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Authors: Guigueno, Mélanie F., Sealy, Spencer G., and Westphal, Ashleigh M.

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RESEARCH ARTICLE

Rejection of parasitic eggs in passerine hosts: Size matters more for a non-ejecter

Mélanie F. Guigueno,[1,2]* Spencer G. Sealy,[1] and Ashleigh M. Westphal[1]

[1] Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba, Canada
[2] Current address: Advanced Facility for Avian Research and Department of Biology, University of Western Ontario, London, Ontario, Canada
* Corresponding author: mguiguen@uwo.ca

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ABSTRACT

The evolution of egg mimicry by parasites and the recognition of foreign eggs by hosts are important components of the coevolutionary arms race between brood parasites and their hosts, which is one of the most behaviorally complex of all host–parasite interactions. To examine cues used by the Yellow Warbler (*Setophaga petechia*), a non-ejecter that buries or deserts eggs laid by parasitic Brown-headed Cowbirds (*Molothrus ater*), we added model eggs of different sizes and colors to nests. We also reviewed the literature to investigate the effects of model egg surface color (background and maculation) and size on the response of hosts that eject. We predicted that size would be more important for Yellow Warblers as they likely use tactile cues to bury or desert parasitized clutches and color cannot be assessed tactilely. In Yellow Warblers, rejection frequency increased as size and color diverged more from real warbler eggs. Egg size was not generally used as a criterion for egg rejection, however, across different species that eject parasitic eggs. Color was the only model egg parameter, out of color and size, that significantly affected rejection in these ejecter hosts. Tactile cues are therefore not used by ejecters but are more important in a host that uses methods of rejection that do not require egg discrimination, such as burial and desertion. Of metrics that took into account the ultraviolet range, achromatic Just Noticeable Differences (brightness) in Yellow Warblers better predicted rejection of model eggs based on color than chromatic Just Noticeable Differences (hue). The high costs of burial and desertion may have led to multiple (size and color) egg discrimination abilities in the Yellow Warbler.

Keywords: avian perceptual modelling, Brown-headed Cowbird, burial, desertion, egg color, egg size, ejection, *Molothrus ater*, *Setophaga petechia*, Yellow Warbler

Rejet des œufs parasites chez les passereaux hôtes: La taille importe davantage pour une espèce qui n'éjecte pas

RÉSUMÉ

L'évolution du mimétisme des œufs par les parasites et la reconnaissance des œufs étrangers par les hôtes sont des composants importants de la course aux armes co-évolutive entre les parasites de nichée et leurs hôtes, ce qui est l'une des interactions hôte–parasite les plus complexes sur le plan comportemental. Afin d'examiner les signaux utilisés par la paruline jaune (*Setephaga petechia*), une espèce qui n'éjecte pas les œufs parasites pondus par le vacher à tête brune (*Molothrus ater*) mais les enterre ou les déserte, nous avons ajouté des modèles d'œufs de différentes tailles et couleurs aux nids. Nous avons également effectué une revue de la littérature pour examiner les effets de la couleur en surface (couleur de fond et maculation) et de la taille des modèles d'œufs sur le comportement de rejet des hôtes qui les éjectent. Nous avons prédit que la taille serait plus importante pour la paruline jaune car cette espèce semble utiliser des signaux tactiles lors de la décision d'enterrer ou de déserter les nichées parasitées, la couleur ne pouvant être évaluée tactilement. Chez la paruline jaune, la fréquence de rejet augmentait à mesure que la taille et la couleur divergeaient des œufs réels de la paruline jaune. La taille des œufs n'était cependant généralement pas utilisée comme un critère pour le rejet des œufs chez des différentes espèces qui éjectent les œufs parasites. La couleur était le seul paramètre des modèles d'œufs, entre la couleur et la taille, qui affectait significativement le rejet chez ces hôtes. Les signaux tactiles ne sont par conséquent pas utilisés par les éjecteurs mais ils sont plus importants chez un hôte qui utilise les méthodes de rejet ne requérant pas la discrimination visuelle des œufs, telles que l'enfouissement et la désertion. Le seuil de perception achromatique (luminosité) chez la paruline jaune, qui prenait en compte la gamme des ultraviolets (UV), a prédit le rejet sur la base de la couleur mieux que le seuil de perception chromatique (teinte). Les coûts élevés d'enfouissement et de désertion ont possiblement mené à des habiletés de discrimination multiple (taille et couleur) des œufs chez la paruline jaune.

Mots-clés: couleur de l'oeuf, désertion, éjection, enfouissement, modélisation de la perception aviaire, *Molothrus ater*, paruline jaune, taille de l'oeuf, *Setophaga petechia*, vacher à tête brune

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"The arch-enemy of the yellow warbler is undoubtedly the cowbird."

Arthur Cleveland Bent, 1953

INTRODUCTION

Host–parasite interactions play an important role in shaping ecosystems and creating linkages within communities (Lafferty et al. 2006). The interactions between some hosts and their parasites are characterized as coevolutionary arms races (Vikan et al. 2010). An important aspect of the host–parasite arms race is the evolution of the ability of hosts to detect parasites and of parasites to avoid detection (Aviles et al. 2010). Interactions between brood parasites and their hosts are among the most behaviorally complex of host–parasite interactions and, as such, host recognition plays an important role in determining the outcome of the particular arms race (Lovászi and Moskát 2004, Davies et al. 2006). Many brood parasites have evolved stunning levels of egg mimicry to counter host egg-recognition abilities (Brooke et al. 1988). To overcome this mimicry, hosts use a wide range of visual and tactile cues to recognize parasites, such as counting eggs and recognizing their patterns (Hauber et al. 2006, Shizuka and Lyon 2010). Hosts recognize the parasitic egg visually either by discordancy or true recognition (Moskát et al. 2010, reviewed in Sealy and Underwood 2012, Moskát et al. 2014). Recognition by discordancy is based on differences in egg phenotypes within the same clutch (Rothstein 1974, Sealy and Underwood 2012). Eggs that are the most dissimilar and are in the minority are recognized as the parasitic eggs. True recognition, which does not require the simultaneous presence of host and parasitic eggs, requires neural encoding of the recognition template of the hosts' own eggs (Hauber and Sherman 2001, Moskát et al. 2010).

The Common Cuckoo (*Cuculus canorus*), a widespread brood parasite in Eurasia, has had a longer coevolutionary relationship with its hosts than the Brown-headed Cowbird (*Molothrus ater*) in North America (Krüger 2007). The Common Cuckoo parasitizes small hosts, lays relatively small eggs, and groups of individuals (gentes) specialize in parasitizing a particular species, laying eggs that mimic the host's egg (Davies 2000, Krüger 2007). Brown-headed Cowbirds are not as specialized as cuckoos, although in some instances they preferentially parasitize higher-quality hosts (Grant and Sealy 2002, Woolfenden et al. 2003). Host quality depends on the probability the host will reject the parasitized clutch or egg, competition for resources between host and parasite nestlings, and the suitability of the host's diet (Woolfenden et al. 2003). Regardless, cowbirds parasitize nests containing host eggs that vary in color (background and/or maculation), size, or both compared with their own eggs (Davies 2000).

Although humans and most other mammals cannot see in the ultraviolet (UV) range (300–400 nm), some birds are UV sensitive, with a peak UV sensitivity at 365 nm (Chen et al. 1984, Tovée 1995, Cuthill et al. 2000, Aidala et al. 2012). Some hosts of brood parasites use UV signals to discriminate parasite eggs from their own eggs (Honza et al. 2007, Cassey et al. 2008, Honza and Polaciková 2008); however, not all hosts use UV signals (Underwood and Sealy 2008). It is important, therefore, to incorporate the spectral reflectance of eggs in the avian visible range (300–700 nm) when assessing the importance of color in egg discrimination in hosts of avian brood parasites.

Most studies of parasitism on cowbird hosts have focused on species that either accept or reject in the context of natural parasitism (Peer and Sealy 2004). As such, it is often unclear whether parasite recognition traits evolved in tandem or whether one trait evolved to secondarily reinforce rejection once the primary trait was already in place. We addressed egg recognition in the Yellow Warbler (*Setophaga petechia*), an intermediate rejecter (~40% rejection frequency) of eggs laid by the brood-parasitic Brown-headed Cowbird (Sealy 1995, Guigueno and Sealy 2011). The Yellow Warbler is unique among known Brown-headed Cowbird hosts as its primary method of rejection is consistently burial (Sealy 1995, Guigueno and Sealy 2010), whereas other rejecters normally remove parasitic eggs by grasp- or puncture-ejection. Yellow Warblers are not known to eject cowbird eggs. Rejection frequencies in Yellow Warblers are conditional on environmental factors, with time-consuming burial or nest desertion more likely to occur early in the laying season, when there is more time for replacing lost clutches (Sealy 1995, Guigueno and Sealy 2010). However, more time is needed for initiation of a new clutch during desertion (7.3 days) than burial (2.7 days), therefore, it is more adaptive for warblers to accept or bury their parasitized clutch at the end of the clutch-initiation period than to desert the parasitized nest (Guigueno and Sealy 2010). The basis on which the Yellow Warbler recognizes the parasitic egg is unknown. Warblers accept blue, warbler-sized model eggs, but reject up to 30% of model cowbird eggs, which are twice the size of warbler eggs but similar (as perceived by humans) in color and maculation (Sealy and Lorenzana 1998, Kuehn 2009, Guigueno and Sealy 2011). In addition, Yellow Warblers reject 37% of American Robin (*Turdus migratorius*) eggs, which are immaculate blue and are about five times the size of warbler eggs (Stewart et al. 2011).

We hypothesized that egg size is a more important rejection cue for Yellow Warblers (a non-ejecter) than for

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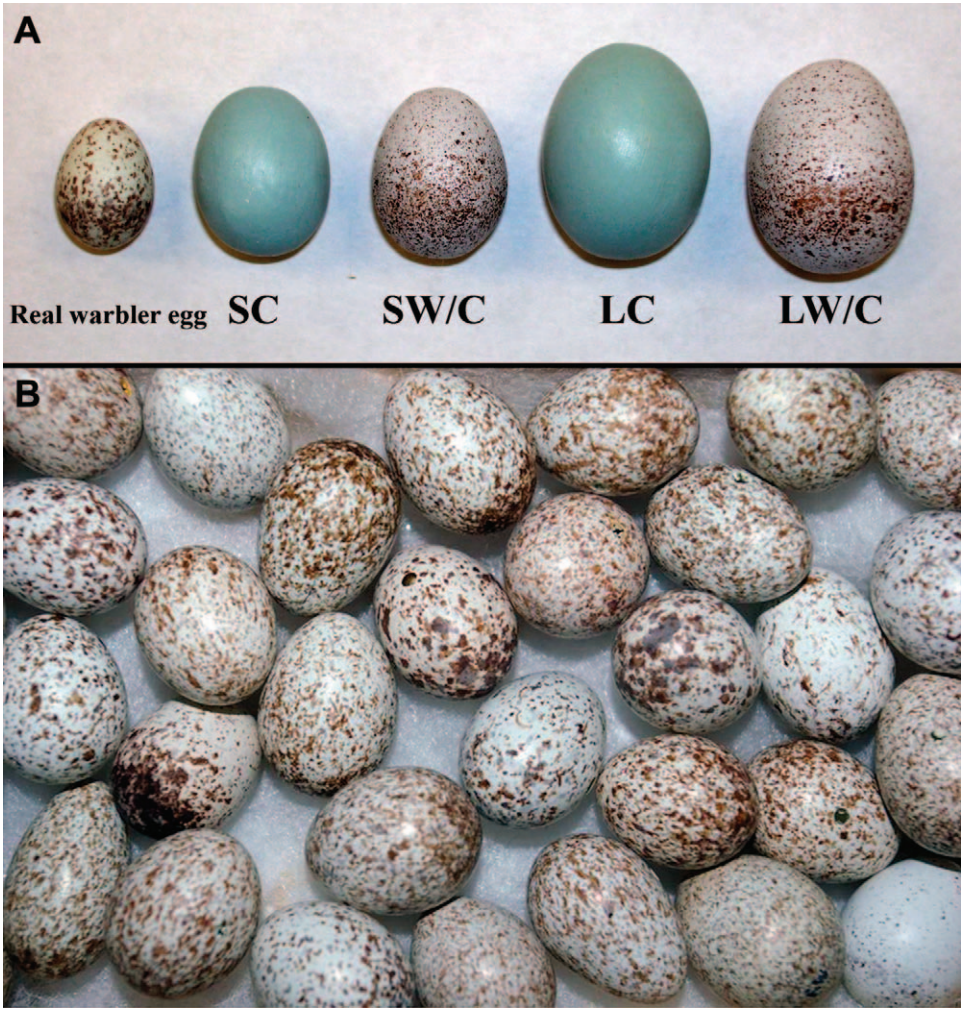


FIGURE 1. (**A**) Real and model eggs used in the experiment. Left to right: real Yellow Warbler egg; cowbird-sized, cuckoo-colored egg (SC); cowbird-sized, warbler/cowbird-colored egg (SW/C); cuckoo-sized, cuckoo-colored egg (LC); and cuckoo-sized, warbler/cowbird-colored egg (LW/C). (**B**) Real Brown-headed Cowbird eggs from our field site (Delta Marsh). Photo credit: Justin L. Rasmussen

ejecters because an ejecter must visually identify the egg to be removed, but a non-ejecter can use tactile cues to simply reject the entire clutch. Indeed, Yellow Warblers that probed their manipulated clutches more (i.e. a tactilely-induced behaviour) were more likely to bury or desert (Guigueno and Sealy 2012) and warblers likely do not visually recognize their own eggs (Sealy and Lorenzana 1998). We predicted that differences in size between the parasitic and host eggs would be more important than differences in color in eliciting egg rejection in Yellow Warblers. In addition, we reviewed the literature for studies involving ejecters that manipulated both egg size and color to determine the relative importance of size and color for rejection in ejecter species. Because ejecters do not require a tactile stimulus to eject the foreign egg, we predicted that size would be less important for these hosts than for Yellow Warblers.

METHODS

Field Site

We conducted our experiment in May and June 2010 at Delta Marsh, Manitoba, Canada (50°1′N, 98°19′W), where Yellow Warblers and Brown-headed Cowbirds are common and have been sympatric for at least 200 years (Thompson 1891). The frequency of cowbird parasitism on warblers at our field site has varied from year to year (14–31%, Sealy 1995; 8–35%, Woolfenden et al. 2003).

Model Eggs

The model eggs used for our experiment diverged from Yellow Warbler eggs either in color, size, or both, and our predicted levels of rejection depended on the relative importance of size versus color (Figure 1A, Table 1). Our model types were chosen based on two possible foreign

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TABLE 1. Predicted levels of rejection that depend on the relative importance of color (C) versus size (S), followed by recorded rejection percentages in response to clutch manipulations (model eggs added to nests on laying day 2). Groups are represented in an order of increasing divergence from Yellow Warbler eggs. For predictions, order of rejection frequency is lowest at 1 and greatest at 4. Cowbird-sized warbler/cowbird-colored eggs (SW/C) and cowbird-sized cuckoo-colored eggs (SC) were about twice the volume of warbler eggs. Cuckoo-sized warbler/cowbird-colored eggs (LW/C) and cuckoo-sized cuckoo-colored egg (LC) were 4–5 times the volume of warbler eggs. Coefficients of determination (r^2) indicate strength of correlation between recorded rejection percentages and each prediction. ΔAIC values indicate the most parsimonious model after penalizing for over parameterization. Prediction 5 correlates most strongly with the data (r^2 and ΔAIC are in bold).

	SW/C	SC	LW/C	LC	r^2	ΔAIC
Predictions						
1. Color only (C)	1	2	1	2	0.28	17.53
2. Size only (S)	1	1	2	2	0.72	13.76
3. Both equal (C=S)	1	2	2	3	0.95	6.91
4. Both, but C>S	1	3	2	4	0.73	13.63
5. Both, but S>C	1	2	3	4	**0.99**	**0**
Recorded rejection % (*n*)*	16 (25)	36 (25)	48 (27)	68 (25)		
Acceptances, burials, desertions	21, 3, 1	16, 7, 2	14, 11, 2	8, 8, 9		

*Includes rejections by burial and nest desertion. We recorded rejection (one burial) at 5% of control clutches ($n = 18$).

egg types Yellow Warblers naturally encounter in their nests: eggs of the Brown-headed Cowbird and of the Black-billed Cuckoo (*Coccyzus erythropthalmus*), a facultative intraspecific brood parasite that occasionally and erroneously lays eggs in Yellow Warbler nests (Figure 1A; Hughes 1997, Dearborn et al. 2009). Black-billed Cuckoo eggs are immaculate blue-green and are 4–5 times the size of warbler eggs, whereas cowbird eggs are about twice the size of warbler eggs and their coloration consists of an off-white background with brown maculation (Lowther 1993, Lowther et al. 1999, Hughes 2001, Lorenzana and Sealy 2002).Yellow Warbler and cowbird eggs both have an off-white background with dark brown maculation, therefore, we refer to 2 of our models as being small warbler/cowbird colored (SW/C) and large warbler/cowbird colored (LW/C) (Figure 1A). We also used small cuckoo-colored (SC) and large cuckoo-colored (LC) eggs (Figure 1A).

The mean and standard error for length (22.9 ± 0.04 mm), width (17.9 ± 0.02 mm), and mass (3.0 ± 0.03 g) of the cowbird-sized model eggs ($n = 85$) were similar to sizes 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). Out of the 85 cowbird-sized models (SW/C and SC), 52 randomly chosen models were used in successful clutch manipulations. The mean length (28.5± 0.04 mm), width (21.8 ± 0.05 mm), and mass (6.3 ± 0.02 g) of cuckoo-sized model eggs ($n = 85$) were similar to real cuckoo eggs (length: 27.55 ± 0.14 mm, width: 20.77 ± 0.15 mm, mass: 6.3 g; $n = 102$; Hughes 2001). Out of the 85 cuckoo-sized models made (LW/C and LC), 50 randomly chosen models were used in successful clutch manipulations. Yellow Warbler eggs averaged 16.80 ± 0.08 mm in length and 12.60 ± 0.04 mm in width, respectively, with a mass of 1.43 ± 0.01 g (Sealy 1992). We painted models light blue-green or off-white with brown maculation with waterproof acrylic paints (FolkArt Opaque Acrylic Paints; Plaid Enterprises, Norcross, GA, USA). Models were made by shaping floral foam into an egg and placing it in a cowbird or cuckoo egg mold with a thin layer of plaster of Paris, which permits puncture-ejection (similar to Lee et al. 2005), although warblers are not known to eject eggs (Sealy 1995).

Avian Perceptual Modelling

We measured the spectral reflectance of the model eggs and of real warbler and cowbird eggs, including the UV range (300–700 nm) with a UV and visible light spectrometer (USB2000 UV–VIS; Ocean Optics, Dunedin, FL, USA) and a deuterium–tungsten light source (DT-1000-MINI; Analytical Instrument Systems, Flemington, NJ, USA) (Figure 2). We used a spectralon reflectance standard (WS-1; Ocean Optics), which reflects 99% of UV and visible light, prior to measuring each egg, as well as a dark standard, which measures the baseline "noise" in the spectrophotometer. We recorded these light and dark measurements to standardize measurements of reflectance. We measured the spectral reflectance of all eggs under a black cloth to eliminate potential interference from ambient light. Nine reflectance measurements were taken from each egg: three from random locations on the side of the egg, three from the blunt end, and three from the pointed opposite end. We measured 10 eggs per group.

Although model eggs increasingly diverged in color from a human perspective from host eggs (Figure 1A), both warbler/cowbird-colored (SW/C and LW/C) and cuckoo-colored (SC and LC) model eggs diverged from real warbler eggs in the UV range (300–400 nm) (Figure 2A). We used Avicol (Gomez 2006) to measure chromatic

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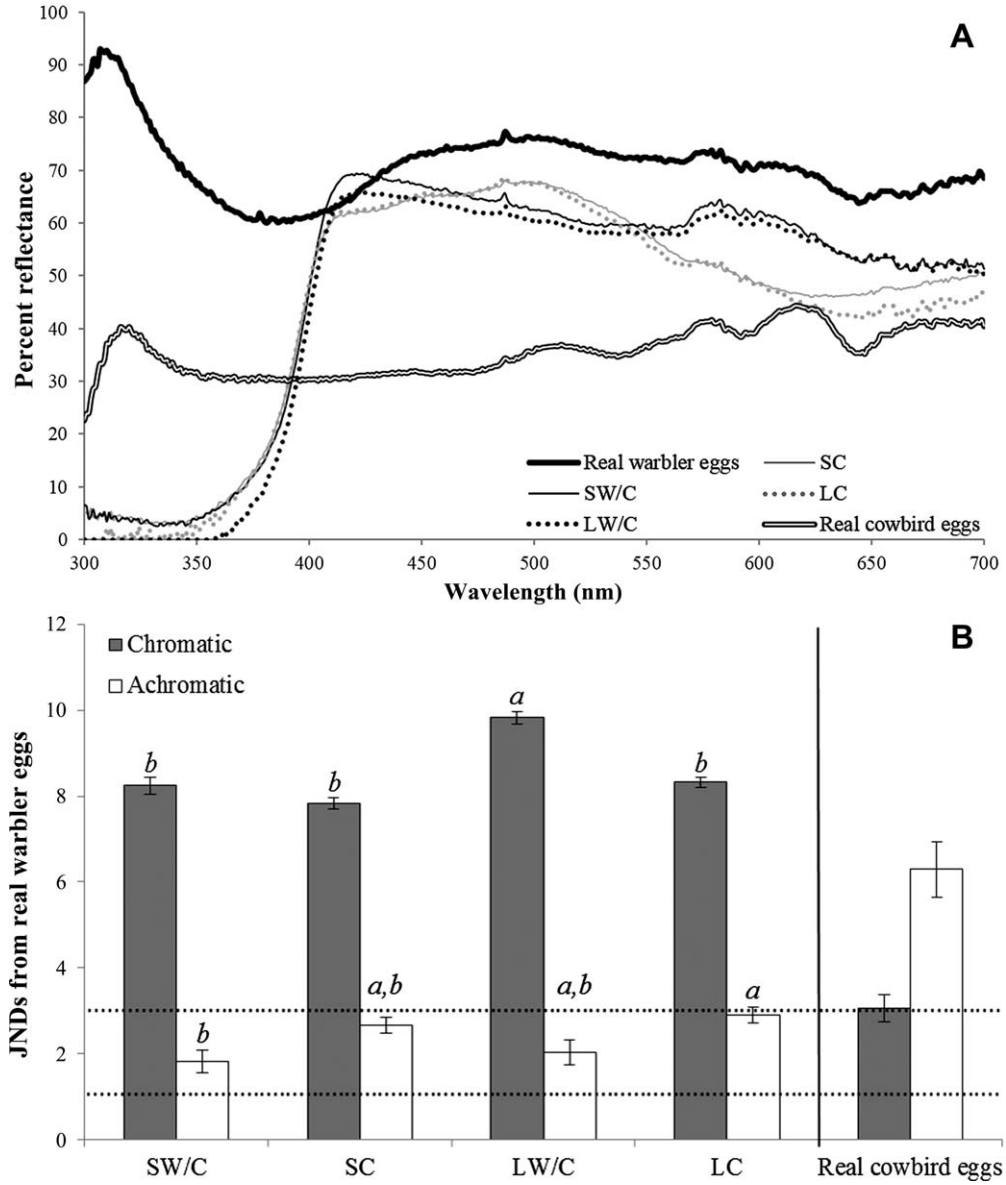


FIGURE 2. (**A**) Spectral reflectance of cowbird-sized warbler/cowbird-colored (SW/C) and cuckoo-colored (SC) model eggs, cuckoo-sized warbler/cowbird-colored (LW/C) and cuckoo-colored (LC) model eggs, and real Yellow Warbler and Brown-headed Cowbird eggs. A small artifact appeared at 480 nm; however, all eggs types were affected similarly and, thus, the Just Noticeable Differences in (**B**) were likely unaffected. (**B**) Just noticeable differences (JNDs) from real Yellow Warbler eggs for all 4 model eggs for chromatic and achromatic portions of color. Bars represent means and error bars are ± SEM. Lower dotted line (JND = 1) indicates minimum JND required for warblers to discriminate between their own eggs and model eggs and higher dotted line (JND = 3) indicates minimum JND required for warblers to easily discriminate between their own eggs and the model eggs. Therefore, if 1<JND<3, 2 eggs are difficult to distinguish. Letters indicate results from Tukey's post hoc tests. The same letters within each color type (chromatic and achromatic JNDs) indicate that 2 model types are not significantly different from each other.

Just Noticeable Differences (JNDs) (hue) and achromatic JNDs (brightness) visual contrasts between the model eggs and real warbler eggs, but also between real cowbird and warbler eggs to assess cues that warblers may use to detect natural parasitism. Avicol permits differences in spectral data to be measured as viewed by the avian tetrachromatic visual system (Gomez 2006). Following Gomez (2006), we extracted cone densities from Stuart-Fox et al. (2008). Those values were based on the mean ratio for birds with a UVS visual system because Yellow Warblers are predicted to possess UV-sensitive SWS1 cones (Aidala et al. 2012). Cone densities were as follows: UVS – 1, SWS – 2, MWS – 3, and LWS – 3. We assumed a Weber fraction of 0.1 based on Vorobyev et al. (1998). A

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TABLE 2. Review of studies examining host responses to model eggs that varied in size and color from hosts' own eggs and the parasites' eggs. These hosts all eject parasitic eggs, unlike the Yellow Warbler. Colors of model eggs differed from host eggs in both background and maculation (score = 0), background or maculation (0.5), or neither in background nor maculation (1). This review is meant to be representative, but not exhaustive.

Brood parasite	Host	Range in color differences[a]	Model egg volume relative to host egg[a]	Range in rejection	Source
Dideric Cuckoo *Chrysococcyx caprius*	Red Bishop *Euplectes orix*	0–1	100–150%	10–75%	Lawes & Kirkman (1996)
Lesser Cuckoo *Cuculus poliocephlus*	Hume's Yellow-browed Leaf Warbler *Phylloscopus humei*	0.5–1	100–175%	0–100%	Marchetti (2000)
	Yellow-browed Leaf Warbler *Phylloscopus inornatus*	0–1	100–250%	8–100%	Marchetti (1992)
Common Cuckoo *Cuculus canorus*	Reed Warbler *Acrocephalus scirpaceus*	0–1	100–510%	0–81%	Davies & Brooke (1988) Stokke et al. (2010)
	Marsh Warbler *Acrocephalus palustris*	0–1	100–175%	38–92%	Antonov et al. (2006)
Brown-headed Cowbird *Molothrus ater*	Gray Catbird *Dumetella carolinensis*	0–1	50–100%	0–100%	Rothstein (1982)
	American Robin *Turdus migratorius*	0–1	75–100%	0–100%	Rothstein (1982)

[a] We tested Yellow Warblers with model eggs that differed between 0 and 1 in color and were 200–500% the volume of their own eggs.

JND less than 1 indicates that 2 eggs look similar to the bird (Gomez 2006) and a JND between 1 and 3 indicates that 2 eggs are difficult to distinguish, even under ideal light conditions (Cassey et al. 2009). A JND greater than 3 indicates that a bird should be able to easily discriminate between the 2 eggs.

Criteria for Acceptance and Rejection

Each nest was used once and models were warmed by hand for 10 seconds before being placed into nests (Guigueno and Sealy 2012). To minimize variation in rejection due to the stage of the nesting cycle and the breeding season, egg addition or control visits commenced on the warblers' laying day 2 (LD2) and the experiment was conducted during the first half of the breeding season (May 26–June 12; Guigueno and Sealy 2011). Yellow Warblers infrequently abandon parasitized clutches later in the breeding season, when they may not have enough time to bury or desert and renest (Sealy 1995, Guigueno and Sealy 2010). All nests were manipulated on the warblers' LD2 because cowbirds usually parasitize nests early in the laying cycle and hosts are more likely to accept cowbird eggs as the nesting cycle progresses (Sealy 1995, Guigueno and Sealy 2010). Each nest was checked every 24 hours 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 after the manipulation (Sealy 1995, Guigueno and Sealy 2011).

Nest Measurements

We recorded nest volume, minimum nest width, and nest depth (i.e. depth of interior cup) of all nests because a smaller cup may allow Yellow Warblers to better detect a foreign egg tactilely during egg turning (Deeming 2002, Guigueno and Sealy 2012). We measured the inner volume of the nest by pouring rice into a thin plastic bag that was placed inside the nest cavity and then measuring the volume of rice with a graduated cylinder (see Stewart et al. 2011 for additional details).

Review

We reviewed the literature to compare the responses of various hosts to eggs that differed in both size and color from their own eggs. We reported the responses of 7 host species (from 7 studies) that are hosts to 4 obligate brood-parasitic species: Brown-headed Cowbird, Common Cuckoo, Dideric Cuckoo (*Chrysococcyx caprius*), and Lesser Cuckoo (*Cuculus poliocephlus*) (Table 2). Studies that were included in our review met the following criteria (to maximize the similarity in methods with our own experiment): Model eggs or natural eggs with their surface painted were used and experimental groups included model eggs that differed from host's egg and the parasite's egg in both color and size. We searched for the following key words and phrases in databases of scientific articles: "egg size," "egg color," "brood parasitism," and "egg rejection." Not all articles provided enough information necessary for statistical analysis on egg discrimination cues, therefore, we used reference texts, species guides,

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and other publications (e.g., *Birds of North America Online*; *The Handbook of Birds of the World*, Lynx Edicions, Barcelona, Spain) to provide measurements of missing eggs and data on appearance for both host and parasite eggs.

Data Analysis

Control clutches and nest dimensions. We conducted a continuity-adjusted χ^2 test to demonstrate that adding a model egg to warbler nests increases nest abandonment (via burial or nest desertion) relative to control clutches. Nests in the control group did not have an egg added or removed, but the eggs were touched by the researcher and these nests were inspected in the same manner and at the same frequency as those of the treatment groups. We used a 4×2 Fisher exact test (see Grieef and Sealy 2000) to analyze the method of rejection across egg-addition treatments because more than 25% of the cells had an expected value of less than 5. Nest dimensions were lognormally distributed and we used *t*-tests on log-transformed data to examine whether cup volume, minimum width, and depth were greater for accepters. We pooled all experimental groups as there was no difference in cup volume ($F_{4,116} = 0.61$, $P = 0.66$), minimum width ($F_{4,116} = 0.87$, $P = 0.49$), and depth ($F_{4,115} = 0.22$, $P = 0.93$).

Avian visual modelling. We ran an ANOVA with Proc ANOVA in program SAS (SAS Institute, Cary, North Carolina, USA) with Tukey's post hoc tests to determine the relative differences between each model egg type and real warbler eggs.

Importance of color versus size. We used a general linear model (PROC GLM in SAS) to determine the importance of size and color and their interaction on the frequency of rejection (burial or nest desertion for warblers; burial, nest desertion, or ejection in the literature review). For the data in the review, "host species" was also added as a discrete factor in the GLM model. For all GLM models, we used stepwise regression using backward elimination (SAS Institute 2009). *P*-values < 0.05 were considered significant.

For the warbler experiment, color was assessed in 3 ways. First, we used criteria based on our own color discrimination abilities (human vision; see Table 1 for details of our predictions based on the relative importance of color [human vision] versus size in warblers and an outcome that would support each prediction). We measured the coefficient of determination (r^2) and the ΔAIC values between the data and each of the predictions to determine which of the predictions was most strongly supported (Anderson et al. 2000). An egg model was given a score of 1 if the background and maculation color(s) matched the host eggs (LW/C and SW/C), whereas a score of 0 was given if the background color and maculation were not the same as host eggs (LC and SC) (Table 1). The second and third methods of assessing color were the achromatic JNDs (brightness) and the chromatic JNDs (hue), respectively, from our avian perceptual modelling. The JNDs value for each egg type was included in the GLM model.

For the review data, we used human vision to assess color as we did not have data from avian perceptual modelling. As such, we only compared results from our human vision GLM for warblers to the data from the review. Maculation and background color were each given a score from 0 to 1 and their averages were calculated for the analysis. Maculation was given a score of 1 if both pattern and color matched the host eggs, a score of 0.5 if the pattern or color (but not both) matched the host egg, and a score of 0 if neither color nor pattern matched the host egg. Background color was given a score of 1 if it was visually the same as host eggs and 0 if it was not the same.

To measure the difference in size (i.e. volume) between the experimental eggs and host eggs, we divided the experimental egg volume by the host egg volume. Parasitic and host eggs that were the same size had a proportionate value of 1, whereas parasitic eggs that were larger than host eggs had a value greater than 1, and parasitic eggs that were smaller than host eggs had a value between 0 and 1.

RESULTS

Natural Parasitism, Control Clutches, and Nest Dimensions

Warblers naturally parasitized in early egg laying ($n = 6$) rejected real cowbird eggs at 50% of nests by burial. Nests that received a model egg elicited significantly more burial and nest desertion than control clutches (continuity-adjusted ${\chi_1}^2 = 7.89$, $p = 0.005$; Table 1).

Individuals with larger minimum nest width (accepters: 44.5 mm ± 0.4 versus rejecters 43.3 mm ± 0.5; $t_{119} = 2.11$, $p = 0.04$) tended to accept model eggs. However, there was no significant difference in inner nest volume (accepters: 51.5 ml ± 1 versus rejecters 48.9 ml ± 1.2; $t_{119} = 1.94$, $p = 0.06$) or depth (accepters: 38.4 mm ± 0.5 versus rejecters 37.1 mm ± 0.5; $t_{118} = 1.82$, $p = 0.07$). Most rejections were by burial (68.2%, $n = 44$) and rejection type, i.e. burial versus desertion, did not differ significantly between groups (3×2 Fisher exact test, $p = 0.144$).

Avian Visual Modeling

The spectral reflectance curves in Figure 2A indicate that our model eggs did not reflect light in the UV wavelength range, whereas real Yellow Warbler and Brown-headed Cowbird eggs did. We further investigated these differences in Figure 2B. For achromatic visual contrasts, all model eggs ranged mostly between 1 and 3 JNDs, indicating that it was difficult for the warblers to distinguish between their

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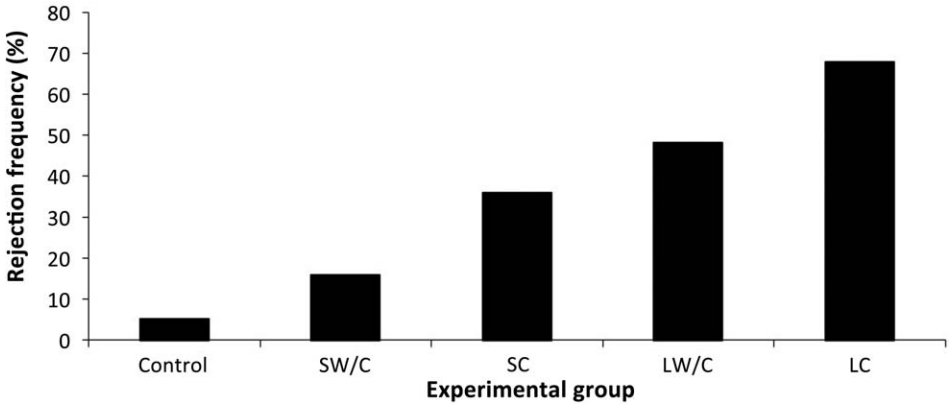


FIGURE 3. Rejection frequency increased as model eggs increasingly diverge in color and size from Yellow Warbler (host) eggs. Abbreviations for egg types are as in Figure 1A and statistical details reported in Table 1.

own eggs and the model eggs in terms of brightness. For achromatic visual contrasts (brightness), LC models differed the most, followed by SC models, whereas SW/C models were most similar to real warbler eggs ($F_{3,36} = 4.73$, $p = 0.007$; Figure 2B). For chromatic visual contrasts (hue), we found that all model types appeared different from real warbler eggs in the avian visible spectrum, but that LW/C models differed the most ($F_{3,36} = 32.19$, $p < 0.0001$; Figure 2B). Chromatic visual contrasts were >3 JNDs for all model types, indicating that all model eggs were easily distinguishable in the avian visual spectrum from real warbler eggs in terms of their hue (Figure 2B). Finally, unlike the models used in our study, real cowbird eggs differed from warbler eggs more in achromatic visual contrasts than in chromatic visual contrasts (Figure 2B).

Importance of Color versus Size

Yellow Warblers. The rejection frequency increased as model eggs diverged more in color and size from the warblers' own eggs (Table 1, Figure 3). The prediction that both color and size affected rejection, with size being more important than color (Prediction 5), had the strongest correlation with our data and was the top AIC model as the next-best model differed by more than 2 (Anderson et al. 2000; Table 1). Both color and size were significant in our human vision and JNDs achromatic GLM models (Table 3). However, only size was a significant factor in our JNDs chromatic GLM model (Table 3).

Review. Changes in color and size of model eggs relative to host eggs elicited rejection that varied between 0 and 100% for many of the species (Table 2). Host species and size did not have a significant effect on rejection, whereas color significantly affected rejection (Table 3). To determine whether phylogeny affected our results, we analyzed the data with the 2 groups of 2 hosts from the same genus merged under a single species per group, but the results did not change.

DISCUSSION

As model eggs diverged in size and color from the Yellow Warblers' own eggs, rejection frequency increased (Table 1, Figure 3). The results from our experiment matched the predicted pattern described in Prediction 5 (Table 1), indicating that size was more important than color in eliciting rejection in warblers. The achromatic JNDs model

TABLE 3. Summary of statistical effects of host species (review only), model egg size, model egg color, and interaction between model egg size and color for Yellow Warblers from the study and for the literature review. For Yellow Warblers, statistical effects were tested using color values based on human vision (also used for review), Just Noticeable Differences (JNDs) for achromatic vision, and JNDs for chromatic vision. Results are based on stepwise regression using backward elimination with a general linear model. Effects that remained in the top models have test statistics and *p*-values in bold. Raw data were used for analyses with Yellow Warblers, whereas averages for each model type were used in the review.

	Color	Size	Color*Size	Host
Yellow Warblers				
Human vision	$\mathbf{F_{1,101} = 4.70\ P = 0.033}$	$\mathbf{F_{1,101} = 12.18\ P = 0.00070}$	$F_{1,101} = 0.00\ P = 0.99$	N/A
JNDs achromatic	$\mathbf{F_{1,101} = 4.70\ P = 0.033}$	$\mathbf{F_{1,101} = 7.99\ P = 0.0057}$	$F_{1,101} = 0.00\ P = 0.95$	N/A
JNDs chromatic	$F_{1,101} = 3.50\ P = 0.064$	$\mathbf{F_{1,101} = 11.47\ P = 0.0010}$	$F_{1,101} = 1.15\ P = 0.29$	N/A
Review				
Human vision	$\mathbf{F_{1,49} = 6.22\ P = 0.016}$	$F_{6,49} = 0.32\ P = 0.57$	$F_{6,49} = 0.34\ P = 0.56$	$F_{6,49} = 1.22\ P = 0.32$

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also reported that size and color were significant but the chromatic JNDs model only reported size as a significant factor, suggesting achromatic visual contrasts between the warblers' own eggs and the model eggs were used as a cue for rejection, but not chromatic visual contrasts (Table 3). The background coloration may be less salient than the degree of maculation. Indeed, real cowbird eggs differ more achromatically (brightness) than chromatically (hue) from warbler eggs, so differences in brightness, which are likely due to cowbird eggs generally being more heavily maculated than warbler eggs, may reinforce the decision to reject naturally parasitized clutches (Figures 1B and 2). There was no significant effect of interaction between size and color in Yellow Warblers, therefore, size and color influenced rejection independently and additively rather than acting multiplicatively (de la Colina et al. 2012). For the brood-parasitic hosts in our review, only color based on human visual perception, out of the possible parameters of color and size, was used as a cue for rejection (Table 2).

In Yellow Warblers, increased rejection tended to occur in nests with smaller cups, indicating possible tactile responses to egg crowding (Deeming 2002). Because egg discrimination is not required for the 2 methods of rejection used by Yellow Warblers (burial and nest desertion), a tactile cue from the larger parasitic egg is likely the most important cue in eliciting rejection in the wild. Egg size is the primary parameter used for ejection by some cavity or dome nesters, as color is less visible in dark environments (Mason and Rothstein 1986). Rufous Horneros (*Furnarius rufus*) assess the overall egg-size variation in their clutches and eject Shiny Cowbird (*Molothrus bonariensis*) eggs that have widths less than 88% of the width of their own eggs (Mason and Rothstein 1986). Yellow Warblers may use a similar tactile strategy to detect cowbird eggs. Yellow Warblers increasingly shuffled and probed eggs more when cowbird egg-sized models were added to their nests relative to clutches in which no eggs were added (Guigueno and Sealy 2012). In addition, warblers that probed more were more likely to reject their experimentally parasitized clutch, indicating an important role in tactile cues in eliciting rejection in this host (Guigueno and Sealy 2012).

The results from our review (Tables 2 and 3) demonstrate that color is more important than size for ejecter hosts of brood parasites such as cowbirds (Rothstein 1982, Marchetti 2000) and cuckoos (Brooke and Davies 1988, Davies and Brooke 1989, Lotem et al. 1992). American Robins eject model eggs that differ (from a human visual perspective) from their own eggs in 2 out of 3 parameters (size, background color, maculation), but size is the least important parameter, as sizes of cowbird and robin eggs overlap (Rothstein 1982). Unlike cowbirds and their hosts, the coevolutionary relationship between Common Cuckoos and their hosts is more advanced as individual cuckoos specialize on one host species (Lotem et al. 1992, Davies and Brooke 1988). Common Cuckoos parasitize small hosts and lay eggs that are smaller than nonparasitic cuckoos, but color varies according to the cuckoo gentes (Payne 1974, Krüger 2007). Indeed, differences in color between parasite and host eggs are the most reliable and most used cues by hosts of different cuckoo species in Europe and Africa (Krüger 2007, Honza et al. 2014).

Brown-headed Cowbird hosts included in our review were larger than cowbirds, ejected nearly all cowbird eggs added to their nests, and sometimes ejected an egg before settling onto their clutch (Rothstein 1982, Rasmussen et al. 2009; J. L. Rasmussen personal communication; Table 2). Hence, relying on an egg parameter that can also be assessed tactilely (size) would not be as important in these species, as differences in color are sufficient for egg discrimination and subsequent ejection. Both background and maculation of American Robin and Gray Catbird (*Dumetella carolinensis*) eggs differ from cowbird eggs, however, cowbird eggs may overlap in size with robin and catbird eggs (Rothstein 1982, Lowther 1993, Smith et al. 2011, Vanderhoff et al. 2014). In addition, a parasitic egg that is larger than host eggs (i.e. cowbirds parasitizing Yellow Warblers) is likely more detectable tactilely than a parasitic egg that is smaller than the host eggs (i.e. cowbirds parasitizing American Robins and Gray Catbirds). Therefore, differences in color are a more reliable and noticeable cue for these ejecters.

Our study provides insight into the evolution of egg rejection. Parasitic cuckoos lay eggs that are about 3 times smaller than eggs laid by nonparasitic cuckoos, as cuckoos parasitize smaller host species (Payne 1974). Thus, before individual cuckoos specialized on one host species, cuckoos may have evolved small eggs to reduce rejection by all small hosts, and as cuckoos increasingly specialized color differences were also minimized to reduce rejection by the species upon which they specialized (Davies and Brooke 1988, Lotem et al. 1992, Hosoi and Rothstein 2000). Color was the only important cue for the hosts in our review possibly because the cuckoo species already evolved eggs that were small enough to minimize rejection based on size. Thus, we propose that (1) rejection frequencies based on egg size increase as the difference in size between host and parasite eggs and the reliance on a tactile cue increases; (2) rejection based on color is constant across a gradient of sizes; and (3) as the differences in size diminish, due to coevolutionary convergence by parasites, for example, size as a cue becomes less reliable.

In conclusion, Yellow Warblers use primarily size and secondarily color as cues for rejection, whereas ejecter hosts of multiple parasites only use color. Color differences

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may not be enough to elicit rejection in warblers because they may not visually recognize their own eggs (Sealy and Lorenzana 1998) and, thus, also rely on nonvisual cues, such as tactile cues, and on methods of rejection that do not require egg discrimination, such as burial and desertion. Burial and desertion are generally more costly than ejection, so warblers likely must rely on more cues to minimize the probability of burying and deserting in the absence of parasitism. Indeed, in addition to egg size and color, warblers also use the presence of an egg-removing cowbird at their nests as a cue to reject (Guigueno and Sealy 2011).

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