Aggression towards egg-removing cowbird elicits clutch abandonment in parasitized yellow warblers, *Dendroica petechia*

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The proximate causes triggering nest abandonment have important implications in the host−parasite arms race. Cowbird parasitism and rejection of parasitism are costly to some hosts; therefore, cues affecting their responses have important evolutionary implications. Experimental addition of a cowbird egg to the nest of a yellow warbler, a host that abandons nests parasitized by cowbirds via burial or desertion, elicited a rejection frequency similar to that of naturally laid cowbird eggs. Eggs experimentally added before sunrise (time of natural parasitism) were rejected at the same frequency as eggs added after sunrise; therefore, timing of parasitism did not influence rejection. Interaction with a robotic egg-removing cowbird increased the probability of abandonment, and the most aggressive individuals were likely to bury the model cowbird egg. Individual behaviours, therefore, were correlated across contexts. Host–parasite interactions and aggression are the two most important components in host defence. Future work should focus on the physiological aspects of individual variation, such as differences in hormone levels between individuals that accept and reject parasitized clutches.
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Insects (Zink 2003), fish (Kynard 1978; Coleman & Gross 1991) and birds (Hill & Sealy 1994; Hosoi & Rothstein 2000) abandon nests. Parental investment theory suggests that parents decide to abandon if the benefits of staying with their current nest are outweighed by the possible benefits gained by abandonment (Trivers 1972; Coleman & Gross 1991; Winkler 1991). Cues that elicit nest abandonment, however, are generally unclear (Peer et al. 2005). Cues activate specific cognitions in working memory, which dispose individuals to respond in ways that enhance their fitness (Schaller et al. 2007). Decreases in clutch or brood size apparently elicit abandonment in insects (Zink 2003), fish (Jennions & Polakow 2001) and birds (Armstrong & Robertson 1988; Sealy 1992; Hill & Sealy 1994; Kosciuch et al. 2006), although not always, especially in birds (Peer et al. 2005). Bird clutches may be abandoned in the context of brood parasitism, but the stimulus for abandonment apparently involves more than the mere presence of the parasitic egg in the nest for many cowbird hosts (Graham 1988).

Natural selection should favour the development of defences against brood parasitism because of the costs imposed on the hosts (Rothstein 1975; Sealy 1992; Lorenzana & Sealy 1999; Rasmussen & Sealy 2006). Hosts may eject the egg or abandon the parasitized clutch and thus reduce fitness costs (Sealy 1995; Rothstein 1990; Hosoi & Rothstein 2000). Abandonment usually involves other cues that are largely unknown within and outside the context of cowbird parasitism (Rothstein 1975; Hosoi & Rothstein 2000; Peer et al. 2005). Factors such as life-history traits and gape-size limitations may account for the prevalence of abandonment (Servedio & Hauber 2006). Species that do not grasp-eject cowbird eggs may not be able to discriminate between their own eggs and the parasite's egg, or their bills may be too small to grasp the egg (Sealy 1996; Peer et al. 2005; Underwood & Sealy 2006; Rasmussen 2008). Species unable to discriminate between their own eggs and the parasite's eggs may rely on other cues, such as an interaction with the brood parasite (Moksnes & Røskaft 1989; Sealy 1995; Hosoi & Rothstein 2000), to determine whether they have been parasitized.

The yellow warbler, *Dendroica petechia* (hereafter warbler), is the only host of the brown-headed cowbird, *Molothrus ater* (hereafter cowbird), known to regularly abandon parasitized clutches by burying cowbird eggs, often with its own eggs, and then lay a new clutch in a superimposed nest (Clark & Robertson 1981; Sealy 1995; Mico 1998). Warblers also may abandon their nest and nest site

(nest desertion) (Sealy 1995), which is another possible anti-parasite defence (Hosoi & Rothstein 2000; Guigueno & Sealy 2010). Sealy (1995) combined experimental parasitism and placement of a female cowbird mount in laying position on warbler nests but the rejection frequencies recorded at experimental nests ($\sim$8%) were not as high as those at naturally parasitized nests ($\sim$45%).

Addition of a cowbird egg to nests, interaction with a taxidermic mount of a cowbird in laying position (Sealy 1995) and removal of a host egg (Sealy 1992) elicit considerably less rejection than that recorded at naturally parasitized nests (Sealy 1995). We predicted that these cues are not sufficient for making the decision to abandon. We hypothesized that interactions with cowbirds during acts of laying and egg removal (see below), together with clutch manipulations at natural laying times, provide the key stimulus and, hence, are the most important cues (Hypothesis 1), as increased interaction in addition to clutch manipulation increases abandonment in a common cuckoo, *Cuculus canorus*, host (Moksnes & Røskaft 1989; Moksnes et al. 2000). Warblers on our study site are usually present at their nest around sunrise when cowbirds lay (Neudorf & Sealy 1994; Sealy et al. 2000). We predicted that visits before sunrise to add a cowbird egg and place a mounted female cowbird in laying position on the nest in combination with visits to nests after sunrise on the same day to remove a host egg and present an egg-removing cowbird would elicit the most rejection among all groups. Abandonment (burial or desertion) would be recorded most frequently at nests with the most parasitic disturbance (i.e. with all four factors present), and rejection at these nests should be similar to that of naturally parasitized nests.

Warblers respond more aggressively to a perched cowbird after being exposed to an egg-removing cowbird than after exposure to a laying cowbird (Campobello 2008), suggesting that interaction with an egg-removing cowbird is more likely to elicit rejection of a parasitized clutch. Cowbirds remove one host egg, most frequently during the host's laying day 2 (LD2), from about one-third of warbler nests parasitized (Sealy 1992), unlike predators that usually remove all eggs (Sealy 1994). Individual warblers vary in the rate of seet calling and in the number of strikes on a cowbird mount (Campobello 2008). Warblers utter seet calls preferentially towards cowbirds, which may startle cowbirds and deter them from nest searching, and they utter chip calls towards nest predators (Sealy et al. 1995; Gill & Sealy 2003, 2004). Individual variation in aggression may influence which birds accept or reject parasitism (Hypothesis 2). We predicted that females that seet-called and struck cowbird mounts most frequently would be more likely to bury or desert a 'parasitized' nest. Individuals may be more aggressive relative to others across contexts, and aggressiveness may be correlated with other behaviours (behavioural syndromes; Riechert & Hedrick 1993; Maupin & Riechert 2001; Sih et al. 2004). Aggressiveness may be a behavioural syndrome in warblers if the more aggressive individuals, in addition to attacking the cowbird mount, also abandon their clutch. Host aggression against adult cuckoos and egg rejection behaviour evolve in tandem, and, thus, accepter species are less aggressive than rejecter species (Røskaft et al. 2002). Similarly, cowbird hosts are increasingly aggressive with increasing parasitism frequency (Robertson & Norman 1976).

We added a cowbird egg before sunrise at some nests and after sunrise at other nests during the same breeding season to examine temporal shifts in rejection behaviour. We hypothesized (Hypothesis 3) that adding cowbird eggs to nests before sunrise would elicit rejection because parasitism naturally occurs at this time (McMaster et al. 2004). We predicted that naturally parasitized nests and nests experimentally parasitized before sunrise would elicit similar frequencies of rejection and that they would elicit more rejection than nests experimentally parasitized after sunrise (Sealy 1995).

Our objectives were to determine which aspects of brood parasitism (i.e. clutch manipulations, interactions with brood parasites, timing of parasitism) elicit rejection and whether aggression influences rejection. Although we examined cues associated with parasitism that elicit abandonment by a host, we also gained insight into the level of disturbance tolerated by a nesting animal.

METHODS

Study Site and Species

We conducted our first experiment in May and June 2008 and a second experiment in 2009 at Delta Marsh, Manitoba, Canada (50°1′N, 98°19′W), on the properties of the Delta Marsh Field Station (University of Manitoba), Portage Country Club, Delta Waterfowl Station, and Bell Estate (MacKenzie 1982; Briskie et al. 1992). Warblers and cowbirds have been recorded at Delta Marsh since at least the 1800s (Thompson 1891) and they are common there every year. This long interaction with cowbirds has resulted in the evolution of two host behaviours that are elicited by the presence of cowbirds: seet calls and nest-sitting behaviour (during which the warbler returns quickly and sits tightly on its nest) (Hobson & Sealy 1989; Gill & Sealy 2004). Each year through the mid-1980s, frequency of parasitism on warblers at Delta Marsh averaged about 21%, but ranged from 14% to 31% (Sealy 1995). Parasitism frequency is positively correlated with overall host abundance, so the availability of other host species is likely to influence the level of parasitism experienced by each host species (Woolfenden et al. 2004).

Criteria for Acceptance and Rejection

We included four experimental groups (groups 2a, 2b, 3a, 3b) and one control group (group 1) in 2008, each containing a before-sunrise component (Table 1). Model cowbird eggs were recorded as accepted if warblers completed their clutches and tended them for 6 consecutive days (Sealy 1995). This criterion is a trade-off between excluding rejections related to factors other than parasitism, such as predator interference or inclement weather, and includes rejections delayed as a result of experimental parasitism; less than 1% of rejection responses occur after 5 days (Rothstein 1982), although individuals of some species take longer to respond to parasitism (Peer & Sealy 2000). Each nest was checked every 24 h after the addition of a model egg or after initial disturbance (controls) on LD2 (Sealy 1995). If a model egg appeared to be rejected, we inspected the nest for a few more days to confirm the type of response because a nest may seem deserted one day, but the adults may be tending the eggs the next day, and because burial of the clutch can take more

Table 1
Experimental groups: all tests were conducted on the day that yellow warblers laid their second egg (LD2); nests were visited daily for 6 days to record acceptance or rejection of the 'parasitized' clutch. Females from all groups were flushed from their nests

Group	Before sunrise (0415–0530 hours)	After sunrise (0700–1200 hours)
1	Host egg touched	Host eggs touched
2a	Cowbird egg model added	Host eggs touched
2b	Cowbird egg model added	Host egg removed
3a	Laying event simulated[*]	Host eggs touched
3b	Laying event simulated	Egg-removing event simulated[†]

All times are Central Daylight Time.

[*] A female cowbird mount in the laying position was placed on the nest after a cowbird egg model had been added to the nest.

[†] A robotic female cowbird in the egg-removing position (with an artificial host egg in the bill) was placed on the nest rim and a host egg was removed.

than 1 day to complete (Guigueno & Sealy 2009, 2010). We removed model eggs from nests when the test was over, unless they had been buried, and we examined models for peck marks indicating that the hosts had attempted to puncture-eject them (Rothstein 1977). We looked into each experimental nest during daily nest checks to see whether a model cowbird egg was gone and, if so, gently pressed the bottom of the inside of the nest cup to determine whether it had been buried. Nests were considered deserted when the putative parents were not observed nearby for 3 consecutive days and the eggs were cold (Sealy 1992, 1995).

Time of Manipulations Relative to the Nesting and Breeding Cycles

All nests were manipulated on the warbler's LD2, as responses to parasitism change during the nesting cycle and cowbirds frequently parasitize nests on the first or second day of the host's laying (Clark & Robertson 1981; Sealy 1995; Guigueno & Sealy 2010). Yellow warblers are less likely to abandon parasitized clutches later in the breeding season because they may not have enough time to renest; therefore, acceptance could avoid delays associated with egg burial or desertion (Clark & Robertson 1981; Sealy 1995; Guigueno & Sealy 2010). To minimize this effect on abandonment frequencies, we conducted tests during the first half of the breeding season (6–20 June) in 2008 and 2009.

Model Egg Addition

Most cowbirds parasitize nests during a 0.5–1-hour 'window' before sunrise and before egg laying by warblers (McMaster et al. 2004). To properly simulate parasitism, we added model eggs to nests before sunrise. Cowbirds at Delta Marsh lay a mean ± SE of 31.2 ± 2.0 min before sunrise, and warblers lay 13.3 ± 2.8 min after sunrise (McMaster et al. 2004). Sunrise times between 6 June (2008 clutch initiation date) and 20 June 2008 ranged from 0523 to 0530 hours Central Daylight Time, CDT (Astronomical Applications Department, U.S. Naval Observatory, Washington, D.C.: http://www.usno.navy.mil/USNO/astronomical-applications/data-services/rs-one-year-us). Experimentally parasitized nests received a model egg between 0415 and 0530 hours CDT (68–75 min before sunrise to 0–7 min after sunrise). This interval probably encompasses all times when cowbirds parasitize warbler nests at Delta Marsh (Sealy et al. 2000; McMaster et al. 2004).

We inspected nests the afternoon before parasitism to confirm each nest's precise location, which had been marked nearby with numbered flasher tape. Treatments were randomly assigned to assistants conducting manipulations by rolling a dice the night before the tests were to begin. We monitored 11 nests naturally parasitized early in laying (LD1 or LD2) to determine the rejection frequency for comparison with experimental nests.

In May and June 2009, we added model cowbird eggs before sunrise at some nests and after sunrise at other nests (Hypothesis 3) to determine whether the timing of clutch manipulation relative to sunrise and host egg laying affected rejection frequency. We also monitored six nests naturally parasitized in early laying (LD1 or LD2) to compare rejection frequencies between experimentally and naturally parasitized nests.

Model Eggs

All model eggs were made of plaster and painted with nontoxic, water-resistant acrylic paints (Folk Art Opaque Acrylic Paints by Plaid®; Plaid Enterprises Inc., Norcross, GA, U.S.A.; product numbers and colours below) to resemble cowbird eggs. The background of cowbird eggs was off-white (Wicker White 1643 mixed with

Figure 1. Mounts of a female brown-headed cowbird (a) in laying position on a yellow warbler nest and (b) during a host egg-removal event (with an artificial yellow warbler egg in its bill).

Licorice 1506) with brownish markings (Burnt Umber 1618 mixed with Wicker White) that varied in diameter (Lowther 1993; Guigueno 2010). The colours were mixed to resemble closely the coloration of real cowbird eggs (which resemble warbler eggs) to a human observer.

Model eggs had a Styrofoam centre to match the weight of real cowbird eggs. The dimensions and weights of the models (length: 22.50 ± 0.05 mm, width: 17.05 ± 0.05 mm, mass: 3.1 ± 0.02 g, $N = 212$) were similar to 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). All models were sanded three times, each with finer sandpaper, before they were painted to ensure that their surfaces were smooth. Each model was heated in the hand for 10 s before being placed into a nest, and each nest was used for only one test.

Behavioural Responses

Behavioural responses of warblers to laying and egg-removing taxidermic mounts (Fig. 1) were videorecorded using Sony DCR-SR62 and DCR-SR65 camcorders (Sony of Canada Ltd., Toronto, Ontario, Canada) to determine whether individuals with the most aggressive response (i.e. more strikes and seet calls) were more likely to reject parasitized nests. Laying and egg-removing cowbird mounts were placed on nests for 1 min of interaction, or for up to 5 min if the parents were not seen within 5 m of the nest. Laying lasts about 1 min (Sealy et al. 1995; McMaster et al. 2004), and cowbirds take less than 1 min to remove a host egg (S. G. Sealy, unpublished data). We recorded behaviour at all nests, including

controls, to be consistent across experimental groups. We recorded the warblers' behaviour for 1 min from natural cover (Höhn 1993), about 7.5 m from the nest, wearing camouflage clothing and hats. We waited up to 5 min for the adults to appear if they were not immediately in the vicinity of the nest. Hosts may silently watch a cowbird mount (Hobson & Sealy 1989; Neudorf & Sealy 1992; Gill et al. 1997) or be 'out of the area' during presentations of cowbird or sparrow mounts, depending on the stage of the nesting cycle (Hobson & Sealy 1989; Gill et al. 1997). Therefore, warblers do not always attack cowbird mounts placed near their nest. To be consistent across all groups, we visited each nest as a control, to manipulate the eggs or to place a cowbird mount at the nest. Then, after recording the warbler's behaviour, we returned to the nest to manipulate the eggs again and/or to remove the cowbird mount. No additional disturbance was created in groups 3a and 3b compared to groups 1, 2a and 2b because we used the same method across all groups (see Table 1).

We recorded from videos the number of seet calls and chip calls given during 1 min. Seet calls denote cowbirds, whereas chip calls denote any nest predator (Gill & Sealy 2004), so by recording calls, we determined whether warblers perceived the mounts as cowbirds before sunrise (laying) as well as after sunrise (egg-removing). We also recorded the number of times each female warbler struck the cowbird mount with its bill or body. Before sunrise, built-in infrared light in the camcorders, supplemented with an external infrared light (Sony of Canada, model number: HVL-IRM), produced a clear image.

Freeze-dried mounts of female cowbirds were used for treatments 3a and 3b (Fig. 1). Two mounts of females in laying position (Fig. 1a) and two egg-removing mounts (Fig. 1b) were made from salvaged cowbird carcasses, which were appropriately positioned, frozen and freeze-dried for about 4 days. The egg-removing mounts stood upright and had an artificial warbler egg (prepared as described above, but without the Styrofoam centre) secured in the open bill. The feet of each mount were attached to a dowel connected to a radiocontrolled servo, which was attached to a nearby branch. The receiver and the external battery were either affixed to the ground or secured to a nearby tree or branch. The robotic egg-removing mount was positioned in the warbler's nest with its head oriented into the nest. When the servo was activated, the head rotated upward about 10 cm from its original position.

Statistical Analyses

We used a Fisher's exact test to compare the highest rejection frequency recorded at an experimental group in 2008 with the rejection frequency at naturally parasitized nests in 2008 because more than 20% of the cells had expected values of less than five (Zar 1999). We used a 3 × 2 Fisher's exact test to compare the rejection frequencies at nests experimentally parasitized before and after sunrise and at naturally parasitized nests in 2009. We report means ± SE throughout the text. All P values ≤0.05 were considered significant.

To determine which factors influenced rejection in warblers, we used the 'PROC LOGISTIC' procedure in SAS (SAS Institute, Cary, NC, U.S.A.) and performed logistic regression on four potential predictor categorical variables (add cowbird egg, remove host egg, laying cowbird, egg-removing cowbird) (Kosciuch et al. 2006). Models predicted the probability of rejection given the presence or absence of each categorical variable. All variables were absent for group 1, 'add cowbird egg' was present for groups 2a, 2b, 3a, 3b, 'remove host egg' was present for groups 2b and 3b, 'laying cowbird' was present for groups 3a and 3b, and 'egg-removing cowbird' was present for group 3b. We used Akaike's Information Criterion corrected for small sample sizes (AIC_C) to rank various general linear models using logit link functions (Kosciuch et al.

2006). We used a backward stepwise logistic regression based on AIC values to select a best-supported model. The most parsimonious model had the lowest AIC_C value ($\Delta AIC_C = 0$); however, additional models with ΔAIC_C less than or equal to 2 were considered equally parsimonious (Anderson et al. 2000). Also, the strength of support for each model was determined by calculating Akaike weights (ω_i). We determined the direction and strength of each effect from the odds ratio (e^β). An odds ratio less than 1 indicates that the factor reduced the odds of an effect, an odds ratio greater than 1 indicates that the factor increased the odds of an effect, and an odds ratio of 1 indicates that the factor had no effect (Stokes et al. 2000; Kosciuch et al. 2006).

Seet calls and strikes were recorded in group 3b. We used exact logistic regression to determine whether there were differences in the number of strikes, seet calls and chip calls between individuals that rejected or accepted parasitism because the sample sizes in each group (accepted versus rejected) were small and thus the data did not fit a regular logistic model (Hirji et al. 1987; Stokes et al. 2000). Hirji et al. (1987) programmed this technique, which was originally devised by Cox (1970) for SAS within the 'PROC LOGISTIC' procedure. Analysis of small, sparse and skewed data is frequently unreliable if general linear models, mixed-effect models, or other asymptotic methods of analysis are used (Derr 2000; Stokes et al. 2000). AIC values, however, cannot be computed in exact logistic regression; therefore, we analysed each behavioural measurement (strike, seet call, chip call) in a separate model, then determined the direction and strength of each behavioural characteristic on rejection behaviour using the exact odds ratios.

Ethical Note

Our experiments were approved by the University of Manitoba Committee on Animal Care (Animal Care Utilization Protocol, references F08-005 and F09-004). Scientific permits were issued by the Canadian Wildlife Service, Environment Canada (permit numbers CWS 08-S0010 and 09-MB-SC009).

RESULTS

A total of 158 experimental nests (including two 'egg ejections') survived for 6 days (Table 2). Warblers apparently did not attempt to puncture-eject accepted egg models because none showed peck marks. In the two cases of 'egg ejection', the model eggs were probably removed by a predator rather than by the warblers because (1) at one nest, the model egg disappeared between the fifth and sixth daily checks and the adults were not seen on day 5 or 6, and (2) at the other nest, the model egg went missing on the fifth day and the nest was

Table 2
Responses of yellow warblers to clutch manipulations and cowbird mount presentations

Group	Treatment	Rejection[*]		Acceptance	Total nests	Rejection frequency (%)
		Burial	Desertion			
1	Control	1	1	54	56	3.6
2a	Add egg	6	1	15	22	31.8[†]
2b	Add+remove eggs	2	1	20	23	13
3a	Laying mount	1	0	22	23	4.3
3b	Laying+egg-removing mounts	3	3	26	32	18.8

[*] Two 'ejections' were recorded. Group 2a: an artificial cowbird egg disappeared on the 6th daily check, but the adults were not seen on day 5 or 6. Group 3a: an artificial cowbird egg disappeared on the 5th daily check, but the nest was damaged on day 5 or 6.
[†] Similar to the frequency observed at nests that were naturally parasitized during the first 2 days of host laying (LD1 or LD2) in 2008 (27%, N = 11).

damaged. Therefore, we did not include these two 'ejections' in the statistical analyses. To qualify as a host 'ejection', host eggs must remain intact and be tended by the host (see Rothstein 1975).

Most rejections occurred in group 2a, with abandonment recorded at about the same frequency as that at naturally parasitized nests (Table 2), and these frequencies did not differ significantly (Fisher's exact test: two-tailed $P > 0.999$). The top logistic regression model (ΔAIC_C) contained all four factors (Table 3). Models with 'add cowbird egg' received 98% of the support among models, 'laying cowbird' received 74%, 'egg-removing cowbird' received 56% and 'remove host egg' received 29% of the support (Table 3). The only supported single factor model contained 'add cowbird egg'. Four models were considered equally as parsimonious ($\Delta AIC_C \leq 2$; Table 3).

Warblers whose nests received an egg before sunrise (group 2a) were 12.60 times (95% CI = 2.37, 67.10) more likely to reject parasitism than warblers that did not receive such an egg (group 1) (Table 2). Warblers at nests from which a host egg was removed (group 2b) were 0.32 times less likely to reject parasitism than warblers at nests with no host eggs removed (group 2a) (Table 2), but the 95% CI surrounding this estimate included one (0.07, 1.45). Warblers from nests at which the laying cowbird mount was presented (group 3a) were 0.10 times (95% CI = 0.01, 0.88) less likely to reject parasitism than warblers at nests with no mount present (group 2a) (Table 2). Warblers at nests at which the egg-removing cowbird mount was presented (group 3b) were 15.80 times (95% CI = 1.10, 226.06) more likely to reject parasitism than warblers at nests with no egg-removing mount present (groups 3a, group 2b). For the last variable ('egg-removing cowbird'), the rejection frequency for group 3a was multiplied by 0.32 ('remove host egg'), then multiplied by 15.6 ('egg-removing cowbird') to acquire the approximate rejection frequency for group 3b because the effects of these factors are additive (Table 2). The top parsimonious equation containing all factors is presented below. Positive β estimates indicate that a factor increased the probability of rejection, whereas negative β estimates indicate that a factor decreased the probability of rejection:

$$Logit(P) = -3.30 + 2.53(\text{add cowbird egg})$$
$$- 1.14(\text{remove host egg}) - 2.33(\text{laying cowbird})$$
$$+ 2.76(\text{egg-removing cowbird})$$

Laying cowbird mounts presented before sunrise did not elicit attacks or seet calls. Most warblers from groups 3a and 3b (89%, $N = 55$) flushed from their nests, and none were seen within 5 m of their nest (i.e. they moved out of sight) following placement of the laying mount. Warblers in the other treatments showed a similar response to a 'control' disturbance (group 1: 84% flushed, $N = 56$; groups 2a and 2b: 89% flushed, $N = 22$, $N = 23$). However, the laying

Table 3
Results of the logistic regression models for the probability of rejection of a parasitized clutch by yellow warblers, in response to clutch manipulations and cowbird mount presentations

Logistic regression model	AIC_C*	ΔAIC_C†	w_i‡
Add egg+remove egg+laying cowbird model+egg-removing cowbird mount	112.10	0.00	0.29
Add egg+laying cowbird model+egg-removing cowbird mount	112.31	0.20	0.26
Add egg	112.51	0.41	0.24
Add egg+laying cowbird mount	113.02	0.91	0.19
Intercept only (null model)	117.62	5.52	0.02

* AIC corrected for small sample sizes.
† Difference between current and most parsimonious models.
‡ Akaike weights.

mount decreased the probability of rejection, strongly suggesting that it influenced the warblers' response. Egg-removing mounts presented after sunrise elicited attacks, seet calls and chip calls from most individuals (68%, $N = 32$), and all individuals were nearby (i.e. they could see the mount) when the egg-removing cowbird was present. Three warblers simultaneously attacked the egg-removing cowbird mount at one nest. Individuals that buried the eggs in their nest or that deserted their nest following the addition of a model egg chipped less frequently than those that accepted the model eggs ($\beta = -0.5039$, $P = 0.0467$). For every chip call, individuals were 0.604 times (95% CI = 0.117, 0.998) less likely to reject. The number of strikes ($\beta = 1.6609$, $P = 0.0605$) and seet calls ($\beta = 0.0905$, $P = 0.1323$), however, had little effect on the probability of rejection.

Results differed, however, when we compared acceptances versus burials only. The egg-removing mount elicited responses from most individuals that either buried or accepted model eggs (76%, $N = 29$). Individuals that buried model eggs struck the mount more than individuals that accepted model eggs ($\beta = 2.566$, $P = 0.0148$). For every strike, individuals were 13.010 times (95% CI = 1.338, ∞) more likely to bury the eggs. Individuals that buried model eggs seet-called more than individuals that accepted model eggs ($\beta = 0.1389$, $P = 0.0307$). For every seet call, individuals were 1.149 times (95% CI = 1.011, 1.359) more likely to bury model eggs, however, the number of chip calls ($\beta = -0.255$, $P = 0.4431$) had no effect on the probability of burial. For every chip call, individuals were 0.775 times (95% CI = 0.185, 1.056) less likely to bury, but the confidence interval included one.

Rejection was recorded at 21.9% ($N = 32$) of the nests that were experimentally parasitized before sunrise and at 21.1% ($N = 38$) of the nests that were experimentally parasitized after sunrise in 2009. These frequencies did not differ significantly from rejection at naturally parasitized nests (33.3%, $N = 6$) in 2009 (3×2 Fisher's exact test: $P = 0.7659$).

DISCUSSION

Influence of Cowbird–Host Interactions and Clutch Manipulations on Abandonment

Our most surprising result was that the laying cowbird mount elicited the opposite response to what we expected: fewer rejections occurred when a laying female cowbird mount was placed on the nest at the time of experimental parasitism. The addition of a model egg before sunrise (group 2a) elicited the most rejection among treatment groups, whereas the addition of a model egg and placement of a laying cowbird mount on the nest (group 3a) elicited the fewest rejections (Table 2). During placement of the laying cowbird mount for groups 3a and 3b, most females (89%, $N = 56$) were flushed from their nests before sunrise, and none of these females returned to attack the mount. In a previous study, more than half of the female hosts roosted in their nest overnight and averaged 28 min in their nests during the 30 min 'critical period' when cowbirds were most likely to parasitize nests (Neudorf & Sealy 1994). However, by flushing in low light and not returning, the yellow warblers in our study may not have recognized the mount as a cowbird. Adult warblers have been observed attacking laying cowbirds in nature (Sealy 1995; Sealy et al. 2000). Thus, cowbirds may be intercepted by some of their hosts as they approach the hosts' nests and, thus, before the cowbirds can physically remove the host's egg and parasitize the nest (Tewksbury et al. 2002).

Warblers in groups 3a and 3b apparently saw the mount (if they had not, no effect would have been expected), but they may not have recognized it as a brood parasite. Instead, they may have recognized it as a nonspecific stressor (i.e. an unknown threat). For birds in

treatment groups 1, 2a and 2b, we simply waited for up to 5 min at a distance of 7.5 m from nests and placed nothing on the nest ('control disturbance'). In contrast, the birds in groups 3a and 3b were exposed to the laying cowbird mount on their nests for 5 min. Thus, this prolonged exposure to an unknown threat could have resulted in a potentially different response from that of the other treatment groups (Siegel 1980; Harvey et al. 1984; Whittow 2000). Many other animals forgo nonessential behaviours in situations with unknown stressors (Siegel 1980; Whittow 2000; Korte et al. 2005), so the warblers in groups 3a and 3b may have simply 'ignored' the potential cue to reject because of the higher stress level. It is also possible that a mobile cowbird mount, a robotic bird capable of intercepting the warbler at the nest or a trained live bird would have better simulated natural laying than the stationary cowbird mount used in our study. Alternatively, warblers may have been less aggressive, and therefore less likely to reject (see below), when confronted with a laying cowbird mount whose position resembled that of the submissive preening invitation display used by cowbirds to reduce host aggression (Selander & La Rue 1961; Robertson & Norman 1976). It is difficult to know whether interaction with a laying cowbird in a natural context influences a host's decision to reject. Interaction with a laying cowbird after sunrise elicited few rejections (~8%) in a previous study (Sealy 1995), suggesting that interaction with a laying cowbird may not be as important as interaction with an egg-removing cowbird, although in Sealy's study, the laying mount was not placed on hosts' nests at sunrise, which is the natural parasitism time.

The egg-removing cowbird mount, unlike the laying cowbird mount, had a positive effect on egg rejection and it elicited more responses and more aggression than the laying mount (see also Campobello 2008). Our logistic regression model controlled for the presence of the laying cowbird mount in group 3b and revealed an increase in rejection from group 3a, which suggests that interaction with an egg-removing cowbird is necessary to elicit egg burial behaviour in warblers. After a cowbird egg has been laid in a nest, interaction with an egg-removing cowbird seems to be the most important cue used by warblers in making the decision to reject. This is not surprising, considering that parasitism through cowbird egg addition and host egg removal costs on average 0.6 fledglings per nest at Delta Marsh (Sealy 1992; Lorenzana & Sealy 1999) and egg-removal alone accounted for at least half of this cost in a warbler population in Montana (Tewksbury et al. 2002). In addition, warblers are much more effective at preventing cowbirds from removing their eggs than they are at preventing them from parasitizing their clutch (Tewksbury et al. 2002). It is presumably the egg-removing cowbird, not the removal of a host egg per se, that is the cue for rejection because 'remove host egg' was the least important factor in our logistic regression model. This is consistent with Sealy's (1992) results showing that the probability of warblers accepting a parasitic egg was not affected by the removal of a warbler egg at the time of parasitism. The effect of the egg-removing mount supports the hypothesis that increased interaction with the adult parasite in combination with the addition of a parasitic egg increases the probability of rejection (Davies & Brooke 1988; Moksnes & Røskaft 1989; Moksnes et al. 2000). A cuckoo mount at the nest promotes host egg discrimination (Davies & Brooke 1988; Moksnes & Røskaft 1989; Moksnes et al. 2000). To our knowledge, ours is the first study to demonstrate an increase in rejection with interaction with an egg-removing cowbird. In addition, the increased probability of egg burial by individuals that were more aggressive towards the egg-removing cowbird (see below) further supports the hypothesis that interaction with the parasite plays an important role in eliciting rejection in yellow warblers.

It is unlikely that a witnessed egg-removal event alone elicits egg burial, as yellow warblers rarely bury their own eggs (6 of 1885

nests examined; Sealy 1995). Adding a model egg to a nest is essential in eliciting rejection, because 'add cowbird egg' was the most important factor in our logistic regression model. Approximately 33% of cowbirds remove a warbler egg from nests they have parasitized (Sealy 1992), and rejection occurs at about 40% of parasitized nests, depending on the year and when the nest was parasitized relative to the host's laying cycle (see Results; Sealy 1995). The similarity between these two frequencies and results from the present study suggest that interaction with an egg-removing cowbird and the addition of a cowbird egg are important cues used by warblers to abandon parasitized clutches.

Adding a model cowbird egg to nests before sunrise elicited a rejection frequency nearly identical to that at naturally parasitized nests in 2008 and 2009, which was higher than that recorded in previous studies (Sealy 1995; Sealy & Lorenzana 1998). However, rejection did not differ between nests parasitized before and after sunrise in 2009. Therefore, the timing of egg addition did not affect abandonment of parasitized clutches by yellow warblers. Warblers rejected more experimentally added cowbird eggs in 2008 and 2009 (23.9%, $N = 92$) than they did 20 years ago (8.5%, $N = 47$) when Sealy (1995) added cowbird eggs to nests on the same laying day as in the present study (chi-square test with continuity correction: $\chi_1^2 = 3.89$, $P = 0.0485$). This increase in rejection of experimentally added eggs could be due to methodological differences because Sealy (1995) used real eggs, whereas we used artificial cowbird eggs in our experiments. However, model eggs in the present study were identical to real cowbird eggs in size, mass, colour and texture, and both real eggs and artificial eggs experimentally added to yellow warbler nests are rejected at identical frequencies (Stewart 2003). If the difference is not attributable to a difference in methodology, it may involve phenotypic plasticity or genetic changes. Data on cowbird abundance were lacking in our study as well as in Sealy's (1995) study; however, brood parasite abundance does not necessarily need to increase for egg rejection to increase in a host population (Soler et al. 1994). Our conclusion mirrors Soler et al.'s (1994), who explained a rapid increase in the frequency of ejection by European magpies, *Pica pica*, on the basis of phenotypic plasticity or genetic change, although the increase was unrelated to the local abundance of cuckoos.

Aggression is Correlated with Egg Rejection within a Species

Aggressive individuals, as measured by their interactions with the egg-removing cowbird mount, were more likely to bury parasitized clutches. This supports the prediction that aggression and rejection are correlated. The upward motion of the egg-removing cowbird elicited many of the attacks; therefore, movement may be an important cue for aggressive responses. Aggression against cuckoos and egg rejection behaviour may evolve in tandem, so that accepter species are less aggressive than rejecter species (Røskaft et al. 2002). This correlation can now be applied to between-individual comparisons within the same species of cowbird host. Yellow warblers are deemed intermediate egg rejecters because their rejection frequencies are less than 80% (Peer & Sealy 2004). Individual warblers that reject may have more experience recognizing a cowbird as a threat and, hence, react more aggressively towards it (Sealy 1995). Sealy (1995) found no difference in the frequency of rejection between yearling female warblers and older female warblers, however, age and experience do not necessarily go hand in hand because all nests are not parasitized every year (parasitism frequency varied from 14% to 31% between 1974 and 1987; Sealy 1995). Yearling warblers have no prior experience with parasitism, but they potentially have the opportunity to interact with egg-removing cowbirds at their nests without being parasitized, or with cowbirds at neighbouring nests,

because warblers may attack cowbirds cooperatively. Experience with previous clutch manipulation decreases the acceptance threshold of great reed warblers, *Acrocephalus arundinaceus*, a cuckoo host, when discriminating between experimentally modified host eggs and unmodified host eggs (Hauber et al. 2006; but see Hauber et al. 2004). A key test would be to track individual yellow warblers through many breeding seasons, collect data on previous parasitism history as a measure of experience, and compare aggression and rejection responses between experienced and inexperienced individuals.

Some warblers chip-called when they reacted to the egg-removing mount, which suggests they were not focused on the immediate threat at their nest (a cowbird removing an egg), but possibly considered us, or the cowbird, as a general threat (i.e. a predator). Despite being concealed behind natural cover (Höhn 1993) and wearing clothing that blended with the natural environment, warblers were probably still aware of our presence. We did not use blinds because of time constraints, but low levels of chip calling have previously been recorded in the presence of a cowbird mount in which blinds were used in other studies (Hobson & Sealy 1989; Gill & Sealy 2004); thus, blinds may not have reduced the amount of chip calling. Our results suggest that individuals that were more focused on their nests (i.e. that chipped less) were more likely to reject parasitism. They may have been more experienced with the threat of parasitism and reacted by seet calling and striking the cowbird instead of chip calling. Yellow warblers in naïve populations seet-called less frequently in response to a cowbird mount than individuals in sympatric (more experienced) populations (Gill & Sealy 2004; Kuehn 2009).

Aggression by warblers across contexts and the correlation between aggressive responses to cowbird mounts and aggressive responses to experimentally parasitized clutches may be an example of a behavioural syndrome (Sih et al. 2004; Dingemanse et al. 2010). Although both of these aggressive responses occur within the context of brood parasitism, they can be considered responses to different threats: rejecting a parasitized clutch versus attacking a cowbird that may remove a host egg (Sih et al. 2004; A. Sih, personal communication). A behavioural syndrome is defined as two or more behaviours that are correlated across situations, and a situation is defined as 'a given set of conditions at one point in time' (Sih et al. 2004, page 372). Therefore, responding to a parasitized clutch over a few days involves a different set of conditions than responding to the immediate threat of egg loss. The concept of behavioural syndromes may now be applied to the host of a brood parasite in which correlated behaviours (aggression towards a brood parasite and burial of the parasitized clutch) are both adaptive. Nevertheless, stronger evidence for a behavioural syndrome would be provided by additional observations of similar behaviour in a nonadaptive context (such as aggression towards offspring). Behavioural types have important evolutionary implications, such as effects on species distribution, phenotypic and environmental plasticity, and on speciation rates (Sih et al. 2004).

Future Research

We found that more aggressive individuals were more likely to reject parasitism. There may be a physiological basis for this individual variation, such as hormone levels that vary with age, experience and aggressiveness (Hutchinson et al. 1967; Wingfield & Soma 2002; Love et al. 2004; O'Dwyer et al. 2006). Testing whether egg rejection frequencies are influenced by differences in hormone levels would allow us to gain insight into the proximate mechanisms underlying these behaviours. Such studies should enhance our understanding of the physiological factors influencing

rejection and clutch abandonment in hosts of brood parasites and in birds that abandon their clutches outside the context of brood parasitism (Hoi et al. 1994).

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