy 2010). Although all our manipulations were conducted during the first half of the clutch initiation period, reparasitism events occurred near the midpoint of this period. Reproductive success generally remains stable and high in the first half and declines over the second half of the breeding season in passerine birds (Verhulst et al. 1995, Guigueno and Sealy 2010). The clutch initiation period of warblers at our study site, based on a related study that analyzed nesting data from 13 breeding seasons, is ~35 days; on average, it takes 2.7 days to initiate a new clutch after burial, but 7.3 days after desertion (Guigueno and Sealy 2010). The cost of raising a cowbird chick does not take into account the fledgling period, during which costs of parasitism may persist (Lorenzana and Sealy 1999, Rasmussen and Sealy 2006). Therefore, the cost of acceptance is likely greater than initially predicted, but likely stable over time. Based on the curve of reproductive success (see Guigueno and Sealy 2010), warblers would be expected to bury or desert parasitized clutches in the first half of the clutch initiation period when reproductive success remains stable over time, because the time to initiate a new clutch costs little or no decrease in their reproductive success. Warblers should accept or bury during the second half, when reproductive success decreases with time, instead of spending 7 days to desert and reinitiate a clutch, which would lead to little or no reproductive success (see Guigueno and Sealy 2010: fig. 1). Other species forgo renesting later in the clutch initiation period because of limited time; in fact, the most important predictor of renesting by female Mallards (*Anas platyrhynchos*) was seasonal timing (Arnold et al. 2010). A similar situation seems to be operating in Yellow Warblers, in which the decision to abandon clutches is also plastic and apparently involves weighing the costs and benefits of rejection versus acceptance.

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