

# An experimental test of preferences for nest contents in an obligate brood parasite, *Molothrus ater*

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We conducted a series of experiments designed to examine the stimuli to which female brown-headed cowbirds (*Molothrus ater*) attend when selecting a nest for parasitism. We gave hand-reared juvenile and wild-caught adult females opportunities to assess nests containing different numbers and types of mock eggs. We measured female interest in nests by recording the number of times they approached nests (experiments 1 and 2), and also, we maintained 5 groups of adult and 2 groups of juvenile females in outdoor aviaries where we could measure patterns of laying in nests (experiment 3). Results from both types of experiments were similar. Females of both age classes preferred nests with eggs over nests without eggs, nests containing 3 eggs to nests containing 1 egg, small eggs to medium sized eggs, and medium eggs to large eggs. In addition, there was an age-related effect in how females responded to a nest that already contained a cowbird egg. Adult females avoided nests containing cowbird eggs, whereas juveniles preferred these parasitized nests. Taken together, the results provide evidence of the adaptive nature of decision processes involved in host nest selection. *Key words*: brown-headed cowbird, cognition, decision processes, host selection. [*Behav Ecol* 18:922–928 (2007)]

Fitness of generalist obligate brood parasites depends on the ability of females to lay their eggs in suitable host nests. Selecting a suitable nest can be a challenge. There are more ways of choosing a nonsuitable host nest than a suitable one. Only hosts that will feed their young an insect diet, incubate their clutches for an appropriate amount of time to allow the parasite young to hatch, and have young of a size that can be effectively outcompeted for food by the parasite young will raise the parasite successfully. Errors in host nest choice by parasites can result in a failed opportunity for reproduction. Selection therefore may have favored abilities in female parasites that would allow them to select host nests that offer the best chance of survival for their offspring. Once a suitable host species is selected, it is also important that the parasite times egg laying such that her young will hatch successfully. Parasitizing a nest too early or too late may result in their young being at a developmental disadvantage compared with the host young. Because of these demands in selecting a nest, parasites provide a good model to study how selection pressures arising from breeding biology can shape cognitive abilities and decision processes (Sherry et al. 1993).

In addition to the problem of finding a suitable nest, parasites must overcome the hosts' defenses (Gill, Grief, et al. 1997). A variety of species behave in ways that decrease their likelihood of being parasitized. Hosts can reject parasite eggs (Rothstein 1975; Hosoi and Rothstein 2000; Peer and Sealy 2004), respond aggressively toward parasites (Neudorf and Sealy 1992), abandon nests (Rothstein 1990), or bury a clutch of parasitized eggs (Sealy 1995). For example, yellow warblers, *Dendroica petechia*, are sensitive to the presence and sounds of female cowbirds (Gill and Sealy 1996, 2004; Gill, Neudorf, Sealy 1997). The presence of cowbirds can induce yellow war-

blers to defend (Gill and Sealy 2004) or burying their nests (Sealy 1995). Given such defenses, parasites must assess a nest quickly and unobtrusively.

Although it makes sense to expect that parasites can detect suitable nests, it is possible that they may have no such sensitivity to nest characteristics. If the overwhelming challenges for females are to locate a nest (Payne 1977) and avoid being detected by the host, then they may have no opportunity to be choosy. As long as the energetics involved in producing eggs are low enough (Carey 1996), female parasites may benefit from using a strategy of overproducing eggs and laying in any nest that they encounter (the "shotgun" strategy; Rothstein 1975). Although some parasite species have been reported to employ such a strategy (Kattan 1997), evidence from brown-headed cowbirds from the field suggests that cowbirds can be discriminating in host selection. Grant and Sealy (2002) showed that female cowbirds preferentially parasitize the nests of high-quality red-wing blackbirds over low-quality red-wings. Woolfenden et al. (2003) used genetic markers to determine patterns of cowbird host selection. They found that cowbirds in the wild used a mixed strategy, where some females have preferences for specific host species, whereas others parasitized a variety of host species.

We hypothesized that one way parasites could assess the acceptability of an opportunity for parasitism as well as avoid the defenses of hosts would be evaluate the contents of nests they encounter. Assessing nest characteristics could be done when the host was away from the nest. Specifically, the number of eggs present and the size of the eggs could be used as indicators of nest suitability. The number of eggs present in a nest could be used as a cue to indicate the readiness of a nest for incubation. Cowbird hosts have clutch sizes ranging from 2 to 8 (most commonly 4) and incubation times that range from 11 to 16 days (Friedmann 1929, 1963; Friedmann et al. 1977; Terres, 1980). In most passerines, incubation commences after the laying of the host's last egg (Podulka et al. 2004). Therefore, although there is variability here, some information about the nest's readiness for incubation could be provided from the number of eggs in a nest.

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The size of eggs could also be an indicator of an acceptable host. Hosts producing eggs of similar sizes as the parasite's own would be more likely to produce chicks of similar sizes as the parasite's chicks. We hypothesized that parasites would prefer nests containing eggs slightly smaller than their own. Smaller eggs would produce smaller host chicks, and thus the parasite's young's larger body size could potentially provide an advantage over the host's young in begging for food.

In addition to egg number and egg size, we were also interested in whether female cowbirds would attend to the presence of another cowbird egg in a nest. Because cowbird young are extremely vigorous competitors for food (Hauber 2003), it may benefit females to avoid parasitizing a nest that already contained a cowbird egg, an effect reported in the field (Ortega et al. 1994).

We were also interested in any age- or experience-related effects on nest selection. Were adult females superior to juveniles in selecting suitable nests? Individual learning about the quality of a nest would be unlikely because there would be very little possibility for reinforcement or feedback for the female as a result of making either a good or a bad nest selection (but see Hoover and Robinson 2007). There could, however, be a number of ways by which adults were better than juveniles at selecting a host nest, for example, they could be better at finding nests or competing over nests. If adults were superior in some way in selecting a quality nest for parasitism, it might be possible for juvenile females to learn socially from adults when selecting a nest.

We conducted a series of studies with captive juvenile and adult brown-headed cowbirds. Juveniles were hand reared and adults were wild caught, so they most likely differed in their experiences with nests. We tested birds in indoor flight cages and in large outdoor aviaries prior to and during the breeding season. We examined females' interest in approaching and laying eggs in various nests containing different mock egg stimuli. If selection has acted on the females' nest selection decision processes, we should be able to detect preferences for nests containing eggs that indicated the suitability of a host for rearing young, the readiness of a nest to be incubated, and whether the nest had already been parasitized.

## EXPERIMENT 1

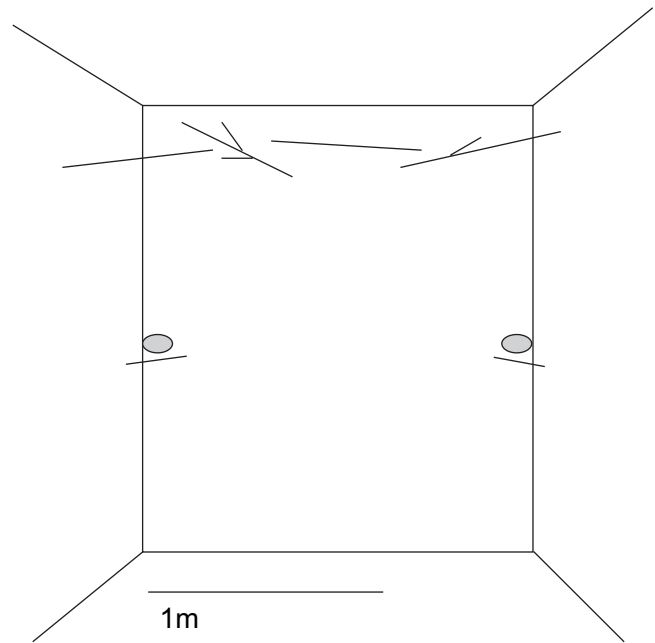
The first series of trials took place in February 2004 in an indoor flight cage. We housed and tested juvenile and adult females together. We conducted a series of choice tests and examined female approaches to nests varying in egg number and egg type.

### Subjects

In all, 8 hand-reared juvenile and 11 wild-caught adult female brown-headed cowbirds served as subjects for experiment 1. Each female wore unique combinations of colored leg bands to permit individual identification. Adults were wild caught and juveniles were hand reared in the summer of 2003. All females resided in large outdoor aviaries with males until October 2003, when we placed them into the flight cages for this experiment. Prior to the experiment, 7 males were also housed with the females. We moved the males to their own cage adjacent to the females for the duration of testing.

### Apparatus

The flight cage was  $4.26 \times 1.67 \times 2.13$  m, containing ad lib food and water, refreshed daily. The cage had perches situated approximately 0.25 m from the roof. Birds spent the majority of their time on these perches when experimenters were in



**Figure 1**  
Front view scale schematic of the indoor flight cage apparatus used in experiments 1 and 2.

the room. At the beginning of a trial, we placed 2 nests 1 m above the ground in the rear corners of the cage (see Figure 1). Nests were 9-cm-diameter canary breeding nests filled with Straw Weavers Spanish moss. We placed branches within 20 cm of the 2 nests so that females could land near and investigate the nests.

### Procedure

Beginning 9 February 2004, for each trial we provided 2 nests containing different types or numbers of mock eggs on either side of the cage. We then observed patterns of female approaches to the 2 nests for 20 min. We tested each stimulus pair twice with the locations in the flight cage counterbalanced; thus, for each pair of stimuli tested, we assessed female approach patterns for 40 min. The 2 tests for stimuli pairs were separated by at least 1 h. To be scored as an approach, females had to land on the nests or on the branches situated near the nest. We then compared, for each female, how many times she approached each nest.

### Stimulus presentations

**Egg number.** To test female preferences for the number of eggs present in nests, we used "medium"-sized mock eggs. These were white almond M&Ms (Masterfoods, Hackettstown, NJ) from a promotion where M&Ms were sold in packages containing only white and black color variants. Medium eggs were approximately 2.25 cm in length, the same approximate size as cowbird eggs (see Figure 2). We conducted 3 trials. First, we compared one nest containing 2 eggs with one nest containing no eggs (2 vs. 0). Second, we compared one nest containing 3 eggs with one nest containing 1 egg (3 vs. 1). Finally, we compared one nest containing 6 eggs with one containing 3 eggs (6 vs. 3). This last trial evaluated 2 clutch sizes within the range of cowbird hosts. We made this last comparison to detect whether females were preferring nests with more eggs to nests with fewer eggs, irrespective of the information that egg number may provide about hosts' incubation timing.



**Figure 2**

Candies used as mock egg stimuli. From left to right: real cowbird egg, medium M&M, large yogurt-covered almond used in experiments 2 and 3, small M&M, experimentally speckled M&M, black M&M. Also shown is a canary breeding nest containing Spanish moss and 3 medium M&Ms.

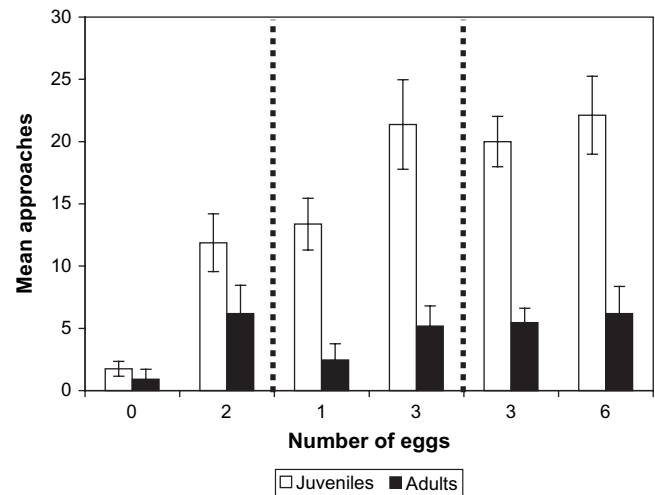
**Egg type.** Here, we used mock eggs of different colors and sizes. We conducted 4 trials. First, we compared one nest containing 2 white (W) medium eggs with one nest containing 2 black (B) medium eggs (2W vs. 2B). Given that there are no species on record that lay black eggs, we expected a large preference for the white eggs in this comparison. Second, we compared one nest containing 3 white medium (M)-sized eggs with one nest containing 3 white small (S) eggs (3M vs. 3S). Small eggs were M&M peanuts that were approximately 0.5 cm smaller in length than the medium eggs (Figure 2). We expected females to prefer the smaller eggs as such a nest would give their young a competitive advantage over the smaller host chicks. We then compared one nest containing 3 white medium eggs with one nest containing 3 white large eggs (3M vs. 3L). Large eggs were white-painted Cadbury eggs that were approximately 200% larger than the medium eggs. Given such a large discrepancy in size, we expected the females to show strong preferences for the nest containing medium eggs. Alternatively, if eggs served as a releasing stimulus, the large eggs could serve as super releasers that attracted the females to the large egg nests. Finally, we compared one nest containing 3 white medium white eggs with one nest containing 2 medium white eggs and one real cowbird egg (3W vs. 2WIC) to simulate a nest that had already been parasitized. Cowbird eggs are white with black speckles (see Figure 2).

### Statistics

For each of the trials, we used Wilcoxon signed-rank tests to analyze within-female comparisons. We used nonparametric tests because of indeterminate forms in approach data and nonnormal distributions.

### Results

Females were highly motivated to approach nests, and juveniles did so significantly more than adults. (Egg number trials: mean juvenile approaches =  $90.5 \pm 9.83$ , mean adult approaches =  $26.4 \pm 8.21$ ; Mann-Whitney  $U$ -test,  $U = 6$ ,



**Figure 3**

Mean ( $\pm 1$  SEM) approaches per female (juvenile and adult) to nests for egg number comparisons in experiment 1. Dashed lines represent separate experiments.

$N_1 = 8$ ,  $N_2 = 11$ ,  $P < 0.001$ .) Patterns of approaches are shown in Figures 3 and 4.

### Egg number trials

**2 versus 0.** Both juvenile and adult females approached the nest with 2 medium eggs significantly more frequently than they approached the empty nest (Wilcoxon  $T$ -test, juvenile females,  $T = 0$ ,  $N = 8$ ,  $P < 0.05$ ; adults,  $T = 0$ ,  $N = 11$ ,  $P < 0.005$ ).

**3 versus 1.** Both juvenile and adult females approached the nest containing 3 eggs significantly more frequently than they approached the nest containing 1 egg (juvenile females,  $T = 0$ ,  $P < 0.05$ ; adults,  $T = 8$ ,  $P < 0.05$ ).

**6 versus 3.** Neither juvenile nor adult females showed any significant preference for approaching one nest over the other in this trial (juvenile females,  $T = 8$ , not significant [NS]; adults,  $T = 21$ , NS).

### Egg type

**2W versus 2B.** Juvenile but not adult females approached the nest containing the white eggs significantly more than they approached the nest containing the black eggs (juvenile females,  $T = 0$ ,  $P < 0.05$ ; adults,  $T = 16$ , NS).

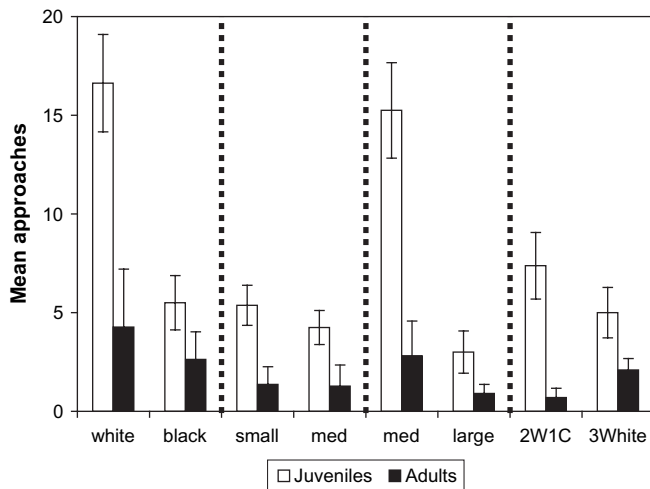
**3M versus 3S.** Neither group showed a preference in this trial, though both tended to have more approaches to nest containing the smaller eggs (juvenile females,  $T = 8.5$ , NS; adults,  $T = 6.5$ , NS).

**3M versus 3L.** Juvenile females approached the nest containing the medium eggs more frequently than they approached the nest containing the large eggs ( $T = 0$ ,  $P < 0.05$ ). Adult females did not show a significant preference ( $T = 4.5$ , NS).

**3W versus 2WIC.** Juveniles showed a significant preference to approach the 2WIC nest ( $T = 4$ ,  $P < 0.05$ ), whereas adults showed no significant preference, though they had a trend to approach the nest with 3 white eggs more often ( $T = 4$ ,  $P = 0.088$ ).

### Discussion

Females preferred to approach nests with eggs over nests without eggs and they also preferred nests with 3 eggs over nests with 1 egg but showed no preference for nests with 3 eggs over



**Figure 4**  
Mean ( $\pm 1$  SEM) approaches per female (juvenile and adult) to nests for egg-type comparisons in experiment 1. Dashed lines represent separate experiments.

nests with 6 eggs. In addition, they tended to prefer nests with eggs smaller than their own, and they preferred nests with eggs similar in size to their eggs over nests containing eggs larger than their own. Although adult females had significant differences in approaches in the first 2 trials and, in general, they showed the same patterns as the juveniles throughout, they approached nests less frequently than did the juveniles. The adults thus had nonsignificant patterns of approaches through most of the trials, including some where we expected to see the largest results (black vs. white, large vs. medium). This lack of interest in approaching nests by the adults may have occurred because the trials occurred prior to the breeding season and thus prior to egg laying. Thus in experiment 2, we retested more adults in the breeding season.

## EXPERIMENT 2: REPLICATE FLOCKS

We repeated the trials from experiment 1 with 2 new flocks of birds during the breeding season (beginning 5 May 2004). One flock again contained adult and juvenile females. The other flock contained only juvenile females that had no experience with adult females. This group allowed us to determine whether the adult females were in some way influencing the juvenile females' patterns of approaches in experiment 1.

### Subjects

One flight cage, similar in dimensions as the cage used in experiment 1, contained 6 juvenile females and 8 adult females. A second flight cage contained 7 juvenile females. All juveniles were hand raised and all adults were wild caught in the summer of 2003. All females had been housed in large outdoor aviaries with males prior to the experiment.

We conducted the same trials as in experiment 1, except for the following changes. First, we made a more conservative test of the large versus medium trials. The large egg used in experiment 1 was much bigger than the medium egg, and thus, it was a stimulus that lay outside the range of egg sizes typical for cowbird host species. Here we used a new stimulus to serve as the large egg. We used a yogurt-covered almond, approximately 0.5 cm larger than the medium egg (see Figure 2) for the large versus medium trials in experiment 2.

In addition, we added 2 comparisons to experiment 2 that we had not tested in experiment 1. One comparison was a con-

trol for using a cowbird egg. Because this was a real egg, it was a different stimulus than the other mock eggs we had been using. To control for this difference, we conducted a trial where we used a white mock egg that was painted to look like a cowbird egg instead of using a real cowbird egg. We experimentally "speckled" a white medium egg with black paint. We then compared one nest containing 2 white eggs and 1 white egg with black speckles with a nest containing 2 white eggs and 1 white egg that had been speckled with white paint. This last egg was speckled with white paint to control for the painting manipulation and did not appear any different from the other white eggs. We also conducted a comparison of a nest containing 2 white eggs and 1 white egg speckled with black paint to a nest containing 2 white eggs and 1 real cowbird egg. If females evaluated an experimentally speckled egg as similar to a real cowbird egg, then they should find no difference between these 2 nests. Due to potential order effects in experiment 1, we conducted the trials in reverse order for experiment 2.

## Results

Patterns of approaches for the 2 flocks in experiment 2 were similar to experiment 1 (see Table 1 for a summary of approaches). Here, however, the new group of adult females approached nests significantly more frequently than did the adults in experiment 1 ( $U = 13.5$ ,  $N_1 = 11$ ,  $N_2 = 8$ ,  $P < 0.01$ ).

### Egg number

As depicted in Table 1, all 3 groups of females (juveniles with adults, adults with juveniles, and juveniles alone) showed significant preferences for approaching the 2-egg nest over the empty nest. All 3 groups showed preferences to approach nests with 3 eggs as opposed to nests with 1 egg. No group showed a preference in the 6 versus 3 case.

### Egg type

All 3 groups approached the nest with small eggs significantly more than they approached the nest with medium eggs. This differed from experiment 1, where they showed nonsignificant trends in the same direction. All 3 groups approached the nest with medium-sized eggs more frequently than they approached the nest with large eggs, although only the juveniles housed alone did so significantly. Adult females approached the nest with 3 white eggs significantly more than they approached the nest containing 2W1C. In contrast, both groups of juveniles approached the 2W1C nest more frequently than they approached the nest containing the 3 white eggs, though not significantly more.

When we compared the nest containing the 2 white eggs and 1 black-speckled egg with the nest containing the 2 white eggs and 1 white-speckled egg, we found similar patterns as in the 3W versus 2W1C trials. Adults preferred the nest containing 3 white eggs ( $T = 2$ ,  $P < 0.05$ ), and the juveniles showed a trend to approach the nest with the black-speckled egg more frequently (juveniles with adults  $T = 5.5$ ,  $P = 0.29$ ; juveniles housed alone  $T = 3$ ,  $P = 0.115$ ). Finally, no group showed any differences in approaching a 2W1C nest versus a nest containing 2 white eggs and 1 black-speckled egg (all  $T_s \leq 2$ , all  $P_s \geq 0.14$ ).

Given the small sample size and nonparametric analyses, it was possible that the tests above were not powerful enough to detect subtle differences within some trials. Because in experiment 2, all 3 groups of females showed similar patterns of behavior, we combined data across the groups to increase sample size in order to determine whether there were significant differences in the trials that only showed trends when investigated within groups. For the 6 versus 3 trials, collapsing

**Table 1**  
**Patterns of nest approaches for females in experiment 2**

Egg number		2 eggs		1 egg	3 eggs		3 eggs	6 eggs	
Juvenile and adult group									
Juveniles	4.00	<b>14.17</b>	$T = 0, N = 6,$	4.00	<b>16.33</b>	$T = 0, N = 6,$	8.17	9.17	$T = 4, N = 6,$
SE	1.26	<b>4.53</b>	$P < 0.05$	0.68	<b>2.64</b>	$P < 0.05$	1.35	1.49	NS
Adults	9.88	<b>17.50</b>	$T = 2, N = 8,$	5.38	<b>13.38</b>	$T = 0, N = 8,$	8.38	10.63	$T = 9.5, N = 8,$
SE	2.21	<b>3.20</b>	$P < 0.03$	1.63	<b>2.70</b>	$P < 0.02$	2.06	2.22	NS
Only juveniles group									
Juveniles	3.00	<b>17.71</b>	$T = 0, N = 7,$	10.43	<b>17.57</b>	$T = 1.5, N = 7,$	9.43	10.86	$T = 11, N = 7,$
SE	0.82	<b>2.81</b>	$P < 0.02$	1.80	<b>1.59</b>	$P < 0.05$	1.36	1.55	NS
Egg type									
Small		Medium		Medium	Large	2W1C		3 White	
Juvenile and adult group									
Juveniles	<b>8.00</b>	5.17	$T = 0, N = 6,$	9.00	7.33	$T = 3, N = 6,$	8.63	5.75	$T = 4.5, N = 6,$
SE	<b>1.93</b>	1.58	$P < 0.05$	1.77	1.52	NS	2.04	1.79	$P = 0.21$
Adults	<b>8.50</b>	7.25	$T = 0, N = 7,$	9.25	5.50	$T = 4.5, N = 8,$	3.67	<b>6.33</b>	$T = 0, N = 8,$
SE	<b>1.81</b>	1.68	$P < 0.05$	1.96	1.79	NS	1.17	<b>0.88</b>	$P < 0.02$
Only juveniles group									
Juveniles	<b>9.71</b>	5.86	$T = 1.5, N = 7,$	17.29	13.29	$T = 3.5, N = 7,$	12.00	8.00	$T = 2.5, N = 7,$
SE	<b>1.85</b>	1.01	$P < 0.05$	2.45	3.18	NS	1.80	0.95	$P = 0.093$

Mean approaches per female for adults and juveniles in the 2 groups in experiment 2. Conditions in bold reflect statistically significant differences. Only juveniles group refers to the group of juvenile females housed without adult females. 2W1C = nest containing 2 white eggs and 1 cowbird egg.

across groups did not reveal any significant preferences ( $T = 64.5, N = 21, P > 0.129$ ). For the 3M versus 3L comparison, there was a significant preference for the 3 medium egg nests ( $T = 31.5, N = 21, P < 0.05$ ). Combining only the juvenile female groups in experiment 2 revealed a significant preference for the 2W1C nests over the 3 white nests ( $T = 12, N = 13, P < 0.05$ ).

## Discussion

The 2 new groups of females replicated the patterns seen in experiment 1. Here, however, the adult females engaged in more approaches and showed significant patterns of approaches similar to the juveniles. Housing with adults did not influence the juveniles' approach patterns. The additional control trials in experiment 2 revealed that adult females approach a nest less frequently if it contains a cowbird egg or 1 black-speckled egg. Furthermore, females did not treat a cowbird egg differently than an egg artificially speckled.

## EXPERIMENT 3: EGG-LAYING PATTERNS

To this point, it remained untested whether approaching a nest more frequently was a valid measure of preference to parasitize the nest. The final series of trials was conducted during the breeding season in large outdoor aviaries where females lived in functional flocks with males. We designed these tests to replicate some of the findings from the indoor flight cages using actual egg-laying patterns as an assay of females' nest selection preferences. In the breeding season, females would lay eggs in artificial nests set out by experimenters. By manipulating the nest contents, we could test whether patterns of approaches seen in experiments 1 and 2 would correspond to preferences for parasitism.

## Subjects

We housed 56 females across 6 aviaries (8–11 in each) for the breeding season of 2004. One aviary contained only hand-

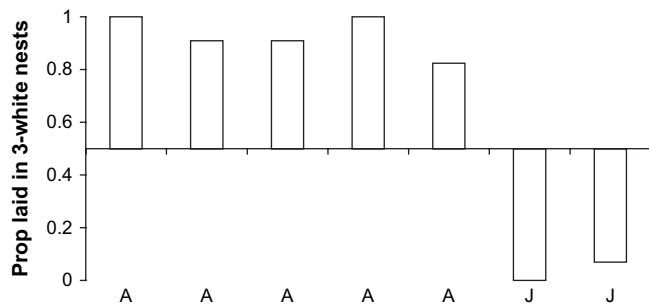
reared juvenile females ( $N = 8$ ), and the others contained only wild-caught adults. Thus, although we did not have data on which individuals laid the eggs within an aviary, we could be certain of juvenile and adult egg-laying patterns. For statistical purposes, we treated the egg output for each aviary as a single data point. All aviaries contained 7–12 males. In the breeding season of 2005, we added one more aviary containing hand-reared juvenile females (11 juvenile females, 9 juvenile males).

## Apparatus

Aviaries were large outdoor enclosures ( $9.1 \times 21.4 \times 3.4$  m) located in Monroe County, Indiana. The aviary containing hand-reared juvenile females added in 2005 was located in Montgomery County, Pennsylvania. Each aviary contained trees, grass, shrubs, indoor shelters, and feeding stations. We provided the birds daily with vitamin-treated water, a mixture of white millet, red millet, and canary seed as well as a modified Bronx zoo diet for blackbirds. We placed 10 nests in each aviary and at 05:30–06:00 AM each morning, we collected all eggs laid.

## Procedure

Because we did not have unlimited time to test the birds in the aviaries and it was unknown how many eggs females would lay and when, we only used 3 of the comparisons from experiments 1 and 2. For egg number trials, we selected the 3 versus 1 comparison. For egg-type trials, we selected 3M versus 3L (the large eggs from experiment 2). Finally, we compared 3 white eggs versus 2W1C. We began with the comparison of egg number. In each aviary, we placed 5 nests containing 1 egg and 5 nests containing 3 eggs, positioning them at randomly selected locations in trees and shrubs throughout the aviaries. To avoid the possibility that females would remove any of our mock eggs, we secured them to the Spanish moss using nontoxic glue. Each morning, we would collect the eggs that had been laid in the nests and then move the nests to new



**Figure 5**  
Proportion of eggs laid in 3 white egg nests in the 3W versus 2W1C trials in experiment 3. “A” indicates aviaries containing adult females, and “J” indicates aviaries containing juvenile females. The final bar represents the aviary added in 2005.

locations in the aviaries. After 4 days of collection, we tested the large versus medium eggs in a similar fashion. We again collected eggs for 4 days. Finally, we commenced with the cowbird egg trials. We placed 5 nests in each aviary containing 2 white eggs and 1 real cowbird egg and 5 nests containing 3 white eggs. Each morning, we removed any cowbird stimulus egg that had been pecked and replaced it with a new one. For the additional juvenile female aviary in 2005, we only conducted this final test comparing 2W1C nests with nests containing 3 white eggs. Here we collected eggs from the aviary for 14 days.

## Results

We collected on average 2.57 eggs per aviary per day (range 0–7). Females in all 6 aviaries from 2004 laid more eggs in 3-egg nests than in 1-egg nests, on average, laying 83% ( $\pm 4.7$ ) of eggs in the 3-egg nests ( $T = 0$ ,  $N = 6$ ,  $P < 0.03$ ). Similarly, females in all aviaries laid more eggs in the nests with medium eggs than large eggs (85%  $\pm 6.4$  eggs laid in medium nests,  $T = 0$ ,  $N = 6$ ,  $P < 0.03$ ).

Egg-laying patterns for the trial comparing nests with a cowbird egg with nests containing 3 white eggs are depicted in Figure 5. Adult females laid 92.8% ( $\pm 3.3\%$ ) of their eggs in the nests with 3 white eggs ( $T = 0$ ,  $P < 0.05$ ). Juvenile females in the 2 aviaries, however, laid 96.6% of their eggs in the 2W1C nests. Although it was impossible to have enough groups of hand-reared juveniles for statistical analysis, the patterns in the 2 groups were pronounced. Overall, juvenile females laid 38 eggs in 2W1C nests compared with a total of 2 eggs in the nests with 3 white eggs. In contrast, adult females laid 5 eggs in 2W1C nests and 52 in the nests with 3 white eggs.

## Discussion

By varying the numbers and types of mock eggs in nests, we determined that female cowbirds could evaluate the contents of nests and could use that information to influence their nest selection. Measures of approaching and laying eggs in nests revealed similar patterns: females were sensitive to egg number, egg type, and whether a nest had been previously parasitized. There were 2 age-related effects. First, juveniles were more interested in nests prior to the breeding season than adults. Second, the patterns of assessing nests for both juveniles and adults were similar except in the case of past parasitism. Adults preferred nests that had not been parasitized, whereas juveniles showed a preference for nests that had been parasitized.

### Egg number

Females showed preferences for nests containing eggs compared with empty nests. In addition, across all the experi-

ments females showed preferences for nests containing 3 eggs compared with nests containing 1 egg. This suggests that there may be a cost to parasitizing a nest too early. It is possible that laying early may increase the likelihood of the host abandoning the nest or of losing the egg to predation. It could also give the host more opportunities to reject the egg.

Another possibility is that females prefer nests with the greater numbers of eggs because cowbird chicks benefit by having more host chicks present. Kilner et al. (2005) report that increased numbers of the host's young in a nest also increases the amount of parental care provided by the host parents to the cowbird. However, females did not display a preference for nests with more eggs versus fewer eggs in the 3- versus 6-egg trials.

### Egg type

Females showed preferences for nests containing eggs similar in size or smaller to their own. Larger eggs could indicate a host more likely to produce young that could outcompete the cowbird for food and may also indicate a host with a higher likelihood of employing an egg-rejection strategy (Peer and Sealy 2004). Comparing across experiments 1 and 2 (though not experiment 3), the effects of egg type were less pronounced than the effects of egg number. It is possible that other cues are more important than egg characteristics for cowbirds when evaluating the type of host species that owns a nest, such as using the sights or sounds of the host itself (Clotfelter 1998). Observing the type of bird that owns a nest may not provide information about the timing of the nest for incubation however, and therefore, cowbirds may rely on the characteristics of the host for choosing to parasitize a nest, whereas using characteristics of the nests to evaluate the timing for laying.

### Past parasitism

Field studies have indicated that cowbirds are less likely to parasitize an already parasitized nest (Ortega et al. 1994), though multiple parasitism seems to occur more often in some populations than in others (Robinson 1992). Our tests revealed that adult females, but not juveniles, avoided laying in nests that had already been parasitized. Juveniles showed no such aversion and in fact approached and laid more often in nests containing another cowbird egg. This age effect may indicate that although birds may not have an opportunity to use individual learning for nest quality assessment, it may be possible for social learning to play a role. Juvenile females may employ a “nest copying” strategy. They may be “parasitizing” information from more knowledgeable conspecifics and selecting a nest and a host that another female has judged to be suitable for her young. Juveniles might be exposing their chicks to more intense competition in the nest with another cowbird present, but this cost could be outweighed by the benefits of laying in a high-quality nest. Admittedly, in our experiment, juvenile females seemed to have no problems selecting appropriate nests.

We assessed females in groups to investigate competition among females. Although this caused problems for independence among the data points, we did test a number of independent groups and the effects were unambiguous in most cases, especially in the patterns of laying in experiment 3. It is unclear what the effects of the group had on individual nest selection. At some points it was probably true that a few females led the rest of the group to approach the appropriate nest, but at other times there were many fights and displacements at the popular nest, leaving some females with no choice but to approach the less popular nest. We have begun to test females in pairs to increase independence, and although we are seeing the same patterns of approaches, the

lower number of females has led to far less interest in approaching nests overall (White DJ, Ho L, Freed-Brown SG, unpublished data). This suggests that the female competition may be an important aspect of nest selection in these experiments and thus will be the subject of future experiments.

Numerous studies have revealed that ecology can provide selection pressures on cognitive abilities (Shettleworth 1998). For example, demands associated with foraging (Sherry 1988), mating (Gaulin et al. 1990), and social interactions (Emery and Clayton 2001; Bergman et al. 2003) have been shown to favor such cognitive abilities as spatial memory and the ability to use transitive inference. Here we have developed a technique to begin to analyze how selection imposed by the demands of the cowbirds' parasitic breeding system may have influenced adaptations for cognition, memory, and learning abilities.

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