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When are egg-rejection cues perceived? A test using thermochromic eggs in an avian brood parasite host

Mark E. Hauber[1] · **Miri Dainson**[1] · **Alec Luro**[1] · **Amber A. Louder**[1] · **Daniel Hanley**[2]

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Abstract

At the core of recognition systems research are questions regarding how and when fitness-relevant decisions made. Studying egg-rejection behavior by hosts to reduce the costs of avian brood parasitism has become a productive model to assess cognitive algorithms underlying fitness-relevant decisions. Most of these studies focus on how cues and contexts affect hosts' behavioral responses to foreign eggs; however, the timing of when the cues are perceived for egg-rejection decisions is less understood. Here, we focused the responses of American robins *Turdus migratorius* to model eggs painted with a thermochromic paint. This technique modified an egg's color with predictably varying temperatures across incubation: at the onset of incubation, the thermochromic model egg was cold and perceptually similar to a static blue model egg (mimicking the robin's own blue–green egg color), but by the end of an incubation bout, it was warm and similar to a static beige egg (mimicking the ground color of the egg of the robin's brood parasite, the brown-headed cowbird *Molothrus ater*). Thermochromic eggs were rejected at statistically intermediate rates between those of the static blue (mostly accepted) and static beige (mostly rejected) model eggs. This implies that at the population level, egg-rejection relevant cues are not perceived solely when arriving to or solely when departing from the nest. We also found that robins rejected their own eggs more often when exposed to color-changing model eggs relative to static eggs, suggesting that recognizing variable foreign eggs entails costly rejection errors for this host species.

Keywords Brood parasitism · Egg rejection · *Molothrus ater* · Recognition systems

Introduction

Some of the best understood aspects of animal decision making involve the perception and recognition of salient cues used to effect different alternative behavioral responses (Mendelson et al. 2016); for example, ongoing research (e.g., Caves et al. 2018) is expanding our knowledge of the role of categorical perception in shaping sexually selected traits, including the red beak of male zebra finches *Taeniopygia guttata*, building on prior knowledge of multimodal sexual displays in this species (e.g., Simons and Verhulst 2011).

From a signal-detection perspective, the timing during which salient information is both available and reliable is a critical factor for reducing recognition errors (Reeve 1989). Yet, a far less explored aspect of the decision process is the timing at which recognition cues are gathered and evaluated, except for the series studies that focus specifically on cue exposure during critical or sensitive periods (e.g., Batista et al. 2016).

Here, we tapped into an increasingly well-characterized study system of information gathering and decision making, namely, the foreign-egg-rejection responses of hosts of avian brood parasites (reviewed by Manna et al. 2017). Our aim here was to understand the timing at which salient cues are gathered for this particular perceptual and decision-making process. Obligate avian brood parasites including cuckoos, cowbirds, indigobirds, and honeyguides, as well as other facultative heterospecific and conspecific brood parasites, impact many bird species (i.e., hosts) by laying their eggs

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✉ Mark E. Hauber
mhauber@illinois.edu

[1] Department of Evolution, Ecology, and Behavior, School of Integrative Biology, University of Illinois, Urbana-Champaign, Urbana, IL 61801, USA

[2] Department of Biological and Environmental Sciences, Long Island University-Post, Brookville, NY 11548, USA

in another bird's nest (Lyon and Eadie 2017). In turn, some hosts respond to natural or experimental brood parasitism by removing the parasitic egg from or marginalizing it within the nest (Rothstein 1975a, b; Davies and Brooke 1989). Most such egg-rejecter hosts show patterns consistent with a template-based egg recognition mechanism, whereby rejection thresholds are based on the avian-perceived coloration and maculation of the foreign egg relative to a mental representation of the acceptable range of eggshell appearances (Ban et al. 2013; Stevens et al. 2013; Hanley et al. 2019). Therefore, experimental manipulation of eggshell appearance typically results in predictable variation in the acceptance/rejection decisions of natural or model parasitic eggs (Hauber et al. 2015; Lahti 2015).

However, egg rejection is rarely instantaneous, with studies indicating a lag of up to 6 days to assess whether parasitic eggs can be deemed accepted or rejected (e.g., Grim et al. 2011). Therefore, there are likely repeated inspections of the clutch with the foreign egg by the evaluating hosts (Antonov et al. 2008; Pozgayova et al. 2011; Soler et al. 2017). Such repeated opportunities to evaluate the relative appearance of each egg against a mental template and/or the other eggs in the nest can then guide egg-rejection decisions by discriminating hosts. Opportunities to inspect eggshell appearance occur across the nesting period, and each inspection may provide valuable information for a discriminating host, because the light conditions and contextual information can differ across the laying and incubation periods (Honza et al. 2011). Inspections can occur at, but may not be limited to, the arrival to and settling onto the nest by the incubating host, the departure to forage from the nest after an incubation bout, and/or during incubation (e.g., when hosts rotate or inspect eggs) (e.g., Scharf et al. 2019).

The American robin *Turdus migratorius* (hereafter robin) lays a blue–green immaculate egg and is parasitized occasionally by the brown-headed cowbird *Molothrus ater*, which lays a beige egg with brown speckles (Rothstein 1982) (Fig. 1). Previous research has found that this host typically accepts blue–green-painted model eggs that appear visually similar to their own, and rejects maculated or immaculate beige model eggs that appear similar to those of their parasites (Lang et al. 2014; Dainson et al. 2017; Luro et al. 2018). Here, we designed an experiment to address whether salient cues for decision making are gathered at distinct timepoints relative to the onset vs. the end of incubation bouts of female robins. Specifically, we used thermochromic paint to predictably modify model-eggs' ground colors, such that at the onset of incubation, the model egg was perceptually similar to the robins' own eggs in color, while by the end of incubation bouts, it was more similar to the parasitic brown-headed cowbirds' eggs in ground color (see "Results"). We did not to use cowbird-like maculation patterns in our experimental setup, because our thermochromic treatment was only able to change the ground color of the model eggs. Nonetheless, ground color differences alone between cowbird-like and robin-like model eggs are sufficient to elicit predictable variation egg-rejection behaviors in this species, especially of smaller, cowbird-sized eggs (e.g., Igic et al. 2015; Luro et al. 2018).

We predicted that if recognition cues for egg inspection are gathered at the onsets of incubation bouts, then thermochromic eggs would be mostly accepted (when the thermochromic eggs display blue coloration), whereas if recognition cues are gathered upon departures from the nest following incubation bouts (when thermochromic eggs display beige coloration), these same egg types would be mostly rejected. We used static blue (known to be mostly accepted: Igic et al. 2015) and beige model eggs (mostly rejected) as experimental controls in this study.

Methods

Egg models

General All eggs were ordered from a commercial 3D-printing source, using the "Cow bird egg smooth" polished nylon model available at www.Shapeways.com. This egg type resembles the shape, size, and mass of a natural Brown-headed Cowbird egg (for details, see Igic et al. 2015). All model eggs were primed with white acrylic paint, and then lightly sanded to remove imperfections. Eggs then received their experimental treatment paints, as detailed below. We removed any uneven edges by sanding and reapplying the paint as needed. Then, all eggs were finished with a light satin coat that included a drop of "Flock Off" clear UV reflective solution (Ware, UK).

Static blue control eggs Robin-mimetic light blue eggs were painted with a blue latex paint [2050-40 Florida Keys Blue mixed by Benjamin Moore; Montvale, USA], previously known to be accepted by robins nearly in all nests when experimentally tested (e.g., Croston and Hauber 2014; Igic et al. 2015; Luro et al. 2018). They were given 2–3 coats and dried before receiving their finish. We also assessed whether these and/or the other egg types showed temperature dependence in their reflectance spectra and avian-perceivable color in the laboratory (see below).

Static beige control eggs Beige was chosen as a cowbird-like model-egg color, previously known to be rejected nearly in all experimental trails (Croston and Hauber 2014). We did not apply cowbird-like maculation patterns to these models (see above). These eggs were also painted with 2–3 coats of a beige latex paint (1002 Featherstone mixed by Benjamin Moore) and dried before receiving their finish.

Thermochromic experimental eggs Thermochromic eggs were painted with a white acrylic base and then one coat of

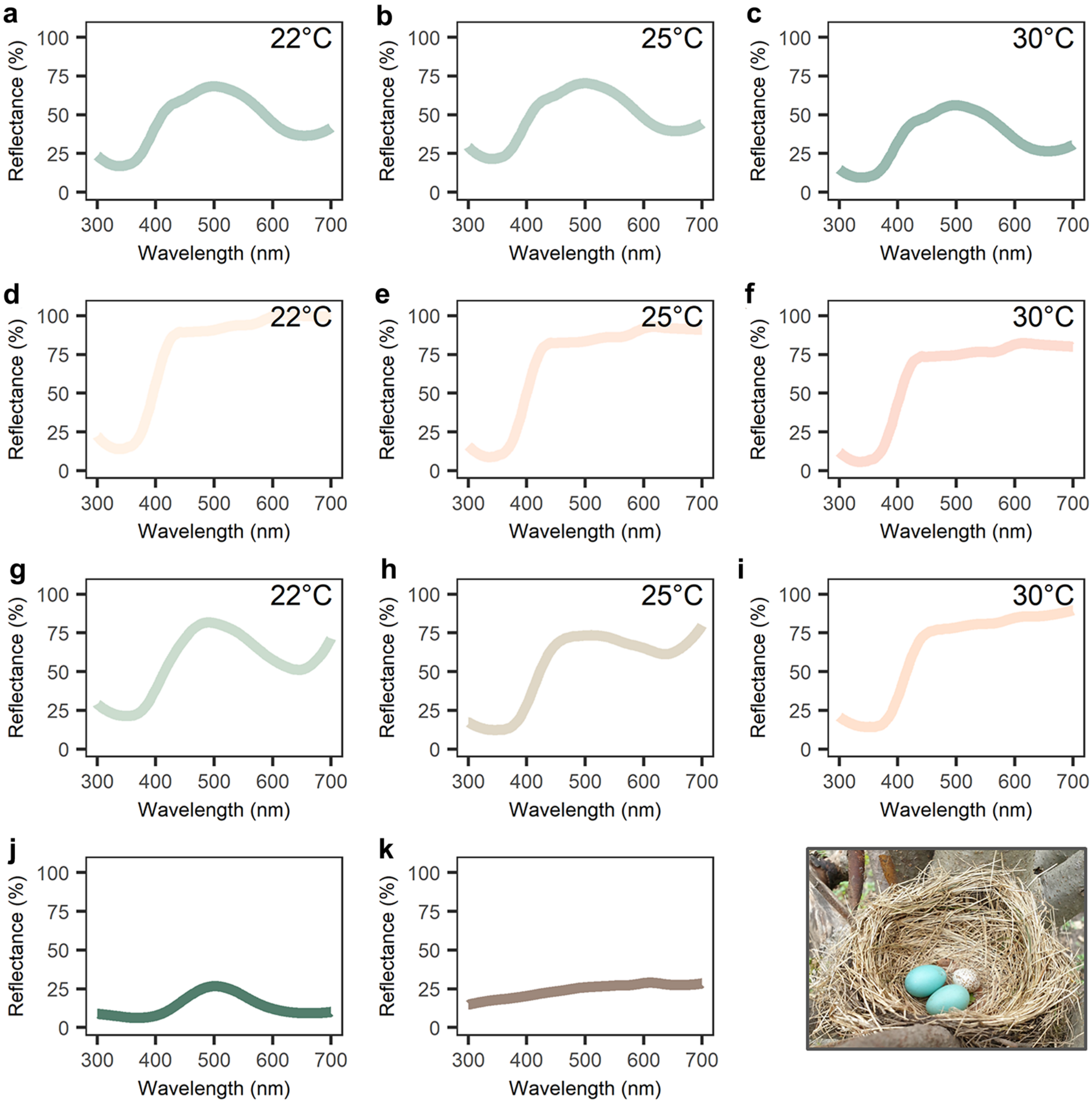

Fig. 1 Representative reflectance spectra of each type of static (blue, **a**–**c**; beige, **d**–**f**) and the thermochromic egg (**g**–**i**) across a range of experimentally relevant temperatures. The bottom row shows representative reflectance spectra of a natural American robin (**j**) and a brown-headed cowbird (**k**) eggshell's ground coloration [from Croston and Hauber (2015)], and a naturally parasitized robin nest (lower right corner; photo credit: MEH). For illustrative purpose, we plotted each spectrum to reflect the human-visible appearance of the eggs as calculated from each shell's average reflectance spectrum (color figure online)

the static beige paint. They were then given the thermochromic treatment paint coat. Thermochromic color treatment was designed to match the control static blue below 24 °C, and change to match the control static beige when the egg's temperature rose above 24 °C. Therefore, the mixing process was done in a room with temperatures below 24 °C, so that the thermochromic color did not have an intermediate appearance during the mixing process. Solar dust thermo powder (Thermal-Dust; Lake Wales, USA) must be suspended in a clear or light-colored paint, so that when they are heated, they "disappear" and reveal the color underneath or the color that they are mixed into. A high ratio of powder to suspension material is necessary to achieve full coverage. In this case, a batch of paint consisted of 2.8 mL of the control beige paint combined with 20 drops of DecoArt Dura Clear Polyurethane Satin Varnish and included Solar Color Dust color codes in the amounts of 0.5 g of teal, 0.5 g of grass green, 0.1 g of dark blue, and 0.05 g of brown. With the ground color beige as the mixing base, it contributed to the resulting hue, adding a small amount of yellowness to the thermopowders, so that there could be a lower dust to paint ratio. This mixture was reapplied to coat the model eggs a minimum of three times and then carefully dried using a fan. Creating a dense thermochromic paint mixture can yield chunky and uneven coats and this is particularly apparent with the clear coating.

We stored all eggs in a cool, dark place when not in use.

Egg color measurements

We measured avian-visible reflectance spectra (300–700 nm) from static blue ($n=2$), beige ($n=2$), and thermochromic ($n=2$) model eggs at temperatures ranging from 21 to 27 °C in 1-degree increments, and at 30 °C, 34 °C, and 38 °C. Eggs were placed in a plastic bag and heated in a water bath, then cooled with ice to change surface temperatures. Egg surface temperatures were monitored using an infrared laser thermometer and taking three measurements at different locations on the egg surface for 3 s to ensure a stable temperature reading, and the reflectance spectra were taken within 5 s of the last temperature measurement. Spectra were plotted using the *pavo* package in *R* with spectra lines colored using an RGB transform of the spectra using the *spec2rgb* function for plotting graphs (Figs. 1, 2). In addition, reflectance spectra for $n=22$ natural American robin eggs were taken from Croston and Hauber (2015), and avian-perceivable differences of the experimental eggs from the natural robin eggs were calculated as just noticeable differences (JNDs) using a receptor-noise limited model (Vorobyev and Osorio 1998) of the European blackbird (*Turdus merula*, a congener of the robin) visual system following Hanley et al. (2017). Reflectance spectra were measured using a 400 µm fiber optic reflection probe fitted with a rubber stopper with a measuring distance of 3 mm and area of 2 mm^2 at a 90° angle to the surface of the egg. Measurements were taken using a *JAZ* spectrometer with a pulsed-xenon light source (Ocean Optics, Dunedin, USA) and all measurements were made relative to a diffuse reflectance white standard (Spectralon WS-1-SL, Labsphere, North Sutton, USA).

Study area and protocol

The fieldwork was conducted in Champaign County, Illinois, USA, during the robin breeding seasons of 2017 and 2018. Robin nests were opportunistically located in tree nurseries, arboretums, and private gardens (e.g., Luro and Hauber 2017; Scharf et al. 2019). Nests were predominantly found in young trees and bushes. Nests were considered suitable for videotaping and artificial parasitism if they were found active (with female robin attending or defending the nest, with eggs warm to the touch, and/or with egg numbers increasing between subsequent daily visits) for at least 2 consecutive days and contained ≥ 2 robin eggs. In addition, eggs were deployed when the weather forecast predictions for the week of experimentation were below 24 °C to avoid spontaneous fluctuation in the appearance of the thermochromic eggs independent of robin incubation behavior. We did not capture and band robins individually as part of this experiment, but assured that experiments took place in concurrently active neighboring nests to avoid pseudoreplication through reuse of the same study subject(s).

We selected a static blue ($N=18$), static beige ($N=20$), or thermochromic egg model ($N=17$) and placed it into each robin nest. Data from depredated or abandoned nests were

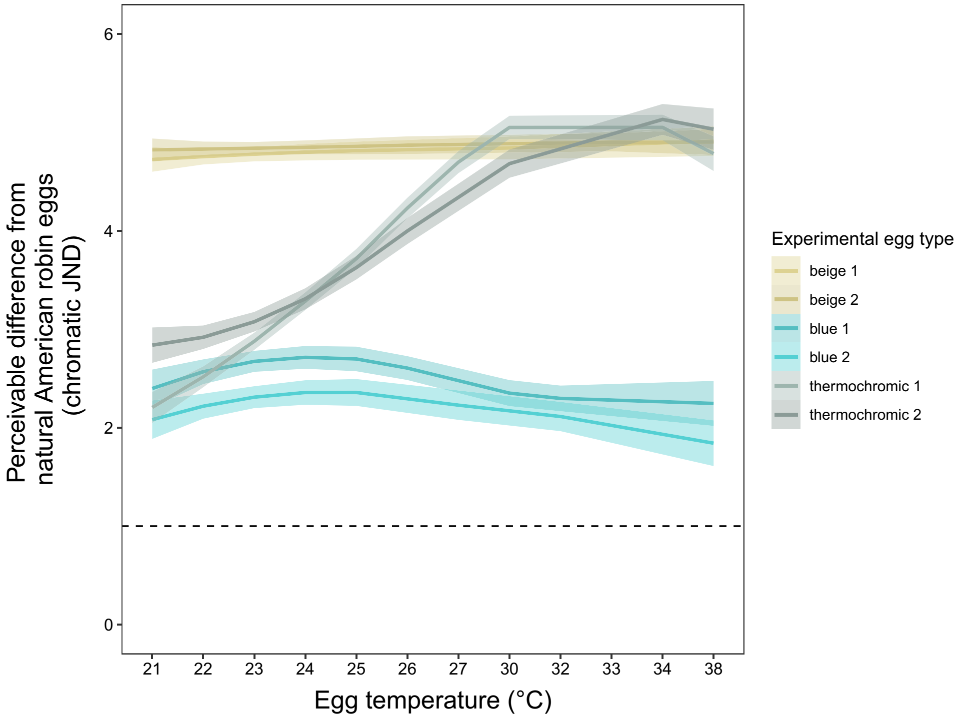

Fig. 2 Just noticeable differences (JND) between colors of static blue ($N=2$), beige ($N=2$), and thermochromic ($N=2$) model eggs relative to $n=22$ natural American robin eggs (means and ± SE) each, across a range of avian incubation-relevant temperatures. Lines and intervals drawn using nonlinear locally estimated scatterplot smoothing (LOESS) with a span = 1.2 (color figure online)

not included in the analyses, because Croston and Hauber (2014) showed that experimentally introduced eggs do not induce nest abandonment in this species (also see Igic et al. 2015 and Hanley et al. 2017). Therefore, our final sample sizes for analyses were smaller (as reported in the Fig. 3 legend).

We aimed to videotape potential rejection attempts and other nest visitation events following the insertion of a model egg at a subset of nests across the three treatments (*N* = 15 nests), and a GoPro camera was set up on a camouflaged extended flexible gooseneck and wrapped around a nearby branch, ideally positioned 15 to 60 cm away from the nest with the clamp of the gooseneck latched to a nearby branch, depending on the environment. A Lasergrip 630 Dual Laser digital infrared thermometer (Anaheim, USA) was used to measure the temperature of natural eggs already in the nest as well as the model egg prior to its placement into the nest. The model egg was added to the clutch of natural eggs already present as removing or adding experimental eggs can yield similar egg-rejection responses in this species (Croston and Hauber 2015). For brevity of disturbance at the nest, the researcher set up the experiment and left the nest site in under 3 min.

After 3 h, the researcher returned to the nest, measured the temperature of the eggs in the nest, removed the camera, and left the site. We did not record any additional footage of the same nests. After the field season ended, an observer reviewed each camera's footage for the following information: the time of arrival or departure by the incubating robin, and the percentage of human-visible beige color of the surface of the static or thermochromic eggs (in bins of 0, 25, 50, 75, and 100%).

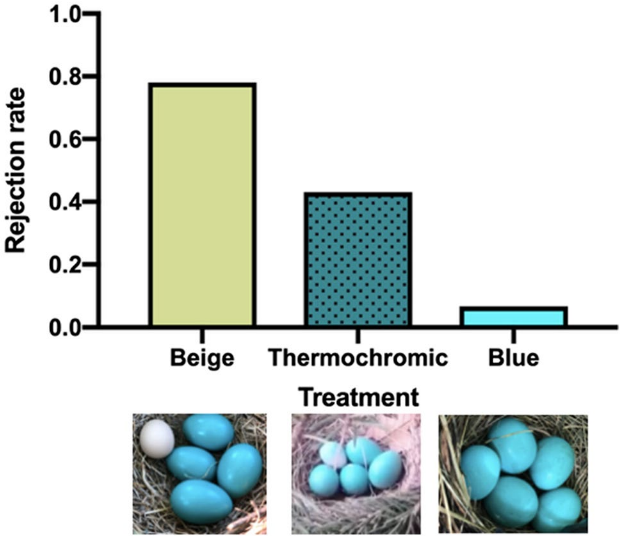

Fig. 3 Relative proportions of the rejection outcomes (by day 2 following the experimental addition) in response to model eggs (beige *N* = 18 nests, thermochromic *N* = 14, and static blue *N* = 15; predated or abandoned nests were excluded from the data set). Respective experimental clutches are shown underneath each bar, with the model eggs in the upper left quadrant of each image; the thermochromic egg shown is phased at the ~ 50% beige/blue stage (color figure online)

Each nest was revisited and its contents monitored daily to record the presence of natural and model eggs for up to 3 days (Luro and Hauber 2017). The mean, modal, and median latency until rejection of the beige eggs were all less than 2 days (mean ± SD = 1.6 ± 0.8 days, mode = 1 day, median = 1 day, range = 1–3 days). Therefore, we considered an egg accepted if it was still present in the nest on the 2nd day following initial insertion (day 0) or rejected if it became absent at any point during this period. We assumed that missing eggs were removed by incubating (female) robins (Vanderhoff et al. 2016; Scharf et al. 2019), rather than served as evidence for partial clutch predation. We did not monitor nests past our experiment and so we do not always know the exact stage of the incubation period at which our experiments occurred; nevertheless, prior work in this species confirmed that the timing of parasitism within the incubation period was not statistically related to rejection rates of model eggs (Croston and Hauber 2014).

Analyses

We used visual representations of the laboratory-collected avian-visible range reflectance spectra, the calculated avian-perceivable JNDs, and video-based human assessment of model-egg color to document temperature- and incubation-dependent variation in the appearance of thermochromic and control eggs (Fig. 2).

To analyze the temperature of un/incubated model eggs, we conducted one-sample *t* tests with 24 °C (the half-way point for color change; see "Results") as the null expectation. We applied linear mixed models to analyze the video-based human-assessed color change between the onset and end of incubation bouts; here, we coded incubation bout phase as the predictor and used repeated measurements per nests, with nest ID as a random effect. Finally, we used logistic regressions and Fisher's exact tests to analyze treatment-dependent egg-rejection data. Statistical analyses were conducted in JMP 12.0.0 (SAS Institute Inc., Cary, NC, USA). The data are available as Supplementary File 1.

Results

Temperature-dependent appearance of thermochromic and static egg colors

We qualitatively confirmed that under laboratory conditions, both the reflectance spectra (Fig. 1) and the avian-perceivable ground color difference from the natural robin egg color (chromatic JND) of the thermochromic eggs have shifted from more closely matching the static blue egg at room temperature (~ 21 °C) to more closely matching the static beige egg at nearing avian incubation temperatures (~ 38 °C) (Fig. 2). Thermochromic eggs attained an intermediate (half-way) color at ~ 24 °C (Fig. 2).

In the field, the temperatures of unincubated model eggs were consistently below the color-changing half-way point of 24 °C and had a mean ± SE of 21.7 ± 0.8 °C ($N = 17$ measurements; $t = -4.8$, $p = 0.0002$) and the temperatures of incubated model eggs were consistently above 24 °C at 27.8 ± 1.1 °C ($N = 32$; $t = 2.8$, $p = 0.019$).

Color change during field experimentation

We confirmed through field videos of the experimental nests that the human-perceived proportion of beige of the static blue (mean ± SE: 0% ± 0; $N = 3$ nests) and beige (100% ± 0; $N = 3$ nests) eggs did not change from the onsets to the end of robins' incubation bouts (Fig. 1, insets). By contrast, the portion of beige of the thermochromic eggs shifted significantly from mostly blue (10.9% ± 6.4) at the onset of incubation bouts to mostly beige (93.5% ± 5.4) the end of incubation bouts ($F_{1,32.8} = 136$, $N = 9$ nests, $p < 0.0001$; for a representative video of thermochromic egg color change, see Supplementary File 2).

Rejection responses to model eggs

Color treatment had a significant effect on the rejection rate of model eggs (logistic regression: $\chi^2 = 19.8$, $p < 0.0001$; post hoc comparisons: blue beige: $p < 0.0001$, blue thermochromic: $p = 0.032$, beige thermochromic: $p = 0.047$; Fig. 3), and robin nests with fewer eggs in the nest (3 vs. 4 eggs) at the onset of the experimentation showed lower rejection rates ($\chi^2 = 4.48$, $p = 0.034$). However, this did not contribute to a bias in our rejection data, because when the treatment * clutch size was included in the model, it did not yield a significant interaction term ($\chi^2 = 2.97$, $p = 0.23$).

Finally, we detected the loss of one or more of the hosts' own eggs without nest abandonment at five of all the nests monitored; these were statistically associated with the color treatment of the model eggs ($\chi^2 = 14.4$, $p = 0.0007$), but not with initial clutch size ($\chi^2 = 0.63$, $p = 0.43$). All instances of clutch reductions were associated with the thermochromic treatment only (36% of nests), such that rejection errors occurred more often in nests with thermochromic eggs than those with blue (0% of nests) or beige static eggs (0% of nests), but the lack of these errors was otherwise equivalent between the two static treatments (Fisher's exact $p_{\text{blue vs. thermochromic}} = 0.002$, $p_{\text{beige vs. thermochromic}} = 0.06$, $p_{\text{blue vs. beige}} = 1.0$). Rejection errors occurred both in nests where the thermochromic egg was accepted ($N = 3$) or rejected ($N = 2$).

Discussion

Our results show significant differences between the rejection rates of thermochromic and both the static model eggs (Fig. 3). This suggests that the timing of cue acquisition for egg-rejection decisions is likely non-exclusive to solely the time of the onset of incubation or the departure from the nest across all individuals in this population.

A range of non-mutually exclusive alternatives exists to explain these findings. One possibility is that roughly half of the female robins inspect their nest contents and make decisions (to accept) prior to incubation bout(s) when the thermochromic egg is cold (and blue), while the other half inspect their nest contents make decisions (to reject) after incubation bout(s) when the thermochromic egg is warm (and beige). It is also possible female robins inspect the eggs at a timepoint half-way through the color-changing phase of the thermochromic egg model and make decisions to reject based on the perceived color at the time of inspection. Alternatively, a ~ 50% rejection rate could occur if only half the thermochromic eggs changed from blue to beige; however, our video recordings reject this possibility by demonstrating that robin incubation was sufficiently long and warm enough to allow for the full color-phasing from blue to beige (see "Results"). Finally, there is a possibility that females integrate the appearance of the model eggs at the onset, during (when the thermochromic egg is changing its color: Fig. 3), and/or at the end of incubation. To assess these alternative predictions, new experimentation with continuous video-tracking is necessary to capture the timing and the details of egg inspections, touches, ejection attempts, and ejection events fully (e.g., Roncalli et al. 2019).

If birds integrate the appearance of model eggs using visual cues at both the onset and end of incubation bouts, the inconsistent color cues of the thermochromic egg would be unreliable for egg recognition. From a signal-detection perspective, the fitness outcome of egg-rejection decisions should closely track cue reliability: signal-detection theory predicts a narrower egg acceptance threshold as the salient recognition cue's reliability decreases (e.g., Campbell and Hauber 2010), resulting in more egg-rejection errors (i.e., mistaken rejection of own eggs; Davies et al. 1996). Here, we experimentally decreased egg the coloration cue's reliability using a color-changing thermochromic paint and found that robins exposed to thermochromic color-changing eggs were more likely to reject one or more of their own eggs than robins whose nests were artificially parasitized by a single-static (blue) model egg. This suggests an increase of uncertainty in assessing own vs. foreign eggs in the nest, which can thus result in increased recognition errors, and the associated rejection costs of removing own eggs, in this and in other rejecter hosts of avian brood parasitism (e.g., Lorenzana and Sealy 2001; Stokke et al. 2002). For example, robins exposed to color-changing eggs may have shifted to a narrower egg acceptance threshold (Reeve 1989; Hauber et al. 2006) than robins exposed to static-colored eggs, potentially resulting in the greater likelihood of such recognition errors made. However, rejection errors occurred both in nests where the thermochromic egg was accepted and nests where it was rejected; thus, it does not appear that birds rejected their own eggs only in the course of rejecting the thermochromic eggs. Future research should investigate whether rejection errors occurred at a time when the thermochromic eggs were blue, beige, or phase transitioning (Fig. 3, Supplementary File 2).

Although our thermochromic treatment is highly artificial, less extensive changes to egg appearance can and do occur in bird nests from laying onwards and throughout incubation: for instance, fecal matter may land and dry onto the surface of the eggs (Mayani-Paras et al. 2015), yolk or shell from other, broken eggs may also discolor or slip over the surface of the eggs (Hauber 2003), and in particular in the mud-walled nests of robins, dirt and detritus may alter the eggshells' appearance (Luro and Hauber 2017). There is also evidence of ongoing and avian-perceivable changes in eggshell coloration within hours and days following egg-laying due to fading (Moreno et al. 2011), including in nests of hosts of other brood parasitic species (Hanley et al. 2016). One implication of our work here might be that robins are able to track the changes in the appearance of the full clutch across time, and adjust their egg-rejection/acceptance thresholds accordingly. Explicit tests of this hypothesis should subtly alter the appearance of model eggs at time scales across hours and days, rather than minutes.

Perceivable cues for anti-parasitic egg-rejection decisions in robins do not appear to be integrated solely at either the time of nest arrival or nest departure by all incubating females. Thus, future research should also address whether egg recognition cues are collected at different timepoints of nest attendance, integrated across longer periods, and/or show inter-individual variation in the use of cues at either the arrival or departure from the nest. In turn, experimentally induced temporal unreliability about the identity of the foreign egg in the nest appears to be associated with fitness costs for discriminating eggs through rejection errors made by robins that have removed their own eggs instead or in addition to the foreign egg from the nest.

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Compliance with ethical standards

Conflict of interests All authors declare no conflicts of interests.

Ethical approval We followed the guidelines of the Animal Behavior Society for ethical treatment of research animals. The research was approved by the University of Illinois (IACUC #17049), the USA Department of the Interior (#23681), and the Illinois State Department of Natural Resources (#NH17.6099) issued to MEH.

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